About the Author

Dr. Hamel worked for the State of Tennessee until February 1993, when he accepted a position as a Research Wildlife Biologist with the U.S. Department of Agriculture Forest Service at the Southern Research Station’s Center for Bottomland Hardwoods Research. There he studied response of wildlife, particularly Neotropical migratory birds and small mammals, to forest management of bottomland hardwood forests. He retired in January 2015.

EDITOR’S NOTE AND DISCLAIMER: This book was first published in 1986 by Smithsonian Institution Press. In July 2018, Smithsonian issued a reversion of rights letter to the author, thereby permitting the publication of an updated edition of the book. This second edition provides links to electronic support materials, including measurement data and standardized photographs on Bachman’s Warbler specimens. Aside from minor updates described in the preface to the second edition, text from the original book has been retained.
BACHMAN’S WARBLER
A Species in Peril

Paul B. Hamel

2nd edition

Smithsonian Institution Press  Washington, D.C.  London
I dedicate this work to those involved in the struggle to preserve natural diversity.
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Preface

This work was intended originally to be simply a bibliography in which all sources were presented and listed under appropriate subject headings; where disagreements or other circumstances necessitated, works were to be cross-referenced to each other. Recent reviewers have urged a more active authorship in which I evaluated the literature and identified important issues concerning the species. This I have done with some trepidation, but also with enthusiasm. Where my own researches have yielded new ideas or summaries, I present them as well.

The work comprises two Parts, (1) an introductory discussion of the biology and history of the birds, and (2) a list of publications that mention the species. The first Part is a brief introduction to and analysis of the literature dealing with the biology and history of Bachman's Warbler. Certain works cited in the introduction do not mention the species. Such citations are marked by asterisks and the works are listed in a separate Literature Cited section that accompanies Part 1. Part 2 constitutes the bibliography of the species in which works are listed in two ways. First is an alphabetical listing, by author, of papers that treat the Bachman's Warbler. Second is a listing by subject categories. The subject classifications are patterned loosely after those employed in recent volumes of the *Zoological Record*. Subject classifications in Part 1 and the subject-heading section of Part 2 are labelled the same to enable ready comparison. I provided many categories so that works might be referenced as specifically as possible. Readers expecting each reference to contain a substantial amount of information must be patient, however; information about this very rare species is far more often recorded in phrases than in paragraphs.
Copies of unpublished reports listed in the bibliography have been placed in a file in the R. M. Cooper Library at Clemson University. Readers wishing to examine such works may do so by writing to the Reference Librarian, R. M. Cooper Library, Clemson University, Clemson, South Carolina 29631.

I have used a number of other important sources of unpublished reports or original field notes in compiling this work. These include the field notes of Arthur T. Wayne at the Charleston, S.C., Museum; the extensive correspondence between Wayne and William Brewster in the collections of the Library of the Museum of Comparative Zoology at Harvard University; the correspondence of Witmer Stone at the Academy of Natural Sciences of Philadelphia; original field notes and correspondence of personnel of the U.S. Bureau of the Biological Survey in the Archives of the Smithsonian Institution; files of the Big Lake National Wildlife Refuge, Manila, Arkansas; files of the U.S. Fish and Wildlife Service Endangered Species Field Office in Asheville, North Carolina; and the files of the Wildlife, Fisheries, and Range staff unit of the U.S. Forest Service in Atlanta, Georgia.
Preface to 2nd edition

The opportunity to place this otherwise-out-of-print book online for future scholars was too good to overlook. Online publication permitted inclusion of a color illustration on the cover. Electronic publication further made possible the inclusion of electronic support materials including measurement data on 312 specimens of Bachman’s Warbler collected between 1832 and 1949, and standardized photographs of 308 of them. Inclusion of these support materials corrects an error in the original work, in which I indicated that that set of photographs had been donated to VIREO at the Academy of Natural Sciences of Philadelphia; I never finalized the arrangements to complete that donation.

I have made small changes to the text of Part 1, to incorporate results of continuing search of collections to locate specimens of Bachman’s Warbler. Table 1 is more complete than before, and Table 2 includes more data. I redrew Figures 2 and 3 using electronic graphic presentations of the original data.

I added three publications to the list of papers that mention Bachman’s Warbler in Part 2 (Hamel 1995, Am. Ornithol. Union 1998, Lovette et al. 2010). Each in its own way extends the original work to the present. I wrote an account of the species for the Birds of North America series that extends the account in Part 1 of this book (Hamel 1995). The current Check-list of North American Birds (Am. Ornithol. Union 1998) declares what I was not able to allow myself to state in 1986, that the species is “Probably extinct.” Lovette et al. (2010) used mitochondrial DNA gathered from one of the specimens measured in the present study to include *Vermivora bachmani* in their comprehensive study of relationships in Parulidae. That work confirmed the close relationship of *V. bachmani* with *V. chrysoptera* and *V. cyanoptera*. 
Acknowledgments

I am indebted to many people for helping to bring this effort to fruition. Julian Harrison's preliminary bibliography was the starting point. Brooke Meanley and Paul Opler sent additional material. The following librarians were extremely generous with their time, insight, and energies in locating and verifying various publications: Donald Miles and Genevieve Reidy of the R. M. Cooper Library, Clemson University; Ruth Hill and Jane Baldwin of the Museum of Comparative Zoology Library, Harvard University; Janet Hinshaw of the Van Tyne Library, University of Michigan Museum of Zoology; Carolyn Hahn of the Smithsonian Institution Libraries; and Nancy Hackney and Sharon Bennett of the Library of the Charleston Museum, Charleston, South Carolina. I cannot thank these individuals and their institutions enough.

William Canine and Gordon Henry of Newberry College provided the photograph of the sculpture by Willard Hirsch. Walter Dawn graciously permitted use of his significant photographs of a singing male Bachman's Warbler. Keith Russell kindly permitted use of his drawing as the cover illustration. Sidney Gauthreaux and Michael Lennartz provided logistical support. Gertrude Corder typed difficult initial drafts of the manuscript. Gordon Howard, Pamela Purcell, and Maxine Romsa coordinated production of parts of the manuscript. Ruth Spiegel and Maureen Jacoby of Smithsonian Press have patiently guided me through the latter stages of the preparation of the manuscript.

The research for this bibliography was supported by the USDA Forest Service Southeastern Forest Experiment Station; the Clemson University Faculty Research Committee; the National Audubon Society; the Charleston, South Carolina, Natural History Society; and the Tennessee Department of Conservation.
An earlier draft of Part 2 (30 October 1978) was read by James Bond, Eugene Eisenmann, Robert Hooper, Thomas Imhof, Vernon Kleen, Kenneth Parkes, and Henry Stevenson. As a result of their suggestions the manuscript has been improved in numerous respects. Two anonymous reviewers of a second draft of that chapter urged the addition of a narrative account of the species. Millicent Ficken, Orlando Garrido, Robert Hooper, and Henry Stevenson read the draft narrative in Part 1. Each made a significant contribution to this final product.

In the end, of course, the work is mine, and I take responsibility for all the analyses and particularly for the frequent speculations. I believe this work is virtually complete, and regret any omissions I have made.
Acknowledgments to 2nd edition

I thank these kind people for helping me with this project. Stephanie Summerhays of Smithsonian Press alerted me to the possibility of converting this work to an online publication. Ginger Minkiewicz of Smithsonian Institution Scholarly Press facilitated the transfer of rights. David Sibley generously permitted use of his painting of Bachman’s Warbler. Maureen Stuart of the U.S. Department of Agriculture Forest Service Southern Research Station publications unit made the online publication happen. Ironically, now 40 years after the Forest Service took a flyer on a graduate student at Clemson University interested in warblers and funded my research on Bachman’s Warbler, this work returns to the agency that started the process. I am grateful to Ted Leininger of the Center for Bottomland Hardwoods Research and his supervisors in the Southern Research Station for supporting me during the intervening time and for encouraging me to complete this project in my retirement. Maureen Stuart and Stephanie Worley Firley shepherded the project to completion.

Inclusion of the support materials resulting from examination of specimens in North American museums provides me the opportunity to thank the institutions, curators, and others who made that examination possible. Words of thanks are inadequate to express the many courtesies, insights, corrections, and advice these kind people provided. In addition to the institutional help, I received kindness from many others; as an example I cite the Zak family of Lynn, Massachusetts, who provided me lodging during my extended work at the Museum of Comparative Zoology at Harvard University in 1978.

I am especially grateful to my three children, who, with their mother, endured my absences during the work that produced this book originally. Each child has contributed significantly to this edition. Renée
edited, Peter commissioned the cover art, and Patrick offered statistical advice.
Part 1. History and Biology of Bachman's Warbler

Interest in Bachman's Warbler (*Vermivora bachmanii*) has waxed and waned as populations of the species have seemed to appear and disappear over the 154 years since John Bachman collected the first specimen south of Charleston, South Carolina. Passage of the Endangered Species Act in 1973 by the U.S. Congress has sparked the most recent round of investigations of the species. No breeding populations are known, the specter of possible extinction is unavoidably present, and a storm of controversy has developed over proper management of South Carolina lands where Arthur T. Wayne found a large number of nests in the early decades of this century.

