SPECIES RELATIONSHIPS IN THE AVIAN GENUS *AIMOPHILA*

BY

LARRY L. WOLF

Museum of Vertebrate Zoology
University of California

ORNITHOLOGICAL MONOGRAPHS NO. 23

PUBLISHED BY

THE AMERICAN ORNITHOLOGISTS' UNION

1977

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ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk*. Publication has been made possible through the generosity of Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. John William Hardy, Department of Natural Science, The Florida State Museum, University of Florida, Gainesville, Florida 32611.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Glen E. Woolfenden, Department of Biology, University of South Florida, Tampa, Florida 33620. (See price list on back and inside back cover.)

Ornithological Monographs No. 23, viii + 220 pp.

Editor of A.O.U. Monographs, John William Hardy

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First received, 24 January 1974; accepted, 2 February 1976; final revision completed, 9 January 1976

Issued February 23, 1977

Price (includes long-play phono-disc album) $12.00 prepaid ($10.50 to AOU Members)

Library of Congress Catalogue Card Number 77-73658

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

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INTRODUCTION

Although there is some disagreement regarding the application of the biologic species concept to classification, taxonomists and evolutionists generally agree as to what constitutes species. Genera, on the other hand, are subjective taxa set up by us to aid in categorizing species, to facilitate study of their biology, and to further show their possible evolutionary pathways. The genus as a category depends to a large extent on differences between groups of organisms that arise through evolutionary divergence and extinction of intermediate forms (Mayr *et al.* 1953). Gaps between groups of species can be defined in terms of characters from the cellular to organismal level of organization. The characteristics used to define genera may exist at almost any level of organization. In most cases various gross morphological characters, both internal and external, are used to classify vertebrates at this level. Recent attempts have been made to use cytological, behavioral, and biochemical evidence in vertebrate classification (Mayr 1958; Sibley 1960, 1962, 1970; Gorman 1965).

Our greater knowledge of processes and factors affecting patterns and rates of evolution places increasing emphasis on studies of directions and effects of evolutionary changes in populations and on selective forces producing such changes. These populations provide natural experiments for our theories of evolution. Among the vertebrate groups, birds are perhaps the best known taxonomically, as well as morphologically, ecologically, and behaviorally. With this background it should be possible to assess possible significance of these data in classification above the species level and to begin to formulate more precise ideas on generic classification.

One of the most recently diversified groups of birds is the emberizine finches of the family Fringillidae (Storer 1959). Within this group I studied the genus *Aimophila,* a taxon that some taxonomists feel is an unnatural assemblage of species and probably represents several groups or even rather widely divergent forms (Ridgway 1901, Dickey and van Rossem 1938, Storer 1955).

Marshall (1964), in studies of species thought to be related to *Aimophila,* stated that "the ground-dwelling fringillids should be studied from all standpoints of their biology before generic realignment." Such is the aim of this study, although it will necessarily be more limited in scope than Marshall idealized. Nevertheless, it may provide a basis for future work and information leading toward generic classification of most of the emberizines and reflecting something of their biologic attributes.

By assembling as many data as possible from zoogeography, general biology, and morphology, I have tried to show the evolution within the genus, as presently constituted, particularly in establishing groups of species that might be thought of as evolutionary units. In addition, I have attempted to contribute to theories about the multiple evolutionary pathways and end products that characterize animal genera. I have assumed (1) that the goal is to arrive at a genus that in some way represents a single aggregation of similar evolutionary units, in the sense of a divergence from a recently common gene pool, and (2) that certain types of biologic continuity, when viewed in their proper perspective, ought to reveal some measure of historical continuity. In *Aimophila* the evolutionary units are based on common zoogeographic and ecologic histories. As too few specimens in museums and essentially no published information were available on the South American *Aimophila strigiceps* (however, see Navas 1965), I have considered only the North American members of the genus (*sensu* Ridgway 1901).

ACKNOWLEDGMENTS

This study was initiated and pursued for several years under the guidance of the late Alden H. Miller; John Davis kindly aided me in the final stages. O. P. Pearson and Paul Hurd read drafts of this monograph and have contributed to the final form. I offer them my sincere thanks

Several other people deserve special thanks for their help during this study. George Chaniot, Gene Christman, and Robert Payne discussed the problem with me and helped clarify the material. Christman was of further and especial aid in planning and executing the figures. John Hubbard and Richard Sage helped me in the field in the summers of 1963 and 1964, respectively. Their company and help were invaluable. Rudolfo Hernández Corzo, Director of the Departmento de Forestal y Caza in Mexico was instrumental in obtaining the necessary permits for us to collect in Mexico. Clarence Cottam and Caleb Glazener generously allowed us to use the facilities of the Welder Wildlife Foundation in Sinton, Texas. They also were very helpful during our stay at the Foundation. The wardens at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas assisted in many ways during our stay there. Richard Root allowed me to accompany him on several trips to Arizona, giving me a chance to study the Rufous-winged Sparrow (*A. carpalis*) during the nonbreeding period. Patrick Gould and Robert Ohmart provided information on the habits of *A. ruficeps* and *A. cassinii* in Arizona. Allan R. Phillips and Howard Cogswell permitted me to use their manuscript materials on *A. ruficeps* and *A. carpalis.* Miwako Tamura helped with some aspects of the analysis of the vocalizations. Wesley Lanyon sent a copy of a tape recording of the song of *A. mystacalis* made in Oaxaca, Mexico by Charles Bogert.

The Associates in Tropical Biogeography provided financial support for two field trips to Mexico. A fellowship from the Elsie Binger Naumberg

Fund of the American Museum of Natural History and a National Science Foundation grant (GB-7611) aided during the writing of this report. The Museum of Vertebrate Zoology, University of California, Berkeley, provided equipment both for work in Berkeley and for field work. The Department of Zoology at Berkeley and Peter Marler, formerly of that department, provided additional equipment and facilities.

I thank the following curators and their respective institutions either for sending materials on loan or making available their collections for study at the institution: Philip Humphrey, George Watson, and Richard Zusi (United States National Museum, USNM); Wesley Lanyon and Dean Amadon (American Museum of Natural History, AMNH); Robert W. Storer and Harrison B. Tordoff (University of Michigan Museum of Zoology, UMMZ); Richard F. Johnston (University of Kansas Museum of Natural History, UKMNH); Emmett R. Blake (Chicago Natural History Museum, CNHM); George H. Lowery, Jr. (Louisiana State University Museum of Zoology, LSU); Richard C. Banks (San Diego Society of Natural History Museum, SDSNH); Thomas R. Howell and O. M. Buchanan (Dickey Collections at the University of California at Los Angeles, UCLA); J. William Hardy (Moore Laboratory of Zoology, Occidental College, MLZ); Joe T. Marshall (University of Arizona, UA); and California Academy of Science, CAS.

The number of other people who have contributed to this study in various capacities is too great to mention each individually, and they receive only my combined acknowledgment here. However, this in no way diminishes my gratitude for their help.

METHODS AND MATERIALS

FIELD WORK

Field trips were made from June to August, 1963 and 1964. In 1963, I worked in Arizona, New Mexico, and western and southern Mexico; in 1964, I worked primarily in Texas, near Cuernavaca, Morelos, Mexico, and through southern Mexico. Short field trips were made to Arizona in January and December, 1963 to study *A. carpalis* and *A. ruficeps* in the nonbreeding season. Some field work was carried out intermittently near Berkeley, California from 1962 to 1965.

During each of the summer field trips in 1963 and 1964, time was divided between collecting and observing. Primary emphasis was on social systems, foraging behavior, and vocalizations. Recordings of vocalizations were made with a Uher 4000s tape recorder and a 24-inch parabolic reflector. All recordings were made at 9.3 cm/sec. The recorded material was analyzed from sound spectrograms made on a Kay Electric Company Sonagraph with wide band pass filter and high shape equalization (HS) settings. Most of the specimens taken during these trips are in the collections of the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, but a few are in the collections of the University of Michigan Museum of Zoology (UMMZ). All tape recordings are in my possession, but a composite reference copy has been deposited in the Bioacoustic Archive, Department of National Sciences, Florida State Museum, Gainesville, Florida.

MEASUREMENTS

The following measurements were made on all specimens from the known or presumed breeding grounds and on which an accurate measurement was possible: *Length of wing.*—Measured as the chord from bend of wing at wrist to tip of longest primary. The longest primary varied from number 5 to 8. *Length of tail.*—Measured from point of insertion into skin of middle pair of rectrices to tip of longest tail feather. In most cases this was the second pair. *Tarsus.*—Measured from posterior of middle point of tarsus at junction of tarsus and tibiotarsus to the most proximal scute covering toes 3 and 4. The last undivided scute was less constant in position and is not equidistant at all points from the upper joint. This measure is slightly (1 mm for largest species) longer than the tarsal measurement given by Baldwin *et al.* (1931). *Middle toe.*—Measured on ventral surface from distal end of pad to the same point as distal end of tarsal measurement. *Hallux.*—Measured from distal end of pad to distal end of the same scute as for the tarsus. *Bill length.*—Measured from anterior edge of nostril to tip of bill. *Bill width.*—Measured on specimens in which the bill was judged to be naturally closed, in a plane at right angles horizontally to the length and passing through anterior edge of the nostril. This measurement is the widest portion between the two tomia at that point. *Bill depth.*—As for width, vertical to length of bill.

All measurements on the appendicular skeleton were made of the longest extent of the bone. The total length of each appendage was obtained by summing values for each component. This obviously gives a slightly greater length than in the living bird, but the difference should not affect the results given here.

The width of the temporal fossa was the only skull measurement analyzed. This is the greatest width of the concave area in which *M. adductor mandibularis* is situated (see Fig. 57 of Bowman 1961: 206).

Measurements of a selected sample of the individuals of each species were treated statistically. To put values of the several species on more nearly similar bases, or to eliminate the factor of size differences among the species, I calculated equated values for pertinent measures by dividing the mean value by the cube root of body weight for the species (Amadon 1943).

Body weights were calculated for the species as a whole. This may slightly bias weight values, but I attempted to include weights in about equal proportions from the several populations of a geographically variable species. None of the species becomes noticeably fat, so this was not considered in obtaining weight values. Females with enlarged ovaries were not included.

NOMENCLATURAL BACKGROUND

In his original description of the genus *Aimophila,* erected to include *A. rufescens* and *A. superciliosa,* Swainson (1837) defined the group primarily in terms of bill character, only briefly mentioning wings, tail, and feet. Gray (1840) later designated *A. rufescens* as the type member of the genus, after which Ridgway (1898) designated *superciliosa* as the type and only species of his genus *Plagiospiza* [= *Oriturus* of Miller *et al.* 1957].

Meanwhile, Audubon (1839) erected the genus *Peucaea* to include *Fringilla bachmanii* [= *Aimophila aestivalis*] and *Fringilla lincolnii,* basing it primarily on bill characteristics; he also considered other external morphological characters to some extent. (*F. lincolnii* has subsequently been removed from this genus and placed in *Melospiza.*) Baird (1858) later included *A. cassinii,* first described as a *Zonotrichia* (Woodhouse 1852), in *Peucaea* along with *Aimophila aestivalis* and *A. ruficeps*; the latter was described originally in the genus *Ammodramus* (Cassin 1852, Heerman 1859). Baird defined the enlarged genus *Peucaea* primarily on characters of wing, tail, and feet, with scant mention of the bill. He included in *A. cassinii* the species *A. botterii* (described by Sclater 1857 as a *Zonotrichia*), as did Coues (1872), i.e. as *Peucaea aestivalis,* var. *cassinii.* In the United States *A. botterii* was known at that time only from the vicinity of Los Nogales, Sonora. Ridgway (1873) called this population *P. aestivalis arizonae,* whereas Sclater and Salvin (1868) assigned the Mexican *A. botterii* to *Peucaea.*

Sclater and Salvin (1868) also included their new species, *A. notosticta,* in *Peucaea.* Coues (1873) named *A. carpalis* in the genus as well, and in his key to North American birds (1884) he listed *aestivalis, cassinii, ruficeps,* and *carpalis* in *Peucaea.* Ridgway (1883) noted that *Peucaea notosticta* approached some of the *Haemophila* (a name introduced by Cabanis (1851) in place of *Aimophila*) species in size but that it appeared to be a true *Peucaea,* though not closely related to any known species. By 1885, Ridgway included specimens of *mexicana* [= *A. botterii*] from Texas in *Peucaea,* although Merrill (1878) had called this population *P. arizonae.*

Ridgway (1883) was of the opinion that *Zonotrichia quinquestriata,* described by Sclater and Salvin (1868), was really an *Amphispiza*, a conclusion also reached with regard to *Z. mystacalis.* Salvin and Godman (1886) later followed Ridgway in retaining *quinquestriata* in *Amphispiza* and *notosticta* in *Peucaea*, but they removed *mystacalis* to *Haemophila* and included *petenica* (= *botterii*) in the genus *Coturniculus*. Except for the *botterii* group, *Haemophila* was eventually expanded to include all of these species, plus *Zonotrichia ruficauda acuminata* and *Chondestes ruficauda*, the latter described by Bonapart (1853); the race *Aimophila ruficauda lawrencii* was initially placed in *Haemophila.* The *botterii* group, *carpalis*, and other United States species were considered to belong to *Peucaea.*

In 1898, Ridgway stated that he was unable "to discover any characters sufficient to separate *Peucaea* from *Aimophila*, unless the form be restricted to *P. aestivalis*, *P. botterii*, and *P. cassinii.*" By 1899, he was convinced that *Aimophila* must include *ruficeps* and *carpalis*. He thought that *carpalis* was closer to *sumichrasti* than any other species, but was still uncertain where to place *quinquestriata*, *mystacalis*, *humeralis*, and *ruficauda.* In his inclusive work on the fringillids and other birds of North and Middle America, Ridgway (1901) erected the genus in what is now the modern treatment; however, in a footnote on page 36, he stated that the group was "a very heterogeneous and probably unnatural genus, which, however, I am unable to divide." Hellmayr (1938) added the South American *strigiceps* to *Aimophila* and suggested that *Rhynchospiza stolzmanni* (also South American) might belong to the genus.

Ridgway's (1901) usage has been questioned in succeeding years. For example, Dickey and van Rossem (1938) in their treatment of the birds of El Salvador retained *ruficauda* in *Aimophila*, but modified their arrangement by stating that, "Although so listed here, we do not believe for a moment that this sparrow is an *Aimophila.*" The most recent author to suggest that the genus be divided was Storer (1955), who acknowledged that the group was indeed heterogeneous but declined to make any changes until "a series of studies of the life history and anatomy of the little-known members of the group" could be done. More recently Phillips *et al.* (1964) placed two additional members, the Black-throated Sparrow (*Amphispiza bilineata*) and the Sage Sparrow (*Amphispiza belli*), in the genus. In a discussion under the Lincoln Sparrow (*M. lincolnii*, p. 208), they intimated that perhaps the whole *Aimophila-Amphispiza-Junco-Zonotrichia-Passerella-Melospiza* complex might be better placed in one genus. Finally, Paynter (1970) includes *Rhynchospiza* but not *Amphispiza* in *Aimophila*, while admitting that the expanded group is "a poorly known genus whose species require much more field study before their taxonomy may be unraveled."

Besides the problem of generic limits of *Aimophila*, a few problems of specific limits exist in the genus. *Aimophila botterii* and *A. b. petenica*, and *A. ruficauda lawrencii* and *A. r. acuminata,* are different enough to have been recognized as distinct species by early workers. Both of these pairs are composed of allopatric forms, so the question of specific identity can not be resolved by the natural test of sympatry. For purposes of this report I consider *petenica* as conspecific with *botterii,* and *lawrencii* and *acuminata* as populations of *A. ruficauda.* In addition I am not concerned with the generally clinal subspecies that have been described in many of the species of *Aimophila.* Consequently, I separate in my discussions only those forms mentioned above, as they may prove to be species in their own right.

In the following discussion I segregate species of *Aimophila* into four units within the genus: the *Haemophila* complex, the *ruficeps* complex, the *botterii* complex, and *A. quinquestriata.* The reasons for this treatment are apparent later in this presentation.

DISTRIBUTION

SPECIES ACCOUNTS

STRIPE-HEADED SPARROW, *A. RUFICAUDA*

Geographic distribution.—Resident from the vicinity of Tepic, Nayarit, Mexico, southward to the dry northwestern lowlands of Guanacaste Province, Costa Rica (Fig. 1). The northern population (*A. r. acuminata*) occurs in the drainage of the Río Balsas of west-central Mexico, from sea level to about 2000 m elevation (Davis 1953). Southward along most of the Pacific coast of Oaxaca to the Isthmus of Tehuantepec there is a hiatus that is rather difficult to explain. A narrow strip of habitat seemingly suitable for the species stretches along the coast in the foothill region of the Sierra Madre del Sur (J. Sarukhan pers. comm.), but to date the limited collections have not yielded *A. ruficauda* from this area.

Another population (*A. r. lawrencii*) occurs in the Pacific coastal plain of Oaxaca (vicinity of Tehuantepec) and Chiapas, ranging into the foothills to approximately 760 m in southern Chiapas. The most southeasterly records are specimens (UMMZ) taken around Pijijiapan, Chiapas.

The most southerly population (*A. r. ruficauda*) occurs along the Pacific coastal plain from Guatemala south and east to the dry lowlands of northwestern Costa Rica.

Finally, another population (*A. r. connectens*), isolated north of the central mountains of Guatemala, occupies the lowland area of the upper valley of the Río Motagua, east to Gualán (Griscom 1932). This arid region on the Caribbean slope is in the rain shadow of the Sierra de las Minas, which runs inland perpendicularly to the east coast for some

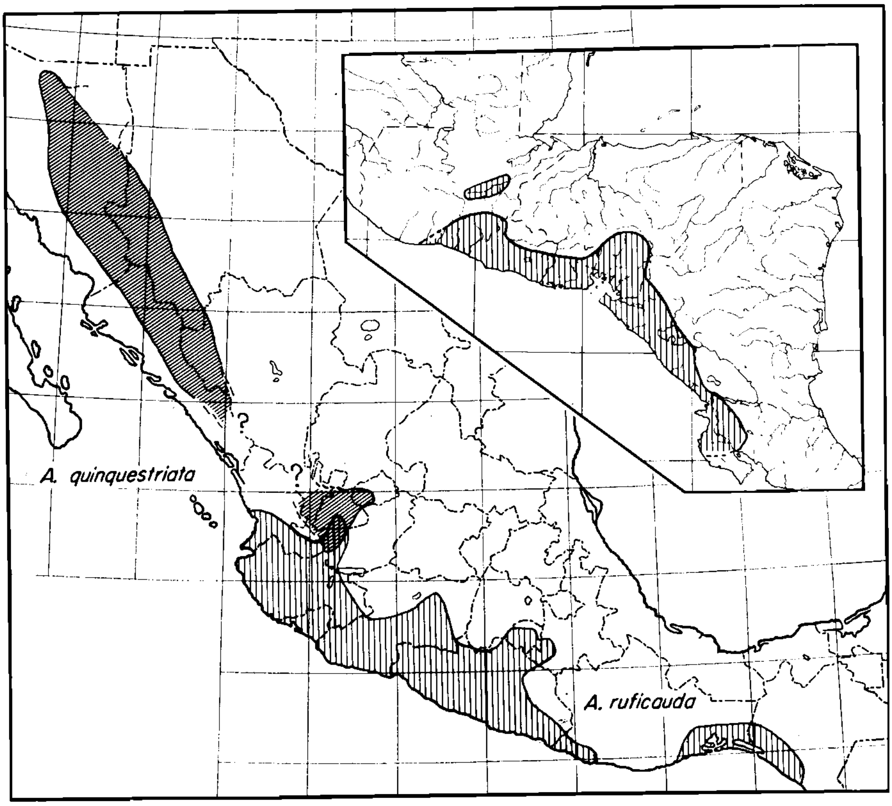

FIGURE 1. Geographic distribution of *A. ruficauda* and *A. quinquestriata.*

160 km (Griscom *op. cit.*). The more humid lower portion of the valley is not influenced by the mountains and the mesic vegetation there is not occupied by *A. ruficauda.*

Ecologic distribution.—According to the vegetation map of Mexico prepared by Leopold (1950), the range occupied by the northern population of *A. ruficauda* is dominated by arid tropical scrub and tropical deciduous woodland with lesser amounts of thorn forest and savanna. In Nayarit, the species apparently penetrates the interior only slightly; I found it about 48 km southeast of Tepic in a pastureland with scattered fencerow shrubs and small trees.

In Jalisco the sparrows follow several river systems at least as far inland as the Barranca de Oblatos northwest of Guadalajara. Here Selander and Giller (1959) reported them at approximately 3000 feet on the floor of the barranca "in shrubs bordering fields, especially in the vicinity of cacti and agaves. A few were seen at Ixcatán, but the species was absent from hillsides and was not noted in the riparian vegetation." On 31 July 1963 I found a pair about 11 km south of Ixtlahuacán del Río in the upper reaches of the barranca. On the other side of the river I heard a chatter duet of *ruficauda* from a rocky, legume-dominated slope above the road where it wound along the rim of the barranca. It seems that where scrubby vegetation occurs in disturbed habitats, *ruficauda* can occupy the slopes of the barranca to about 1350 m.

Habitat for this species is more extensive toward the Pacific coastal plain. About 56 km northeast of Autlán, Jalisco at about 1200 m we encountered several individuals in an extensively overgrazed area that was dominated by flat-pad cactus (*Platyopuntia*). The country is decidedly more moist over the range of mountains just west of Autlán, and here the sparrows were in disturbed sites along the road. They were limited primarily to leguminous woody vegetation with surrounding open areas along fences at the edges of cultivated fields or pastures. We also found them commonly along the road about 10 km southwest of La Huerta.

In Colima, J. Davis (1960) reported *A. r. acuminata* from several coastal localities, and Schaldach (1963) noted that this species is a "brush inhabitant which may be found from the Thorn Scrub of the coastal plain up to the edge of the Tropical Deciduous Forests but is absent from heavy Thorn Forest" and "a common resident of the lower, more tropical areas of the region."

Reports of this species along the coastal plain in Michoacán and Guerrero are only scattered. Storer (1955) wrote that the species "preferred" the "thorn scrub" habitat. W. B. Davis (1944) reported it from 1000 feet and 3250 feet in Guerrero "in areas of scattered brush." I found it commonly in the region of the first foothills about 8 km from the ocean around Coyuca, Guerrero, at less than 150 m elevation. Here it occurred in cleared pastures with a few trees and scattered shrubs. It also occurred along fencerows bordering pastures and swampy areas. This area was perhaps the wettest in which I found *A. ruficauda.* Many freshwater marshes and lakes were nearby, and the vegetation was much more lush than at other localities, except possibly around Manzanillo.

Inland from the coastal plain in the center of the range, *A. r. acuminata* probably reaches its highest elevation and its farthest extension into the interior. In Zacatecas, Webster (1959b) found a flock in a weedy field beside the Río Juchipila. J. Davis (1953) reported it from 6500 feet in the vicinity of Tzitzio, Michoacán, near the head of the Río Chinapa, a tributary of the Río Balsas, where clearing operations created open habitats that were being invaded by leguminous shrubs and other bushy growth. Apparently *A. ruficauda* follows the rivers into the highlands and spreads as more habitat is created.

A sizeable population of *acuminata* is at the dry, south end of the Cañón de Lobos, Morelos. The cañón opens into the valley of the Río Yautepec, a tributary of the Río Balsas. The sparrows occur in cleared areas that have been partly overgrown by shrubby and arboreal legumes. Rowley (1962) found them nesting in mesquites about 11 km south of Cuernavaca. W. B. Davis and Russell (1953) noted that *A. ruficauda* was a "residente frecuente en la communidad de latorral desértico" of Morelos and included localities from the Yautepec region.

The populations of *A. ruficauda* in the Pacific coastal plain of Oaxaca and Chiapas occupy relatively open vegetation, such as open grassy areas with a scattering of various legumes (*Acacia, Prosopis, Caesalpinia*) and other tree and shrub species in the area around Tehuantepec, Oaxaca. Often pairs are scattered along cart paths, powerlines, and in other disturbed sites, and neither there nor farther east does the species appear to occupy more mesic woodlands (Edwards and Lea 1955). According to Selander (1964) this xeric savanna-type vegetation ends in Mexico just northwest of Tonalá, Chiapas, but *A. ruficauda* occurs farther to the southeast, probably where clearings in lusher woodlands have grown up with scrubby vegetation.

In the Caribbean populations along the Río Motagua in eastern Guatemala, A. W. Anthony (Griscom 1932) found *A. ruficauda* quite common at Progreso, "haunting the cactus fences and brushy thickets along the edges of the fields." Around Usumatlán and slightly farther east, Land (1962) found it "common in overgrown fields and hedgerows," up to an elevation of 900 feet. Still farther to the east and nearly to Zacapa, Tashian (1953) found it in "desert scrub" on Finca San Jorge.

In Costa Rica, *A. ruficauda* is a member of what Slud (1964) termed the Arid Pacific Fauna, restricted to the arid coastal plain and extending only slightly into the foothills. Slud says it is a "bird of bushy and thickety, grassy and brushy semi-open, [where] it frequents edges of scrubby growth, shrubbery, and overgrown ravines." Wetmore (1944) found it "common in [the] region about Liberia," where it occurred "near the ground in the brushy, tangled growths of pastures and old fields . . . mainly not far from the water." In the area around Playa del Coco on the Pacific coast of Costa Rica, I found *A. r. ruficauda* in fields and pastures, some of which were so overgrown with brush 2–3 m tall that they were nearly impenetrable. Generally the sparrows occurred on the edges of these brush patches and retreated into them when pursued. Here and on the Finca la Pacífica just north of Cañas, I found the birds along fencerows and cutover areas at the edges of tropical deciduous woodlands.

Tashian (1953) said that the population in southeastern Guatemala occurred in "savanna thicket" and "in savanna bushes." In El Salvador, A. H. Miller (1932) found the species in brush along stream courses at Sonsonate, at 1500 feet, in what Dickey and van Rossem (1938) called the Arid Lower Tropical region. Dickey and van Rossem noted that the species was exceedingly common in brushy tracts, about the edges of clearings, hedgerows, and in cultivated lands generally. In Nicaragua, Nutting (1883) reported that the species was rather common in hedges on the west shore of Lake Nicaragua.

CINNAMON-TAILED (SUMICHRAST'S) SPARROW, *A. SUMICHRASTI*

Geographic distribution.—This sparrow occurs on the coastal plain and slightly into surrounding foothills of the southern, arid portion of the Isthmus of Tehuantepec, Oaxaca, Mexico north along the Pan American Highway as far as 94 km northwest of Tehuantepec (Fig. 2). Contrary to Storer (1955), *A. sumichrasti,* within its limited geographic range, is one of the most common passerine species and probably the most common emberizine.

Ecologic distribution.—*A. sumichrasti* is resident in one of the more xeric regions of Mexico, with a dry season marked by a nearly total lack of rain. The rainy season extends from June to October (Duellman 1960), and rain may fall nearly every day during this period. However, the rains are light and the annual rainfall averages less than 1100 mm (Contreras 1942).

Aimophila sumichrasti occupies vegetation consisting largely of tropical deciduous forests, composed of species of such genera as *Jatropha* and *Ipomoea* and ranging up to 5–6 m tall. The trees are bare during the dry season, giving the woodland a very open appearance that is heightened by the scant shrub layer and the fact that the herb layer is nearly nonexistent during the dry season. Trees and shrubs leaf out rapidly after the rains begin, and the herb layer becomes nearly continuous and sometimes grows to more than 60 cm tall. Interspersed are cleared areas, many of which are grassy pasturelands, some showing evidence of secondary succession with legume shrubs and various other woody plants.

A. sumichrasti reaches its greatest abundance in slightly open areas of tropical deciduous forest where there is some grass in the herb layer vegetation. In the forest interior the species normally occurs along trails, stream gullies, roads, and moderate clearings made by man. Pasturelands and their successional stages typically are left to *A. ruficauda.*

BLACK-CHESTED SPARROW, *A. HUMERALIS*

Geographic distribution.—*A. humeralis* is resident in nearly the same range as *A. ruficauda* (Fig. 2), although the two differ in how far inland they penetrate, and the latter species occurs farther north. The southeastern limits of *A. humeralis* are along rivers that drain south and west from the highland areas of central and southern Puebla. We found it commonly

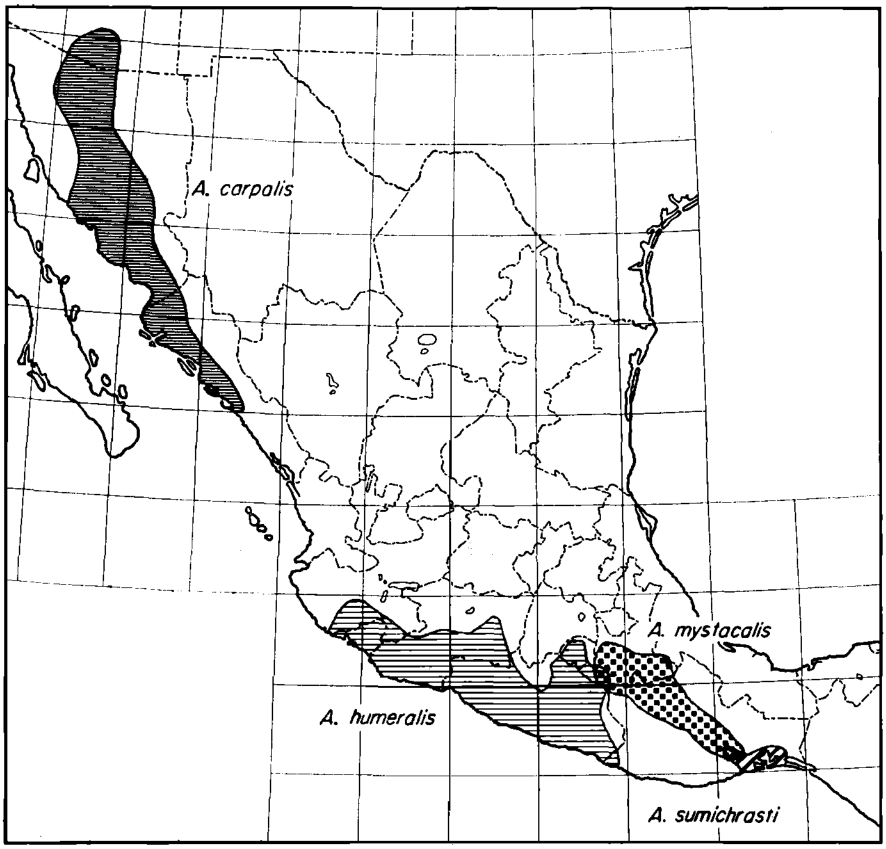

FIGURE 2. Geographic distribution of *A. sumichrasti*, *A. humeralis*, *A. mystacalis*, and *A. carpalis*.

11 km south of Piaxtla, Puebla, and rarely (one pair in about 12 ha) approximately 14 km south of Izúcar de Matamoros, Puebla.

Ecologic distribution.—A. humeralis occupies arid tropical scrub, tropical deciduous forest, and thorn forests, which are the dominant vegetations in its range (see vegetation map of Leopold 1950). The tree layer in these vegetation types usually ranges from 11 to 32 m tall and is sparse enough to allow growth of a dense, continuous herb layer and varying proportions of shrubs.

In the Cañón de Lobos, near Cuernavaca, Morelos, the species occurred mainly on the east-facing slope, where shrubs and small saplings formed a nearly continuous layer. *A. ruficauda* was present in open grassy areas with scattered legumes, and the two species were often seen within 8 m of each other where open brushy areas were adjacent to the tropical deciduous woodland. Even under these circumstances, *A. humeralis* was in the more closed portions of the habitat, although in one case a pair was bounded on two sides by pairs of *A. ruficauda.*

Where allopatric, *A. humeralis* may expand into the habitat of *A. ruficauda.* For example, in 1963 *A. humeralis* was the commonest fringillid at a site approximately 11.5 km south of Piaxtla, Puebla, and a pair used rather dense legume and broadleaf trees along streambeds, as well as grazed grassy areas along the streambed and on small hillocks between streams. Other pairs of *A. humeralis* were restricted to the closed canopy, tropical deciduous forest on surrounding hillsides.

BRIDLED SPARROW, *A. MYSTACALIS*

Geographic distribution.—This species is resident on arid slopes south of the Mexican plateau from Puebla into northwestern Veracruz (vicinity of Orizaba) and southwestward in Oaxaca to where the mountains drop toward the Isthmus of Tehuantepec (Fig. 2).

Ecologic distribution.—Although Goldman (1951) listed *A. mystacalis* from the Lower Austral Zone, where it apparently is restricted to arid highlands mainly above 900 m, I found no published records regarding its habitat preferences. In general I found habitats of this species rather varied, but characterized by trees. In 1963, I found the species on an arid hillside about 14 km southeast of Izúcar de Matamoros, Puebla, where it occurred with, but outnumbered, both *A. rufescens* and *A. humeralis. A. mystacalis* occurred in relatively open leguminous thorn forest interspersed with large cacti; the species less commonly occupied more closed areas of the same habitat. About 48 km southward in a valley ultimately connected with the Río Balsas, only *A. humeralis* was present in the same type of vegetation.

A. mystacalis was also found in a hilly area dominated by scrubby oaks 6.5 km southwest of Matatlán, Oaxaca (about 64 km southeast of Oaxaca City). Clearings resulted from firewood cutting and agriculture were also present, and in some of these, thorny vegetation had grown up as the early stages of secondary succession. These successional areas were occupied by *A. mystacalis,* while *A. ruficeps* was found on naturally open, rocky hillsides and *A. notosticta* in scrub oaks. *A. mystacalis* occurred most commonly on east-facing slopes, which are scrubbier than west-facing slopes.

Farther southeast in the mountains along the Pan American Highway, about 26 km southeast of Matatlán, I found *A. mystacalis* common only on rocky hillsides in arborescent, arid tropical scrub and in open deciduous forest. A nearly closed canopy about 3 to 5 m high existed at some localities. A shrub layer of about 1 to 3 m formed a less-than-50% canopy.

In some places herbs and grasses were about a meter high in August, but undoubtedly ground vegetation is nearly absent at the peak of the dry season. Vegetation does not vary much with exposure, and the birds occur on all slopes. One pair had a territory in a maguey (*Agave* sp.) field in which grass several feet tall grew luxuriantly between the 1.5-m-high plants; the maguey served as song perches in the absence of trees.

RUFOUS-WINGED SPARROW, *A. CARPALIS*

Geographic distribution.—A. carpalis ranges from central southern Arizona south to near Elota, Sinaloa (Fig. 2). The Arizona populations seem to fluctuate in abundance, and the localities of occurrence vary from year to year. The species is much commoner in Mexico, where it is limited to the Sonora and Sinaloa Biotic Provinces (Goldman and Moore 1945).

Van Rossem (1945) was of the opinion that in *A. carpalis* "breeding is limited to the northern part of the range" and that the more southern records were of populations that shifted southward "from late fall until early or even midsummer." *A. carpalis* has since been found breeding in Sinaloa, and the race *A. c. cohaerens* was named from this part of the range (Moore 1946). In Arizona some populations are larger in winter than during summer, suggesting that some migration occurs. Extent is not known, but regular migrations are of doubtful occurrence.

Ecologic distribution.—Mesquite (*Prosopis juliflora*) is probably the most characteristic woody vegetation in areas inhabited by *A. carpalis.* The birds are usually in more open mature stands, comprised of trees up to about 6 m tall. Mesquite trees are used as song perches and nest sites and the birds rest in the shade of foliage. In 1963 lepidopteran larvae on leaflets of mesquite were a common food source for *A. carpalis* in Sonora. Ground cover in *A. carpalis* habitats depends to a large extent on season of year and pattern of land use. Most areas of mesquite woodlands probably had a grassy understory originally; this persists, or did so in the recent past, in some places. Pitelka (1951a) reported that at Pitahaya, Sonora, *A. carpalis* occurred in mesquite areas with "largely grassy" interspaces, and Phillips (1951a) said that the birds in Arizona could survive "given a patch of grass." The latter implies that grass is a necessary requirement of this sparrow, but outside of Arizona this may not be true.

In addition to mesquite, other woody species in the habitat include plants such as hackberry (*Celtis* sp.) and *Acacia,* with cholla and beavertail cacti (*Opuntia* spp.) relatively common in some more open areas. The population of *A. carpalis* is smaller where cholla dominates than in more open mesquite woodland.

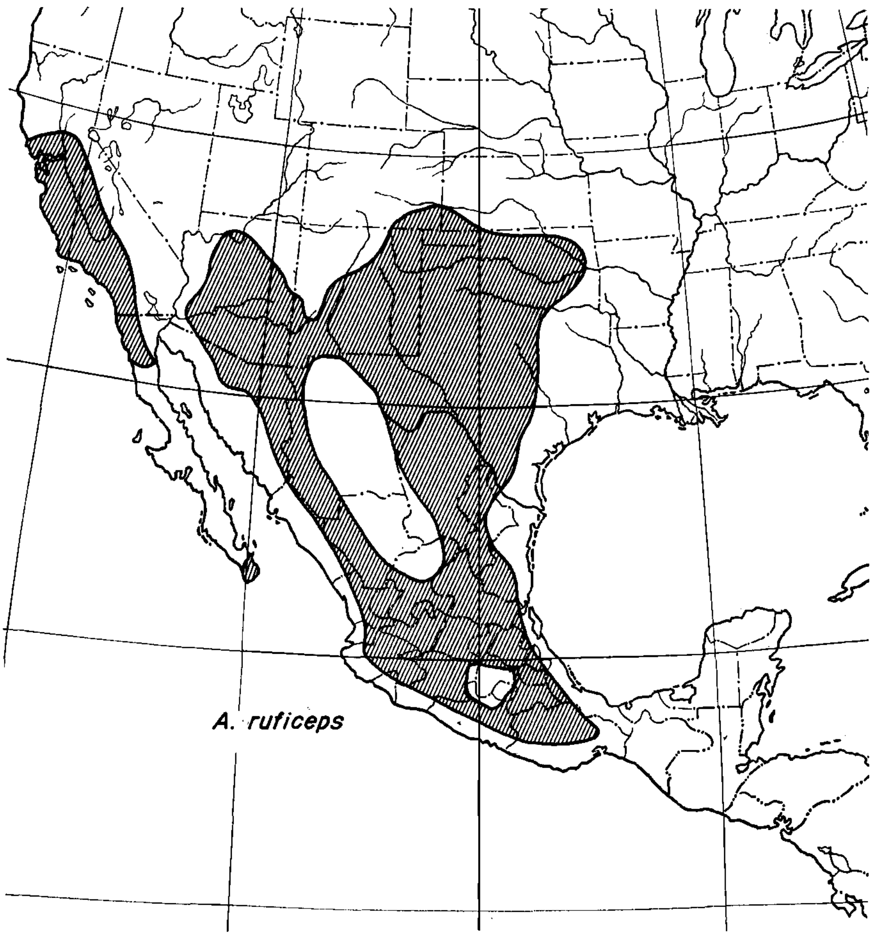

FIGURE 3. Geographic distribution of *A. ruficeps*.

RUFOUS-CROWNED SPARROW, *A. RUFICEPS*

Geographic distribution.—The Rufous-crowned Sparrow occurs from "central California, central northern Arizona, southwestern New Mexico, southeastern Colorado, and northwestern and central Oklahoma, south discontinuously to southern Baja California, Guerrero, Oaxaca, and Veracruz" (A.O.U. 1957; Fig. 3). Casually, it ranges into southwestern Kansas, and it has been reported in Zion National Park, Utah (Wauer 1965).

In the United States, some birds seem to shift ranges in winter, such as in California (Cogswell 1968) and in Arizona (Phillips *et al.* 1964, Phillips

1951b). However, there is little evidence of regular migration and it is doubtful that even the northeastern race (*A. r. eremoeca*) has truly different winter and summer ranges, as stated by the A.O.U. check-list (1957). Sutton (1967) reported no evidence of migration in that form in Oklahoma, and such would appear the case elsewhere. Recently, Hubbard (1975) re-examined specimens of supposed migrants of *eremoeca* from southern Mexico (A. H. Miller *et al.* 1957) and found that they are examples of southern, resident races.

Ecologic distribution.—In the United States *A. ruficeps* is an indicator species of the Upper Sonoran Life Zone, while in Mexico, Goldman (1951) listed it from the Upper and Lower Austral Zones.

In California the Rufous-crowned Sparrow frequents areas with low shrubs interspersed with various smaller nonwoody plants; sometimes interstices between bushes are almost bare. Its habitat seems to be approximately the same throughout its California range, with a predilection for patches of California sage (*Artemisia californica*) where these occur (Grinnell and Miller 1944). In northern California *A. ruficeps* usually occurs on open, grassy hillsides with scattered brush and rocks. In the more arid inner coast ranges and western foothills of the Sierra Nevada the grass is sparser and shrub species change. In mesic areas the birds may occur on hillsides devoid of rocks but with small shrubs that serve as elevated, exposed perches. In Marin County, Mailliard (1900) noted an apparent shift from sagebrush in spring to poison oak (*Rhus*) and blackberry (*Rubus*) vines on grassy hillsides away from sagebrush in late summer. In an area around Fresno, *A. ruficeps* used rock piles or other outcroppings for perches and hiding places on hills devoid of brush and trees (Swarth 1917).

In southern California Cogswell (1968) found *A. ruficeps* in "moist coastal scrub areas near Santa Barbara." Willett (1933) thought they were "partial to grass-covered hillsides." Farther south in the northern section of Baja California, Grinnell (1926) noted they "kept to a low, sparse, dry hillside type of chaparral."

On Santa Cruz Island, California, the habitat is "grassy hillslopes and canyon walls where there are scattered bushes or clumps of cactus" (Grinnell and Miller 1944). However, Dawson (1923) reported that *A. ruficeps* occurred in the thickest patches of prickly pear (*Opuntia*) cactus when he visited the island in the spring of 1915. The birds shift habitat slightly during winter months. At the tip of Baja California *A. ruficeps* occupies "grassy hillsides above 2,500 feet" (Belding 1883).

There are very few reports on habitat of *A. ruficeps* outside of California. To the east in Arizona, western New Mexico, and northern Mexico, the species principally occupies chaparral and oak woodland, at times reaching the piñon-oak-juniper association. Scott (1886) reported birds as high as 10,000 feet in "warmer months," but this is exceptional even for areas where xeric vegetation reaches high altitudes on dry slopes. Scott (1887) mentioned that the species extended from 3000 feet up to the pine woods in the Santa Catalina Mountains. I found *ruficeps* at about 1350 m in the Santa Catalina Mountains where the oaks met remnants of drier vegetation from the desert floor. Most of the region is covered with grasses, scattered oaks from 3–9 m tall, and some leguminous trees, with rocks throughout the area. In Cochise County, Arizona the species was found on southern exposures of scantily vegetated lower ridges and foothills among a scattering of oaks, madrone, and scrubby mountain mahogany, with abundant beargrass and mescal on the ground (Willard 1912). The birds also occur along Cave Creek Canyon on the eastern slope of the Chiricahua Mountains. Occasionally they come down to forage in riparian vegetation on the floor of the canyon, but are usually heard from dry, rocky slopes above the stream. To the west in the Baboquivari Mountains, Arizona, Sutton and Phillips (1942) found *A. ruficeps* in live oak-piñon-juniper-grass-agave habitat in the saddle just west of the peak. In his extensive survey of pine-oak woodland of the southwestern United States and adjacent northern Mexico, Marshall (1957) found the species in grassy places that were broken up by boulders, scattered trees, or clumps of low bushes. In Arizona they were limited to south-facing canyon walls as the other sides were usually too densely vegetated. They became more numerous in Mexico where more brush and increasing amounts of grass and *Ceanothus* were present.

According to Ligon (1961) the habitat in New Mexico was arid canyons and mountain slopes of "desert land character" between 5000 and 7500 feet, usually where scrub oak and similar brush grew. North of Silver City, Grant County, I found *A. ruficeps* in open pine-oak woodland with large bare spaces and extensive shrubbery. At another nearby locality, they were in an area dominated by oaks, junipers, pines, and *Ceanothus*; the birds seemed to be centered on hillsides that lacked pines where the ground was approximately half bare. About 16 km northwest of Cliff, Grant County, I found several singing males and a female on rocky hillsides covered with scrub oak, *Ceanothus*, and juniper but with little grass and much bare ground. In the Peloncillo Mountains of western New Mexico, I found the birds most common on arid hillsides dominated by pine-oak. In Guadalupe Canyon in the southwest corner of New Mexico and the southeast corner of Arizona, the birds inhabited both slopes on rocky hillsides covered with mesquite, cactus, yucca, agave, grasses, and creosote bush. (See Johnston and Hardy 1959 for a more detailed description of the habitat in Guadalupe

Canyon.) *A. ruficeps* were seen foraging on the floor of the canyon, but singing was heard only from hillsides.

Ragsdale (1892) noted that in Cooke County, Texas the species inhabited dwarf post oak and blackjack oak stands, where there was a growth of chaparral in sandy soil. Attwater (1892) said it was a common summer resident, and nests were found in hilly country around San Antonio among tumbled rocks of worn limestone cliffs (Quillin and Holleman 1918). Around Boerne in southwestern Texas, Salvin and Godman (1886) reported the species in rocky localities, usually near a creek but up to 1.5 km or more from water.

In Oklahoma, Sutton (1934, 1967) found the species along rims of mesas "among big boulders and at the bases of cliffs" and nesting in areas "among grass on rocky slopes." Nice (1931) reported that *A. ruficeps* "lives only in rocky broken country in Oklahoma," where "granite boulders, small cedars, stunted oaks, and parched hillsides suit its fancy."

In Tamaulipas *A. ruficeps* occurs along the eastern slope of the Sierra Madre Oriental and onto the Mexican Plateau. There is an isolated population in the Sierra de Tamaulipas, a mountain range in the Atlantic Coastal Plain east of the Sierra Madre and just north of the Veracruz border (Martin *et al.* 1954). Here *ruficeps* was found in arid pine-oak woodlands on the upper slopes. These authors reported that less than 50% of the area was covered with woods and that many ridges and high meadows were covered with short grass, while others graded into either pine or oak savannas, which then merged into woods with a complete crown closure. The birds favored "fallen trees, clumps of cycads, and any brush available for cover in the open woods." Lamb (MS) reported that there was little understory except in some arroyos and that sparrows were taken on rocks or in low branches of oaks.

To the west in Nuevo León, Sutton *et al.* (1942) found *A. ruficeps* in a "dry gully" below Mesa de Chipinque, and Burleigh and Lowery (1942) reported it as "common in mountainous areas and to some extent in arroyos of open desert country." According to Lamb (MS) *A. ruficeps* occurred on rocky hillsides in low oak bushes at the east base of Mt. Potosí and in brush growth including chaparral and manzanita, with possibly a few oaks in the arroyos.

To the northwest Miller (1955) reported the species up to 7000 feet on south-facing slopes within the oak belt of the Sierra del Carmen, Coahuila. Here yucca, cactus, and tussock grass among rocks afforded cover.

In Chihuahua, *A. ruficeps* occurs in the Sierra Madre Occidental. Stager (1954) found it on the west slope of the Barranca del Cobre, from 6300 feet down to 4300 feet, where pines gave way to larger oaks. The sparrows were common throughout higher elevations. Along the western slope of the Sierra Madre Occidental *A. ruficeps* extends southward into northern Jalisco. At Rancho Batel, near Santa Lucía, Sinaloa, I found several individuals on open pine-oak hillsides where the herb layer was well grazed. The conditions were more mesic than those in places I visited in Arizona, New Mexico, and other parts of Mexico. Pitelka (MS) also found the birds at Rancho Batel "on dry, open slopes where the woodland had been partially cleared and where there were scattered, low brush thickets, and a broken, low plant cover." He thought that "in physical character the habitat resembled closely that occupied by the species in . . . Berkeley [California]."

In the highlands of Jalisco around the Barranca de Oblatos, *A. ruficeps* was in relatively open, flat oak-pine-juniper woodland with an abundant grass and herb layer. Webster and Orr (1954a) reported the species about three miles southwest of Sombrerete, Zacatecas, where it was common and apparently breeding in mesquite-prickly pear vegetation.

The species reaches the southern limit of its distribution in the mountains of Oaxaca. Lamb (MS) collected specimens in the heavy growth on the hills surrounding Tamazulapan. I found it in the same area in 1964 in relatively open hard chaparral and scrub oaks. It occurred with *A. notosticta*, which seemed to be more nearly restricted to denser scrub vegetation. Just south of the Valley of Oaxaca, about 7 km southeast of Matatlán, *A. ruficeps* was found in open grassy areas on rocky, scrub-oak hillsides, but was found infrequently in denser scrub oaks.

RUSTY SPARROW, *A. RUFESCENS*

Geographic distribution.—The Rusty Sparrow occurs in the highlands from northern Mexico south to northwestern Costa Rica and in the eastern lowlands from Tamaulipas south along the Gulf coast through Guatemala, and in Honduras and Nicaragua (Fig. 4). The altitudinal distribution is from near sea level to more than 2400 m.

Ecologic distribution.—The northernmost populations of this species occur in northern Chihuahua and Sonora. There Marshall (1957) found the birds in pine-oak woodland, in logged pine forest, on a desert slope, and in open pine forest with low patches of *Ceanothus* and bracken (*Pteridium aquilinum*). Van Rossem (1945) listed the species as occurring in the upper Sonoran Zone (canyon oak association) of the mountains of Sonora.

In Zacatecas, Webster (1958) found *A. rufescens* in a region west of Monte Escobedo, where tall bunchgrass flourished beneath oaks 10 to 20 feet tall. In nearby Jalisco, Selander and Giller (1959) reported small numbers in the understory of clumps of small trees in dry gullies high on the side of the Barranca de Oblatos northeast of Guadalajara. I found it

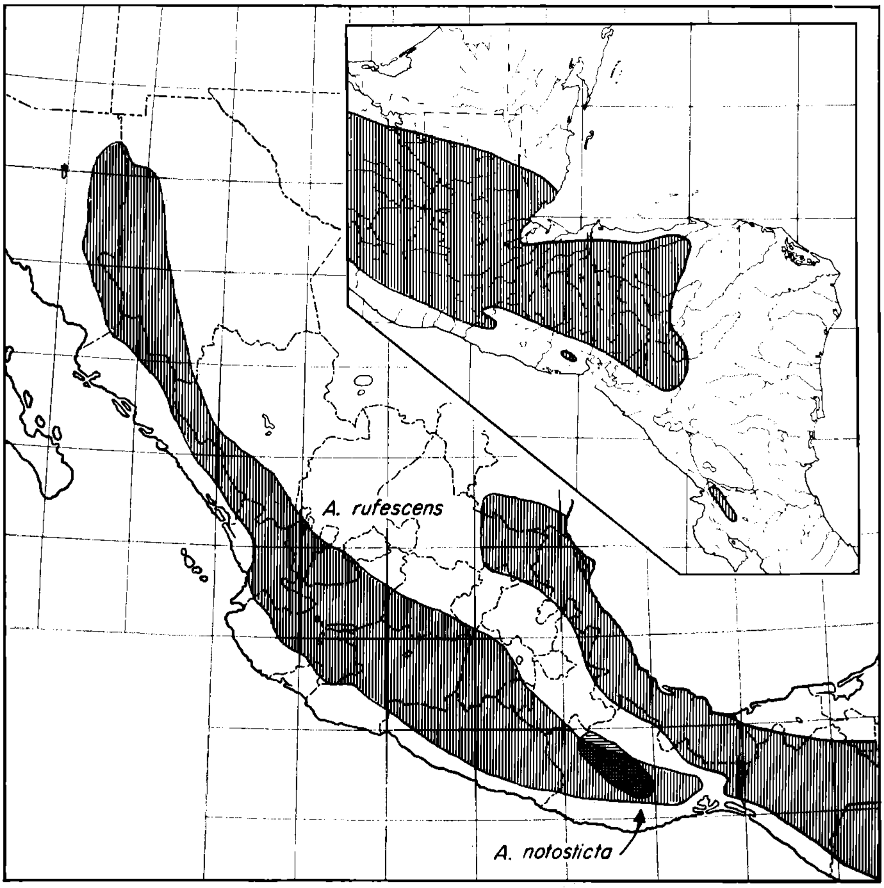

FIGURE 4. Geographic distribution of *A. rufescens* and *A. notosticta.*

in the same region on open, legume- and oak-dominated grassy hillsides in late July 1963. Farther west in Colima, Schaldach (1963) noted that the bird was uncommon in brushy barrancas at the edge of pine-oak forest on the flanks of the Volcanes de Colima.

In Michoacán, *A. rufescens* was common in dense thorn scrub thickets and heavy brush of the Tzitzio region (J. Davis 1953). When I visited there in 1963, the bird was most common in relatively open pine-oak forest. Oak seedlings occupied part of the cleared area, and some legumes and other shrubs were also present. In some places grass was 10 to 15 cm tall. Gullies were densely grown with shrubs and brush, but the sparrows tended to spend most of their time on the more open hillsides.

A. rufescens is rather common in deciduous forests east of Cuernavaca, Morelos, and in the pine-oak zone of the mountains to the north (Rowley 1962). On Rowley's directions, I returned to this locality and found the vegetation was second-growth deciduous forest, with many *Ipomoea* and few scattered oaks. In many places the woods were essentially closed at 3 to 5 m above the ground, but sufficient light penetrated to support a thick growth of shrubs and small trees, making walking very difficult. Generally the birds stayed in openings of the woods that had grown up in grass or in annual herbs that formed a thick layer about 15 cm tall at this time of year. The birds usually were found at the edges of the woods, to which they escaped. I heard several male *A. rufescens* singing on the upper slopes of the Cañón de Lobos, about 14.5 km east of Cuernavaca. These hillsides are generally dominated by tropical deciduous forest, except on the dry slopes of the southeastern end where there are extensive grassy spots and scattered oak trees. North of Cuernavaca, in the pine-oak zone, *A. rufescens* occurred where earlier logging operations left the area relatively open, but with some shrubs. Early in the century, A. P. Smith (1909) found the birds in a deep barranca near Cuernavaca. He said the bottom of the barranca was covered in places with fallen leaves and the sparrows spent much time scratching through them. Davis and Russell (1953) reported that in Morelos the species seems to be a resident along the lower border of the mixed woodland.

South of Chilpancingo, Guerrero, as the Sierra Madre del Sur drops to the Pacific coastal plain to the south, *A. rufescens* was moderately common on grassy hillsides at about 750 m. Pines predominated in a pine-oak community with many of the trees less than 6 m tall. Shrubs were scattered throughout the park-like area and the grass layer formed a canopy at about 45 to 60 cm. Slightly farther to the north (15 km south of Chilpancingo), W. B. Davis (1944) reported that the species was common in rolling, grassy, and brush-dotted hills.

To the east, *A. rufescens* ranges into the highland regions of Veracruz. Here Sumichrast (1869) found it common in the "temperate" region where it was most abundant between 2000 and 5000 feet. Lowery and Dalquest (1951) reported that *A. rufescens* usually occurred on or near the ground along edges of fields in the Upper Tropical Life-zone.

In Chiapas, Edwards and Lea (1955), working on the plateau country about 64 km north of Arriaga, said *A. rufescens* was "the common sparrow in the thick brush in the pine-oak woods," around El Fénix in August and La División in April.

A. rufescens also occurs in the highlands of parts of Guatemala (and south into Nicaragua), and Land (1962) said it occurred fairly commonly in brushy second growth and pine forest. In El Salvador, "the chief requirement of [*A. rufescens*] seems to be rocky grasslands or rough terrain covered with a relatively scanty growth of low brush and weeds" (Dickey and van Rossem 1938). An isolated population (*A. r. pectoralis*) occurs on Volcán de San Miguel on the lava flows that are cut by numerous gullies and are covered mostly with bunchgrass, agave, scrub oaks, waxberry, and similar growth (*op. cit.*). It was apparently common when van Rossem visited there.

The populations that occupy the eastern lowlands of Middle America from Mexico southward into Honduras were reported by Griscom (1932) from pine forests in Guatemala, while Land (1962) found them at the edge of an extensive grassland. Russell (1964) said these birds were "common residents" in the "extensive grassy areas of the pinelands of the Mountain Pine Ridge, especially near brush-filled ravines and small thickets."

Along the Pacific slope of the Guanacaste Cordillera in Costa Rica, *A. rufescens* is typically found in open habitats, particularly boulder-strewn volcanic slopes and grassy fields and pastures dotted and patched with wiry bushes, undersized trees, and thicket scrub (Slud 1964).

OAXACA SPARROW, *A. NOTOSTICTA*

Geographic distribution.—This rare and little-known species is apparently confined to the mountains of central and northern Oaxaca (Fig. 4). However, the type specimen may be from Puebla or Mexico (Miller *et al.* 1957).

Ecologic distribution.—According to Goldman (1951), *A. notosticta* occurs in the Lower Austral Zone, but the localities in Oaxaca where I found it are clearly in Goldman's Upper Austral Zone. The two places where I observed *A. notosticta* are near Tamazulapan and near Matatlán, both on the Pan American Highway at approximately 1850 m elevation. The hillsides in the two regions are rather steep and in many places nearly bare of herbaceous vegetation. Some areas have rock outcrops. The habitat is hard chaparral with scattered scrub oaks of the *Quercus rugosa* type. In places the scrubby trees are dense enough to form a closed canopy at 1 to 3 m, making walking nearly impossible. The oaks average 2 to 3 m tall; the tallest are 4.5 to 6 m. Trees taller than 4.5 to 6 m are limited to streamsides and are not in areas used extensively by *A. notosticta.* One such site, however, was used by a male as a song perch. Manzanita (*Arctostaphylos* sp.) occurs with oaks on all slopes and is dominant on some hillsides.

This habitat occurs along the highway on the upper slopes south of Tamazulapan for some kilometers, but is limited in extent around Matatlán. In both areas, farming is rapidly taking over much of the land and habitat, for *A. notosticta* is disappearing. Although *A. mystacalis* occurs sparingly

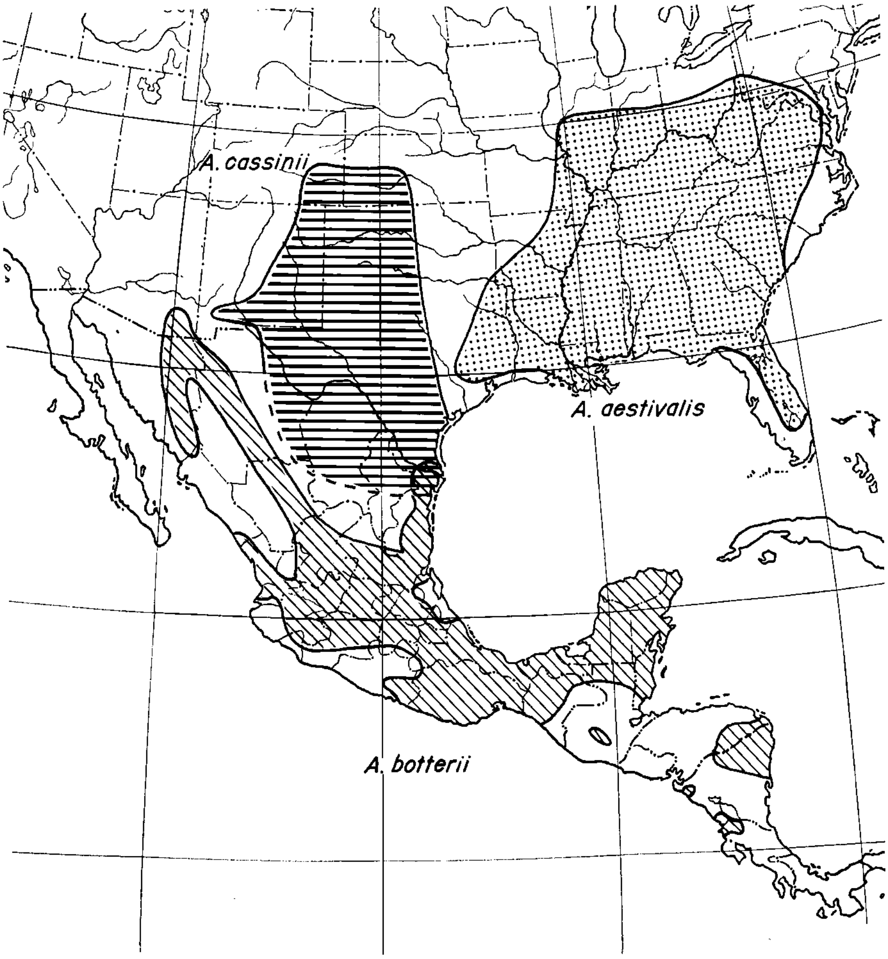

Figure 5. Geographic distribution of the *botterii* complex—*A. aestivalis, A. botterii,* and *A. cassinii.*

in *A. notosticta* habitat, I have yet to discover *A. notosticta* ranging out into the dry, legume-dominated hillsides that are so extensively inhabited by *A. mystacalis.*

Bachman's (Pinewoods) Sparrow, *A. aestivalis*

Geographic distribution.—This species is limited to the south and central portions of the eastern United States (Fig. 5). It normally occurs in breeding season from central Indiana and central Ohio, southwestern Pennsylvania, and central Maryland south to the Gulf coast and central Florida.

It occurs from the east coast throughout this north-south range west to Missouri and northeast Texas. There is a record, perhaps erroneous, from eastern Concho County, Texas (Lloyd 1887).

This is one of the migratory species in this genus. From available records, it appears that by August northern populations begin to move south to the Gulf coastal states and the southern Atlantic seaboard for the winter. Brooks (1938) summarized some records of spring arrival dates in the north-central part of the range.

Ecologic distribution.—Brooks (1938) noted that *A. aestivalis* is very local and selective in breeding places in the north-central part of the range. He characterized the habitat preference as "brushy hillsides or wooded borders on fairly steep slopes." This seems to be true for much of the northern portion of the range from Missouri east to Pennsylvania and south to Tennessee, Kentucky, and the Virginias. The birds seem to rely heavily on open foraging sites.

In the more southern parts of its range, *A. aestivalis* is restricted primarily to open pine stands with a grassy substrate and scattered shrubs, oaks, and other hardwoods. In South Carolina the species occurs in "scattered stretches of open pine woods" (Burleigh 1935), and Sprunt and Chamberlain (1949) noted that undergrowth and bushes are essential elements of the habitat. Sprunt (1954) stated that the species occurs in pinelands and in association with palmetto stands in Florida. Mills (1905) found *A. aestivalis* in an old field partly overgrown with pines and shrubs. In Louisiana Lowery (1955) noted that the species occurs primarily in pine and pine-oak woods. Meanley (1959) found it in open park-like areas in sites with scattered pine trees, clumps of shrubs, and brush piles.

Ragsdale (1892) reported the species in the eastern third of Cooke County, Texas, where post oak and black oak grew on the uplands and hickory, ash, and elms along the streams. In Angelina National Forest, Jasper County, Richard Sage and I found *A. aestivalis* common in open forests of replanted longleaf pine, and an essentially complete grass cover and scattered shrubs. One pair used a stand of oaks along one edge of its territory primarily as a retreat; the male sometimes used one of the edge trees for a song perch.

