wing bars and the stronger yellow edgings on the inner remiges of *minimus*, but incorrectly stated that it shares the form of the nostril with *minor*. Also, when distinguishing *minimus* from *minor*, Todd concentrated his attention on minor differences in variable characters, leading Zimmer to consider only those differences in his discussion of *minimus*.

In conclusion, the name of the taxon previously known as *Hemitriccus aenigma* is *Hemitriccus minimus* based on the 15 years priority that *Snethlagea minima* Todd, 1925 has over *Euscarthmornis aenigma* Zimmer, 1940. The name of the subspecies of *Hemitriccus minor* previously known as *minimus* should now be *snethlageae* Snethlage, 1937. The name *snethlageae* appears to be based on a population of *minor*, and not of *minimus*, as the wing lengths ranged from 49 to 53 mm, and tail from 42 to 43 mm (Snethlage 1937). I recommend that the English name of *Hemitriccus minimus* remain Zimmer's Tody-Tyrant, as used for *H. aenigma*, since Zimmer was the first to distinguish it correctly from the population of *Hemitriccus minor* that occurs alongside it.

In addition to the four specimens at the Carnegie and Zimmer's type and paratype of *aenigma*, a male specimen at the Museu de Zoologia da Universidade de São Paulo from Fordlandia (MZUSP 47086) and a male specimen (ANSP 133117) at the Academy of Natural Sciences, Philadelphia, from Tauari (mentioned in Griscom and Greenway 1941) are examples of *Hemitriccus minimus*. Since I discovered these specimens, which extend the range of *Hemitriccus minimus* to the west bank of the Rio Tapajós and upstream about 180 km, Parker and Bates have found and collected *minimus* in Bolivia (Parker et al. 1991), so the range is much broader than previously believed.

I thank Paulo Vanzolini, Helio Camargo and Regina Rebouças-Spieker (Museu de Zoologia, Universidade de São Paulo), Ken Parkes and Scott Wood (Carnegie Museum), Mark Robbins (Academy of Natural Sciences), and Allison Andors and George Barrowclough (American Museum of Natural History) for assistance in using the specimens under their care and for providing important information about those specimens. This paper benefitted substantially from comments by Richard Banks, Ken Parkes, Tom Schulenberg and an anonymous reviewer, as well as from discussions with John Bates, Ted Parker, and Tom Schulenberg. Ken Parkes located and examined specimens of Todd's original series at Carnegie that had been exchanged to other museums, for which I am most grateful.

LITERATURE CITED

- BERLEPSCH, H. G. VON. 1909. Über eine neue Gattung aus der Familie der Tyrannidae. J. Ornithol. 57: 104–107.
- GRISCOM, L., AND J. C. GREENWAY, JR. 1941. Birds of lower Amazonia. Bull. Mus. Comp. Zool. 88:85– 344.
- PARKER, T. A., III, A. CASTILLO U., M. GELL-MANN, AND O. ROCHA O. 1991. Records of new and unusual birds from northern Bolivia. Bull. Br. Ornithol. Club 111:120–138.
- SNETHLAGE, H. 1937. Ein neuer Tyrannidae aus Amazonien. Ornithol. Monatsber. 45:174–175.
- TODD, W. E. C. 1925. Sixteen new birds from Brazil and Guiana. Proc. Biol. Soc. Wash. 38:91–100.
- TRAYLOR, M. A., JR. 1979. Tyrannidae. Pages 1-240 in Checklist of birds of the world, vol. 8 (M.A. Traylor, Jr., Ed.). Harvard Univ. Press, Cambridge, Massachusetts.
- ZIMMER, J. T. 1940. Studies of Peruvian birds. No. 34. The genera Todirostrum, Euscarthmornis, Snethlagea, Poecilotriccus, Lophotriccus, Myiornis, Pseudotriccus and Hemitriccus. Am. Mus. Novit. No. 1066.

Received 1 July 1991, accepted 19 February 1992.

The Auk 109(4):917-919, 1992

Extensive Folivory by Thick-billed Saltators (Saltator maxillosus) in Southern Brazil

ERIK S. MUNSON¹ AND W. DOUGLAS ROBINSON Department of Ecology, Ethology, and Evolution, University of Illinois, 606 East Healey Street, Champaign, Illinois 61820, USA

Although folivory is a successful foraging strategy for numerous taxa (e.g. Ellison 1960, McNaughton 1979, Otte 1981, Watt 1981, Brown 1984), few birds are folivorous. In part, this is because flight is ener-

getically too expensive to be feasible on an energypoor diet of leaves (Tucker 1971, Morton 1978); the energy content of leaves is only about one-half that of fruits and one-fourth that of arthropods (reviewed in Jenkins 1969). Furthermore, because digestion of leaves is slow, large storage chambers in the gut are necessary (Grajal et al. 1989). Volant birds, however,

¹ Deceased.