Until breeding populations of the species are found, only the available literature, field notes, and correspondence can be used to guide the thinking of scientists, managers, and environmentalists alike concerning the conservation of the species. Bibliographies of previous literature were published by Sharpe (1885) and Ridgway (1902). No complete summary or synthesis of the literature has appeared since 1902, although Dingle (1963) and Stevenson (1972b) made strong contributions. Unfortunately much of the literature lies in old journals and works which are not easily accessible to most workers. Consequently, many recent popular treatments of the species suffer from inadequate summarization of known information about the birds.

This part is organized into sections and subsections after the *Zoological Record*. The same organization appears in the list of papers by subject heading in Part 2.

GENERAL

The greater majority of the General Works on this endangered species are not primary works but rather are
works that mention the species, or works that give a general overview of their author's knowledge of the species. Most of the sections in this category are self-explanatory. Field Guides and Illustrations are evaluated and compared by Hamel and Gauthreaux (1982). Biographies are those of individuals who worked on the birds, and whose biographers mentioned the species in the memorial account. In addition to the numerous illustrations, Bachman's Warbler has been the subject of a sculpture (Hirsch 1973) as well as the focal point for the social commentary of a popular comic strip (Trudeau 1981).

MORPHOLOGY

Bachman's Warbler morphology is described in the standard treatises of the late 19th and early 20th centuries (Baird 1858, Coues 1903, Ridgway 1902, Sharpe 1885). The original description by Audubon (1834), the account by Dingle (1963), and a recent summary of illustrations by Hamel and Gauthreaux (1982) serve as guides to the numerous descriptions of plumage.

At least 375 Bachman’s Warblers were collected. Some 333 study specimens are presently housed in North American museums (Table 1); no fewer than 28 more are located in European institutions; Meanley and Mitchell (1958) list 14 stomachs. The type specimen is held by the U.S. National Museum, as is the only known skeleton. Each of 318 specimens was examined, 312 were measured, and 308 photographed under standard lighting conditions. See Appendix for information about pertinent locality and measurement data of these specimens, as well as digital scans of 193 original photographs, which are available at https://srs.fs.usda.gov/pubs/bachmans-warbler-materials/.

Analyses of measurements of a sample of these skins indicated that sex differences exist among individuals in first basic plumage and among older birds as well (Table 2). Typically the male birds are larger. I attempted to use plumage variables to determine differences between birds collected on the breeding grounds along the Atlantic Coast and in the
### Table 1. Specimens of Bachman's Warblers in United States and Canadian Museums.

<table>
<thead>
<tr>
<th>Institution</th>
<th>Number of specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Academy of Natural Sciences of Philadelphia</td>
<td>13</td>
</tr>
<tr>
<td>American Museum of Natural History</td>
<td>80</td>
</tr>
<tr>
<td>California Academy of Sciences</td>
<td>18</td>
</tr>
<tr>
<td>Carnegie Museum</td>
<td>10</td>
</tr>
<tr>
<td>Charleston, S.C., Museum</td>
<td>15</td>
</tr>
<tr>
<td>Cornell University</td>
<td>5</td>
</tr>
<tr>
<td>Earlham College</td>
<td>1</td>
</tr>
<tr>
<td>Field Museum of Natural History</td>
<td>32</td>
</tr>
<tr>
<td>Louisiana State University Museum of Zoology</td>
<td>2</td>
</tr>
<tr>
<td>Massachusetts Audubon Society</td>
<td>1</td>
</tr>
<tr>
<td>Museum of Comparative Zoology</td>
<td>81</td>
</tr>
<tr>
<td>Museum of Vertebrate Zoology</td>
<td>8</td>
</tr>
<tr>
<td>Peabody Museum of Natural History</td>
<td>4</td>
</tr>
<tr>
<td>Reading, Pa., Public Museum and Art Gallery</td>
<td>2</td>
</tr>
<tr>
<td>Royal Ontario Museum</td>
<td>5</td>
</tr>
<tr>
<td>Tall Timbers Research Station</td>
<td>1</td>
</tr>
<tr>
<td>U.S. National Museum</td>
<td>39</td>
</tr>
<tr>
<td>University of California at Los Angeles</td>
<td>2</td>
</tr>
<tr>
<td>University of Georgia</td>
<td>3</td>
</tr>
<tr>
<td>University of Michigan Museum of Zoology</td>
<td>8</td>
</tr>
<tr>
<td>University of Wyoming Museum of Zoology</td>
<td>1</td>
</tr>
<tr>
<td>Virginia Polytechnic Institute and State Univ.</td>
<td>2</td>
</tr>
</tbody>
</table>

Total\(^2\) 333 specimens in 22 North American collections

\(^1\)I learned about this specimen after the book was originally published.

\(^2\)At least 28 additional specimens are housed in no fewer than 7 European collections in France, Germany, Russia, Sweden, and the United Kingdom.
Table 2. Comparison of external mensural characteristics of female and male Bachman's Warblers.

<table>
<thead>
<tr>
<th>Measurement, in mm</th>
<th>Females</th>
<th>Males</th>
<th>¹N=24</th>
<th>¹N=104</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.D.</td>
<td>Mean</td>
<td>S.D.</td>
</tr>
<tr>
<td>Wing chord</td>
<td>57.0</td>
<td>1.54</td>
<td>60.2</td>
<td>1.58</td>
</tr>
<tr>
<td>Wingspan³</td>
<td>187</td>
<td>5.34</td>
<td>193</td>
<td>4.43</td>
</tr>
<tr>
<td>Length of tail</td>
<td>41.8</td>
<td>1.54</td>
<td>43.3</td>
<td>1.88</td>
</tr>
<tr>
<td>White patch</td>
<td>9.4</td>
<td>4.02</td>
<td>15.3</td>
<td>4.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sexes Similar</td>
<td></td>
</tr>
<tr>
<td>Exposed Culmen</td>
<td>11.8</td>
<td>0.62</td>
<td>11.7</td>
<td>0.64</td>
</tr>
<tr>
<td>Diagonal of Tarsus</td>
<td>16.0</td>
<td>0.72</td>
<td>15.9</td>
<td>0.64</td>
</tr>
<tr>
<td>Hallux</td>
<td>5.3</td>
<td>0.24</td>
<td>5.5</td>
<td>0.33</td>
</tr>
</tbody>
</table>

¹Sample, except for wingspan, consists of potentially breeding birds taken N of 30 degrees north latitude. ²All differences significant at p=0.05. Sexes also differ in the shape of the patch of white in the outermost and second outermost rectrix. In each case the patch in males is larger than that in females. ³Sample of all 14 female and 45 male specimens for which wingspan was available.

Mississippi Valley. No dependable differences were found so I do not present the tests. The results suggest that Bachman's Warblers constitute a single monotypic species, as has been assumed by all earlier workers.

The birds have curved culmens that are distinct among Vermivora. They acquire full adult plumage only in the second prebasic molt, rather than the first (Hamel and Gauthreaux 1982). The single skeleton was part of the material used in a dissertation study on
warbler morphology conducted by Shirley Ostroff (1985) that I have not seen. However, Jon Barlow (pers. comm.) indicated that the study revealed that Bachman’s Warbler was phenetically similar to Blue-winged (V. cyanoptera) and Golden-winged Warblers (V. chrysoptera).

Bachman's Warbler eggs are well-described by Dingle (1963). They are usually pure white, although at least one with a few faint spots on the large end has been collected.

No Bachman's Warbler has ever been weighed, and none has ever been captured and banded.

EVOLUTION AND PHYLOGENY

Bachman's Warblers have been placed in Vermivora by all workers. Stein (1968a) presents a cladogram in which he associates the species most closely with Blue-winged and Golden-winged Warblers on characters of their vocalizations. I here suggest that the song of Bachman's Warbler may be additional evidence of relationship to those two species, on the following anecdotal grounds. In 1976, I conducted a song playback experiment using Type-I songs of Blue-winged and Golden-winged Warblers (*Lanyon and Gill 1964; figured by Stein 1968a), Bachman's Warbler song, and songs of a "Brewster's" hybrid. The "Brewster's" song was similar to the Type-II songs of V. chrysoptera and V. cyanoptera (*Lanyon and Gill 1964). Bachman's Warbler songs have never been distinguished into categories. Harry LeGrand assisted with the work, in which the songs were played in random sequence to territorial males. Allopatric Blue-winged and Golden-winged Warblers in southwestern North Carolina and southeastern Tennessee were the subjects of the tests. Our quantitative notes were lost when a tape-recorder malfunction occurred.

Two qualitative results of the work were (1) that the birds of both species responded to conspecific song most strongly and (2) that individuals of each species
responded to Bachman's Warbler songs as strongly as to heterospecific Type-I Blue-winged or Golden-winged Warbler song. In several cases, both Blue-winged and Golden-winged Warblers responded to Bachman's Warbler song with Type-II trill songs very much like Bachman's Warbler song. I therefore believe that Bachman's Warbler song is homologous with Type-II songs of the other two species. All three species appear to share the Type-II trill song figured for *V. bachmanii* by Stein (1968a, in his Figure 2); Blue-winged and Golden-winged Warblers have distinct additional Type-I songs. This similarity of Bachman's Warbler song to Type-II songs of Blue-winged and Golden-winged Warblers is further evidence of the relatedness of the three species noted above (Ostroff 1985). Unfortunately, the similarity is not such that it can confirm or refute the cladogram of Stein (1968a). Lovette et al. (2010) provided the confirmation with their analyses of warbler relationships using DNA sequence data.