BOTTERI'S SPARROW, *A. BOTTERII*

Geographic distribution.—Webster (1959a), Dickerman and Phillips (1967), and Monson (1968) discussed in detail distribution of this species, which occurs from southern Arizona and southeastern Texas south to Nicaragua in the east and Costa Rica in the west (Fig. 5). The populations of Central America are more discontinuous and isolated than those of Mexico.

Those include the dark forms (*A. b. petenica*) of the eastern lowlands of southern Mexico and Central America, which I follow recent authors (Webster 1959a, Russell 1964, Howell 1965, Dickerman and Phillips 1967, and Monroe 1968) in including as races of *A. botterii.*

According to Webster (1959a), "the few, scattered winter and migration records seem to show that . . . the northern populations spend the period from November to May in the arid tropical zone of southern Mexico." The northern birds apparently do migrate, although actual wintering specimens are limited. Phillips *et al.* (1964) listed the bird as a "summer resident" in Arizona, but noted that nothing was known about the winter range of that population.

Ecologic distribution.—In the eastern lowlands of Nicaragua, Howell (1965) said that *A. botterii* is found in the pine savanna (*Pinus caribea*), whereas in the highlands near Chinandega it was found in grassland (W. DeW. Miller 1925). In the northern portion of the Guanacaste Cordillera of Costa Rica, Slud (1964) said this species occurs among the smooth rust-colored volcanic boulders well up on the bare southwestern slope. At Orosi it occurs among the rough black volcanic rocks on the western approach. As expected, it apparently does not occur on the moister eastern slopes.

In the central highlands of Guatemala, *A. botterii* occurs in the region of Antigua (see Dickerman and Phillips 1967), but the habitat is not reported. The species also occupies the plains of the Petén in northern Guatemala that Van Tyne (1935) described as "a lowland region covered with a tropical forest which is, however, broken by sharply marked areas of poor soil characterized by savannas and open pine forests." The specimens of *A. botterii* that Van Tyne collected probably came from savanna and open pine-forest habitat.

To the south in British Honduras, Russell (1964) reported that the species is an "uncommon local resident of the lowland pine ridges from Hill Bank south to the savannas near Monkey River." However, "many extensive areas of apparently suitable habitat are not occupied," and it did not occur on the low pine hillsides above 3000 feet elevation.

From the more northern portions of the range, the form was recorded in the "rather extensive grassy areas studded with scattered low trees, numerous thickets, or dense shrubbery, tangles of vines and medium sized trees" near Las Choapas, Veracruz (Zimmerman 1957). In Tabasco I found the bird about 11 km south of Chontalpa in an extensive grassy field at the edge of a cutover rain forest. The grasses, averaging about 15 cm tall but as high as 45 to 50 cm, grew mostly in clumps and almost completely shadowed the ground throughout much of the area. There were scattered shrubs in the field, and two of the three birds that I saw were flushed from the base of one clump of shrubs. Paynter (1955) reported the habitat on the Yucatán peninsula only as "low arid scrub."

A. botterii occupies the open grassy areas in forested regions at middle elevations in the southern highlands of Mexico. I saw *A. botterii* near the city of Oaxaca in heavily grazed areas essentially denuded of grasses and dominated by annuals, cacti, leguminous shrubs, and other scrubby vegetation. Webster (1955a) reported *A. botterii* nearby in approximately the same conditions. Bangs and Peters (1928) reported that W. W. Brown took some birds, among which were specimens of *A. botterii*, that were characteristic of "pine ridge" vegetation, near Chivela, Oaxaca. Edwards and Lea (1955) found *A. botterii* in grassy upland fields on the plateau near Monserrate, Chiapas. A singing male I observed approximately 24 km west of Izúcar de Matamoros, Puebla was in thorn scrub with a well-grazed grass layer, where trees and shrubs were rather far apart. This is the most closed habitat in which I found *A. botterii*.

On the high central Plateau of Mexico, *A. botterii* is apparently limited to grassy and weedy expanses at moderate to high elevations. Edwards and Martin (1955) reported the species singing in a grassy field along the southwestern side of Lake Pátzcuaro, Michoacán. D. A. Zimmerman, on the label of a specimen from Michoacán ("UMMZ 151553; nine miles west of Jacona, 5300 feet"), noted that the habitat was arid scrub with cacti and thorny shrubs to 12 feet tall. Grassy patches were small and cover was primarily shrubs. On the old road from Morelia to Toluca that passes through Zinapécuaro, Michoacán, *A. botterii* were common in fields bordering the road. Most of this land is used for cultivation or grazing, but fallow ground had grown up in weeds, grass, and shrubs. The sparrows were usually found in these overgrown fields, but when frightened would escape to weed patches in the midst of cultivated fields. Going north from Ixtapan de la Sal, Mexico toward Toluca, we found *A. botterii* on fences and in roadside fields in the same sort of habitat as in parts of Michoacán. Weedy agricultural fields at about 1850 m on the plateau are apparently prime habitat. Probably available habitat increased considerably after man cut much of the woody vegetation.

Webster (1959a) reported that "in Zacatecas, Durango, Jalisco, and Guanajuato, I found the race *mexicana* most numerous at elevations of 6400 to 7500 feet. In these regions the sparrows were sheltered in stone walls or scattered bushes (*Prosopis* or *Acacia*, usually) or hedgerows or bushes along a creek, wash or irrigation ditch; but they did most of their feeding in the grassy (*Bouteloua* sp.) or weedy fields. Breeding pairs were collected in an outlying group of piñon pines (alt. 7900 feet) west of Fresnillo, Zacatecas, and in a thicket of morning glory trees (*Ipomoea* sp.), north of Colotán, Jalisco at 6100 feet. These areas apparently represented marginal habitats, but at both spots there was considerable open grass nearby." At a point 50 km northeast of Autlán, Jalisco, on 28 July 1963, I found these birds in very open, grazed grassland or cultivated fields with scattered trees that served as song perches for males. On the plateau above the Barranca de Oblatos on the road toward Moyahua, Zacatecas, we found the species in a grazed pastureland dotted with shrubs and trees.

A. botterii inhabits tropical, palm-dotted savanna near sea level on the coast of Nayarit and semitropical grassland with scattered *Acacia* bushes near Compostela, at 2500 feet (Webster 1959a). I also found it in a slightly cutover oak parkland on the dry slopes north of Tepic, where grass and weeds grew thickly on hillsides where the ground vegetation had not been eroded.

In Arizona, *A. botterii* is an uncommon summer resident, with only one published nest record (Ohmart 1968). The species was not found in the state during the early 1900's, being "rediscovered" in the southeastern part of Arizona in 1939 (Monson 1947). Monson reported, "Nearly all Botteri's Sparrows noted were inhabiting stands of sacaton (*Sporobolus wrightii*), a tall grass which occurs along the Babocomari River and in parts of the southern end of the Sulphur Springs Valley. Singing perches used most frequently were mesquite (*Prosopis juliflora*), catclaw (*Acacia greggii*), and whitethorn (*Acacia constricta*), which shrubs occur with the sacaton stands or on their borders. In some instances, the birds were occupying swales of sand dropseed (*Sporobolus cryptandrus*) intermingled with mesquite and catclaw." On 27 June 1963 I found *A. botterii* less than a km west of Fort Huachuca, Cochise County. There were at least two singing males; one occupied an overgrazed grassland partly overgrown with perennial weeds, but with scattered patches of sacaton grass and mesquite; the other was in a fenced plot with a solid grass layer averaging about 30 cm high. There were a few trees and some small dead twigs and shrubs that were used for song perches. I also heard a bird singing in similar habitat just south of Nogales, Sonora in early July 1963.

Although *A. botterii* occurs along the Gulf coast from southern Texas to southern Tamaulipas and inland in Tamaulipas east of the Sierra Madre Oriental, the only habitat records are from the very restricted range in southern Texas in the region of the Rio Grande delta. Harper (1930), in his historical review of the species around Brownsville, Texas, characterized the habitat as wide salt prairie covered with low grasses and herbs, plus a few prickly pears and small mesquite. He also found the birds in a slightly higher and drier prairie. There "the mesquite bushes were taller and more numerous, there were more prickly pears, and a new element appeared in the shape of yuccas." There was still an abundance of salt grass. Ripley (1949), revisiting the area in March 1946, found over-grazing very apparent and good salt prairie limited to the borders of the sea and lagoon both at Port Isabel and Boca Chica. He did not find any *A. botterii* during his visit and remarked that the summer range of the sparrow had been seriously damaged. However, this apparent absence was probably because the birds had not returned from their wintering grounds or that they were not yet singing. During early July 1964, we found *A. botterii* locally common on the borders of Laguna Atascosa, Cameron County, and in nearby areas. Here it was almost entirely limited to salt grass association where there were few trees and shrubs. As grass dropped out away from the lake shore and mesquite and cactus became more frequent, *A. cassinii* became predominant. We did find several *A. botterii* in rather bare-ground habitats along a drainage canal; here they were surrounded by *A. cassinii*. *A. botterii* probably is closely tied to salt grass prairie in this portion of its range.

CASSIN'S SPARROW, *A. CASSINII*

Geographic distribution.—The A.O.U. check-list (1957) outlines a large breeding range for this species, extending from Texas, Kansas, and Oklahoma west to Arizona and south to Chihuahua, Coahuila, and Tamaulipas (Fig. 5). However actual breeding records are more restricted. Phillips (1944) found one bird building a nest near Tucson in late August, but the nest was not completed. Ohmart (1966) found 3 successful nests around Tucson in August and September 1965, and intimated additional nesting there subsequently (Ohmart 1968). The early summer breeding range that has been documented by nests or recently fledged young is the Gulf coast of Texas, southwestern Kansas, parts of Oklahoma and Colorado, and sites in eastern New Mexico (Hubbard 1970). There also is evidence that the species breeds in spring and early summer locally in southwestern New Mexico (Zimmerman pers. comm.). It probably breeds south into Mexico, but extent of the range there has not been documented. Urban (1959) presented some evidence, based on gonad condition and early summer occurrence, that Cassin's Sparrow breeds in Coahuila. About 45 miles south of Villa Ahumada at 4700 feet, A. H. Miller collected a male with enlarged gonads on 21 June. The date and activity indicate that the birds may have been breeding, but the lack of females at the site (none recorded by Miller, MS) suggests that these males were early migrants.

The postbreeding migration appears to be westerly and southward in late summer and fall, but some birds winter in southern parts of the breeding range. Phillips (1944) discussed in detail migration and wintering in *A. cassinii*, but much remains to be learned about this species.

Ecologic distribution.—Throughout its breeding and wintering ranges

Cassin's Sparrow generally occupies very similar habitats. Typically there is a ground layer dominated by grasses, although in some overgrazed areas grasses may be replaced by herbs. Within the grassy region shrubs or small trees appear to be essential, as they are used for song perches and concealment. Openness of the habitat varies from nearly uniform grassland to dense mesquite woodland around which the birds probably forage in the more open border areas. The species seems to be restricted to semiarid plains and usually does not penetrate the eastern deciduous woodlands or riparian lands within its range.

We found Cassin's Sparrow in mesquite-hackberry grassland around Sinton, San Patricio County, Texas. Most of this land presently is used for cattle grazing. Much of the original grass is gone, and large patches of ground are bare or dominated by *Opuntia* cactus and various herbs. On the Welder Wildlife Foundation we found groups of singing males in habitats from low mesquite in open range land to dense patches of mesquite 6 to 7.5 m tall. The birds were commoner in more open habitats.

Near the Rio Grande delta of southern Texas, *A. cassinii* was restricted to more xeric habitats characterized by *Opuntia* and hackberry and occurred in salt grass vegetation where mesquite trees existed. It was absent from the nearly pure salt grass regions occupied by *A. botterii.*

On 16 June, several singing males were spaced at about 90-m intervals in juniper, mesquite, grass, and thorny bushes about 13 km west of Davis Mountain Junction, Jeff Davis County, Texas. On surrounding hillsides the ground was rockier and sparsely covered by grass; shrubs were denser and taller where water collected than in intervening areas. The birds seemed to concentrate in the middle region but used sites with dense shrubs as refuges. On the same day we found another group of these sparrows 19 km southwest of McCamey, Pecos County, Texas. I heard at least two males, and one gave the flight song performance. Habitat was open and dominated by legume shrubs and some grass, most of which was around bases of shrubs.

Johnston (1964) reported *A. cassinii* as a "common summer resident" in open shrub and grassland edge south and west of Wallace and Comanche counties, Kansas.

In southwestern New Mexico I saw what probably were early migrants in several locations around Silver City. On 4 July 1963, a single bird was in an overgrazed area with about 35 to 50% cover of bear grass, juniper, and oaks. On 7 July, approximately 22 km north of Separ, we found at least four and possibly five singing males in habitats dominated by perennial composites and mesquite. The next day, as we drove toward Arizona on U.S. 70, we found a group of 30 or more singing males (apparently no females) in mesquite-grassland vegetation. The grass was approximately

38 cm tall and formed a 50 to 75% cover. The scattered mesquite was up to 2 to 2.5 m tall. The birds essentially avoided, until chased, all places with bare ground or ground covered only by short herbs and mesquite. In eastern New Mexico similar habitats are used, but in addition an alfalfa field was occupied near Maxwell, Colfax County, in June 1971 (Hubbard pers. comm.).

This sparrow occurs in grassland in southeastern Arizona from late summer through spring. Around Tucson, birds have been taken in grassland dominated by mesquite and hackberry. Henshaw (1875) reported *A. cassinii* on dry plains covered with short grass, small shrubs, and bushes.

Little information on habitat of the species in Mexico is available. Webster and Orr (1954b) reported an adult male in full breeding condition taken on 10 July about 24 miles northeast of Ciudad San Luis Potosí at 1815 m. The bird was giving song flight performances in mesquite grassland. Miller (MS), found at least three singing males in "the thicker vegetation" of tussock grass, mesquite, catclaw, desert willow, and dry composites 45 miles south of Villa Ahumada, Chihuahua, at 1450 m. There was some green annual growth. Finally, in March 1974, several birds were singing in thorn scrub-grassland north of Monterey, Nuevo León (Hubbard pers. comm.).

FIVE-STRIPED SPARROW, *A. QUINQUESTRIATA*

Geographic distribution.—This species is limited to the Sierra Madre Occidental Biotic Province (Goldman and Moore 1945) in northern and western Mexico and, in recent years, Arizona. The first record for the latter area was of a bird taken in the Santa Rita Mountains (Binford 1958); since then the species has been found breeding at Patagonia, Santa Cruz County. The nearest breeding ground to the south appears to be near Imuris, Sonora (Binford *op. cit.*), and the species ranges south to Jalisco along the foothills and lower slopes of the western Sierra Madre (Fig. 1).

The altitudinal range of *A. quinquestriata* extends from around 240 m to about 1850 m. There are several records (Webster 1958, Selander and Giller 1959) in the interior along river valleys where suitable climatic and vegetational conditions prevail. Highest altitudinal records are from the extreme southern portion of the range in Jalisco and Aguascalientes. The lowest record is from the Río Mayo drainage near Camoa, Sonora. There is no evidence that *A. quinquestriata* migrates.

Ecologic distribution.—In general, I found *A. quinquestriata* in dense deciduous woodland averaging about 6 m tall. In more arid areas it is often found in wetter sites along stream courses or on north-facing slopes. In Arizona the species has been found in dense mesquite stands along Sonoita Creek, Santa Cruz County. About 123 km east of Hermosillo, Sonora, above the arid mesquite-dominated floodplains in the foothills of the Sierra Madre, I found *A. quinquestriata* common on hillsides dominated by tropical deciduous woodland. They were limited to forests with a nearly closed, 3-to-6-m canopy composed largely of leguminous trees. The understory was almost clear of shrubs, but was covered with annuals that were just coming up in mid-July 1963. When I returned to the same site in late August, the herb layer was 1 to 2 m tall in most unshaded places. Some of the land under the canopy was still open. The birds did not forage where there was an impenetrable tangle of weeds up to 1 to 1.5 m tall, but seemed to prefer the denser shrubs and herbs under the canopy. Buchanan (in litt., 16 December 1965) took three birds in Sonora (Miña Promontorio, Sierra de Álamos, altitude 510 m) "on a spit of land running out into a fairly steep-sided barranca in a big inter-montane basin on the (southwest) side of the Sierra [de Álamos]. The obvious vegetation here was Pochote (*Ficus goldmanii*) (on the upper flats), *F. petiolaris* (in barranca), *Acacia* sp. and *Lemairocereus* sp. (the foothill [species]—not . . . *L. thurberi* of the lower Arid Thorn Scrub association), plus the introduced *Prosopis chilensis.*"

Lamb (MS) collected the species at Rancho Guasimal, Durango, in an area where the "brush is exceedingly heavily foliaged; and the ground covered with vines and weeds; also the country is exceedingly steep."

The remaining information on habitat is from central Mexico. Webster (1958) found *A. quinquestriata* in brush on a cliffside near Moyahua, Zacatecas in September. Selander and Giller (1959) reported the species from the Barranca de Oblatos near Guadelajara, Jalisco. In an area at about 1230 m they saw a "pair . . . in low shrubs and herbs in a grassy area [?] at the side of the road." In July 1964, I found several singing males in this same area. The birds were limited to wooded ravines on grassy, open-wooded hillsides at about 1200 m. Where there was sufficient moisture in the ravines, luxuriant growth of deciduous trees, formed a closed canopy. Thick stands of shrubs were present where some trees had been removed and on the slopes between grassy hillsides and woods. Singing birds were in wooded sites, although a male that I pursued for 5 to 10 minutes gradually moved into the shrubby region. We did not hear birds from the open grassy places and saw no birds that were not singing.

N. K. Johnson (MS) saw three individuals and collected one male about one-half mile south of La Labor, Aguascalientes at approximately 1850 m on 27 July 1959. He found the birds in a "subtropical ravine." The bottom of the ravine was a shady tangle of unknown shrubs and a leafy tree mixed with mesquites and an occasional yucca. The nearby area was arid with some trees, but mostly cacti, mesquite, and low green grass.

DISCUSSION

Geographic distribution.—The genus, as constituted by Hellmayr (1938), occurs primarily north of Panama. The only exception is *A. strigiceps* in Argentina, which I did not consider in my study. (Also not considered was *A.* [cf. Paynter 1970] *stolzmanni* of arid western Peru and Ecuador, a species that may well be aimophiline.) On the basis of number of species, the center of distribution of the genus is central Mexico. From there the number of species decreases both to the south and north, but more occur in the north. Of the entire group considered here, only three (*A. cassinii*, *A. aestivalis*, and *A. carpalis*) do not reach this central Mexican region as breeding birds. These three species seem to be offshoots of groups common in the area.

The genus can be divided rather subjectively into highland and lowland groups. There are several intermediate forms, and several species have representatives in both altitudinal regions. The highland forms are *A. rufescens*, *A. ruficeps*, *A. notosticta*, *A. mystacalis*, and *A. botterii*; these species represent the three major groups in the genus. The entire *ruficeps* complex is included here and probably originated in the highlands, perhaps in the pine-oak zone. Toward the northern end of the range, principally in California, *A. ruficeps* occurs near sea level at some localities. In the more central part of the range it usually occurs from 600 m to about 2450 m. *A. notosticta* is restricted to an altitude of about 1850 m in the mountains of Oaxaca where it is associated with a particular vegetation type that also seems to be limited altitudinally. *A. rufescens*, on the other hand, is nearly restricted to the highlands in the north and central portions of Mexico, but in the south populations occur along the eastern seaboard of Mexico, British Honduras, and Guatemala, at or near sea level. This situation is paralleled by the *botterii* (including *petenica*) group, suggesting that the two species groups have somewhat similar evolutionary and geographic histories. The distribution of *A. botterii* also reaches sea level where mountain populations extend north into the Gulf lowlands of Texas and adjacent Mexico. Here mountain ranges probably are too arid to support *A. botterii*, and the species has invaded salt prairie grasslands of the Rio Grande delta and adjacent coastal Mexico. *A. mystacalis*, a member of the *Haemophila* group, is limited to the arid mountains of southern Mexico north and west of the Isthmus of Tehuantepec.

Lowland forms include *A. carpalis*, *A. cassinii*, *A. aestivalis*, *A. ruficauda*, *A. humeralis*, and *A. sumichrasti*. *A. carpalis* is isolated in northwestern Mexico and southeastern Arizona, where it apparently is limited to the Sonoran desert region except for slight incursions into the more humid tropical scrub woodlands of northern Sinaloa. It occurs in the foothills of the Sierra Madre Occidental, but only where river floodplains provide an arid woodland habitat. The contact with *A. cassinii* in Arizona has not been examined. *A. cassinii* occupies the plains region of south-central United States and extends southward into Mexico. It occurs at moderate elevations but probably invades these areas only where the moisture regimen produces arid grassland and scrub habitats. *A. aestivalis* is essentially limited to low elevations, although Mengel (1965) reported a specimen from 4000 feet in Kentucky. *A. ruficauda* occurs perhaps to 600 m in the portion of the range south and east of the Isthmus of Tehuantepec, but *A. r. acuminata* is found as high as 1850 m or more at the western edge of the Mexican Plateau. This seems to be a rather recent range expansion, that has occurred as man cleared the forests on the edge of the Plateau. *A. humeralis* similarly is based in lowlands, but reaches into highlands along the edge of the Plateau. *A. sumichrasti* occurs, but for only a short distance, above the plains of the southern Isthmus of Tehuantepec area.

The only species that is essentially limited to middle elevations is *A. quinquestriata.* It occurs from about 240–1850 m, primarily in tropical deciduous woodlands. Its isolation in the northwestern part of Mexico (and adjacent Arizona) makes it difficult to place zoogeographically in relation to the remainder of the genus.

On the basis of the size of the range, this genus is divisible into several types. Species such as *A. sumichrasti* and *A. notosticta* occupy very limited geographic ranges even though the potential range seemingly extends farther. *A. notosticta* is rare enough that the actual range may be greater than is known at present.

The species with "medium-sized" ranges include *A. mystacalis*, *A. humeralis*, *A. carpalis*, *A. cassinii*, and *A. quinquestriata.* The northern limit of the range of *A. mystacalis* may be determined in part by competition with *A. humeralis*, although *A. mystacalis* seems to occur in slightly more arid habitats. *A. humeralis* is limited to the arid basin of the Río Balsas drainage. As already mentioned, *A. carpalis* is restricted largely to the Sonoran desert. *A. cassinii* is limited as a breeding bird to the south-central and southwestern United States and northern Mexico. Probably it is restricted in part by competition with *A. botterii* in the southern parts of its range. Finally, *A. quinquestriata* is limited to the western slope of the Sierra Madre Occidental.

The species *A. aestivalis*, *A. botterii*, *A. rufescens*, *A. ruficeps*, and *A. ruficauda* have large ranges. *A. aestivalis* is limited to the eastern half of the United States, primarily in the south but extending as far north as Ohio, Pennsylvania, and Maryland. It does not quite contact *A. botterii* in southwestern Texas. *A. botterii* occurs in highlands and lowlands as far as Costa Rica. The presence of an isolated highland population across the Nicaraguan gap in Costa Rica suggests their habitat was once more continuous. The recent discovery (Howell 1965) of a population in the lowlands of Nicaragua suggests that at one time the coastal savanna was nearly or completely continuous along the Caribbean coast as far south as Nicaragua.

A. rufescens has nearly the same distributional pattern as *A. botterii*, but does not occur as far north in eastern Mexico and does not extensively invade the moister oak woodland of the Sierra Madre Oriental. This species is apparently more widely distributed in the regions southeast of the Isthmus of Tehuantepec than is *A. botterii*. *A. ruficeps* does not cross the Isthmus into the pine-oak woodland of the Chiapas highlands as do other forms, but it does extend much farther north in the western United States. *A. ruficauda* is the one member of its group that has a wide distribution. However, its range is different from others that cross the Isthmus. It is limited to the lowlands on the Pacific slope in the region of the Isthmus and is not faced with a discontinuity of habitat. The races from southern Mexico and farther south seem to form a group that may have evolved since the smaller, more clear-breasted *A. r. acuminata* was isolated in the lowlands of the Río Balsas. The population of the Río Motagua valley of eastern Guatemala probably is a derivative of the nominate form that nearly comes in contact with it in the southwest.

Each species group has a wide-ranging form that crosses the Isthmus (in two cases these species break into lowland and highland populations), each has at least one species that occupies a rather limited range, and each has one or more species that have intermediate-sized ranges. *A. aestivalis* is the only species that is limited to the United States as a breeding and wintering bird; it is isolated from all other *Aimophilae*. *A. cassinii* breeds at the northern limit of the range of the genus in the plains of the United States and northern Mexico. Species occurring principally on the Plateau of Mexico are *A. ruficeps*, *A. rufescens*, and *A. botterii*. All three have representatives in other areas. Two endemic forms, *A. mystacalis* and *A. notosticta*, are found in the mountains south of the Plateau. The lowlands of western Mexico seem to be the stronghold for members of the *Haemophila* complex. *A. carpalis* and *A. quinquestriata* occur in northwestern Mexico—*A. carpalis* in lowlands and *A. quinquestriata* at middle elevations.

Ecologic distribution.—The three species groups of *Aimophila* occupy distinct habitats. The *Haemophila* group, including *A. carpalis*, occurs in arid tropical lowland vegetation, characterized by thorny trees and shrubs and varying amounts of grassland and tropical deciduous woodland. *A. humeralis* and *A. ruficauda acuminata* are nearly limited to these habitats in the Río Balsas drainage. *A. humeralis* is restricted to tropical deciduous woodland, while sympatric *A. ruficauda* is in more open habitats, dominated by legumes. It appears that they are so similar as to be competitively exclusive. Even though *A. mystacalis* occupies higher elevations than other members of the group, it still occurs in arid thorn scrub vegetation. It is equally at home in the nearly closed-canopy deciduous woodland that is also common on some of the hillsides. It does not use the heavy, hard chaparral and scrub oak-covered hillsides. Its lower limit along the Río Tehuantepec overlaps that of *A. sumichrasti* to some extent, but the two probably segregate by habitat. *A. sumichrasti* and sympatric *A. ruficauda* occupy the arid lowland of the Isthmus and extend south and east into Chiapas. They segregate by habitat in sympatric situations, but *A. ruficauda* occurs in more dense habitats in tropical deciduous forests to the southeast along the coast of Oaxaca beyond Tapanatepec. Finally, *A. carpalis* is isolated in the Sonoran desert regions in vegetation that probably was once phenotypically similar to that in the range of *A. ruficauda* but which is now drier.

The *ruficeps* complex is based in pine-oak woodland of the central Plateau of Mexico. *A. notosticta*, being limited to scrub oak habitat of the mountains south of the Plateau, is the only species of the complex that occurs solely in the pine-oak zone. *A. ruficeps* occupies other sorts of habitats, in addition to pine-oak woodland, especially in the northern part of its range. *A. rufescens*, with both highland and lowland forms, is the most unusual species in this complex. The highland forms are found mostly in pine-oak woodland, but also in pines and down into nearly pure oaks. In lowlands the bird is almost always found in savanna-like regions with some scattered brush cover and elevated perches.

The *botterii* complex is most common in weedy, grassy sites within its range, where there are large expanses of low ground cover, but also some scattered brush for cover and perches. The three species differ in their requirements or tolerances for woody vegetation. The southern populations of *A. aestivalis* are found mostly in open pine woods. *A. cassinii* and *A. botterii* may occur either in open country with few shrubs or scattered trees, or in habitats more nearly dominated by woody vegetation. Both require some open areas for foraging.

A. quinquestriata is unique in occupying the tropical deciduous woodland along the western slope of the Sierra Madre Occidental. It does not appear to be related by habitat preference to any other species in the genus, although *A. humeralis* also occupies tropical deciduous woodland sometimes. I place *A. quinquestriata* alone primarily because it is the only species that is restricted to middle elevations and tropical deciduous woodland. *A. humeralis* is most common in lowlands, but extends into highlands where habitat has been altered appropriately.

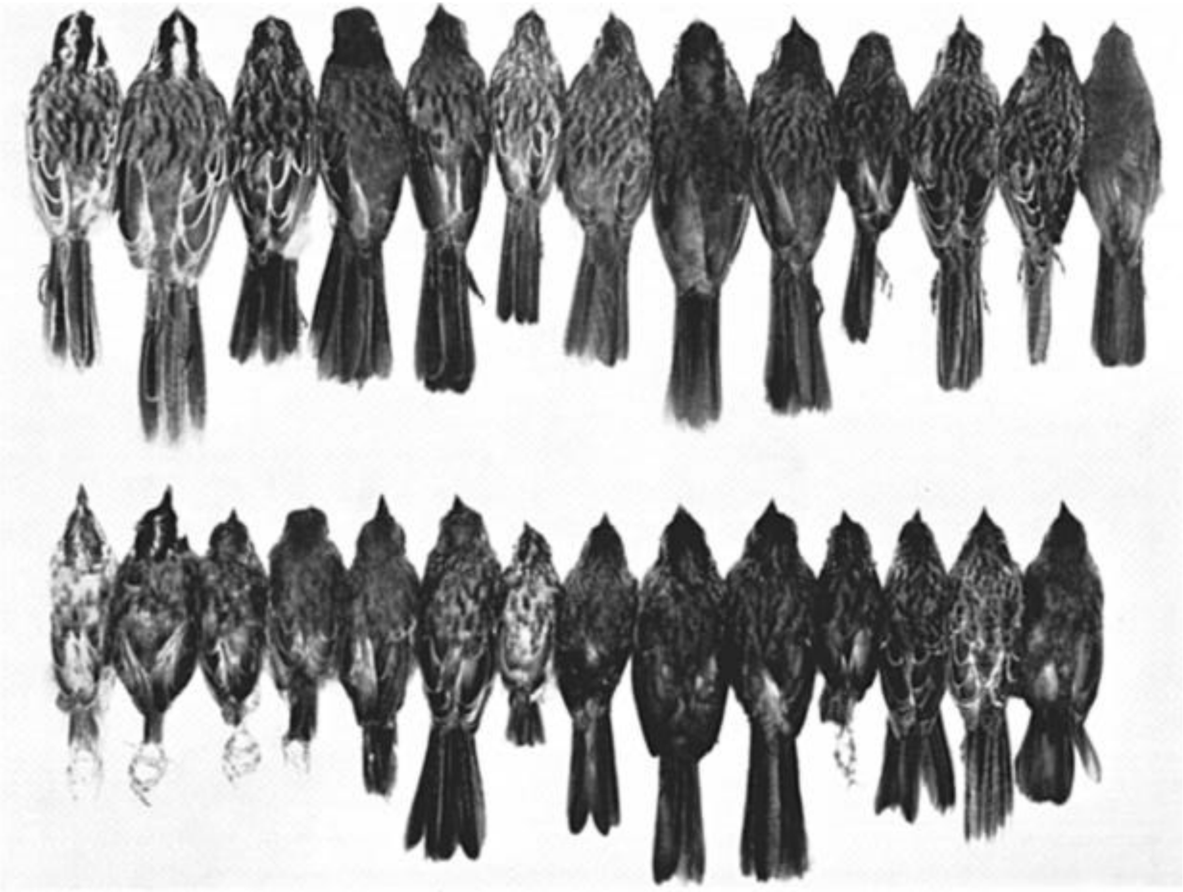

PLATE 1. Dorsal view of adult (above) and juvenal (below) plumages of 12 species (13 forms) of *Aimophila*. Left to right: *ruficauda acuminata*, *ruficauda lawrencii*, *sumichrasti*, *humeralis*, *mystacalis*, *carpalis*, *ruficeps*, *rufescens*, *notosticta*, *aestivalis*, *botterii*, *cassinii*, and *quinquestriata*.

PLUMAGES AND MOLTS

PLUMAGES

The following accounts are modified from Ridgway (1901). They are in no way assumed to be complete descriptions of plumages. The purpose of this section is not to examine plumages in detail, but to evaluate some plumage characteristics for use in generic classification. (See plates 1 and 2 for photographs of the adult and juvenal plumages.) In all species of *Aimophila*, as in many emberizines, the sexes are not dichromatic and only a single description of each plumage is necessary. Adult plumage is attained by the second breeding season and sometimes by the first. Juvenal plumage is the first composed of true contour feathers. The first winter plumage is acquired by a postjuvenal molt and worn until the first prenuptial (= prealternate) or postnuptial (= prebasic) molt.

A. RUFICAUDA

Adult.—A single description will be given although certain obvious differences between several of the races will be noted: Head marked with four broad stripes of black or dusky, sometimes with brown feathers intermixed, alternating with three narrow stripes of white or brownish white; back pale brownish and rusty, broadly streaked with black; tail cinnamon-brown; lesser wing coverts and adjacent scapulars cinnamon-rufous; underparts mainly white, passing into tawny-buff or clay color on the flanks and crissum; chest and sides of breast vary from nearly completely white to gray, forming a dark pectoral band edged and margined with white; wing reddish brown; bill: maxilla blackish, mandible yellow.

Juvenal.—Storer (1955) first described this plumage for *A. r. acuminata.* Essentially like adult, but black of adult replaced by brown; back more brown and sides and flanks with ochraceous buff; pectoral band of adult replaced by brown streaks that are finer in *A. r. acuminata,* in which the adults tend to a reduction of the band; white areas of adult replaced by varying approaches to buff in young; greater and median upper wing coverts tipped with dusky (instead of whitish in adult).

First winter.—Like adult but tending to brown suffusion on black and gray areas; usually brown tips on black feathers.

A. SUMICHRASTI

Adult.—Pileum with two broad lateral stripes of chestnut-brown, streaked with black, a median stripe of grayish; back and scapulars light brown or grayish brown, broadly streaked with black; broad superciliary stripe, auricular region, sides of neck and sides of chest light gray, fading into

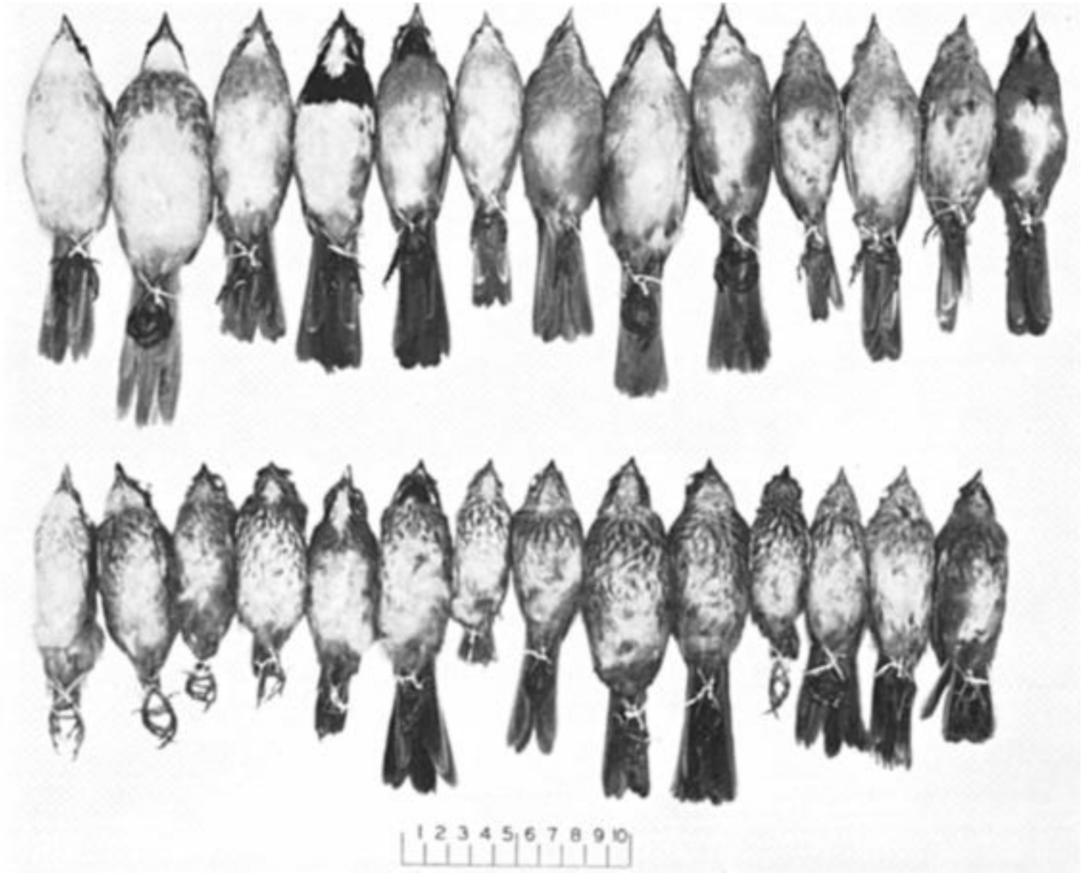

PLATE 2. Ventral view of adult (above) and juvenal (below) plumages of 12 species (13 forms) of *Aimophila*. Left to right: *ruficauda acuminata*, *ruficauda lawrencii*, *sumichrasti*, *humeralis*, *mystacalis*, *carpalis*, *ruficeps*, *rufescens*, *notosticta*, *aestivalis*, *botterii*, *cassinii*, and *quinquestriata*.

paler gray on median portion of chest; suborbital crescent, anterior half of malar region, chin, upper throat, and abdomen white; a broad postocular streak of dark brown; a loral, rictal, and submalar streak of black; flanks grayish buff, femoral region and undertail coverts clear buff; lesser wing coverts cinnamon-rufous; upper tail coverts and tail cinnamon; wings dusky, two wing bars; bill darker brown above than below.

Juvenal.—Similar to adult, but dorsal surface to lower back streaked with dark brown; rump buffy; upper tail coverts rufous; black streaks of adult brownish; breast and sides streaked with brown, these streaks more prominent in younger birds than noted by Storer (1955).

First winter.—Similar to adult; apparently achieved by complete postjuvenal molt.

A. HUMERALIS

Adult.—Head and neck dusky, becoming darker anteriorly; a supraloral spot and malar stripe white; auriculars dusky, becoming darker below; narrow stripe on the side of the throat and a broad band across chest black; rest of underparts chiefly white; flanks and undertail coverts buffy brown; back and scapulars mostly cinnamon-rufous, more or less streaked with black; rump and upper tail coverts light grayish brown, the coverts more or less margined terminally with paler grayish brown; tail dusky, with grayish edgings; lesser wing coverts cinnamon-rufous; middle and greater coverts with white bar; remiges dusky; bill: maxilla black, mandible light colored; legs and feet brownish.

Juvenal.—First described by Storer (1955) from a bird which had nearly completed postjuvenal body molt. Similar in patterns to adult, the similarity more pronounced in some individuals than in others. Upper parts generally uniform brown with faint darker brown streaks on the midback; black areas of throat and breast replaced by brown or grayish; streaks of breast and sides either strong when pectoral band essentially lacking, or nearly obsolescent when brown pectoral band well developed; wing coverts with bar of buffy brown; sides and flanks brown, becoming buffy posteriorly.

First winter.—Same as adult.

A. MYSTACALIS

Adult.—Pileum and hind neck grayish, streaked with dusky; loral spots and central streak on forehead white; sides of head dull brownish gray or dusky with a white supraloral stripe and a white malar stripe; chin and throat black with varying amounts of white mixed in; lower throat and chest light olive-gray or dull ash-gray; sides, flanks, and undertail coverts cinnamon-buff; breast and abdomen dull white; back brown streaked with black; scapulars rufous; rump plain cinnamon-rufous or rusty; wings and tail dusky, with light edgings; the middle and greater wing coverts tipped with white, forming two wing bars; bill: maxilla black, mandible light grayish blue; legs and feet light brown.

Juvenal.—Similar to adult, but throat whitish with dark brown lateral stripes; chest, dull whitish streaked with brown, usually heavily; sides and flanks brown becoming buffy posteriorly; edging of greater secondary coverts buff.

First winter.—Essentially like adult, but with feather tips lighter gray on pectoral band; all juvenal plumage apparently replaced before the first breeding season.

A. CARPALIS

Adult.—Pileum streaked broadly with chestnut-rufous or rusty and narrowly with grayish, the latter forming a more or less distinct median line; a broad superciliary stripe and sides of head generally light grayish, the latter with a postocular streak of rusty and a rictal and submalar streak of blackish; upperparts including upper tail coverts and tail brownish gray or light brownish gray, the back and scapulars streaked with blackish; lesser wing coverts cinnamon-rufous; underparts grayish white, except flanks buffy gray, with a slight suggestion of a grayish pectoral band; crissum light buff; slight whitish tips of greater and median secondary coverts suggest two wing bars; wing brown; bill: brown, maxilla slightly darker than mandible; legs and feet light brownish becoming darker distally.

Juvenal.—Crown and back light brown heavily streaked with dark brown; slight suggestion of brownish submalar streak, remainder of underparts whitish with brown spotting on throat and breast; flanks and thighs streaked with brown; margins of wing coverts buff; crissum whitish.

First winter.—Essentially like adult. Usually all of remiges and varying numbers of rectrices retained from juvenal plumage. All body plumage replaced at postjuvenal molt.

A. RUFICEPS

Adult.—This form is rather variable in color depending on geographic source of specimens. The following is for the nominate form. Pileum clear chestnut, darker on forehead, where sometimes blackish anteriorly, with a median whitish line at base of culmen, and usually with buffy-grayish streaks along middle of crown and occiput, forming a slight indication of a median stripe; back and scapulars buffy grayish brown (to darkish gray), broadly streaked with chestnut, but usually without distinct dusky shaft streaks; tail light cinnamon-brown or deep wood-brown; sides of head, neck, and most of underparts pale buffy-brown; the chin, throat, supraloral line, narrow orbital ring, malar stripe, and abdomen paler, but not white; crissum buffy; a chestnut postocular streak and a distinct black submalar streak; wing dark brown; wing coverts dark brown with lighter outer margins; bill: brown, maxilla slightly darker than mandible.

Juvenal.—Much like adults, but pileum dull brown, obsoletely streaked with darker brown; back more narrowly streaked with darker brown; chest narrowly streaked with dusky brown, and an indistinct or obsolete submalar stripe of brown.

First winter.—Similar to adult, but variable number of juvenal rectrices, primaries and wing coverts retained. (See Hubbard 1975 for subspecific revision of this species.)

A. RUFESCENS

Adult.—Again rather variable, but not as much as is *A. ruficeps.* Description taken from Ridgway's (1901) account of the nominate form. Pileum chestnut, divided by a more or less distinct median stripe (rarely obsolete) of olive-grayish or dull buffy and streaked with black, at least posteriorly or along the exterior margin; back and scapulars brown, more or less distinctly streaked with black; wings brown, inclining to chestnut on secondaries and proximal greater coverts; tail chestnut-brown or russet; sides of head, including a broad superciliary stripe (whitish anteriorly) olive-grayish; a whitish eye-ring surrounded by dusky; a dusky postocular streak and a very distinct black submalar streak; malar region, chin, throat, and abdomen dull white or pale buffy; rest of underparts dull grayish buffy, becoming deeper and more brownish on sides and flanks; crissum buffy; bill: maxilla black and mandible grayish blue; legs and feet brown.

Juvenal.—Varies from adult in essentially the same manner as in *A. ruficeps*; most populations show a strong tendency to yellow suffusion on the underparts.

First winter.—Same as adult, but some individuals may retain a few juvenal body feathers.

A. NOTOSTICTA

Adult.—Pileum rusty brown with fine black streaks and narrow gray median line; back grayish brown broadly streaked with black; wings mainly grayish brown, tertials inclining to chestnut-brown on edges; tail dark brown; sides of head and neck, including broad superciliary stripe, brownish gray, this passing into a more brownish hue on sides of breast; distinct white eye-ring, surrounded by dusky; broad postocular streak of dark brown; malar stripe, chin, throat, and abdomen dull buffy-whitish; a black submalar streak; no wing bars, greater wing coverts dark brown with light outer margins; bill: black; legs and feet brown.

Juvenal.—Similar to juvenal of *A. ruficeps* (see Storer 1955).

First winter.—Same as adult?

A. AESTIVALIS

Adult.—The description is of *A. a. aestivalis,* which differs from other forms of the species in being grayer and having more dark back streaks. Above gray, broadly streaked with chestnut-brown, feathers of the back with blackish central spots and streaks; tail dusky with broad gray edgings, middle pair of rectrices gray with median stripe of dusky; sides of head and neck smoke-gray or dullish gray, the latter streaked with chestnut or dark chestnut-brown; a narrow chestnut or chestnut-brown postocular stripe; chin and throat very pale dull grayish buff or buffy-grayish white, deepening on chest, sides, and flanks into pale grayish buffy; flanks sometimes streaked with brown; crissum buffy; dusky submalar streak sometimes present; wing dark brown with rufous edgings; wing coverts dark brown with lighter outer margins and no evidence of a distinct wing bar; bend of wing yellow; bill: maxilla dusky, mandible paler; legs and feet very pale brownish buffy.

Juvenal.—Dorsum brownish with midback more reddish brown, all heavily streaked with brown; sides of neck, throat, breast, sides, and onto flanks heavily streaked with brown; underparts whitish becoming buffy on flanks and crissum; greater secondary coverts margined with rusty to form a slight wing bar.

First winter.—Similar to adult, but some individuals with light brownish spots on breast.

A. BOTTERII

Adult.—Description is that of *A. b. botterii*; lowland *A. b. petenica* forms are much grayer on the back nearly approaching a gray-black condition. The markings and general pattern are the same as the nominate form except that some populations do not show yellow, but white, at the bend of the wing. Underparts grayish buff on breast (pectoral band), lightening on throat; sides and flanks more buffy with buffy crissum; abdomen white; (the color of the underparts may become essentially gray in place of the buff); wing brown with no wing bars; greater secondary coverts broadly edged with rusty as are most of the secondaries; tail dusky with light edge on middle pair in a "ladder-shaped" pattern; back, rump, upper tail coverts, and pileum reddish brown; pileum with fine black streaks and gray edges of feathers; black streaks broad on middle back; no streaks on hind neck, but gray predominates on reddish central portion; superciliary and lores light as throat; rusty postocular streak; bill: brown, mandible lighter than maxilla; legs and feet light brown.

Juvenal.—Like adult, but back essentially dark brown with broad buffy edges on feathers; underparts buffy-white to yellowish in *A. botterii* types with dark brown streaks on the breast and sometimes extending onto throat and down sides; few streaks on posterior flanks; bend of wing yellow in some forms; greater secondary coverts margined with rusty and tipped with buff.

First winter.—Like adult, but some individuals with light brown spots on breast.

A. CASSINII

Adult.—Above light brown, broadly streaked with light gray, the pileum streaked also with black or dusky; scapulars and interscapulars light brown, marked with dusky subterminal spots or bars; margins of feathers light gray; upper tail coverts with roundish, cordate, or transverse subterminal spots of blackish and margined terminally with pale grayish; middle rectrices light brownish gray with a narrow, pointed median stripe of dusky, this more or less irregular or serrated along the edges, with more or less distinct indications of darker lines across the gray on either side; outer pair of rectrices with white tips; wing brown; wing coverts dark brown with grayish outer margins; edge of wing pale yellow; chest, sides, and flanks very pale brownish gray, flanks sometimes streaked with brown or dusky; rest of underparts dull white, except crissum buffy; sides of throat sometimes marked with a dusky submalar streak; sides of head buffy and grayish; bill: brown, maxilla darker than mandible; legs and feet brown.

Juvenal.—Essentially like adult, but ground color of back brown, feathers with buffy tips and darker brown central streaks; greater wing coverts margined with white; median secondary coverts margined with grayish buff; remiges of adult margined with buffy-brown, those of juvenile margined with whitish; bend of wing yellowish; small amount of buffy color around margins of lores and auriculars; light streaking on the breast and probably faint markings on throat.

First winter.—Like adult, but some individuals have small brownish spots on breast.

A. QUINQUESTRIATA

Adult.—Above plain purplish grayish brown, inclining to chocolate on the back, the rump and upper tail coverts more grayish; superciliary streak, malar streak, stripe down the middle of the chin and throat, and abdomen

TABLE 1

OCCURRENCE OF SOME JUVENAL AND FIRST WINTER PLUMAGE CHARACTERISTICS AMONG THE SPECIES OF *AIMOPHILA*

Species	Plumage characters (X = presence; O = absence) Juvenal like adult	 Juvenal heavily streaked	 First winter spotted
ruficauda	X	O	O
sumichrasti	X	O	O
humeralis	X	O,X	O
mystacalis	X	X	O
carpalis	O	X	O
ruficeps	O	X	O
rufescens	O	X	O
notosticta	O	X	O
aestivalis	O	X	X
botterii	O	X	X
cassinii	O	X	X
quinquestriata	O	O	O

white; broad stripe on each side of the chin and throat, and spot in the middle of the chest, black; rest of underparts plain dull slate-gray; crissum gray, broadly margined with white; wings and tail dark brown, tail with light outer tips; bend of wing whitish; no wing bars, greater wing coverts dark brown with light outer vanes; bill: maxilla black, mandible bluish.

Juvenal.—Phillips (1961) described the plumage, and I draw from his account with slight modifications based on specimens from Sonora and Zacatecas. Similar to adult, but with the crown and back brown, back spotted with darker brown; the lower back and rump are uniformly brown with no streaks; tail brownish black, tips of the outer pair of rectrices white; underparts yellowish with a brownish pectoral band with faint brown streaks; sides and flanks brownish; crissum brownish, broadly tipped with yellow; wings dusky, primaries edged with whitish becoming dusky on inner feathers, secondaries edged with rufous; upper wing coverts dusky margined with buffy-brown; alula dusky, margined laterally with whitish.

First winter.—Similar to adult, but with some remiges, rectrices, and wing coverts retained from juvenal plumage.

DISCUSSION

The subject of plumages can be approached from several viewpoints. Here I will treat some characteristics of color and patterns of plumages of three age classes: juvenile, first year, and adult. The information is sum-

TABLE 2

OCCURRENCE OF CERTAIN ADULT PLUMAGE CHARACTERISTICS AMONG THE SPECIES OF *AIMOPHILA*

	Plumage characters (X = presence; O = absence)											
Species	Patterned head	Rufous shoulders	Black submalar	Pectoral band	Wing bar	Eye-ring	Back streaks	Rufous tail	Yellow “wrist”	Buffy flanks	Patterned tail	Bill bicolor (B) monocolor (M)
ruficauda	X	X	O	X	X	O	X	X	O	X	O	B
sumichrasti	X?	X	X	X	X	O	X	X	O	X	O	B
humeralis	X	X	X	X	X	O	X	O	O	X	X	B
mystacalis	X	X	O	X	X	X	X	O	O	X	X	B
carpalis	O	X	X	X	X	O	X	O	O	X	O	M
ruficeps	O	O	X	X	O	X	X	X	O	O	O	M
rufescens	O	O	X	X	O	X	X	X	O	O	O	B
notosticta	O	O	X	X	O	X	X	O	O	O	O	M
aestivalis	O	O	X	X	O	O	X	O	X	X	O	M
botterii	O	O	X	X	O	O	X	O	X	X	X	M
cassinii	O	O	X	X	X	O	X	O	X	X	X	M
quinquestriata	X	O	X	X	O	X	O	O	O	O	?	B

marized in Tables 1 and 2. Other items such as molt and feather shape will be considered in other sections.

Not all species appear drab; several have strikingly colored or patterned plumage, especially in the head region. *A. ruficauda* has a black-and-white pattern on the top and sides of the head of the adult; in the juvenile these same areas are marked brown and buffy, respectively. First-year birds generally show the black-and-white markings, but both colors are muted by brownish tips on the feathers. The head pattern contrasts sharply with the reddish-brown, streaked back plumage, the whole of the throat, and much of the ventrum. The pectoral band of *A. ruficauda* differs among races from a rather dark gray in the southern populations (*A. r. lawrencii, A. r. ruficauda* and *A. r. connectens*) to a clear white breast in some individuals of *A. r. acuminata.*

A. ruficauda is the only member of the genus that never has a black submalar, malar, or throat stripe in adult plumage. Probably the striking white throat acts as a contrast to the top and sides of the head. A black submalar might detract from the head-throat contrast and may have been eliminated in the evolution of this pattern.

The top of the head of *A. humeralis* is essentially uniformly colored. The dark crown contrasts sharply with the brightly marked throat and breast. With the bill pointing directly at the observer, there is a pattern of white lines radiating from the bill and bounded on all sides by black. This is set off from the rest of the ventral pattern by a very distinct black pectoral band. *A. mystacalis* has a black throat bounded laterally by white and black stripes and a darkly streaked gray head. The chest is crossed by a gray pectoral band that is much less striking than that of *A. humeralis*, but nonetheless serves to separate the markings of the head from the rest of the ventral pattern. Of these species with striking head patterns, only *A. mystacalis* has an eye-ring. An eye-ring would be obscure in *A. ruficauda* and would alter the line pattern of *A. humeralis.* The pattern of *A. mystacalis* is probably the most subdued of the three species and the eye-ring may have been selected for because of its contribution to the contrasting pattern of black and white.

A. sumichrasti has a less marked head pattern and shows a similar reduction in the distinctiveness of the pectoral band. The intensity of the pectoral band is correlated with that of the head pattern suggesting that the breast band has been selected for as an integral part of the total head pattern.

The plumage of *A. quinquestriata* also is rather distinctly marked for a sparrow. It is discussed alone, as it combines several features not found in the four species just mentioned. The pattern, which is primarily limited to the throat and sides of the head, is set off by the uniformly colored top of the head, just the reverse of the pattern found in *A. ruficauda.* The throat pattern of the Five-striped Sparrow is set off by a prominent pectoral band which merges into the flanks and sides more than in the other species so the pattern is not broken as abruptly into head and body regions. The black chest spot is unique among these sparrows and further focuses attention toward the body proper rather than the head. There is no contrast between the top of the head and the remainder of the dorsal plumage.

Pectoral bands of most other species in the genus are only slightly developed. The band in *A. carpalis* is reduced, probably related to duller plumage overall. In the remaining species the pectoral band is a gray or dark buffy wash across the chest. The band is only slightly differentiated in color from the remainder of the underparts and probably has little or none of the special significance suggested in the other species.

These bright head patterns probably are used in displays that involve head-on views of partners or opponents. Viewed head-on, the lines of color seem to flare back from the bill. The only possible display I have seen involving the head is during the chatter duet when two birds often turn and face one another. These duets occur in *A. ruficauda, A. humeralis,* and *A. mystacalis,* but not in *A. quinquestriata.* However, the pattern of *A. quinquestriata* does not seem to radiate as much from the bill, being more restricted to the ventrum and perhaps having an entirely different function and evolutionary background. The apparent importance of the bill as a focal point of the pattern provides a selective basis for the bicolored bill in these species of *Aimophila.*

A well-differentiated part of the plumage of several species is the presence of reddish or rufous shoulders. The upper marginal and some of the upper lesser secondary coverts in *A. ruficauda, A. humeralis, A. sumichrasti,* and *A. carpalis* are rufous, while *A. mystacalis* has rufous scapulars. In both cases, the effect is approximately the same.

I mentioned earlier that *A. ruficauda* is the only species in which the adult never has a black streak along the side of the throat. All three members of the *botterii* complex often have the streak, but it is not present in all individuals. The streak is also present in varying degrees in some juveniles of the *botterii* complex. The remaining species apparently always have a streak, although its size varies.

Wing bars, when they are present in the group, are usually limited to the greater and median secondary coverts. They are not present in the three species of the *ruficeps* complex and are only slightly developed in *A. cassinii,* the only member of the *botterii* complex in which they occur. All members of the *Haemophila* group have some sort of wing bar, but it usually does not contrast enough with the remainder of the coverts to be distinctive. In *A. mystacalis* wing bars are white and rather prominent. *A. quinquestriata* lacks wing bars.

I already mentioned the well-defined eye-ring of *A. mystacalis*, which is the only member of the *Haemophila* complex that has an eye-ring. All three members of the *ruficeps* complex have eye-rings, but that of *A. notosticta* is pronounced and usually complete, while in *A. ruficeps* and *A. rufescens* the ring is less well marked and usually incomplete. Eye-rings do not occur in the *botterii* group or in *A. quinquestriata.*

All species except *A. quinquestriata* have dorsal streaks. Dorsal streaks may be correlated with general lack of importance of highly patterned dorsal plumage, provide contrast to the striking ventral patterning, and function in protective coloration. Degree of dorsal streaking in *A. humeralis* varies from heavy to none and does not lessen the contrast between the back and head; this contrast probably is the most important feature of the back pattern. Apparently no geographic correlation to amount of dorsal streaking exists.

Only three species of *Aimophila* show yellow at the bend of the wing. The significance of this color patch is not known, but Moynihan (1963) showed several Green-backed Sparrow (*Arremonops conirostris*) displays that exhibit the patch. Several forms of *A. botterii* have lost much of the phaeomelanin component of plumage color, having become mostly black and grayish rather than brownish and reddish. Some of these forms have white rather than yellow at the carpal joint (Howell 1965).

The final character considered here seems to be loosely tied to general pigmentation. Members of the *Haemophila* and *botterii* complexes have buffy colored flanks. The flanks are slightly darker and contrast less with the remainder of the abdomen in the *botterii* complex than in the rather white-bellied *Haemophila* group. Again the significance is not known.

Two supragroups can be erected in the *Aimophila* genus primarily on grounds of pattern and/or brightness of adult plumage. Each group contains possible subdivisions. The first group is composed of species that either have striking head patterns or seem to be related to species that do. This group includes *A. ruficauda, A. humeralis, A. mystacalis, A. sumichrasti, A. carpalis,* and *A. quinquestriata. A. quinquestriata,* although included in this group, is discussed separately.

It is partially the striped pattern of the head and throat that seems to link *A. humeralis, A. mystacalis, A. ruficauda, A. sumichrasti,* and *A. carpalis.* Each of the last two forms has a similar but much reduced head pattern, and overall color of the plumage is much duller. This head pattern is not limited to this group of birds and may be convergent or else indicative of wider relationships than are suggested here. Members of the genera *Arremon, Arremonops,* and *Rhynchospiza* have similar but differently colored patterns. To some extent head patterns of the *ruficeps* complex are similar. Probably the striped head pattern itself is not as significant a difference as the black-and-white color combination and total pattern of the foreparts.

Several other plumage characters seem to hold the group together. All have rufous coloration in the shoulder region. Each species has a wing bar, and each has warm buffy flanks in contrast to a whitish abdomen. The only form which seems to vary significantly is *A. carpalis,* whose overall appearance is much grayer than the other species. This difference probably has been accentuated in the habitat of the species, and it does not eliminate the possibility of relationship with the group.

The second division within the genus includes those species that are dull-colored with essentially plain, dingy underparts and streaks on the back. Most species do not have wing bars and have dark, rather than rusty-colored tails. Included here are *A. ruficeps*, *A. rufescens*, *A. notosticta*, *A. aestivalis*, *A. botterii*, and *A. cassinii.* Although I grouped these species together on the basis of similarity, I do not feel that they are all equally related. The group can be further subdivided according to several characters.

Species in the *ruficeps* group all have rusty dorsal head patterns, in many cases consisting of two rusty, lateral crown stripes separated by a grayish median line. In some populations, especially in many forms of *A. ruficeps* and to a lesser degree of *A. rufescens,* the crown is nearly concolor with little indication of a median line, especially in worn spring birds. I have not found examples of *A. notosticta* that approach this condition. Both *A. notosticta* and *A. rufescens* have pronounced dorsal streaks in adult plumage. These streaks are reduced in *A. ruficeps* and may be missing in some forms. Each species has some indication of a pectoral band, but it is only a darker wash across the breast and is not of the intensity of those in the *Haemophila* and *botterii* groups. The black bill of *A. notosticta* differentiates it from the other two species. Bill color may facilitate species recognition in the region where *A. notosticta* and *A. ruficeps* are sympatric. The bill of *A. rufescens* is black above and bluish gray below; the bill of *A. ruficeps* is brownish. A striking difference between *A. notosticta* and the other two forms is the already-mentioned white eye-ring of *A. notosticta,* which is very obvious even in the field. However, many *A. ruficeps* and *A. rufescens* show a slight white eye-ring, and it is easy to see how the eye-ring might appear exaggerated in the otherwise darker plumage of *A. notosticta.*

The other subgroup of dull-colored types includes the three species of the *botterii* complex. For some time the close morphological similarity between some populations of *A. botterii* and *A. aestivalis* confused taxonomists about the specific distinctness of the two forms. Both have a buffy chest band of varying intensity and a strongly patterned middle back. Some forms of *A. aestivalis* show a heavily streaked crown. *A. cassinii* tends much more to grays and has neither a strongly streaked back nor a buffy chest band; the latter consists of a slight band of gray. The barred or ladder pattern of the middle part of the rectrices of *A. cassinii* apparently is an accentuation of the pattern of *A. botterii.* The large white patches on the outer rectrices of *A. cassinii* are unusual in the genus, but are also present to some extent on *A. humeralis*, *A. quinquestriata*, *A. mystacalis*, and occasionally on sparrows of several other species. During the song flight display of *A. cassinii* the tail is spread and the white appears as a patch, suggesting that the pattern has been selected for because of its importance in this display. The bill of all forms in the *botterii* complex is essentially brownish, with more gray or black in the darker *petenica* forms. An evident link among these species is the presence of a yellow patch at the bend of the wing. It occurs in all forms of *A. aestivalis*, in *A. cassinii*, and in most forms of *A. botterii*; it is a characteristic shared with other species of sparrows but not with other members of the genus.

A. quinquestriata stands alone as judged by plumage. The pattern has some characteristics that are shared with no congener, and some that are common to one or more species. The black breast spot is unique in *Aimophila*, as is the concolor appearance of the head and back. *A. humeralis* also may have an unmarked head, but it contrasts with the color of the back.

The similarity of *A. quinquestriata* to *Amphispiza bilineata* has led some authors to unite the two genera (Phillips *et al.* 1964). However, Storer (1955) pointed out several differences between the two forms and the similarity may be due to convergence. The marked difference in the juvenal plumages and in some adult plumage characteristics make it unlikely that the two forms are that closely related.

Juvenal plumages in *Aimophila* provide some evidence of intrageneric relationships. In general the types of juvenal plumage fall into the same four groups outlined above for adult plumages. All show marked similarities to adult plumage, particularly in those forms in which adult plumage is highly patterned, so that a similar pattern is easily seen in juvenal plumage. All forms show streaks on the breast and usually on the sides. A few have heavy streaks extending onto the throat region.

The selective value of strongly patterned juvenal plumage is uncertain. It occurs in those species where the adult is strongly patterned, and apparently it is an advantage for young to acquire the adult plumage pattern, although not the colors, as early as possible. Early acquisition of the pattern may represent early maturation of the physiological mechanisms that are responsible for the pattern. This might be selected for in relation to some other system that matures earlier than other physical attributes. It may also have some value in parental-offspring relationships that influence the length of time young remain with their parents. In *ruficauda* and *humeralis* young may remain with their parents for 1 year or more and may aid in the parents' reproductive efforts during their first breeding season. Similarity of pattern also may aid in species recognition by adults in regions of sympatry, and it may be effective in promoting intraspecific gregariousness prior to the time young acquire complete first winter plumage.

