———, & N. T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-Petrel. Condor 81: 157–165.

DIXON, W. J., & F. J. MASSEY, JR. 1969. Introduction to statistical analysis, 3rd ed. New York, McGraw-Hill.

HELWIG, J. T., & K. A. COUNCIL (Eds.). 1979. SAS user's guide, 1979 ed. Raleigh, North Carolina, SAS Inst. Inc.

MANUWAL, D. A. 1978. Effect of man on marine birds: a review. Proc. J. S. Wright Forestry Conf., Wildlife and People, West Lafayette, Indiana, Purdue Univ.

———, & P. D. BOERSMA. 1977. Dynamics of marine bird populations on the Barren Islands, Alaska. Pp. 294–420 *in* Environmental assessment of the Alaskan Continental Shelf. Annual reports of principal investigators, vol. 4. Boulder, Colorado, NOAA, Environmental Res. Lab.

MANUWAL, N. J. 1979. Vegetation of the Barren Islands, Alaska. Syesis 12: 131–146.

MURRAY, K. G., K. WINNET-MURRAY, & G. L. HUNT, JR. 1979. Egg neglect in the Xantus Murrelet. Proc. Colonial Waterbird Group (3): 186–195.

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978–983.

———. 1968. Patterns of growth in birds. Ibis 110: 419–451.

SIMONS, T. R. 1980. Discovery of a ground-nesting Marbled Murrelet. Condor 82: 1–9.

WEHLE, D. H. S. 1983. The food, feeding, and development of young Tufted and Horned puffins. Condor 85: 427–442.

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Was Bachman's Warbler a Bamboo Specialist?

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Although the virtual extinction of the Bachman's Warbler (*Vermivora bachmanii*) has been considered to be natural (Stevenson 1972), a satisfactory explanation has yet to be proposed. Destruction of forest habitat per se does not seem to be involved in the decline. The riverine swamps of the southeastern United States have been extensively logged and drained, but there is no direct evidence that destruction of virgin forest habitats was a key factor in the warbler's disappearance. What little we know about the habitat preference of Bachman's Warbler does not indicate that it was as restricted to virgin forest as was the Ivory-billed Woodpecker (*Campephilus principalis*), whose dependence on mature forest follows from our knowledge of its feeding ecology (Tanner 1942). The degree to which the warbler occurred in second-growth forest is controversial (Hooper and Hamel 1977, Shuler 1977, Shuler et al. 1978). Urbston et al. (1979) found that one of the last strongholds of Bachman's Warbler, the I'On Swamp of South Carolina, was not a mature forest when most Bachman's Warblers were collected there and that most forest that was there had been logged extensively. However, the most recent observations of presumed breeding birds were in mature forest (Shuler et al. 1978; but see Hamel 1979 concerning validity of recent reports in I'On Swamp). Nevertheless, it seems unlikely that a small passerine would be completely dependent on virgin bottomland forests and find no other habitat type suitable: we have no parallel situation in any other bird of eastern North America, except the Ivory-billed Woodpecker. Therefore, it seems possible that some critical habitat or microhabitat upon which Bachman's Warbler was dependent has escaped identification.

Throughout the Neotropics, from Mexico to Argentina, bird species occur that are restricted in their habitat preference to bamboo thickets (*Chusquea* and *Guadua*; Bambusoideae); these bird species are primarily insectivores that glean arthropods from bamboo foliage and stems, although a few eat bamboo seeds (Parker 1982, Parker and Remsen MS). One species of bamboo, "cane" (*Arundinaria gigantea*), once occurred in extensive stands throughout the seasonally flooded swamplands of the southeastern U.S. Although cane is still present in much of its former range, the vast "canebrakes" that were the scourge of farmers and travelers are now greatly diminished.