Bachman's Warbler may have been a hybrid, but the plumages are so consistent across the specimens I have examined that I believe that hybridization is an unlikely possibility for the origin of the species. Where and how the species evolved, whether it is an earlier or later derivation from *Vermivora* stock, whether Mengel's (1964) glaciation hypothesis is applicable to the species, and other questions about evolution and phylogeny remain unaddressed.

**ECOLOGY**

**General**

The single, most salient feature of knowledge of the ecology of these rare birds is the lack of hard, quantitative data. This lack of data dooms us to confusion, speculation, and often to controversy (see PROTECTION, below).

Understanding of the ecological role of Bachman's Warblers is hampered severely because no quantitative work has been published, because most of the
qualitative work was done by individuals whose primary interest was documenting occurrence and not examining habitats, and because the great preponderance of work on the species was done before knowledge of the role of succession was widespread. Unfortunately, the birds have become extaille (*Banks 1976) before detailed, scientific work can be conducted on them.

Breeding Habitat

More than any other area of the ecology of the species, breeding habitat has been the subject of intense speculation and some analysis. Efforts directed toward protection and management of the species on the North American mainland have concentrated on examination of the meager first-hand accounts of nesting. These are Widmann (1897, 1898), Wayne (1907a, 1910a, 1918, and his field notes at the Charleston, S. C., Museum), Embody (1907), Holt (1919), and Stevenson (1938). Hooper and Hamel (1977) and Shuler (1976, 1977b) examined these data, none of which are quantitative, and came to different conclusions concerning what constitutes breeding habitat for the species:

"The overstory of areas chosen for nesting appeared to have been subjected to disturbance, either natural or man caused, that stimulated development of a relatively dense understory . . ." (Hooper and Hamel 1977);

"To avoid the conclusion that these nests were found in the interior of a relatively mature, dense-canoped swamp forest one must assume Wayne was not describing what he saw." (Shuler 1977b).

Important habitat elements appear to be the presence of trees for song perches and some foraging; and dense understory thickets for foraging and nesting; in a swamp, wetland, or area subject to periodic flooding. Differences of opinion result from attempts to identify the size and density of the canopy trees,
and the size of the understory thickets. Shuler (1977b) echoed Wayne (Bassett 1941) that timber cutting is disastrous for the birds, yet Widmann (1897) found them in areas that had been selectively logged. Hamel et al. (1977), on the other hand, suggested that the birds may breed in secondary successional areas in swamp forests. Remsen (1986) raises the interesting hypothesis that the birds were specialists on cane (Arundinaria gigantea). The photograph taken by Howell (1911) is instructive in this regard (Figure 1) for it shows both a relatively open canopy of large trees and a dense understory thicket composed most obviously of cane. Wayne's statements seem conflicting, for he discusses the habitat as including piles of fallen logs (Wayne 1901) and then indicates that cutting the swamp caused the birds to leave (Bassett 1941). Likewise, the field notes of A. H. Howell are confusing. He observed [Missouri: St. Francis River (west of Senath), April 25-30, 1909, notes in Smithsonian Institution Archives] "Three specimens . . . and another one heard, all in a brushy clearing in the drier part of the swamp some two miles back from the river." Later he noted (Arkansas: Big Creek, May 6-10, 1910, notes in Smithsonian Institution Archives) "I located two males . . . They were all seen in heavy primitive timber with few openings and many dense cane thickets." These notes and the comments of Wayne are open to more than one interpretation.

A possible synthesis of the various opinions on breeding habitat may be that the birds' original habitats were secondary successional (i.e., gap-phase) openings in the swamp forest canopy, such as might be
Figure 1. Breeding habitat of Bachman's and Swainson's Warblers in northeastern Arkansas, 1910. Photograph from Howell (1911).
caused by storms or insect damage\textsuperscript{1}. All authors agree that the birds bred in swamps but no clear discussion has been made of where in a flooding regime the birds' optimum habitat occurred. Allen and Starr (*1982) suggest that differences in perception of the same data set may represent differences in the scale of examination. In my opinion, the scale of the disturbance is the issue here. We will never have a satisfactory explanation until breeding birds can be studied.

More quantitative observations have been made on single birds in a Virginia creekbottom (Barnes 1954, see Foraging and Feeding, below) and cutover woods of longleaf pine (*Pinus palustris*) in South Carolina (Chamberlain 1958). Neither of these birds was demonstrated to have bred, however; the one in South Carolina was in atypical habitat as well. Breeding was suspected of birds in a pond pine (*Pinus serotina*) pocosin on Fairlawn Plantation in South Carolina during 1948-1953 (Burton 1970).

Millicent Ficken (pers. comm.) suggests some general inferences that can be drawn from comparison with *V. chrysoptera* and *V. cyanoptera*, the two supposed

\textsuperscript{1}For example, Williams (*1975) described such an area in the Hatchie River bottoms of Tennessee. Estimated to be 300 acres (120 ha) in extent, it was called in 1828 the "Big Hurricane." "'It is about a mile and a half--perhaps more--long, and about one-third as wide... The Hurricane will best describe itself when you see it and go into it. I will say, however, that there is not an original tree in it. All were blown down or topped off by the tornado that passed over it; when, no one knows. From the appearance of the undergrowth, it must have been ages ago. Near the river it is thick cane; the middle and outer portion, every variety of scrubby undergrowth, filled up with briers. Except for the rotting out of the old fallen trees, or logs--many, however, are yet in a sound state of preservation---egress into, or out of it, would be impossible.'"
closest relatives of *V. bachmanii*. The former two are "'successional species' restricted to certain stages of old field or bog succession" that "probably shift breeding areas frequently." They also "nest in 'colonies' where a number of pairs are often found if the habitat is suitable." Bachman's Warblers may share these traits with their congeners (see Breeding Habits, below).

** Territory **

Widmann (1897) reported that one bird's territory was 2 acres (0.8 ha). Barnes (1954) indicated an area of 430 x 150 ft (1.5 acres, 0.6 ha). Two birds reported by Chamberlain (1958) had territories "200-300 yards in extent" (8-18 acres, 3-7.5 ha) and 1.3 acres (0.5 ha). These were apparently Type A territories of Nice (*1941) although none of these estimates distinguishes a defended area from an undefended home range.

** Migration **

Bachman's Warblers were early migrants, leaving Cuba in late February and returning as early as July. Most of the movement through Florida took place in March and August. Detailed observations of the birds in the spring were made by Brewster (1891), Brewster and Chapman (1891), and Wayne (1893, 1895). Atkins (in Scott 1888b, 1890a) studied them on migration in the fall. Birds struck the light at Sombrero Key in 1887 (Scott 1888b) and at Tybee Island, Georgia, in 1924 (Wayne 1925). No lighthouse or tower kills have been reported since 1924. Jon Barlow (pers. comm.) has suggested that the birds may be physiologically capable only of short overwater migratory flights.

** Winter Habitat **

Unlike the case of breeding habitat, no detailed descriptions of the winter habitats of the species have been published. Most of the listed references discuss limitations of winter habitat or restriction of the
birds' winter range. Amadon (1953) was the first to suggest that a restricted winter range was a possible cause of the species' rarity. Gochfeld (1979) points out that this is the only North American migrant warbler restricted in winter to Cuba. It is, of course, possible that the winter range extended to other islands in the Caribbean, such as Hispaniola, although no records have been made there. Terborgh (1974) and others assume that the birds' primary winter habitats were in the Cuban lowlands, especially in the extensive Zapata Swamp. Perhaps they were, but no quantitative surveys have ever been conducted. Qualitative observations, such as those of Gundlach (1876) and Garrido (1985) and the collections of Oscar Tollin for Charles Ramsden (specimens in the U.S. National Museum), indicate that the birds were found throughout the island from the western lowlands to the mountainous Oriente Province. They have been reported from native forest, planted forests, and gardens. Gundlach (1893) notes the birds as occurring in 'majaguales' (forests of Hibiscus tiliaceus) and states that cutting of the majaguales caused the birds to disappear. It is not certain whether this cutting was done for timber harvesting or as clearing for agriculture. Isolated winter records come from Okefenokee Swamp and from Melbourne, Florida (Dingle 1963).

Ecological Associates

Many writers, particularly among the early workers, mention lists of species that they encountered in the area in which they found Bachman's Warblers. Generally, the lists include species typical of the avifauna of bottomland hardwood and swamp forests. Except for the cases of direct interactions between species (see Competition, below), however, the lists do not indicate which species were actually syntopic with Vermivora bachmanii. Several nests found by Wayne (1907a, 1910a) were near those of Swainson's Warblers (Limnothlypis swainsonii), and he found nests of
Bachman's Warblers on the same day on which he first proved that Black-throated Green Warblers (*Setophaga virens*) nested in the Coastal Plain. Observations of both species were made in I'On Swamp. Garrido (1985) notes that the birds sometimes associated in winter with flocks of Yellow-headed Warblers (*Teretistris fernandinae*).

The species has never been recorded on a Breeding Bird Census, Breeding Bird Survey, or Christmas Bird Count.