Importance of juvenal plumage to classification and phylogeny was known to Darwin (1859). He also pointed out possible complications, such as convergence, inherent in such characters. Storer (1955) used juvenal plumage to suggest groupings within the genus, and Pitelka (1951a) used juvenal plumage to suggest a relationship of *A. carpalis* to the genus *Spizella.* In view of the apparent strong selective pressure to produce juvenal plumage that closely approximates adult plumage, I question the validity of using juvenal plumage for classification in *Aimophila.* It seems to represent the same problems of evolutionary divergence as do adult plumages. Highly streaked juveniles are common among emberizines and are hardly significant for our purposes. However, the fact that several members of what is thought to be a closely related group of birds all show the same tendency to approximate adult plumage as closely as they do may be significant. Parkes (1957) used the similarity of the juvenal to adult pattern of *Atlapetes* in his discussion of relationships of Red-eyed Towhees (*Pipilo*) to *Atlapetes, Melozone,* and Brown Towhees (*Pipilo*). It now seems imperative to discover the possible importance of early maturation of plumage pattern.

Occurrence of yellowish ground color in juvenal plumage of several forms (*A. botterii, A. rufescens, A. quinquestriata*) for which there is little evidence of a close relationship suggests that it is independently derived in each form. This is especially clear when one considers that the character is present in only some forms of *A. rufescens* and *A. botterii,* these being especially the southern populations; it occurred in all populations of *A. quinquestriata* that I examined.

The similarity of the juvenal plumage of *A. quinquestriata* to that of *Melozone kieneri* may be fortuitous, but the resemblance is so close that I suspect it shows a close relationship. Both juvenal forms have a strong chest band, although adult *M. kieneri* have no band. Both have a buffy-to-yellowish cast on the light areas and a marked reduction of the streaks on the dorsum, especially on the head. Part of this similarity can be attributed to similarity of the adult plumages in certain respects, but the common occurrence of the breast band and yellowish ground color suggests to me a close tie between these species.

Within the genus, as with most other emberizines, the character of the first winter plumage (some species may replace part of this plumage at a prenuptial molt, but this does not influence markedly either color or pattern of the plumage) is essentially the same as the adult plumage. In several species, such as *ruficeps* and *quinquestriata*, there is good evidence that juvenal wing feathers may be entirely or partly retained through the first breeding season. However, these differ little from those of the adult. The only major, and seemingly important, differences are found in *cassinii*, *botterii*, and *aestivalis*. Each species has some first-winter birds with light brown spotting on the breast. It is not present in all freshly molted birds and probably is worn off somewhat rapidly, so that by the first breeding season most or all of these birds are indistinguishable from adults. Significance of this distinct plumage is not known, but may reduce aggression between adults and young of the year during the early period following postjuvenal molt. Among the other species only *ruficauda* has a noticeably divergent first-year plumage. Here the blacks and grays, especially on the head pattern, are muted by brownish tips on the feathers. Again, the pressure seemingly has been to reduce the pattern from that of the brightly colored adult, possibly allowing first-year birds to associate more freely with adults through one breeding season.

MOLT

Extent of molt among north temperate fringillids varies, even within a genus (Dwight 1900). All species investigated have a complete postnuptial molt, but extent of postjuvenal molt varies as does presence or absence and extent of a prenuptial molt. Published molt data are limited for all *Aimophila* species except *carpalis*, for which Phillips (1951a) presented the basic outline. This section considers timing and extent of the three molts and attempts to assess the value of these data for the systematics of the genus.

POSTJUVENAL MOLT

The following account is based on specimens of *A. cassinii*, the only species for which sufficient material representing the entire sequence of body plumage replacement (Table 3) was available. This description serves as a generalized description for the genus; specific variations from the pattern outlined here are mentioned later in the text.

Molt commences on the dorsal tract just below a line connecting the shoulders; at the same time new feathers are appearing on the scapulars. Molt of forehead feathers begins soon after it starts on the midback. Molt progresses posteriorly, and to a lesser degree anteriorly on the back and posteriorly on the head. In these sparrows the upper tail coverts usually molt in sequence, as the molt loci proceed down the back. While some specimens have new upper tail coverts prior to onset of molt on the lower

TABLE 3

POSTJUVENAL BODY MOLT OF *A. CASSINII*

Stage	Dorsum	Ventrum	Forehead and crown	Coverts
1	Begin midback and scapulars.	Begin to some new on breast and sides.	Begin.	No molt.
2	Mixed to most new on midback and scapulars.	Few to most new breast and sides.	Few new.	Marginals molting, greater and medial secondaries beginning if they molt at all.
3	Spreading posteriorly.	Breast, sides and throat most new.	Forehead new, crown few new.	Some new medial coverts, marginals new.
4	Back most new.	Breast and sides new to most new posteriorly.	Forehead new, crown mixed.	Continuing.
5	Most new, begin molt of hind neck.	New except flanks, midabdomen and throat.	Crown mixed.	Greater secondary sheathed at base.
6	Hind neck still some old.	Molt on crissum and lower abdomen.	Hind crown old.	New.
7	New to few old.	New to light molt posteriorly.	Superciliary molt with auriculars.	

back and rump, birds essentially through dorsal molt may still have old upper tail coverts. Early molt of upper tail coverts does not appear to be symmetrical. The last dorsal regions to molt are the cervical area on the spinal tract and the occipital portion of the coronal tract.

Soon after molt starts on these dorsal areas, the forehead, breast, and sides begin to show new feathers, and pinfeathers appear on the midline of the throat where the line of new feathers merges with the new feathers on the breast. Once started, ventral molt progresses posteriorly along the sides and flanks and then toward the midline of the abdomen and to the crissum. Meanwhile replacement of throat plumage continues spreading anteriorly and laterally. The last ventral areas to molt are the midline of the abdomen and the crissum. Occasionally the crissum is replaced prior to the most posterior portions of the abdomen.

The lateral head region is replaced late in molt. Coincident with completion of molt on dorsal and ventral surfaces, new feathers appear on the superciliary region and sides of the head, including the auriculars.

Molt of upper wing coverts begins at about the same time as dorsal molt. The first coverts to be replaced are the marginals. These are sheathed or new by the time the dorsal molt spreads posteriorly. The remainder of the coverts to be molted at this time, usually all except the greater primary and occasionally the greater secondary coverts, are lost about midway through molt and are new before dorsal and ventral surfaces finish molting. The alula and its coverts do not molt at this time. I did not examine molt of the underwing coverts.

There is no evidence of flight feather molt in *A. cassinii* by the time body molt is essentially complete. Molt of these feathers is variable in the genus and will be discussed separately for each species.

A. ruficauda.—I examined 10 specimens in various stages of body molt and 18 specimens in stages of flight-feather molt. I found no general differences in pattern of molt compared to that of *A. cassinii.* Two individuals (*A. r. acuminata*) from Morelos (MVZ 150147, 150148) showed early completion of feather replacement on the sides in relation to other portions of the body, and some late-hatched birds in early stages of molt had incompletely grown flight feathers. Most specimens in all populations molt the remiges and wing coverts, but less than half apparently molt the rectrices. Flight-feather molt does not commence until after body molt is essentially complete. However, a few birds may molt from one to three inner secondaries (7–9) near the end of body molt. Initiation of rectrix molt, when it does occur, is variable. In general, birds molting rectrices were about half through molt of primaries, but one bird had new tail feathers by the time primary 3 was new; this may have been adventitious replacement.

The four races of *A. ruficauda* fall into two groups with regard to general timing of the flight-feather molt. *A. r. connectens* and *A. r. ruficauda* may not start to molt the flight feathers by mid-January, while *A. r. acuminata* and *A. r. lawrencii* have at least two or three new primaries by this time. Some *A. r. ruficauda* may molt as early as *A. r. lawrencii.*

Available data show that body molt takes about 2 to 3 months and molt of flight feathers may take 4 months or more. The latter figure is a population estimate and probably is slightly longer than for any individual. Total time to complete postjuvenal molt is perhaps 5 to 7 months. Some birds finish molting only two or three months before some members of the population begin the prenuptial molt.

A. sumichrasti.—The single specimen (UMMZ 139821) in the early stages of molt shows that the initial pattern is essentially the same as in *A. cassinii.* The tail was still sheathed at the base, indicating an early inception of body molt. Body feather replacement in this molt is complete. A male through postjuvenal body molt had the first primary erupting from its sheath in the initial stages of a postjuvenal flight feather molt. Another male (RTM 54749) was through postjuvenal body molt and showed new secondaries 8 and 9. The rectrices were all old. Primaries 1 and 2 were new and 3 was missing; of the greater primary coverts, only 5 through 9 were still old. Spring birds are mostly too worn or are in prenuptial molt, but some material indicates that rectrices are not always replaced and that remiges usually are completely replaced.

A. humeralis.—Six specimens in body molt and ten in flight feather molt were examined. The ventrum usually begins molting before the dorsum or molts faster than the dorsum, thus deviating slightly from the generalized molt pattern for the genus. This difference is not significant. If wing coverts are molted during body molt, only some secondary coverts and marginals are new before flight feather molt. The first birds to show complete body molt were taken in mid-August and were undoubtedly from the first breeding effort in May, indicating that body molt may be completed about two months after fledging.

Body molt is finished before molt of flight feathers starts and before replacement of wing coverts continues. Six birds with only a few juvenal body feathers remaining show no signs of molt of either wing or tail feathers. Assuming that flight feather molt begins soon after body molt is completed, late August or early September is the earliest date to expect young of the year to begin molt. The first dates at which molt was completed are in early January, indicating that three months may be required for the process. However, it would be impossible to differentiate from adults any birds that finished earlier and retained no juvenal feathers. Among juvenal birds molting remiges, less than half (5 of 14) showed tail molt or new tail feathers. Possibly others that renewed their tail feathers earlier were incorrectly aged and classed as adults, but some probably do not replace tail feathers at this time.

A. mystacalis.—I examined 11 specimens in molt. In juveniles hatched late in the breeding season, molt begins before growth of the juvenal flight feathers is completed. I saw no early summer specimens in molt. The midback, scapulars, breast, and sides start molt essentially coincidentally. Variation within species shows either ventral or dorsal regions beginning slightly earlier. Otherwise, molt progresses as outlined for *A. cassinii.*

No replacement of flight feathers is found on the six specimens in late stages of body molt. The alula and its coverts and the greater primary coverts were retained by all these individuals. Usually the greater secondary coverts are not replaced at this molt. Apparently the remiges and rectrices are replaced sometime after molt of body plumage is completed, although a few spring birds still had juvenal greater primary coverts and one had rather worn juvenal primaries.

A. carpalis.—I examined 21 specimens in molt. The general pattern of body plumage molt is the same as in *A. cassinii.* Usually back and forehead molt is initiated slightly after ventrum molt. Body molt often begins before growth of some flight feathers is completed.

Molt of much of the body plumage may occupy little more than one month. A juvenile taken in late August 1963, was in a late stage of body molt. A survey of breeding over much of the range of *A. carpalis* during this year showed a late breeding season beginning in early to mid-July. This individual was probably not hatched until at least early July. I am not sure of the time span of molt in this species.

All wing coverts are replaced except the greater primary coverts, and most individuals retain the juvenal alula and its coverts. Molt of flight feathers is usually limited to three or less inner secondaries, but one bird was replacing primaries 7–9 on the right wing and 8–9 on the left wing. The remainder of the primaries were old. Phillips (1951a) reported a September female from Arizona that was molting the inner primaries (6–9 were still old, 5 was missing, 4 was about one-half grown, 3 was nearly full grown, 1 and 2 were new, by my examination). It is possible that this bird was undergoing complete primary molt. I found no birds that had symmetrically molted the rectrices, although one mid-December bird had all new rectrices except for right 2, which was of the acute juvenal form and noticeably more worn than other tail feathers. Phillips (*op. cit.*) reported that the September female referred to above was molting the outer pair of rectrices as well as the primaries. These birds either were abnormal individuals undergoing a regular rectrix molt, or, more likely, they were replacing feathers that had been accidentally lost.

A. ruficeps.—I examined 148 specimens in molt. No major differences from the general pattern were noted in postjuvenal molt of *A. ruficeps.*

About the time body molt is completed, replacement of flight feathers begins. The number of remiges that are molted is variable and seldom includes the entire complement. Molt of wing feathers usually begins with the secondaries. Secondary molt normally includes only proximal feathers, at least 8 and 9. Primary molt normally involves the distal feathers. Some birds do not molt any primaries, while most replace at least the outer two or three. The greater secondary coverts are lost as the wing feathers start to drop. The greater primary coverts are shed when the primaries are replaced, but the relation does not seem to be as synchronous as during postnuptial molt. In general, fewer coverts are molted than primaries. There is some geographic variation in degree of replacement of the wing feathers.

Tail molt, normally starting soon after molt of wing feathers, occurs in the centrifugal pattern common to many passerines and usually includes the entire tail. There is often a slight disarrangement and possible asynchrony between the right and left sides, probably partly related to accidental loss.

In central California, molt may start in early June and be completed by early September. I found marked variation in time of molt within a population of this species; birds in any particular stage of molt may be taken as much as three months apart. This in part relates to length and timing of the breeding season. Among the different forms, those of the northern populations along the western coast of North America and the eastern portion of the Plateau and the Sierra Madre Oriental in Mexico start to molt earliest. Birds from southwestern Mexico are among the last races to begin molting; one bird (MLZ 54754) from Oaxaca in an early stage of molt was taken on 27 October.

A. rufescens.—I examined 72 specimens in molt. With its large geographic range, one might expect this species to show a long postjuvenal molt period. Indeed, my records show that at any particular molt stage, individuals may be four months apart. I recorded birds in early stages of molt from mid-June to mid-October and these dates are nearly matched in some areas in Mexico alone. The latest date, 31 January, is for a male from Chichicastenango, Guatemala (AMNH 397911) that was nearly through molt. Thus, the range of dates for postjuvenal molt is at least eight months and possibly slightly more. Geographic variation in timing or extent of molt was not investigated.

Body molt progresses as outlined for *A. cassinii.* The greater primary and secondary coverts and alula and its coverts are not molted until after body molt is essentially complete. Some individuals have a few juvenal feathers, usually on the midabdomen, in the next breeding season.

As body molt is completed, the flight feathers begin to drop. Normally secondaries do not molt until after the first primary or two have dropped, but one bird had all new secondaries while only about half of the primaries had been replaced; some body molt was still occurring, suggesting that the secondaries began to drop earlier than usual and that the primaries were in their normal temporal sequence. The greater secondary coverts are molted prior to the greater primary coverts and are usually lost in a group, while the latter are molted sequentially with their respective primaries. This species, though thought to be closely related to *A. ruficeps*, carries very few juvenal wing feathers into first breeding season. I found two cases of secondaries 1–6 being retained and one case each of the following primaries being retained: 1–9, 1, 1–3, 1–2, and 8–9. The rectrices may be retained more often than either the secondaries or the primaries. The tail usually starts to molt last and is normally replaced in the 1 to 6 sequence. Generally, tail molt is protracted, but there are specimens with most of the regrowing tail feathers of only slightly different lengths. It is possible that these few birds accidentally lost their tail feathers. A few birds deviate from the 1 to 6 sequence, but this is also found in other members of the genus, and Miller (1961) reported similar circumstances for postnuptial tail molt of *Zonotrichia capensis* in Colombia. He thought that accidental loss only partly explained the deviation, implying that it may be natural for *Z. capensis.*

A. notosticta.—The only juvenal specimen of this form that I examined was just beginning the postjuvenal molt. A few new feathers were present on the midback. There was no evidence of molt of the ventral tracts.

A. aestivalis.—I examined 21 specimens in body molt and 16 in flight feather molt. This species may have as many as three broods a year and has a long period of postjuvenal molt. In some parts of the range, birds begin to molt as early as May or June, while a bird (AMNH 55180) from Greensboro, Alabama was still in the late stages of flight feather molt on 13 December. The molt period is much shorter for an individual.

The four birds in early stages of molt show little, if any, difference in molt pattern compared with other members of the genus. The midback begins first and is soon followed by the sides of the breast and forehead. One bird nearly through body molt had old upper tail coverts. Usually the alula and its coverts, and the greater wing coverts are not molted during general body molt.

Molt of flight feathers usually begins when body molt is nearly completed, but may vary among individuals. The greater wing coverts molt at this time, greater secondary coverts early, and greater primary coverts coincidentally with their primaries. Loss of primaries usually starts prior to loss of the eighth secondary, the first of these feathers to drop. The last flight feathers to begin molting are the rectrices.

A. botterii.—I examined 24 specimens in molt. The known period of molt for *A. botterii* is more limited than expected due to a lack of specimens in late stages, especially during flight feather replacement. Molt undoubtedly begins in late May or early June in the Texas portion of its range and extends at least until late December as observed in a female *petenica* taken 7 December near Chontalpa, Tabasco, Mexico (K. A. Arnold, in litt.). This bird sitll had old primaries 7 through 9 and would require several more weeks to finish molting.

The major departure of molt pattern in this species from the generalized pattern is the rapid completion of ventral molt. Although mid-dorsal molt apparently begins as early as, or often slightly ahead of that of the sides of the breast, the ventral areas progress faster and may be almost entirely new while dorsally the molt has progressed little beyond the midback, scapulars, and forepart of the crown. Replacement of the marginal and lesser wing coverts is coincident with body molt. The alula and its coverts and the greater secondary and primary coverts are not molted until body molt is complete.

Although the female *petenica* mentioned previously is the only late molt cycle specimen, there is every reason to believe that this species undergoes a complete molt with flight feather replacement after body molt is complete. I found no spring birds that retained juvenal flight feathers. K. A. Arnold (in litt.) informed me that two young of the year (LSU) taken in November were in flight feather molt on all the regions—rectrices, primaries, and secondaries. The greater primary coverts were molting synchronously with their respective primaries, while the greater secondary coverts were all new. The alula and its coverts were still old.

A. cassinii.—I examined 45 specimens in molt. Their postjuvenal molt served as the model for the genus and does not need to be repeated here. *A. cassinii* shows more coincidence of inception of dorsal, ventral, and forehead molt than do members of the *ruficeps* and *Haemophila* groups. Occasionally the ventral molt proceeds more rapidly to near completion, while some dorsal and head areas lag behind. This may result from a slight delay in molt associated with migration. There is some evidence that molt is no less complete in late-hatched birds, but tends to be compressed so that molt at various loci is more nearly synchronous.

Molt of flight feathers begins after body molt is nearly or entirely completed. Usually the secondaries start before the primaries, and the first rectrices are dropped about the time the sixth primary is regrowing. Birds with molting primaries have been taken from 15 August (primaries 4–9 old) to 12 November (primary 9 missing). Molt begins in some individuals by late May or early June, and in others not until much later. On 10 November a bird (AMNH 401609) still had primaries 4–9 old. Tail molt begins about midway through molt of the primaries. It apparently occurs more rapidly than remigial molt and may be completed by the end of primary molt. Since birds in late stages of molt are often difficult to distinguish from adults this last point is not fully documented.

A. quinquestriata.—Seven specimens in molt. Most available specimens are either in the very early stages of molt or are through molting. Replacement begins on the midback, but soon spreads to the breast and sides. In one bird about one-third through molt the breast and sides are more nearly complete than the midback. A bird (CAS 62877) collected on 12 August 1961, near Moyahua, Zacatecas and most of the birds that I collected near Mazatán, Sonora at the end of August 1963 were in early stages of molt. Birds from near Huassa, Sinaloa in early December, had completed molt; at least they showed no missing or growing feathers. Molt often begins in young birds before the juvenal tail feathers are completely grown.

TABLE 4

NUMERICAL SCORING FOR PRENUPTIAL MOLT IN *AIMOPHILA*

Region	Extent	Value
Rectrices	None	0
	1	1
	2	2
	1,2,3	3
	Other[c]	4
Body	Part[a]	0
	Most[b]	1
	All	2
Secondaries	None	0
	8	1
	8,9	2
	7,8,9	3
	Other[c]	4
Upper wing coverts	None	0
	Some greater secondary	1
	All greater secondary	2
	Greater, middle secondary	3
	Other[c]	4

[a] Part means all or most of the ventrum and limited dorsal molt.
[b] Most means an increased amount of dorsal molt, but not complete.
[c] Included here are categories of greater amounts of molt and a few exceptional cases of lesser amounts of molt.

Extent of molt in 16 specimens in complete first winter plumage varies slightly. Usually the entire body plumage is replaced, although a few yellowish feathers may be retained on the midabdomen. All rectrices are usually retained, and the only flight feathers normally replaced are some of the inner secondaries. Six birds that had completed the molt had replaced the innermost secondary (9), while three had replaced 8 and 9, and seven had replaced 7 through 9. Apparently the feathers are lost in order from 9 to 7. The alula and its coverts and the greater secondary coverts are replaced. Rarely, a variable number of primaries and their corresponding greater primary coverts may be replaced.

PRENUPTIAL MOLT

In *Aimophila* only members of the *Haemophila* complex show a regular, extensive prenuptial molt, although some individuals in populations of *A.*

TABLE 5

AVERAGE NUMERICAL VALUES OF PRENUPTIAL MOLT

Species	Rectrices	Body	Secondaries	Coverts	Total
mystacalis	0.58	1.31	1.69	0.56	4.14
sumichrasti	1.88	1.21	1.49	1.41	5.99
carpalis	1.37	1.42	2.47	1.72	6.98
humeralis	1.56	1.96	2.94	1.26	7.72
r. acuminata	2.50	1.70	2.91	2.93	10.04
r. other	1.78	1.70	2.91	3.19	9.58
Total	9.67	9.30	14.41	11.07	
Average	1.61	1.55	2.40	1.84	
Range	0–4	0–2	0–4	0–4	

botterii undergo limited body molt. New feathers noted on some specimens of other members of the genus appear usually to represent adventitious replacement. Hubbard (1975) found several specimens of *A. ruficeps* from Jalisco that were relatively fresh plumaged in the late spring and early summer. Whether these were birds that had undergone a prenuptial molt is unclear, but possibly they had such a molt.

The extent of prenuptial molt was examined in a large number of specimens taken at onset of the breeding season. Molt was essentially completed by this time, giving a valid indication of populational variation in extent of molt. To facilitate interspecific comparisons I scored each specimen in four molt regions (Table 4). These scores were then summed for all specimens of a species, the average taken (see Table 5), and percentages of specimens in each category calculated (Table 6).

In all species the same tracts are molted, but to varying degrees. Some-to-all body plumage is replaced; when only some of the contour feathers are molted the ventral surface usually appears to be entirely new, while parts of the dorsal surface are worn. Extent of molt of rectrices, secondaries, and wing coverts is likewise variable. Sequence of feather replacement within any given region generally follows that of postnuptial molt with the exception of the reduced dorsal body molt. In some species initiation of molt is more coincident at the several loci than in postnuptial molt. Molt normally begins on the back and at about the same time on the breast, throat, and sides. Inception of tail molt and covert replacement is more variable.

A. r. acuminata.—Although there is some evidence that breeding seasons are slightly different for coastal and inland localities, both populations are considered as one here. Some individuals begin body molt in the first

TABLE 6

% Distribution of Individuals of *Haemophila* Group in Categories of Prenuptial Molt

	Categories																		
	Rectrices					Body			Secondaries					Coverts					
Species	0	1	2	3	4	0	1	2	0	1	2	3	4	0	1	2	3	4	N
r. acuminata	4	20	30	16	30	5	19	76	2	2	5	88	3	0	12	23	25	40	114
r lawrencii	20	29	27	2	22	10	10	80	6.5	13	6.5	37	37	2	8.5	19	8.5	62	45
sumichrasti	38	19	2	2	39	32	15	53	44	8	15	24	9	29	34	21	0	16	48
humeralis	7	60	16	4	13	1.5	1.5	97	0	1	11	80	8	8	68	18	0	6	70
mystacalis	53	40	5	0	2	26	18	56	29	20	9	38	4	76	9	6	0	9	43
carpalis	8	59	27	1	5	19	21	60	19	0	4	70	7	12	33	38	5	12	78

week of April. Only 15% (2 of 13) of all April birds showed any evidence of molt; these were in the initial stages of body molt. All early May birds were in body molt, and most had begun tail and/or secondary molt. Of 5 mid-May birds, only one showed slight amounts of body molt, and none of the others was molting. Specimens from late May generally were molting, while some had completed the molt on one or more regions. One male (MLZ 28778), with testes marked as "full" on the label, was in worn plumage. This suggests that birds reaching breeding condition early have a reduced molt and that breeding and molt are essentially mutually exclusive activities. Molt continues through June, with some individuals showing traces of body and tail molt into early July. Rectrices, secondaries, and wing coverts molt after the body and apparently finish in less time.

Each region of molt is independent of the others. For example, the amount of wing covert molt was not related to the number of remiges replaced. No birds showed molt on all 4 regions, but the 4 birds that did not replace any rectrices molted normally on the other 3 regions. However, the most extensive molt category in each of the four regions contained the largest percentage of the individuals. Thus for *A. r. acuminata* selection has operated independently on the four regions to maximize the extent of the molt.

A. ruficauda (other races).—Although there is some evidence that prenuptial molt in the three races is not synchronous, all three are lumped here because the number of available specimens was limited.

Early stages of body molt appeared on seven birds taken in mid- to late April in Chiapas. Three had begun tail molt, and none of the seven showed any signs of secondary covert molt. By early May some birds had new body feathers, secondaries, and wing coverts. Others appeared to have new feathers on the alar tracts, but these were relatively unworn parts of the plumage replaced several months earlier during the postnuptial or postjuvenal molt. A single female from Tonalá, Chiapas on 13 May was very worn and had not initiated molt. She may not have molted until after the breeding effort. Some birds complete the molt, especially on the secondaries and wing coverts, during mid- to late May, while most birds are still undergoing body and rectrix molt. The only molting June specimens are two from Costa Rica that showed body and rectrix molt. One was molting secondaries, while both had completed molt of the wing coverts. Some birds from northern Central America probably also are molting into June, but most are finished by that time.

Average covert replacement is highest in these forms of the *Haemophila* group, and there is a high incidence of full secondary replacement. However, numerous birds replace fewer than three secondaries. The even spread of individuals in categories of rectrix molt is surprising in view of the high numbers showing extensive molt in the other three regions. Again this suggests a high degree of independence of the four regions as was shown for *A. r. acuminata.*

A. sumichrasti.—Among the few prenuptial molt specimens available are a single bird from late April, ten from May, and two from June. All of them except one early June bird show evidence of molt. The single April specimen (USNM 144026) was starting to molt about simultaneously on three of the molt regions—the body, rectrices, and secondaries. As shown by a late May bird (USNM 144030), molt of the coverts normally begins later. Birds showing symmetrical feather replacement in mid- to late August were judged to be initiating postnuptial molt.

Molt in *A. sumichrasti* is not as complete as in most other species of the group; replacement of feathers on the body averaged less complete than for any of the other species. Most birds (68%) underwent complete or nearly complete body molt, while 32% showed only part replacement. Most individuals showed no or very little secondary (44% and 8%, respectively) and wing covert (29% and 34%, respectively) replacement. If more coverts than the greater secondaries were replaced, the molt involved at least the marginals and the secondary coverts. No birds showed new feathers on only the greater and median secondary coverts. The difference observed between percentages of birds that did not molt any secondaries (44%) and those that did not molt any coverts (29%) shows independence of molt in these tracts. This is also supported by the greater percentage of birds extensively molting coverts (16%) than molted more than three secondaries (less than 9%).

A. humeralis.—Body molt begins as early as mid- to late April. The first record of tail molt is in late May, and it is still apparent in some early July individuals. Wing molt starts by about mid-May. Molt in *A. humeralis* is more rigidly timed in the several regions examined than in other species of this complex.

Body molt is complete in most individuals in this species. By early July (when most of the specimens were collected) the exceptionally abrasive conditions make it difficult to judge whether some feathers had been molted two months earlier. Only two birds—probably abnormal individuals—had an obviously incomplete body molt.

A. humeralis generally replaces few feathers on regions other than the body. Most of the birds molt either rectrix pair 1-1 or pairs 1-1, 2-2; very few replace no tail feathers. Ninety-two percent had from one to three new inner secondaries; the remainder apparently molted more distal secondaries in addition to the normal 7–9. Several birds had only secondary 9 new, suggesting independent molt loci for secondaries 8 and 9. This normally is not evident as 8 molts earlier than 9. *A. humeralis* shows some coincidence between the extent of secondary and wing covert replacement, although more specimens molted all the greater secondary coverts than molted more than three secondaries. Apparently the correlation between replacement of secondaries and secondary coverts results from common selective pressures rather than interdependence of factors initiating molt.

A. mystacalis.—Molt begins by late April or early May. An early May specimen (USNM 135974) had light molt on the forehead and throat; the inner rectrices were just beginning to erupt from their sheaths. By the middle of May body molt is well underway. Some birds still showed molt in mid-June while others were finished by this time. Birds in July and August showed minor amounts of molt, probably replacing accidental feather losses, and were not in prenuptial molt.

More than half (56%) of the specimens examined that had completed prenuptial molt had completely new body plumage, 26% had only partly new plumage, and even fewer birds showed mostly new plumage; all individuals replaced some body plumage. The majority (53%) did not replace any rectrices at this molt; of those that did, most molted only 1 or 2 pairs of tail feathers, although 1 bird replaced rectrices 1–5. The preponderance of birds showing no new tail feathers is noticeably different from other species in the group. Only *A. sumichrasti*, with 38% of the specimens not molting any rectrices, approaches *A. mystacalis* in this regard. Generally either no secondaries or the inner three (7–9) are replaced. The majority replace 7–9. Fewer replace only secondary 8 or 8 and 9. One bird apparently molted all nine secondaries, but this is difficult to judge because the distal secondaries are more protected from wear than are other remiges. A single bird replaced secondaries 7 and 8 rather than 8 and 9 as is more usual when only two are molted.

Molts of wing coverts and secondaries are apparently not directly correlated. While fewer than 30% molted no secondaries, over 75% of the specimens had no new wing coverts. Small numbers replaced inner secondary coverts, some corresponding approximately to the secondaries that were replaced, but others showing nearly all new coverts, while the number of new secondaries was three or less.

Differences in completeness of molt may reflect habitat differences among these sparrows. All other members of the *Haemophila* complex have centers of distribution in lowland regions, while *A. mystacalis* is restricted to mountains, usually above 900 m. Increased altitude may result in decreased harshness of habitat and hence decreased abrasion of feathers between molts. This is suggested by the generally less-worn appearance of those feathers in breeding *A. mystacalis*, especially in the tail, which are not molted by some or all individuals of species in the complex. Decreased wear also could result from different foraging behavior or other factors.

A. carpalis.—By the latter part of April some individuals begin prenuptial molt; during the molt period, which extends into early July, the birds are paired and territorial. Nests have been found as early as May (Bendire 1882) around Tucson, Arizona and a bird (MLZ 9434) taken 3 May at Reforma, Sinaloa had a "well-developed" ovary. It appears that periods of molt and breeding can overlap in a population of this sparrow. A photograph by E. Porter (*in* Phillips *et al.* 1964) shows an adult with the first pair of rectrices about three-fourths grown feeding nestlings. Relation of breeding to spring rains is discussed elsewhere. It seems possible that early summer rains may initiate early breeding while some birds are in prenuptial molt. Whether such birds would discontinue the molt is not known. However, prenuptial molt in most individuals is essentially complete by the start of breeding. Some birds show a few pinfeathers on the body, probably replacements for feathers accidentally lost. Females reaching breeding condition in early May probably have a reduced molt or none at all. The May bird with the "well-developed" ovary was fairly worn and probably did not have a prenuptial molt. Males in molt may show enlarged gonads. Sutton and Phillips (1942) noted males with enlarged testes in early June that were finishing the molt; they thought the gonads were not of maximum size. Birds that I collected near Tucson in June had testes of 6 × 4 mm, the size of the gonads of males known to be paired with nesting females.

Molt usually begins on the body, but soon includes the tail. In 60% of the specimens examined, body molt appeared to be complete; the remainder of the birds showed some old feathers on the hind neck and upper and lower back. The crown and ventrum are always replaced. Replacement of the latter is sometimes difficult to judge in July birds as it rapidly becomes worn in incubating females. The number of wing coverts molted varies from none to nearly all except the greater primary coverts. Twelve percent of the specimens examined showed no evidence of covert molt. Over half the birds molted only the greater secondary coverts. An appreciable number of birds replaced some or most secondary coverts, but did not molt more than two secondaries. Seventy percent of the birds molted secondaries 7–9 but only 33% replaced only those greater secondary coverts. Nineteen percent had no new secondaries. No spring birds symmetrically replaced primaries or their coverts; the few cases of irregular molt were classed as nonmolt. Several birds taken in Sonora in late August (MVZ) showed symmetrically new inner primaries; whether they were molted in the prenuptial molt period or whether they represented an early postnuptial molt cannot be determined. Tail molt usually occurs after body molt starts, but the relationship is irregular. In 86% of the specimens it involves the inner one or two pairs of rectrices. Only 8% showed no replacement of rectrices during prenuptial molt. Birds in tail molt were taken from mid-May to the end of June.

POSTNUPTIAL MOLT

Although there is individual variation in time of initiation of molt at loci on the body and appendages, there is sufficient consistency to construct a "typical" molt pattern. The following description is based on individuals of *A. ruficeps* from California and Arizona.

Since molt of the primaries generally covers the entire period of molt, it has been used to define arbitrary stages in the molt (Table 7). The primaries consistently start molting with number 1 (the innermost) and progress distad. Timing of molt of adjacent primaries varies slightly among individals, so that in one bird primaries 1, 2, and 3 may be lost consecutively and nearly exclusively, while in another individual all three may drop nearly simultaneously. Molt of the greater primary coverts is synchronized with molt of the corresponding primary.

Replacement of the secondaries usually starts soon after the primaries, but occasionally earlier, and is normally completed slightly after full growth of the last primary. Some individuals have completely new secondaries before the last primary is fully grown. The replacement sequence for all the species seems to be about the same and shows similar variations. Secondary 8 is always lost first, followed by either 9 or 7 and both of these are lost before secondary 1; then 2 through 5 molt in sequence. The position of 6 in the sequence is the most variable. It may molt at the same time as number 1, shortly after number 2, or at the end of the sequence. Usually if it is not molted by the time number 3 is growing, it will be replaced last in the series.

The greater secondary coverts are dropped about simultaneously in the early stages of primary molt. They are usually all replaced by stage 3 or slightly later. Median secondary coverts molt after the greater coverts and are completely new before the end of primary molt. The alula and its coverts molt from about stage 3 to stage 6 and are new by the end of primary replacement. The underwing coverts were not studied.

The rectrices are replaced centrifugally beginning with number 1. Rectrix molt may begin about the same time as primary replacement or may be delayed until primary 4 or 5 has been dropped. The molt is usually complete by the time the last primaries are partly replaced. Birds delaying rectrix molt may replace these feathers more rapidly than those beginning tail molt at an earlier stage. Rectrices in molt usually show up to four or five, infrequently six, feathers in various stages of growth. This suggests that for short periods the tail, functionally, is rather limited.

TABLE 7

STAGES OF POSTNUPTIAL MOLT IN *A. RUFICEPS*

	Stage							
	1	2	3	4	5	6	7	8
Primaries	1, 2 missing to part grown.	1, 2 new; 3 part grown; 4 old to missing; 5–9 old.	1–4 new, 5 part grown.	1–5 new, 6 part grown.	1–6 new.	1–7 new; 8, 9 replacing.	1–8 new, 9 almost grown to sheathed base.	New.
Secondaries	Old.	8 missing, 1–7, 9 old.	8 part to new, 7 missing to part, 9 old to missing, 1–6 old.	7–9 new, 3–6 old, 1 part to full, 2 missing to part.	7–9 new; 6, 1, 2 - partly new.	7–9 new; 6 part; 1, 2 new to part; 3 old to part; 4, 5 old.	New to 4–6 sheathed.	New.
Coverts	Old to some missing.	Greater secondary sheathed.	Molt, greater secondary new.	New; some still sheathed.	New.			
Rectrices	Old.	Old to #1 drops.	1 sheathed, 2 part to sheathed, 3 missing to part, 4–6 old.	1–3 new, 5 ⅔, 6½ to old.	1–4 new, 4–6 sheathed bases.	New.		
Ventrum	Begin to part new on breast, sides.	Light-heavy on breast, sides, throat, flanks.	Spreading anteriorly and posteriorly.	Posterior moderate to light.	Light posteriorly.	New.		
Dorsum	Begin to part new on midback.	Light to heavy midback and spreading anteriorly, posteriorly.	To anterior and posterior.	Posterior moderate to heavy.	Moderate to heavy.	Light to moderate.	Light posteriorly.	New.
Head	Begin to part new, medium forehead.	Heavy on forehead.	Crown molt.	Complete hind crown.	New.			

Body molt may start slightly before or at about the same time as primary molt. In either case body molt is completed by the time the flight feathers are replaced and usually by the time the outer primaries are growing. Body molt begins on the midback, scapulars, breast, throat, and sides and progresses as in the postjuvenal molt. The last areas to molt are the hind crown, lower back, upper tail coverts, midline of the abdomen, and the crissum.

A. ruficauda acuminata.—There were 28 specimens in postnuptial molt. Molt is not started until early to mid-October, and the first completely molted birds are from mid-January. Different birds may be in the same molt stage for up to three months, probably related to different breeding seasons in coastal and inland populations.

Body molt generally starts just prior to primary molt and is completed by stage 5. The rectrices begin molting either slightly before or soon after the first primary drops. Termination of tail feather replacement is slightly more variable and may occur by stage 4–5 or may be prolonged until stage 7. The secondaries molt in the usual sequence, beginning with secondary 8 and progressing in order: 8–9–7–1–2 = 6–3–4–5. Secondary 8 is lost sometime during the molt of the first three primaries, and the end of secondary replacement seems to correspond rather closely to the termination of primary molt. Timing of molt of the greater secondary coverts in relation to the primaries is somewhat variable. Generally they are all replaced by stage 2. The other coverts are replaced after the greater secondary coverts.

A. ruficauda (other races).—I examined 15 specimens in molt. The earliest bird in postnuptial molt was taken in mid-August; the first birds that have completed the molt are represented in material taken in mid-January. *Aimophila r. connectens* and *A. r. ruficauda* probably have later nesting and molt periods than *A. r. lawrencii* (Tashian 1953, Dickey and van Rossem 1938, Land 1962). Dickey and van Rossem noted that "the fall or 'postnuptial' molt is well under way at a time when second sets are being laid," because "a female taken on October 29 was laying, although in the midst of the fall molt at the time, and a male taken September 3 was in full breeding condition although at the same time in molting plumage."

Body molt begins before or about the same time as primary molt and is usually completed slightly before the last primary is fully grown. The molt pattern seems to be similar to that of the postjuvenal molt.

Secondaries do not begin to molt until after the primaries; the usual sequence is 8–7 = 9–1–2–3–4 = 6–5, although 6 may molt slightly earlier. The last secondaries are replaced just before the end of primary molt. The greater secondary coverts are molting by stage 1 or sometimes slightly before and are finished by stage 4. The median secondary coverts molt slightly later. The alula and its coverts molt together during the middle of primary replacement. The rectrices usually drop before the primaries and may be as much as ¼ grown by the time the first primary is being replaced. Rectrix molt seems to require more time than in some other species and is not finished until stage 6–7 or 7. The sequence of replacement may be in the regular 1–6 sequence or slightly asymmetrical.

A. sumichrasti.—Specimens were available only in initial stages of molt which begins in early August. Little more can be said than that molt usually begins on the body before the first primary is lost. There is some evidence that tail molt is variable and may not necessarily follow the 1 to 6 sequence of tail molt in *A. ruficeps.*

A. humeralis.—I examined 18 specimens in molt and 6 in intermediate stages. The earliest birds in molt (stage 0–1) were taken in mid-October. Molt is apparently completed by early to mid-December in some individuals. Body molt normally begins before the flight feathers and proceeds in essentially the same pattern as in *A. ruficeps.* Some individuals are finished by the time the fifth primary is partly grown; others may continue slightly longer. The rectrices usually start molting before the first primary is lost and are finished by stage 5–6. The general pattern of tail molt does not differ from that of *A. ruficeps.* Some individuals show slight deviations from this pattern, but this is probably due to accidental loss, especially during the molt. Secondaries begin molting during stage 1 and usually finish just before the primaries complete their growth. The usual sequence of replacement, except for number 6, is 8–7=9–1–2–3–4–5. Number 6 may be lost either before or after number 3, most often before, but always after number 1. The greater secondary coverts are dropped before the first primary. These coverts usually molt simultaneously and are completely new by stage 3. The other secondary coverts are less synchronous, but are usually replaced by the end of primary molt. The alula and its coverts are molted about midway through primary molt.

A. mystacalis.—I examined seven specimens in molt. Individuals apparently begin to molt by early September, after the young of the first brood become relatively independent. Molt may be at stage 5 by early October, and it probably takes between 2 and 3 months for the average individual. No birds were available in stages 6 through the end of molt.

Body molt starts before primary molt and is finished by stage 5. One bird (MVZ 119183) with new body plumage by stage 2 may be an unusual case. The secondaries may begin molting before the first primaries are lost or not until after stage 1–2. No specimens were examined that had completed secondary molt. The sequence of replacement of secondaries, 8–9–7–1=6–2=5–3–4, deviates slightly from that of other species as 5 is usually replaced before 3 and 4 rather than in ascending order from 1. Greater secondary coverts are replaced early in the molt followed by the other coverts, except the greater primary coverts, which molt with their respective primaries, and the alula and its coverts. The rectrices are molted in sequence from 1 to 6 starting at stage 1 or as late as stage 2–3. They are entirely new in two birds in stages 4 and 5, respectively.

A. carpalis.—I examined 24 specimens in molt. Since the breeding season of this sparrow may vary depending on time of the summer rains, and time of initiation of molt may be extended when birds are raising two broods, one might expect that the period of molt would also vary. While I have found birds beginning to molt in Sonora in late August and early September, Pitelka (1951a) and Moore (1946) reported nests or newly fledged young into early November. A male collected in early November with young "at most two or three days out of the nest" was in early stages of postnuptial molt (Pitelka *op. cit.*). An adult female taken on 2 October in stage 2–3 of the molt was at an active nest with 3 eggs. The total period of molt for an individual probably is 3 months or slightly less.

Some birds begin body molt prior to starting replacement of the primaries, while others begin after primary 3 is partly grown. The general sequence follows that of postjuvenal body molt. Body molt may terminate as early as stage 4 for certain birds that began to molt early. I am not certain when the last birds complete this part of molt. Secondaries are replaced beginning about the time the second or third primary is lost. The usual sequence is 8–9–7–1–2–3–5–4; the sequence between 1 and 4, especially the timing of 6, varies. The greater secondary coverts begin molting before the first primary is lost and are new by stage 2. Marginals are molted early while the other coverts are replaced after the greater secondary coverts. Timing of molt of tail feathers is also variable. All old rectrices were noted on birds in stages 1 to 3 while molting feathers were found on birds in stages 1 to 4. Some birds show all new rectrices by stage 4 while others do not until slightly later. There is no evidence that molt sequence deviates from the pattern in *A. ruficeps.*

A. ruficeps.—I examined 48 specimens in molt. A "typical" molt pattern for this species has already been given. Birds in the northern part of the range, in California, may finish the molt in early September, while populations in southern Baja California and in southern Mexico may still be in late stages of molt in mid-December. Some birds in new adult plumage in early September were aged by collectors as adults on the basis of skull ossification. As young of the year would still have unossified skulls in September, it is apparent that some adults complete the postnuptial molt this early. There are not enough specimens in early stages to determine the approximate time required to complete feather replacement.

Except for the general comments made above, there are too few specimens to reveal any racial or geographic variation in timing of molt.

A. rufescens.—I examined 13 specimens in molt. With its wide geographic range, one might expect marked variations in dates of initiation of molt. At stage 3 two-and-one-half months separate the earliest and latest of 6 birds. Stage 6 would show a range of 4 months or more, if one extrapolated the stage 7 bird (Mexico) taken in early November, so its molt is similar to the stage 6 bird (El Salvador) taken in March.

Body molt begins before that of the primaries and may be completed as early as stage 2 or 3. Pattern of this molt does not deviate markedly from the postjuvenal molt or the postnuptial molt of *A. ruficeps.* Rectrices generally do not begin molting until after several primaries are dropped and at least primaries 1 and 2 have been replaced; regrowth of new tail feathers is complete in the single bird at stage 6. Loss of rectrices often is nearly synchronous, leaving the bird with all or most tail feathers growing during the middle stages of primary molt. Sequence of rectrix molt is from 1 to 6. Molt of the secondaries starts soon after the first primaries are regrowing. Replacement begins with 8 followed by either 7 or 9 and then moving in sequence from 1 to 6. Six is usually the last secondary to be lost and regrown. Replacement of the secondaries requires only slightly less time than that of the nine primaries, and growth of the last secondaries is completed shortly after the ninth primary is fully grown. The greater secondary coverts are new by stage 3 and probably sooner. By the same time a few lesser and median coverts are still old. While the greater secondary coverts molt nearly synchronously, there is less synchrony in the other secondary coverts. The alula and its coverts molt at about stage 4–5.

A. notosticta.—No birds in this molt were available. Most adults were taken in midsummer and had very worn plumage.

A. aestivalis.—From the three specimens in molt, it appears that molt pattern is essentially the same as for the other species.

A. botterii.—Few molting specimens were available. I examined three specimens from mid-September that were in early stages of molt. All showed that body molt begins prior to primary molt. One had initiated secondary molt with number 8 either missing or in a sheath. Another had begun replacing the rectrices with number 1 about full grown; the others were still old. A bird in early October had not started to molt. Howell (1965) reported that seven birds taken in Nicaragua in early February were all "in fresh, unfaded plumage," while four birds from British Honduras in November had new body plumage and primaries (K. A. Arnold, in litt.).

A. cassinii.—I examined 14 specimens in molt. Molt begins by late August or early September in Arizona and Texas. Body molt starts at least by the beginning of primary molt and sometimes slightly sooner; it is completed by the late stages of primary molt. Timing of initiation of secondary molt varies. Some birds lose secondaries before primary molt while others may not drop the first secondaries until after primary 3 is partly regrown. The greater secondary coverts all molt about the same time and are replaced by stage 3. The other coverts are lost after the greater secondary coverts. Rectrix molt may begin by stage 1 or not until after stage 2. Rectrices may be completely replaced by the time primary 5 is regrown and number 6 is partly grown, or not until the end of primary molt.

A. quinquestriata.—I examined seven specimens in stage 1. The initial stage of the molt is about the same as for its congeners. I have no birds in intermediate or late stages of molt. Flight feather molt begins with the inner primary, or the first two primaries may drop nearly synchronously so that both are missing. It appears that the first 2 or 3 primaries molt as a group before the 4th is dropped.

Phillips (1961) reported that an adult male beginning the postnuptial molt was collected 14 September 1952, along with a young bird in early stages of postjuvenal molt. I found birds with dependent young in early stages of postnuptial molt near Mazatán, Sonora in late August 1963, and on 1 September 1964. A bird taken on 11 November at Rancho Guasimal, Durango, had recently completed the molt.

DISCUSSION

Four types of molt cycles in *Aimophila* are depicted in Figure 6. Little consistent difference in pattern occurs in postjuvenal molt. One might outline statistically some departures from the "normal" pattern, but there is a similar degree of individual variation within a species. *A. botterii* shows a rather rapid and early replacement of the ventral plumage. Variations noted in timing and pattern are probably not significant in understanding relationships within the genus.

The major differences between the species are in degree of completeness of molt. Most forms show a complete or nearly complete postjuvenal body molt (Table 8), probably because the first winter body plumage provides more protection for the young than the laxer juvenal plumage. With regard to flight feathers, a few specimens of *A. rufescens* that recently had molted still had some juvenal tail feathers. *A. carpalis* retained some tail feathers, all primaries, and the distal secondaries. Some individuals of most or all of the other species in the *Haemophila* complex retained some rectrices. *A. quinquestriata* and *A. ruficeps* apparently usually retained at least some of the secondaries, primaries, and greater primary coverts. In *A. ruficeps* the number of feathers retained seems to vary geographically.

The significance of varying retention of juvenal plumage at the postjuvenal molt to the classification of the group is negligible. Such retention is highly adaptive, and it probably represents an attempt to economize

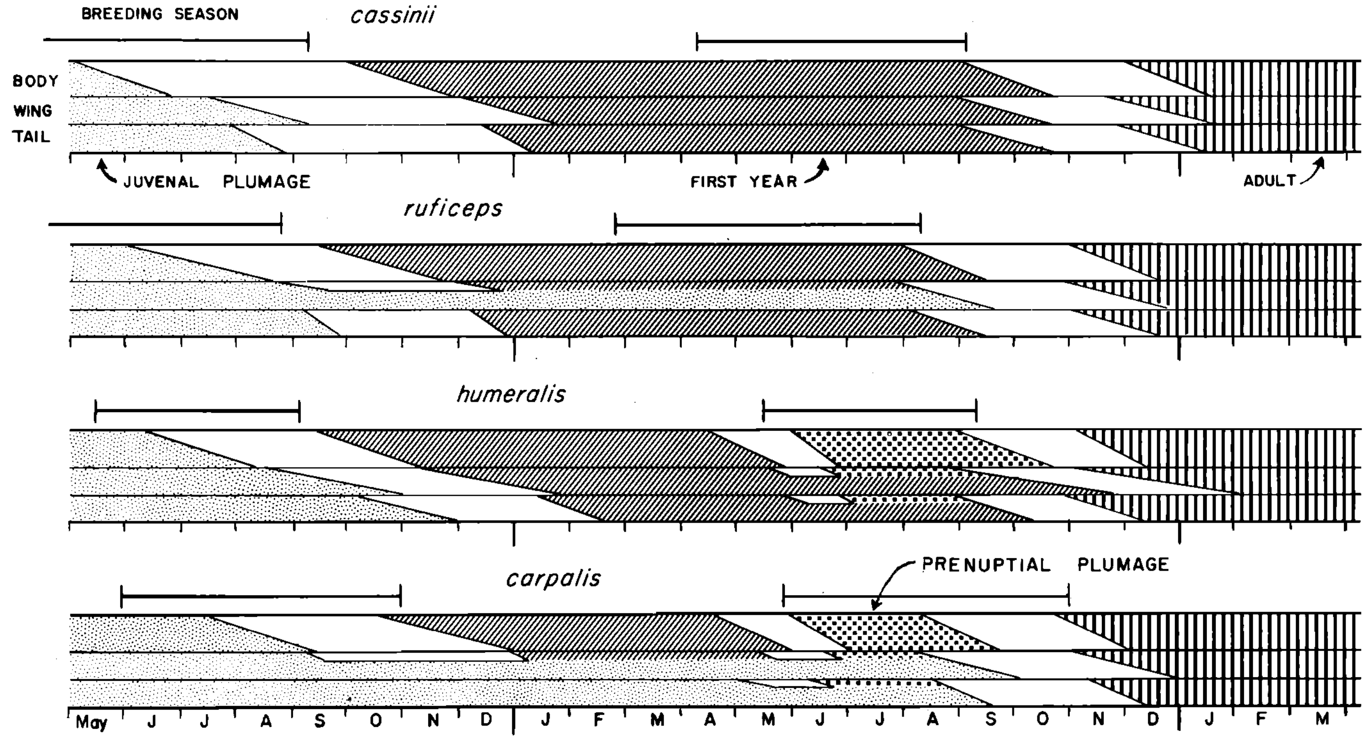

FIGURE 6. Examples of molt cycles in four species of *Aimophila*. Note the different degrees of completeness of the postjuvenal molt and the presence or absence of a prenuptial molt. The breeding seasons of each species are indicated by a line above the molt charts. The upper portion of the chart for each species shows the sequence of molt of the body plumage; the middle portion, the wing feathers; the lower portion, the tail feathers. White areas are periods of molt.

TABLE 8

SUMMARY OF MOLT EXTENT FOR ALL SPECIES OF *AIMOPHILA*

	Postjuvenal			Prenuptial				Number feather generations in plumage at:	
Species	B[1]	W	T	B	W	T	Postnuptial	1st breeding	2nd breeding
ruficauda	c[2]	c	c,p	p	p	p	c	2–3	2
sumichrasti	c	c	p?	p	p	p	c	2–3	2
humeralis	c	c	c,p,n	c	p	p	c	2–3	2
mystacalis	c	c?	c?	p	p	p	c	?	2
carpalis	c	p	p	p	p	p	c	3	2
ruficeps	c	p	c	n	n	n	c	2	1
rufescens	c	c	c,p	n	n	n	c	1–2	1
notosticta	c?	?	?	n	n	n	c	1?	1?
aestivalis	c	c	c	n	n	n	c	1	1
botterii	c	c?	c?	p?	n	n	c	2?	1–2?
cassinii	c	c	c	n	n	n	c	1	1
quinquestriata	c	c?,p	n	n	n	n	c	2	1

[1] B = body, W = wing, T = tail.
[2] c = complete, p = partial, n = none.

energy during the period of peak strain on the resources of the population. In *Aimophila*, as in shrikes (*Lanius*; A. H. Miller 1928), wrens (*Campylorhynchus*; Selander 1964), and jays (*Aphelocoma*; Pitelka 1945), the flight feathers replaced are those most likely to become worn during subsequent months. Selander (*op. cit.*) also thought that birds with shorter breeding seasons might retain more feathers.

One interesting phenomenon in *Aimophila* is that replacement of juvenal flight feathers, when it occurs, begins about the time body molt is completed and at about the same time adults begin postnuptial flight feather molt. A. H. Miller (1928) noted that postjuvenal molt in the Loggerhead Shrike (*Lanius ludovicianus*) was delayed, and that the few outer primaries molted were lost at about the same stage as they were in the postnuptial molt. However, this did not hold for the Phainopepla (*Phainopepla nitens*), which molted the innermost primaries first, but still initiated molt late (A. H. Miller 1933). The Boat-tailed Grackle (*Cassidix major*) molts the body and flight feathers coincidentally in the postjuvenal molt (Selander 1958), and the same is essentially true for the House Finch (*Carpodacus mexicanus*; Michener and Michener 1940). It may be that juveniles of some species must stagger the two processes, as they are not only molting into a new plumage, but are finishing growth—both energy-demanding processes. It can be argued that molt of body feathers occurs earlier in the postjuvenal molt, so that the bulk of the plumage is molted at a time of

TABLE 9

SUMMARY OF EXTENT OF POSTJUVENAL MOLT IN SELECTED EMBERIZINES

Genus	Extent of molt	Authority
Aimophila	Partial to complete	This study
Ammodramus		
savannarum	Complete	Dwight, 1900
Ammospiza		
caudacutus	Partial	Woolfenden, 1956
maritima	Complete	Woolfenden, 1956
Calamospiza	Partial	Dwight, 1900
Calcarius (2 species)	Partial	Dwight, 1900
Chondestes	Complete	Dwight, 1900
Junco hyemalis	Partial	Dwight, 1900
Melospiza		
melodia	Partial to complete	Dwight, 1900
lincolnii	Partial	Dwight, 1900
georgiana	Partial (sometimes rectrices)	Dwight, 1900
Passerculus		
sandwichensis	Partial "only body"	Sutton, 1935
Passerella iliaca	Partial	Dwight, 1900
Passerherbulus		
henslowi	Complete	Sutton, 1935
Pipilo		
erythrophthalmus	Partial (including tail and tertials)	Dwight, 1900
fuscus	Partial	J. Davis, 1951
Plectrophenax	Partial	Dwight, 1900
Pooecetes	Partial	Sutton, 1935
Spizella arborea	Partial	Dwight, 1900
passerina	Partial	Sutton, 1935
pusilla	Partial	Sutton, 1935
Zonotrichia capensis	Partial	A. H. Miller, 1961
albicollis	Partial	Dwight, 1900
leucophrys	Partial	Dwight, 1900

peak food supply. The slow replacement of flight feathers in postjuvenal molt may relate to reduced energy available above maintenance level at a time of decreasing food availability and increased population size. The more experienced adults, which complete both body and flight feather molt simultaneously and in a shorter period than postjuvenal flight feather molt, would be less influenced by these factors. It also happens that postjuvenal body molt often begins as the last of the flight feathers are finishing their growth, meaning that the follicles of all flight feathers of juveniles have been active much more recently than those of adults. This may also delay onset of flight feather molt in juveniles.

A survey (Table 9) of North American emberizines for which adequate data were available showed that most undergo only a partial postjuvenal molt. Those for which a complete molt is reported include: *Ammodramus savannarum*, *Passerherbulus henslowi*, *Ammospiza maritima* (but not *A. caudacutus*), *Chondestes grammacus*, and some species of *Aimophila*. The only tropical emberizine for which I could find adequate data, *Zonotrichia capensis* (A. H. Miller 1961), has an incomplete molt as do its north temperate congeners. On this basis it may be that an incomplete molt is the ancestral condition in the sparrow complex, and those species with complete molts perhaps have acquired them secondarily. If a partial molt of wing feathers is adaptive in the sense of replacing plumage that is most subject to wear, one might expect to find a complete molt among species in which wear is most prevalent. Woolfenden (1956) felt that the harshness of the habitat of *Ammospiza maritima*, with the resultant wear of the plumage, was the factor selecting for the complete molt of that species, as compared to the partial molt of its congener, *A. caudacutus*. The species of *Aimophila* that show a complete postjuvenal molt also normally inhabit somewhat abrasive habitat.

If potential plumage wear is a strong selective force on molt, one might expect some correlation between extent of postjuvenal molt and occurrence and extent of prenuptial molt. In reality, prenuptial molt is limited to those forms, i.e. *A. sumichrasti*, *A. carpalis*, *A. mystacalis*, *A. humeralis*, and *A. ruficauda*, that are inhabitants of arid tropical regions and make up the southern-based *Haemophila* complex within the genus. Additionally, the very worn appearance during the breeding season of the species which have no prenuptial molt suggests that it is difficult to evolve a prenuptial molt and that this trait probably has not arisen independently in all these forms. In this regard it is interesting that few passerines sympatric with members of the *Haemophila* group show a prenuptial molt.

In total extent of prenuptial molt, *A. ruficauda* ranks highest and *A. mystacalis* lowest (Table 5). Also, within each molt category *A. ruficauda* usually ranks highest. This suggests that this species may encounter the harshest environment of the group. The limited molt of *A. mystacalis* is interpreted here to mean that there has been a reduction in the degree of molt from the ancestral form within a less harsh environment in the montane regions of the southern plateau and the Sierra Madre del Sur, or that molt in *A. ruficauda* has diverged to the greatest extent from the ancestral condition. While *A. mystacalis* still inhabits thorny vegetation, it may be actually in a less continuously abrasive environment than the lowland forms. Most individuals show comparably less wear than the other members of the complex. As more specimens become available, it will be interesting to see if a decline in extent of molt occurs in those populations of *A. ruficauda acuminata* and *A. humeralis* that are penetrating the highlands surrounding the Río Balsas basin.

It is hard to imagine that extent and presence of this prenuptial molt is related to need to replace feathers to increase or maintain efficiency of flight. The outer primaries are not molted as one might expect, since these and the rectrices are probably most important to flying efficiency. Furthermore, one might expect to find prenuptial flight feather molt in *A. cassinii* in which the flight song display plays such an important role in courtship and probably in pair formation.

Prenuptial molt of the tail feathers most often includes at least the inner pair. In individuals that do not molt rectrices, this pair is usually much more worn than the other five pairs. At first I thought it may have been retained from the juvenal plumage, while the outer five pairs were replaced; however, this is not the case. The causes of increased wear of the central rectrix pair are obscure. However, since the molt tends to follow the pattern of postnuptial molt, if only one pair was replaced it would be the central pair.

The extent of prenuptial molt within the *Haemophila* complex may be related to length of time an individual has to complete the molt. Such a time period in these sparrows might be influenced by several factors, some directly related to the environment and others less so. In *A. carpalis* it appears that molt terminates about the time individuals begin the breeding effort. This suggests that individuals beginning the molt late may show lesser amounts of molt than birds that molt earlier and have longer to replace feathers. Also, if the onset of summer rains is important in stimulating breeding (Marshall 1963) then early rains might markedly influence extent of molt, by terminating molt earlier than usual.

Selective forces acting on prenuptial molt as compared to postjuvenal molt probably are more varied. This does not exclude the importance of abrasiveness of environment. However, it may also be that certain feathers are replaced to enhance the plumage used in various courtship or species recognition displays. It seems likely that this consideration plays an important role in molt of the head and throat feathers in species such as the White-crowned Sparrow (*Zonotrichia leucophrys*; Banks 1964), the *Haemophila* group, and the Orange-crowned Warbler (*Vermivora celata*; Foster 1967), all of which have special markings in those areas.

In a series of *A. botterii* taken by H. H. Kimball (UMMZ) in the summer of 1932, some individuals from May and June show new and molting feathers on the midback, forehead, breast, and throat. It appears that some individuals, the number possibly varying with locality, undergo a partial prenuptial molt of a limited amount of the body plumage. Although he makes no such statement directly, Webster (1959a) implies that the species does not have a prenuptial molt. In fact, this is the only member of the genus outside of the *Haemophila* group that has such a molt, although the situation in certain Jalisco *A. ruficeps* (Hubbard 1975) was mentioned earlier.

The postnuptial molt is complete and follows essentially the same pattern in all species with no significant differences among them. In at least one migratory form, *A. cassinii*, molt in most cases apparently occurs after migration, even though degree of wear of the flight feathers would seem to make it more efficient to molt prior to migrating. Perhaps the pressure to leave the region exerted by the rapid increase in population size after the young are independent, and a consequent reduction in available food, make it advantageous to leave early in the summer (see Holmes 1966 for a more extended discussion). Probably some selective pressure is produced by advent of summer rains and consequent increasing food supply in areas to the west.

Some individuals (probably in all species) may begin postnuptial molt before their young are independent (Pitelka 1951a, Phillips 1961, Webster 1959a, pers. obs.). It is perhaps not coincidental that most of these records occur late in the breeding season of the particular species and that birds with late broods, either supernumerary or replacement ones, may reduce the usual time lag between molt and breeding. It suggests that two energy-demanding processes, reproduction and molt, can in fact overlap, but that normally it is more advantageous to make them temporally exclusive (Pitelka 1958). The early postnuptial molt of late breeding birds may be related to the hormonal control of molt. Hormonal changes may be hastened in late breeders to the extent that the two processes, reproduction and molting, overlap.

It appears that those species, primarily of the *ruficeps* and *botterii* groups, and birds that finish breeding early, may also not begin molt as soon after breeding as do many sparrows of the *Haemophila* complex. This may be related to the intercalation of a prenuptial molt in the annual cycle of the *Haemophila* group. This extra molt may require closer synchronization of end of breeding season and initiation of postnuptial molt to allow at least a short time after postnuptial molt when there is no energy drain from either molting or breeding.

Whereas flight feather replacement during postjuvenal molt occurs subsequent to body feather renewal, during postnuptial molt the process may start before molt of body feathers. In *A. botterii* the molt may begin with a substantial replacement of body plumage, but in other species if body molt begins prior to flight feather replacement it is only very shortly followed by loss of the first primary.

Except for slight variations in timing of postjuvenal molt in *A. botterii*, it appears that the general differences in molt patterns and cycles exhibited by these forms are all adaptive to their particular modes of life. As discussed later, this may or may not have an effect on use of such information in unravelling the phylogeny of these forms. Sibley (see Parkes 1957) and others probably are picking distinctions that are too fine when they discuss such differences as timing of molt of the throat as evidence for generic relationships. My own results show too much individual variation within the group considered to use these distinctions in working out relationships. However, I am convinced that general characteristics of molt patterns and cycles, present inconsistencies within North American genera notwithstanding, are highly useful in outlining group relationships within the genus *Aimophila.*

GENERAL BIOLOGY

AIMOPHILA RUFICAUDA

Territoriality and pair bond.—Territoriality in this species is rather difficult to define precisely. As Storer (1955) noted, birds in the breeding season are often found in groups of more than two adults.