William Bartram (*in* Harper 1958) frequently wrote of the extensive canebrakes encountered in his travels through the southeastern U.S. in the late 18th century. He used phrases such as "an endless wilderness of cane," "cane meadows always in view," "cane forests," "vast cane meadows," "wide-spreading cane swamps," and "cane swamps, of immense extent." Scenes such as that described at the turn of the century by Roosevelt (1962) along the Tensas River in northeastern Louisiana are essentially nonexistent today: ". . . canebrakes stretch along the slight rises of ground, often extending for miles, forming one of the most striking and interesting features of the country . . . ."

A variety of factors seem to have been involved in the decline of the great canebrakes. Canebrakes were valuable for cattle forage, and overgrazing of this resource contributed to their destruction (Hughes 1951, 1957). Because they were located on fertile floodplain soil and were more easily cleared than forest, many canebrakes were destroyed by clearing for agriculture (Hughes 1951, Meanley 1971). Fire control

also may have played a role; Hughes (1957) found that "cane stands thin out and decline in productivity when unburned for a decade or so." Flood-control projects along southeastern rivers eliminated much of the seasonal flooding in which bamboo thrives. Furthermore, once removed, cane "comes back so slowly that it will not restock for several generations," partly because of its unusual mode of sexual reproduction (Hughes 1951). As is typical for most bamboos (McClure 1966), *Arundinaria gigantea* produces seeds only after long periods of vegetative growth and dies completely after flowering.

Considering the former extent of bamboo in the southeastern U.S. and the degree to which many birds are specialized on bamboo elsewhere in the New World, it seems curious that no species were known to be restricted to cane. Swainson's Warbler (*Limnothlypis swainsonii*) is especially common in cane thickets but is by no means restricted to them (Meanley 1971, Eddleman et al. 1980). What about Bachman's Warbler?

Virtually every detailed account of the nesting habitat of Bachman's Warbler mentioned the presence of cane. Hooper and Hamel (1977), in their review of existing nest records, found that most came from more elevated areas of the swamps that were inundated for relatively short periods of time, i.e. areas most likely to contain cane. They also found that the overstory was usually subjected to disturbance, which stimulated dense understory. Cane was mentioned specifically in many cases and was a prominent plant in the undergrowth of the I'On Swamp. The recent observations in the 1970's from the I'On Swamp were in seasonally flooded areas where cane and palmetto predominated in the understory (Shuler et al. 1978; cf. Hamel 1979). Howell (1911) collected two specimens in Arkansas in May "in heavy timber with a dense undergrowth of cane," and his figure caption for a "canebrake in primative hardwood forest" is followed by "Home of Bachman and Swainson Warblers." The distribution of *Arundinaria* (Gilly 1943) corresponds closely to the known or suspected breeding range (A.O.U. 1983) of Bachman's Warbler. (This applies equally to the range of many other plants characteristic of bottomlands of the southeastern United States.) A survey of plants used as nest material and for supporting the nest of Bachman's Warbler would be useful, although we know virtually nothing about the nests of neotropical bamboo specialists for comparison (Parker and Remsen MS). Of the six Bachman's Warbler nests described by Wayne (1907), five contained cane leaves and two were supported by cane stems. At least two additional nests were supported by cane (Embody 1907, Arnow 1908).

In spite of the frequent mention of *Arundinaria* in accounts of Bachman's Warbler, only Meanley (1972: 70) speculated on the possible restriction of this bird to bamboo: "Possibly the disappearance of the canebrakes that formed the understory in many of the primitive bottomland and swamp forests inhabited by this warbler may be one factor related to its extirpation in some areas. During the 1940s and 1950s, I visited the three areas where Bachman's Warbler was formerly known to be a common breeding bird .... Cane used to be prominent in the understory of all three places. Parts of these areas still had some fine forests but a paucity of cane understory." Other authors, however, seem to have come close to making such a hypothesis. King's (1981) distillation of what is known about Bachman's Warbler habitat mentioned that *Arundinaria* was especially prominent but did not propose restriction to it. S. A. Gauthreaux's painting of Bachman's Warbler accompanying Hooper and Hamel's (1977) review of its habitat preferences portrays a pair perched in cane.