**Competition**

Three authors mention interactions between Bachman's Warblers and other species. Atkins (in Scott 1890a), Barnes (1954), and Dawn (1958) note that the Bachman's Warblers were very aggressive toward other species, both on migration and on the breeding grounds. Barnes (1954) and Dawn (1958) each were dealing with a single individual.

Hamel (1981) discusses association in time or space and behavior between Bachman's Warblers and four other small, foliage-gleaning warblers, Orange-crowned Warblers (*Oreothlypis celata*), Northern Parulas (*Setophaga americana*), Black-throated Green Warblers, and Prairie Warblers (*S. discolor*), on the birds' breeding grounds in I'On Swamp in South Carolina. Orange-crowned Warblers, in particular, are nearly identical morphologically to the Bachman's Warbler by Hamel's (1981) measures of external morphology, and occur in coastal South Carolina nearly throughout the breeding season of Bachman's Warblers. He speculates that these species might have been brought into competition by ecological crunches of the sort described by Wiens (*1977*).
Breeding Habits

Widmann (1897) presents the clearest available observations of the breeding habits of Bachman's Warblers, and Wayne (1910a) also gives invaluable data. These observers, as well as Embody (1907) and Holt (1919), call attention to an unexplained aspect of the breeding of the birds. Each observer notes several pairs in close proximity. Observers at Fairlawn Plantation near I'On Swamp in the late 1940's also noted more than one pair of birds in a habitat patch (Burton 1970). Several speculative explanations for this trait involve the notions that breeding habitat for these birds appeared in limited patches, that patches might be occupied for a limited number of years, or that a pair might occupy a patch and a small deme of its descendants continues to occupy that patch over the period of availability of the patch; other explanations are equally plausible.

The only certain knowledge of the breeding habits of these birds is that the males sang advertising songs from the trees in their territories and the nests were placed in shrubs. After Widmann, Wayne, Embody, Howell, and Holt, none has been privileged to study populations of breeding Bachman's Warblers. Stevenson (1938) found the nest of a single pair. Barnes (1954), Chamberlain (1958), and more recent workers were observing only single isolated individuals. No one has had the opportunity to examine Widmann's (1897) hypothesis that the older males acquired mates before the younger ones did. As far as known, the birds were monogamous; but even this statement reflects more the general case in wood warblers than specific fact about V. bachmanii.
Clutch and Brood Size

Disagreement exists as to how many nests of Bachman's Warblers were discovered. Shuler (1979a) suggests 37 while Hamel (1977d) believes 40 is the correct number. The difference relates to interpretation of the field notes of Arthur Wayne. Shuler (1979a) interprets three entries in the notes as referring to three nests already discovered while Hamel (1977d) considers those entries to constitute distinct nests. The uncertainty is a result of Wayne's method of recording his notes. Shuler (1979a) gives a clutch size of 4.2 +/- 0.7 (range 3-5) eggs for 24 nests.

Timing of clutch initiation is a topic of some interest but one whose investigation requires rather a large number of assumptions. Length of time required for nest building, incubation, and raising young to fledging are unknown, as is the time taken between completion of the nest and laying of the first egg. Shuler (1979a) presents a projection of clutch initiation dates, and another is presented here (Figure 2). I have assumed that one egg is laid per day, incubation begins with the laying of the last egg and lasts 11 days, and that the nestling period lasts ten days. The assumptions are based upon the data in Bent (1963, see Dingle 1963). These projections for 29 nests indicate that the birds in South Carolina began clutches before 1 April in 18 cases and before 15 April in 26 cases. Three nests in Kentucky and Missouri were begun in the first two weeks of May. One of two Alabama nests was begun in the second week of April and the other about 20 May. These data suggest that the birds on the Atlantic Coast bred earlier, by perhaps a month, than those in the Mississippi Valley. Sufficient data exist in the notes of Wayne to compare timing of clutch initiation for four years, 1906 (four estimates), 1907 (seven estimates), 1908 (seven estimates), and 1915 (three estimates; Figure 2). The comparisons indicate that within a local population the initial egg-laying periods in adjacent years may not overlap.
No data exist to clarify the question of whether the birds have a second clutch after successfully raising a first brood.

**Parental Care**

Most nests of Bachman's Warblers discovered by people were destroyed by their discoverer before the eggs could hatch. Wayne (Brewster 1905) noted in one case that the male parent was feeding the male offspring and the female parent was feeding the female fledgling; then he collected both of the young. Embody (1907) discovered a nest by following the female, and Stevenson (1938) noted that the male fed the young in the nest. Thus, both adults were involved in the care of the young, but quantitative data are lacking on the relative contributions of the two parents.

**POPULATION**

**Size**

Populations of Bachman's Warblers in historical times have probably never been large, but noticeable differences between populations at one time and those at another seem to have occurred. An overwhelming

Figure 2. Clutch initiation dates of Bachman's Warblers, inferred from the field notes of Arthur T. Wayne. All data from I'On Swamp, South Carolina. A. Date and condition when found, 35 nests; not shown is nest found on 2 June 1906 from which young had fledged. B. Estimated dates of initiation of 29 clutches. Bars show estimates of date of initiation; numbers indicate year after 1900, e.g., 13=1913. Only estimates accurate to within four days are included. C. Estimated dates of clutch initiation for all years for which at least three estimates were available. Bars show contiguous estimated periods of clutch initiation, numbers indicate number of clutches initiated during the period.
Condition when Found:
- Empty, new construction
- Empty, deserted
- Eggs in nest
- Young in nest
- Deserted, eggs in nest
- Young fledged from nest

A

\[
\begin{array}{ccccccccccc}
& & & & & & & & & & \\
\text{March} & 26 & 31 & 5 & 10 & 15 & 20 & 25 & 9 & 12 & \\
\text{April} & & & & & & & & & & \\
\text{May} & & & & & & & & & & \\
\end{array}
\]

B

\[
\begin{array}{cccccccccccc}
\text{March} & \ldots & 20 & \ldots & 25 & \ldots & 30 & \ldots & 5 & \ldots & 10 & \ldots & 15 & \ldots & 20 & \ldots & 25 \\
\text{April} & \ldots & \ldots & 7 & \ldots & 8 & \ldots & 6 & \ldots & 6 & \ldots & 6 & \ldots & 15 & \ldots & 15 & \ldots & 15 \\
\end{array}
\]

C

\[
\begin{array}{cccccccccccc}
1906 & \ldots & \ldots & 1 & \ldots & 2 & \ldots & 1 \\
1907 & \ldots & \ldots & 5 & \ldots & 1 \\
1908 & \ldots & \ldots & 7 \\
1915 & \ldots & \ldots & 1 & \ldots & 1 & \ldots & 1 \\
\end{array}
\]

\[
\begin{array}{cccccccccccc}
\text{March} & 20 & \ldots & 25 & \ldots & 30 & \ldots & 5 & \ldots & 10 & \ldots & 15 & \ldots & 20 & \ldots & 25 \\
\text{April} & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\
\end{array}
\]
number of accounts of the species point out that, after the discovery of the birds in 1832 and 1833, more than 50 years passed before any were found again in the United States. "Rediscovery" is a popular word in this context. Gundlach (1855) had, of course, observed them in Cuba in the interim. After Galbraith's (1886) collections showed that the birds were present, collectors and scientists found the birds in some numbers during 1890-1920. Subsequent to that time the populations have been very low. At the present time no breeding populations are known, and the species has been described as "essentially extinct" on Cuba (Garrido 1985).

This historical record falls into three periods, pre-1890, 1890-1930, and post-1930. Interpretation of the record is essentially speculation, but I believe interpretation may shed some light on the status of the species and its decline. Two assumptions about the record are as follows: (1) that the historical record of observations reflects actual populations of the birds, and (2) that the record reflects ornithological interest and opportunity to observe the birds. These assumptions are not mutually exclusive but they do represent the endpoints of a spectrum of possible interpretations of the historical record of the Bachman's Warbler.

Under assumption (1), Bachman's Warbler numbers have gone through a cycle in the past 150 years, from low in the time of their discovery to high at the turn of the century, to lower in the 1930's-1950's, to extremely few now. Explanation of such a cycle requires a controlling factor capable of causing population increases or reductions. Such factors could include periodic Cuban hurricanes, disease, failure of food supplies either on the breeding or the winter grounds, and catastrophe during migration.
Only one of these factors can be examined in any detail, the frequency of Cuban hurricanes. Absence of such storms indicates a possibly favorable wintering environment. Presence of such storms only indicates the possibility that large-scale losses of wintering Bachman's Warblers occurred. Fluctuations in the frequency of intense storms would then lead to population fluctuations in Bachman's Warblers, other things being equal. The record of storms for the 19th century is not as good as that for the 20th, but it becomes increasingly good in the latter part of the 19th century. Tannehill (*1945) reports the most destructive Cuban storms to be usually late season storms in October or November. Four such storms were recorded in the 19th century, in 1812, 1844, 1846, and 1865 (Table 3). Those in 1844 and 1846 were particularly strong. Thirteen such storms crossed Cuba in the first 44 years of the 20th century, and five of them occurred between November 1932 and October 1935. Two such storms struck western Cuba in October 1933; that in November 1932 is considered one of the most destructive and intense ever recorded (*Tannehill 1945). These storms may have destroyed large numbers of Bachman's Warblers as they did of other species (*Huntington and Barbour 1936). Cry (*1965) presents another view of the record of hurricanes that is not entirely in accord with that of Tannehill (*1945). Whether severe hurricanes actually caused significant mortality of Bachman's Warblers is unknowable; they did lead Griscom (1948) to suggest first that hurricanes may have been a factor in the decline of the species.