The few breeding season flocks of which I collected a substantial portion were composed of one female and several males. Usually there was a single male with an ossified skull, which suggests that it was two years old or older (see pp. 189), and one or more males with partly ossified skulls, which were probably only a year old.

Near La Huerta, Jalisco, in 1963, the flock members foraged and were active as pairs in early morning and moved into a flock only as morning progressed. A feeding flock observed at Cuernavaca, Morelos apparently was composed of birds that I had observed only a short time earlier as independent pairs, apparently on territories. Some flock members returned to sites where I had watched pairs earlier. This suggests that in some flocks members are more evenly distributed between the sexes and that there may be two different kinds of flocks: integrated, unit flocks that are active at a single nest and others—usually larger—that are mainly, and probably entirely, temporary feeding flocks.

Several other pairs that I watched in the same area around Cuernavaca, Morelos showed no signs of admitting others to their "territories." Thus, there is a good deal of variability in the composition of groups that are formed even in the same region. In part this probably reflects carrying capacity of the site and population size. Assuming auxiliary members of the breeding groups are first-year birds that do not breed, but join with breeding adults, then in years with high recruitment of young birds there is probably a greater number of groups of more than two birds, while in years following a low production of young, the proportion of pairs probably increases. Selander (1964) found groups of wrens (*Campylorhynchus*) in the breeding season that he thought were composed of adults and young of the previous year ("family groups"). The situation in *A. ruficauda* seems rather similar, except that I am uncertain of the genetic relationship of the auxiliary birds to the breeding pair.

Near Cuernavaca, during July 1964, I frequently noted territorial disputes involving pairs of birds. A dispute usually started when one pair or a single bird flew into or approached the territory of the adjacent pair. All four birds normally participated in a dispute. Usually members of each pair were together, but they were isolated from the other. The dispute most often consisted of duet chatters back and forth, with the chattering pairs facing each other, and occasionally individual chatters. Chatters were occasionally heard at other times, but they were often answered by an adjacent pair or stimulated an adjacent pair to fly toward the common territorial boundary. Frequently during a territorial dispute between two pairs a third pair about 50 m away started to chatter. Chases, usually by single individuals from each pair, occasionally climaxed an encounter, but more often after a dispute the pairs silently moved back to their respective territories.

Flight.—Flight is direct with no apparent pumping or undulations, either on short or very long flights ranging from less than 3 m to over 90 m. However, flight does not seem to be exceptionally strong.

Foraging and food.—During the summers of 1963 and 1964 detailed observations were made on foraging behavior of *A. ruficauda*, and more limited data were gathered on its food. It is important to emphasize that these observations were made during the summer months, as this sparrow may change its diet seasonally, especially in relative amounts of animal and plant matter, and food items sought will influence to some extent method of foraging. Observations were made on *A. r. acuminata* in the vicinity of Cuernavaca, Morelos and La Huerta, Jalisco, and on *A. r. lawrencii* near Tehuantepec, Oaxaca.

At this time of year 75% or more of the foraging took place on the ground. Some feeding was in trees and even less in shrubs; in both, the feeding actions were directed at the foliage. Most ground foraging was done in open places so the birds were usually visible to the observer. While moving on the ground the birds normally hopped; they ran very little.

Many kinds of food were found in stomachs of collected birds. I did not identify the items, but calculated ratios of animal to vegetable material. The average was 40% animal (range 98 to 5%) to 60% vegetable (N = 15). Although I saw only insect material being brought to nestlings, adults ingested a fairly large proportion of vegetable food during breeding season.

AIMOPHILA SUMICHRASTI

Territoriality and pair bond.—Only once did I observe more than two adult birds together in the breeding season. Apparently the social unit of this species during breeding season is the pair. Members of a pair often foraged together. Sometimes one bird (presumed to be the male) sat singing or calling while the other bird foraged nearby. Close ties between adults were especially evident when the female was nest building. The male nearly always was in the immediate vicinity and sang from a nearby shrub when the female added material to the nest. He often followed her in flights away from the nest and then would accompany her partway to the nest. At no time was there more than a single attendant bird. The only time I saw three adults together was in an apparent territorial dispute involving two males and the female of the resident male. Shortly after the two males came together, they were joined by the female and then separated. Within two minutes only two birds were in the territory, both calm and acting as a mated pair. Some groups of birds were encountered, but collecting and close observations always showed that birds in excess of two adults were young of the year, although some of these were in essentially adult plumage, having almost completed the postjuvenal body molt.

The chatter duet of *A. sumichrasti* is usually given from an elevated perch. I heard duets from near or on the ground when two birds were foraging together, but usually the perches were 1.5 m or more above the ground and rarely as high as the canopy. In early morning the birds sometimes chattered from above the canopy but later in the day were invariably below the canopy in the shade. Chatter did not require the two birds to come together but started *in situ,* especially if given in response to a chatter by a neighboring pair. Usually the performing pair was within 30 cm of each other. Once I heard a complete chatter from a pair separated by 3 to 3.7 m. Solo versions of the chatter were often given by the male while the female was foraging and sometimes by the male during a disturbance when the female was absent.

I heard several chatter performances during an apparent territorial dispute, but I only observed one actual confrontation. At other times, neighboring pairs chattered, one after the other, as if one pair stimulated the next. Although chatter also occurs in disturbance situations, these performances were very like counter-singing and so judged to be a form of territorial proclamation. Evidence is not completely conclusive, but points to a territorial, pair reunion, and/or some sort of alarm function for the chatter.

Food and foraging.—Observations on eight days in August of 1963 and 1964 showed that the birds spent nearly all their foraging time on the ground. I did not see any bird move up into tree or shrub vegetation to forage. Apparently the birds move over the ground mostly by hopping.

Stomachs of 20 birds from August of 1963 and 1964 contained an average of 36% animal material (range = 0 to 95%). Four individuals from 4 August averaged 94% animal food, and 16 birds from 16–25 August ate an average of 21% animal food. These very limited data indicate that diet of adults may change drastically as young become independent.

AIMOPHILA HUMERALIS

Territoriality and pair bond.—Adult birds are spaced throughout suitable habitat during the breeding season, in a way that suggests they are holding territories. Usually two birds were associated in a given area. As Storer (1955) also noted, more than two adult-plumaged birds occupied some areas, but less frequently than in *A. ruficauda.* On the basis of detailed observations in the Cañon del Lobos near Cuernavaca, Morelos, in summer, 1964, I found that most groups of more than two adults were formed during territorial disputes or were of very short duration. Only one group of three was together each time I saw them. From their behavior, I was sure that fledged young were nearby, and the extra adult each time may have been attracted by alarm calls. Relaxation of aggressiveness in alarm situations may account for some observations of groups of birds. Several times I saw three adults foraging together with no apparent antagonism. In most other cases of threesomes, a pair was joined for a short time by a third bird. Usually the reaction by one of the pair (male?) was aggressive, but not strongly so, and the new bird often remained nearby for a short time.

Foraging and food.—All my observations were in summer. Over half (32 of 56) of my recorded foraging behavior observations were of individuals in the tree layer; remaining observations were divided equally between ground and shrub layers. I think these observations fairly accurately reflect the differential use of various levels by the birds. Propensity for tree foraging is related both to abundant insect food and seeming difficulty with which these birds move through dense lower vegetational layers. At other times of the year, especially in the dry season, they probably spend a much greater percentage of time foraging on the ground.

Foraging in trees was done much in the manner of a vireo, i.e. as a deliberate foliage gleaner. Captures were usually made by a rapid peck at the surface of the foliage or, less often, at a woody portion of the tree. Rarely, a bird flew up and hovered just below a leaf while attempting to catch prey. Most tree branches that the birds used were horizontal and probably reflected the limited ability of the forager to cling in a vertical position or to use irregularities in the bark to move up more inclined branches. When foraging through shrubbery the birds used essentially the same technique. While foraging on the ground the birds hopped.

I was unable to identify most food items. The stomach contents of 20 adults (mostly from near Cuernavaca, Morelos) in July and August of 1963 and 1964 were predominately animal remains ($\bar{x}$ = 89.4%; range = 70–100%). Lepidopteran larvae, ranging from 2 to more than 3 cm long, were identifiable and seemed to compose a larger portion of the diet of *A. humeralis* than of *A. ruficauda.* A few other identifiable insects included several species of caterpillars, grasshoppers, and termite workers.

AIMOPHILA MYSTACALIS

To my knowledge there is no previously published information on the habits of *A. mystacalis.* I studied these birds along the Pan American Highway south of Oaxaca City during August of 1963 and 1964.

Territoriality and pair bond.—In both years, pairs were between first and second broods. At this time I encountered the spaced birds as pairs of adults or as family groups, including one or two adults and up to three young. The social system of *A. mystacalis* in the breeding season probably is based on the pair as the primary unit. I found no threesomes or larger groups of adults.

Male territorial proclamation is usually by primary song given from an exposed perch in the territory. Active defense and pair proclamation of the territory was by pair reunion chatter, which is common in this species. On several occasions I watched adjacent pairs counter-duetting, and a duet by a neighboring pair often stimulated an answering chatter from the pair I was watching. I did not see any chases or fighting between adjacent pairs.

Foraging and food.—Even though the birds were common, it was difficult to observe foraging behavior, because the sparrows were timid and disappeared when the observer approached. In addition, I was seldom able to follow birds for longer than 2 or 3 min before they moved out of view in the dense vegetation.

Mode of feeding depended both on character of surrounding vegetation and kind of food for which the birds were searching. A pair with a territory in a maguey field was limited to ground foraging, as there were no trees or shrubs within its area; maguey was rarely used as a foraging substrate. The grass layer was very dense and of a different character from the surrounding, heavily grazed hillsides. In August 1963, I watched a pair (presumably male and female) foraging on a hillside above the Pan American Highway. From their activities over several hours, I judged that they had not commenced breeding. They foraged only on the ground, most frequently in the dense herb layer around the bases of shrubs. Normally, they hopped while foraging and covered short distances. Several times they flew up about a meter, hovered before a branch or leaf, pecked at something, and dropped back to the ground. Another pair that I watched in August 1964 was feeding at least one fully grown fledgling. This pair foraged almost entirely in woody vegetation up to 6 m above the ground, generally between 30 cm and 2.5 m up in shrubs and in low branches of trees. They occasionally foraged on the ground. When foraging they generally moved methodically along bare, horizontal branches. Their movements reminded me much more of the slow foraging of a vireo than of a wood warbler. Much food was taken from leaf clusters in the tree canopy. Several times a bird dropped to the ground after a dislodged insect. I watched another pair eating small red berries in a shrub. Most animal food items that I saw captured were orthopterans, at least one species of which was abundant in the foliage of the trees in which the birds were foraging.

Stomachs of 19 adults from August of 1963 and 1964 contained an average of 55% animal material (range = 1–100%). Even among specimens taken at the same time on the same day, contents varied from 10% to 100% animal items per stomach.

AIMOPHILA CARPALIS

Territoriality and pair bond.—During the breeding season and for an undetermined period before and after, the pair is the social unit in *A. carpalis.* I am not sure when winter flocks form or begin to break up or when pair formation occurs. There is some evidence, discussed later, that a loose pair bond may hold, at least for some pairs, during the winter season. Anderson (1965) reported pairs by mid-April. By mid-June in Arizona, pairs are spaced territorially.

The members of a pair usually forage together. Single birds are found less often, but are not uncommon when males are singing or females are incubating. Usually lone birds soon join, or are joined by, a second bird. Likewise singing males, when approached, move off to join or be joined by the female. This was the time when I was most successful in collecting the less obvious females.

The nonbreeding biology of *A. carpalis* was studied 11 km east of Tucson, Pima County, Arizona from 24 to 29 January 1963, on 17 December 1963, and in the summers of 1963 and 1964.

Winter habitat types corresponded almost identically to those occupied during the breeding season—open mesquite-hackberry woodland with a ground layer of dried, mixed grasses and perennials. Although apparently not heavily grazed in the previous 2 to 3 years, only a small area had substantial ground cover, while most of the remainder had a sparse ground cover of short dried grasses. The only shrub or tree with leaves at this time of year is the hackberry. Around Tucson, mesquite does not leaf out until mid- to late April (Marshall 1963).

I usually found birds in intraspecific groups of 5 to more than 50 birds, most commonly in groups of 5 to 10. Single birds, pairs, and groups of fewer than 5 were also present, but less frequently. Several pairs in one group seemed to stay together and occupy a fixed area. Occasional singing by individuals suggested a low level of territorial behavior at this time of year. Birds sang at all times of the day to at least 1700. Most songs were given from exposed, elevated perches, as is typical of territorial song bouts during the breeding season. Generally single birds sang, but occasionally a second sang soon after the first, and once I heard 3 birds singing simultaneously. Anderson (1965), on the other hand, reported songs only from birds disturbed by the approach of the observer. Some sparrows sang in a flock, but I never heard more than one member of a flock sing at a time. Songs were of all types, including the duet, heard during the breeding season, but the *tzzlip* call was more common in winter than in summer. It is the introductory portion of a common song type, and its prevalence in winter probably indicated the low level of song motivation.

Interspecific flocks were as common as intraspecific ones. Brewer's Sparrows (*Spizella breweri*) were the most common associates, and Black-throated (*Amphispiza bilineata*), Lark (*Chondestes grammacus*), and White-crowned (*Zonotrichia leucophrys*) Sparrows occurred with *A. carpalis* less frequently and in smaller numbers. Only infrequently was there obvious aggression by either *A. carpalis* or any associated species. Usually a mixed flock moved off together as I approached, but sometimes the birds moved off in intraspecific groups. When flushed, the sparrows usually flew preferentially into a hackberry, cholla, or mesquite. They only infrequently resorted to palo verde. Hackberry and cholla are probably the best refuges at this time of year, cholla because the birds can disappear into the center of a branching plant in a network of thorns, and hackberry because of its spiny branches and dense foliage.

Foraging and food.—In summer *A. carpalis* foraged principally on the ground in open, relatively bare areas; winter foraging was all done at or just above the ground. Most feeding is done by pecking at the ground. I saw no birds scratching the ground surface or moving objects lying on the ground. When undisturbed, actively foraging birds hop about the feeding area. In general they move slowly and do not cover large areas of ground rapidly. One bird that I watched in January 1963 worked for more than 15 minutes in a roughly circular area of about 2.8 sq. m. Stomachs of all but two of the birds collected in winter contained nearly 100% seeds. In the exceptions, numbers of hard parts of ants were present. These birds undoubtedly use animal food when readily available, but generally take seeds. Brewer's and Black-throated Sparrows collected at the same time had eaten the same types of seeds. I examined stomach contents of 23 *A. carpalis* adults taken during June, July, and August of 1963 and 1964. Average animal material was about 85%, with about 15% vegetable material. In four juveniles taken in late August percentages of plant and animal material were approximately the same (79% animal, 21% vegetable). This species, like many others, changes its diet from seeds in the winter to animal material (mostly insects) in the summer. Most food for the young, at least until the birds are foraging independently, is animal material.

AIMOPHILA RUFICEPS

Very little is known about the biology of this shy, retiring sparrow, and only a few miscellaneous notes have been published. Most of the published material appears in the accounts of the species by Cogswell and Phillips in Bent's *Life Histories of North American Birds* (1968). In the following account much information is drawn from my observations during two summer field trips in 1963 and 1964, as well as more extensive observations near Berkeley, California from 1962 to 1964. Most of the latter observations were made in the spring months.

Territoriality and pair bond.—Cogswell (1968), on the basis of seeing pairs early in the year, thought the birds might remain paired throughout winter. Some birds are paired by early February in the Berkeley area, while others do not pair until later in spring. Adults probably remain paired through the winter, while young do not pair until the spring before their first breeding season. If this were the case one would expect to find either scattered birds and/or some organization within flocks during the winter. So far there are few records of Rufous-crowned Sparrow flocks. The flock reported by Esterly (1920) of about 20 that stayed for several months around his house was probably a misidentification of a flock of *Zonotrichia*, which he noted as curiously missing from the environs until the departure of the *A. ruficeps* in middle March. Linton (1908) took a specimen of *A. ruficeps* from a flock of 40 to 50 birds, but he did not state whether the remainder of the flock was made up entirely of *A. ruficeps*; he probably took the bird from a mixed flock of sparrows. A flock of several species of sparrows, including *A. ruficeps*, was noted around the Calaveras River (Cassin 1852). I saw *A. ruficeps* sporadically attached to a mixed flock of *Zonotrichia*. The Rufous-crowned Sparrows temporarily joined the flock when it was in particularly favorable foraging locations. In general, these birds do not flock after breeding season, except as family groups. It is not entirely clear when these family groups begin to break up. Around Berkeley, I have seen fully grown young in juvenal plumage being attended by adults in September. Another juvenile on 21 September seemed to be independent of any adults. I collected two young of the year and one adult from a group of at least five in the Santa Catalina Mountains of Arizona on 19 December 1963. These flocks indicate that family groups stay together well into the winter months in both areas.

During the breeding season, pairs were strictly territorial. Where *A. ruficeps* occurs with *A. rufescens* or *A. notosticta,* there was no evidence of interspecific territoriality or mutual aggression (Marshall 1957, pers. obs.).

Singing males usually use song posts of some sort. In California these include shrubs, trees, brush piles, and rock outcrops. A. H. Miller (1955) reported that in the Sierra del Carmen of Coahuila the birds used song perches ranging from 2 to 8 feet above the ground, and one male sang in flight. I found that males often sang from the ground while foraging. Usually the songs were much softer than the advertising song and the male often sang with closed mandibles.

Flight.—Flight is floppy and seemingly labored. Grinnell and Miller (1944) noted that "flights over the bush tops are rapid and short and usually down hill." Cooper (1870) reported that on Santa Catalina Island the birds "flew short distances only." I noted that birds often flew 6 to 15 m when flushed. Cogswell (1968) noted flights of as much as 165 m. Undoubtedly the length of a flight depends on motivation for the flight and nature of terrain between origin and destination. However, flight in this species is poorly developed, while ground locomotion is highly developed.

Foraging and food.—Most foraging by this species is done on or very near the ground. I often found birds foraging in the nearly continuous grass layer, in which they were invisible for long periods. At other times they spent proportionately as much time in the open, where the ground vegetation was very short or virtually lacking. Less commonly, the birds foraged in the taller woody vegetation. Cogswell (1968) noted them "in taller shrubs and short (oak) trees, apparently seeking food." I watched single sparrows moving through *Baccharis* bushes pecking at the substrate apparently searching for food. The birds do this in the foliage of the tree or shrub, but may also peck along branches where they probably are taking insects. Cogswell (1968) thought that *A. r. canescens* might be seen less often in trees than *A. r. ruficeps.*

While foraging on the ground the birds usually walk, moving one foot ahead of the other, over short distances at a fairly slow pace. Faster movements, as across open areas, are made by hopping. The birds do little flying during active foraging. In contrast, J. Davis (1957) found that the Rufous-sided Towhee (*Pipilo erythrophthalmus*) in California hopped almost entirely, while the Brown Towhee (*P. fuscus*) had a "step-hop" motion when foraging slowly and ran when moving long distances or making quick movements.

Food consisted of seeds and other plant material and insects, both imagoes and larvae. Williams (1897) reported that two females taken in May were eating "alfilaria seeds and small pieces of some grass stem." A. Martin *et al.* (1951) reported that stomachs of 25 specimens of *A. ruficeps* taken in summer contained 80% plant material. Barlow (1902) noted a similarly high content of plant material during the breeding season. Apparently these birds show little change toward animal material in the diet in the summer months as is seen in other species. I watched an adult male in the spring catch alate ants emerging from a crack in the ground. Crops of birds collected in Arizona in December and January contained only plant material. Insects probably comprise the diet of the young. Myers (1909) reported adults feeding young nestlings green worms about an inch long. Simpson (1925) photographed adults carrying "white grubs" to fledglings.

AIMOPHILA RUFESCENS

Territoriality and pair bond.—During the breeding season one almost always finds two adult *A. rufescens* together. In the few cases when both birds were collected, they were male and female, and we assumed that this was the composition of all pairs at this time. Members of a pair usually are separated only when the female is incubating or in the early morning, and less frequently at other times of the day when the male is singing. Slud (1964) reported that in Costa Rica single birds were less frequently observed than pairs or small groups. He did not specify dates of the observations or composition of the "small groups." Only in instances of apparent disturbance have I seen three adults together without overt aggression. In El Salvador, Dickey and van Rossem (1938) noted *A. rufescens* "in pairs throughout the year, each pair keeping to its own, usually very limited, grass-grown lava flow or brushy ravine." It is apparent that *A. rufescens* is territorial during breeding season and possibly territorial or very sedentary when not breeding.

Flight.—The usual flight of *A. rufescens* is very floppy with much tail pumping in the manner of a Song Sparrow (*Melospiza melodia*). Slud (1964) characterized the flight as of the "hedge hopping, twisting, fluttery type and of short duration." Most flights are short and unhurried; only a few flights that I witnessed were of more than 25 m.

Foraging and food.—From 45 records of the foraging position of individuals (each bird recorded only once per observation period), I found only nine (20%) in shrubs or trees rather than on the ground. Ground foraging usually occurs in relatively open areas of grass or herbaceous vegetation from 7 to over 30 cm tall. While on the ground the birds usually hop, but I saw them move through thick vegetation by short flights. In a tree they forage from leaf clump to leaf clump in the slow deliberate manner of a vireo.

A. P. Smith (1909) reported these birds scratching in the leaf litter of a deep, shaded, and secluded barranca near Cuernavaca, Morelos. I have seen similar motions that appear to be the same as used by towhees (*Pipilo*) (J. Davis 1957). There was little leaf litter where I made most of my observations, and the birds did not use this foraging technique frequently.

Eighteen stomachs, all from August and probably containing more animal material than is present at other times of the year, averaged 59.4% animal matter (range 30 to 90%).

AIMOPHILA NOTOSTICTA

Because the species is exceedingly scarce where it occurs, there is no published information on its habits, and my few field data are based on chance observations. The males that we collected and recorded on tape were scattered through the habitat, and they are apparently territorial during breeding season. Usually I saw a single bird at a time, but once called in a pair. The independent juvenile that I collected on 9 August 1963, was just beginning postjuvenal molt, suggesting that these birds may not stay in family groups for extended periods.

AIMOPHILA AESTIVALIS

Territoriality and pair bond.—Early in breeding season, paired birds are spaced in the habitat. Later, family groups become more common. Lowery (1955) mentioned that these sparrows occur singly and in pairs during the winter in Louisiana, which suggests that some individuals may be paired permanently.

Brooks (1938) reported 4 (perhaps 5) singing males in a field of about 12 acres in West Virginia. My own observations in eastern Texas suggested that the average territory size was about 180 by 45 m. In this area various natural and artificial boundaries produced elongated territories, but 8100 m^2 approximates the size of each of 4 territories.

The male actively proclaims his presence by singing from an elevated perch, usually most persistently in the early morning. I often heard neighboring males counter-singing, and they approached one another in such performances. A recorded song played in a territory usually stimulated the resident male to sing and approach the recorder. With birds so widely spaced in the habitat (which is rather closed at the low height of most activity) it appears that song and other vocal communication have become very important in the social organization of this species—probably more important than for the more southern species, which live in more open habitats and have smaller territories. This may explain, in part, the remarkable development of song in *A. aestivalis* in contrast to that in other species. It may also be reflected in the drab plumage of *A. aestivalis* compared to plumages of some southern forms.

Flight.—Although habitat is more open than those of several other species in the group, the power of flight does not seem to be any greater. The longest flights I recorded were of only 27 and 36 m. Flight is weak and floppy with pumping of the tail. Usually the line of flight is slightly undulating, because of the slightly irregular wing beat. Escape is usually by movement into a nearby clump of bushes or flying for a short distance.

Foraging and food.—Most birds that I watched foraged entirely on the ground. It was very rare to find a bird foraging above ground, although it is sometimes difficult to determine whether a bird is foraging when it is moving around in a shrub or the limbs of a tree. Brooks (1938) noted "the parent birds divided their time between the oak tree and the ground, feeding in both . . . ." Although the species is primarily a ground forager, Brooks' statement may indicate that some habitat, geographic, or seasonal variation exists.

Food brought to nestlings in Texas was insect material, usually orthopterans. The adults apparently take a range of food items. Meanley (1959) recorded weed seeds and beetles in stomach contents of birds taken in Louisiana in winter. He noted that a minor item of the diet was pine seeds. This suggests that the presence of pines as an indicator of suitable habitat is not because these trees are important as a food plant, but rather correlates with some other aspect of the environment. Sprunt and Chamberlain (1949) noted that birds in the southern states preferred insects but took some seeds. They did not give season of year or percentage values for the two food types. A. Martin *et al.* (1951) reported that the stomachs of 7 winter birds contained about 76% plant food, while 8 spring and 5 summer birds ate more than 80% insects—a marked change in the major food items for developing young and adults during the course of a year. Seven stomachs of adults collected in Texas in June 1964 contained an average of 68% animal (range = 10% to 100%) and 32% plant material.

AIMOPHILA BOTTERII

My only detailed observations were made on the salt grass prairies of the coastal strip of southeast Texas during early July 1964, when nesting was underway.

Territoriality and pair bond.—Observations at several nests showed no more than 2 birds at any nest, although the pair was often there together. I saw 4 birds together only once, and this was in response to a song playback at the boundary of several territories. The playback apparently attracted at least 2, and perhaps 3 males. After a short time with all 4 birds together, they separated and departed in three directions from this central point.

Singing males were spaced at about 70-to-92-m intervals. They sometimes approached closer, but normally did not approach the territory boundary at this time. The singing pattern of neighboring males often suggested that they were counter-singing.

Flight.—Most flights are jerky and pumping with a short wing stroke and the body level, the birds seemingly fluttering through the air. When a bird darts up from the grass or flies to another foraging site, flight is very jerky. The birds do make longer, more direct flights up to 90 m without any tail pumping, but still with short wing strokes. These longer flights are usually just above grass level and are common when adults are feeding young in a nest.

Foraging and food.—In this habitat it would have been nearly impossible for the sparrows to forage anywhere except on the ground as few trees and shrubs were present. Ground cover was so dense and tall that it was usually impossible to observe birds while they foraged. I presume that the birds spent most of their time foraging in corridors on the ground between clumps of salt grass. Since much of their foraging at this time was to feed young, I am not sure how it may have differed from winter foraging.

The birds always hop along the ground except when moving rapidly or crossing an open place, when they run. Slud (1964) reported them "progressing in small leaps and a hopping shuffle."

The only food items that I saw these birds catch were brought to the young and probably were not the same types as the adults ate. The young received various green orthopterans, green larvae, a green grasshopper, and several walking stick insects or items of similar shape. The stomachs of 10 birds taken at this time contained approximately 70% animal food (range = 10% to 100%) and 30% plant food. The main food items identified were beetles, orthopterans, lepidopteran larvae, and several types of seeds. A. Martin *et al.* (1951) reported that 19 birds taken during the summer had approximately 15% plant food; the differences are probably not important.

AIMOPHILA CASSINII

Territoriality and pair bond.—Within their preferred habitat, Cassin's Sparrows may occur in colonies. Migrant groups also are distributed locally even though other areas appear equally suitable. This probably reflects subtle habitat differences and a degree of sociability by the sparrows.

In a group of these birds, either on the late summer migration or on the breeding grounds, one finds singing males spaced at distances of 45 to 90 m or more. Early in the breeding season one finds pairs of birds and later family groups in mutually exclusive areas. *A. cassinii* probably is territorial during breeding season, and the basic units of social organization during breeding season are the pair and family groups. The species occurs in "flocks" during the nonbreeding season.

Male territorial proclamation is usually by a song flight or by a song given from a perch within his territory. The song flight is the most highly developed in the genus, and this is the only species in which the song flight plays a major role in territorial proclamation. Observations of an unmated bird late in breeding season suggest that this flight song performance also plays a major role in pair formation.

Perhaps the most striking feature of this species is the occurrence of a generally east-to-west migration of birds soon after the early summer breeding season (Phillips 1944). Migration also occurs southward, but the extent of this has not been as well documented. Migrating males have enlarged gonads and cloacal protuberances, indicating that they are reproductively active; I have not examined any to see if they were producing quantities of viable sperm. Generally only males are seen or collected during the summer migration, and the few females that are available from the critical periods have no gonadal data on the labels. The geographic origin and reproductive status of these males is not known. They may be males that did not mate during the breeding season and are migrating earlier than the remainder of the population, without undergoing gonadal regression. Birds on the breeding grounds at this time may still be raising their second broods. Much more study needs to be done on this aspect of the biology of *A. cassinii*, as it seems to be unique among North American sparrows, especially now that this species has been found to breed successfully after migrating (Ohmart 1966).

Flight.—Flights (not song flights) on the breeding grounds are usually not long in either distance or time. Occasionally birds fly up to 90 m, and many fly 15 to 25 m or more during flight song performances. Short flights are usually jerky with tail pumping, and the line of flight undulates slightly. Longer distance flights are less jerky, and may be free of pumping motions.

Food and foraging.—Foraging occurs entirely or almost entirely on the ground. The birds hop along the ground and usually stay in relatively bare areas. Most food is obtained directly from the ground with some coming from standing plant stems. The occurrence of various insect larvae in the diet indicates that some foraging is done in mesquite and other shrubs, especially for food for the young.

The only items that I saw taken during the latter part of breeding season were grasshoppers and lepidopteran larvae. Stomachs of 10 adults from the breeding grounds in late June and early July contained animal and vegetable material in about equal proportions (52 and 48%, respectively; range = 5% to 95%). Five migrants had about 99% animal material (range 90% to 100%). The stomach of a single January bird taken near Tucson, Arizona contained only seeds and grit.

AIMOPHILA QUINQUESTRIATA

This species is uncommon even in suitable habitat within its range and in collections. The little published information refers primarily to habitats and is included in a previous section. I obtained some information in 1963 in an area about 125 km east of Hermosillo, Sonora and 32 km east of the village of Mazatán. This region is in the foothills of the Sierra Madre Occidental, but still has arid vegetation reminiscent of the Pacific coastal plains. We spent several days there in mid-July 1963, and the morning of 26 August 1964.

Territoriality and pair bond.—In July, these birds were spaced in pairs throughout the habitat, and the males sang from elevated perches during portions of the day, especially in the early morning. The males had preferred song perches that were separated by as much as 20 m or more from the next singing male.

I often saw two birds foraging together and assumed that they were mated. Apparently this species maintains a pair bond during the breeding season, but the duration of the pair bond is not known. In August, pairs were accompanying young of the year that foraged independently.

Foraging and food.—In several days of observation during the early stages of the breeding cycle in mid-July, I never saw a foraging bird move high into the 5–6-m-tall trees that are common in this habitat. The majority of foraging occurred on or within a few feet of the ground, usually in open places, including rocky outcrops along the side of a small hill, under closed tree canopy vegetation, and in various small piles of dead shrubs and tree branches. These were not grown up in dense herb layer vegetation and hence were easy to move through. Movement over the ground or along branches was by hopping.

Birds foraging on the ground usually focused their attention on the ground or the sparse, short vegetation nearby. Movement along the ground was slow; several timed and measured foraging distances averaged 2 to 3 m per minute. Occasionally birds alternated foraging between the ground and the lower shrub or small tree layer; usually this involved more time above than on the ground. In woody vegetation, the birds foraged like vireos. They hopped slowly through the vegetation by moving to a perch and looking around at the foliage in the immediate vicinity, and then either pecking at prey or moving to another perch a short distance away.

The only food items I saw captured were lepidopteran larvae and one small moth. The stomachs of 20 adults taken 32 km east of Mazatán, Sonora in July 1963 and on 1 September 1964 contained an average of 66% animal material (range = 0 to 100%) and 34% vegetable material. The predominant animal foods were Orthoptera, larvae of Lepidoptera, and a few ants. Lepidopteran larvae were most abundant; they were in 8 of 9 stomachs collected on 13 July but were in only 2 of 11 stomachs collected on 1 September. In September, 11 stomachs averaged about 40% animal matter, mostly in 3 birds. Seeds were much more common in the diet in September than in July.

VOCALIZATIONS

The importance of voice in bird species recognition and its use in taxonomy has been appreciated for some time (Marler 1957, Stein 1958, Johnson 1963). However, its application to studies of generic classification has been limited (e.g. Thorpe and Lade 1961), and there have been few detailed studies of voice in large genera to judge its taxonomic value (see for example Selander 1964).

In studies of most fringillids, song has played a minor role in outlining relationships. In regard to *Aimophila* Pitelka (1951a) commented on the similarity of the song of *A. carpalis* and that of members of the genus *Spizella*, and Storer (1955) mentioned vocalizations in his discussion of relationships within *Aimophila.* Most recently, Borror (1971) used song to analyze relationships in the United States species. Finally, Marshall (1964) commented on possible relationships between *Aimophila* and the Brown Towhee group (*Pipilo* spp.) as suggested by voices.

In discussing vocalizations, one faces a problem of terminology. Sophisticated studies in this field for the most part have been conducted only recently. As a consequence some dissimilarity in terminology used by various workers still exists. For this report the types of vocalizations will be divided primarily on the bases of their supposed function and internal complexity. Following Lister (1953) singing is subdivided into primary and secondary song, and I have lumped the remaining sounds, mostly shorter calls, under the category "other vocalizations."

Further definitions, except for "figure" rest primarily on quantitative characters of the vocalizations. Figure is defined as a continuous tracing on the sound spectrograph; the term note is avoided, because of its established meaning of a sound of constant pitch. I follow Mulligan's (1963) definition of whistle and vibrato. Without presenting any quantitative data for *Aimophila*, I follow the definitions of Isaac and Marler (1963) for syllable and song. A song bout is used here to mean a sequence of songs preceded and followed by silent periods much longer than between songs within a sequence. Duetting "refers to the simultaneous singing of two individuals" (Selander 1964).

I have no information on the inheritance of vocalizations in *Aimophila*; this information is important in assessing value of sounds in solving taxonomic problems (Löhrl 1963). Without this information, I assume that some portion of the characteristic of the song is inherited and hence subject to change via changes in the genetic character of the individuals.

The primary songs of *Aimophila* sparrows conform to those of many temperate zone fringillids, apparently functioning to proclaim territories and warn away other males. Under secondary songs I include what I have already termed "chatter calls." These are present in many species of *Aimophila* and are frequently given as a duet between members of a pair or between adjacent pairs. These duets appear to reinforce territorial boundaries or pair bonds and are homologous to the pair reunion ceremony of the Brown Towhee group (Marshall 1964). In species such as the members of the *Haemophila* group, duet or chatter call is at least as conspicuous as primary song in the vocal repertoire. In fact, in disturbance situations—such as caused by the presence of humans—the chatter calls are characteristic, and this has led to their being identified more or less as primary songs (e.g. Edwards 1972, L. E. Davis 1972, Peterson and Chalif 1973). This misconception is perhaps understandable, but nonetheless it is an error and should be redressed as the following will show. In *A. ruficauda* and *A. sumichrasti* there is a kind of intergradation between chatter and primary songs, but in other species these remain distinct.

The sound recording published as a supplement to this monograph will aid the reader in understanding terminology and descriptive accounts given of the voices in the following pages.

AIMOPHILA RUFICAUDA

Primary song.—At least two types of songs are given from exposed perches, in loud performances by single males; one type of song often induces neighboring males to sing. *Pechew* song.—This involves an introduction and a "trill" of syllables sounding like *pechew* (Plate 3) and was heard only from *A. r. acuminata.* Near La Huerta, Jalisco in July 1963, there were at least 2 recognizable introductions to this song, composed of 1

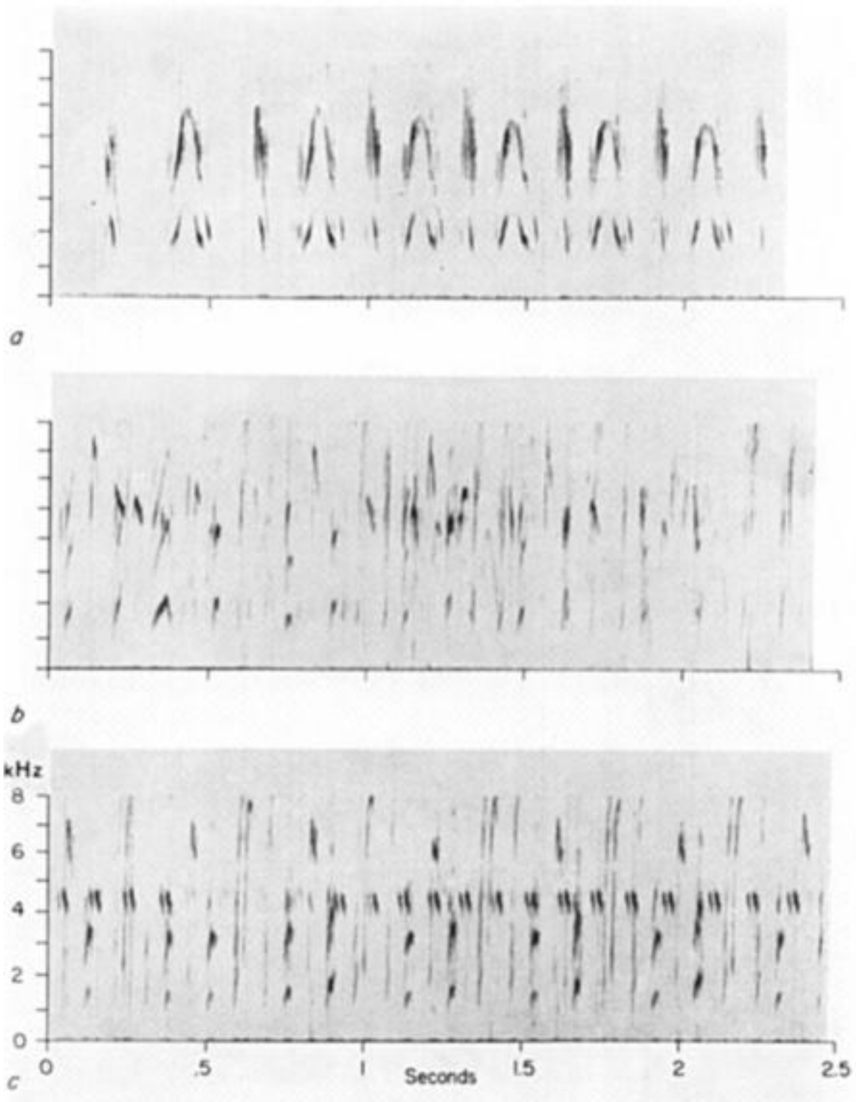

Plate 3. Vocalizations of *A. ruficauda.* (a). *Pechew* song of *r. acuminata*; recorded 10 km southwest of La Huerta, Jalisco on 25 July 1963. (b) Solo chatter of *r. lawrencii*; recorded 7 km east of Tehuantepec, Oaxaca on 22 August 1964. (c) Chatter duet of *r. lawrencii*, recorded 7 km east of Tehuantepec, Oaxaca on 17 August 1963.

or 2 different syllables. One male began singing one type of song and switched to the second when another male began singing the second type. Singing was most common in the early morning. Birds near Cuernavaca, Morelos in July 1964 gave a much simpler song without an introduction and seldom of more than six *pechew* figures. The song was heard less frequently and not at all as a dawn performance. Differences in song may relate to breeding status of individuals in each population. At Cuernavaca, breeding had commenced up to six weeks earlier, and most pairs undoubtedly were formed and probably had bred or were in the process of breeding. At La Huerta, breeding had not started, and possibly some males were unmated. I did not hear this song from *A. ruficauda* around Tehuantepec (*A. r. lawrencii*) in August or in Costa Rica (*A. r. ruficauda*) in July, and I found no published references to such a song for either of these populations. This may reflect lack of study at the right time of year.

The second type of song (Plate 3) sounds like the male contribution to a chatter duet. Around Tehuantepec it is given by lone males from exposed perches. I did not hear *A. r. acuminata* sing in such a manner. From the latter form I occasionally heard what sounded like solo chatters, but these came from a group of at least two birds and it was impossible to tell whether only one bird contributed. Song and chatter of *A. r. acuminata* are so different that I doubt if further analysis will show the *pechew* song to be the same at solo chatter, if the latter vocalization actually occurs in this form. That this solo chatter is the only song heard in Tehuantepec probably results from my being too late in the breeding season for any pairing songs, and/or the possibility of the other song type being reduced in, or absent from, the repertoire of *A. r. lawrencii.* I am uncertain why *A. r. acuminata* apparently does not give the solo chatter.

Secondary song.—Included in this category is the very prominent and frequent chatter call. This vocalization is given either as a solo or duet performance within the limitations noted above. Storer (1955) twice mentioned the chattering song of *A. r. acuminata*, apparently referring to this reunion duet. He said it was frequently given in duets and choruses. In my experience this is the most common vocalization of *A. r. acuminata*, but less common than the solo chatter in *A. r. lawrencii.* It is often given as a counter-vocalization between two pairs occupying adjacent territories. When a bird intrudes into a territory, there is usually a bout of chattering, apparently often including the intruder. The intruder then returns to its territory uttering a subsequent chatter with its mate. When a pair enters a neighboring territory there is a series of chatter duets as the pairs approach each other. It seems clear that the chatter duet is a ritualized form of territorial defense and proclamation. Less commonly than in an obviously announcing or defending situation, two members of a pair chatter when

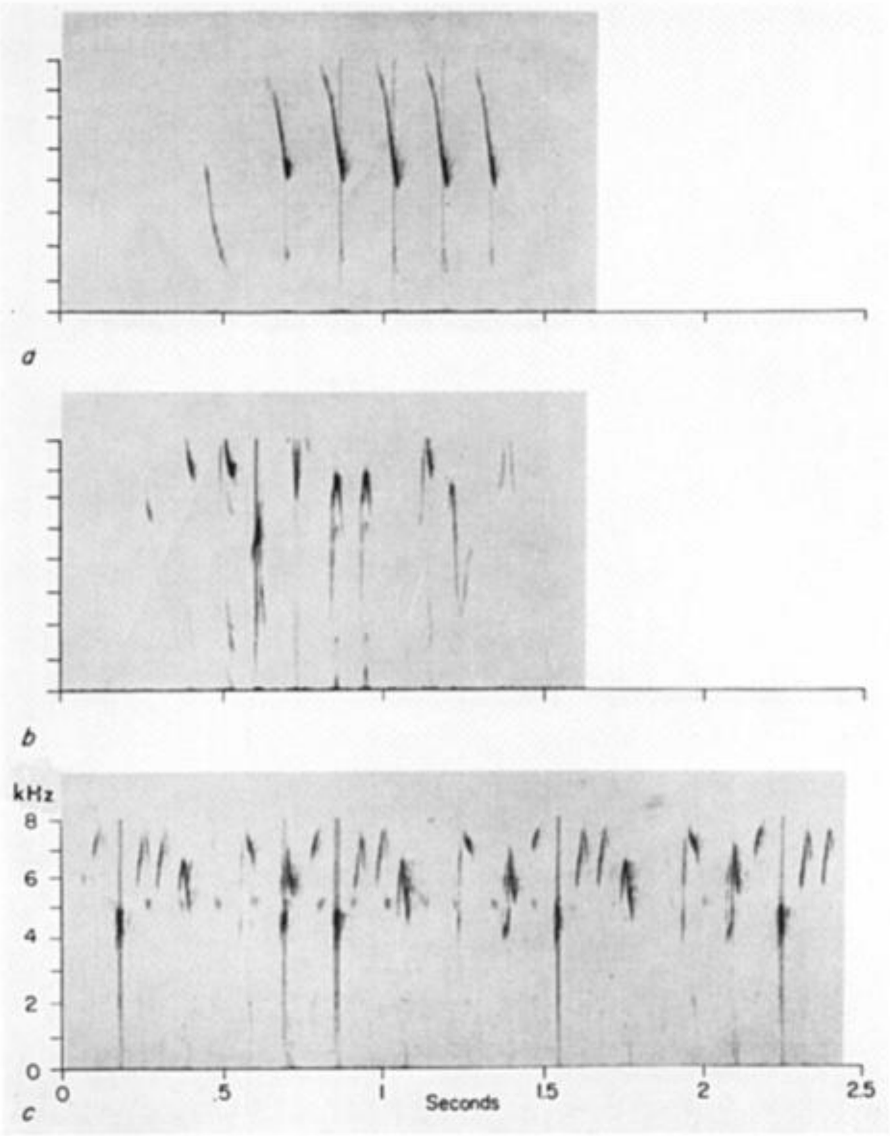

PLATE 4. Vocalizations of *A. sumichrasti*. (a) Simple song; recorded 7 km east of Tehuantepec, Oaxaca on 23 August 1964. (b) Chatter song; recorded 7 km east of Tehuantepec, Oaxaca on 23 August 1964. (c) Chatter duet; recorded 7 km east of Tehuantepec, Oaxaca on 23 August 1964.

they come together after being separated for a period of time. This is the pair reunion situation for the chatter and apparently serves to maintain the pair bond.

Visually (Plate 3) and aurally chatter seems to be fabricated of different contributions by each sex. I assume that the most elaborate portion is given by the male, but so far I have been unable to collect a bird that was known to be giving this component. The material available shows that one bird (male?) produces short phrases of several syllables that may or may not be repeated immediately. Changes between phrases do not seem to be of much magnitude. The other bird (female?) gives a series of identical syllables producing a trill-like sound. The utterances of the two sexes are not synchronized.

Other vocalizations.—*Chip.*—This call is given in alarm situations when motivation is low. It has been heard during bouts of preening and infrequently with *chup* calls. *Chup.*—This is an alarm call given in high motivational states. It is often given in a long series, especially when the observer is around a nest. *Chee-up.*—This may be a variation of *chip.* It was heard during bouts of preening. *Tzeet.*—This call is given very softly during bouts of preening. It may be a pair communication call. If so, it is uncommon and was not heard while members of a pair were foraging.

AIMOPHILA SUMICHRASTI

Primary song.—Two distinct types of primary song are given by this species: a simple song and a chatter song. The simple song (Plate 4) is composed of various combinations of introductory figures followed by a trill of 4 to 7 (rarely more) figures and lasts from 1 to 2 seconds. An actively singing male gives approximately 10 of these songs per minute. The trill component is a series of simple, downward-inflected, abrupt figures. Generally these figures span more than 1000 cycles per second, but one song was recorded in which the frequency range of the trill figures was constructed, while the length was greater than usual. The figures are identical within a trill phrase, thus setting apart the trill from the introduction by both type and repetition of figures. The introductory portion of the song varies from 1 to 5 figures. Except when it is a single note, the introduction contains one or more whistle-like notes. Introductions of 4 or more notes had 2 consecutive notes that were identical and shorter, but they covered a broader frequency range than the other introductory notes.

The chatter song is a variable array of figures, all rather short (Plate 4). No figure is repeated more than twice, and once used it is not repeated in the same chatter. Eight consecutive chatter songs from a much longer sequence delivered by a single individual showed the same figure pattern and differed only in number of figures in a given chatter. A chatter of another individual did not share any figures with the first. The chatter ranges from 1½ to more than 2 seconds long; an actively singing male gives about 8 chatter songs per minute.

The chatter song may communicate more than territorial and sexual information. It is often given during disturbances, as when a gun is fired or a truck passes along a nearby road. While trill song is normally given from an elevated, exposed perch, chatter song may also be given from on or near the ground. It was given once in flight as the bird changed perches while a truck was passing. Undoubtedly, this is the "sprightly tinkling song" that Amadon and Eckelberry (1955) heard along the Pan American Highway near Tehuantepec, Oaxaca.

Amadon and Eckelberry (*op. cit.*) also mention seeing "two birds . . . perched close together and singing a 'whisper song' in duet." I have heard one duet whisper song, but solo whisper songs, presumably by the male, are not uncommon. Both the trill and chatter are given as whisper songs, but I heard no special whisper song. In all instances except one, whisper songs were delivered by the male in association either with a female known to be actively nest building or a female that was collecting nesting material. The single exception was a male (sex verified by dissection) of a pair that was attracted to noises made by the observer. After 5 to 7 repetitions the bird flew off 3 m and gave a song of normal volume. The whisper songs undoubtedly function as communication between a mated pair. The reduced volume is probably related to its delivery in potentially dangerous situations. Full-volume songs are also given at this time.

Secondary song.—When two members of a pair come together after being separated, a duet chatter performance often follows. Both in the field and when physically reproduced it seems that one bird (presumably the male) gives a rapid version of the chatter song or something very similar; however, I do not have recordings of the chatter song and the male portion of a chatter duet from a single male to confirm this. The second bird (female?) makes a trill, usually a single note rapidly repeated (Plate 4).

This duet performance usually occurs in a pair reunion situation and probably serves to maintain the pair bond. Once I heard a chatter duet from 2 birds 3 to 3.5 m apart, one on either side of me. A minute later, I heard a softer version of the chatter from this same pair. Except for the distance separating the two birds, this was probably the whisper song in duet referred to by Amadon and Eckelberry (*op. cit.*).

Rapid succession of duets from different pairs of birds suggests that this performance functions also in territorial advertisement. On 14 August 1963 I watched and listened to 3 pairs apparently chattering in response to one another; the pairs were spaced at 9-to-11-m intervals along a linear clearing for an electric line. When a 4th pair called from across the clearing, 1 pair of the 3 flew in that direction. Later the same day three spaced pairs were chattering one after the other in such a way that I noted they were answering one another. Since these pairs were also spaced, it was obviously not a reunion performance of more than two birds from adjacent territories. Furthermore, the two members of the pair were already together and the chatter was not always preceded by flight to a new perch as is the case in a pair reunion performance. I could detect no obvious differences in vocalizations in the two situations.

Also on 14 August near Tehuantepec, I watched two presumed males in adjacent territories. One began singing, followed shortly by the second; they then approached each other and finally came together in the top of a nearby tree and sang. While singing, both males stretched slightly and sleeked the body plumage; following this both males chattered. They were joined shortly by a third bird and all flew off. Soon after, the first bird was back on his territory and singing. The chatter here was probably a territorial defense vocalization.

Other vocalizations.—Tzee (*chip*).—This is the note given by either member of a pair while foraging and serves to maintain contact between adults. It is sharper than the corresponding call of *A. carpalis* and *A. ruficeps*. *Chip.*—This is a sharp, short alarm call given by the female after she has flushed from a nest. While watching a female gradually work back to her nest, I noted that the repetition rate of the *chips* often increased sufficiently to be classed almost as a trill. This may represent a high level of stimulation. Following a preening bout a female uttered a *tee, tee, tee* call that probably was three shortened *Tzee* calls.

AIMOPHILA HUMERALIS

Primary song.—The song is an introductory figure or phrase followed by a trill of varying length (Plate 5). Usually the trill and introductory notes are different. Although I heard no other type of primary song, Zimmerman and Harry (1951), Sutton (1952), and Storer (1955) all mention that the song is often performed in duet. The description by these authors leaves no doubt that they were referring to the "chatter duet" that is described below. At no time in the course of my field work did I hear the primary song given as a duet.

In Morelos in July 1964 at dawn on several days, the first vocalizations of *A. humeralis* were the primary songs from single birds spaced through the habitat. Shortly after sunrise, chatter duets gradually became the dominant vocalization. During the day occasional birds gave one or more primary songs in sequence or uttered widely spaced repetitions of the introductory

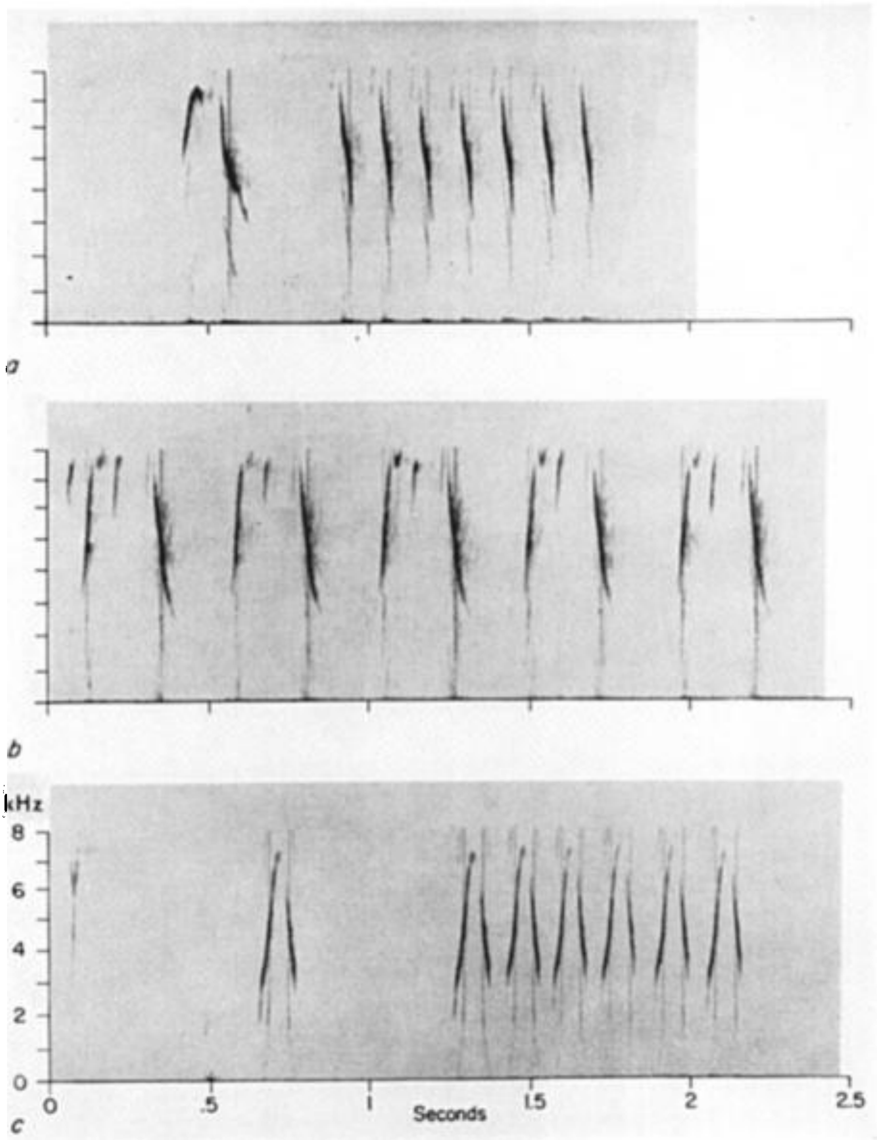

PLATE 5. Primary song (a) and chatter duet (b) of *A. humeralis*; both recorded 11 km south of Piaxtla, Puebla on 8 August 1963. Primary song (c) of *A. mystacalis*; recorded at km 616 on Pan American Highway southwest of Oaxaca City on 17 August 1964.

figure. When the birds are paired or nesting, the song may be less common than earlier in the year during pair formation. A male, possibly unmated, sang for more than 5 minutes at 1145 on 9 August. This was the longest song bout after the dawn chorus that I heard during the breeding season.

Secondary song.—The only secondary song is what I call the chatter duet (Plate 5), but which other authors have considered to be the song. In the full performance of the chatter duet each sex produces a different syllable or phrase that is constant for each sex throughout any performance. Since the duetting pairs are bisexual, I think the more variable portion, at least as recorded in Morelos, belongs to the male. This phrase is repeated while the female produces a softer, thinner trill. In a recording from Puebla, both birds trilled, one upward-inflected and the other downward-inflected.

Other vocalizations.—*Pit-za.*—This is a common call and sounds similar to the contribution of some males to the chatter duet. Physically this call and the chatter duet, which the *pit-za* often precedes, are similar enough that one may be derived from the other. Sometimes it is given in flight as one bird approaches its mate and is followed by a chatter when the flying bird lands. It probably occurs in alarm situations of high-to-medium intensity. Soft trill and *chip* followed by a trill.—Both are given in alarm situations. The *chip* was also probably a reaction to my presence. The *chip*-trill was also heard after *pit-za* calls, suggesting a relationship to the *pit-za* call on a motivational continuum of alarm calls. The *chip*-trill occurs in low motivation situations. I grouped these two calls together because the soft trill is very likely a *chip*-trill given at reduced volume such that I did not hear the introductory *chip*; the *chip* may not be given in low volume calls. *Tzeet* and *Chip* calls.—These, given while foraging, undoubtedly function as pair communication calls. The *tzeet* sounds thinner and more drawn out than the various types of *chip* calls. Probably the two types are physically different, but I did not obtain recordings of either. *Tzeet.*—Fledglings produce a higher, thinner version of this pair communication call.

AIMOPHILA MYSTACALIS

Primary song.—Almost all songs of this species are preceded by a short, high *tzit.* The remainder of the song consists of one or more different syllables arranged as a single figure or syllable followed by a short pause and a trill (Plate 5). The first syllable may be the same as the trill syllables or, if different, is usually a whistle. The trill is a series of rapidly repeated syllables of downward- and upward-inflected figures that sound like a series of *chip* calls.

In marked contrast to *A. ruficauda* and *A. humeralis,* the commoner song of *A. mystacalis* is the primary song which is heard at all times of day, but

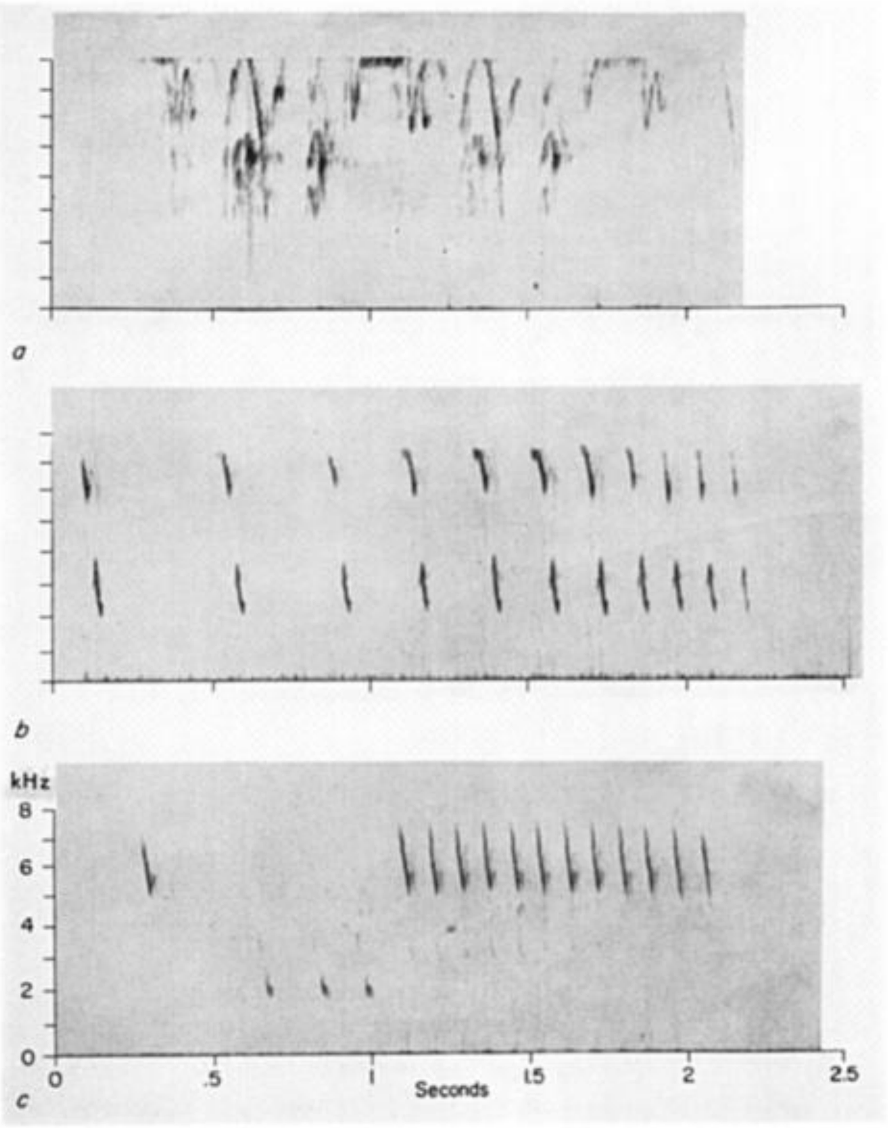

PLATE 6. Chatter duet (a) of *A. mystacalis*; recorded at km 616 on Pan American Highway southeast of Oaxaca City on 17 August 1964. Two types of primary song of *A. carpalis*: (b) the wrentit song; recorded at Tucson, Arizona on 25 June 1963 by John P. Hubbard; (c) a type 4 song; recorded 29 km north of El Oasis, Sonora on 16 July 1963.

more frequently in the morning. The chatter is much less frequent but occurs throughout the day. The primary song is given in sustained bouts by males from exposed perches. All or most birds that gave this song were paired and the female was usually nearby. It apparently serves for territorial proclamation in addition to sex recognition and probably mate attraction.

Secondary song.—*A. mystacalis* has a chatter duet (Plate 6) which is similar to the duets of *A. sumichrasti, A. ruficauda,* and *A. humeralis.* Each member of a duetting pair (probably a male and female) produces a different sound. The presumed male gives a 3- or 4-figure sequence rendered *pe, pe, chee* while the female gives a 3-figure trill sequence. The chatter of *A. mystacalis* differs from that of *A. sumichrasti* and *A. humeralis* in being composed of repeated sequences, apparently not synchronized by the two birds, while the other species have a continuous, nonsequential pattern.

The chatter of *A. mystacalis* apparently occurs only when two birds come together after a change of position or after being separated during normal activity. Even when two pairs are counter-chattering, each pair flies a short distance before starting a second chatter. The frequency of chattering in response to chatter from adjacent pairs suggests a territorial function for the call. Often the initial flight before a chatter will take the pair toward the territorial boundary beyond which the adjacent pair is calling. I did not see neighboring pairs come closer together than 6 to 9 m during these duets, and no interpair chases were observed. While primary song probably functions in territorial proclamation, chatter apparently serves both as a proclamation and as an active confrontation, in addition to pair reinforcement.

Other vocalizations.—*Tzeet.*—This is a pair communication call that sounds very similar to that of *A. carpalis. Chip.*—The *chip* is a sharper call given in my presence and is undoubtedly an alarm call. *Tzee.*—This call is a thinner version of the adult *tzeet* given by young birds. *Chitter* series.—This is probably a series of softer, thinner *chip* calls. It was occasionally heard from adults while I watched them caring for well-grown young. *Chu, chut,* and *tut.*—The first two calls are given, usually in series, by the female. *Tut* is a similar but shorter call given by the male. The two are probably homologous, but their function is unknown. A female will call, usually from an exposed perch, while a male is singing, but soon drops back to the ground. *Check.*—This call was given by a male as it flew along the slope of a hill. Its relationship to the other calls is not known.