Family	Plant species	Food	Items eaten	Sequences	Foraging time (s)
Bromeliaceae	Vriesea carinata	Fruit	7	2	65
Myrtaceae	Eugenia sp.	Fruit	6	2	93
Melastomataceae	Tibouchina sellowiana	Leaves	9	1	105
Solanaceae	Solanum granulosoleprosum	Leaves	4	1	55
Solanaceae	Cyphomandra sp.	Leaves	31	1	324
Rubiaceae	Psychotria longipes	Leaves	8	5	307
Compositae	Piptocarpha angustifolia	Leaves	67	4	1,660
Compositae	Mikania sp.	Leaves	2	1	50
Compositae	Vernonia discolor	Leaves	43	2	700
Nyctaginaceae	Unidentified A	Leaves	3	1	91
· _	Unidentified B	Leaves	1	1	15
_	Unidentified C	Fruit	4	1	145
—	Unidentified D	Leaves	6	2	60

TABLE 1. Foods eaten by Thick-billed Saltators in August 1991 in Parana, Brazil.

* Number of foraging sequences that include use of a given food.

have little storage space available because large pectoral muscles and a well-developed sternum are necessary for flight (Morse 1975).

Despite the disadvantages of folivory, about 3% of all bird species, from at least 14 families, eat leaves regularly (Morse 1975, Morton 1978). Most leaf-eating birds are terrestrial or aquatic; only five bird families include arboreal members that regularly eat leaves. From these five families, only two species, the Hoatzin (Opisthocomus hoazin, Opisthocomidae, Cuculiformes; Beebe 1909) and the Owl Parrot (Strigops habroptilus, Strigopidae, Psittaciformes; Oliver 1955), receive most of their energy from leaves ("obligate" folivory sensu Morton 1978). Among passeriforms, the arboreal plantcutters (Phytotomidae) and one species of calleid crow (Calleus cinerea) also may be obligate folivores, but no studies have reported the diets of these birds in any detail (Morton 1978). Here, we report observations of extensive folivory by the Thickbilled Saltator (Saltator maxillosus), an emberizid from southern Brazil. This species has not been previously reported eating leaves, and our description of possible obligate folivory appears to be the first for any passerine.

From 2 to 24 August 1991, we studied Thick-billed Saltators in Mananciais da Serra Area de Especial Interesse Turistico do Marumbi, in Parana state, southern Brazil (25°30'S, 49°10'W). The study site, at about 1,050 m elevation, is part of a mostly contiguous, second-growth forest of greater than 500 km². We encountered foraging saltators in a forest-edge habitat along 4 km of a lightly traveled dirt road, where we were able to view the birds clearly without disturbing them. We noted the kinds of foods eaten, the number of food items taken per perch, the number of perches used per foraging sequence, and whether leaves were torn or eaten whole. We did not have permission to color-mark individual saltators, so we mapped each observation. Observations separated by more than 300 m were considered to be of different birds. We believe

this is a conservative measure of separation because birds generally moved less than 100 m along the road during observation periods of <1 to 38 min. We marked foraging sites and returned later to identify plants. Four tree species were inaccessible and could not be identified, but these appeared to be distinct from each plant we identified and distinct from one another. Each of these four trees was treated as a separate morphospecies in our analysis.

Of 191 food items that we observed eaten by Thickbilled Saltators, 91% were leaves (Table 1). This sample is from 24 foraging sequences from approximately 16 individual birds. All leaves were from woody plants and, in nearly all cases, leaves were plucked and consumed whole. The only leaves that were not ingested whole were from *Vernonia discolor*, a tree with leaves 5 to 9 cm wide that were torn before ingestion. The saltators ate leaves from 10 species of plants, and fruits from 3 species. Leaves of the tree *Piptocarpha angustifolia* were the most common food, accounting for 35% of the items we saw eaten. The saltators also spent more foraging time in *P. angustifolia* than in any other plant species.

When handling leaves, a saltator first grasped the leaf near its middle and plucked it, petiole included, from the twig. The leaf was initially held flat, intact, and crosswise in the bill. The bird then pinched along the leaf's full length, working the leaf slowly back and forth through the bill. Folding the leaf parallel to the petiole-to-tip axis, the bird then pinched the leaf repeatedly, eventually forming a small, mashed ball which was then eaten. Handling time was 5 to 26 s per leaf. The birds ate as many as 25 leaves per perch ($\bar{x} = 4.5 \pm SE$ of 0.8, n = 42 perches) in this manner. On a few occasions, saltators dropped parts of the processed leaf to the ground, possibly intentionally. Unfortunately, we could not recover the dropped leaf portions for inspection, but we suspect that some were petioles too tough for digestion.