Under assumption (2), the lack of records of the birds between the 1830's and 1880's reflects only the lack of opportunity for collectors to encounter the birds. However, no evidence exists that collectors' interest in the birds changed between this and the later period. Population sizes in the interim are unknown but they were potentially as high as when the
Table 3. Cuban hurricanes of the 19th and early 20th centuries, from Tannehill (*1945).

<table>
<thead>
<tr>
<th>Era</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
</tr>
</thead>
<tbody>
<tr>
<td>19th century</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total storms¹</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td>3</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>1900-1945</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strong storms</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Weaker storms</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Total storms</td>
<td>5</td>
<td>1</td>
<td>3</td>
<td>11</td>
<td>16</td>
<td>9</td>
</tr>
</tbody>
</table>

¹Two additional storms were reported but the time was not indicated for them.

Birds were studied during 1890–1920. This assumption and the other do not differ in the projection of population sizes subsequent to 1920. Under this assumption the destructive hurricanes of the 1930's appear as a serious blow to populations already reduced to low numbers by some other cause. Indeed, under this assumption no natural cause of the decline of the species is a likely one.

**Endangeredness**

Bachman's Warblers are considered to be nearing extinction by biologists who have worked on them in the breeding season (Stevenson 1982) and in the winter (Garrido 1985). No individuals have been found on territory since 1962 or 1963 (Shuler 1977d). A female reported in Cuba in 1981 (Ripley and Moreno 1981) was the first bird observed on that island in 15 years.
Numerous suggestions, theories, and speculations have been put forward to explain the decline of the species. Each has focused upon a particular concern of its author, but no comprehensive attempt to relate the theories to each other has been made. The commonly cited reasons for the decline of Bachman's Warblers are as follows: habitat destruction, both on the winter (Terborgh 1974, Rappole et al. 1983) and breeding grounds (Korte and Fredrickson 1977, Shuler 1977b, Remsen 1986, many others); restricted winter range (Amadon 1953); overcollecting (Wright 1976); and hurricanes (Griscom 1948). Henry Stevenson (pers. comm.) considers none of these to be a very satisfactory or plausible explanation of the decline of the species. Millicent Ficken (pers. comm.) suggests that ecological specializations, indicated by their sharp bills and apparently narrow habitat requirements, made these birds "especially vulnerable if specific habitats were destroyed."

Any explanation of the decline of the species must also include discussion of the pre-Columbian habitat and range of the species, the geologic history of the birds' range, climatic change and weather, the possible roles of interactions with other species, failure of food resources, disease, and the interaction of these factors. No comprehensive data exist concerning the validity of any inference, however. A chronicler of these birds can do nothing more than arrange a mutually consistent set of speculations. I present these speculations to stimulate readers to think in ways that may enable action to prevent other species from needlessly reaching the perilous condition of the Bachman's Warblers at the time of this writing.

Prior to colonization of the Western Hemisphere by European and African peoples, Bachman's Warblers migrated to and from winter grounds somewhere in Cuba or nearby islands to breed in the southeastern United States. Breeding habitats that met the descriptions of
Widmann (1897), Wayne (1907a), Howell (notes in U.S. National Museum), and Holt (1919) were present at those times, and were produced in a frequency capable of supporting populations of the species. Winter habitats also existed in sufficient quantity to support the species. Possible agents involved in the production of breeding habitats were thunderstorms and tornados, hurricanes, fire, natural mortality of trees, and possibly the actions of Native American peoples. Each of these factors is capable of producing disturbance to the forest canopy such that a mosaic of small openings is created in swamp forest. Under such openings would flourish the canebrakes proposed as important to the birds by Remsen (1986). Although winter habitat requirements are unknown, similar forces are likely to have produced them.

One factor not yet associated with Bachman's Warbler decline is the decrease in gross area of winter habitat at the end of Pleistocene glaciation. At the peak of the last glaciation, sea levels in the Atlantic Ocean were as much as 100 m lower than they are now (*Flint 1957). At that time the total area of potential winter habitat in western Cuba was much greater than it is today, particularly in the region of the great Zapata Swamp thought to be an important winter habitat by many (cf. Terborgh 1974, Ripley and Moreno 1981). The Isle of Pines may even have been connected to the main island. Simultaneously and even more strikingly, the extent of the Bahama Islands was several fold greater than it is at present. At the time of glacial retreat the extent of each of these areas began to recede, as did those of other as yet undiscovered wintering sites. A first reason for the decline of the birds' numbers is thus probably the restriction of winter habitat (Amadon 1953).

Whatever the evolutionary reason for the restriction of Bachman's Warblers to a small winter range, other associated and unknown circumstances
caused the birds to migrate north early in the spring and to return south early in the fall as well. The early spring migration meant that the birds moved at a time when favorable southeast winds generally prevailed in the northern part of the Caribbean (*Bradley 1972). Fall migration in August occurred just before and during hurricane season.

The causes for the timing of these movements are unknown, but some of the potential effects of weather on populations of the birds are obvious. Adverse weather on migration has caused innumerable groundings of migrants; tower and lighthouse kills are known even among Bachman's Warblers (Bassett 1941, Atkins in Scott 1888b). Adverse weather in winter may have been an even more serious threat. Tannehill (*1945) reports that the most serious hurricanes that hit Cuba do so in October and November; the entire Bachman's Warbler population is on the island at that time. Devastating hurricanes may well have decimated populations of the birds periodically. Huntington and Barbour (1936) describe the effects of one particular storm that virtually eliminated bird populations in one part of Cuba for a time.

We must assume that Bachman's Warbler populations had experienced the effects of shrinking winter range, periodic creation of breeding habitat, and periodic severe storms on the winter grounds before colonization of the Western Hemisphere. It is uncertain whether the birds' populations were in equilibrium with these factors, or whether populations were declining from the action of these factors.

Possible insight into the situation may come from landscape-scale considerations. For example, Shugart (*1984) examines the equilibrium of vegetated landscape systems as an interaction of land area with extent and frequency of disturbance. He suggests that perhaps only Cuba among Caribbean islands may be able to support a landscape in equilibrium despite hurricane
disturbance. An equilibrium landscape on Cuba would be expected to provide a relatively constant supply of winter habitat for Bachman's Warblers at the present time. Other, smaller islands would not. In previous times of greater land extent, particularly in the Bahamas, equilibrium conditions may have existed such that Bachman's Warbler winter habitat was dependably present in other islands as well as Cuba.

After colonization of Cuba and the southeastern part of the United States, permanent habitat destruction became a factor both on the breeding grounds and in the winter range. Korte and Fredrickson (1977) graphically portray the destruction of bottomland forests in the Mississippi Valley using Missouri as an example. Kochtitsky (*1957) gives a firsthand account of the motivation of those who eradicated these forests. Terborgh (1974) and Rappole et al. (1983) both point out the clearing of large areas of lowlands in Cuba for sugarcane production. This clearing may have created disequilibrium vegetation conditions on the Cuban wintering grounds. Habitat destruction on breeding and winter grounds probably had a depressing effect on Bachman's Warbler populations.

The nature of human intervention into the birds' habitats requires additional discussion, particularly on the breeding grounds. Bachman's Warbler populations persisted in I'On Swamp in South Carolina alongside agricultural interests (Urbston et al. 1979), and in spite of some logging. Wayne (Bassett 1941) believed that logging in the swamp was what finally extirpated the birds from I'On Swamp (see below for an alternate speculation). Most perplexing in this regard are the populations in southern Missouri and northeastern Arkansas. From the time Widmann (1896, 1897) discovered the birds breeding there until the time Howell (1911, Figure 1) studied the birds, the bottomlands of the Mississippi River were undergoing high-grade logging.
in which only merchantable timber was cut. The birds reached their greatest local population densities during these times, densities great enough that Widmann (1907) and Howell (1911) both labelled the species as "common". I believe that the logging served to create the moderate disturbance to the forest canopy under which Bachman's Warblers could flourish. Proof of these assertions can probably never be musteried. Some considerable circumstantial evidence is available. In 1887 a logging tram railroad was begun which ran east from Paragould, Arkansas, toward the St. Francis River (*Horner 1973). The purpose for building the railroad was the removal of timber to sawmills in Paragould. By 1895 the line had been extended to Cardwell, Missouri. In the early 1890's a sawmill was constructed 10 mi (16 km) down that tram by Mr. A. R. Byrd on Buffalo Island in Dunklin County, Missouri. In 1896 Widmann rode that train and discovered Bachman's Warblers in Greene County, Arkansas. A year later he rode the train to Buffalo Island (also called Kolb or Culp Island) and found the first nest of the species in a clearing created by the logging. Today, Arbyrd, Missouri stands on the site of Mr. Byrd's sawmill. Further circumstantial indication of the appearance of Bachman's Warbler habitat in those areas is available in the form of the photograph by Howell (1911; Figure 1) of both Bachman's and Swainson's Warbler habitats. Had the birds been as common in those areas in earlier times we should have some record of them, but none exists. I believe that the initial high-grade logging practices created Bachman's Warbler habitats in bottomland forests.