AIMOPHILA CARPALIS

Primary song.—Four recognizable song types were recorded from singing males. All were heard 29 km north of El Oasis, and near Ciudad

Obregón, Sonora. Around Tucson, Arizona and in northern Sinaloa only 3 of the 4 were heard. While there may be statistical differences in frequency of the four types over the range of *A. carpalis,* most are represented throughout the range. The fourth song type is relatively uncommon and was heard from only two or three males. The other 3 types were all common; often all 3 types can be heard within a 5-minute period. Several males observed for extended periods sang 2 song types, and 1 male sang 3. All three song types heard around Tucson during the breeding season were heard also in the same locality in December and January.

While these primary or advertising songs are usually given by males from elevated, exposed perches, P. J. Gould (MS) reported that after a chase that ended in an aerial fight "a second chase followed during which the aggressor sang a full song while in flight." This and Bendire's (1882) report of birds singing "while hovering a few feet in the air" are the only records of which I am aware of songs given in flight by *A. carpalis.*

The 4 types of advertising song heard are as follows: (1) The "wrentit" type.—This is a series of short similar figures (Plate 6). It begins with figures widely enough separated in time to be called individual syllables. With each succeeding call the interval between them decreases until a short enough interval is reached to produce a trill effect. The interval between separate figures of the trill is maintained essentially constant. (Here I disagree slightly with the definition given by Mulligan (1963) in that I would reserve the term trill for a repeated series of figures or syllables with a constant or nearly constant interval between syllables.) This song type was normally given at the rate of 7 to 10 songs per minute. This is Borror's (1971) type 1 song, which he likened to the song of the Field Sparrow (*Spizella pusilla*). (2) One to three, usually distinct, introductory notes followed by a trill.—This is the song type described by Anderson (1965). Variations, in addition to changing the number of introductory notes, are one of the following types: (a) Introductory figures on the same pitch as the trill (this variation differs from song type 1 only in having 2 distinct figures followed by a trill while type 1 is a series of distinct notes gradually becoming a trill); (b) introductory figures on the same pitch, which is different from that of the trill; (c) introductory figures on different pitches. (3) The third song type, which I call the "drink your tea" song because of its resemblance to the song of the eastern form of the Rufous-sided Towhee (*Pipilo erythrophthalmus*), consists of an introductory figure followed by a whistle, which in turn is followed by a trill and perhaps the *chip, chip, whecoo* variation described by Anderson (*op. cit.*). While the whistled call sounds to me as if the pitch varies, sonagrams show that it is essentially of constant pitch. Variations include: (a) Reversing the order of the introductory figures; (b) introductory figures followed by a *chink* call. The latter variation was given several times by a single male on 25 June near the end of a bout of song activity of approximately three minutes. This song is usually given at a rate of 10 to 12 per minute. Borror (1971) also likens this song to that of the Rufous-sided Towhee, and he called it type II. (4) The fourth and least common of the four types is another simple song. It begins with a short introductory figure followed by three figures on a lower pitch and finally a trill on the pitch of the introductory figures (Plate 6). I did not hear this song frequently and noted no obvious variations. It was given at a rate of 10 to 13 songs per minute.

Secondary song.—(1) Whisper song.—On 24 June an adult (sex?) flew to an exposed perch 1 to 1.5 m above the ground and commenced preening. During the pauses in preening activity this bird gave faint trills, but although I was reasonably close, I am uncertain whether there were accompanying introductory calls. This was the only instance of a possible whisper song that I recorded. (2) Subsong (here used in the sense of practice song).—This may correspond to the juvenile song of Brown Towhees (Marshall 1964), but I am not sure of the age of the singer in *A. carpalis.* I have only one record—this from a bird (sex?) foraging on the ground at 1100 about 2.5 m from me on 26 January near Tucson, Arizona. My field notes describe this song as "a warbly and variable version of the drink your tea song." The warbled pattern and pitch varied, but the song was always classed as a "drink your tea" type. (3) Duet (warbled song).—While this, on the basis of volume, belongs with the primary song I hesitate to place it there as that category also implies a rather narrow function of the vocalization. Hubbard (MS) describes a duet performance of this song as follows: The male begins with a series of alternating higher and lower notes and the female joins in with a high-pitched trill. At other times the male may give his portion of the performance alone; such solo performances have been heard both with the female present and absent. In general, this performance seems to occur in a pair reunion situation. A lone male giving the warble is usually joined in a short time by a second bird, a female in the instances in which the birds were collected. It may occur also in a territorial encounter between neighboring pairs. Anderson (*op. cit.*) reported that a fledgling flew immediatey to an adult that had just given a "brief warble."

Other vocalizations.—The location call of *A. carpalis* is a high, thin *tzeet.* This is apparently the alarm call mentioned by Pitelka (1951a). I agree with Pitelka that its figure is very similar to the location call of *Spizella.* However, I was able to identify these calls as given by either *A. carpalis* or *S. breweri* after listening to both for part of a day. A similar call in *Zonotrichia leucophrys* is less sharp, but also very similar.

Several other vocalizations are given by *A. carpalis* that are not properly discussed with those above or for which I am uncertain of function, frequency of occurrence, or context.

The first primary song type has been rendered as *tzlip, tzlip, trill.* Especially in winter and occasionally in early summer, birds give one or more *tzlip* calls without ending in a trill. These calls undoubtedly represent incomplete songs reflecting a low motivational state. Sometimes the series of *tzlip* figures extends to five or more with no trill. This suggests that the introductory ones are given during periods of low motivation, but that the trill threshold is high. Thus, birds with an intermediate motivational level might produce extended series of introductory notes.

The *tzlip* and *tzeet* calls may be on a contextual and physical continuum. Occasionally in alarm situations I heard calls that sounded intermediate between the two types. Marshall (1964) noted that Brown Towhees have two distinct location calls that are physically different. The second figure, when more intense, signifies alarm. The few times I heard a sharper *tzit* note from *A. carpalis* were also in alarm situations.

Another vocalization, usually composed of a rapid succession of *tzeep* calls, sounds similar to a chatter series given by Brown Towhees. I heard this only once and am not sure of the behavioral context.

AIMOPHILA RUFICEPS

Primary song.—Primary song of *A. ruficeps* is usually delivered from an exposed perch, but the same song may also be given from the ground while the male is foraging. Miller (1955) reported that a male sang in flight over a canyon. An actively singing male delivers 7 to 10 songs per minute.

The song is a series of 5 to 11 syllables, each of which may be repeated up to 6 times (Plate 7). In an 11-syllable song, 5 syllables were given only once and 1 was repeated 6 times. Several songs contained a trill sequence either at or near the end of the song (Plate 7). A 5-syllable song ended in a long, 16-note trill. Occasionally the song followed a series of *chur, chur* calls. The songs analyzed gave no indication of significant differences among the three populations studied from California, Arizona, and New Mexico. A male singing continuously may repeat the same song one or more times before switching to another song type. While the same syllables may be repeated in a song there are often slight modifications in length of song, number of different syllables included, and number of times a syllable is repeated.

Secondary song.—Soft versions of complete primary songs are sometimes given by the male while a pair is foraging on the ground. This may serve for pair bond reinforcement and/or intrapair communication as the volume is not sufficient for territorial proclamation.

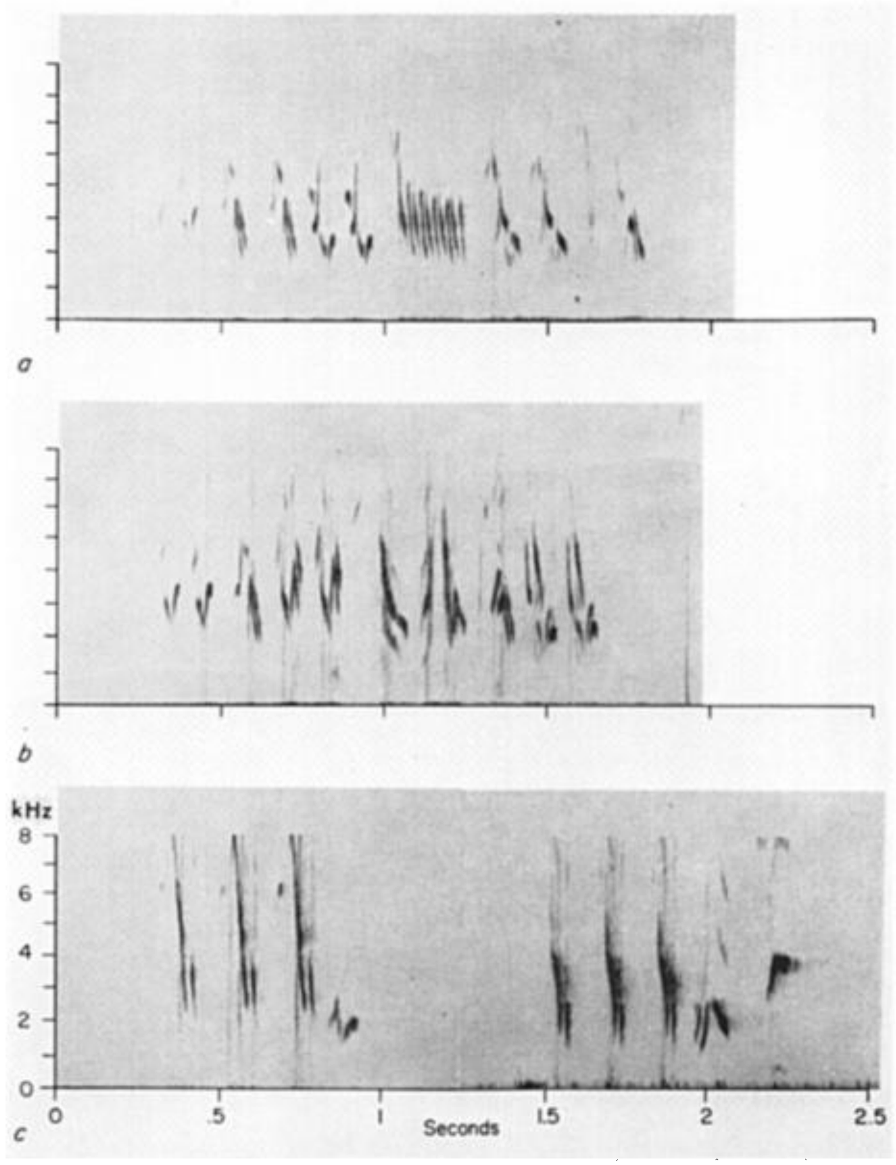

PLATE 7. Trill (a) and nontrill (b) songs of a single male of *A. ruficeps*; recorded on 14 June 1964 at Bear Creek Campground, Santa Catalina Mountains, Pima County, Arizona. Two primary songs (c) of *A. rufescens*; recorded 8 km east of Cuernavaca, Morelos on 4 August 1964.

Marshall (1964) reported a pair reunion duet for this species. I have heard a warbling call, which may have been the duet, given as two birds flew up onto adjacent fence posts. In another case the same call was followed by a *dear, dear* call. J. Tramantano and M. Manns (pers. comm.) both reported the occurrence of pair duet by *A. ruficeps* from near Tucson, Arizona and Mt. Diablo, California, respectively. Willard (1912), presumably referring to the squeal duet, reported that during chases *A. r. scotti* gave a chattering call similar to that of the Brown Towhee. The duet is apparently not a common call in *A. ruficeps*, but may function in the same fashion as a pair reunion call reported for other species of *Aimophila.* Hubbard (MS) heard a chattering call suggesting "half" a duet from an adult near Silver City, New Mexico when the bird was disturbed by a dog in an area harboring a fledgling.

Other vocalizations.—The most characteristic call of *A. ruficeps* is the alarm call, *dear, dear.* Sometimes this is followed by a long chatter of a minute or more in duration. It is given in flight, while the bird is perched, and often as it flushes from the grass. This call carries farthest and probably has carrying power nearly equal to that of primary song. A somewhat musical rattle followed by the *dear, dear* call was given during a chase right after the second bird was joined by a third. Similar "twitterings" were heard at the end of a *dear, dear* call after the bird landed. These may have represented the pair reunion duet of *A. ruficeps.*

Another alarm call is an upward-slurred *tzit* that is harsher in quality than the *tzeet.* The call may be given either while the bird is foraging or perched. Occasionally it is followed by a similar call from a second bird—probably the other member of the pair. Once I heard an almost continuous version of this call after a second bird flew into a nearby bush and gave the *dear, dear* call followed by a long chatter.

AIMOPHILA RUFESCENS

Primary song.—This is normally given in sequences of several to many songs by males singing from exposed positions. Physically the song consists of 3 to 5, rarely 6 syllables in rapid sequence with about the same interval separating the syllables (Plate 7); occasionally one figure is set off as an introduction. The number of different syllables ranges from one to three. A distinct note may precede a sequence of 2 to 3 identical notes, which in turn is followed by 1 or 2 syllables or figures, each of which is distinct from any previous ones. One peculiar song transcribed near Cuernavaca, Morelos consisted of 3 individually distinct syllables followed by a sequence of 3 identical figures. An actively singing bird in August gave 12 to 15 songs per minute.

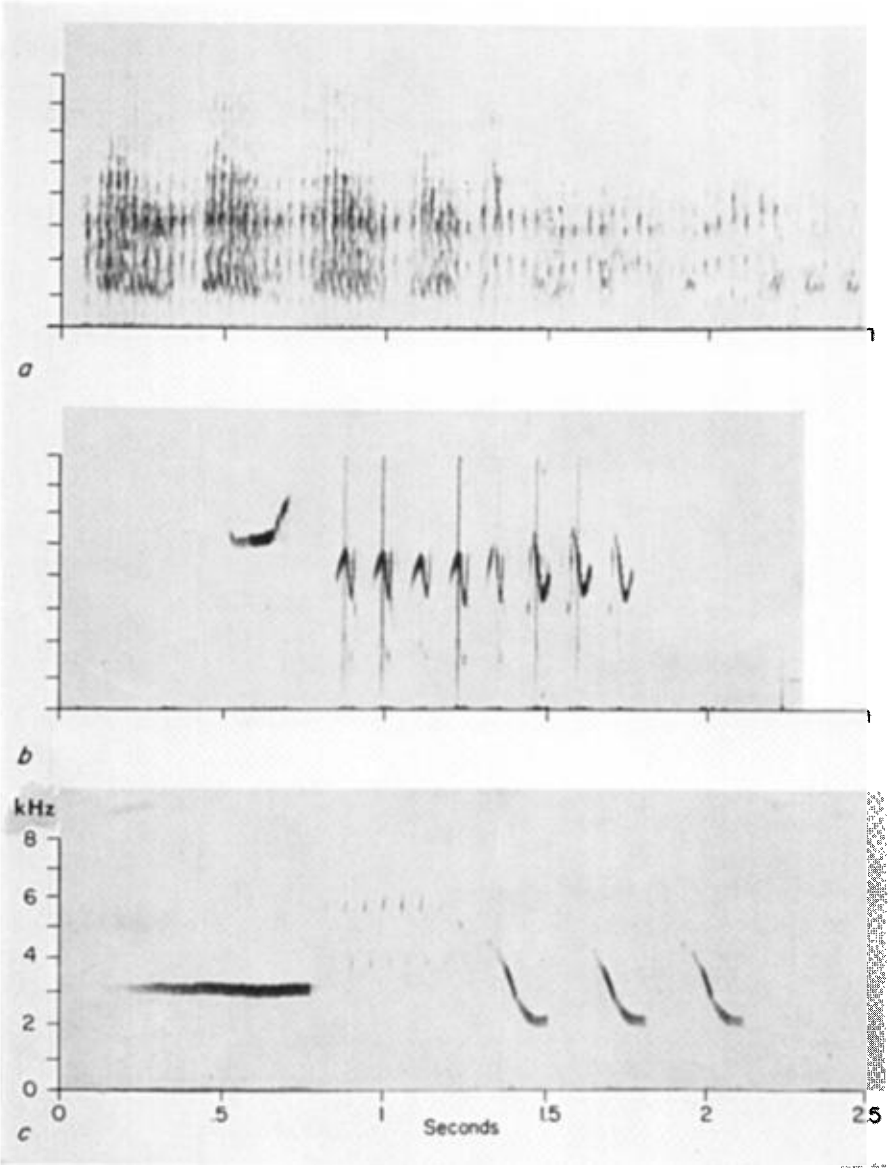

PLATE 8. Chatter or squeal duet (a) of *A. rufescens*; recorded 8 km east of Cuernavaca, Morelos on 4 August 1964. Primary song (b) of a male *A. notosticta*; recorded 7 km southeast of Matatlán, Oaxaca, on 10 August 1963 by John P. Hubbard. One song type (c) of a male *A. aestivalis*; recorded 2 km south of Boykin Springs, Angelina National Forest, Jasper County, Texas on 18 June 1964.

Near Guadalajara, Jalisco, in July 1963, two adjacent males sang continuously for 5 to 7 minutes, each singing a distinct song type. The two songs were similar in that each had an introductory syllable followed by three identical trill figures, which differed between the two birds, followed by a third figure much different and lower in pitch. This stereotypy of a unique song allowed easy individual recognition. Near Cuernavaca, Morelos during August 1964, the birds generally gave at least two song types in a bout of singing, usually alternating types. It sounded to me as if several birds had the same pattern of song, but probably the syllables differed. While the song is most often given from elevated perches, these may be just above the ground. Usually song bouts delivered from a low perch were of short duration between periods of feeding activity. Often a foraging male sings from the ground or moves onto a nearby low shrub, weed stalk, or pile of brush.

Flight songs of constant form, repeatedly performed in a particular fashion, are not known for *A. rufescens.* Twice birds (undoubtedly males) sang during chases or after disputes. After a territorial dispute the intruder sang two short songs as it flew just over the shrubs back to its own territory. The second instance probably was a sexual chase involving a mated pair. While one followed close behind the other, one gave a *churr* noise and the other sang. Each dropped to the ground and continued to chase with hops and short, fluttering flights, while continuing either to *churr* or sing, respectively.

Secondary song.—Whisper song.—This song does not differ in any obvious way, except in volume, from the primary song, except that it may be preceded or followed by *churr* noises. Both recorded instances of a whisper song were probably alarm situations in which soft male songs were less likely to reveal the exact location of the singer or of a nearby bird. Squeal duet.—This is composed of distinct parts from each member of the contributing pair (Plate 8). One, presumably the female, gives a continuous trill while the other, presumably the male, gives phrases that sound and graphically appear to be very similar to the *churr* calls. Often a duet begins with or follows a series of *churrs.* Hubbard (in litt.) thought that the performance "sounded very typical of *Aimophila,* especially . . . *sumichrasti,*" when he heard it in Chiapas. That the squeal and *churr* are distinct, at least functionally, is indicated by the performance of the *churr* call by both sexes while only one sex contributes a *churr*-like phrase to the squeal.

The squeal is heard only when two members of a pair come together. In some cases a reunion duet probably occurred in response to a similar performance by an adjacent pair. Several playbacks of a recording of the duet brought the resident pair into nearby trees, where they duetted. Thus, defense of a territory may be accompanied by the squeal duet rather than by the primary song. Marshall (1964) commented that the song and squeal duet of Brown Towhees have similarly diverse functions.

Other vocalizations.—Churr.—This is a very common alarm or agitation call given by either sex. Usually it is performed as a series of spaced phrases, but these may run together at the beginning, presumably when motivation is highest. Birds *churr* from any height in the vegetation and sometimes in flight. An infrequent performance of reduced volume may serve as an alarm call. It often precedes the squeal duet and leads into the duet essentially unchanged. In this case only one bird is *churring*, but solo *churr* performances are not uncommon. *Tzee* (*seee* of Marshall 1964).—Marshall reported this as similar to the pair communication call of Brown Towhees. I have heard it only as a long drawn-out figure followed by a squeal. It may occur in duet performances as it does in the towhees (Marshall *op. cit.*) but I do not have any recordings of such a squeal from *A. rufescens.* I did not hear the *tzee* given solely as a pair communication call between separated individuals. (3) *Chip* (*tzeek*).—Heard from adult birds that had young hiding nearby.

AIMOPHILA NOTOSTICTA

Primary song.—This is the only known vocalization. Generally it is given from elevated, exposed perches either in small trees or shrubs. The only birds heard singing were males spaced at intervals. The song probably functions in territoriality and pair formation. An actively singing male in August gave eight to ten songs per minute.

The song usually consists of one, sometimes two, introductory figures and a trill-like chatter (Plate 8); occasionally it is followed by several figures of a distinctly different quality from the trill. The trill itself can be of one or two (or more?) types of sounds. In the recorded songs, which are all of one type, the trill has two kinds of figures. The first is repeated 3 to 5 times before the second type is likewise repeated 3 to 5 times. The total number of figures in the trill is seven to eight. The figures of the trill in *A. notosticta* are more complex than those of the trill among the members of the *Haemophila* complex. The quality of the song is remarkably similar to that of *A. ruficeps.*

AIMOPHILA AESTIVALIS

Primary song.—This is the advertising and territorial vocalization. Borror (1961, 1971) and Thorpe and Lade (1961) noted the extreme variability of this song. Borror (1971) recorded 39 types from a single Florida bird and 244 song patterns from birds in Florida and Ohio. Several songs occurred in different birds from the same state, but no song patterns from Florida birds appeared in the vocabulary of Ohio birds or vice versa. In 77 consecutive songs from a single male in Texas, I recorded 23 different song patterns, only 4 of which were repeated with one or more different song types between repetitions. An actively singing male gives from six to ten songs per minute.

Physically the song usually consists of a whistle or vibrato introductory figure followed by a trill of various types of syllables (Plate 8). The whistle or vibrato may either have a constant frequency range throughout or may change in pitch. In relation to the trill the introductory part may average about the same or lower or higher in pitch. The other song patterns from the Texas bird included: (1) Songs that began with a trill, in which case a second trill was set off from the first by a downwardly inflected whistle; (2) the introduction was followed by two different types of trills, and the trills may or may not be separated by a whistle; (3) rather than ending in a trill, several slurred or inflected whistles followed the trill.

It is not uncommon for a singing male to produce several songs without a pause. Such "consecutive songs" seem to occur most frequently in highly motivated territorial situations such as counter-singing or actual defense. On 20 June 1964 in Jasper County, Texas, what I thought to be two males reacted as follows during a chase that occurred after one approached to within 23 m of the nest of the other. The account is quoted from my notes taken at the time: "Heard chips and series of chitters. Bird dropped to ground near halfway pine [= about 75 feet from nest]. Male (resident) flew down and [I] heard another series of chitters and rustling in the grass. One bird flew out . . . giving continuous series of songs. Second followed with same songs."

F. E. Brooks (quoted in M. Brooks 1938: 104) may have heard consecutive song for he reported "when I approached a little nearer he discovered me and changed his song into a fine, mixed-up combination of slurs, whistles, and trill." Except for songs given in flight during chases, all daytime singing is done from a perch and perhaps occasionally from the ground (Brooks *op. cit.*, pers. obs.).

Mengel (1951) reported a song flight to a height of 150 feet just after sundown. The song, which may have been a consecutive song, reminded him "of a much speeded-up Indigo Bunting (*Passerina cyanea*) song of wren-like quality." Flight songs in *A. aestivalis* are not common.

Counter-signing is common, especially between adjacent, territorial males. The territorial function of primary song is further suggested by the ease with which males were stimulated either to sing against and approach a tape recording of a singing male.

Secondary song.—A "whisper" song or soft rendition of primary song is common during nest building. While giving whisper songs the male often sits 15 to 30 m from the nest on an exposed perch. These soft songs, in large measure, seem to coincide with times when the female is actually at the nest with new materials (pers. obs.), or while the female searches for material (Blincoe 1921). F. E. Brooks (quoted in M. Brooks 1938) mentioned hearing a "whisper song" a number of times on 23 April, the recorded date of arrival of *A. aestivalis* at that locality. Brooks also noted that whisper songs were "not uncommonly interspersed" in bouts of loud songs.

Brooks (*op. cit.*: 104) mentioned "broken twitterings" that may be some sort of subsong or consecutive song.

Other vocalizations.—*Chitter.*—This is a series of *chip* calls run together with sufficiently short intervals between them that the result sounds like a trill of the Chipping Sparrow (*Spizella passerina*). The trill is somewhat slower than in *Spizella* and changes pitch slightly at the end. During late June in Texas, this was a not uncommon call from a pair of nest-building birds. One bird, presumably a female, gave such a call, perhaps in alarm, while flying by me. On 17 June, two birds foraging separately began the call. Both then flew and landed only 2 to 3 m apart, and each gave a long *chittering* series. Occasionally after a female added some nesting material, she flew to a shrub and *chipped* and then to another shrub where two birds gave a low *chitter.* I have already mentioned *chitter* associated with an apparent territorial dispute. Compared to primary song, *chitter* was not common enough to be segregated quantitatively into functional categories. This call probably is an aggressive as well as pair reunion call. *Chip, tzink,* and *chink.*—While all three renditions appear in my field notes, they probably refer to the same alarm call. Adults carrying food *chipped* when an observer was near a nest or fledglings. During nest building a female *chipped* going to and from the nest. No high, thin *tzee* was heard, and I found no published reports of such a note. *Chip.*—A softer call than given by the adults is given by the young. *Chur.*—This call was heard only from a female flushed from a nest containing young or eggs. The female did not leave the vicinity of the nest but ran through the grass 3 to 5 m away sometimes giving an "injury-feigning" display with the *chur.* I described it as a gravelly "meow," but Bendire (1888) quoted Avery, undoubtedly referring to the same call, as saying that it was a distinct hissing. It sounds remarkably like a snake, and its occurrence with movements through the grass heightens a snake illusion. Sibley (1955) commented on behavioral mimicry of this sort in certain species, particularly hole-nesting parids.

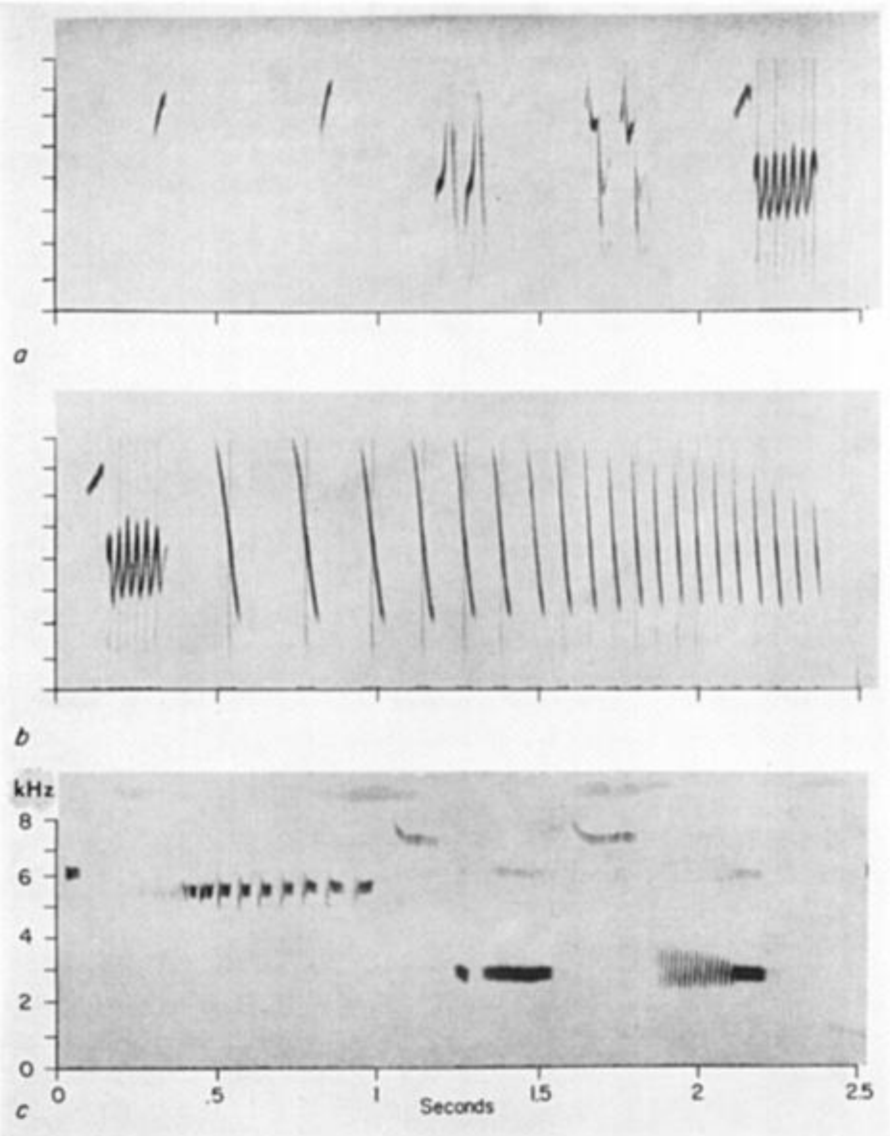

Plate 9. Primary song (a), (b) of *A. botterii.* (a) and (b) together comprise one song of about 4¾ seconds duration; recorded on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas on 7 July 1964. Flight song (c) of *A. cassinii*; recorded at Welder Wildlife Foundation, Sinton, San Patricio County, Texas on 30 June 1964.

AIMOPHILA BOTTERII

Primary song.—The advertising song of *A. botterii* occurs in two distinct patterns. The first is a short song of less than five seconds. The song is composed of groups of 2 identical syllables (more rarely 1 syllable) with each group usually differing from other groups in the same song, followed by a trill of single-figure syllables and often 1 or 2 whistle notes (Plate 9). The song and calls are variable; some songs begin with a series of high, thin introductory *chips* and/or trill syllables, and some have single figures or syllables interspersed throughout the series of two-syllable groups. There is also considerable variation in the figures and syllables composing a song, but the pattern is usually constant. An actively singing male generally repeats a song several times and may return to a song performed earlier. Although the song is more complex, the trill near the end and the ordering of the song types are reminiscent of *A. aestivalis.*

In the second song type the performance is not broken into distinct songs. I call this pattern the "continuous song." A singing male may give phrases and single syllables for up to three minutes without breaking into a trill. Harper (1930), Monson (1968), and Borror (1971) do not mention this song. Sometimes a continuous song will end like a regular song with a trill and 2 whistles. The continuous song was heard from males otherwise giving trill songs and from a male while the female was around the nest. Undoubtedly the trill song is used for mate attraction and territorial proclamation, while the continuous song may be reserved for situations involving a paired male and female, probably for pair reinforcement.

Storer (1955) and Monson (1968) did not mention the occurrence of a flight song in *A. botterii.* Harper (1930) noted that while *A. botterii* did not have a flight song of the magnitude of the performance in *A. cassinii,* "at least one [bird] sang as it flew along in a direct course low over the salt grass." My observations in Texas, Arizona, and Mexico corroborated those of Harper and indicated that the song given in flight is not physically different from a song by a perched bird. Flight songs were most frequently heard as a singing male changed perches and continued singing from the new perch. One flight song occurred at the end of a chase just before the paired birds dropped into the grass. The flight song does not seem to have a special function, nor does it seem to be an important part of the singing performances.

In Texas, perches used for singing ranged from 2.5 cm to 6 m above the ground, but most were between 1 and 2 m. One bird sang from the ground on a gravel road approximately 3 m from a tape recorder playing the advertising song. Song perches used were either just above the grass in weeds and low shrubs or in or near the tops of 2- to 3- m hackberries and mesquites.

Occasionally birds moved into the taller *Acacia* and *Prosopis* when they occurred within the territory. Generally the perches raised the birds above the level of the grass.

Secondary song.—A soft version of the continuous song was heard from a bird approximately 3 m from the observer after it approached in response to playback of the primary song. As this was the only time a whisper song was heard, its significance is uncertain and apparently it is an uncommon vocalization.

Other vocalizations.—*Chitter.*—I am not entirely certain if this is correctly treated as a vocalization distinct from a rapid series of *chip* calls, but I think it will prove to be different. Apparently the call is given primarily as two birds come together after being separated by some distance. I heard it as a duet performance when two birds landed 15 to 20 cm apart in low mesquite. More commonly it sounded as if only a single bird were calling; this usually occurred as the male and female came together near a nest. Some instances were obviously solo performances, e.g. when a resident male *chittered* while it flew to chase an intruding male. This is the only example of the call being given when both male and female were not in the immediate vicinity. *Chip.*—This is an alarm call of varying intensities and is given, especially by adults, while an observer is around the nest. Adults may give this call before going to a nest with food. One bird gave a rapid series of *chip* calls as it flew away from an aggregation of four birds drawn to a territorial boundary by playback of male songs. *Chup.*—Adults gave this call while I was holding their young; probably it is a call of extreme alarm. *Churr.*—This "reunion" call near the nest sounded as if it were being given by only one of the two birds present. *Squalling.*—A sound heard from a pair hidden in the grass. I am uncertain what behavior coincides with this call. I have heard pairs of caged Rufous-collared Sparrows (*Zonotrichia capensis*) give a call of this sort in aggressive intrapair situations. Usually the male is the aggressor and the female apparently gives most or all of the squall (Miller and Miller 1968).

AIMOPHILA CASSINII

Primary song.—Peterson (1961) renders the song as *ti ti tzeeeee tay tay*, or 1 or 2 introductory figures followed by a high, sweet trill and 2 lower figures. Actually there are several song types that can be classified under the general type mentioned by Peterson, and as Borror (1971) states, the terminal part of the song is more complicated than *tay tay* implies. In essence, there are two additional elements, as shown in Plate 9. Borror has analyzed the song variation of this species in detail.

Secondary song.—A second pattern is the *chitter* flight song. It sounds like a rapid series of *chips*, that change to a warbled sound near the end. This call is more warbled than the *chitter* call. One such flight song ended as in the more common song.

In late June and early July 1964, in San Patricio County, Texas, unmated, actively singing males did not perform any *chitter* flight songs. These came only from males that did not engage in long singing bouts and were judged to be mated, probably with fledged young. The *chitter* flight song may function to strengthen pair and family ties, perhaps as renesting begins. The *chitter* flight song usually elicited a marked approach response from a neighboring, unmated male, and it is possible that this song is an alarm vocalization. Thus, one song may be associated with territoriality and initial pair formation, while the second is more important in maintaining the pair bond.

The normal song of *A. cassinii* is given from a perch or in a flight performance, referred to by Peterson (*op. cit.*) as "skylarking." Stationary or perched songs are most commonly given from elevated perches on shrubs, tall weed stalks, or trees. Some individuals also sing from on or near the ground. Most elevated perches were less than 3 m tall. There is an inverse relation between sun intensity and exposure of a song perch.

Flight song performances were of two types, horizontal and with a marked vertical component. Horizontal flights were usually performed within 3 m of the ground. Vertical performance was much commoner than horizonal and began with a shallow, regular wingbeat in a fluttery flight upward at an angle of 60 or more degrees above the horizontal (30° according to Borror 1971). At the apex of the flight the bird began a flat-winged glide back to a perch or to the ground, or it descended close to the ground and flew off normally. The actual song performance usually began on the upward flight just before the apex and ended before the bird reached the perch. Song flights varied from 2 to 6 or more m ($\bar{x} = 4.6$ m; $N = 42$) above ground at the apex. Infrequently a bird may climb to 12 or 15 m. These exceptional performances most often followed a boundary dispute and accompanied long flights from the edge of the territory back to the usual song perches.

During 2 consecutive mornings, the percentage of perch songs in the song bouts of an unmated male increased until it was nearly 100%; over short intervals 100% perch songs are common. The reasons for decline in frequency of flight songs are obscure, but there seemed to be an inverse correlation with wind speed that began to increase at approximately 0730. Probably increased insolation during the course of the morning was also significant. There also seemed to be fewer flight songs from mated than from unmated males.

Other vocalizations.—Chitter.—The circumstances in which *chitter* occurred were varied and more than one vocalization may be masked under this inclusive term. I was not able to tape record any *chitter* calls. If there are two calls—a series of *chip* or several-noted syllables and a warbled call—I think they are two extremes of a vocal continuum. Several times a *chitter* call became more warbled or a *chitter* call was warbled throughout, and sometimes this call sounded similar to the warbled "duet" of *A. carpalis.* Although solo (or apparently solo) performances were given, *chitter* was heard more often when two or more birds were together. When more than two birds were together, some were obviously young; but when only two birds were present, I often could not tell if both were adults or whether at least one was a young of the year. Solo performances of a *chitter* series that probably was a rapid series of *chip* calls occurred while adults were caring for fledglings. In this case the calls may have been either in alarm or to alert young to a subsequent feeding. Twice during what I thought were territorial disputes I heard the *chitter* call. At other times a *chitter* or warbled call was given by two birds when they came together in a bush or during a flight with one bird right behind the other. Early one morning two groups of adults separated by 27 to 36 m were *chittering.* These last instances seemed to be concerned with pair bond reinforcement and territoriality. Exact patterns and functions of these vocalizations require further study, but they clearly include alarm calls and some sort of reunion call. *Chip.*—*Chip* calls are single figures given by adults when an observer is around young and probably in other alarm situations. *Ship* (soft).—What seemed to be a rather soft version of the adult *chip* was given by dependent fledglings.

I did not hear *tzee* or other soft location calls from foraging birds.

AIMOPHILA QUINQUESTRIATA

Primary song.—This highly variable vocalization is given only by males. Singing birds usually are on an exposed perch, but I did hear males sing from on or just above the ground when I was following them.

The pattern of the song is characteristic of the species. An actively singing bird gives from 2 to 6 figures in sequence and then pauses for 2 to 4 or 5 seconds and gives another phrase of 2 to 6 figures differing from the first (Plate 10). In 10 sequences of 2 actively singing males there was an average of 18 phrases per minute. Since a phrase is 1 second or less long, this means an average silent period of 2 to 3 seconds. All phrases are simple and involve 1 or 2 major syllables joined together in various patterns. The syllables range from simple inflected calls to more complex ones with several variations in pitch. The following is a rendition of 12 consecutive phrases given by a single male. Each different letter refers to a different syllable

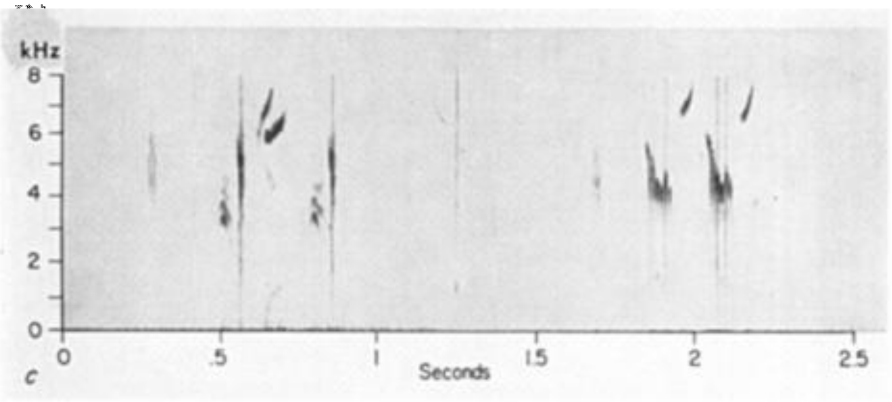

PLATE 10. Two series of notes from a song sequence of *A. quinquestriata*; recorded 32 km east of Mazatán, Sonora on 13 July 1963 by John P. Hubbard.

type. The small letters are for minor introductory figures that are of much less volume than the major figures of the phrases: AA, bCCC, AA, bDD, EEEECC, DD, EEEFFF, bDD, gEEEEAA, EEEEDD, AA, EEEEDD. Frequently used syllables differ among individual males and the number of variations among all males was probably sufficient to permit individual recognition. I was unable to detect any differences in the specific pattern of singing between males in Sonora and Jalisco (see also Borror 1971).

Secondary song.—Binford (1958) mentioned a male singing "a faint whisper song with its bill closed." He characterized the song as "a high, musical, varied series of short trills and phrases." The descrpition suggests a whisper performance of the primary song. The bird sang after flushing when three observers approached.

A warbling song, or a continuous outpouring of notes varying markedly in pitch, was heard once from a male singing 2 m up at the edge of a wooded hillside. When I retrieved the specimen, a female (later collected) moved, on the ground, slowly uphill, from just below where the male was singing earlier. This song may be similar to the warbling song of *A. carpalis.* Undoubtedly it functions in part to reinforce the pair bond.

Other vocalizations.—A slurred chatter was given by one of two birds during a chase down a small gully. The call was most likely given by the aggressor. No calls were heard during two interspecific chases, in both of which *A. quinquestriata* was being chased.

In this category are 5 calls composed of 5 different figures given either singly or in series. No recordings were made. *Tzit.*—A location call. *Tziiit.*—A long version of the location call. Heard once from a foraging, possibly agitated, bird as a second individual approached from uphill; function uncertain. *Tzeep.*—A harsh, loud sound given singly that serves as an adult alarm call. *Chup.*—Given by the foraging bird mentioned above while .5 to 1 m up in shrubs; probably also an alarm call, as this was the second of two birds that were present as I approached; the other flew over the crest of a nearby hill. *Chip.*—Harsh and given in series; this alarm call was heard only once, when I flushed a family group of two adults and three young into some shrubs. I was not certain which members of the group gave the calls.

DISCUSSION

Primary song of these sparrows is of two main types, based on song pattern and syllabic structure of the trill or the major portion of the song. In general, members of *Haemophila*, excluding *A. ruficauda*, have a song with an introductory figure and a very simple-figured trill that appear as a series of slash marks on a sonogram. These slashes sound like a rapidly repeated *chip.* Most of the others have a more complicated structure of figures or syllables in the major portion of the song, and the song pattern is less simple and more musical. Some figures of the trill of *A. botterii* have the same general appearance as those of the *Haemophila* group, but those at the beginning of the song are much more complicated. In general, song of *A. botterii* might be classed in some ways as intermediate between the two types, but the common occurrence of whistle figures in songs of *A. aestivalis*, *A. botterii*, and *A. cassinii* set these species apart from the other members of the genus. Songs of the *botterii* complex seem to be variations on the common theme of introduction, trill, and terminal flourish.

The song of *A. ruficauda* does not comply with this classification, but is uncommonly used and apparently is not the major vocalization of the species. The history of this vocalization is difficult to understand, but possible explanations for the divergence will be advanced later. This species is also peculiar in the apparent difference in the primary song of *A. r. acuminata* from the *A. r. lawrencii-A. r. ruficauda* group.

The only species that has two very distinct primary songs, used interchangeably, is *A. sumichrasti.* One song has the usual introduction and trill while the other is much more like the songs of the *A. ruficeps* type with complex syllables and a warbling sound; I suspect that this song is part of the chatter duet of this species. I am not including here the consecutive or continuous songs of *A. botterii* and *A. aestivalis*, as these probably are merely modifications of primary song.

Phillips (Phillips *et al.* 1964) stated that the song of *A. quinquestriata* is like that of *Amphispiza bilineata*, and he used this as evidence in placing *Amphispiza* in *Aimophila.* From the description in Peterson (1961), the song of *A. bilineata* is of the introduction and trill type of the *Haemophila* group. Miller and Stebbins (1964) called the song "tinkling" and lacking in vigor and persistence. The similarity of this song to that of *A. quinquestriata* is not apparent to me, a conclusion also reached by Borror (1971).

Within this genus is the previously mentioned vocalization variously called the pair reunion duet, the squeal duet, or the chatter duet. Although the terms in part refer to calls made in many cases under similar circumstances, it appears that the calls themselves may be different. In *A. rufescens,* sonograms of this call suggest that it is most similar to the duets of the Brown and White-throated Towhees (*Pipilo fuscus* and *P. albicollis*; Marshall 1964). I do not have recordings of the squeal duet of *A. ruficeps*, but apparently it also suggests that of *Pipilo fuscus* (Cogswell 1968; J. Tramantano and J. P. Hubbard, pers. comm.).

The complete behavior pattern in duetting involves calls produced by both members of the pair (in most instances either known or thought to be a mated pair). This may not be true in *Pipilo albicollis* and *A. ruficauda* because more than two birds may participate. In species for which information is available, it appears that each participant of the duetting pair makes a different sound. In *Aimophila* the presumed female makes a trill that is usually a series of sharp notes. The male usually gives a more varied pattern of sounds. In *A. sumichrasti* and *A. ruficauda* this more varied call is very reminiscent of the chatter song that the male bird gives as the primary song, and the two vocalizations may be structurally related. The pattern in *A. mystacalis* is similar, but the male portion does not occur as a primary song. *A. humeralis* often uses the syllable that is given during the *pit-za* performance of agitation by the two members of the pair. When the *pit-za* performance is given by both sexes, they produce the same note at asynchronous intervals; during the chatter duet the same vocalization is given by the male (?) while the female (?) gives the simpler trill notes.

A similar vocalization for the *botterii* group is much simpler than that of either of the other groups of the genus. It generally was described in my notes as a *chitter* sound given when two adults (or adult and young?) came together. The call may be related to duets given by other members of the genus, but I have no tape recordings and found no mention of this call in the literature. It seems to function as a reunion call between members of a mated pair, and it may also have some function in the family group.

The male portion of the chatter duet of the *Haemophila* group is more complex than that of the *ruficeps* group, but may be a modification of that type. In both species groups the female member of the duetting pair apparently gives a similar vocalization, a simple trill.

The other notes produced by members of this genus are harder to describe and compare, partly because I have been unable to make the necessary recordings and partly because many calls seem to grade into one another. Hence a thorough analysis must await a more detailed survey of the situations in which the calls occur. Several distinctive calls are represented in one or more species in the genus and seem to set off species from one another. The alarm call of *A. ruficeps* is a *dear, dear* vocalization which, as far as I know, is not found in the vocal repertoire of other species of *Aimophila.* It seems to be given in the presence of an intruder and usually by a single bird. There seems to be little geographic variation in this call. The figure given by the female *A. mystacalis* while the male is singing (see page 106) is apparently unique to this species, and *A. humeralis* has the *pit-za* call that probably is not similar to any other calls in the genus. The only call that may be related is the *chut* figure of *A. mystacalis.* The fact that the *pit-za* call may be the male portion of the chatter duet relates it functionally to the songs of *A. sumichrasti* and *A. ruficauda.*

Various authors have commented on use of song in outlining species relationships. Thorpe and Lade (1961) presented a very limited analysis of primary songs of 18 genera of emberizines and concluded that certain types of calls (e.g. wheezing and bussing), duration of song, and tendency to deliver songs in bursts of one type may be generic characters. In *Aimophila* structure of figures and syllables within the song (e.g. slash figures or more complex), pattern of song (e.g. introduction and trill, several syllable types, etc.), and complexity of the chatter duet and its relation to other vocalizations appear to be the most important vocal characters in establishing species relationships.

The value of vocalizations to taxonomy will undoubtedly rest on importance of the sounds to the species and degree to which they are subject to divergent selective pressures. In sibling species such as in the flycatcher genus *Empidonax* (Stein 1958, Johnson 1963), song is very important for species recognition, because plumage colors and patterns are very similar. However, this is not the case for some species of *Aimophila,* which have distinctive plumage marks and patterns or size differences that can aid in species recognition. If calls are important for species recognition, and if two species are sympatric, one might expect calls that may have evolved from a common ancestor to have diverged to a greater or lesser degree. A similar divergence could occur if the vocalization had territorial functions, and if it were selectively disadvantageous to maintain interspecific territories. With the marked habitat separation generally occurring in sympatric forms, one might expect selection to operate against interspecific territoriality (Orians and Willson 1964). (This may explain the major differences between the chief vocalizations of *A. ruficauda acuminata* and *A. humeralis.*) This obviously could obscure relationships based on song characteristics. Such divergences may not carry over into other vocalizations of the species that are not used for species recognition and/or territoriality. In fact, there may be selection for some calls to remain similar (see Moynihan 1968 for a discussion of similar ideas on convergence of plumage patterns). The relationships of function to types of selective pressures make it obvious that one must know something of the functions of vocalizations before trying to use them in classification.

The same vocalization can subserve different functions, depending on the particular behavioral situations in which it occurs. This may suggest a close relationship between situations when the call is given. It emphasizes the importance of combinations of signals for increasing the amount of information that can be conveyed using a limited set of signals. It also is of interest in considering the repertoire needed to send the same number of signals, given one or more media of communication. (See Marler 1961 and Smith 1963 for a further discussion of this problem.) Within *Aimophila* primary song apparently is used in species recognition and proclaiming and perhaps defending a territory. Hence with the amount of sympatry reported in the genus one would expect primary songs to be different in detail, if not in overall pattern. I think the marked similarities in primary songs (pointed out earlier) must, in fact, reflect a close relationship within these species groups.

The chatter or squeal duet in the *Pipilo fuscus* group leads me to think that they may be closely related to the *ruficeps* group of *Aimophila* (see also Marshall 1964). If the duet of *Melozone kieneri* is as similar to that of *Pipilo aberti* as thought (Wolf in Marshall *op. cit.*), then this genus may also belong to this group of species. The divergences noted in the duet of the *Haemophila* complex seem to indicate an early split of this group from the main stock of *Haemophila*, but the marked similarity within the complex points to a close relationship of the various species.

While similarities of duets within groups in the genus strongly point to close relationships, it is possible that occurrence of the chatter or squeal duet in the various groups is not evidence of relationships. In fact, it may be that the *Pipilo-A. rufescens* line is entirely distinct from the *Haemophila* line of evolution. Immelmann (1961, 1963) has shown that this duet call is not uncommon among birds occupying the arid portion of Australia and having long pair bonds, and that the call may be a primary means of pair bond reinforcement. In the *Aimophila* and *Pipilo* species in which this duet is most developed, the circumstances probably also involve a long pair bond as well as arid environments. Also involved may be the facts that the sexes are alike externally, territories are held year around, and habitats are relatively dense. Together, these factors may account for duetting, which aids in pair recognition and territorial reinforcement. (For discussion of significance of duetting in African birds, see also Payne and Skinner 1970 and Thorpe 1972.)

In *Aimophila* and *Pipilo* the function of duetting in territoriality may represent an extension from its original use in pair reinforcement. That the male portion of the call has also taken on the function of male advertisement in *A. ruficauda*, *A. sumichrasti*, and possibly *A. humeralis*, is also understandable if the call has gradually increased in importance in the species. It appears that the call has been elaborated in the *Haemophila* complex as it has taken over diverse functions in these species. It seems to have been placed secondarily under selective pressures that might be anticipated for the primary song, which may explain the marked divergence of this vocalization of the *Haemophila* complex from the pattern of the duet of the *ruficeps* group.

BREEDING SEASONS

The following information was used to judge breeding status of each species: Nests and nest building, young, ovarian condition, and presence or absence of a brood patch on females. Age of young, both in and out of nests, was estimated and probable date of egg-laying calculated from available data on incubation, nestling periods, and timing of postjuvenal molt, both for these sparrows and other fringillids (Michener and Michener 1940, A. H. Miller 1961). The significance of the condition of brood patches was judged from Bailey (1952) and Selander and Kuich (1963). Reproductive condition of males, as judged by testis size, was not used. Before using such information one must know the size of testes capable of producing functional spermatazoa and how long before nesting begins the males produce sperm. This information is not available for the subtropical and tropical species considered here.

SPECIES ACCOUNTS

A. ruficauda.—Since this species is composed of several allopatric, morphologically distinct populations, I shall treat each as a separate entity in outlining breeding seasons.

Guatemala (*A. r. connectens*).—Males with enlarged gonads are reported from the Motagua Valley in July, October, and November (Tashian 1953, Land 1962). I found no nest records for this form.

El Salvador, Costa Rica (*A. r. ruficauda*).—In El Salvador, A. H. Miller (1932) reported a nest and three eggs at Sonsonate on 21 July 1925, and Dickey and van Rossem (1938) found young on the wing as early as mid-July; a female with an egg in the oviduct was taken at Rio Goascoran on 19 October. In Costa Rica, Wetmore (1944) noted postbreeding flocks with young of the year in late October in the region around Liberia. During July 1965, I found birds that had not yet started breeding about 32 km south of Liberia, although I watched one adult carrying nesting material. Douglas Gill and I found two nests with three eggs each on 9 and 10 July 1966, near Cañas and Liberia.

Southern Mexico (*A. r. lawrencii*).—During the second half of August 1963 and 1964, juveniles were in developmental stages from fledglings prior to postjuvenal molt to first winter birds essentially through postjuvenal molt. At the same time some females (with recently ruptured follicles) were laying eggs, and we found two nests with eggs. In this population egg-laying must stretch over a four-month period, from late April and early May through at least late August. Most birds starting to nest late in the season probably also attempted to breed earlier, but none obviously preparing to breed again was collected with young close at hand. Dates of early nesting probably vary from year to year depending on climatic conditions.

Central Mexico (*A. r. acuminata*).—This small northern form begins egg-laying in late May and early June. A female, taken by W. W. Brown on 28 April in Morelos had the notation "breeding" on the label, indicating that in some years breeding may begin by this time. However, no gonadal data were on the label. Eggs, or females that had recently laid eggs, were taken as late as 14 November. The few specimens of juveniles corroborate approximate dates of onset of egg-laying. With the long span of egg-laying, at least two broods could be raised per season, although I found no supporting data. Schaldach (1963), with no firm evidence, suggests that this form may raise as many as three broods in Colima.

I can add very little to the suggestion (J. Davis 1960) that coastal populations may initiate and finish breeding later than inland populations. Birds taken near Coyuca, Guerrero, on the Pacific coast on 31 July, and 1 and 2 August 1964 were just beginning to breed. Near La Huerta, Jalisco, in the foothills above the Pacific coastal plain, breeding had not started by late July 1963. In Morelos, birds were breeding in June 1963 (juveniles in early August). Apparently the total length of breeding season is about the same in coastal and inland populations, but phenological differences in environment shift the seasons out of phase.

A. sumichrasti.—Young nearly through postjuvenal molt, nestlings less than one day old, recent fledglings, and nests with eggs were found near Tehuantepec in mid-August. Several females accompanied by fledglings showed signs of second nesting in the near future, and nest building was noted on 23 August. The earliest definitive record of breeding is a female (UMMZ) taken on 3 June with an egg "about ready to lay." Females taken in mid-May were in prenuptial molt and showed no evidence of gonadal enlargement. Probably actual time of initiation of breeding from year to year reflects local climatic conditions. Usually June is the wettest month (Duellman 1960), but time of onset of rains is variable.

Evidence points to egg-laying from late May and June to early September. In all cases for which data are available the late nestings are second clutches, often by birds accompanied by juveniles.

A. humeralis.—Nests and eggs are present from May until at least late August and early September. There are juveniles in nearly complete first winter plumage in the first week of August and birds not yet in postjuvenal molt as late as mid-July. Several females in late July and late August showed signs of an imminent breeding attempt. Two females from Morelos with small ovaries had no sign of a brood patch in mid-July and probably had not bred that year. Both birds were alone and may have been unpaired. Undoubtedly the two females were late nesters, perhaps first-year birds. On 22 August 1963 near Cuernavaca, Morelos one female had an unshelled egg in her oviduct preparatory to laying, several others had postbreeding ovaries and brood patches, and two females were beginning postnuptial molt. Also near Cuernavaca, premolt juveniles and two nests were found in mid-July 1964, and a female on 26 August had three ruptured follicles.

Available evidence indicates a prolonged breeding season, with females attempting several broods. Whether these several broods represent replacement nestings or several successful attempts is not known. Some females, probably first-year birds, do not initiate breeding until mid- to late July and probably attempt only a single brood.

A. mystacalis.—No nest of this species was found, and all dates are inferred from females and young. Young collected from late July to mid-August either were in early stages of postjuvenal molt or were finishing the molt. Adult females in August included birds with no brood patch that had not yet bred and ones beginning postnuptial molt. One female with no brood patch and a slightly enlarged ovary was with an adult male and a young bird in postjuvenal molt. Perhaps this female replaced another female with which the male had nested earlier. Nesting must begin in May and early June, followed by some second broods in August or early September, at which time other members of the population are initiating breeding.

A. carpalis.—Bendire (1882) reported nests and eggs from the Tucson, Arizona region from 14 June to 1 September 1872. Information supplied by C. Robbins (in litt. from L. Short, November 1965) gives egg dates in Arizona from 25 May to 11 September. In Sonora, nests are known from mid-July to at least 11 September. Three young "two or three days out of the nest" near Pitahaya, Sonora, on 1 November 1950 (Pitelka 1951a) hatched from eggs probably laid in late September or early October. There are very few nesting records from Sinaloa, and only recently was it discovered that the birds breed in the southern part of their range. The available records from Sinaloa extend from the initiation of nesting in early July (pers. obs.) to a nest and three heavily incubated eggs from which the female was flushed on 2 October (Moore 1946). My own records over the breeding seasons of 1963 and 1964 show that egg-laying started approximately synchronously in mid-July from the Tucson area to Sinaloa. We found nests with eggs and under construction in mid-July and collected stub-tailed young and birds well into postjuvenal molt in late August. In late August 1963 several adult females with dependent young, had enlarged ova, apparently for a second breeding effort. Females taken in late August 1964 showed positive evidence of a subsequent second breeding effort, and several males taken at the same locality were beginning postnuptial molt.

Marshall (1963) stated that *A. carpalis* "nests *only* after the summer rains" around Tucson. His data for 1959 and 1961 show that the onset of summer rains varied from early July to mid-August. Unfortunately, he presents no data on breeding of *A. carpalis* in these years to provide a basis for his statement. If *A. carpalis* does nest only after the summer rains, then early rains could explain the records of eggs in May and June. These records might also be correlated with exceptionally heavy rains during the spring rainy period (March and April) near Tucson. In mid-July 1963, nests and eggs were found in Sonora and Sinaloa the day before and the day after the first rains of the season. Thus the individuals did not wait until onset of summer rains in this particular season.

While there are few data on the subject, I postulate that *A. carpalis* is physiologically capable of breeding soon after a sufficiently heavy rainfall during the late spring and early summer. No published information is available on range of dates during which such a response is possible and time which must elapse after a rain before breeding begins. It undoubtedly is not of the small magnitude reported by Farner and Serventy (1960) and Immelmann (1963) for certain Australian desert birds. Since Marshall's data show rains in late March to mid-April, the period of physiological reproductive capability must begin no sooner than May, or one might expect even earlier breeding records than are now extant. This raises the question of which environmental features are responsibile for initiation of breeding and why a spring rain as late as mid-April does not trigger breeding in mid- to late April.

Another question is status of breeding in years such as 1961 when the only major rains in the Tucson region came in late March and mid-August. My own data from all parts of the species' range show that if the rains have not arrived by early to mid-July, breeding commences prior to the rains. The species probably is only partly timed by the rains and then only inasmuch as the birds are capable of initiating breeding slightly earlier than "usual," should the summer rains begin early. Should the rains be delayed until late summer, breeding commences prior to the rains. These forms probably have not been emancipated from the seasonality of breeding, to the point that they are entirely dependent on rain for timing of breeding.

A. ruficeps.—Egg-laying in California begins by late February or early March and continues into July. Arizona populations begin nesting about mid-May and continue through mid-August (Phillips 1968). Most populations begin breeding in April and May and continue to July. The records suggest a sufficiently long breeding season for a pair to fledge two broods. Much of the seasonal diversity of egg-laying may reflect different climatic conditions in the various years.

The early laying dates from California and Texas probably relate approximately to the early spring rains before the hot, dry summer. In Arizona, New Mexico, and Mexico, the rains occur in summer. The dependence of these forms on an abundant insect and seed crop for food may partly restrict the breeding season. The dry, hot summers in California offer a harsher, less favorable climate for rearing young than that in late spring when insect food is abundant.

A. rufescens.—Egg-laying probably begins in early to mid-May in Morelos, Oaxaca, Sinaloa, Veracruz, and probably throughout most of the range of the species. Nests with eggs have been reported at least into early July (Rowley 1962), and several juvenile specimens from southern Mexico probably hatched in mid- to late September. The limited data do not indicate any marked altitudinal or latitudinal variation in time of onset or length of breeding season. The occurrence over several months of juveniles in about the same stage of molt, plus Rowley's (*op. cit.*) dates for nests with eggs, suggests a prolonged breeding period with little synchrony among birds, even over a limited geographic area.

A. notosticta.—A female taken 9 July had large eggs in her ovary and a female on 14 August had already laid. A juvenile on 9 August was just beginning postjuvenal molt and probably had hatched in June.

A. aestivalis.—Young are present as early as 9 May (Bendire 1888), and some in initial stages of postjuvenal molt by mid-May. Egg-laying must begin in the southern part of the range in April and probably increasingly later as one goes north to Ohio and Pennsylvania (May 10, Todd 1940). Egg dates from Alabama, Florida, Kentucky, North Carolina, and Tennessee, supplied by C. Robbins (in litt. from L. Short), show that first sets may be laid from 20 April to 11 May, with the later dates from the more northern states. By mid-May to June, some pairs are beginning second broods. Sprunt and Chamberlain (1949) reported that in some years there may be three broods in South Carolina. Two broods are often raised, at least in the more southern populations, but I found no documented evidence for three broods. Late July and August nestings could represent third broods, replacement nests, or second nests of birds that initiate breeding later than other individuals.

A. botterii.—C. C. Lamb (unpublished field notes) noted that a female collected in San Luis Potosí on 4 May was nesting. This is the earliest nesting record for Mexico. In Texas, egg dates range from 16 April to 9 July (in litt., L. Short; pers. obs.). Generally egg-laying begins in late May or early June and first clutches are laid into early July. Second nestings may be attempted in August and early September in parts of the range. A record of a nest and set of eggs from Baja California (MVZ 7019) is undoubtedly a misidentification of either *Aimophila ruficeps* or *Amphispiza bilineata.* The earliest laying dates as judged by appearance of juveniles are early to mid-May. These dates were obtained only from a series of birds taken in 1932 in Cameron County, Texas and may represent a local early breeding season in response to special climatic conditions that year. The set of eggs from 16 April may be similar or may represent a misidentification and refer to *A. cassinii,* which is known to breed at that time. In 1964 in Cameron County, nesting began in early June and clutches in early stages of incubation were present in the first third of July.

Breeding may not be well synchronized in local populations. Three of four birds taken at Charco Redondo, Jalisco, on the same day had small ovaries, while the fourth bird was nesting. The three sexually inactive birds were probably at least two weeks away from egg-laying. Four nests found in Cameron County on 8 to 10 July 1964 were started within a period of two to three weeks.

A. cassinii.—Egg-laying begins in April and early May and extends to late July, August, and early September; undoubtedly some of the late records are second clutches and some may be replacement nests. Two of five adult females taken in late June and early July 1964 in Texas were laying or had just finished laying, and two others had edematous brood patches and were probably incubating eggs or caring for recently hatched young. Females that are active on the breeding grounds at this time probably are attempting second broods or replacement nests. Ohmart (1966) found three nests in Arizona in late August and September. These are the first nests from Arizona, which previously was considered only as part of the winter range (Phillips 1944). The birds probably occasionally, but perhaps not regularly, breed in Arizona. Birds off the breeding grounds either on or en route to winter quarters are known from late June to mid-July (Phillips *op. cit.,* pers. obs.). As far as I can ascertain these reports of early migrants are mostly of males. The time of arrival and the gonadal condition of females in Arizona is not known.