That naturalists did not notice if Bachman's Warbler was restricted to bamboo is not surprising. Most bamboo specialists are not completely restricted to bamboo plants but are regularly seen away from the thickets themselves (Parker and Remsen MS). Even species that are seldom seen away from bamboo foliage only recently have been recognized as being so specialized [e.g. the Plush-capped Finch (*Catamblyrhynchus diadema*), a common bird over a wide elevational range in the Andes from Venezuela to Bolivia (Hilty et al. 1979)]. Many bamboo specialists are among the rarest neotropical birds in museum collections (Parker 1982, Parker and Remsen MS).

A restriction of Bachman's Warbler to breeding in canebrakes would help to explain why observations of this species on the breeding grounds were rare. Not only are canebrakes located in swamps with difficult access, but cane thickets themselves are nearly impenetrable. Roosevelt (1962) described canebrakes in 1907 as "well-nigh impenetrable to a man on horseback; even on foot they make difficult walking unless free use is made of the heavy bush-knife. It is impossible to see through them for more than fifteen or twenty paces, and often not for half that distance." Thus, it is not surprising that in spite of intensive searching by oologists for the highly sought-after prize of a Bachman's Warbler nest, only 40 were found, 35 by a single skilled and persistent collector, A. T. Wayne (Hooper and Hamel 1977). Although generally considered a rare bird even in the 1800's, observations of relatively large numbers in migration (see Stevenson 1972) indicate that it may have been much more common than realized. A tabulation of records almost certainly would show that the majority of observations were of migrants. So, again, it is understandable that restriction to canebrakes for breeding could have gone unnoticed, especially considering that Bachman's Warbler was not an easy species to detect. For example, a female built a nest within a few feet from Widman's (1897) daily observation point without his knowing it for a week; Widman, whose field experience with Bachman's Warbler was extensive, stated that it was "very easily overlooked, even in a region where it is common."

I speculate that Bachman's Warbler was a bamboo-thicket specialist that has become virtually extinct as the canebrakes of the southeastern U.S. were destroyed by agriculture and flood control. Seasonal flooding is extremely important to bamboo ecology (Marsh 1977, as cited by Eddleman et al. 1980). Unfortunately, the timing of the disappearance of the large canebrakes apparently has not been chronicled. Although cane is still found throughout most of the region, it now occurs primarily in small patches that may not be of sufficient size for Bachman's Warbler territories. It is also possible that optimal habitat for Bachman's Warbler was the extensive canebrakes (no overstory) or their interface with forest rather than the patches that still may be found in forest undergrowth. Is it possible that the irruptive nature of our recorded history of this warbler was linked to the episodic nature of bamboo reproductive cycles? Did Bachman's Warbler require the presence of bamboo over a large geographic area so that it could move from a region of postflowering die-offs to one at a different stage in the cycle? Could the very early arrival of Bachman's Warbler in spring be related to a specialization on (nearly) evergreen bamboo foliage? Similarly, could the unusually (for a wood-warbler) thin, decurved bill of Bachman's Warbler (see plates in Hamel and Gauthreaux 1982) reflect some specialization for foraging in bamboo? Although the diet of Bachman's Warbler has been studied (Meanley and Mitchell 1958), observations of selection of foraging substrates have been restricted mainly to migrant birds (e.g. Brewster 1891) or to individuals at the periphery of their range (e.g. Barnes 1954, Meanley and Mitchell 1958). In these situations it foraged in many kinds of plants, searched dead leaves, and gaped into terminal leaflets in a manner similar to other *Vermivora* (Brewster 1891, Barnes 1954, Meanley and Mitchell 1958).