The nature of the disruption of the original bottomland forests in Missouri and Arkansas changed as the emphasis changed from logging to clearing and planting. Formation of drainage districts, construction of levees, and channelization of streams followed the initial logging with incredible rapidity (*Nolen 1913). By 1920 much of what had been apparently ideal breeding
habitat had been completely cleared and drained for agricultural purposes. It was at this time that habitat destruction became a possible factor in the decline of the species.

Wright (1976) and some others suggest that scientific and economic collecting may have been an important factor in the decline of Bachman's Warblers. My own speculation is that collecting was probably not an important factor in the range-wide decline of the species. However, in selected local areas, particularly in I'On Swamp in South Carolina, local populations may have been adversely affected by collectors. Wayne (letter to Brewster, 4 June 1912, in collections of Library of Museum of Comparative Zoology) assumed that these birds would renest after a clutch was collected. His notes and the dates of collections reflect this belief, but he left no notes to indicate that he returned to the swamp to verify his assumption. The pattern of collections in his notes (Table 4) is consistent with the view that his persistent collecting reduced the population to a low level; 21 nests with eggs or young were taken in I'On Swamp, in 1906-1908, but he found no more than three nests in any subsequent year. This pattern is, unfortunately, also consistent with the view that the habitat changed through succession to a stage unfavorable to these birds, and consistent as well with a view that the market for clutches of eggs became flooded and the reduced price made other specimens more valuable. This third view is perhaps less likely than the others because of the high value ($75-200) that individual egg sets brought to Wayne (Shuler 1977d; Wayne letter to Brewster, 10 September 1911, in collections of Library of Museum of Comparative Zoology).

A summary of the forces involved in the decline of Bachman's Warblers, as I see them, is as follows. In times of glacial advance during the Pleistocene the
birds had a significantly larger winter range on Cuba and the Bahamas, and perhaps elsewhere in the Caribbean as well. Population levels were in equilibrium with environmental factors that created habitats and caused mortality on migration and winter grounds. Under certain circumstances of unfavorable conditions the birds may have experienced ecological crunches during which they may have competed for resources with other species.

<table>
<thead>
<tr>
<th>Year</th>
<th>1905</th>
<th>1910</th>
<th>1915</th>
<th>1920</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of nests</td>
<td>1 6 6 9 0 3 1 1 1 0 3 1 2 1 1 0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


In post-glacial times the winter range of Bachman's Warblers shrank with increases in sea levels. The reduced winter range may have increased the amplitude of population fluctuations resulting from winter mortality that was due to hurricanes. This alone may have been the single most important ultimate cause of the decline in the numbers of these birds. Colonization of both winter and breeding habitats by non-native peoples set in motion a sequence of events by which habitat availability monotonically decreased. Current evidence suggests that not only the amount of habitat but also its quality decreased, viz-a-viz loss of canebrakes or some other unknown requirements (Remsen 1986). Holder (*1970) points out that canebrakes were the first target for land clearing.
activities because they grew on fertile soil and the absence of trees made the canebrakes easy to clear. These habitat losses apparently widened the amplitude of population fluctuations such that a major catastrophic mortality event, such as that suspected from the Cuban hurricanes of the early 1930's, may have eliminated most of the population. Populations are so small today that individuals may be unable to find each other on the breeding grounds, that normal nest predation may be disastrous, that inbreeding may interfere with reproductive success, that Brown-headed Cowbird (Molothrus ater) parasitism may be significant, or that other, stochastic processes may have potentially serious consequences.

Protection

Legal protection is afforded Bachman's Warblers by the various Migratory Bird Treaties, by the Endangered Species Act of 1973, as amended; and by the endangered species laws of the states within the birds' historic range in North America. Much of the recent history of attempts at protection of the birds and their habitats is unpublished and largely unknown.

Beginning as early as 1975, disagreement developed concerning whether applicable endangered species statutes were being followed in South Carolina on the Francis Marion National Forest. The Santee Preservation Society of McClellanville, South Carolina, questioned the land management practices conducted by the U.S. Forest Service in the I'On Swamp area of the Francis Marion. Controversy over the difference between the Society and the Forest Service led to the formation of a blue-ribbon panel in 1976 at the urging of Robert Golten, an attorney for the National Wildlife Federation. Composed of the late Fred Evenden of the Wildlife Society, David Marshall of the U.S. Fish and Wildlife Service, and William Zeedyk of the U.S. Forest Service, the panel met to discuss issues pertaining to the protection and management of Bachman's Warblers and
their habitats. In March 1977, the panel convened a hearing on the species at Charleston, South Carolina.

As a result of their deliberations and the hearing, the panel tendered a series of reports (Evenden et al. 1976a, 1976b, 1977) in which they evaluated available literature concerning the land-use history of I'On Swamp (Urbston et al. 1979, Shuler 1976) and the biology of the Bachman's Warblers. Their final report included recommendations for Bachman's Warbler preserves in I'On Swamp and in nearby areas in the Little Wambaw Swamp and Wambaw Swamp, and for instigation of carefully controlled habitat manipulations to create breeding habitat conditions similar to those described by Wayne (1907a), Widmann (1897), Hooper and Hamel (1977), and others as discussed above.

Subsequent to the final report of the panel, the Forest Service entered into consultation with the Fish and Wildlife Service under Section 7 of the Endangered Species Act. The initial opinion rendered by the Fish and Wildlife Service (Vaughn 1978) was that Forest Service management was likely to jeopardize the continued existence of Bachman's Warblers on the Francis Marion. Based in part on findings of Urbston et al. (1979), and particularly the negative results of the searches for the birds on the Francis Marion (Hamel et al. 1976; Hamel and Hooper 1979a, 1979b), the Forest Service petitioned the Fish and Wildlife Service to reinitiate consultation over management of the Francis Marion National Forest. The final opinion rendered by the Fish and Wildlife Service in 1979 (Black 1979) is still in effect. Pending certain management activities to be conducted by the Forest Service, the opinion is one of non-jeopardy. The opinion includes recommendations for Bachman's Warbler management areas, for a series of experimental cuttings in specified areas of the National Forest, for annual monitoring for the species' presence, for a five-year review process, and for a
system to encourage searches by the bird-watching community.

In 1982 and 1983, the Forest Service contracted initial bird surveys (Forsythe and Tyler 1982) and instituted experimental cuttings in the recommended area. At about the same time, two of the areas suggested originally as Bachman's Warbler management areas, Wambaw Swamp and Little Wambaw Swamp, were declared wilderness areas by act of the U.S. Congress. No specific monitoring program for the birds was subsequently established and a number of the recommended habitat manipulations were not conducted.

In 1985, the Santee Preservation Society appealed the Francis Marion Land Management Plan (USDA Forest Service 1985a) on grounds, among others, that Bachman's Warblers should not be considered extirpated from the Francis Marion. The Forest Service responded by agreeing to modify the Francis Marion Land Management Plan to comply more fully with the recommendations of the 1979 biological opinion of the Fish and Wildlife Service. The Santee Preservation Society applauded the Forest Service decision to manage more actively for the species.

In August 1985, the Forest Service managers of the Francis Marion National Forest, the representative of the U.S. Fish and Wildlife Service, and personnel of the Southeastern Forest Experiment Station met to discuss progress made in carrying out the 1979 non-jeopardy opinion. As a result of this meeting, the parties agreed to carry out more fully the recommendations of the 1979 biological opinion (Black 1979) and to meet after another five years to discuss results of the efforts.

The most complete records of these proceedings are in the files of the U.S. Fish and Wildlife Service Endangered Species Field Office in Asheville, N.C., and in the files of the Wildlife, Fisheries, and Range
staff unit of the U.S. Forest Service Southern Regional Office in Atlanta, Ga.

Searches

Searches of all sorts are mounted every spring in the southeastern U.S. for these, the American Birding Association's most wanted, birds (Tucker 1979). One such search was conducted for several years in the 1970's by members of the Northeast Arkansas Audubon Society in cooperation with personnel of the Big Lake National Wildlife Refuge (records in the files of the Refuge, Manila, Arkansas). The search was unsuccessful. Only one extensive, systematic search for Bachman's Warblers has been conducted, that in South Carolina, Missouri, and Arkansas in 1975-1979 (Hamel et al. 1976; Hamel and Hooper 1979a, 1979b). That search also was unsuccessful.

Future systematic searches are desirable, in spring in Alabama, Arkansas, Louisiana, Mississippi, and Tennessee, and in winter in Cuba, the Isle of Pines, and perhaps in the Bahamas and Hispaniola as well. The probability for success of any of these searches is, however, probably very low. Because the probability for success is so low, any systematic search must be well-designed and careful records of effort and coverage kept. The work of Hooper and Hamel (1974) is a guide to design of a search in the breeding season.