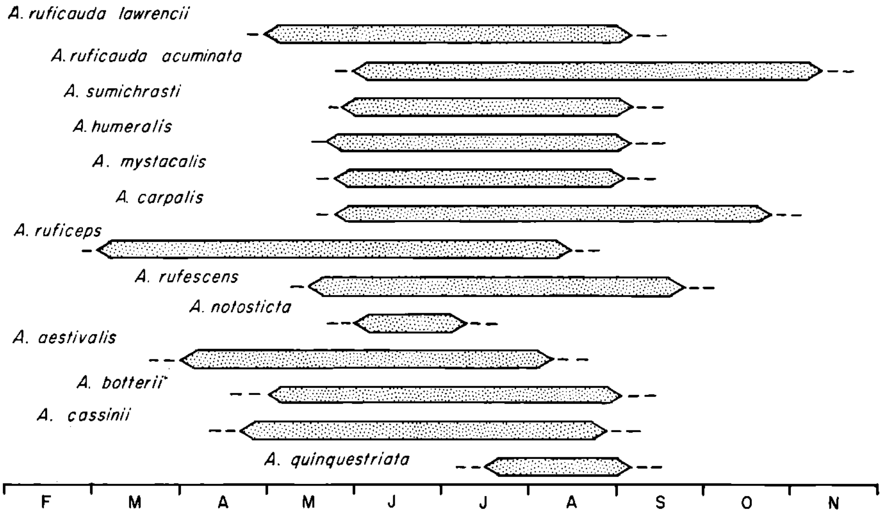

FIGURE 7. Breeding seasons of 12 species (13 forms) of *Aimophila*. Horizontal scale is months; dashed lines represent possible minor extensions of breeding from major periods.

A. quinquestriata.—In Sonora breeding began in early to mid-July in 1963 and 1964. Second nestings started in late August and early September in 1963; there was no evidence of second broods in early September 1964. Males with enlarged, sperm-filled cloacal protuberances are known from Jalisco and Zacatecas in July and September (pers. obs.; Webster and Orr, 1954a), so breeding probably occurs at a similar time at the northern and southern ends of the range. Several males taken on 1 September 1964 in Sonora were in the initial stages of postnuptial molt and probably had terminated breeding.

DISCUSSION

Breeding seasons for all species of *Aimophila*, as they are presently understood, are summarized in Figure 7. Species of *Aimophila* occupying the same geographic regions usually have the same breeding seasons. Although not evident from the summary graph, an exception may be *A. botterii* and *A. cassinii* in the Rio Grande Delta of Texas; there *A. cassinii* lays, on the average, at an earlier date. However, both species probably are responding to local environmental conditions. These are nearly the same throughout the early summer breeding range of *A. cassinii*, and nesting begins at about the same time. However, *A. botterii* reaches the northeastern limit of its distribution in Texas, and this population may be influenced by gene flow from more southerly populations where the breeding season is later. If timing of breeding is under some genetic control, then it seems probable that two factors are operating to fix the breeding season. One is gene flow from the southern populations, which breed later than *A. cassinii*; the other is adaptation of local populations to ensure proper timing to local conditions. Difference in time of nesting probably has little to do with potential competition between the forms, as they occupy essentially different habitats in the same localities.

General similarity in breeding dates indicates that the birds have similar reactions to local and general climatic conditions and other factors that regulate time of breeding. Marshall (1963) noted the relation of summer rains and breeding in *A. carpalis*, Phillips *et al.* (1964) suggested that a similar relation may exist in *A. ruficeps* in Arizona, and I discussed earlier the probable relationship between rain and time of breeding in *A. carpalis*. My own data suggest that both species are influenced, at least to some degree, by rains or some aspect of the environment dependent on rains, and this is probable for other members of the genus (Phillips 1968), especially for the late summer and autumnal breeding of *A. cassinii* in Arizona.

I find no strong indication of latitudinal variation in onset of breeding activity in species other than *A. aestivalis* and possibly *A. ruficauda*. Most of the species occur where most months are climatically suitable for nesting. Hence, breeding periodicity can be timed to other critical environmental factors during potential nesting periods. For many grass-inhabiting and granivorous species, one especially critical factor appears to be rain (Moreau 1950, Skutch 1950, Benson 1963), which influences availability of nesting material and food supply for adults and young. Another critical factor may be temperature extremes that occur in the northerly range of *A. aestivalis*. In this species, breeding apparently is correlated with latitudinal variations in environment. The birds apparently begin nesting as soon as conditions are suitable, and they probably are proximally timed by temperature, as has been suggested for other north temperate species (von Haartman 1963).

Thus breeding seasons and their apparent timing offer little information that one might use to group species that have adapted in various ways to environment. In addition, there apparently has been little selection for marked differences in breeding season in areas of sympatry.

NEST STRUCTURE

Behavioral characteristics are being used more and more to clarify taxonomic relationships in birds. One such characteristic is reflected in nest structure and placement. Dilger (1960) showed the existence of some genetic bases for nest-building behavior in the lovebirds (*Agapornis*). Stein (1958) noted the difference in nest type of the two forms of Willow Flycatcher (*Empidonax traillii*) near Ithaca, New York and used it as evidence of possible specific distinctness between the two forms. Mayr and Bond (1943), Lack (1956), Moreau (1960), Orr (1963), and Collias and Collias (1963) all noted the usefulness of nest structure as evidence of taxonomic relationships in their discussions of genera of swallows, swifts, and weaverbirds. At yet a higher level of classification, Tordoff (1954) commented on nest structure in his discussion of the relationships of cardueline finches. In the following paragraphs I present information on placement, style, and materials of the nests of the species of *Aimophila*. To date I have not found nests or discovered any published information about nests of *A. notosticta, A. quinquestriata, A. mystacalis,* and the *petenica* forms of *A. botterii.*

Of the nests that are known, all except some nests of *A. aestivalis* have the typical cup shape common to many passerine birds; exceptions are noted in the text, but a general nest description is not repeated for each species.

SPECIES ACCOUNTS

A. ruficauda.—Nests are reported from mesquite, *Acacia,* and other dense, thorny trees or bushes (A. H. Miller 1932, Zimmerman and Harry 1951, Storer 1955, Rowley 1962, pers. obs.). The nests ranged from about 32 cm to 1.5 m above the ground. Materials used included twigs (Storer 1955), twigs and grass (Zimmerman and Harry 1951), sticks and hair (Miller 1932), and grasses or grasses and weedstalks (Rowley 1962, pers. obs.). Undoubtedly choice of nest materials is primarily determined by availability at time of construction. In general all nests had finer materials in the lining than in the exterior; nine of ten nests were lined with some animal hair. Storer (1955) noted that the nest discovered by E. K. Miller in Michoacán in 1950 was "lined with a few finer twigs and rootlets." He did not mention any animal hair.

Nests of *A. r. acuminata* are bulky (inside diameter/outside diameter = 0.4–0.5), with nest material protruding from the sides rather than being neatly woven into a rounded side. This is more evident in twig nests; the general disarray of the nest is less when the main material is grass. Rowley (1962) noted that nests of *A. ruficauda* in Morelos were bulkier than those of *A. humeralis,* even though both species used essentially the same materials. Two nests of *A. r. lawrencii* did not seem to be as bulky as those of *A. r. acuminata* (inside diameter/outside diameter = 0.44), but fell within the range cited for that form. One nest of *A. r. ruficauda* was "neatly built" and deep (Miller 1932). For two nests of *A. r. lawrencii* and one of *A. r.*

acuminata the ratios of inside diameter to inside depth were 1.14, 1.27, and 1.36, respectively. The depth of these somewhat exposed nests probably makes the sitting female less conspicuous.

A. sumichrasti.—Four nests discovered near Tehuantepec, Oaxaca in late August, ranged from 20 to 38 cm above the ground. All were placed in small, usually thorny bushes. This species, like *A. humeralis*, occupies areas dominated by broad-leafed trees and apparently chooses the small bushes as denser, more protected nesting sites. The nests were constructed of grasses, with and without weed stems. One nest was in the low crotch of a shrub and incorporated a few dead vines that had grown up the side of the shrub. The nests often are compact (inside diameter/outside diameter = 0.62 to 0.67), less bulky than those of either *A. humeralis* or *A. ruficauda*, but with loose ends of material protruding. The lining of two nests was of plant material (in one case rootlets) that was finer than the main body of the nest. Three nests had no evidence of animal hair in the lining; each had a thin bottom through which one could see easily. Such flimsy workmanship may be an adaptation to the hot climate in which this species nests. The nests were deep; two averaged 1.31 (range = 1.22–1.40) in internal width-to-depth ratio.

A. humeralis.—Apparently nests have been reported only from Morelos. Two were found in "thick weed growth" (Rowley 1962) at heights of 15 and 30 cm, and two were placed in small bushes 46 to 68 cm above the ground. The low height of these nests in comparison to those of *A. ruficauda acuminata* in the same area probably is related to the fewer *Acacia* and more broad-leafed, nonthorny trees, which are less suitable as nesting sites, in the habitat of *A. humeralis*. A similar difference may hold for *A. r. lawrencii* and *A. sumichrasti* in the southern Isthmus region of Oaxaca.

The four nests were constructed of grasses, finer in the lining than the exterior. The lining in all cases included a few animal hairs. The only nests for which measurements were available were slightly smaller and less bulky (inside diameter/outside diameter = 0.55 and 0.59) than nests of *A. ruficauda.* The nest which Rowley pictured in his report and one that I found in Morelos were both substantial, compact structures, while R. D. Sage (MS) reported a nest that was "not very well put together." *A. humeralis* nests are wide inside in relation to inside depth (ratios of 1.44 and 1.97 recorded). They usually are well concealed, although built above the ground.

A. carpalis.—Nests have been found from about 15 cm to 2 m above the ground. Near Tucson, Arizona, Bendire (1882) noted them in low bushes, particularly small mesquites. In Mexico, the species used similar sites with the exception of one nest under construction about 1 m up on a dead cholla (*Opuntia* sp.) and two nests in pad-type *Opuntia* cactus. In many areas where the Rufous-winged Sparrow is common, mesquite is a dominant woody plant and is a site frequently used for nests. In areas where cholla or other *Opuntia* are common these also serve as nest sites. Nests in mesquite are often fully exposed to view from the side and seemingly are vulnerable to predation. They are shaded from the sun by overhead foliage.

The cup nests of *A. carpalis* usually are built of weed stems and grasses, but apparently only dead and dried plant material is used. The exterior is coarser than the interior, although the plants in the two portions are essentially the same. There may be more grasses in the lining, which also includes some long animal hair.

Bendire (1882) made no mention of how tightly woven the nests were. My own observations showed that most are compactly constructed. The ratio of outside to inside diameter on the only nest measured was 0.56, similar to the values for *A. humeralis* nests. Incubating females often seemed to be nearly engulfed within the nest structure. Bendire stated that the nests were 2 inches wide and 3 inches deep, giving a depth-to-width ratio of 1.5, but he was probably referring to external measurements. The nest I measured was essentially equal in width and depth with the ratio of 1.00. Both values indicate extremely deep nests, which may provide protective cover for the sitting female. It is often difficult to see her until one is close enough to see the tail, which usually protrudes slightly above the rim of the nest.

A. ruficeps.—*A. ruficeps* usually nests on the ground. Some authors noted that nests were flush with the ground (Barlow 1902, Dawson 1923, Grinnell and Wythe 1928), in a slight hollow that had been scraped by the birds (Williams 1897), or in an apparently natural hole (Pemberton 1910), but all nests are not in depressions in the ground. The only above-ground nests reported were never more than 45 cm up in shrubs (Carmel Valley, California—Linsdale MS; Texas—Phillips 1968). Generally nests are on a hillside, but only Williams noted any particular nest site orientation. He found six nests oriented to catch the "morning sun." Most nests are built close to vegetation that provides cover and an escape route for the adults.

Nests are composed primarily of dried grasses and weed stems with some small twigs and other plant fiber, and more than half of them had varying amounts of animal hair in the lining. Williams (*op. cit.*), reporting on six nests, noted that they usually were "flabby." A nest found by Carpenter (1907) was much wider than deep (width/depth = 1.8).

A. rufescens.—Two ground nests of *A. rufescens* were composed primarily of grasses and lined with finer grasses. No authors recorded animal hair in the lining. Griscom (1932) quoted A. W. Anthony that a nest found in Guatemala was "well woven." Another nest (MLZ), which was made of wide grass stems and pine needles, was compact and neatly assembled. Rowley (1962), who found 8 nests over a 3-year period in the vicinity of Cuernavaca, Morelos, said that the 3 July nests were placed "up to eight feet above the ground." He correlated above-ground nests with occurrence of the rainy season.

A. aestivalis.—Only ground nests are known for *A. aestivalis*, and most are protected or hidden by vegetation (Blincoe 1921, Brooks 1938). A nest which Meanley (1959) observed being built was placed at the base of a milkweed plant.

Blincoe (*op. cit.*) observed little vegetation surrounding the nest site except for some weeds, briars, and grass growing up through the brush under which the nest was located. All nests found in Texas in 1964 were placed at the outer edge of clumps of grass approximately 30 cm high. The nests were positioned in grass clumps so that little herb layer vegetation was found in a semicircle of at least 30–40 cm in front of the nest entrance. While this may allow the female a less obstructed view and better escape path, it would seem to put the nest in a more exposed situation than if it were hidden in a continuous grass layer. Two nests in Texas showed definite evidence that the female (only the female builds) had scraped the ground clean and made a slight depression in the sandy substrate. Lloyd (1931) and Mills (1905) mentioned nests "partially sunk" or "partly embedded" in the ground.

Two of four nests in Texas faced north, one northeast, and one west. Stoddard (in Burleigh 1958) reported one nest that faced north, and Mills (*op. cit.*) stated that the entrance of a nest he found in Georgia was from the west. Building a nest to face away from the sun or to be exposed only to late afternoon sun has two apparent advantages: (1) When the female is absent from the nest neither eggs nor young are exposed to excess heat. (2) With the adult absent the white eggs are probably less noticeable to predators if shaded than if illuminated by direct sunlight. This same advantage also may hold for newly hatched young with pink skin and a little down, but doubtless becomes less important as protectively colored juvenal plumage is acquired.

Brooks (1938), in his summary of information on Bachman's Sparrow in the northern part of its range, noted that the more southerly, pineland populations more consistently build domed nests than do the more northerly, second-growth, shrubby-field populations. Whether the difference in nest shape is caused by lack of suitable overhanging material in which to incorporate nest material in the northern breeding areas or to some other environmental factor, such as weather or predators, is not known. Sprunt (1954) reported a nest in Florida that was "under a palmetto leaf" and "open above, like most sparrow nests." Perhaps the presence of a suitable "roof" in the form of the palmetto leaf sufficed for an arch. A nest under construction in Texas showed that in the first stage, the female placed a circle of grasses near the front of the nest site to form the front edge of the nest and arch.

All nests reported were constructed mainly of grasses. The lining generally was of grasses finer than those in the exterior, and Blincoe (*op. cit.*) and Brooks (1938) mentioned three nests that contained at least some "horsehair" in the lining. Several nests included such items as small weed stems, shreds from cornstalks and pine needles in the lining.

One nest in Texas was 15 cm from front to back, with the cup occupying 7 cm of this distance; from the bottom of the cup to the top of the back of the arch was 16 cm; the total width of the front was 16 cm of which the diameter across the widest part of the opening to the cup was 6 cm.

A. botterii.—Merrill (1878) reported that the first known nest of *A. botterii* was "made of blades and stems of grasses and was rather deep. . . ." He noted that this nest was "very frail." Four nests discovered near Laguna Atascosa, Cameron County, Texas in 1964 were composed of dry grasses and had no animal hair in the lining. The nests were compactly built (inside diameter/outside diameter = 0.65; range = 0.61–0.71) and had the deep cup (width/depth = 1.2; range = 0.86–1.60) on which Merrill commented. In nests in clumps of salt grass, the portion closer to the center of the grass clump was much thinner than the front. A single nest from Guanajuato, Mexico was composed of dead grasses and weeds, with some leaves in the outer layer; the lining was of fine grasses (MLZ).

In general, *A. botterii* is a ground-nesting sparrow. One nest in 1964 was found in a slight depression on the ground in a patch of crabgrass; 2 others were nestled slightly off the ground in clumps of salt grass with blades of the grass shading the nests; the 4th nest was in a 30-cm bush, about 10 cm above the ground. The nest was shaded by a small succulent plant to the east and south. All nests opened to either the north or northwest. Probably nest placement with respect to adjacent vegetation offers protection from the sun.

A. cassinii.—The nests found by Merrill (1878) were "composed of dried grasses, lined with finer ones and a few hairs, but were very frail." Hershey and Rockwell (1907) presented a more detailed account of a Colorado nest composed of dry grass blades and stems, weed stems, bark, and vegetable fibers. The lining consisted of fine grass blades and a very few fine grass stems, but no animal hairs. Sides of the deep-cupped nest were essentially perpendicular. The exterior was 3½ inches tall and 3½–4 inches in diameter, and the interior was 2½ inches deep and 2 to 2½ inches in diameter (width/depth = 1.00; inside diameter/outside diameter = 0.57).

Except for nests in Tom Green County, Texas, which were "in low bushes not higher than one foot from the ground" (Lloyd 1887) and a nest in Arizona (Ohmart 1966), all other known nests were placed on the ground.

They may be concealed in weeds (Johnson 1956) or at the base of small bushes (Hershey and Rockwell, *op. cit.*). Only the last authors specifically mentioned that the nest was not sunk below ground level.

DISCUSSION OF NEST STRUCTURE

Members of the *Haemophila* group build elevated nests, usually in a thorny tree or shrub. The remaining species in the genus for which nests are known normally nest on the ground, with the exception of *A. rufescens* which may vary nest position during the nesting season. Ground-nesting forms seem to be rare among passerines sharing the habitats of *Haemophila.* This may result from predation pressure by the numbers of ground-dwelling vertebrates, especially snakes (Skutch 1949), lizards, and small mammals in these tropical and subtropical lowland areas.

Another apparent correlation is between average environmental temperature and nest site. Most species that nest in warm lowland areas build elevated nests, and several build flimsy nests with especially thin bottoms that may aid in keeping nest temperatures below a critical maximum. Collias (1964) found that roofed nests of tropical weaverbirds were several degrees cooler inside and that the efficiency of this system increased as lining width increased. In open nests this insulation would keep heat from incident sunlight in the nest cavity, rather than outside the nest. That several members of the group that build elevated nests also reach 1200 to 1850 m elevation in the mountains of Mexico is unimportant as far as nest site is concerned. These forms, except *A. mystacalis* for which the nest is unknown, are only recently invading these highland areas and retain characteristics inherent in the population as a whole.

The deep cup shape of the nest of several species in two of the groups suggests an independent derivation of this characteristic. As already mentioned, it probably serves to conceal the incubating female. A deep cup-shaped nest might also shade the eggs during absences of the female. The deeper the structure in relation to internal width, the more nearly overhead the sun must be to shine directly on the eggs. Finally, the degree of diversity shown in nest depth by, for example, *A. botterii* suggests that the characteristic is variable and may depend primarily on nest placement and substrate. In this case the nests in Texas may be used for examples. The raised nest was the only one which was deeper than wide, the ground nest was the shallowest, and the two nests in clumps of salt grass were of intermediate depth.

Given selective pressures to build elevated nests, it is necessary to explain ground-nesting habits of other species in the genus, especially as raised nests are occasionally built by ground nesters. Although a few populations or individuals may be limited from building elevated nests by lack of woody vegetation, this is rarely true and not an important factor. This suggests that the ground is the safest place for these species to build, probably related to amount and type of ground cover available. For most species of *Haemophila*, ground vegetation is composed primarily of annual herbs that appear after the rains. In some years this vegetation is sparse or lacking and does not provide adequate cover for ground-nesting forms. The other species all occupy habitats in which grass is included to a greater or lesser degree in the ground cover. It is a permanent cover that provides excellent protection.

While the separation of ground and elevated nesting habits among the three groups is not perfect, it appears that the *Haemophila* group is unique in the genus in consistently building elevated nests. Since in large part nest placement and structure is adaptive to the environment in which the bird lives, it seems that for groups thought to have radiated in common habitat types, nest-building habits can be an important character in defining the genus. If a group has radiated into different habitat types, then selection pressures may have been sufficient to modify nest building so that it no longer is consistent within the group.

EGG COLOR

For a survey of egg ground color and degree of marking or patterning of eggs of some North American and neotropical emberizine genera, see Table 10. Most have some degree of marking on the generally light, occasionally white, eggs; *Aimophila* is just the opposite, and only a few other emberizines shares its white egg trait.

The question of sequence of evolution in emberizines of patterned versus unpatterned eggs is not resolved here. Among the sparrows, most species have patterned eggs, which suggests an early origin and subsequent maintenance of the trait as various populations took otherwise divergent evolutionary paths. However, this does not rule out the possibility of independent origin of patterned eggs in ancestral forms of several groups at a later point in time. A few eggs of *Melozone kieneri* with faint reddish dots appear in clutches of otherwise unmarked eggs (Rowley 1962). Whether the species is in the process of acquiring spotted eggs or has not completely lost the trait is unknown. In either case it is of variable expression even in a single female. On the other hand it does not seem probable that selective pressures for egg concealment would permit a loss of patterning and subsequent evolution of other devices to protect the eggs, unless there was either a relaxation of the selection pressure or a strong selective pressure against the energy-demanding process of pigment deposition (Averill 1924).

TABLE 10

EGG CHARACTERISTICS OF SOME EMBERIZINES

Species (or genus)	Color	Pattern*
Aimophila spp.	White to pale blue	U
Amaurospiza concolor	Pale blue	U
Ammodramus spp.	Whitish	M
Ammospiza spp.	Whitish to greenish blue	M
Amphispiza belli	Pale blue-greenish blue	M
Amphispiza bilineata	White	U
Arremon aurantiirostris	White	M
Arremonops spp.	White	U
Atlapetes spp.	Pale blue to white	U
Calamospiza melanocorys	Pale blue	U
Calcarius spp.	Whitish to brown	M
Chlorura chlorura	Whitish to pale greenish blue	M
Chondestes grammacus	Whitish	M
Emberiza spp.	Whitish to light brown	M,m
Junco (except *phaeonotus*)	Whitish to pale blue	M
Junco phaeonotus	White	m
Melozone kieneri	Pale bluish white	U (m occasionally)
Oriturus supercilosus	Whitish	M
Passerella iliaca	Pale greenish	M
Passerculus sandwichensis	Pale greenish blue	M
Passerherbulus spp.	Pale greenish white	M
Pipilo erythrophthalmus	Whitish to pale greenish blue	M
Pipilo fuscus	Pale bluish to whitish	M,m
Plectrophenax spp.	Whitish to brownish	M
Pooectes graminicola	Whitish	M
Rhynchophanes mccownii	Whitish to light brown	M
Spizella spp.	Blue	M
Sporophila torqueola	Pale blue to pearl-gray	U,m
Tiaris olivacea	Dull white	M
Volatinia jacarina	Whitish to pale blue	M
Zonotrichia spp.	Pale blue to bluish green	M

* Pattern legend: U = unmarked, M = distinctly marked, m = finely marked.

White probably is a very conspicuous color for eggs under a variety of conditions. The majority of bird species with white eggs are cavity-nesting birds, and white may help the parents locate the eggs (Lack 1958). It is also possible that there is little or no selection to maintain colored and patterned eggs. For other birds the strongest selection pressure on patterning and color of eggs probably is predation (Lack *op. cit.*). This does not eliminate physiological parameters, but among emberizines these seem to be of only minor importance.

For birds nesting in the open, the problem of egg concealment can be solved in a variety of ways. The most frequent among the emberizines seems to be to evolve patterned eggs as a method of protective coloration. However, Hicks (as quoted in Brooks 1938) said:

> "the percentage of success [of Bachman's Sparrow nests] is distinctly higher than that which Mrs. Nice has found for the Song Sparrow, and which I have found for the Field Sparrow and the Vesper Sparrow.
>
> "The causes of predation losses we know to be rather complex, and not so easily explained as being due to the color of the eggs. I doubt very much if the species' nesting success would be significantly altered if the eggs looked like those of the Vesper Sparrow."

To counteract selection pressures for patterned eggs would involve finding other means of protecting unpatterned eggs.

Some white eggs are unpalatable to predators in comparison to nonwhite eggs (Swynnerton 1916). The reason for this is not known, nor have such tests been made for the eggs of *Aimophila.*

Parental behavior may help conceal white eggs and might be an alternative to patterned eggs (Cott 1940) or might operate with patterning to further reduce predator pressure. Most emberizines with unpatterned eggs nest above ground, where eggs are less visible to ground predators. While aboveground nesting may be related to other environmental factors, such as amount of rainfall, in addition to predator pressure on eggs, a raised nest may reduce selective pressures for patterning as protective coloration. A bulky nest structure placed in a raised position would most likely be noticed by a ground and arboreal predator before eggs in a nest cup, and selection would operate to make raised nests less conspicuous. After a predator locates the nest, egg color probably is of little significance. Several species of *Aimophila* build deep nests placed in trees. Such raised nests unprotected by branches or foliage from above are open to aerial predators such as jays.

A majority of raised nests of *Haemophila* are in thorny trees and shrubs, or shrubs with sharp sclerophyllous leaves. Selection of such plants may serve to discourage ground predators from clambering in vegetation containing nests. However, ground squirrels (*Citellus*) do climb about such thorny bushes as cholla (*Opuntia*), and they are known to take eggs as part of their food (S. B. Benson, pers. comm.). Thus thorny vegetation may not be an effective deterrent.

Two species of *Arremonops* (*rufivirgatus* and *conirostris*) and *Aimophila aestivalis* (in part) are among the ground-nesting emberizines that have white eggs and build arched or "roofed" nests. This nest type helps conceal eggs. A trend toward a greater percentage of arched nests built by *A.*

TABLE 11

MEASUREMENTS OF WING LENGTH (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	x̄	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	54	65.26	2.00	0.27	61.5 –69.2	21.26	3.06
	F	49	63.22	1.51	0.22	60.4 –66.2	20.93	2.40
r. lawrencii	M	35	73.43	1.55	0.26	71.2 –76.9	21.60	2.11
	F	34	70.24	1.92	0.33	64.6 –73.3	21.03	2.73
sumichrasti	M	21	66.68	1.96	0.43	63.1 –70.0	22.08	2.94
	F	15	63.99	1.53	0.40	61.4 –67.1	21.47	2.39
humeralis	M	60	65.80	1.71	0.22	58.7 –68.8	22.61	2.60
	F	57	63.63	2.15	0.28	59.3 –70.5	22.33	3.38
mystacalis	M	17	69.55	1.71	0.42	67.4 –72.9	24.56	2.46
	F	12	65.11	2.03	0.59	62.1 –68.6	23.09	3.12
carpalis	M	62	59.30	2.53	0.32	52.8 –64.1	23.91	4.26
	F	38	56.99	2.83	0.46	52.6 –64.7	23.17	4.96
ruficeps	M	55	62.89	2.70	0.36	57.5 –70.1	23.47	4.29
	F	48	59.89	2.82	0.41	55.6 –67.2	22.77	4.70
rufescens	M	42	73.73	2.84	0.44	67.7 –79.9	21.56	3.85
	F	33	69.14	2.50	0.44	64.4 –73.8	20.58	3.61
notosticta	M	5	67.66			63.5 –71.0	22.18	
	F	3	63.23			61.5 –65.4	20.94	
aestivalis	M	45	60.13	1.85	0.28	56.6 –65.7	22.11	3.08
	F	22	58.42	2.09	0.45	55.2 –62.4	21.88	3.58
botterii	M	55	63.20	2.65	0.36	57.0 –67.9	22.49	4.19
	F	41	61.90	2.52	0.39	55.6 –65.5	22.27	4.06
cassinii	M	43	63.77	1.23	0.19	61.6 –67.3	24.53	1.93
	F	16	61.97	1.69	0.42	58.8 –65.6	23.30	2.73
quinquestriata	M	9	66.99	2.79	0.93	63.1 –70.2	25.00	4.16
	F	18	64.28	2.45	0.76	60.5 –69.8	24.16	3.81
Species groups:								
Haemophila	M					21.26–24.56	22.67	
ruficeps	M					21.56–23.47	22.40	
botterii	M					22.11–24.53	23.04	
quinquestriata	M					25.00	25.00	

aestivalis in the southern part of its range as contrasted to the northern part (Brooks 1938), if true, may reflect either a decrease of selective pressure exerted by terrestrial predators for building domed nests as concealment for the white, unpatterned eggs, or changes in substrates in which nests are built.

Another method of protecting the nests and eggs from ground predators is through modified behavior in the vicinity of the nest. Skutch (1949) noted that the Ruddy Quail-dove (*Geotrygon montana*), one of the few pigeons that leaves the nest between laying of the first and second eggs, lays buffy eggs rather than white as for most columbids. Birds also can conceal their eggs by being very reluctant to leave the nest when a predator approaches or by being very secretive in approaching and leaving a nest. While these behaviors are not restricted to birds with white eggs, they are found among species of *Aimophila* for which I have found nests. In ad-

TABLE 12

MEASUREMENTS OF TAIL LENGTH (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	$\bar{x}$	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	56	75.90	2.53	0.34	70.2–82.0	24.72	3.33
	F	35	73.21	2.75	0.44	67.8–79.4	24.24	3.76
r. lawrencii	M	36	86.92	3.74	0.62	78.4–95.8	25.56	4.30
	F	19	83.10	4.03	0.92	76.0–92.1	24.88	4.84
sumichrasti	M	11	67.50	2.19	0.66	64.5–71.5	22.35	3.25
	F	8	62.79			57.6–65.9	21.07	
humeralis	M	32	74.09	2.29	0.41	70.2–80.4	25.46	3.10
	F	35	70.70	2.18	0.37	67.6–76.4	24.81	3.08
mystacalis	M	16	78.04	2.02	0.50	74.5–81.3	27.58	2.59
	F	13	72.79	1.87	0.52	69.1–75.4	25.81	2.57
carpalis	M	42	62.96	2.39	0.37	58.2–69.2	25.39	3.80
	F	32	60.90	2.98	0.53	56.7–66.7	24.76	4.89
ruficeps	M	48	67.74	3.42	0.49	62.4–78.6	25.28	5.05
	F	38	64.75	3.32	0.54	56.6–72.5	24.62	5.12
rufescens	M	39	79.74	4.50	0.72	72.1–88.8	23.32	5.64
	F	28	75.04	3.51	0.66	68.8–80.8	22.33	4.68
notosticta	M	3	78.97			73.5–83.5	25.89	
	F	2	71.20			66.1–76.3	23.58	
aestivalis	M	31	63.34	2.14	0.38	59.3–67.2	23.29	3.37
	F	16	61.49	2.56	0.64	57.0–65.5	23.03	4.17
botterii	M	41	64.54	3.41	0.53	56.4–70.7	22.97	5.28
	F	21	62.93	4.09	0.89	51.8–71.0	22.64	6.49
cassinii	M	13	67.85	2.17	0.60	63.9–71.0	26.10	3.20
	F	13	66.44	2.50	0.70	62.0–71.2	24.98	3.77
quinquestriata	M	7	68.33			65.9–71.3	25.50	
	F	16	66.56	2.94	0.73	61.1–71.2	25.02	4.41

dition, several species have rather well-developed distraction displays. In general these are observed in forms that nest in open habitats where nest and young are more exposed and hence an injury-feigning or other distraction display would be effective.

It is evident that given white, unpatterned eggs and a positive selective force to produce a means of egg protection, various protective devices can be and actually are employed among emberizines. Equally, egg color is another factor that may influence to a greater or lesser extent various behavioral attributes of the species, position and construction of nest, and adult behavior around the nest, and must be considered in analyzing these features for their significance in elucidating relationships.

Thus, while the question of time and direction of evolution in egg color and marking among the emberizines is not resolved, it seems that Pitelka (1951a) may have too rapidly dismissed egg color as an important character in the genus *Aimophila*. This character is probably not independent of other evolutionary changes in the species and may hold a key to the relationships of the genus. Generic relationships are more difficult to decipher if

TABLE 13

TARSAL LENGTH MEASUREMENTS (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	x̄	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	59	24.24	0.66	0.09	22.5–25.3	7.90	2.71
	F	63	23.88	0.58	0.07	22.7–25.0	7.91	2.42
r. lawrencii	M	46	24.46	0.69	0.16	22.9–26.3	7.19	2.82
	F	45	23.93	0.67	0.10	22.1–25.1	7.16	2.79
sumichrasti	M	47	21.11	0.77	0.11	19.7–23.0	6.99	3.65
	F	30	20.50	0.75	0.14	19.2–21.8	6.88	3.65
humeralis	M	71	21.29	0.63	0.07	20.0–23.1	7.32	2.94
	F	62	20.94	0.72	0.09	18.4–22.4	7.35	3.46
mystacalis	M	43	22.34	0.78	0.12	20.9–24.0	7.89	3.48
	F	28	22.16	0.88	0.17	19.3–24.0	7.86	3.98
carpalis	M	58	19.08	0.58	0.08	17.9–21.4	7.69	3.04
	F	47	18.81	0.55	0.08	17.6–20.0	7.65	2.91
ruficeps	M	60	20.71	0.81	0.10	18.5–22.5	7.73	3.93
	F	58	20.61	0.88	0.12	18.5–22.3	7.84	4.29
rufescens	M	53	26.42	1.30	0.18	23.2–28.7	7.72	4.94
	F	52	25.85	1.25	0.17	22.8–28.1	7.69	4.85
notosticta	M	5	24.80			23.8–25.3	8.13	
	F	4	24.18			23.7–25.0	8.01	
aestivalis	M	48	19.98	0.68	0.10	18.5–21.5	7.34	3.42
	F	36	19.52	0.57	0.10	18.1–20.5	7.31	2.91
botterii	M	54	21.89	0.61	0.08	20.6–23.3	7.79	2.80
	F	41	21.95	0.62	0.10	20.6–23.0	7.90	2.83
cassinii	M	45	19.87	0.66	0.10	18.5–21.4	7.64	3.30
	F	37	19.80	0.60	0.10	18.8–21.4	7.44	3.00
quinquestriata	M	14	20.63	0.63	0.17	19.9–22.1	7.70	3.06
	F	19	20.72	0.74	0.17	19.1–22.2	7.79	3.55

various members of the genus have acquired or retained the ability to produce spotted eggs as Selander (1964) found in wrens (*Campylorhynchus*). However, even in this latter genus the major subgroups, *Campylorhynchus* and *Heleodytes*, are differentiated by egg color, one having patterned and the other unpatterned eggs. Egg patterning probably also follows lines of close relationship among some neotropical emberizines, such as *Atlapetes*, *Melozone*, and *Aimophila*.

EXTERNAL MORPHOLOGY

With limited study on, and limited variability of, internal morphology among higher passerines, most taxonomists have relied largely on external morphological characters to separate and define bird genera. In this section I discuss some characteristics of major appendages to assess their importance in classifying *Aimophila*.

Since this is not a study of geographical variation within species, I have lumped all populations of each species, with the exception of the large and small forms of *A. ruficauda*, to arrive at the values presented in Tables

TABLE 14

Measurements of Hallux (mm) in 13 Forms of *Aimophila*

Species	Sex	N	$\bar{x}$	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	48	12.84	0.44	0.06	11.8–13.8	4.18	3.40
	F	61	12.54	0.33	0.04	11.5–13.2	4.15	2.63
r. lawrencii	M	52	13.72	0.37	0.05	12.8–14.6	4.04	2.71
	F	41	13.32	0.42	0.06	12.2–14.1	3.99	3.13
sumichrasti	M	42	11.45	0.48	0.07	10.5–12.5	3.79	4.19
	F	29	11.11	0.35	0.06	10.3–11.7	3.73	3.13
humeralis	M	69	11.49	0.41	0.05	10.6–12.6	3.95	3.59
	F	34	11.25	0.43	0.07	10.2–12.0	3.95	3.83
mystacalis	M	39	11.22	0.45	0.07	10.4–12.1	3.96	3.99
	F	20	11.18	0.31	0.07	10.6–11.6	3.96	2.80
carpalis	M	64	9.67	0.32	0.04	8.8–10.4	3.90	3.34
	F	46	9.53	0.17	0.02	9.0–10.3	3.87	1.75
ruficeps	M	60	10.48	0.51	0.07	9.4–11.6	3.91	4.90
	F	55	10.39	0.53	0.07	9.5–11.6	3.95	5.06
rufescens	M	52	13.25	0.54	0.07	11.7–14.3	3.87	4.04
	F	50	13.07	0.44	0.06	12.0–14.6	3.89	3.40
notosticta	M	5	11.80			11.6–12.1	3.87	
	F	4	11.98			11.6–12.3	3.97	
aestivalis	M	48	11.38	0.40	0.06	10.5–12.2	4.18	3.52
	F	33	11.25	0.42	0.07	10.5–12.3	4.21	3.71
botterii	M	43	11.46	0.41	0.06	10.5–12.3	4.08	3.54
	F	36	11.64	0.44	0.07	10.5–12.4	4.19	3.74
cassinii	M	36	10.61	0.34	0.06	10.0–11.6	4.08	3.18
	F	30	10.63	0.33	0.06	9.9–11.3	4.00	3.08
quinquestriata	M	12	10.16	0.23	0.07	9.7–10.5	3.79	2.28
	F	17	10.12	0.25	0.06	9.7–10.7	3.80	2.43

11 through 19. I attempted to include approximately equal numbers of individuals from various populations of each species to make the values as meaningful as possible. Only adults were measured in those species in which adults and first-year birds are distinguishable. *A. quinquestriata*, for which there were limited numbers of specimens, was the only exception, and as there was little difference in values for young and adults the two age groups were combined. All correlations (r_s) are based on the Spearman rank correlation coefficient (Siegel 1956; Table 20). Equated values presented in the tables are mean measurements divided by cube root of body weight; these values are thus relative and linear (see Amadon 1943).

WING LENGTH

The wing of a bird is the primary appendage for flight; its importance to a bird is obvious. Since the efficiency of a wing is largely dependent on the total area and shape (Savile 1957) that are reflected, to some degree, in wing length, one might expect this dimension to be under strong selective pressures. Assuming a constant flying ability (not necessarily true for this

TABLE 15

MEASUREMENTS OF MIDDLE TOE (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	x̄	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	41	16.13	0.57	0.09	15.3–17.4	5.25	3.55
	F	41	16.03	0.46	0.07	15.0–16.7	5.31	2.85
r. lawrencii	M	42	17.67	0.54	0.08	16.2–18.5	5.20	3.06
	F	35	17.30	0.56	0.09	15.4–18.2	5.18	3.22
sumichrasti	M	32	15.24	0.50	0.09	14.4–16.4	5.05	3.27
	F	24	14.68	0.59	0.12	13.1–15.7	4.93	4.02
humeralis	M	56	14.83	0.59	0.08	13.3–16.0	5.10	4.00
	F	43	14.74	0.69	0.10	12.9–16.9	5.17	4.67
mystacalis	M	33	14.81	0.58	0.10	13.7–16.2	5.23	3.88
	F	20	14.68	0.54	0.12	13.6–15.4	5.20	3.66
carpalis	M	60	12.77	0.44	0.06	11.7–13.5	5.15	3.41
	F	42	12.66	0.49	0.08	11.5–13.2	5.15	3.89
ruficeps	M	59	14.37	0.60	0.08	13.2–16.0	5.36	4.18
	F	56	14.04	0.74	0.10	12.2–15.5	5.34	5.24
rufescens	M	48	18.22	0.82	0.13	16.4–19.6	5.33	4.48
	F	44	17.82	0.73	0.11	16.6–19.2	5.30	4.08
notosticta	M	3	16.70			16.3–17.1	5.48	
	F	3	16.07			15.6–16.7	5.32	
aestivalis	M	46	14.41	0.55	0.08	13.1–15.3	5.30	3.79
	F	33	14.42	0.56	0.10	13.1–15.6	5.40	3.90
botterii	M	43	15.37	0.56	0.08	14.5–16.8	5.47	3.62
	F	32	15.86	0.66	0.12	14.3–17.0	5.70	4.18
cassinii	M	34	14.28	0.52	0.09	13.5–16.1	5.49	3.67
	F	32	14.25	0.38	0.07	13.6–15.0	5.36	2.69
quinquestriata	M	10	13.97	0.36	0.11	13.5–14.5	5.21	2.60
	F	18	14.13	0.33	0.08	13.5–14.7	5.31	3.05

genus), as body size of a bird increases, one expects area and length of the wing to increase to provide the necessary increase in lifting force required for the added weight. However, weight increases as the cube of a linear measure, while area of the wing increases only as the square, and length only linearly; therefore birds might be expected to show positive allometric changes in wing length to compensate for the more rapidly increasing weight. That this is not the case, and that larger birds tend to have larger values for wing loading was shown by Poole (1938).

Wing measurements in this study are only from bend of wing to tip of longest primary and are not strictly comparable to wing-loading indices. However, it seems safe to assume that among most groups of closely related forms there will be little important change in the proximal portion of the wing; at least this seems to hold in *Aimophila* (see section on internal morphology). The wing type is elliptical in the classification of Savile (1957). I have not studied the pattern of wing slots in these forms so am unable to judge the influence this might have on flying efficiency.

In *Aimophila* there was a highly significant positive correlation between

TABLE 16

MEASUREMENTS OF BILL LENGTH (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	x̄	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	63	9.18	0.42	0.05	8.1–10.4	2.99	4.58
	F	57	8.96	0.30	0.04	8.1– 9.5	2.97	3.32
r. lawrencii	M	46	10.63	0.36	0.05	10.0–11.6	3.13	3.42
	F	45	10.39	0.40	0.06	9.7–11.2	3.11	3.85
sumichrasti	M	47	10.12	0.41	0.06	9.1–11.2	3.35	4.08
	F	27	9.66	0.33	0.06	8.8–10.3	3.24	3.40
humeralis	M	70	8.95	0.35	0.04	8.2– 9.8	3.08	3.90
	F	61	8.65	0.33	0.04	7.7– 9.6	3.04	3.77
mystacalis	M	44	8.83	0.21	0.03	8.2– 9.4	3.12	2.33
	F	26	8.54	0.37	0.07	7.9– 9.4	3.03	4.32
carpalis	M	58	7.40	0.30	0.04	6.8– 8.1	2.98	4.12
	F	50	7.25	0.27	0.04	6.7– 7.7	2.95	3.75
ruficeps	M	60	8.14	0.52	0.07	6.7– 9.4	3.04	6.35
	F	57	7.96	0.60	0.08	6.7– 9.3	3.03	7.60
rufescens	M	53	10.73	0.57	0.08	9.3–12.1	3.14	5.29
	F	49	10.45	0.54	0.08	9.2–11.6	3.11	5.20
notosticta	M	5	9.00			8.4– 9.7	2.95	
	F	4	8.68			8.0– 9.1	2.87	
aestivalis	M	48	7.95	0.30	0.04	7.3– 8.7	2.92	3.84
	F	36	7.87	0.35	0.09	7.2– 8.7	2.95	4.42
botterii	M	53	8.11	0.33	0.04	7.6– 9.0	2.89	4.04
	F	38	8.04	0.38	0.06	7.3– 8.8	2.89	4.70
cassinii	M	44	7.68	0.36	0.05	6.8– 8.3	2.95	4.70
	F	37	7.48	0.28	0.05	7.0– 8.2	2.81	3.81
quinquestriata	M	14	8.77	0.36	0.10	8.0– 9.5	3.27	4.16
	F	19	8.61	0.32	0.07	8.1– 9.1	3.24	3.77

mean wing length and cube root of body weight ($r_s = 0.76$; $P < 0.01$). Ten samples were lower in wing rank than in weight rank, or put another way, either weight increased more rapidly than wing length relative to the other species, or these forms had a relatively shorter wing than would be expected from their weight. Of the 10, seven were females and only 3 were males; each species for which there were males was represented also by females, showing that the change is characteristic of the species rather than of a particular sex. *A. botterii* and *A. aestivalis* were represented by both sexes suggesting that this subgeneric group is characterized by relatively short wings and rather poor flight. However, this may be compensated for by the more pointed wings found in these same species (discussed later). *A. cassinii* is in the group having wings longer than expected.

Another way of assessing relative wing length is to consider equated values (Table 11). Within species groups in this genus, individual species have wings of different relative lengths with as much similarity between groups as within groups. Selander (1964) found that within a subgeneric group in wrens (*Campylorhynchus*), equated wing lengths were similar and

TABLE 17

MEASUREMENTS OF BILL WIDTH (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	x̄	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	48	5.12	0.24	0.03	4.5–5.9	1.67	4.61
	F	56	5.11	0.21	0.03	4.5–5.8	1.69	4.19
r. lawrencii	M	45	5.53	0.27	0.04	5.1–6.0	1.63	4.83
	F	42	5.45	0.26	0.04	4.9–5.9	1.63	4.84
sumichrasti	M	45	4.80	0.33	0.05	4.3–5.4	1.59	6.83
	F	25	4.68	0.28	0.06	4.2–5.2	1.57	5.94
humeralis	M	71	4.70	0.23	0.03	4.2–5.4	1.62	4.83
	F	63	4.58	0.28	0.04	4.0–5.3	1.61	6.20
mystacalis	M	42	4.45	0.23	0.04	3.7–4.8	1.57	5.19
	F	27	4.31	0.22	0.04	3.7–4.6	1.53	5.20
carpalis	M	63	4.07	0.21	0.03	3.6–4.5	1.64	5.11
	F	49	3.96	0.22	0.03	3.4–4.3	1.61	5.63
ruficeps	M	60	3.96	0.33	0.04	3.4–5.0	1.48	8.26
	F	57	3.95	0.36	0.05	3.4–4.8	1.50	8.99
rufescens	M	52	5.56	0.41	0.06	4.5–6.5	1.62	7.32
	F	52	5.43	0.33	0.04	4.8–6.1	1.62	6.04
notosticta	M	5	4.30			4.2–4.4	1.41	
	F	4	4.25			4.0–4.4	1.41	
aestivalis	M	48	4.17	0.20	0.03	3.7–4.7	1.53	4.58
	F	36	4.15	0.19	0.03	3.9–4.7	1.55	4.58
botterii	M	53	4.20	0.18	0.02	3.8–4.7	1.49	4.34
	F	37	4.27	0.24	0.04	3.7–4.8	1.54	5.25
cassinii	M	45	3.95	0.21	0.03	3.5–4.3	1.52	5.37
	F	37	3.91	0.21	0.03	3.4–4.2	1.47	5.29
quinquestriata	M	14	4.29	0.16	0.04	3.9–4.5	1.60	3.82
	F	18	4.41	0.19	0.04	4.1–4.7	1.66	4.33

that they differed between subgroups. In wrens each subgroup is composed of essentially allopatric species occupying the same habitat type. Sparrows are more sympatric, but often occupy different habitat types within the same general plant formations and may forage differently. These differences are apparently reflected in relative wing lengths, so that various species within a subgroup show more divergence than is found in closely related forms that are more ecologically similar.

Hamilton (1961) has presented a more detailed discussion of adaptive trends in wing length than will be attempted here, but I would like to mention certain parameters, in particular, that seem to influence interspecific trends in wing length in *Aimophila*. Since the species generally have wide latitudinal ranges, Allen's rule is not pertinent.

In *Aimophila*, considered only interspecifically, relative wing length shows a highly significant negative correlation ($r_s = -0.76$, $P < 0.01$; Fig. 8) with mean body weight, showing that the positive correlation based on absolute length depends primarily on body weight variation in the genus. In reality, increase in wing length is not isometric with weight increase, but

TABLE 18

MEASUREMENTS OF BILL DEPTH (mm) IN 13 FORMS OF *AIMOPHILA*

Species	Sex	N	$\bar{x}$	SD	SE	Range	Equated value	Coefficient of variation
r. acuminata	M	48	7.40	0.43	0.06	6.5–8.7	2.41	5.76
	F	51	7.07	0.30	0.04	6.3–7.6	2.34	4.28
r. lawrencii	M	41	8.18	0.24	0.04	7.6–8.6	2.40	2.96
	F	40	7.94	0.32	0.05	7.3–8.5	2.38	4.00
sumichrasti	M	44	7.23	0.24	0.04	6.8–8.0	2.39	3.33
	F	23	6.87	0.28	0.06	6.3–7.3	2.30	4.15
humeralis	M	65	6.42	0.28	0.03	5.9–7.0	2.21	4.33
	F	59	6.18	0.26	0.03	5.7–6.8	2.17	4.13
mystacalis	M	41	5.90	0.27	0.04	5.3–6.4	2.08	4.58
	F	25	5.78	0.21	0.04	5.4–6.3	2.05	3.70
carpalis	M	56	5.56	0.24	0.03	5.1–6.3	2.24	4.28
	F	43	5.36	0.21	0.03	4.9–5.7	2.18	3.97
ruficeps	M	58	5.17	0.30	0.04	4.5–5.7	1.93	5.74
	F	55	5.10	0.32	0.04	4.5–5.7	1.94	6.20
rufescens	M	49	8.15	0.49	0.07	7.0–9.0	2.38	5.98
	F	46	7.78	0.54	0.08	6.5–8.7	2.32	6.94
notosticta	M	5	6.06			5.7–6.6	1.99	
	F	3	5.60			5.0–6.0	1.85	
aestivalis	M	48	5.56	0.23	0.03	5.2–6.2	2.04	4.21
	F	32	5.56	0.25	0.04	5.1–6.1	2.08	4.57
botterii	M	43	5.51	0.24	0.04	5.2–6.2	1.96	4.31
	F	29	5.48	0.30	0.06	5.0–6.2	1.97	5.42
cassinii	M	38	4.92	0.16	0.03	4.5–5.5	1.89	3.56
	F	25	4.87	0.16	0.03	4.5–5.1	1.83	3.33
quinquestriata	M	13	5.51	0.23	0.06	5.1–5.9	2.06	4.16
	F	18	5.50	0.27	0.06	5.2–6.0	2.07	4.85

is negatively allometric. Then, on the basis of relative wing length, the larger species should be less capable fliers. But flying efficiency is also related to factors other than weight.

In general, several aspects of the biology of the sparrows might affect wing length. One obvious selective factor is seasonal movements; migratory forms might be expected to have relatively longer wings to promote flying efficiency. Among the migratory species—*A. botterii*, *A. aestivalis*, and *A. cassinii*—only the last shows an exceptionally long wing. Wing shape may also influence flying efficiency (Averill 1925), and the three migratory forms have the most pointed wings, or wings with the tip placed most distally. In these three species, primary 7 or 8 is longest and 9 is longer, usually, than at least 1 to 3. The other species have primary 5 or 6 longest, and 9 is usually about the same length or shorter than 1. This obviously does not consider actual differences in feather lengths, which also influence wing shape (Johnson 1963), but it points up a dichotomy that seems to exist in spite of rather marked differences in wing length, either absolute or relative. It suggests that wing shape may be a conservative character in these

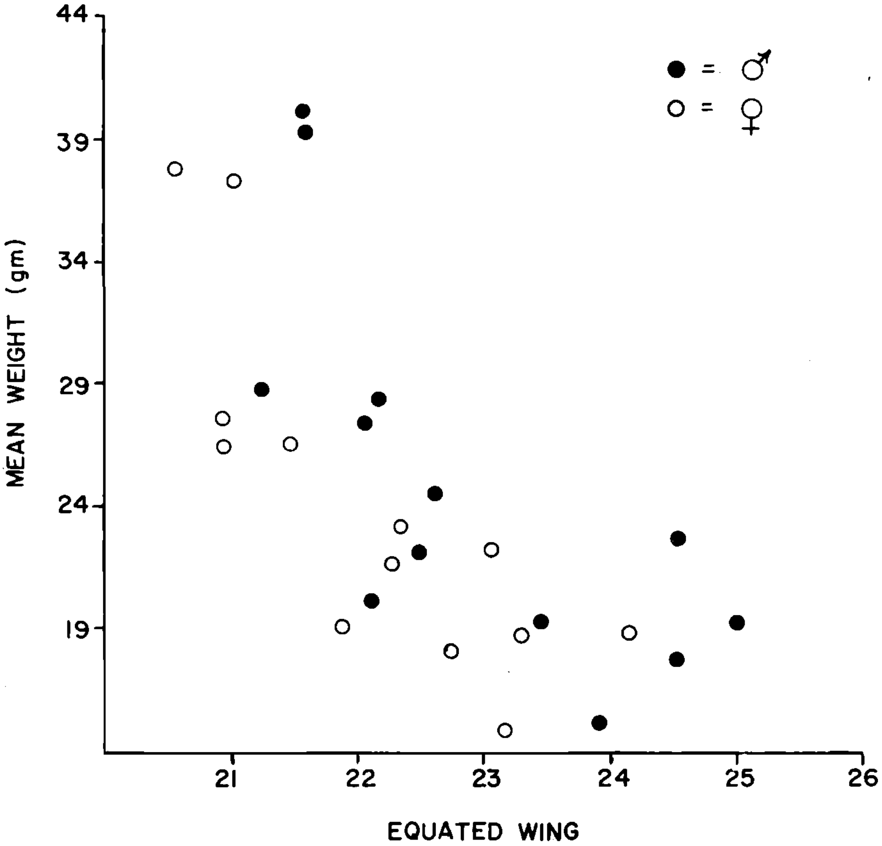

FIGURE 8. Relationship between mean body weight and equated wing length for 12 species (13 forms) of *Aimophila*. Males are represented by dots, females by circles.

sparrows, which changes less than length. It may be, as apparently is true in other forms (Hamilton 1958), that migratory habits of the *botterii* group are the primary selective force for a more pointed wing tip. But as Hamilton pointed out, "the degree of validity of these ideas [relation of wing length and shape to migration] has not been established."

Foraging techniques, while rather uniform within the genus, do show some differences that might be reflected in relative wing length. *A. mystacalis*, compared to other forms, spends long periods foraging in trees and has relatively long wings; however, *A. humeralis*, which also forages extensively in trees, has a wing of average relative length. In general, foraging techniques do not appear to be very influential on wing length in this genus.

TABLE 19

AIMOPHILA BODY WEIGHT

Species	Sex	N	$\bar{x}$	SD	SE	Range	$\sqrt[3]{\ }$
r. acuminata	M	48	28.84	1.76	0.25	25.7–32.4	3.07
	F	25	27.58	1.47	0.29	25.4–30.4	3.02
r. lawrencii	M	34	39.27	2.73	0.47	31.5–44.7	3.40
	F	19	37.30	2.44	0.56	31.5–41.2	3.34
sumichrasti	M	50	27.43	1.34	0.19	24.7–30.1	3.02
	F	31	26.54	1.93	0.35	23.1–30.0	2.98
humeralis	M	45	24.60	1.61	0.24	20.7–27.5	2.91
	F	26	23.23	1.78	0.35	19.1–27.6	2.85
mystacalis	M	36	22.78	1.37	0.23	19.9–25.9	2.83
	F	22	22.19	1.36	0.29	19.3–24.2	2.82
carpalis	M	44	15.02	1.09	0.16	12.6–17.5	2.48
	F	24	14.96	1.15	0.23	13.0–16.9	2.46
ruficeps	M	59	19.33	1.48	0.19	16.0–23.3	2.68
	F	39	18.13	1.31	0.21	15.2–20.3	2.63
rufescens	M	36	40.44	2.51	0.42	36.4–47.9	3.42
	F	28	37.92	1.79	0.34	34.1–41.6	3.36
notosticta	M	8	28.40			26.5–30.0	3.05
	F	2	27.7			26.4–29.0	3.02
aestivalis	M	12	20.16	1.42	0.41	18.4–22.6	2.72
	F		19.08				2.67
botterii	M	21	22.23	1.85	0.40	16.4–25.2	2.81
	F	6	21.60			19.2–23.5	2.78
cassinii	M	20	17.60	1.00	0.22	16.0–19.5	2.60
	F	5	18.84			17.5–19.8	2.66
quinquestriata	M	23	19.33	1.10	0.23	17.1–21.7	2.68
	F	4	18.82			17.9–19.5	2.66

Miller (1931) and Pitelka (1951b) thought that foliage density might affect wing length through its influence on amount of flying, distance of flights, and type of flying. In more closed habitats, birds tend to have short, rounded wings that enhance maneuverability, while birds in more open habitats require longer wings as the amount of flying increases. This is especially evident for *A. mystacalis*, *A. cassinii*, and *A. carpalis*. Other forms, such as *A. ruficauda*, *A. ruficeps*, and *A. rufescens*, that also occur in open habitats forage more on the ground and fly appreciably less than the former three. They are seldom far from cover and rarely make long flights.

It is difficult to determine the influence of altitude on wing length, but it may, in part, account for the relatively long wing of *A. mystacalis*.

The long wing of *A. quinquestriata* is puzzling. While its habitat is closed at canopy height, the understory where the birds spend much of their time is usually more open. The little available information suggests that *A. quinquestriata* is most like *A. mystacalis* in foraging behavior, and it usually sings from elevated perches. Also, *A. quinquestriata* could be descended from a group of relatively long-winged forms.

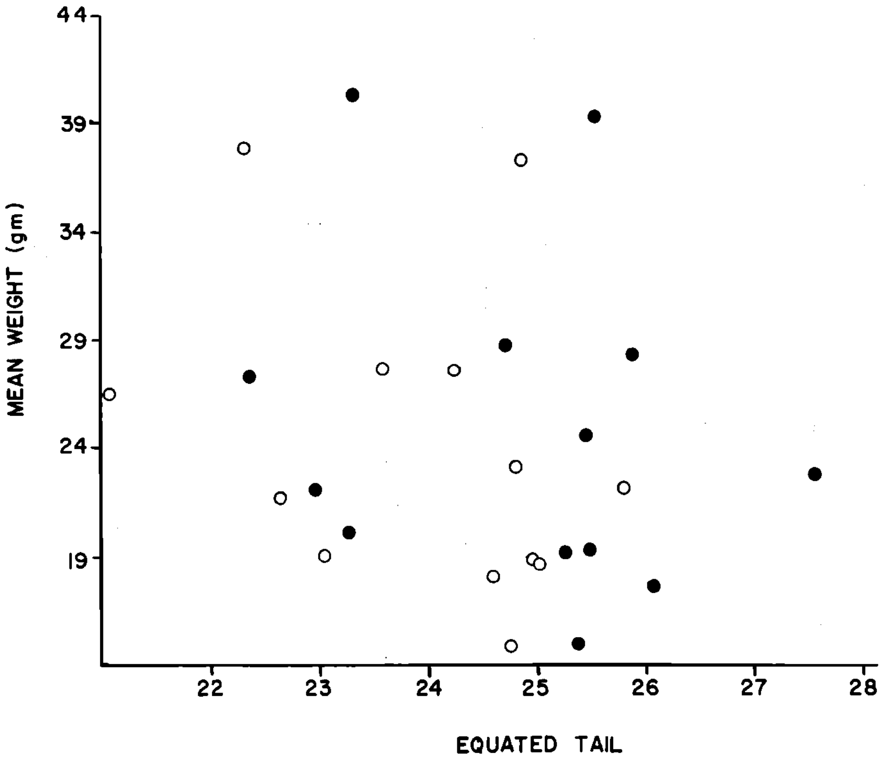

FIGURE 9. Relationship between mean body weight and equated tail length for 12 species (13 forms) of *Aimophila*. Males are represented by dots, females by circles.

Another factor affecting wing length may be actual amount of flying done by a species in daily activites, so the relatively long wing of *A. cassinii* may be correlated with importance of display flight. Similarly, birds that are very active in territorial confrontations may have longer wings. Wing length may also be related to distance between foraging and nesting sites. Differences in these distances among the sparrows are subtle and I do not have sufficient information to evaluate their influence on wing length.

Thus, as discussed by Hamilton (1961) on an intraspecific level, diverse selective pressures act on wing length. Among these sparrows the most critical relation seems to be between body size and relative wing length. However, the relation is not what one might expect, and at present I am at a loss to explain why it apparently overrides other selective forces. It is interesting that this relationship is true both for wing length (as measured from bend of wing to tip of longest primary) and for total wing length (as

TABLE 20

SPEARMAN RANK CORRELATION COEFFICIENTS (r_s) AND PROBABILITY LEVELS FOR VARIOUS COMBINATIONS OF CHARACTERS*

Characters considered	r_s	p
Wing/body weight	0.75	<0.01
Tail/body weight	0.76	<0.01
Tarsus/body weight	0.89	<0.01
Wing/tail	0.63	<0.01
Bill length/width	0.52	<0.01
Bill length/depth	0.61	<0.01
Wing/tarsus	0.09	>0.50
Equated tarsus/weight	0.01	>0.50
Equated wing/weight	–0.76	<0.01
Equated tail/weight	–0.19	>0.05

* N = 26 for all combinations of characters.

shown by the sum of the relative lengths of the three long wing bones—see section on internal morphology).

TAIL LENGTH

The tail is positively correlated with weight ($r_s = 0.76$, $P < 0.01$). However, equated values of tail length show a slight, but not significant, negative correlation ($r_s = -0.19$; $P > 0.05$) with mean body weight (Fig. 9); hence tail length is not strictly a function of body size within the genus. The significant positive correlation of wing and tail length (Table 20) probably indicates their common relationship to body weight and possibly their functional unity. This is not to say that wing and tail sizes cannot be or are not under divergent selective pressures.

Pitelka (1951b) noted that certain jays (genus *Aphelocoma*) in southern Mexico had longer tails than northern representatives of the same species; he attributed it to selection for greater flying ability in the taller, more open southern habitat (Pitelka 1951b: 309, footnote). Tail length probably is important in helping to provide balance and maneuverability in flight. Fisher (1959) showed that tail feathers are important in the braking motion associated with landing in birds. This is especially true of birds that have powerful flight or a relatively heavy body mass. In *Aimophila* the particularly long-tailed forms are those found in relatively open habitats. The only exception is *A. quinquestriata*, which has long wings and tail but occurs in tropical deciduous woodland. The long tail of this species probably is related to maneuverability in the fairly open understory where the birds spend much time.

The tail also may be selected as an important morphological part of certain display patterns in birds (e.g. birds of paradise and trogons). This may be an important factor in *A. cassinii* in which the tail is spread as a brake and apparently also as a display during the flight song performance. Additionally, the tail may be important in the display during the squeal duet by members of the *Haemophila* complex. Usually at some time during the performance, one or both members of the pair depresses and spreads the tail. There are no distinctive markings in the tails of most species, but tail length might be selected to make the tail more conspicuous during the display.

The long tails of *A. mystacalis* and *A. humeralis* are presumably related to amount of time spent foraging in trees. A long tail may be used as a balancing device as the birds clamber through the vegetation (Engels 1940, Selander 1964). For *A. mystacalis* it probably also increases maneuverability in their open habitat. The small white markings on the tip of the tail of *A. mystacalis* may indicate some sort of communicatory value for the tail, in addition to its importance in the duet performance.

Selective pressures also operate to shorten the tail. Short-tailed forms are primarily those occurring in closed habitats with a nearly continuous ground layer at certain times of year. A short tail enables the bird to move more easily through dense ground vegetation. Although *A. botterii* occupies open sites, its short tail is not unexpected as there is often little tall vegetation above the grass layer in its habitat; also, this species makes few long flights, except when feeding young. The male, even when actively singing, does not use particularly high perches, usually because none are available.

The actual shapes of the tail and its individual feathers have been used in various generic diagnoses. In *Aimophila* the tail is rounded or doubly rounded and is essentially identical among the several species. The first pair (1-1) of rectrices is usually shorter than the next two pairs, making the center of the tail slightly notched. The longest pair is either 2-2 or 3-3; this varies individually, but not consistently, among the species. The outer three pairs are progressively shorter than the inner pairs, with the outermost (6-6) approximately 75% of the length of the longest pair, so the tail is slightly graduated. The tail feathers of the *botterii* complex may average slightly narrower than those of the other species. Rectrices of *A. ruficauda*, especially the central pair, may be narrower than those of other members of the complex, but in general the shape of the rectrices does not vary enough to separate the genus into species groups.