Resource use by birds can change seasonally, so it is possible that this extensive use of leaves is only seasonal. Fruits, evidently an alternative food source for Thick-billed Saltators (Table 1), vary seasonally in abundance in tropical rain forests (Hilty 1980, Levey 1988, Loiselle and Blake 1991). Fruit abundance is generally lowest during the dry season (Heideman 1989), and our August study came during the driest time of the year in Parana (Eidt 1969). During the dry season at our study site, at least two normally frugivorous (Sick 1985, Ridgely and Tudor 1989) species of tanagers, the Blue-and-yellow Tanager (Thraupis bonariensis) and the Diademed Tanager (Stephanophorus diadematus), occasionally eat leaves (F. Straube, E. Munson, and D. Robinson, pers. observ.). Thus, our study may have been during an annual period in which fruits were scarce and the saltators were forced to switch to leaves. Similarly, Thick-billed Saltators may switch from leaves to other foods during the nesting season to provide their growing young with higher-quality nutrition. In Costa Rica, three congeners, the Buff-throated (S. maximus), Black-headed (S. atriceps), and Gravish (S. coerulescens) saltators, feed primarily on fruits when not breeding and switch to a diet composed almost exclusively of arthropods when feeding nestlings (Jenkins 1969). Studies are needed during all seasons to gauge the full extent of folivory in the Thick-billed Saltator.

Future studies could provide further insight into avian folivory by analytically comparing the life-history traits of the Thick-billed Saltator with analogous traits of congeners that have different diets. Diets evidently differ among saltator species, as some species are frugivorous (Jenkins 1969, Sick 1985) and at least one is locally folivorous (this study). Unfortunately, the two bird species (Hoatzin and Owl Parrot) known previously to be obligate, arboreal folivores are in monotypic genera and there are no closely related species with which to make comparisons. In contrast, saltators provide an opportunity to control for phylogenetic effects and isolate specific morphological, physiological, and behavioral traits associated with folivory.

We thank Miguel A. Marini for acquainting us with the study area and translating some Portuguese literature. S. Robinson, D. Enstrom, K. Halupka, T. Mc-Cartney, C. Trine, J. Brawn, A. Grajal, and R. Macedo made helpful comments on earlier drafts of the manuscript. Biologists at the Museu de Historia Natural do Capao da Imbuia in Curitiba, Brazil, provided valuable assistance: Jose Tadeu W. Motta identified the plants; Pedro Scherer Neto allowed access to museum collections; and Fernando C. Straube generously shared knowledge on birds. We also thank Carlos Eduardo Pierin of SANEPAR for allowing us to work in Mananciais da Serra. This work was funded by the University of Illinois through a graduate fellowship to E.S.M. and a travel grant to W.D.R.

LITERATURE CITED

- BEEBE, C. W. 1909. A contribution to the ecology of the adult Hoatzin. Zoologica 1:45-67.
- BROWN, V. K. 1984. Secondary succession: Insectplant relationships. BioScience 34:710–716.
- EIDT, R. C. 1969. The climatology of South America. Pages 54–81 in Biogeography and ecology in South America (E. J. Fittkau et al., Eds.). W. Junk, The Hague.
- ELLISON, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26:1–78.
- GRAJAL, A., S. D. STRAHL, R. PARRA, M. G. DOMINGUEZ, AND A. NEHER. 1989. Foregut fermentation in the Hoatzin, a Neotropical leaf-eating bird. Science 245:1236-1238.
- HEIDEMAN, P. D. 1989. Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. J. Ecol. 77:1059–1079.
- HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane rainforest in Pacific Columbia. Biotropica 12:292–306.
- JENKINS, R. 1969. Ecology of three species of saltators with special reference to their frugivorous diet. Ph.D. dissertation, Harvard Univ., Cambridge, Massachusetts.
- LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecol. Monogr. 58:251-269.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180-193.
- MCNAUGHTON, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. Am. Nat. 113:691–697.
- MORSE, D. H. 1975. Ecological aspects of adaptive radiation in birds. Biol. Rev. 50:167-214.
- MORTON, E. S. 1978. Avian arboreal folivores: Why not? Pages 123-130 in The ecology of arboreal folivores (G. G. Montgomery, Ed.). Smithsonian Inst. Press, Washington, D. C.
- OLIVER, W. R. B. 1955. New Zealand birds. Reed, Wellington, New Zealand.
- OTTE, D. 1981. The North American grasshoppers. Vol. 1, Acrididae (Gomphocerinae and Acridinae). Harvard Univ. Press, Cambridge.
- RIDGELY, R. S., AND G. TUDOR. 1989. The birds of South America: The oscine passerines. Univ. Texas Press, Austin.
- SICK, H. 1985. Ornitologia Brasileira, vol. 2, 3rd ed. Editoria Universidade de Brasilia, Brasilia.
- TUCKER, V. A. 1971. Flight energetics in birds. Am. Zool. 11:115-124.
- WATT, A. S. 1981. A comparison of grazed and ungrazed grassland A in East Anglian Breckland. J. Ecol. 69:499–508.

Received 12 December 1991, accepted 13 March 1992.