BEHAVIOR

General

"Typical of a warbler" may be the most apt description of the behavior of Bachman's Warblers. Stewart thought that they were typical Vermivora (Barnes 1954). Ficken and Ficken (1968) also considered their behavior to be typical of Vermivora. On migration they seem to have used available vegetation in
proportion to its availability (Brewster and Chapman 1891, Scott 1890). On the breeding grounds they seem to have concentrated their foraging in the shrub layer as well as using the overstory (Widmann 1897, Wayne 1910, Tanner 1939, Barnes 1954, Chamberlain 1958). James Tanner (pers. comm., field notes for 25 May-3 June 1937), for example, noted

"He sings from the tall trees, . . . Then every short interval he will plunge to the undergrowth for a few moments, move around a little there and then fly up to the tree tops again."

Little quantitative information comes from observations on the winter grounds. Unfortunately, no unified synthesis of the birds' behavior has been, or perhaps can be, made. Observations of the individual in Virginia in 1954 (Barnes 1954) and the one in South Carolina in 1958 (Chamberlain 1958, Dawn 1958) indicate that those birds were particularly aggressive interspecifically, against Prairie Warblers and Indigo Buntings (Passerina cyanea). Widmann (1897) noted only intraspecific aggression. Knowledge or assumptions that the birds were typically interspecifically aggressive leads to a quite different understanding of their biology and inference of their position in the swamp forest avifauna than does a view that they were not. As with so much else about these birds, speculation on this topic is all too easy.

Vocalizations

Bachman's Warbler songs have been recorded twice. Arthur Allen and Peter Paul Kellogg made a recording of the bird along Pohick Creek near Lorton, Virginia, in 1954 (Barnes 1954). Stuart Keith recorded the bird in Charleston, South Carolina, in 1958 (Chamberlain 1958). Copies of both recordings are in the collection of the Laboratory of Ornithology at Cornell University. Stein (1968a) presents a sound spectrogram of the Allen-
Kellogg recording in his analysis of vocalizations in *Vermivora*.

A multitude of anecdotal observations of the songs of the birds are given by virtually every early worker. Songs most commonly are compared with those of Worm-eating Warblers (*Helmitheros vermivorum*), Northern Parulas, and Chipping Sparrows (*Spizella passerina*). Wayne (1907b) reported an aberrant individual that sang like a Prothonotary Warbler (*Protonotaria citrea*). Several authors refer to the call note as a buzzy "zeep."

Songs were given both from stationary perches and while foraging. The birds also sang in flight, usually giving the song just before landing (Howell 1924). Several authors (e.g., Sprunt and Chamberlain 1970) noted that the song had a ventriloquial quality. This quality may have been the result of the birds' habit of turning on the perch during a song bout, as well as the use of flight song. I suspect that the rarity of the species also played a role in this as well, for few modern observers have seen enough of these birds to have a comfortable feel for how to look for a singing male. Henry Stevenson (pers. comm.), for example, found Bachman's Warblers to be no more ventriloquial than other warblers. Singing rate was variable, possibly reflecting the stage of the nesting season when a bird was observed. The range was from one to ten songs per minute. Widmann (1897) presents an interesting observation that the males with the larger throat patches sang more vigorously earlier in his study than did the males with smaller amounts of black on their throats. He assumed, correctly, that the amount of black was an indicator of the males' ages. His observation suggests that older birds may have arrived earlier on the breeding grounds and acquired mates earlier than younger ones.
Foraging and Feeding

Foraging and feeding of Bachman's Warblers have been treated by few authors. Quantitative study of the foraging behavior of the birds on the breeding grounds was done by Robert Stewart (Barnes 1954) and Chamberlain (1958), who recorded the locations at which birds foraged. A composite of their results (Hamel 1981; Figure 3) showed a pattern typical of a species that sang from elevated perches, foraged to some extent in the canopy, and foraged also lower down in the shrub and herb layers. This foraging pattern is not unlike that of either Swainson's Warblers or Prairie Warblers (Hamel 1981). Tanner (pers. comm.) came to the same conclusion. The birds were said by several authors to glean leaves, clumps of dead leaves, and flowers. These behaviors are also typical of their presumed closest relatives, _V. chrysoptera_ and _V. cyanoptera_ (Ficken and Ficken 1968). Rate of foraging varied from extremely active (Atkins in Scott 1890a) to leisurely (Brewster 1891), suggesting that individual birds were under different motivations at different times when observed.

Food of the birds on the breeding grounds consisted primarily of insects and other small arthropods, with a small amount of seeds that may have been taken incidental to the capture of insects and their larvae. Meanley and Mitchell (1958) analyzed the contents of 14 stomachs taken from Alabama, Arkansas, Florida, and Missouri in 1905-1916.

Foraging behavior on the winter grounds in Cuba has not been studied in detail. Barbour (1923) quotes Gundlach (1893) to the effect that the birds foraged in and about the flowers of _Hibiscus tiliaceus_ shrubs and trees. The birds may have sought nectar as well as insects. The birds' curved bills suggest that some such specialization is possible, although none has been demonstrated. I paraphrase Orlando Garrido's comments (pers. comm.), as follows:
Figure 3. Behavior-height profile for Bachman's Warbler. Dashed line indicates distribution of all behaviors observed, solid line indicates that of foraging observations only. Data taken from Stewart (in Barnes 1954) and Chamberlain, E. B. (1958).
You mentioned that the curved bill of the warbler may represent a "specialty." This could be, or not. Our endemic Teretistris fernandinae has a curved bill, and this tool is used for all kinds of purposes. She fills the ecological niches of several migratory warblers . . . She travels in groups, and practically "combs" the territory, from ground to above 4 meters high, assuming the feeding behavior of several other species . . . As a Vermivora, in their transit grounds here, V. pinus, V. chrysoptera, and V. peregrina are middle or high level feeders. However, Bachman's Warbler apparently feeds in the three situations; I have found her at low stages (one meter above the ground); about two and a half meters; and Gundlach mentions feeding on flowers of majagua, which means that she goes to high levels also. My three encounters with her were in trees with small leaves; however, the majagua trees have broad leaves. There is no doubt that she feeds on honey, just as Dendroica tigrina at least. I have seen V. peregrina and V. chrysoptera on flowers of majagua as well. They may also get some insects as well. I have not observed any feedings or aggressive display on my encounters with V. bachmanii. Teretistris sometimes travels in mixed flocks with other warblers and Vireo gundlachii when foraging. When I saw V. bachmanii for the first time in Zapata, a flock of Chillinhas [Teretistris fernandinae] was around. The warbler was within one meter of my head, and I was sitting on the ground. She soon disappeared among the bushes after I stood up . . . The second one was still on a branch for some time. The tree was separate from the rest of the vegetation. She flew a distance away to cover. The one found in Soroa was in the woods, about 3 meters from the ground on a tree near the road. The hill was about 300 m elevation (Sierra del Rosario).
DISEASES

Sciple (1950) collected a female along the Mississippi coast during a 1949 survey for avian encephalomyelitis. The bird had no parasites in its blood.

GEOGRAPHICAL DISTRIBUTION

A very large number of the references in the bibliography record only occurrence of Bachman's Warblers. Each of them is listed under the appropriate Caribbean island or individual state in U.S. Most of the references record actual occurrence of the birds but a few report negative data (e.g., Hooper and Hamel 1979b, Lane 1981), or expectations (e.g., Ganier 1917, 1933; the birds have never actually been recorded in Tennessee).

In several cases confusion exists concerning occurrence of the birds or the interpretation of reports. This confusion is particularly true concerning records from Georgia, Illinois, Indiana, and the Isle of Pines. Thus the early records for Illinois (Ridgway 1874, 1878) are perplexing. Ridgway would certainly have known the significance of his find [it predates the generally acclaimed "rediscovery" of Galbraith (1886) by almost ten years], yet he failed to do more than note a sight record. Confusion over records from Georgia is more substantial. Bailey's (1883) report of a clutch of eggs is generally discounted (Wayne 1910b), but Wayne's (1912) attack on the report by Hoxie (1911) may or may not have been justified. [Fargo (1934) believed that that attack caused Hoxie to forsake ornithology.] The Indiana specimen reported by Butler (1899) cannot be found and the report by Wilson (1918) may be questionable (Mumford and Keller 1975). A similar situation exists with the single record from the Isle of Pines. Read (1909a, 1909b, 1911, 1913; Reed 1911) took a specimen which he kept in his personal collection. The bird was listed in each of his reports.
and subsequently destroyed in a flood with the rest of his collection and notes. Todd (1916) then listed the bird as hypothetical for the Isle of Pines.

Recent sight records pose another problem. Our present knowledge of the rarity of the species leads to a much closer scrutiny of these records than was given to earlier reports. All known published reports are included in the bibliography, without qualification. A sample of the possible disagreement over validity of reports can be seen by comparing the evaluations of Hamel and Hooper (1979a) with those of Shuler et al. (1978). A critical reexamination of some other sight records from earlier times would probably yield similar uncertainty.