As in the Brown and Rufous-sided Towhees (Davis 1951, 1957) and the Scrub Jay (Pitelka 1945), the shape of juvenal rectrices in *Aimophila* sparrows is different from that of adult rectrices. Juvenal rectrices average narrower and the distal ends are more acute than in the adults. For a short period after postjuvenal and postnuptial molts this character is useful for aging specimens, but wear of feathers is so rapid that it soon becomes difficult to determine age accurately. Although juvenal rectrices apparently average slightly shorter than those of adults, this does not affect the shape of the entire tail.

TARSUS LENGTH

The tarsus in these sparrows is the large appendage most highly correlated with body weight ($r_s = 0.89$, $P < 0.01$). It is perhaps most directly responsive to body weight changes because it serves to maintain the stature of a bird. In other words, it is probably the appendage that is most concerned with support of body weight for the majority of time in these birds and is most significant in their ability to exploit the environment. The tarsus does not have this significance for some arboreal and all aerial foragers, which are more dependent on flying ability to achieve the highest degree of foraging success.

While many authors have tried to use wing length as an indicator of body size, the correlations in *Aimophila*, *Aphelocoma* (Pitelka 1951b), *Passerella* (Linsdale 1928), and *Junco* (A. H. Miller 1941) suggest that tarsal length is a more appropriate measure for species in which foot locomotion is more important than flying; arboreal foragers would probably show a stronger correlation between wing length and body weight.

Tarsal length is not correlated with wing length ($r_s = 0.09$, $P > 0.50$), and although both show strong correlations with body weight, the equated values are correlated differently in each case. The lack of correlation between tarsus and wing is further evidence of the independence of the two appendages.

While the absolute values for tarsal length show a marked positive correlation with body weight, equated values for tarsal length are not so correlated ($r_s = 0.01$, $P > 0.50$; Fig. 10). Tarsal length seems to increase nearly proportionately in all species; the equated values remain about the same, with the slight exception of *A. sumichrasti*, which has a noticeably short tarsus relative to the other species. The cause of this is unknown, but may be related to the generally more compact structure of this species with selection for increased leg support by shortening of the tarsus. The short tarsus of *A. humeralis* is probably related to the increased arboreal foraging that characterizes this species, or it may be related to increased bulk at the expense of increased length. While the shorter tarsus may seem to be the reverse of the relationship reported by Selander (1964) in the wrens (*Campylorhynchus*), it is probably valid. This sparrow species, while foraging frequently in trees, does not do so actively. Hence a shorter tarsus may actually be a more advantageous way to meet the dual need of both increased strength for support while on the ground and to promote efficient foraging in arboreal situations. A lengthened tarsus in *A. notosticta* may

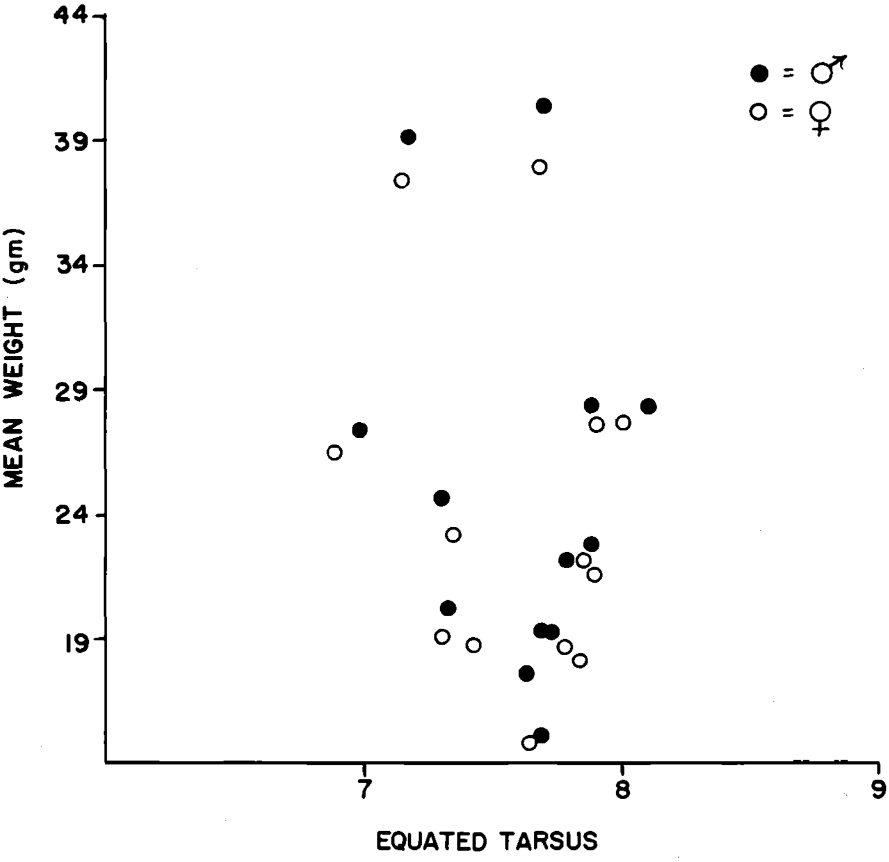

Figure 10. Relationship between mean body weight and equated tarsal length for 12 species (13 forms) of *Aimophila*. Males are represented by dots, females by circles.

correlate with more arboreal habits or more agility in using its feet. It would be interesting to know if this species hops (short tarsus) or runs (longer tarsus) more than its close relatives.

In thrushes (*Catharus*), species with greater body weight tend to have shorter, but bulkier or wider, tarsi relative to body weight to provide more support to the body at the expense of increased length (Dilger 1956). In general the increase in body weight in *Campylorhynchus* tends to be accompanied by an increase in tarsal length, the heaviest birds having relatively the longest tarsi (Selander 1964). This suggests that the relationship between tarsal length and body weight is different for the several types of birds. Most of the wrens are arboreal foragers to a greater degree than either the thrushes or the sparrows, and even within *Campylorhynchus* those species that hop and those that run along the ground have more elongated tarsi than other members of the genus; hence a short, strong tarsus does not seem to be selected by the type of locomotion in which the species engages, but rather the usual substrate and the manner of foraging. Stronger tarsi probably are advantageous to ground foragers while arboreal foragers in general tend to lengthen the tarsus at the expense of increasing strength.

Sparrows and *Catharus* thrushes are both primarily ground foragers, but each has different relative tarsal lengths. The sparrows are under strong selection to maintain an isometric relation between increase in body mass and tarsal length. The difference shown by the thrushes may be related to less stringent selection for tarsal length. Two selective factors may influence tarsal length in these two ground foragers: technique and position of foraging, or comparative construction of the birds. Sparrows are more compactly built than thrushes and forage much more methodically over the ground. J. Davis (1957) and Dilger (1956) have suggested that in ground foragers two interrelated selective pressures act directly on tarsus length. In moving along the ground a bird may either hop or walk (running is a fast walk). However, type of movement may be related to character of the substrate. Walking is more prevalent among species that forage on nearly to completely bare ground, and hopping among species which forage in litter. The bounding motion facilitates movement through the litter. In *Aimophila* most ground foraging is in relatively bare areas, although some species, especially *A. rufescens*, work in varying amounts of litter. Most species move by walking. I think little differential selection on tarsal length has been exercised by either of these factors within *Aimophila.*

In *Aimophila* and possibly other genera, selection for increased bulk of the tarsus as well as for changes in length seems to occur. Length changes usually seem to be related to certain functional needs of movement along a solid substrate or for specialized functions, such as determining depth of wading in shorebirds. However, strength of the appendage may be equally important to species that are primarily adapted for ground foraging. As a consequence, while it may be adaptive to have a longer tarsus, selection for strength may play an active counter-role.

Storer (1955) pointed out marked differences in body size between the northern and the more southern forms of *A. ruficauda*, but tarsal length varies little. The tarsus is slightly longer in the southern forms, but equated values for the two groups of populations show that of *A. r. acuminata* to be nearly the longest of the genus, while *A. r. lawrencii* is essentially the shortest. Therefore, in this particular species, tarsal length is not an adequate indicator of body size. However, even including this species did not render tarsal length less highly correlated than wing or tail.

TOE LENGTH

Toe size is used here as a measure of relative foot size of each species. Foot size should be an important aspect of external morphology for all species and especially so for those in which the foot is important in foraging and locomotion, e.g. jays, which seem to move through arboreal foliage as much by hopping as by flying. In species such as some titmice, parrots, etc., the feet are used in conjunction with the bill in handling some food items and might be under selective pressures for modifications to promote this technique. Most members of *Aimophila* are primarily ground foragers, although some also spend considerable time foraging vireo-like through the trees. It would seem that for all these forms foot size would be important.

As a measure of foot size, I summed values for the hallux (Table 14) and middle toe (Table 15; there is a very strong positive correlation between this measure and body weight ($r_s = 0.94$, $P < 0.01$). However, the same correlation based upon equated values rather than absolute values shows only a slight positive correlation that is not statistically significant ($r_s = 0.22$, $P > 0.05$). Thus, while absolute foot size tends to increase as body size increases, this apparently is not equally true among all forms.

The largest relative foot size is found among members of the *Peucaea* group. These are almost entirely ground and shrub birds, except that song perches of some males, especially *A. aestivalis*, are more elevated. *A. ruficauda* has somewhat large feet and is perhaps the most terrestrial of that group. *A. rufescens* might be expected to have large feet correlated with its well-developed scratching method of foraging. Total foot size is not comparatively large because the hallux is short, but the middle toe is relatively long. In a backward hopping motion the middle toe might produce the most pressure on the substrate and hence be most modified for this purpose.

Foot size can show little more for taxonomic purposes than possible importance in the life of the bird. If one is to use this character for taxonomy, as for example in defining genera on the basis of relative middle toe or hallux sizes, then the supposition follows that the genera are composed of common ecologic types and do not include species with different locomotor or foraging techniques.

BILL PROPORTIONS

In this section I will consider bill types in the genus and how they may reflect the character of the entire jaw apparatus (the latter is treated more fully in the section on internal morphology). Bowman (1961) in his analysis of the Geospizinae presented a discussion of the functional significance of bill shape in these species, in which he carefully pointed out force factors involved in bill shapes (see more recent analysis by Bock 1966). In addition to force factors operating on bill shape, there is another obvious factor (also investigated by Bowman): function in grasping food items. In other words, bill type is influenced by pressures involved in eating and by efficiency of different bill shapes in obtaining food items.

I arbitrarily classed the several equated values for length (Table 16), width (Table 17), and depth (Table 18) of bills of various species and the bill ratios into three size classes: large, medium, and small. By combining the 3 categories I was able to estimate bill type—either strong, medium, or weak—of the 12 species. The three strong bills are deep and usually wide, even though *A. sumichrasti* has a narrower bill than the other two. Usually the bill is also comparatively long, although *A. ruficauda acuminata* has a relatively short bill (low equated value) even when compared to the remainder of the genus. Length would not appear to be an important characteristic of a strong bill, but rather a result of a relationship between growth of bill in length while increasing in width and depth. For these sparrows, it obviously is important to consider amounts of animal and plant foods taken and types of each (see section on general biology). Kear (1962) and Hespenheide (1966) have shown that bill size in certain finches influences efficiency of exploitation of seed sizes.

The smaller, weaker bills belong to two members of the *ruficeps* group—*A. ruficeps* and *notosticta*—and two members of the *botterii* group—*cassinii* and *botterii*. *A. aestivalis* has a deeper bill than the latter two. Probably *A. ruficeps* has the weakest bill, which is narrow and long, the added length probably decreasing the overall strength. The bills of remaining species are classed here as having medium strength. These include three members of the *Haemophila* complex, plus *A. aestivalis* and *quinquestriata.* Hence it appears that the members of the *Haemophila* complex all have rather strong bills while the other two groups, plus *A. quinquestriata,* have generally weaker bills. The major exception, *A. rufescens,* probably results from competition with its close relative, *A. ruficeps,* or evolution into a "vacant" food exploitation type. Each group of sparrows in this genus has apparently had a separate evolutionary pathway in recent times, such that modifications have produced more overlap in bill type in the species now extant, although initially the groups presumably had different general bill strengths.

The relative sizes of the adductor jaw muscles tend to follow those of bill strength. This means, as Bowman found, that the two are probably closely related functionally, and hence bill characters in large part may indicate relative strengths of the total trophic apparatus. By this I do not wish to imply that a single character of the bill, such as culmen length, will give a valid indication of the trophic apparatus. Klopfer and MacArthur (1961) used this character to indicate similarities and differences in trophic apparatus, but it appears that, taken alone, this measure has little relevance to actual relationships between the trophic apparatus of species with markedly different food habits. Bill strength of seed foragers probably is of greatest importance in determining the food most efficiently taken, while actual length may be more important to a probing species. The usual three measurements—length, width, depth—would have to be made on seed eaters before a comprehensive understanding could be gained of the trophic relationships of the species, as judged by this characteristic. While Schoener (1965) considers this possibility but briefly, it may help to explain some of the peculiarities he noted in the fringillids. It is interesting to note that van Valen (1965) used bill width as a measure of structural differences in certain bird species in comparing structural and ecological variability.

DISCUSSION OF APPENDAGES

In addition to correlations of body size with various of the appendages, I correlated various appendages with one another (Table 20). There is a significant positive correlation of wing length to tail length, but there apparently is no correlation of wing to tarsus (Fig. 11). While both wing and tail probably are related via common responses to increasing size, they are actually under quite different selective pressures, as equated values do not show the same relation to body size. Wing and tarsus, on the other hand, both seem to increase in size as body weight increases, but they increase at different rates so they are not positively correlated (Table 20). One might expect such a result with two appendages that functionally are related to moving the body, but in different ways and for different purposes. While both wing and tail are related, at least in part, to flight, the tarsus is primarily concerned with locomotion on a solid substrate. A more marked positive correlation might exist if the two sets of appendages were equally important in the life of the birds.

The decreased correlations of the various appendages among themselves as compared to each on body weight suggests that there is a stronger relation of these appendages to body weight than to each other. Carried to an extreme, this suggests that comparisons of appendage ratios such as wing/tail and wing/tarsus are taxonomic artifacts without biological significance, and such ratios should be given little consideration unless they can be shown to be relevant to the biology of the species being considered. The actual values of several ratios for these sparrows and some closely related emberizine genera appear in Table 21. Using these values as taxonomic characters, the species of *Aimophila* could be placed in *Junco, Ammodramus, Melospiza,* or *Pipilo.* Paynter (1964) has already pointed out the futility

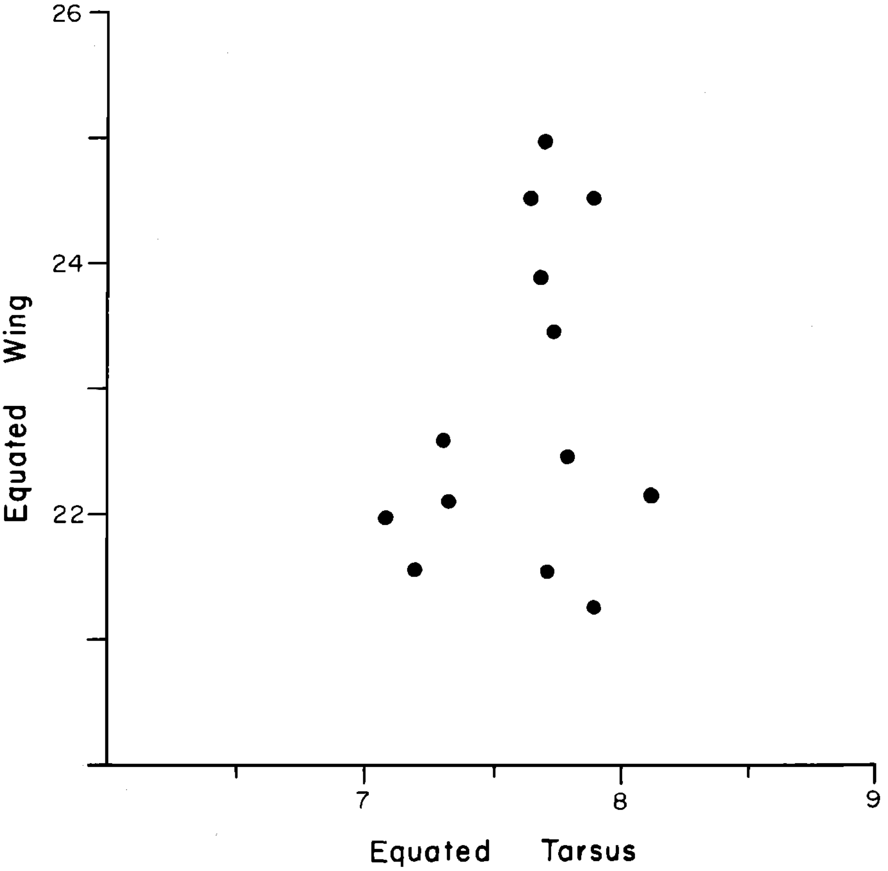

FIGURE 11. Relationship between equated wing length and equated tarsal length for 12 species (13 forms) of *Aimophila*; males only.

of using appendage ratios to separate genera among some emberizines; this probably holds for all emberizines.

Although wing/tail ratios are nearly the same for each sex of a species, the same does not hold for wing/tarsus ratios. In all cases the female averaged smaller, so they had either relatively longer tarsi or shorter wings than the males. Table 11 shows that equated wing values average smaller (females = 22.14; males = 22.87) in the females, while equated tarsal length (Table 13) is more nearly similar in the two sexes (males = 7.62; females = 7.60). The significance of these differences undoubtedly lies in the relative importance of the appendages in daily activities of each sex. The male in general is much more concerned with territorial proclamation and de-

TABLE 21

APPENDAGE RATIOS FOR SEVERAL GENERA OF EMBERIZINES*

Genus	Ratios	
	Wing/tail	Wing/tarsus
Aimophila	⩽1:1	2¾ to 3½:1
Ammodramus	⩽1:1	2⅔ to 3:1
Amphispiza	>1:1	>3:1
Arremonops	>1:1	⩽3:1
Brachyspiza	>1:1	3+:1
Chondestes	>1:1	4½:1
Junco	⩽1:1	<3 – >4:1
Melospiza	⩽1:1	2⅔ to 3:1
Melozone	⩾1:1	2¾ to 3½:1
Passerella	⩽1:1	3½ to 3⅔:1
Pipilo	>1:1	2½ to 4:1
Plagiospiza	≦1:1	<3:1
Spizella	≦1:1	3.2 to 4:1
Zonotrichia	≦1:1	3 to > 3½:1

* Data taken from Ridgway (1901).

fense than the female, while the female is more concerned with the actual reproductive effort and probably does more of the feeding of the young. I have no information that can be interpreted to show a difference in the foraging substrates or repertoires of the two sexes in any of the species, but the possibility exists.

Appendage ratios, however, may be useful in characterizing genera that are thought on other grounds to be evolutionary units and that seem to show the same adaptive responses because they occupy the same sort of habitat and use it in much the same way over the range of the genus. Where there is a large degree of sympatry with consequent shifts in adaptive values for certain types of characters, one might expect these ratios to have little meaning. Selander (1964) found that the ratios are meaningful in wrens (*Campylorhynchus*) in which most of the species are essentially allopatric and hence have diverged little in morphological characters in response to apparent competition from closely related species. The opposite effect is shown by the sparrows reported here.

The correlations of bill measurements are generally lower than those for other appendages, except the wing/tarsus ratio. This suggests that the various elements of bill size—length, width, depth—while parts of a functional whole, can be modified within limits to produce a different sort of trophic apparatus. The low correlations probably reflect diversity of bill structures and increased intrageneric competition encountered in overlapping rather than allopatric ranges. The competition resulting from sympatry that one might expect can in large part be relieved by changes in food preference which may be accomplished by changes in bill structure. This was shown by Bowman (1961) and Lack (1947) for the geospizinae, and others have suggested a similar situation in continental species (Vaurie 1951, Bock 1964b; see review of character displacement by Brown and Wilson 1956).

It is also possible that this reduced correlation does not reflect diversity of trophic apparatus as a result of competition but rather reflects temporal changes that have occurred for other reasons and which have left the bill functionally unchanged but different enough to allow sympatry. In other words, the same bill force or power can probably be achieved by several sorts of bills that differ structurally. This is especially true if one is considering only the external morphology of the bill rather than the entire bill complex. Obviously the character of muscle masses and various aspects of the bony skull influence bill strength. In large part bill structure determines feeding habits but the bill must be able to operate within a certain range of pressures that can be achieved by the other elements of the jaw apparatus. However, one would expect similar bill structures among closely related forms. Although power and size of the bill of the species of *Geospiza* are radically different, there are structural similarities that seem to characterize the genus (Bowman 1961).

Bock (1964b) and Lack (1947) noted that bill shape may play an important role in species recognition in some fringillids. Whether this is a secondary use of a primarily feeding adaptation or has significantly affected bill shape in itself is not known. In *Aimophila* there is no reason to believe that bill structure plays more than a very minor role in species recognition, and hence it probably has been little modified for this function.

Analysis of Variation

The only analyses of variation possible from this study are those based on coefficients of variation calculated for each species taken as a whole, rather than on a populational basis. Most other studies have focused on intraspecific variation and were done on a populational basis. For only three taxa, *Zonotrichia leucophrys*, *Dendrocopos stricklandi*, and *Campylorhynchus*, were numerical values given in the discussion of variation in the group. I have tabulated values and rank order of variation for external measurements in Table 22.

In general, as one might expect of geographically varying species in which the populations are not segregated, coefficients of variation for *Aimophila* are larger for each respective character than for any of the other avian taxa mentioned above. The only exceptions among passerines are variability of hind toe and bill length of *Campylorhynchus*. Selective pressures on these characters in wrens probably are different than in sparrows, probably related to functional significance of these appendages for each

TABLE 22

RANK AND NUMERICAL VALUE OF COEFFICIENTS OF VARIATION OF SEVERAL SPECIES AND GENERA OF BIRDS[1]

	Character							
Genus[2]	Wing	Tail	Tarsus	Bill length	Bill width	Bill depth	Hind toe	Middle toe
Dendrocopus	1(1.74)	3(3.54)	2(3.27)	4(4.73)	—	—	—	—
Aphelocoma	1	2	3	8	7	6	5	4
Campylorhynchus	1(2.31)	2(2.74)	3(3.04)	8(4.57)	7(4.27)	6(4.13)	4(3.48)	5(3.64)
Pipilo	1	2	3	6	—	5	4	—
Junco	1	3	2	4	—	6	8	5
Aimophila	1(3.35)	5(4.12)	2(3.36)	6(4.28)	7(4.50)	8(5.52)	3(3.39)	4(3.71)
Zonotrichia	1(2.38)	—	2(2.52)	4(3.63)	—	—	—	3(3.17)
Range	1	2–5	2–3	4–8	7	5–8	3–8	3–5

[1] All except *Aimophila* are based on intrapopulational variation. Note that there are not equal numbers of characters ranked for each species; the numbers refer only to rank order within the species.

[2] Data from: Banks 1964; J. Davis 1951, 1965; A. H. Miller 1941; Pitelka 1951b; Selander 1964; this study.

genus. Actual bill length in wrens probably could vary more than that of sparrows and still be equally effective as a foraging instrument. In sparrows the bill is probably more completely a functional unit. In wrens bill length probably is mainly concerned with food sources that can be exploited as determined by use of the bill in probing. There is undoubtedly much less rigid selection on length as a functional portion of the bill unit in wrens. The variability of bill length in wrens is much greater in the *Campylorhynchus* division than in the *Heleodytes* division. Species in the former group seem to probe more than those of the latter group, which more often pick items from the substrate in the relative open (Selander *op. cit.*). This leads me to believe that variability may indeed be related to food source exploitation as a means of reducing intrapopulational competition. Similarly, occurrence of selection for variability or reduced selection for conformity might enable a given species to exploit a wider range of food sources than would be possible for the sparrows; intrapopulational competition within the wrens might thereby be effectively reduced (see Selander 1966).

Hind toe differences of *Campylorhynchus* may be related to variety of perches used by wrens. I found no evidence that feet are important in foraging by these birds. Since feet function as support for a bird, one might expect species that use a wide diversity of perches to show more variation than those in which perches are less diverse and the hind toe can specialize for a limited number of substrates. The predominantly ground-foraging sparrows seem to fall into the latter category.

In *Dendrocopos*, only the coefficient of variation of bill length is greater than the corresponding measure in *Aimophila*. Davis (1965: 565–568) presented information on the Strickland Woodpecker (*Dendrocopos arizonae stricklandi*) which supports the hypothesis that the high degree of variability is related to increased sexual dimorphism, and intrasexual variability correlated with a possible expansion of range of foraging techniques used or at least a broadening of the manner of habitat exploitation. Selander and Giller (1963) and Selander (1966) have presented data for other species of woodpeckers, primarily *Centurus* spp. that support the same hypothesis. In general, expansion seems to occur in those species in which there is reduced competitive pressure from other species that share the foraging technique or food items; or put another way, it occurs in those species in which variability of the unexploited habitat is sufficient to select for differences in bill length as a means of broadening the exploitation pattern.

In general, the pattern of variation in *Aimophila* follows that found for other genera of birds. In all these studies the wing was the least variable element, undoubtedly related to the importance of this appendage in flying. Usually the tail and tarsus are the next least variable with the relationships between the two appendages differing from genus to genus. In *Aimophila*, however, the tail measurements are only less variable than those of the bill. In part this may be due to the large number of summer specimens and the resultant number of birds in worn plumage that were measured. To reduce this factor I tried to exclude from my measurements all specimens in which the total length of the tail appeared to be affected by wear, and it should play little role in the high average variability shown. Another minor factor may be the small number of available specimens that could be measured. This probably would increase the standard deviation if the total range of values for the species were included. Seemingly more important would be the especially high values for variation obtained for several species—*A. botterii, A. rufescens*, and *A. ruficeps*. Each of these species is wide ranging, and *A. rufescens* and *A. botterii* are exceptional in that their highland and lowland forms are different. This might indicate that within the genus the tail is much more subject to variation than are other measurements over a broad geographic range. In other words, as the species inhabit new areas the major portions of the body are less affected than the tail. This may be related to importance of other appendages in locomotion and foraging while the tail is probably less important.

The sparrows are generally similar to the other genera in that the legs and feet are less variable than the bill measurements.

Of the three bill measurements, length was least variable in the *Aimophila* sparrows. This was similar in *Junco*, but for the other forms (except *Zonotrichia* for which data were not available) length was the most variable character. Davis (1954) suggested that this, in part, may be due to the effects of wear on the bills of seedeaters. However, two of the three finches show the reverse, possibly related to size, while in nonfringillid genera variability in length may be related to other factors, as discussed earlier.

INTERNAL MORPHOLOGY

In this section, characters of the skull and appendicular skeleton that seem especially relevant to study of evolution in the genus are surveyed. This survey primarily concerns variability of characters within the genus; little reference is made to other genera. I made no attempt to cover the entire skeletal system for possible "generic" characters, and the musculature has been neglected entirely, primarily because an adequate survey would be a report in itself. Where musculature seems to play an important role in the character being considered, I have drawn from the excellent material presented by Bowman (1961) and by Bock (1964a—in more general terms for the skull of birds). The studies of Engels (1940), J. Davis (1957), Eaton *et al.* (1963), and others have served as a partial basis for the survey of the appendicular skeleton.

In general, there seems to be little marked qualitative variation in the

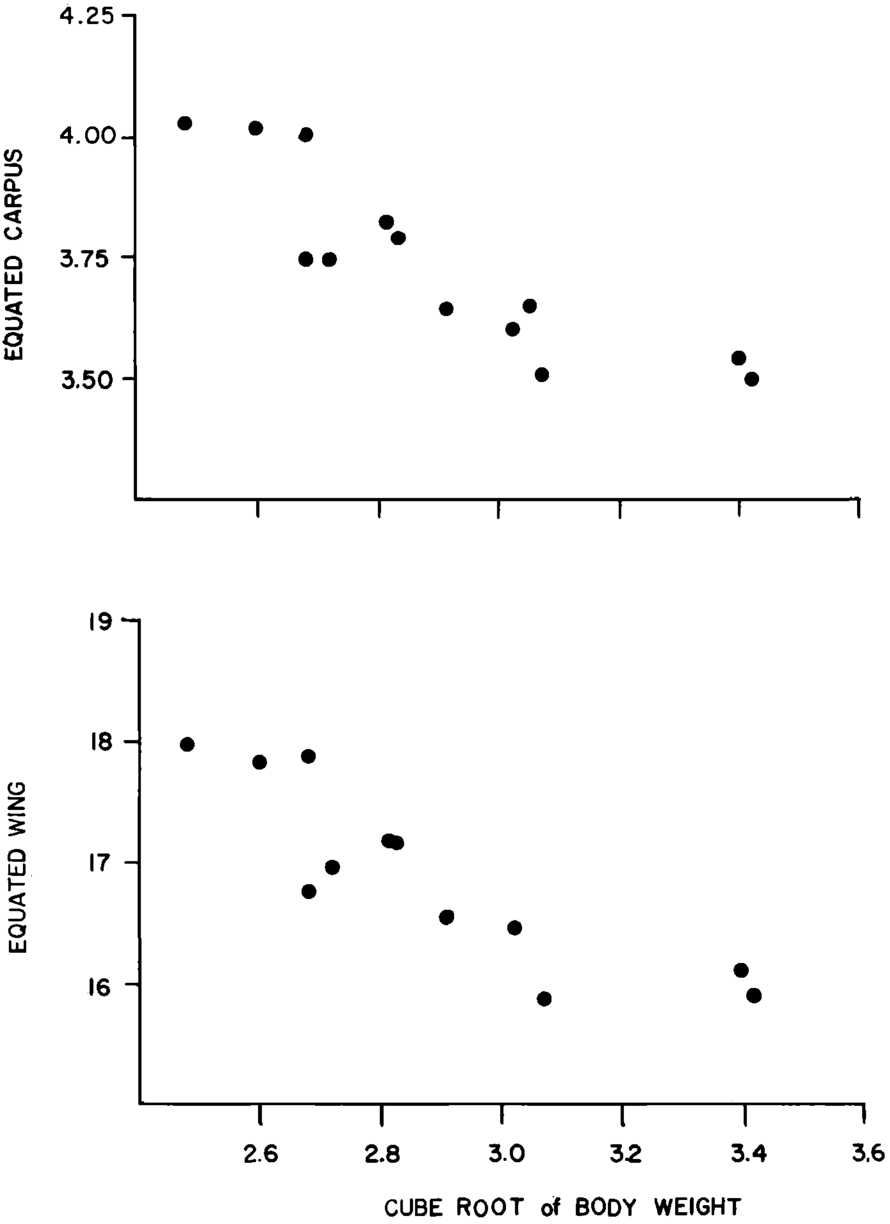

FIGURE 12. Relationships between equated carpus (above) and total equated skeletal wing length (below) and the cube root of body weight of males.

major portions of the skeleton of higher passerines that would be useful for generic classification. Bock (1962) discussed aspects of the humerus of passerines, but this is primarily a family character. Below the family level it seems that skeletal evolution mainly has been in terms of a common adaptation, which is then slightly modified in relation to the ecology and behavior of the particular smaller taxon. Most differences in growth patterns in skeletal elements are associated with differences in habitat exploitation patterns and with behavioral differences. The focus here is to determine whether any of these adaptations are common to the members of groups within the genus and possibly related to some "key" adaptations involved in the initial evolution of the groups and their subsequent radiation. This survey will give an indication of how a limited number of characters varies in this group of sparrows and how these variations can be related to some characteristics that have been presented in other sections of this report.

APPENDICULAR SKELETON

SKELETAL WING AND LEG LENGTH OF MALES AS A FUNCTION OF BODY WEIGHT

By plotting equated values of total length (Tables 23 to 28) against the cube root of body weight, we see a general trend toward relatively smaller wings in the larger, or heavier, species (Fig. 12). This same trend is followed by changes in length of the carpus (Fig. 12). The notable exception, *A. notosticta*, may be the result of the small sample available or of some strong selective forces acting to elongate the distal part of the wing. The correspondence between total wing length and/or carpus length and body weight suggests that the larger birds are less efficient fliers. On the other hand, the change in wing shape may be more specifically involved with the flight feathers themselves. Often more northerly, migratory populations of a species have longer wings (from bend of wing to tip of longest primary) than nonmigratory populations. The migratory species, *A. aestivalis, A. botterii*, and *A. cassinii* have more pointed wings and longer carpi than other species of *Aimophila*, but whether this results from general evolutionary history of the group or from selective pressures of migration is not known. Equated values of wing length, measured from bend of wing to the tip of longest primary, also were negatively correlated with body weight (see p. 150).

Leg and tarsal lengths show no correlation with body size (Fig. 13), except for an apparent increase in variation of length among species as body size increases. This suggests that leg length is much more subject to varying selective pressures and differential growth patterns in this group of sparrows than is wing length. While effective wing length of a bird can

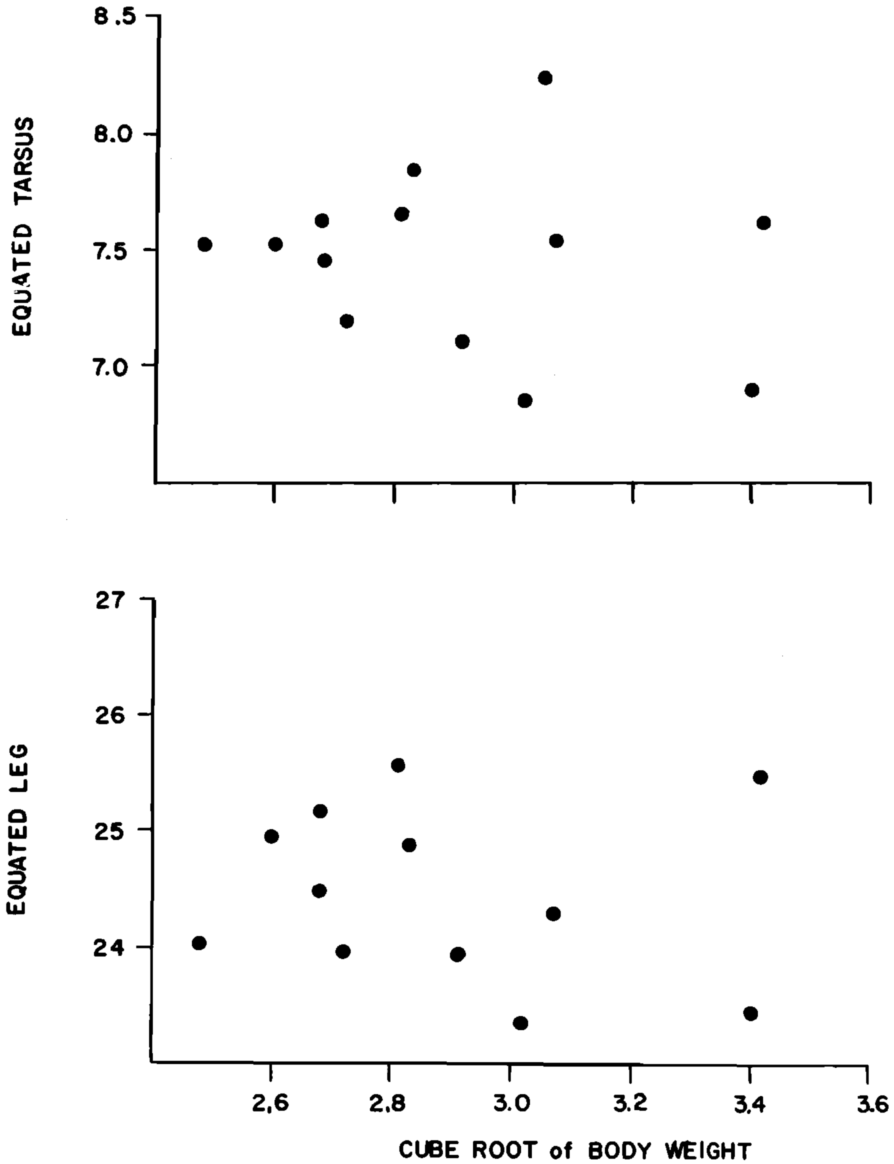

FIGURE 13. Relationships between equated tarsal length (above) and total equated leg length (below) and the cube root of body weight of males.

TABLE 23

MEASUREMENTS OF THE HUMERUS IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	$\bar{x}$	SD	SE	Coefficient of variation	Range	N	Equated value*
r. acuminata	M	19.29	0.33	0.08	1.71	18.9–19.9	19	6.28
	F	18.99	0.45	0.13	2.37	18.1–19.9	13	6.29
r. lawrencii	M	21.51	0.46	0.12	2.14	19.9–22.6	16	6.33
	F	21.19	0.41	0.13	1.92	20.6–21.8	10	6.34
sumichrasti	M	19.14	0.37	0.08	1.93	18.7–20.1	20	6.34
	F	18.68	0.56	0.16	3.00	17.8–19.8	12	6.27
humeralis	M	18.91	0.49	0.12	2.59	18.1–19.8	16	6.50
	F	18.32	0.38	0.09	2.07	17.8–19.0	17	6.43
mystacalis	M	18.55	0.41	0.10	2.21	18.2–19.7	16	6.55
	F	18.28	0.41	0.10	2.24	17.6–19.0	15	6.48
carpalis	M	16.68	0.41	0.08	2.46	15.6–17.5	29	6.72
	F	16.13	0.55	0.13	3.41	15.2–17.3	19	6.56
ruficeps	M	17.24	0.81	0.19	4.70	16.0–18.7	18	6.43
	F	16.53	0.55	0.15	3.33	15.4–17.4	13	6.28
rufescens	M	21.35	0.69	0.15	3.23	19.8–22.5	22	6.24
	F	20.88	0.71	0.20	3.40	19.6–22.2	13	5.70
notosticta	M	19.40					1	6.36
	F							
aestivalis	M	17.68				17.1–18.2	9	6.50
	F	17.47				17.0–18.1	9	6.54
botterii	M	18.55	0.45	0.12	2.42	18.0–19.7	14	6.60
	F	18.40				18.0–19.0	3	6.61
cassinii	M	17.68	0.36	0.09	2.04	17.0–18.3	16	6.80
	F	17.30				16.4–17.7	6	6.50
quinquestriata	M	17.98	0.35	0.11	1.96	17.3–18.4	10	6.71
	F	17.83				17.5–18.1	3	6.70

* Equated value = mean/cube root of body weight.

be increased or decreased either by changing lengths of bones or feathers, leg length of a bird is solely dependent on the bones, and any change must be reflected in changes of bone length.

The increased variation in leg length can result from several selective forces in addition to those for increased or decreased total length. As Dilger (1956) pointed out, force and weight influence the size of the leg. All other things being equal, the larger bird should have a relatively shorter leg to support the increased weight. A second alternative would be to increase the actual bulk of the leg bones so that a longer, yet wider bone can support the same weight. In general, the larger species of *Aimophila* tend to have stouter leg bones than smaller species.

RELATIONSHIPS OF MAJOR BONES IN WING AND LEG (OF MALES)

This includes only the humerus, ulna, and carpus within the wing and the femur, tibiotarsus, and tarsometatarsus within the leg. The radius was not included as it followed the variation of the ulna, and digits of the wing

TABLE 24

MEASUREMENTS OF THE ULNA IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	x̄	SD	SE	Coefficient of variation	Range	N	Equated value
r. acuminata	M	18.68	0.35	0.08	1.87	18.2–19.3	17	6.08
	F	18.08	0.34	0.10	1.88	17.4–18.6	13	5.99
r. lawrencii	M	21.19	0.76	0.20	3.59	19.5–22.6	15	6.23
	F	20.58	0.46	0.14	2.22	19.9–21.3	10	6.16
sumichrasti	M	19.62	0.45	0.10	2.29	18.2–20.3	19	6.50
	F	18.89	0.37	0.11	1.96	18.0–19.3	12	6.34
humeralis	M	18.61	0.38	0.10	2.04	17.7–19.1	16	6.40
	F	17.71	0.31	0.08	1.75	17.3–18.3	16	6.21
mystacalis	M	19.31	0.43	0.11	2.23	18.4–20.2	16	6.82
	F	18.51	0.49	0.13	2.65	17.7–19.4	15	6.56
carpalis	M	17.86	0.34	0.06	1.90	17.2–18.7	29	7.20
	F	17.06	0.60	0.14	3.52	16.2–18.0	18	6.93
ruficeps	M	17.67	0.85	0.19	4.81	16.5–19.4	19	6.59
	F	16.78	0.61	0.17	3.64	15.5–17.8	13	6.38
rufescens	M	21.03	0.66	0.14	3.14	19.5–22.1	21	6.15
	F	20.53	0.78	0.24	3.80	19.5–22.3	11	6.11
notosticta	M	19.30					1	6.33
	F							
aestivalis	M	18.22				17.8–18.6	9	6.70
	F	17.59				16.7–18.2	9	6.59
botterii	M	18.95	0.62	0.20	3.26	18.1–20.0	10	6.74
	F	18.70				18.4–19.2	3	6.73
cassinii	M	18.14	0.43	0.10	2.37	17.5–18.8	18	6.98
	F	17.63				16.4–17.7	6	6.63
quinquestriata	M	19.21	0.27	0.08	1.40	18.7–19.6	11	7.17
	F	18.83				18.5–19.1	3	7.08

were thought to be too small to give meaningful results. All data are considered as percentages of the length of the homologous structure in *A. ruficeps* and are presented only for males of each species.

The relationships can be visualized in two ways. First, given that total length of the appendage changes, what are the contributions of each element to the change? Recorded percentage differences in the ulna exceed by a small amount the differencs in the carpus (see Table 29); the humerus shows the smallest amount of variation of the three wing elements. The leg similarly is more variable distally than proximally. This type of measure of variation is used by Eaton *et al.* (1963) to suggest that distal segments are more responsive to selective forces for changing limb length than are proximal ones. Comparing the degree of interspecific variability of wing and leg bones in the several species (Table 29), it can be seen that both appendages are about equally variable.

Second, one can compare the degree of change within various segments of wing and leg of each species. In other words, as total length for each species changes, how does the relationship of the bones within the wing

TABLE 25

MEASUREMENTS OF THE CARPUS IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	$\bar{x}$	SD	SE	Coefficient of variation	Range	N	Equated value
r. acuminata	M	10.75	0.30	0.07	2.79	10.0–11.4	17	3.50
	F	10.30	0.21	0.06	2.04	9.9–10.7	13	3.41
r. lawrencii	M	12.00	0.56	0.14	4.67	10.3–12.8	16	3.53
	F	11.82	0.34	0.11	2.88	11.2–12.3	10	3.54
sumichrasti	M	10.83	0.26	0.06	2.40	10.2–11.3	19	3.59
	F	10.41	0.26	0.07	2.50	10.0–10.9	13	3.49
humeralis	M	10.57	0.22	0.06	2.08	10.2–11.0	15	3.63
	F	10.05	0.19	0.05	1.89	9.7–10.3	17	3.53
mystacalis	M	10.70	0.62	0.15	5.79	8.6–11.2	18	3.78
	F	10.39	0.21	0.04	2.02	10.0–10.6	15	3.68
carpalis	M	10.05	0.28	0.05	2.79	9.4–10.6	31	4.05
	F	9.59	0.38	0.09	3.96	9.0–10.2	18	3.90
ruficeps	M	10.03	0.46	0.10	4.59	9.4–10.8	20	3.74
	F	9.60	0.34	0.09	3.54	8.9–10.1	13	3.65
rufescens	M	11.93	0.49	0.11	4.11	10.6–12.7	21	3.49
	F	11.62	0.69	0.21	5.91	10.1–12.6	11	3.46
notosticta	M	11.10				10.9–11.3	2	3.64
	F							
aestivalis	M	10.16				9.6–10.7	8	3.74
	F	9.86				9.5–10.1	9	3.69
botterii	M	10.74	0.50	0.16	4.68	10.0–11.7	10	3.82
	F	10.30				10.1–10.6	3	3.70
cassinii	M	10.45	0.30	0.07	2.89	9.9–11.1	17	4.02
	F	10.07				9.6–10.4	6	3.78
quinquestriata	M	10.72	0.13	0.04	1.25	10.5–10.9	11	4.00
	F	10.63				10.5–10.8	3	4.00

change? This can be done by considering each segment as a percent of the same segment of *A. ruficeps* (Table 29). In general, wing variation in the *Haemophila* complex is greater than in the *Peucaea* group (*ruficeps* group plus *botterii* group). At the same time, leg variation of each species is slightly greater in *Haemophila* than in *Peucaea.* Variation of intramembral ratios within the leg ($\bar{x} = 5.15$) is also greater than variation within the wing ($\bar{x} = 3.18$), which suggests that while changes within each limb have obviously occurred, wing changes have been more equally shared by each segment than in the leg.

Length of each element expressed as a percent of total length of the appendage further confirms that the change has been roughly proportionate throughout the length of the appendages, rather than for any one particular element (Table 30). In both the wing and leg the most proximal element is the most constant in length and has the most variable percentage as total length changes. However, the ratios do not compare the actual lengthening of various elements in relation to some standard other than the limb itself (Engels 1940).

TABLE 26

MEASUREMENTS OF THE FEMUR IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	$\bar{x}$	SD	SE	Coefficient of variation	Range	N	Equated value
r. acuminata	M	19.97	0.43	0.10	2.15	19.3–20.8	17	6.50
	F	19.83	0.48	0.13	2.42	19.2–20.8	13	6.57
r. lawrencii	M	22.54	0.84	0.20	3.73	20.2–23.6	17	6.63
	F	22.38	0.48	0.15	2.14	21.9–23.3	10	6.70
sumichrasti	M	20.31	0.43	0.09	2.12	19.0–21.3	21	6.72
	F	20.17	0.62	0.18	3.07	19.2–21.1	12	6.77
humeralis	M	19.50	0.50	0.11	2.56	18.5–20.2	19	6.70
	F	19.22	0.37	0.10	1.92	18.5–19.6	14	6.74
mystacalis	M	18.56	0.44	0.10	2.37	18.0–19.7	18	6.56
	F	18.22	0.39	0.10	2.14	17.6–19.0	15	6.46
carpalis	M	15.76	0.31	0.06	1.97	15.2–16.4	27	6.35
	F	15.50	0.53	0.12	3.42	14.7–16.6	17	6.30
ruficeps	M	18.10	0.77	0.18	4.25	17.0–19.9	19	6.75
	F	17.74	0.60	0.17	3.38	16.6–18.6	13	6.74
rufescens	M	24.02	0.74	0.15	3.08	22.5–25.6	23	7.02
	F	23.91	0.73	0.21	3.04	22.6–24.7	12	7.12
notosticta	M	21.55				21.4–21.7	2	7.06
	F							
aestivalis	M	18.18				17.7–18.9	9	6.68
	F	18.10				17.7–18.6	9	6.78
botterii	M	19.83	0.37	0.10	1.86	19.2–20.5	15	7.06
	F	19.80				19.5–20.4	3	7.12
cassinii	M	17.84	0.39	0.09	2.17	17.1–18.7	18	6.86
	F	17.67				16.6–18.4	7	6.64
quinquestriata	M	17.85	0.27	0.08	1.49	17.4–18.2	11	6.66
	F	18.10				17.8–18.4	2	6.80

A. ruficeps apparently has long legs in comparison to other members of the genus. Legs of most species are between 90 and 99% of the equated length of *A. ruficeps* (Table 29). There seems to be no correlation between relative leg length and openness of habitat. Probably the primary considerations in leg length are type of foraging and amount and kind of ground movements. Most species are primarily ground foragers and would be expected to show some leg modifications. However, the actual modifications would depend in large part on kinds of foraging and position of foraging in relation to various substrate characteristics (J. Davis 1957). *A. rufescens* has relatively long legs that may be crucial in either scratch-type foraging or in moving through layers of leaf litter. The extremely long leg of *A. notosticta* serves an unknown function, as little is known about its foraging behavior. Both *A. cassinii* and *A. botterii* have relatively long legs and commonly forage in the open. The short leg of *A. aestivalis* apparently is achieved by shortening of the distal segments and probably signifies a difference in either mode or amount of ground locomotion as compared to *A. cassinii* and *A. botterii.* Most other species have shorter legs than *A. ruficeps* with decreased

TABLE 27

MEASUREMENTS OF THE TIBIOTARSUS (TIBIA) IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	$\bar{x}$	SD	SE	Coefficient of variation	Range	N	Equated value
r. acuminata	M	31.45	0.66	0.17	2.10	30.3–32.5	15	10.24
	F	30.88	0.79	0.22	2.56	29.3–32.2	13	10.22
r. lawrencii	M	33.67	1.49	0.38	4.42	29.9–35.3	15	9.90
	F	34.04	0.69	0.22	2.02	32.9–35.1	10	10.19
sumichrasti	M	29.55	0.79	0.20	2.67	27.6–30.9	16	9.78
	F	29.28	0.79	0.22	2.70	27.8–30.4	13	9.82
humeralis	M	29.49	0.81	0.20	2.75	19.4–21.7	16	10.13
	F	29.02	0.48	0.12	1.65	28.1–29.9	17	10.18
mystacalis	M	29.60	0.49	0.13	1.66	28.7–30.7	15	10.46
	F	29.19	0.61	0.16	2.09	27.9–30.0	14	10.35
carpalis	M	25.14	0.62	0.12	2.47	23.4–26.5	28	10.14
	F	24.72	0.72	0.18	2.91	23.3–26.0	16	10.05
ruficeps	M	28.86	1.08	0.24	3.74	27.5–31.7	21	10.77
	F	28.74	0.78	0.24	2.71	27.9–30.2	11	10.93
rufescens	M	37.11	0.99	0.23	2.67	35.2–38.9	18	10.85
	F	37.23	1.16	0.37	3.14	25.1–27.0	10	11.08
notosticta	M	34.10					1	11.18
	F							
aestivalis	M	27.44				26.7–28.8	9	10.09
	F	27.39				26.6–28.6	9	10.26
botterii	M	30.50	0.93	0.31	3.05	29.3–31.8	9	10.85
	F	30.63				29.8–31.4	3	11.02
cassinii	M	27.45	0.58	0.14	2.11	25.7–28.5	17	10.56
	F	27.38				26.2–28.1	7	10.29
quinquestriata	M	27.79	0.39	0.12	1.41	27.1–28.4	10	10.37
	F	28.30				28.1–28.6	3	10.64

length occurring in all segments. *A. mystacalis* has an exceptionally long tarsus, the significance of which is unknown. Most *Haemophilae* have generally stronger tarsi and are bulkier birds than the other species; the two characteristics seem to be interrelated. *A. carpalis* has a very short leg but a long wing and occurs in quite open habitat in which it does a great deal of flying. In comparison to most other species in which escape is often via short flights or quick dashes into nearby brush, *A. carpalis* often flies long distances.

Thus the short leg of many sparrows seems to be correlated with increased bulk of body and leg segments and to some extent with behavior. However, most of the species are relatively similar in amount of ground activity and type of ground locomotion. The differences in intramembral ratios of these species are of degree and are not of qualitative importance.

Wing/leg ratio.—This ratio is similar to the wing/tarsus ratio that is so often used in generic definitions. However, here we are considering the major bony elements of the entire wing and leg, with the exception of the feet,

TABLE 28

MEASUREMENTS OF TARSOMETATARSUS (TARSUS) IN 13 FORMS OF *AIMOPHILA* (IN mm)

Species	Sex	$\bar{x}$	SD	SE	Coefficient of variation	Range	N	Equated value
r. acuminata	M	23.14	0.72	0.18	3.11	21.5–24.3	16	7.54
	F	23.05	0.59	0.16	2.56	21.7–23.9	13	7.63
r. lawrencii	M	23.44	1.05	0.27	4.48	20.8–25.0	15	6.89
	F	23.66	0.60	0.19	2.52	22.5–24.8	10	7.08
sumichrasti	M	20.68	0.66	0.16	3.19	18.9–21.7	18	6.85
	F	20.40	0.58	0.16	2.84	19.4–21.4	13	6.84
humeralis	M	20.66	0.60	0.15	2.90	19.4–21.7	16	7.10
	F	20.39	0.54	0.13	2.65	19.5–21.2	16	7.15
mystacalis	M	22.18	0.56	0.14	2.52	21.3–23.6	17	7.84
	F	21.73	0.70	0.18	2.22	20.8–23.2	15	7.70
carpalis	M	18.65	0.52	0.10	2.79	17.4–19.4	28	7.52
	F	18.23	0.52	0.13	2.85	17.4–19.0	17	7.41
ruficeps	M	20.43	0.90	0.20	4.40	19.1–22.0	21	7.62
	F	20.43	0.71	0.20	3.48	19.3–21.6	12	7.77
rufescens	M	25.98	0.77	0.17	2.96	24.7–27.6	20	7.60
	F	25.86	0.64	0.19	2.48	25.1–27.0	11	7.70
notosticta	M	25.10				25.1	2	8.23
	F							
aestivalis	M	19.53				18.9–20.3	7	7.18
	F	19.07				18.5–20.3	9	7.14
botterii	M	21.49	0.69	0.22	3.21	20.7–22.5	10	7.65
	F	21.30				20.8–21.6	3	7.66
cassinii	M	19.55	0.59	0.15	3.02	18.3–20.5	16	7.52
	F	19.26				18.2–20.1	7	7.24
quinquestriata	M	19.94	0.40	0.12	2.02	19.3–20.7	11	7.44
	F	20.47				20.1–21.1	3	7.70

which, within limits, are not particularly crucial in determining stature or locomotor patterns. Within a group of species as similar as these sparrows the wing/leg ratio may indicate relative importance of the two appendages in the life of the birds. It must be emphasized that the measure is only relative, as there is no common denominator to which each appendage is referred; each could vary in tandem with the other and the ratio would show little, if any, change. However, we have already shown that wing length as measured by the longest primary is not correlated with tarsal length, and as tarsal length varies in a similar fashion to the entire leg (Fig. 13), we might expect little correlation between wing and leg in the skeletal elements. Hence, wing/leg ratios probably do present some measure of changes that have occurred. However, it is impossible with this system to determine if the change is via a shortening of one appendage or a lengthening of the other, or both.

The wing averages about 65 to 70% of total leg length (Table 31), but would be increased to some extent if the digits of the hand were included.

TABLE 29

RELATION OF VARIOUS ELEMENTS OF THE WING AND LEG TO THE SAME ELEMENTS IN *A. RUFICEPS*

									Variation in	
Species	Humerus	Ulna	Carpus	Femur	Tibia	Tarsus	Total wing	Total leg	Wing	Leg
r. acuminata	97.7*	92.3	93.6	96.3	95.1	99.0	94.6	96.6	5.4	3.9
r. lawrencii	98.4	94.5	94.4	98.2	91.9	90.4	96.0	93.1	4.0	7.8
sumichrasti	98.6	98.6	96.0	99.6	90.8	89.9	98.0	92.9	2.6	9.7
humeralis	101.1	97.1	97.0	99.2	94.0	93.2	98.6	95.2	4.1	6.0
mystacalis	101.9	103.5	101.1	97.2	97.1	102.9	102.3	98.9	2.4	5.8
carpalis	104.5	109.2	108.3	94.1	94.2	98.7	107.2	95.5	4.7	4.6
ruficeps	—	—	—	—	—	—	—	—	—	—
rufescens	97.0	93.3	93.3	104.0	100.7	99.7	94.7	101.3	3.7	4.3
notosticta	98.9	96.0	97.3	104.6	103.8	108.0	97.4	105.3	2.9	4.2
aestivalis	101.1	101.7	100.0	99.0	93.7	94.2	101.1	95.3	1.7	5.3
botterii	102.6	102.3	102.1	104.6	100.7	100.4	102.4	101.7	0.5	4.2
cassinii	105.8	105.9	107.5	101.6	98.0	98.7	106.2	99.2	1.7	3.6
quinquestriata	104.4	108.8	107.0	98.7	96.3	97.6	106.7	97.3	4.4	2.4
% Variation	8.8	16.9	15.0	10.5	13.0	18.1	12.6	12.4		

* All values are percentages of the value of *A. ruficeps*. Variations are calculated by subtracting the smallest from the largest percentages.

Also the ratio would be more nearly one to one if functional wing length were compared to that of the leg. This would involve adding length of the longest primaries to the skeletal elements of the wing, but would require less change in the leg measurements. Ratios for the individual species range from 62.35 to 74.88 for males and 60.95 to 73.19 for females; in all cases female values are less than male values. This probably is related to the

TABLE 30

INTRAMEMBRAL RATIOS—PERCENTAGES OF THE TOTAL LENGTH OF THE APPENDAGE OCCUPIED BY EACH ELEMENT (BASED ON MALE VALUES ONLY)

Species	Humerus	Ulna	Carpus	Femur	Tibia	Tarsus
r. acuminata	39.6	38.3	22.1	26.8	42.2	31.0
r. lawrencii	39.3	38.7	21.9	28.3	42.3	29.4
sumichrasti	38.6	39.6	21.8	28.8	41.9	29.3
humeralis	39.3	38.7	22.0	28.0	42.3	29.7
mystacalis	37.9	39.9	22.1	26.4	42.1	31.5
carpalis	37.4	40.0	22.5	26.5	42.2	31.3
ruficeps	38.4	39.3	22.3	26.8	42.8	30.3
rufescens	39.3	38.7	22.0	27.6	42.6	29.8
notosticta	39.0	38.8	22.3	26.7	42.2	31.1
aestivalis	38.4	39.6	22.0	27.9	42.1	30.0
botterii	38.4	39.3	22.3	27.6	42.5	29.9
cassinii	38.2	39.2	22.6	27.5	42.3	30.2
quinquestriata	37.5	40.1	22.4	27.2	42.4	30.4
Range (Highest–Lowest)	2.2	1.4	0.8	2.4	0.9	2.2

TABLE 31

WING AS PERCENTAGE OF LEG (TOTAL SKELETAL LENGTH)

Species	Male	Female
r. acuminata	65.34	64.22
r. lawrencii	68.68	66.92
sumichrasti	70.30	68.69
humeralis	69.04	67.14
mystacalis	68.75	68.24
carpalis	74.88	73.19
ruficeps	66.69	64.13
rufescens	62.35	60.95
notosticta	—	—
aestivalis	70.70	69.58
botterii	67.17	66.08
cassinii	71.36	69.97
quinquestriata	73.06	70.72
Average	69.03	67.48

decreased importance of flying in the life of females. As mentioned before, males are more active in territorial defense and also follow the female when she is making trips with nesting material; both sexes feed young. The range of values results both from increased relative wing length (*A. cassinii*, *A. quinquestriata*, and *A. carpalis*) and increased relative leg length (*A. rufescens*, *A. r. acuminata*, and *A. r. lawrencii*). Species with comparatively long wings by this measure also have long wings, as judged by relative length of the longest primary, suggesting simultaneous selection for increased length of the bone and feather portions of the wing.

Using crude estimates of how open or closed the habitat is, I attempted to see if wing and leg length correlated with these environmental parameters. The habitat categories are composites of degree of canopy closure and nearness of individual trees and shrubs that provide elevated perches for the birds. Habitats of most of the species fall into the open category. *A. sumichrasti*, *A. humeralis*, and *A. quinquestriata* occur where vegetation is dense and the ground layer vegetation often is more than 50% shaded. Habitat of *A. mystacalis* approaches this condition in some situations, and the birds may be in open places only after clearing by man. *A. rufescens* may occur in either closed or open woodlands, depending on human disturbance.

In general, species with relatively longer wings than those of *A. ruficeps* occur in open situations; however, the same number of birds with wings shorter than *A. ruficeps* occur in open habitats. Species within groups tend to show relationships similar to those of *A. ruficeps*. The *botterii* group has longer wings while the *ruficeps* group averages slightly smaller. *A. carpalis*, *A. mystacalis*, and *A. quinquestriata* are also larger while the remaining *Haemophila* species are shorter-winged than *A. ruficeps*.

Within the *botterii* group *A. cassinii* has the largest skeletal wing, possibly related to increased importance of flight associated with their very prominent flight song and long migration. *A. botterii* probably occupies the most open habitat of the three and has the next longest wing. Finally, *A. aestivalis*, which occurs in closed pine woods and brushy fields, has wings only slightly larger than *A. ruficeps*. Neither *A. botterii* nor *aestivalis* has a highly developed song flight during the breeding season.

Within the *ruficeps* group the wing varies from 94.7 to 100% of the wing of *A. ruficeps*. At the same time average body weight increases from 19.3 g in *A. ruficeps* to 40.4 g in *A. rufescens*. It seems likely that wing length variation can be accounted for, but not explained by, the inverse correlation of cube root of body weight and wing length. The fluttery flight of *A. rufescens* as compared to that of the other two species probably results from shortened wings.

A. carpalis occupies the most open habitat of the *Haemophila* group and has relatively the longest wing. *A. mystacalis* has a longer wing than *A. ruficeps*, probably related to the rather open hillsides, though often with a well-developed tree layer, on which it lives. All other forms have relatively short wings, are poor, fluttery fliers and occupy the low tree layer and shrub habitat in which strong flight is not at a premium.

A. quinquestriata is very similar to *A. mystacalis* in that it often occurs where there is a closed canopy, but where the strata below the canopy are usually comparatively open. It seems to be a strong flier and probably can be considered to occupy open habitat, especially during the dry season when the herb layer is nearly absent. Its long wings reflect increased flying ability and probable importance of flight in territorial movements.

SEXUAL DIMORPHISM IN THE APPENDICULAR SKELETON

Most of the previous discussion was in terms of male skeletons. One wonders whether the minor differences in bony parts of males and females are related entirely to differences in body weight between the sexes. None of the females has a longer skeletal wing (equated value) than the respective male, but all except three have longer legs (Table 32). This suggests that there is some selective advantage for the females to have a decreased flying ability (or they may have greater change in the wing feathers). However, differences are slight and may be partly accounted for by the advantage of a slightly shorter leg in the slightly heavier males. Usually the degree of difference is greatest in the more distal segments, again showing that these elements are most subject to selective changes. The leg elements generally follow the same pattern as the wing bones.