A major gap in our knowledge of the natural history of Bachman's Warbler is its winter habitat preference. Although some neotropical bamboo specialists are migratory, such movements are from one region of flowering bamboo to another (Parker and Remsen MS). Because habitat destruction has been extensive in lowland Cuba, we may never know what the original habitat was like or whether bamboo was an important component. Anecdotal information indicated that Bachman's Warbler was found regularly in disturbed, riverine habitats, where it probed hibiscus flowers (Gundlach 1876, 1893). Destruction of winter habitat in itself has been proposed as the reason for the demise of Bachman's Warbler (Rappole et al. 1983). Such a hypothesis does not necessarily compete with the one that I propose in this paper. Certainly, habitat destruction on both the breeding and wintering grounds would have acted synergistically toward the decline of the warbler.

A more conservative hypothesis concerning habitat preference of Bachman's Warbler is that it was specialized during the breeding season on seasonally flooded swampy forest, of which cane was merely a prominent component, and that the species disappeared when the habitat was reduced greatly. This hypothesis would help to explain why the limited foraging observations of Bachman's Warbler did not reveal any specialization on cane. On the other hand, although greatly reduced in extent, seasonally flooded, swampy forest is still present in much of the southeastern U.S.; only the Bachman's Warbler and bamboo have declined so drastically.

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Literature Cited

American Ornithologists' Union. 1983. Check-list of North American birds, 6th ed. Washington, D.C., Amer. Ornithol. Union.

Arnow, J. F. 1908. Bachman's Warbler in Camden Co. and breeding in Chatham Co., Georgia. Auk 25: 479.

Barnes, I. R. 1954. A new look at Bachman's Warbler. Atlantic Natur. 10: 18–30.

Brewster, W. 1891. Notes on Bachman's Warbler (*Helminthophilus bachmani*). Auk 8: 149–157.

Eddleman, W. R., K. E. Evans, & W. H. Elder. 1980. Habitat characteristics and management of Swainson's Warbler in southern Illinois. Wildl. Soc. Bull. 8: 228–233.

Embody, G. C. 1907. Bachman's Warbler breeding in Logan County, Kentucky. Auk 24: 41–42.

Gilly, C. L. 1943. A preliminary investigation of the North American canes (*Arundinaria*). Bull. Torrey Botanical Club 70: 297–304.

Gundlach, J. 1876. Contribuciòn a la ornitologìa cubana. Habana, Cuba, La Antilla.

———. 1893. Ornitologìa cubana. Habana, Cuba, La Moderna.

Hamel, P. B. 1979. Status of Bachman's Warbler, a progress report. Pp. 112–121 *in* Proc. Rare and Endangered Wildl. Symp., Athens, Georgia, 1978.

———, & S. A. Gauthreaux. 1982. The field identification of Bachman's Warbler (*Vermivora bachmanii* Audubon). Amer. Birds 36: 235–240.

Harper, F. (Ed.). 1958. The travels of William Bartram. New Haven, Connecticut, Yale Univ. Press.

Hilty, S. L., T. A. Parker III, & J. Silliman. 1979. Observations on Plush-capped Finches in the Andes with a description of the juvenal and immature plumages. Wilson Bull. 91: 145–148.

HOOPER, R. G., & P. B. HAMEL. 1977. Nesting habitat of Bachman's Warbler—a review. Wilson Bull. 89: 373-379.

HOWELL, A. H. 1911. Birds of Arkansas. U.S. Dept. Agr. Biol. Survey Bull. No. 38.

HUGHES, R. H. 1951. Observations of cane (*Arundinaria*) flowers, seeds, and seedlings in the North Carolina coastal plain. Bull. Torrey Botanical Club 78: 113-121.

———. 1957. Response of cane to burning in the North Carolina coastal plain. North Carolina Agr. Exp. Station Bull. No. 402.

KING, W. B. 1981. Endangered birds of the world. The ICBP Red Data book. Washington, D.C., Smithsonian Inst.

MARSH, D. L. 1977. The taxonomy and ecology of cane [*Arundinaria gigantea* (Walter) Muhlenberg]. Unpublished Ph.D. dissertation, Little Rock, Univ. Arkansas.