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Part 2. Literature of Bachman's Warbler

This bibliography contains all of the primary, i.e., original presentations of new data, and secondary, i.e., summarizations or evaluations of original data, ornithological papers, and books published through 31 August 1985. It was compiled by careful search of the following sources:

1. Indices of major English language ornithological journals and the Zoological Record.

2. Major works treating the birds of the Americas and the world.

3. Bird books and bird journals produced in states in the historical breeding range of the species.

4. Unpublished government and other reports concerning this species.

5. Major works on endangered species.

6. General treatises on ornithology.

7. Literature cited sections of all of the above.

In addition, a variety of other leads were pursued. Only a sample of the large number of popular endangered species books is included. I stopped short of including newspaper articles except where no other primary source for the same information was available. Where the information concerning Bachman's Warbler is substantially different in different editions of a work, each edition is listed. Otherwise only the most recent is listed. Where works have been reprinted, the edition listed is the one I examined, even when it was not an original one. It was possible to check the
accuracy of approximately 90% of the citations by reexamining copies of the original works.

In several cases works bear directly upon each other, as reviews, rebuttals, alternate interpretations, or the like. In such cases, annotations point the reader to related views. Examples include works that pertain to the controversy over management of National Forest lands in I’On Swamp, Charleston County, South Carolina, in the 1970's and 1980's.

Five hundred and four papers are listed in this bibliography. Of these, 207 (41%) are referenced under more than one subject heading, and 104 (21%) under more than two. Number of subject headings referenced is one crude guide to the importance of a paper. Twenty-four papers are referenced under six or more subject headings, as follows:

14 times--Widmann 1897;
11 times--Howell 1928, Stevenson 1972b;
10 times--Barnes 1954, Dingle 1963;
9 times--Imhof 1976;
8 times--Brewster 1891, King 1978, Stevenson 1975, Wayne 1907a, Wayne 1910a;

A second estimate of the importance of a particular paper is its appearance in Part 1 of this work. Papers cited there contribute, in my judgment, important information to an understanding of the
biology and history of the species. The large number of references to Widmann (1897) in the third section and the large number of citations of the work in the first section support and reflect my opinion that that is the single most important first-hand account of the Bachman's Warbler yet written.
Bachman's Warbler singing 15 m up in lower canopy of Longleaf Pine, 1958, Charleston Co., S. C.

Photo courtesy of Walter Dawn.
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Bachman's Warbler foraging below 1 m in Post Oak seedling, 1958, Charleston Co., S. C.

Photo courtesy of Walter Dawn.
Listing by Subject

Sequence of subject headings follows that of the Zoological Record.

GENERAL

General Works

Works which are either (a) general works and textbooks; or (2) works containing general information about Bachman's Warblers.

Audubon 1831-1834
Audubon 1841
Baird 1864
Barnes 1954
Berger 1961
Blair et al. 1968
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Buhrman 1977
Chamberlain, E. B. 1958
Chamberlain, E. B. 1974
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1978
Campbell 1977
Chamberlain 1974
Evenden et al. 1976
Evenden et al. 1977
Hamel 1980

King 1978
Natl. Wildl. Fed. 1976
Olendorff and Zeedyk 1978
USDA For. Serv. 1977
USDI Off. Endangered
Species and Int.
Activ. 1973
Vaughn 1978

Searches

Brewster 1886
Curtis 1978
Evenden et al. 1977
Florida Game and Fresh-
water Fish Comm.
Galbraith 1888
Ganier 1916
Hamel 1976
Hamel 1977a
Hamel 1977b
Hamel 1979
Hamel and Hooper 1979a
Hamel and Hooper 1979b
Hamel et al. 1976
Hooper and Hamel 1974
Imhof 1977
LeGrand 1979
Lowery 1974
Meanley 1972
Mengel 1965
Peterson 1948
Ridgway 1878
Stevenson 1972b
Stevenson 1975
Wilson 1940
Wright 1976

BEHAVIOR

General

Audubon 1834
Barnes 1954
Brewster 1891
Brewster 1905
Burleigh 1957
Chamberlain, E. B. 1958
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Dawn 1962
Dingle 1963
Gilbert 1983
Hanes 1958
Horlbeck 1958
Howell 1928
Meanley 1972
Meanley and Mitchell 1958
New Yorker 1950
Scott 1890a
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GEONPHICAL DISTRIBUTION

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Cooke 1905
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Cuba

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Barbour 1943
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Breuer 1860
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Cory 1886
Cory 1889
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Garrido and Garcia Montana 1975
Gochfeld 1974
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Gundlach 1855
Gundlach 1861a
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Gundlach 1865
Gundlach 1876
Gundlach 1893
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King 1978
Lembeye 1850
Ripley and Moreno 1980
Stevenson 1972b

Isle of Pines

Read 1909a
Read 1909b
Read 1911
Read 1913
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Stevenson 1972b
Todd 1916
United States, General

Am. Ornithol. Union 1957
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Hamel et al. 1982
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LeGrand and Hamel 1980

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| Burns 1908 | Pindar 1923 |
| Embody 1907 | Wilson 1922 |
| Figgins 1945 | Wilson 1940 |
| Funkhouser 1925 |

### U. S., Louisiana

| Allen 1888 | Lawrence 1887a |
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| Beyer 1900 | Lowery 1974 |
| Galbraith 1888 | Lowery and Newman 1952 |
| Gee 1977 | Newman 1954 |
| Imhof 1973 | Oberholser 1938 |
| Imhof 1977 | Stevenson 1975 |
| Kopman 1905 | Tanner 1939 |
| Kopman 1915 |

### U. S., Mississippi

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| Howell 1910 | Widmann 1907 |
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| Imhof 1977 | Woodruff 1908 |
| Korte and Fredrickson 1977 |

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| Brimley 1891 | LeGrand 1975 |
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| Cooper et al. 1977 | Potter et al. 1980 |
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U. S., Oklahoma

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U. S., South Carolina

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Shuler 1977d
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Shuler et al. 1978
Shuler et al. 1979
Sprunt 1954b
Sprunt 1958
Sprunt 1965
Sprunt and Chamberlain
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Stansell 1976
Teulings 1978
True 1883
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Southern Region 1985a
USDA Forest Service,
Southern Region 1985b
USDI Fish & Wildl. Serv.
1967
U. S., South Carolina, cont.

Urbston et al. 1979
Wayne 1901
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Wayne 1907a
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Wayne 1910a
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Wayne 1918
Wright 1976

U. S., Tennessee

Eagar and Hatcher 1982
Ganier 1916
Ganier 1917
Ganier 1933

U. S., Texas

Baumgartner 1951
Gunter 1972

Oberholser 1974
Peterson 1963

U. S., Virginia

Bailey 1913
Barnes 1954
Clark 1938
Geffen 1978
Larner et al. 1979
Meanley 1951

Murray 1933
Murray 1952
Palmer 1894
Potter and Murray 1954
Ruch 1954
Bachman's Warbler on a branch of water oak, anodized aluminum sculpture (Hirsch 1973).

Photo by Willard Hirsch.
Appendix

Electronic support materials are available at https://srs.fs.usda.gov/pubs/bachmans-warbler-materials/.

The materials include the following files:

**BachmansWarblerSpecimenData.xlsx** includes three worksheets: “Measurement Data” – the measurement data on 318 specimens, “Format” – a code sheet to the 69 different variables assessed for the specimens, and “Specimen Localities” – a list of known localities for these specimens.

**BachmansWarblerSpecimenDataCoding.pdf** is an explanatory key to the coding of the 69 variables listed in BachmansWarblerSpecimenData.xlsx.

**BAWA.ProtocolPhotos.pdf** is a cross-referenced list of the photos of the specimens.

**One hundred ninety-three photographs (.jpg)** of groups of specimens showing their ventral, dorsal, and lateral sides comprise the bulk of the support materials. Photographs are grouped for convenience into nine folders, labeled “Roll 1 Photos”, “Roll 2 Photos”, etc., with each photograph as a single .jpg file. Specimens shown on each photograph are listed in the “Properties” of each file, on the “Details” tab, in the “Comments” field. Specimens are listed from left to right, defined as the sequence visible when the photograph is rotated so that the bills of the birds are pointing up, and the tags can be read properly. The names of these photographs containing each specimen are listed for that specimen in BachmansWarblerSpecimenData.xlsx, and cross-referenced in BAWA.ProtocolPhotos.pdf.
About the Author

Paul B. Hamel currently holds the title of Zoologist in the Ecological Services Division of the Tennessee Department of Conservation, where he conducts inventory and research studies on endangered and threatened species and their Tennessee habitats.
Bachman’s Warbler: A Species in Peril
Paul B. Hamel

Interest in Bachman’s Warbler (Vermivora bachmanii) has waxed and waned as populations of the species have seemed to appear and disappear since the first specimen was collected in 1832. Congressional passage of the Endangered Species Act in 1973 sparked the most recent round of investigation of this bird.

The book consists of two main parts: Part 1 is a summary and analysis of the history and biology of the species. Part 2 is a comprehensive bibliography arranged both by author and by subject. This bibliography contains all the primary and secondary data, ornithological papers, and books published up through 1985, with inclusion of 1986 materials as well. Dr. Hamel’s analysis also takes into account unpublished field notes and other observations.

This study and bibliography is an invaluable resource for scientists, wildlife managers, and environmentalists.

Bachman’s Warbler: A Species in Peril was awarded the Outstanding Wildlife Book Award, 1987, by the Southeastern Section of The Wildlife Society.

Royalties from sales of this book were donated to the George J. Wallace and Martha C. Wallace Endowed Scholarship Fund of the Department of Integrative Biology at Michigan State University.