TABLE 32

INTRASPECIFIC RATIOS (EXPRESSED AS %) OF FEMALES TO MALES FOR EQUATED VALUES OF ELEMENTS WITHIN THE WING AND LEG

Species	Humerus	Ulna	Carpus	Femur	Tibia	Tarsus	Average	
							Wing	Leg
r. acuminata	100.2	98.5	97.4	101.1	99.8	101.2	98.7	100.7
r. lawrencii	100.2	98.9	100.3	101.0	102.9	102.8	99.8	102.2
sumichrasti	98.9	97.5	97.2	100.7	100.4	99.8	97.9	100.3
humeralis	98.9	97.0	97.2	100.6	100.5	100.7	97.7	100.6
mystacalis	98.9	96.2	97.4	98.5	98.9	98.2	97.5	98.5
carpalis	97.6	96.2	96.3	99.2	99.1	98.5	96.7	98.9
ruficeps	97.7	96.8	97.6	99.8	101.5	102.0	97.4	101.1
rufescens	91.3	99.3	99.1	101.4	102.1	101.3	96.6	101.6
notosticta	—	—	—	—	—	—	—	—
aestivalis	100.6	98.4	98.7	101.5	101.7	99.4	99.2	100.9
botterii	100.2	99.8	96.8	100.8	101.6	100.1	98.9	100.8
cassinii	95.6	95.0	94.0	96.8	97.4	96.3	94.9	96.8
quinquestriata	99.8	98.7	100.0	102.1	102.6	103.5	99.5	102.7

SQUAMOSAL REGION

Tordoff (1954), in his survey of various skull characters of nine-primaried oscines, noted that *Aimophila* was similar to other "more advanced" emberizines in possessing a much inflated squamosal region (S3, the greatest amount of inflation recognized in his study). He examined only *A. botterii, cassinii, humeralis, rufescens,* and *ruficauda.* Tordoff (1954: 10) stated that "some use can be made of the amount of inflation in determining relationships, especially between genera." On the basis of this suggestion a survey was made of all species in the genus. All members of this group show a more inflated squamosal region than do ploceids, but there is still rather marked variability within this group. In some species the degree of inflation approaches that shown by *Spizella* species, and in others the squa-

TABLE 33

OCCURRENCE OF TWO TYPES OF SQUAMOSAL INFLATION IN *AIMOPHILA*

A	B
mystacalis	*ruficauda*
carpalis	*sumichrasti*
ruficeps	*humeralis*
rufescens	
notosticta	
aestivalis	
botterii	
cassinii	
quinquestriata	

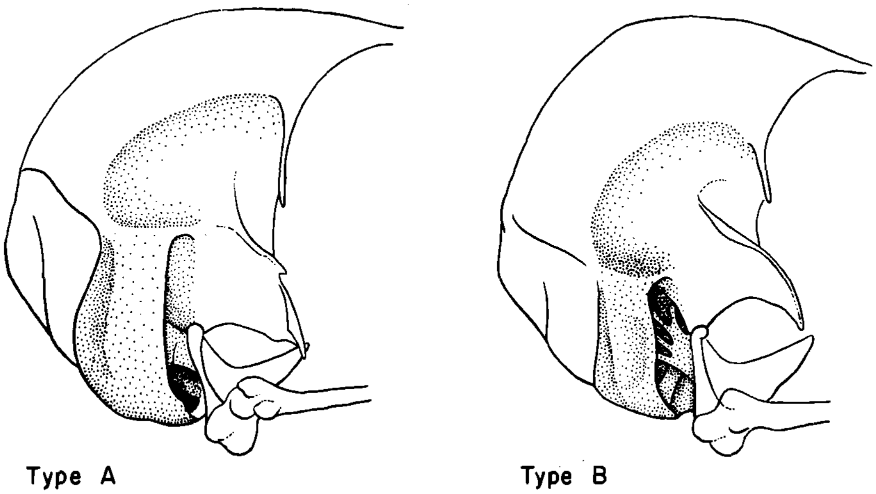

FIGURE 14. Representatives of the two types of squamosal region recognized in this study. (A) Inflated, nonsculptured as exemplified by *A. rufescens.* (B) Less inflated, highly sculptured type as exemplified by *A. ruficauda lawrencii.*

mosal region is inflated but rather dissected (Fig. 14). In the inflated types, there a short portion of adductor muscle inserts within the tympanic chamber and is overlaid by the anterior-dorsal portion of the squamosal. Species could be divided into two categories based on amount of inflation and degree of sculpturing (Table 33).

In his discussion of the significance of the inflated condition in birds, Tordoff (*op. cit.*) drew an analogy with certain open country rodents and suggested that inflated squamosals might relate to auditory acuity. However, he noted that some open country birds did not show the inflated condition. I have not been able to add any information on functional significance of an inflated squamosal region, but would like to discuss the taxonomic value and some possible causes of differences among the species of *Aimophila* in sculpturing and inflation of the squamosal region.

The squamosal region is the site of attachment of *M. depressor mandibularis.* From here the muscle extends downward to the posterior margin of the mandible. It functions, as the name suggests, to depress the mandible during the process of opening the bill. In the Galápagos finches (S1 squamosal), *M. depressor mandibularis* was not extremely variable in size and did not have a strong correlation with the strength of the trophic apparatus (Bowman 1961). Lack of correlation with feeding extended even to species that actively gaped during feeding maneuvers. The only important correlation was a relation to overall lower jaw size and the fact that the de-

TABLE 34

RELATIVE DEVELOPMENT OF THE POSTERIOR BORDER OF THE TRANSPALATINE IN *AIMOPHILA* AND OTHER GENERA OF EMBERIZINES

Species	N	x̄	Range
A. r. acuminata	10	2	2
A. r. rest	10	2.3	2–3
A. sumichrasti	10	2	2
A. humeralis	10	1.9	1.5–2
A. mystacalis	10	2	2
A. carpalis	10	2.4	2–3
A. ruficeps	10	2	2
A. rufescens	9	2	2
A. notosticta	1	2	2
A. aestivalis	6	2	2
A. botterii	8	2.3	2–3
A. cassinii	10	2.2	2–3
A. quinquestriata	8	2	2
Amphispiza bilineata	10	1.95	1.5–2
Spizella passerina	9	1	1
S. breweri	9	1.9	1.5–2
Junco oreganus	9	1.1	1–1.5
Chondestes grammacus	10	2.8	2–3

pressor was working against the inertia of the relaxed, but larger, adductor muscles. In *Junco*, a genus with a markedly inflated squamosal, *M. depressor mandibularis* is essentially bipartite with the anterior portion of the muscle extending in a line along the anterior margin of the tympanic chamber and the posterior portion extending along the ventral margin of the squamosal. The center of the inflated region is essentially bare. The muscle along the anterior margin coincides with the anterior margin of the tympanic chamber so it approaches the point of insertion of the mandible at an acute angle, while if the muscle attaches to the whole bulla the insertion is at essentially a right angle. Angle of attachment may influence the force which a muscle of a given mass can exert on the mandible (Bock 1963). Size and shape of the muscle may also influence shape of the squamosal region by influencing size and shape of the external ear opening. If this were the case it might explain why certain open country forms that one might expect to have the inflated squamosal do not.

The occurrence of the inflated condition in all but three species of *Aimophila* (Table 33) suggests that the forms not showing this character may be related. It is interesting to note that the strong-billed form, *A. rufescens*, has an inflated squamosal (type A), while the relatively weaker-billed *A. humeralis* has a type B squamosal. The apparent dependence of the shape of this region on strength of the trophic apparatus makes it inadvisable to use the characteristic as a means of separating groups within the genus.

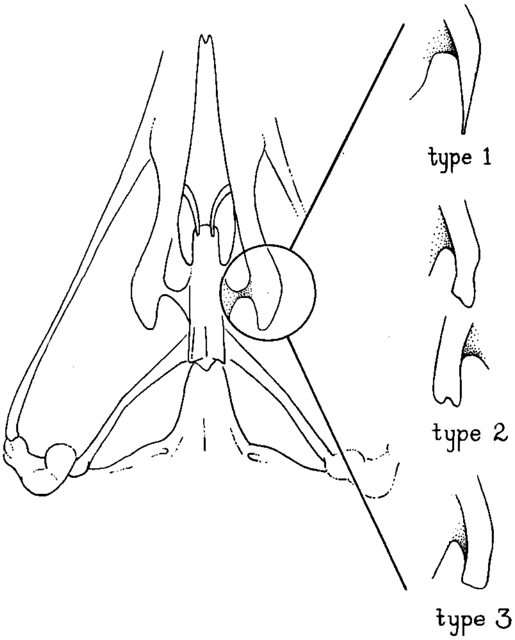

FIGURE 15. Three categories of the shape of the posterior border of the transpalatine. Note the possible variation in the position of the posterior projection in type 2.

TRANSPALATINE PROCESS

Storer (1955) noted that "*carpalis* . . . differs from *Spizella* in having the posterior end of the palatines broad rather than pointed" and that "the broad expansion of the posterior end of the palatines [of *A. carpalis*] are perhaps most like those of *ruficeps* but in some aspects are unique." I surveyed development of this region of the palatines using up to 10 males of each species of *Aimophila* plus several closely related genera (Table 34). I set up three categories based on shape and extent of the posterior border of the transpalatine bone (Fig. 15): (1) a thin spine extending back from the lateral portion of the transpalatine; (2) a spine or broader sheet of bone projecting from the transpalatine, which generally is broader anterior to the projection than in category 1; (3) a broad, essentially flat posterior border. Obviously categories 1 and 3 are extremes on a continuum in which category 2 is approximately intermediate. It is easy to see that several types of palate may be hidden in the various categories depending on shape of the posterior border, shape of the projection, and relative slope of the transpalatine.

The posterior borders of the transpalatine are of similar shape in most species of *Aimophila.* No species has a thin projection as in *Spizella passerina,* but several specimens of *A. humeralis* approached this condition. Several species approached or equalled the category 3 condition in which there is no marked projection from the broad posterior border.

Spizella passerina had a thin posterior border (category 1) while that of *S. breweri* is more similar to that of *Aimophila.* In *Junco,* only *J. oreganus* was examined in detail, and that species had the border most similar to that of *S. passerina.* I examined a few *Junco phaeonotus* and found them to be of category 2. *Chondestes* had a broad, usually nonprojecting border, while *Amphispiza* usually showed some projection. Obviously this characteristic was variable, both intra- and interspecifically within a genus.

I have not attempted dissections to determine functional significance of the differences, so the following information is based on the work of Bowman (1961). There may be a relation between extent of the projection from the border and size of *M. pterygoideus dorsalis, pars lateralis.* Bowman used width of the transpalatine process as a measure of development of *M. pterygoideus ventralis,* the only major muscle to insert there. In general, size of this bone was correlated with other aspects of the skull concerned with adduction. The portions of *M. pterygoideus ventralis* and *p. dorsalis,* that insert on the transpalatine process, function in retracting the palate along the sphenoidal rostrum, thus depressing the mandible. Development of these muscles influences strength of bite, which in seed-eaters could easily influence the types of foods most efficiently eaten.

The transpalatine is part of a character complex concerned with relative strength of the jaw apparatus. The significance of this bone to generic classification would therefore seem to be limited. However, if the genus is composed of forms with bills of similar shape and/or strength then it may be pertinent, depending on what modifications of the jaw apparatus are possible in changing the strength of the jaw.

MUSCLE SCAR IN TEMPORAL FOSSA

In a further attempt to consider degree of development of the skull and bill structure as implements of feeding, an analysis was made of relative development of the temporal fossa, the region occupied by *M. adductor mandibularis, pars superficialis.* The muscle extends downward from its insertion on the skull to attach to the mandible near the posterior angle. It primarily retracts the mandible and hence partly determines bite strength. To determine relative development of this muscle mass, measurements of the greatest lateral extent of the temporal fossa were taken on a series of skulls of each species. These were then averaged and equated values calculated (Table 35).

TABLE 35

RELATIVE SIZE OF THE TEMPORAL FOSSA—INDICATIVE OF THE SIZE OF *M. ADDUCTOR MANDIBULARIS SUPERFICIALIS*

Species	Sex	N	Equated value	Range (mm)	Average length (mm)
sumichrasti	M	17	2.72	7.3–9.5	8.22
rufescens	M	22	2.69	8.3–10.4	9.20
rufescens	F	13	2.66	8.1–9.9	8.93
sumichrasti	F	13	2.60	7.0–8.7	7.75
quinquestriata	M	8	2.56	6.6–7.1	6.85
r. acuminata	M	20	2.55	6.9–8.9	7.84
r. lawrencii	M	9	2.51	7.7–9.3	8.53
r. lawrencii	F	13	2.41	7.5–9.2	8.05
quinquestriata	F	3	2.34	6.2–6.3	6.23
r. acuminata	F	7	2.24	7.2–7.9	7.48
humeralis	M	20	2.13	5.6–7.6	6.19
humeralis	F	19	2.12	5.4–7.2	6.04
carpalis	M	25	1.98	4.1–5.5	4.91
aestivalis	F	8	1.97	4.7–6.1	5.26
botterii	F	3	1.94	5.0–5.6	5.40
carpalis	F	13	1.94	4.3–5.3	4.78
aestivalis	M	10	1.93	4.8–5.9	5.24
mystacalis	M	18	1.92	4.7–6.3	5.42
botterii	M	12	1.86	4.5–5.9	5.23
mystacalis	F	15	1.83	4.5–5.8	5.17
cassinii	F	7	1.57	3.4–4.9	4.17
cassinii	M	17	1.50	3.1–4.6	3.90
ruficeps	F	13	1.32	2.3–4.1	3.47
ruficeps	M	24	1.28	2.7–4.4	3.44
notosticta	M	2	1.10	2.8–3.9	3.35

Engels (1940) and Bowman (1961) used the same sort of measure of strength of *M. adductor mandibularis* in their studies of thrashers (*Toxostoma*) and Galápagos finches, respectively. As the bill became increasingly decurved in *Toxostoma* species, there was a concomitant reduction in strength of the muscle. Engels attributed it to the increased likelihood that the muscle would separate the tips of the maxilla and mandible during adduction. He noted that it was a forceful adductor only in forms with rather straight bills. Bowman found that the finches, with stronger bills and a greater proportion of seeds in their diet, had relatively larger muscle masses, contributing to increased strength of the total muscle-bill complex that determined seeds that could be crushed with the bill.

In *Aimophila* there is a constellation of values for the equated size of this muscle mass, but the range of values is smaller than that reported by Bowman. This is not surprising as he was dealing with an island group that radiated into a larger number of exploitation types than have the continental Aimophilae. The largest muscle mass in *Aimophila* occurs in the southern complex of species. These species also have the greatest development of the bill structure itself (see p. 159). One surprising finding was the relatively strong muscle in *A. quinquestriata.* A larger muscle would increase the strength of the entire trophic apparatus, thereby increasing the force with which the bill is closed, while preserving a probable selective advantage for a longer, thinner bill. The increase operates within limits set by fracture strength of the bill itself. The small muscle scar in *A. mystacalis* suggests that this highland *Haemophila* species has adapted to a different diet from that of its relatives. The reduced adducting muscle is correlated with reduced strength of the bill complex in this form as compared to its close relatives. *A. ruficeps* and *A. notosticta* have relatively the smallest fossae and shallowest bills, suggesting a real difference in food types that are taken and, in part, relative seed sizes that the species select and are able to eat efficiently (Kear 1962, Hespenheide 1966).

Relatively little sexual dimorphism in this character exists within the genus. Several instances of apparent dimorphism are based on samples too small to support firm conclusions. In general, the only major differences between the sexes are correlated with body size differences.

All earlier discussion was based on equated values of size of the muscle mass. In terms of actual strength of the trophic apparatus, absolute size is more important. Absolute values follow essentially the same pattern as equated values. This is what one might expect if size of the trophic apparatus in this genus is related to overall size and there is no stringent selection to produce divergences.

Skull Ossification

For some years ornithologists have used degree of skull ossification to help determine age of passerine birds. By the time of first breeding the skull is double-layered in most north temperate passerines that have a limited and well-defined breeding season; these birds are at least one year old. The ossified condition is known to develop gradually in young of the year (Linsdale 1928), but apparently only Nero (1951) and Serventy *et al.* (1967) have attempted to determine pattern and rate of ossification using birds of known age. In recent years, passerines known to be at least one year old have been reported to have areas in the skull that are not yet double-layered (Selander 1958, 1964; Bowman 1961; N. K. Johnson 1963; A. H. Miller 1963; Grant 1966; Payne 1969). In general, these reports are mostly for tropical species with only scattered reports for north temperate species.

By examining a large number of skulls, Bowman (1961) was able to describe adequately the temporal pattern of ossification in the skull of certain geospizine finches. He found that some individuals of all 12 species

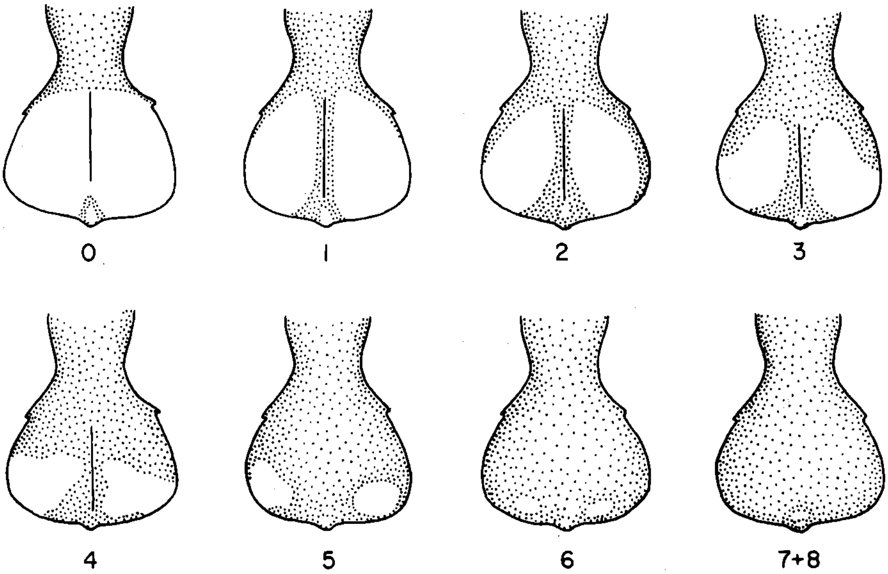

FIGURE 16. The sequence of development of a fully ossified (pneumaticized) skull in several species of *Aimophila*. This sequence holds only for those species in which the last region of the skull to ossify is the parietal. The numbers refer to arbitrary stages utilized in the analysis.

examined did not have fully ossified skulls by the end of one year; the last areas to ossify were the parietals and small "windows" just dorsal to the foramen magnum. This contrasted sharply with the pattern reported by Nero (*op. cit.*) for the House Sparrow (*Passer domesticus*), in which the last areas to ossify were in the frontals just posterior to the orbits.

Within the genus *Aimophila* only one group of species—*A. humeralis*, *A. ruficauda*, *A. mystacalis*, and *A. sumichrasti*—shows delayed skull maturation. This group includes species thought to be closely related within the genus and includes every member of the group, as I constitute it, except *A. carpalis*.

The following discussion will treat each species individually to point out fully the differences that occur in degree of ossification at time of breeding. In general, each species has a clearly defined breeding season with little interspecific variation. Most specimens were adults collected during the breeding season. I arbitrarily constructed 8 stages ranging from no ossification, or the single-layered condition (stage 0), to a completely pneumaticized condition (stage 7; Fig. 16). Each skull was assigned to a category and gonad condition of the specimen noted. For those species that may not have fully ossified skulls by the first breeding season this provides a measure of average degree of ossification. It is impossible to judge in most species whether some birds with fully ossified skulls are first-year individuals. These would obviously influence the average value for a species; values are calculated only from incompletely ossified skulls.

The following five species all show the last skull windows in the parietal region:

A. ruficauda acuminata.—Of 65 skulls examined from summer birds, 68% (38) showed evidence of immaturity. Average degree of immaturity of 31 skulls was 4.8. Even with this maturation rate most individuals probably have completely ossified skulls by the second breeding season. Probably fewer individuals show completely ossified skulls by the first breeding season than in *A. sumichrasti.* The difference between *A. sumichrasti* and *A. ruficauda acuminata* in average amount of ossification probably reflects a substantial difference in maturation rate of the young of the two species.

A. ruficauda lawrencii.—The percentage of individuals showing unossified skulls is even higher than for *A. r. acuminata* (78% or 32 of 41 skulls), but average degree of ossification (4.9) is insignificantly higher.

A. sumichrasti.—Of 62 skulls, 31 (50%) showed varying degrees of immaturity. Degree of immaturity was, on the average, not great (average 5.9; range 5–7). This suggests that complete ossification is achieved shortly after the end of first breeding season in many birds. Some birds may have a fully ossified skull by first breeding season, but it is nearly impossible to determine using other age characteristics.

A. humeralis.—Average degree of ossification (5.5) is about intermediate among the four species. The percentage of birds (N = 65) with incompletely ossified skulls is low (31%), indicating that many more birds have completely ossified skulls by beginning of first breeding season and that the average value is lower than it should be. However, a correction factor would have to be applied to all species and probably would correspond approximately to the percentage of birds that show incompletely ossified skulls. Hence average values may change slightly but relationships of values probably would be the same. The low percentage may also reflect low recruitment of young into the population in sample years.

A. mystacalis.—If two females are eliminated from consideration (neither had a brood patch late in breeding season, both had very slightly ossified skulls, and both probably were young of the year) then the average value is 6.4, the highest of any of the species. This suggests that maturation in this form is usually completed approximately one year after hatching. The 25% of the birds (N = 57) that showed slightly unossified skulls may be either late-hatched birds from the previous year or late-maturing birds that one might expect in a normal population sample when mean time to achieve full ossification is approximately one year.

A. rufescens.—A few individuals showed small unossified regions in the parietals during breeding season. The small number and scattered appearance of "windows" suggested abnormalities in the pneumatization process. Nero (1951) found similar irregularities among caged House Sparrows. It is also possible that *A. rufescens* slightly delays skull maturation with the consequent occurrence of a few, probably late-hatched, individuals with windows.

The three species, the frontal areas of which ossify last, are *A. ruficeps*, *A. cassinii*, and *A. carpalis.* For none of these species did I find breeding birds with unossified skulls. All apparently achieve fully pneumaticized condition before one year of age.

I have no information on pattern of skull ossification in *A. botterii*, *A. notosticta*, and *A. quinquestriata.* I found no breeding individuals with unossified skulls, so all may achieve fully pneumaticized condition before one year of age. In *A. aestivalis* the last region to ossify is not the parietal region, but I do not know whether it is the frontal area behind the orbits.

Although Bowman (1961) suggested a functional relationship between pattern and timing of skull ossification, Selander (1962) noted the functional impracticality of Bowman's hypothesis. Chapin (1949) thought the windows in woodpecker skulls might dampen shocks during hammering. However, most woodpeckers never achieve fully ossified condition, so the relation is not between pattern and timing but is purely a functional relation to pattern. Disney (pers. comm.) suggests a possible correlation between diet and pattern of ossification, again relating the pattern to something associated with feeding—perhaps stress patterns.

In passerines there are at least three patterns of ossification (as judged by position of the last areas of the skull to ossify—Wolf, MS), and perhaps more, as there may be several patterns of ossification in which the last areas to ossify are the same. In *Aimophila* the last regions to ossify are the parietals or the frontals in those species for which information is available. In one aberrant individual of *A. ruficauda acuminata* the last unossified regions were in the middle portion of the skull.

Such patterns of ossification might be used as evidence for phylogenetic relationships. Bowman (1961) surveyed some tropical fringillids (in the sense of Tordoff 1954) and found several in which the parietal region ossified last. He thought this might indicate their relationship to the geospizinae, especially as other authors had suggested relationships of these species on the basis of other characters. However, he thought that the actual pattern of ossification should be known before drawing more definite conclusions. Chapin (1949) noted that most passerine skulls ossify last just behind the orbits. He pointed out that skulls of swallows and geospizines were exceptions, both ossifying last in the parietal region, but in the swallows laterally and in the finches more medially.

Except for *A. rufescens* and *A. carpalis* pattern of skull ossification follows the lines of apparent relationships within the genus. The only specimens of *A. rufescens* in late stages of ossification are from breeding season, and all show small parietal windows. It is possible that these few individuals are aberrant and that the normal pattern is similar to that in *A. ruficeps.* Most birds have achieved a fully ossified condition, suggesting that the few birds with unossified skulls were abnormally retarded.

A. carpalis shows a striking departure from the typical haemophiline ossification pattern. I suspect this is a secondary modification, but it may eventually prove to be a primary character necessitating a shift in generic placement of *A. carpalis.* Within most New World genera so far examined, there is but a single pattern of ossification. For small families the same holds true, but larger families may have two patterns, while fringillids have at least three (Wolf, MS). Further work probably will show the pattern of ossification to be an important character for elucidating relationships. However, we need more knowledge about possible functional significance of pattern of ossification, to explain apparent deviations from the relationships suggested by other evidence.

Delayed skull maturation among closely related forms suggests this character may be a derivation of their common ancestry. In *A. ruficauda* and *A. humeralis* skull maturation may reflect a general level of physiological maturation and be genetically linked with other maturation processes. It is correlated with an apparent delayed entry of first-year birds into the breeding population (see Selander 1964 for a similar phenomenon in wrens of the genus *Campylorhynchus*). On the other hand, it is difficult to explain the delayed skull maturation of *A. sumichrasti* and *A. mystacalis* in this manner. Either it has arisen independently in these species for other reasons, or it represents an ancestral condition. *A. mystacalis* and *A. sumichrasti* may then reflect a general slow skull maturation in this group from which *A. humeralis* and *A. ruficauda* have diverged one way and *A. carpalis* another. A second alternative would be for *A. mystacalis* and *A. sumichrasti* to increase the maturational rate in the skull with changes in social structure and for *A. carpalis* to completely return to the north temperate timing of ossification. Selander (1964) thought that delayed maturation did not reflect phylogenetic relationships among species of *Campylorhynchus.* However, this may be an ancestral trait correlated with a group-type social system that has been selectively eliminated in forms in which the pair now is the social unit during breeding season.

DISCUSSION

At the beginning of this monograph the genus *Aimophila* was split into three subgroups plus the single species, *A. quinquestriata.* These groupings were constructed on the assumption that they include species showing some similarities and that at times it is easier to consider groups rather than to discuss each species separately. I discussed characters that differed among species both qualitatively and quantitatively. Obviously, it is difficult to summarize in a two-dimensional table the results of comparisons of quantitative characters, but comparisons of major characters are summarized for the entire group in Table 36. I think this table shows sufficient evidence to support the initial groupings as evolutionary units. I investigated only a limited number of possible characters, but this should not detract from the applicability of the results to an understanding of evolution within the genus.

All characters studied were considered to be adaptive in one way or another. I did not study any neutral characteristics (i.e. those carried in the genome linked to another functional complex). These characters varied over a broad range from those present among all members of a taxon to those limited to demes or subpopulations of a species. The value of each character to classification of the group must be judged for each case individually. The value to the classification in large part depends on the supposed evolutionary history of the taxon.

Many characters studied are common to the entire genus. In general, features of this type are shared with most or all sparrows and presumably are related to initial emergence of the ancestral emberizine line into its new adaptive zone. In one way or another, most are components of the generalized type of emberizine habitat exploitation.

Similarity of breeding seasons is probably a function of the ecological and environmental factors that determine the most advantageous period of the year in which to produce young. Selection operates to time the breeding effort to coincide with the time of year when the most young can be raised to reproductive maturity (Lack 1954). The similarity of the breeding season of many tropical seed-eating birds (Skutch 1950, Moreau 1950, Benson 1963) indicates very strongly that the primary selective force is availability of food. Breeding seasons in *Aimophila* are not all identical, but they seem to be under similar controls. Most species live under similar conditions of light periodicity and rainfall fluctuations, but temperate regimen differs. As food supply is more stringently regulated by rain than by temperature (provided temperature range is suitable), there is probably little relation of temperature to breeding season. The only species that may be temperature dependent is *A. aestivalis,* in which northern populations seem to be regu-

TABLE 36

SUMMARY OF SOME CHARACTERISTICS OF *AIMOPHILA* INVESTIGATED DURING THE PRESENT STUDY

Species	Altitudinal distribution	Size of range	Habitat	Plumage	Postjuvenal molt	Prenuptial molt	Bill color	Groups	Foraging position	Song	Chatter call	Nest	Egg color	Squamosal	Palate	Skull timing	Skull pattern
ruficauda	L	L	TS	B	p	X	B	X	G	S	P	R	WU	S	2.2	D	P
sumichrasti	L	S	TS	b	p	X	B	O	G	S	P	R	WU	S	2.0	D	P
humeralis	L	M	TS	B	p	X	B	X	GT	S	P	R	WU	S	1.9	D	P
mystacalis	H	M	TS	B	p?	X	B	O	GT	S	P	?	?	I	2.0	D	P
carpalis	L	M	TS	b	p	X	b	O	G	S	?	R	WU	I	2.4	N	F?
ruficeps	H	L	PO	D	p	O	b	O	G	C	I	G	WU	I	2.0	N	F
rufescens	LH	L	PO	D	p	O	B	O	G	C	I	G	WU	I	2.0	N?	?
notosticta	H	S	PO	D	p	O	M	O	?	C	?	G	?	I	2.0	N	?
aestivalis	L	L	W	D	c	O	b	O	G	C	A?	G	WU	I	2.0	N	F
botterii	LH	L	W	D	c?	?	b	O	G	C	A?	G	WU	I	2.3	N	?
cassinii	L	M	W	D	c	O	b	O	G	CS	A?	G	WU	I	2.2	N	?
quinquestriata	M	M	TD	B	p	O	B	O	GS	C	?	?	WU	I	2.0	N	?

Altitudinal distribution = lowland (L), highland (H), or middle elevations (M). *Size of range* = small (S), medium (M), large (L). Subjective analysis based on area included in range. *Habitat* = thorn scrub (TS), pine-oak (PO), grassy-herbaceous (W). *Plumage* = bright (B), dull (D). *Postjuvenal molt* = partial (p), complete (c). *Prenuptial molt* = present (X), absent (O). *Bill color* = strongly bicolored (B), slightly bicolored (b), monocolor (M). *Groups* = occurs in groups of more than two adults in breeding season (X), does not (O). *Foraging position* [primary] = ground (G), trees (T), shrubs (S). *Song* = simple (S), complex (C). *Chatter call* = derived from primary song (P), independently derived (I), derived from alarm notes (A). *Nest* = raised (R), ground (G). *Egg color* = light colored [bluish or whitish], unmarked (WU). *Squamosal* = sculptured (S), inflated (I). *Palate* = average category as mentioned in text (p. 183). *Skull timing* (average period to ossify skull completely) = delayed (D), normal [complete skull ossification in about 6 months] (N). *Skull pattern* (pattern of ossification of skull) = parietal last (P), frontals last (F).

lated by temperature; but the evidence is not as clear for southern populations.

Two aspects of behavior—ground foraging and incubation by the female, followed by care of young by both male and female—are found among most species of emberizines (Kendeigh 1953, Verner and Willson 1969) and probably have been secondarily modified in species where they are not present, as both seem to be related to ecology of seed-eaters. The ground is the most important location of seeds as food for the birds. Secondarily, some species may resort to a greater amount of animal food or various types of vegetative plant structures, or even flowering parts. In *Aimophila* adults switch to predominately insect food during summer months, presumably because of abundance of this rich food source and decreased availability of seeds. They also feed insects to the young. Patterns of parental care among emberizines are related to relative abundance and availability of food, predation pressure, and other factors. Thus these behavioral characteristics are shared by many sparrows and are adaptations of a larger group of species than those of the genus considered here.

Several characters common to all members of the genus are not so easily explained in terms of general adaptations of emberizines. White or light bluish eggs are found in *Aimophila* and a limited number of other emberizines. In some birds there is probably positive selection for unmarked, light eggs to make them more visible in the nest cavity (e.g. woodpeckers), but this is not the case in *Aimophila* or other emberizines with light, unmarked eggs. For these species, selection probably operates to protect the eggs. Presumably there are several possible techniques of protecting eggs, only one of which is protective coloration. Others include choice of nest site and behavior around the nest.

Similarity of the posterior border of the transpalatine process may be due to common ancestry, but probably is more related to type of feeding apparatus evolved in response to the diverse selection pressures involved with feeding. It is possible that this character might remain essentially unchanged throughout a large group of species with different bill structures, but this would require other changes in the skull and jaw apparatus. However, the range of changes of the trophic apparatus over which the palatines could remain essentially unchanged depends on their functional relation to the remainder of the jaw. A functional analysis of the transpalatine has been approached only in a rudimentary fashion (Bock 1960, Bowman 1961).

Postjuvenal molt, like the postnuptial, is shared by all emberizines, but degree of completeness is variable. Most emberizine species, including some species of *Aimophila*, have an incomplete postjuvenal molt; for many the molt is limited to body plumage. All members of the *botterii* complex have a complete postjuvenal molt. The remaining species of *Aimophila* usually have an incomplete molt in which the entire body plumage and varying numbers of flight feathers are renewed. In *A. quinquestriata* and *A. ruficeps*, flight feather molt is usually limited to the innermost secondaries and perhaps the central pair of rectrices. Degree of completeness of molt in some species and populations seems to be related to timing, which in turn is partly determined by time of hatching, the occurrence or absence of migration, and selective pressures to renew potentially heavily worn feathers.

Other characters studied appear in one or more species in the genus, but are more variable and not common to all species or to particular groups. Again, most of these characters concern ecology of the birds and are related to recent adaptations. Some are parts of character complexes and may vary within limits, depending on other parts of the complex. The squamosal region is of two different types; the less common type is limited to three closely related members of the *Haemophila* complex. In addition to its normally proposed function of increased auditory acuity, the squamosal types may be related to jaw musculature and bill characters. Temporal fossa size or the area covered by the insertion of *M. adductor mandibularis, pars superficialis*, is variable throughout the genus. Size, related to strength of the muscle and strength of the entire jaw apparatus, varies directly with other measures of strength of the trophic apparatus. It is dependent on feeding adaptations of the species and is modified by selective forces in relation to minor environmental adaptations. Thus, it would seem to have little relation to the evolutionary history of the groups in *Aimophila*, in which evolution of the jaw apparatus shows differences within groups and convergence among groups.

Many parts of the external and internal morphology, especially those concerned with locomotory functions, would be expected to show similar sorts of variability. Each would be influenced by ancestry of the organism, but could be modified within genetic capabilities of each local population. Thus, wing, tail, and leg measurements would not be expected to reliably indicate relationships, but rather to reflect recent evolutionary changes as populations adapted to various ecological conditions (Linsdale 1928).

Competition in sympatry seems to be a potent evolutionary force that can intensify or reduce differences to allow forms to coexist. Degree of realizable sympatry will depend on potential for change among populations and initial differences that are carried into sympatric situations. Here again we are dealing with a characteristic that probably has relevance primarily at the specific or subspecific level. There may be a "generic preadaptation" for sympatry that allows forms of some genera to become sympatric successfully, while others are maintained only allopatrically; the latter seems to be the case with some wrens (*Campylorhynchus*; Selander 1964). This is probably determined largely by foraging method and potential for successful foraging on other resources. It is also determined by degree of specialization in the trophic apparatus. The sparrows have built-in plasticity in that they normally switch diets during the course of a year and could easily become more specialized in one of several directions given appropriate conditions. It may not be entirely chance that in two classic examples of adaptive radiation on islands i.e. in the Galápagos and in Hawaii, the ancestral form may have been a fringillid or thraupid type (Baldwin 1953, Tordoff 1954). Perhaps it indicates that the finch-thraupid bill can be changed more easily and radically on the basis of initial structure than can other types. It is possible that this preadaptation of the bill permitted the evolutionary success that we see today.

Characters that seem to be limited to one group or another among these sparrows are generally related to adaptation and subsequent radiation of the group in a particular habitat type. Thus, characters that seem to be useful in biologically defining groups within the genus are ecologic and related to habitat exploitation. This suggests that they may have been key adaptations in the habitat type in which the particular group radiated or for the social order associated with exploitation of the habitat. Many characters are not shared by other birds, even other fringillids that occupy the same habitat, suggesting that they are in fact key adaptations for the subgroups of *Aimophila* and are not convergences to a common adaptation necessary for success in the habitat.

The *Haemophila* complex apparently radiated in the lowland thorn scrub that is common along the west coast of Mexico and southward. Many characters peculiar to this group are adaptations to this environment. Prenuptial molt presumably is an adaptation to the abrasive environment that causes marked feather wear in the months between postnuptial molt and the next breeding period. Plumage renewal may be important in courtship or territorial behavior. However, in order to insert this molt into the annual cycle just prior to, and sometimes slightly overlapping with the breeding season, there must be sufficient energy for both processes (Pitelka 1958). Overlap of molt and breeding potential is especially prominent in males. Raised nests are presumably an adaptation to reduce predation or to combat inclement weather, especially summer rains. Occupation of thorn scrub habitat has brought about some changes in social structure; in some cases family groups may stay together for more than a year. Most of the remaining features that characterize the *Haemophila* complex are related to type of social system. Most forms have secondarily lost the group social structure and have returned to the pair as the social unit, but they have retained some group adaptations (see Selander 1964: 205–209, for a discussion of selective advantages of group behavior among wrens). Juvenal plumage probably has been selected for its similarity to that of the adult to decrease antagonism. *A. carpalis* and *A. mystacalis* juveniles probably regained heavy streaking in response to selective pressures of their social systems. Delayed skull ossification probably is related to this group behavior via its relationship to the general overall delay in maturation of young; it is less apparent in forms that lost the group behavior. Bright plumage and chatter duets probably facilitate communication in open habitat and serve to reinforce the pair bond. Immelmann (1963) already noted the apparent correlation between maintaining the pair bond for long periods and presence of a chatter or reunion duet in species living in arid habitats. The important feature of the chatter duet, in those members of the *Haemophila* group in which it has been studied, is that it may have been derived from primary song (or vice versa) and is not an independent acquisition, as apparently is the case in the *ruficeps* group. The simple primary song suggests that visual communication may be more important in these forms than in other aimophiline groups in which plumage is duller and vocalizations more complex. The simple, slash-note song may also be physically the best mode of vocal communication in scrubby habitats.

The *ruficeps* and *botterii* groups seem to have evolved in close relation to dense ground vegetation of either grass or dicotyledonous herbs and consequently share many characters, among which are inflated squamosal area, type of nest site, lack of prenuptial molt, dull adult plumage, and heavily streaked juvenal plumage. All of these characteristics seem to be adaptations to habitat type either as protection (adult and juvenal plumages; nest site) or in relation to character of environment and social and communication systems (squamosal and lack of prenuptial molt). Lack of prenuptial molt possibly is related to decreased importance of plumage in display.

Selection for dull plumage, apparently for protective coloration, reduces the potential communicatory value of the plumage. In species (e.g. some warblers and finches) in which plumage is important in courtship activities, but in which it becomes worn in the interval between postnuptial molt and the subsequent breeding season, there has been selection for a prenuptial molt to renew the plumage, at least that portion that seems to be important in display (see section on molts). Although plumages of members of the *ruficeps* and *botterii* groups become worn by time of breeding, there is no strong selective pressure to renew dull plumage, which has little communicatory importance. Preparations, especially physiological, for breeding may select against channeling energy into molt just prior to breeding.

The *botterii* group is unique in occurrence of flight songs, generally more pointed wings, migratory behavior, yellow at the bend of the wing (in most populations), and spotted first-year plumage in many individuals. Flight songs, long wings, and migration are presumably interrelated through their common denominator of habitat exploitation. Flight songs are not equally developed in all species but would facilitate display in an open environment. Probably they have been enhanced in *A. cassinii* to speed pair formation and establishment of territory in this migratory species. In this sense, flight songs would function in a manner similar to marked sexual dimorphism in certain north temperate warblers and orioles (Hamilton and Barth 1962).

Long wings are probably closely correlated with migratory behavior, which in *Aimophila* is found only in these three species, which are among the most northerly forms of the genus and are probably those most adversely influenced by low temperatures and harsh winter weather. Webster (1959a) has already shown that the more southern (probably resident) lowland populations of *A. botterii* have shorter, more rounded wings than the northern populations. A similar situation may exist for *A. aestivalis*, but this has not yet been investigated. Most populations of *A. cassinii* are migratory to some extent. Migratory habit is undoubtedly related to range and habitat of the species.

The value of the yellow "wrist" among many sparrows is not certain. In some emberizines this area of the wing may be displayed, but occurrence of similar displays among the numerous species with yellow wrists has not been fully documented. Another character that is probably related to the social system of these birds, particularly the relation between young of the year and adults, is spotted first-year plumage. It probably has a signal function in relations between these two age classes. The fact that it occurs in only some individuals suggests that it is being lost or gained evolutionarily.

The three *botterii*-group species have similar plumage patterns; *A. botterii* and *A. aestivalis* once were considered conspecific. The slightly modified, scalloped appearance of *A. cassinii* probably is a response to selective pressures in the comparatively more arid, open habitat that this species occupies.

Characteristics of the *ruficeps* group are harder to relate to ecologic conditions and seem to be more related to common ancestry followed by little divergence. Only the pine-oak habitat can be classed as a major ecological similarity. Similar primary song may be related to decreased selection for divergence based on easy recognition of slight differences of a complex song, and decreased importance of song in species recognition or to carrying quality of these song types in pine-oak habitat. The chatter duet has not been properly investigated from this view. The primary similarity in the *ruficeps* group is plumage pattern, which seems to have been under relatively little selective pressure to change. The plumage apparently has little of the signal function that one might predict for plumage of the *Haemophila* group and hence is under little pressure to diversify; however, the rusty head pattern may have some degree of signal function. Secondly, the plumage pattern probably was well adapted initially for any protective function, and there actually may be selection to retain the pattern.

The discussion of *A. quinquestriata* has been postponed to last, as I am not sure where this species fits in relation to other species of *Aimophila* or even to other sparrows; it probably does not belong with *Aimophila.* The yellowish and dusky juvenal plumage is very different from that of any of the other species. Although one might be tempted to place it with other brightly colored species, the presence of a breast spot, the concolor dorsum, a strikingly distinct primary vocalization, absence of a prenuptial molt, and apparent lack of reunion duet all seem to require that it be placed alone in this study. Its occurrence at middle elevations in tropical deciduous woodlands is also distinctive for *Aimophila.* Probably it is closer to a group of sparrows that includes *Melozone.*

CLASSIFICATION AND EVOLUTION

The three species-groups, plus *A. quinquestriata,* are not as closely related as most recent classifications indicate. However, little can be said about phylogeny of the group as a whole until more studies are carried out on closely related species and genera of emberizines. Each group may well be related to different genera (at least as they are currently delineated) among the emberizines, although I do not feel that an attempt now to place groups in other genera would prove worthwhile. In this section I suggest possible relationships of the groups and likely evolutionary pathways within them (see Fig. 17).

BOTTERII COMPLEX

Relationships of this complex to emberizines other than *Aimophila* are obscure, but these species are probably closest to a group that includes primarily species with dull plumage. In most aspects of plumage pattern they conform rather closely to the large group of "typical" emberizines, which otherwise have diverged in such morphologic features as appendage ratios, tail shape, and feather shapes.

Hubbard (1974) has discussed the evolutionary history of the *botterii* complex, suggesting that the three species may have differentiated as recently as the Wisconsin glacial period, when their habitats probably were disjoined in several refugial areas. The three species in this complex and the *petenica* group of *A. botterii* are essentially allopatric with most other species of *Aimophila. A. botterii* (*sensu stricto*) probably arose from a population in southern Mexico, while *petenica* evolved in grassland and pine savanna of the lowland Caribbean region. Since then, ranges of the two expanded, only to contract again in some areas and leave various relict populations, in-

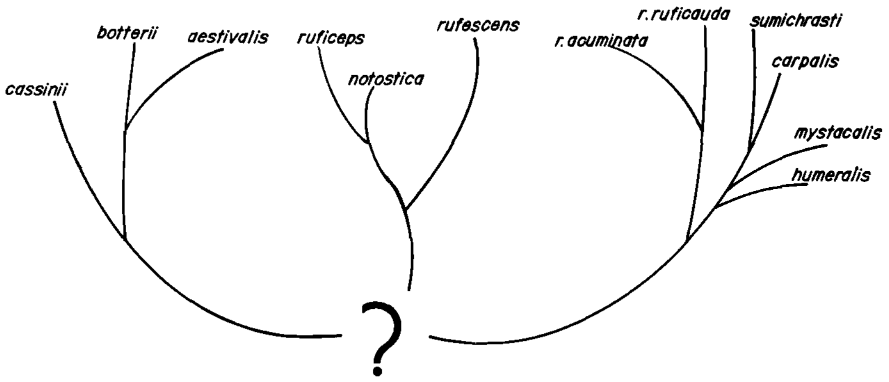

FIGURE 17. A hypothetical phylogeny for 11 of the species of *Aimophila* investigated in this study (*A. quinquestriata* not included). The lines to the central query indicate that the relationships of the three lines of descent are uncertain.

cluding ones in the highlands of Central America. *A. botterii* probably has benefited from man's activities on much of the plateau region of Mexico, where disturbance due to agriculture and settlement have created grassy-weedy habitats where once there were large expanses of pine-oak forest.

A. cassinii is a northern form that may have evolved in a grassland refugium in northern Mexico or along the northern Gulf of Mexico coast (Hubbard 1974). Relationship of its back pattern to its arid, open habitat has been mentioned (p. 198). Flight song performance, migratory habits, and other habitat adaptations seem to be elaborations of similar characters in *A. botterii. A. cassinii* is allopatric with *botterii*, except in Texas and northeastern Mexico, and locally in Arizona (Ohmart 1968). In Arizona, degree of overlap must be studied in more detail to determine extent of breeding of *A. cassinii* in late summer.

A. aestivalis is an eastern isolate that has differentiated very little from *A. botterii* (*sensu stricto*). As with some other species of North American birds, *A. aestivalis* probably was isolated from its relative during the Pleistocene (Webster 1959a), probably in a refugium in southern Florida (Hubbard 1971). From that refugium the species spread northward and westward, while differentiating into intergrading races.

RUFICEPS COMPLEX

Outside of *Aimophila* the *ruficeps* complex seems to be most closely related to the Brown Towhees of the genus *Pipilo*. This is suggested especially by the pair reunion duet and display of *A. rufescens* and that of towhees. The display has not been seen in *A. notosticta* or *A. ruficeps*, but at least the latter occasionally duets. Foraging technique of *A. rufescens* is similar to that of towhees, but this probably is convergence.

Evolutionary history of the *ruficeps* complex is difficult to unravel, because two forms—*A. ruficeps* and *A. rufescens*—are now so widespread. These two probably were separated early in the history of the group and since have reinvaded the ranges of the other. *A. ruficeps* probably evolved farther north than *A. rufescens,* perhaps on the Mexican Plateau. *A. rufescens* may have arisen in the highlands south of the Isthmus of Tehuantepec, with a subsequent occupancy of the lowlands of the Caribbean coastal plain from Mexico south to Guatemala and parts of Honduras and Nicaragua. Timing of the differentiation could be in the Illinoian (penultimate) glaciation, when shrubby habitats for these species may have been disjoined by expansion of forest types (Hubbard 1974). Following expansion of the ancestral *A. ruficeps* in the last interglacial, another change of habitats in the Wisconsin glacial period could have pinched off a population in southern Mexico, that then differentiated into *A. notosticta.* Since then, the more northern *A. ruficeps* reinvaded this area of Mexico to become sympatric with its near relative.

HAEMOPHILA COMPLEX

Relationships of the *Haemophila* group are even more tenuous than those of the *ruficeps* complex. The head pattern of *A. sumichrasti, A. carpalis,* (and to some extent, *A. ruficauda*) seem to ally the group to genera such as *Rhynchospiza* and possibly *Arremonops* and *Arremon*; however, these genera have yellow patches at the bend of the wing, which none of the *Haemophila* complex has. The presence of a wing-up display (see Moynihan 1963) and reunion duet in *Arremonops* that are similar to those of some *Haemophila* tends to support the alliance. In general, habitat seems to be similar to that of *Arremonops,* primarily *Arremonops rufivirgatus.* The similarity of song of *A. rufivirgatus* to that of *A. carpalis* is very striking. However, other species of sparrows have similar songs, and this character may carry little weight in defining relationships.

The *Haemophila* group is a composite of several species in which actual relationships may be somewhat obscured by divergences in plumage coloration, partly as the result of secondary contact. I do not agree with Storer (1955) that *A. sumichrasti* is probably more "primitive" than other members of the group, in spite of its more "conservative" color pattern compared to *A. ruficauda* and *A. humeralis.* This conservatism could be an adaptation to sympatry with the boldly marked *A. ruficauda* which, because of its wide range, may be the oldest member of this complex.

A. carpalis, found primarily in open mesquite woodlands of northwestern Mexico and adjoining Arizona, is similar to *A. sumichrasti* in many adult plumage characteristics, but the juvenal plumage is much more heavily streaked. Song is also similar in the two species.

A. mystacalis seems to be a differentiate from the same ancestor that appears to have given rise to at least *A. sumichrasti* and *mystacalis.* In *A. humeralis* the heavily streaked juvenal plumage and pair form of social unit are similar to those of many other emberizines and probably are secondary modifications.

A plausible evolutionary history of this complex may well follow from Hubbard's (1974) Pleistocene rufugial concept in arid habitats in Central America. At least two stages, or glacial periods, would seem necessary to account for the evolution in the complex, one to split off the ancestors of *A. ruficauda*, on one hand, and that of the remaining four *Haemophila* species on the other. One might visualize the latter perhaps arising in the Isthmus of Tehuantepec and the former somewhere to the north, but both along the Pacific coast of Central America. Following that glacial differentiation, each of these ancestral types may have expanded, as did their habitats, during the interglacial period. The pre-*ruficauda* form may have spread from Sinaloa to Costa Rica, while the other may have moved northward from the Isthmus of Tehuantepec to Sinaloa and inland to Puebla and adjacent areas.

With the advent of the Wisconsin glaciation, pre-*ruficauda* may have died out everywhere but in a northern refugium (e.g. Río Balsas basin) and a southern refugium (e.g. Isthmus of Tehuantepec)—these leading respectively to the *acuminata* and *ruficauda* subspecies complexes. Meanwhile the former isthmian differentiate may have been split into no fewer than four populations, these evolving respectively into *A. carpalis* (Sinaloan refugium), *A. humeralis* (Río Balsas basin), *A. mystacalis* (Valley of Oaxaca), and *A. sumichrasti* (Isthmus of Tehuantepec).

Of course there may have been more or even fewer disjunctions of the stock that produced the species in this complex, but essentially it appears that all of the species, except the widely spread *A. ruficauda*, evolved *in situ.* That species poses interesting questions, including ones relating to the possible extent of its influence on the evolution of sympatric relatives in this complex. For example, the pale chest in *acuminata* complements well the dark chest of *A. humeralis*, but which responded to which? One would suspect that at least *acuminata* adjusted, because all other races of *A. ruficauda* are dark-chested. However, more likely the adjustments were mutual.

All species in the complex could be products of a single separation of ancestral stock, with *A. ruficauda* evolving in its own allopatric refugium (e.g. Costa Rica). The present wide range of the species could then have been attained since the last glaciation, with maximum expansion perhaps occurring in the Altithermal Interval (Deevey and Flint 1957), when arid habitats may have been even more widespread than at present. As a consequence, the races of *ruficauda*, including *acuminata*, could be of recent origin.

A. QUINQUESTRIATA

A. quinquestriata probably is no more closely related to *Aimophila* sparrows than to certain other emberizines. The species shows some resemblance to members of the *Melozone* complex, but it has a much longer tail and a different body form. *A. quinquestriata* occurs in about the same habitats and altitudes (middle), as does *M. kieneri* and the other species of *Melozone* that I have seen (*M. biarcuatum*; *M. leucotis*). The marked difference between *Melozone* and *A. quinquestriata* in general body configuration might be explained by divergent evolution in secondary contact or evolution in allopatry in response to differences in habitat exploitation.

Stronger evidence of similarity between this species and *Melozone* comes from plumage characters. Presence of the black chest spot and nearly uniform dorsum in *A. quinquestriata* may align it with the *Melozone* complex, especially *M. kieneri.* More similarity is shown by the juvenal plumage of the two forms. As the adult plumages do differ in some major degree from each other, it would seem that among a group of birds in which selection has usually operated to match juvenal plumages to divergent adult plumages, one might use the marked similarity of juvenal plumage as strong evidence of a close relationship.

Song of *A. quinquestriata* is distinctive, but to some extent it is similar to that of the Lark Sparrow (*Chondestes grammacus*) with which it also shares certain characteristics in patterning of foreparts. The similarity is tenuous at best. *A. quinquestriata* apparently has enjoyed a long period of isolation and has few emberizine competitors throughout its range. The limited population size and apparent specialization to a limited habitat suggest that it may be an old and relict species. I have no idea of its evolutionary history, other than it may have evolved *in situ.*

GENERIC CLASSIFICATION

This study was designed to formulate a concept of a genus in the avian family Fringillidae. The genus *Aimophila* was chosen as it was thought to be a heterogeneous assemblage of species that might lend itself to an analysis of the sort that would provide a theoretical basis for definitions of fringillid genera. Genera can be approached conceptually as evolutionary units or taxonomic groupings. The latter approach has been championed recently by proponents of numerical taxonomy. Their assumption is that with a vast array of species and with little or no pertinent information from the geologic record, it becomes rather meaningless to construct a phylogeny that can be based only on subjective interpretations of characteristics of the living organism, as there usually is no information concerning directions and rates of evolution. The numerical taxonomist deals with degrees of similarities and differences and hopes that sufficient numbers of characters will be able to replace the subjectivity of the systematist.

This makes it abundantly clear that the genus, as with all categories both above and below the level of the species, is, in fact, a subjective category that has been erected to facilitate study. When one considers the taxon species in terms of the geologic record, this category too becomes one of subjectivity, especially the paleospecies (Simpson 1961). This subjectivity is also evident in modern species where the natural test of biological species—sympatry—is not available. Another complication is the fact that organisms are continually evolving. At a given point in time two populations may or may not have diverged enough genetically to not interbreed in sympatry. Sibley (1950) found in Mexico several populations of towhees (*Pipilo*) in which morphologically distinct types did or did not hybridize, depending on habitat and region. Such populations were near the species-infraspecies borderline, and their actual relationships were problematical in terms of actual or potential gene flow. A similar continuity of evolutionary change plagues the student of higher categories, especially since there is no strictly genetic definition of a genus that can be applied as with sympatric species. As forms radiate from a common ancestor, the degree of divergence will depend on strength and direction of selective pressures on the various populations and on the extinction of intermediate forms. Even if the geologic record were sufficient to supply time factors, evolutionary direction, and actual ancestral forms of the group in question, it still would be a selective matter to determine boundaries for genera and higher categories. Primarily, a more complete geologic record would fuse groups one into another and only confuse the picture. The major aid given by the geologic record would be to provide some assurance that the species being considered were, in fact, related via a more recent common ancestor than some other species. However, recency of common ancestry is not the final test of relationships, because evolutionary rates are too variable, depending on rate of environmental change, size and continuity of the gene pool, and many other factors. The test of relationships is more dependent on roles of the species in future evolution and degree to which species have diverged in their present evolutionary roles or directions.

Given that genera are subjective categories, one must then attempt to formulate what actually comprises a genus in the particular group in which he is working and attempt to assess the various selective pressures on the characters of the species being analyzed. Obviously, there are difficulties in such assessments, primarily because the final judgment must be subjective. If the group of species in question has in fact radiated from or had a recent common ancestor, the group must share some characters that will reflect this common origin. Among the higher categories the evolutionary pattern seems to have been one of basic adaptations that allowed a subsequent series of forms to radiate into the newly achieved adaptive zone (G. G. Simpson 1961). The evolutionary path to such zones is often tortuous and involves many small changes rather than a single, large radical change (Bock 1965). At each higher level of organization the adaptive zone or key adaptation usually has broader potential, but this is judged only in retrospect on the basis of success of radiation and divergence of organisms that share the adaptation(s).

Mayr *et al.* (1953) noted that in many cases a genus also has a type of adaptive zone that they refer to as a "generic niche." The generic niche conceals a multitude of potentialities. Particular adaptation(s) may vary among genera and especially among the various large groups of extant organisms, but probably all (at least in birds) are related to patterns of habitat exploitation. Making a judgment of generic niche is especially crucial as it will markedly influence consideration of the various adaptations apparent in the genus. To illustrate this among bird genera, let us look at the results of several studies showing that type of ecological unit represented by generic classifications varies with evolutionary history of the group.

Bowman (1961) reported in detail on radiation of the Galápagos finches (Geospizinae) in terms of common feeding adaptations, and he divided the group along lines that reflect this concept of genera. His study was concerned with members of an island fauna in which there apparently were ample niche spaces into which forms could radiate. In this island situation the pattern of evolution was determined by the forms (probably finch-like) that were able to colonize, availability of resources, degree of isolation, and subsequent patterns of divergence and reinvasion of the several islands. For an island nearer the source of mainland stock, the pattern would have been influenced more by competitive interactions with additional colonizers, which might have limited the degree of possible divergence from primary stock. It is likely that other colonizers would have been species adapted for other patterns of exploitation and have been competitively superior to primary colonizers in some patterns of habitat exploitation (e.g. *Nesomimus*).

Lack (1947) in an earlier study of the same birds placed them in four genera—*Geospiza*, *Camarhynchus*, *Certhidea*, and *Pinaroloxias*. According to Lack, most of the genera could be differentiated, during breeding season, on the basis of habitat and foraging position within the habitat, two obviously interrelated characteristics. Lack's classification differed from that of Bowman by putting two of Bowman's tree-foraging genera, *Cactospiza* and

Platyspiza, into one large genus, *Camarhynchus.* Lack was more impressed by foraging position than the more refined characteristics of foraging apparatus and technique. Bowman was obviously more interested in foraging apparatus and emphasized it. The two classifications differed primarily in emphasis placed on differentiation within a broad foraging zone.

Another pattern of exploitation has been investigated by Selander (1964) in his study of "cactus" wrens (*Campylorhynchus*). He postulated that these forms initially split into two geographic units, one in Mexico and the other in northern South America. Subsequent evolution of forms in each geographic group was followed by reinvasion of the range of the other where each group occupied a different habitat. Relationships in the South American species are less well-known than those in the Mexican group. In the latter there seems to be almost complete allopatry, suggesting that the forms had successfully specialized to restricted means of habitat exploitation, and when geographic isolates came into secondary contact there was little possibility for divergence from the source phenotype. The range boundaries of the species then seem to be developed via competitive interactions in which the outcome is allopatry rather than divergence and geographic, if not habitat, sympatry. Allopatric distributions often make relationships easier to understand, as evolutionary divergences associated with sympatry are eliminated or reduced.

Yet another form of adaptive radiation seems to have occurred among the groups of the genus *Aimophila.* The species apparently radiated in several distinct habitat types while the centers of distribution (and probably centers of origin) were more nearly coincident than in the wrens. However, following geographic isolation there was secondary contact and "character displacement." So far there has been little evidence that the species can coexist in the same habitat unless there are extreme size differences, such as in *A. ruficeps* and *A. rufescens.* In this case ability to occur in secondary sympatry probably is related to type of habitat exploitation and availability of suitable resources in a variety of habitats. Ability to become sympatric successfully may also depend on plasticity of behavior and morphology of the species in terms of potential competitive interactions.

From these three examples—one island and two continental—it can be seen that evolution of genera in terms of an ecologic unit probably is correct, but that the type of unit depends on pattern of habitat exploitation, degree of specialization of the key adaptation(s), and potential competitors at the time of radiation of the group. From two classic island faunas, Galápagos finches and Hawaiian honeycreepers (Drepaniidae), it would appear that, in large part, radiation of island taxa is determined by the presence or absence of competitors (see Pitelka 1951b: 381 for an example in jays (*Aphelocoma*)). In the presence of competitors, form of habitat exploitation and its plasticity are more important. Thus, although the genus is an ecologic unit it is necessary to have some idea of the evolutionary history or type of ecologic adaptation that has given the genus a zone in which it can radiate. This obviously can lead to circular reasoning, but it is primarily meant as a guide by which one can judge the appropriate taxonomic positions of species. As G. G. Simpson (1961) said, "taxa . . . are not in principle defined by membership but by relationship."

It would seem from this that the definition of genera on the basis of similar characteristics and similar degrees of divergences or gaps that may be negatively correlated in size with numbers of included species (Mayr *et al.* 1953, Simpson 1961), may have relevance only in terms of species that show the same pattern of evolutionary radiation and hence the same type of ecologic adaptation. While it would appear that this is probably the case for most closely related genera (e.g. most members of the same family), it does not follow necessarily in all cases. It becomes especially difficult to make comparisons of sizes of gaps and divergences as the relationships of the forms become more distant. Thus, it probably is not realistic to claim that the generic concept among ducks must necessarily follow the same pattern as in sparrows. Perhaps it is more relevant to discuss generic classification in terms of type of radiation that has occurred. We might be able to compare genera of birds that have evolved in terms of each of the three (probably more) exploitation patterns discussed above for wrens and finches. The selective forces in each case must be judged in terms of the close relatives and included species. However, the species should be grouped as "ecologic units" wherever information is sufficient to support this hypothesis. The problem of generic boundaries still has not been settled satisfactorily. Boundaries obviously will depend on broadness of the ecologic unit, distinctness of the groups, and philosophy of the systematist.

SUMMARY

This study is concerned with various aspects of morphological, ecological, and behavioral variation in members of a heterogeneous assemblage of birds currently united as the genus *Aimophila.* It provides a background for future work on generic classification of fringillids and a possible theoretical framework for generic classification. It deals with those characteristics of the species of *Aimophila* that have been used for classification in the past and those that present meaningful evidence for a classification based on modern evolutionary theory. Primarily, I have tried to incorporate much information from the biology of the birds; most previous studies have neglected this aspect.

The evolution of bird genera can be viewed as the radiation of ecologic

units. Other studies of bird genera have at least two important units: feeding units and habitat units. Type of unit is related to space available to an evolving group. Island genera are often feeding units, while continental genera, faced with increased competition from existing species, are frequently of the habitat type. Both types probably occur in either situation depending on relative availability of diverse habitats and presence or absence of competitors.

Most characters examined fall into two arbitrary categories based on continuity among the species. Most that are useful at the generic level are qualitative and apparently are related to the evolutionary success of the particular group. Mensural characters and those that show slight changes throughout the groups are primarily concerned with adaptations to minor variations in the environment following occupation of the generic space or with the evolution of the progenitor of the ecologic unit.

The species of *Aimophila* have been divided into three species groups—the *Haemophila* complex, the *ruficeps* complex, and the *botterii* complex—which had separate evolutionary histories and probably are not as closely related to each other as some earlier authors thought. *A. quinquestriata* is set off as a single species of unknown affinities. I made no attempt to present other generic classifications for these species, but left them as distinct units, at least until further analyses can be made on related species. I included a discussion of possible lines of evolution within the groups.

I concluded that the groups in *Aimophila* represent the habitat type of ecologic unit. The *Haemophila* complex—*A. ruficauda, A. sumichrasti, A. humeralis, A. mystacalis,* and *A. carpalis*—radiated in the lowland thorn scrub forests of western Mexico and the Pacific lowlands of Central America. They have simple songs, chatter duets that usually seem to be derived from primary songs, prenuptial molt, elevated nests, bright adult plumages, juvenal plumages more similar to the adult pattern than in the other groups, and heavy bills. Maturation of the skull is delayed in most.

The *ruficeps* complex—*A. ruficeps, A. rufescens,* and *A. notosticta*—is set off from the other species by its radiation in pine-oak woodland of Mexico and Central America. The three species have similar primary songs, probably similar chatter duets not derived from primary song, and similar plumage patterns with rusty head stripes that fuse into a cap in *A. ruficeps* and sometimes in *A. rufescens.*

Members of the *botterii* complex—*A. aestivalis, A. botterii,* and *A. cassinii*—from weedy, open country of Middle America and United States—have dull plumages, usually have yellow at the bend of the wing, are migratory, have more pointed wings than the other species, and spotted first-year plumages in some individuals.

A. quinquestriata is retained apart because of peculiarities of plumage, unique song, yellowish, heavily blotched, but lightly streaked juvenal plumage, and lack of a prenuptial molt. The nature of its relationship is left open for the present.

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