MCCLURE, F. A. 1966. The bamboos, a fresh perspective. Cambridge, Massachusetts, Harvard Univ. Press.

MEANLEY, B. 1971. Natural history of the Swainson's Warbler. U.S. Dept. Interior, Bur. Sport Fisheries Wildl. North Amer. Fauna No. 69.

———. 1972. Swamps, river bottoms and canebrakes. Barre, Massachusetts, Barre Publ.

———, & R. J. MITCHELL. 1958. Food habits of Bachman's Warbler. Atlantic Natur. 13: 236-238.

PARKER, T. A., III. 1982. Observations of some unusual rainforest and marsh birds in southeastern Peru. Wilson Bull. 94: 477-493.

RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY III, & J. L. RUOS. 1983. Nearctic avian migrants in the Neotropics. Washington, D.C., U.S. Dept. Interior, Fish Wildl. Serv.

ROOSEVELT, T. 1962. In the Louisiana canebrakes. Louisiana Wildl. Fish Comm., Wildl. Educ. Bull. No. 59. (Reprinted from Scribner's Mag., January 1908.)

SHULER, J. 1977. Bachman's Warbler habitat. Chat 41: 19-23.

———, P. NUGENT, J. TROCHET, & J. VAN OS. 1978. Bachman's Warbler observations continue in I'On Swamp. Chat 42: 23-24.

STEVENSON, H. M. 1972. The recent history of Bachman's Warbler. Wilson Bull. 84: 344-346.

TANNER, J. 1942. The Ivory-billed Woodpecker. New York, Dover.

URBSTON, D. F., D. N. MUDGE, & L. E. LEWIS. 1979. Historical aspects and ecosystem changes of Bachman's Warbler habitat in I'On Swamp, South Carolina. Pp. 169-177 *in* Proc. First South Carolina Endangered Species Symp. (D. M. Forsythe and W. B. Ezell, Jr., Eds.). Columbia, South Carolina Wildlife and Marine Resources Dept.

WAYNE, A. T. 1907. The nest and eggs of Bachman's Warbler, *Helminthophilus bachmani* (Aud.), taken near Charleston, South Carolina. Auk 24: 43-48.

WIDMANN, O. 1897. The summer home of Bachman's Warbler no longer unknown. Auk 14: 305-309.

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Consumption of Largemouth Bass Eggs by Redhead Ducks at Ruby Lake, Nevada

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Dietary preferences and nutrient cycles of breeding ducks are well documented (Krapu 1974, 1981; Serie and Swanson 1976; Drobney and Fredrickson 1979; Reinecke and Owen 1980). Before egg-laying, many species of ducks typically feed on plant foods high in carbohydrates to accumulate lipid reserves for ovarian development and incubation. During the laying period, females feed on animal food to obtain the protein necessary for egg production. Because protein cannot be stored in appreciable amounts, protein for egg formation is obtained principally from the diet (Krapu 1981). Lipid reserves during the laying period provide energy that allows females to feed on invertebrates, the consumption of which may be energetically inefficient (Drobney 1980, Krapu 1981). Because lipid reserves are also needed during incubation, it should be important for female ducks to minimize energy expenditure during egg-laying. Thus, both the protein content of foods and the energetic costs of acquiring them are important factors governing choice of diet.

To my knowledge, breeding waterfowl in freshwater marshes have not been previously reported to eat fish eggs. Utilization of herring (*Clupea harengus*) eggs along the Pacific Coast was reported by Munro (1941) for Greater Scaup (*Aythya marila*) and by Bayer (1980) for several species of diving ducks (*Aythya* spp.), including Redheads (*A. americana*). Peterson and Ellarson (1977) reported that Oldsquaws (*Clangula hyemalis*) wintering on Lake Michigan consumed fish eggs when available.

I report here observations on Redheads during the

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