NOTES

THE WRETCHED RIDDLE OF REDUCED RECTRICES IN WRENS

KEVIN WINKER, University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775; kevin.winker@alaska.edu

Hwat dostu godes a-mong monne?
Na mo þene doþ a wrecche wrenne.

(What good do you do among men?
No more than does a wretched wren.)

(*The Owl and the Nightingale*, Middle English poem, 13th century, lines 563–566; Wells 1907)

Most bird species possess 12 rectrices in six pairs, although the number of rectrices varies among all species from 6 to 32 (Van Tyne and Berger 1976). Within a species, variations from the typical number of rectrices also occur, commonly in some species, and it is this type of variation that has probably attracted most attention. Audubon (1831:139, 140), for example, reported a female Carolina Parakeet (*Conuropsis carolinensis*) with a pair of supernumerary rectrices; he recognized it as an individual aberration and chose to highlight it in his painting of this species. Somadikarta (1984) used the term "polyrectricyly" for supernumerary rectrices, and Hanmer (1985) coined the term "anisorectricial" for an abnormal number of rectrices, whether in an asymmetrical or symmetrical context.

Variation among lineages also occurs. Nitzsch (1867:86) recorded 10 rectrices in these genera: *Cypselus*, *Trochilus*, *Caprimulgus*, *Cuculus*, *Centropus*, *Phaenicophanes*, *Scythrops*, *Crotophaga*, *Bucco*, *Micropogon*, *Pogonias*, *Rhamphastus*, *Buceros*, *Upupa*, *Colius*, *Musophaga*, and *Opisthocomus* (Nitzsch did not report which species of these genera he examined, so I give his partly antiquated nomenclature verbatim). Van Tyne and Berger (1976:137) provided a brief review of the distribution of taxa with 10 rectrices: "hummingbirds, swifts, most cuckoos, most of the motmots, the toucans, etc.," the genus *Dicrurus*, and some Furnariidae. Also, the family Acanthisittidae of New Zealand has only 10 rectrices (Newton 1896). It seems that a modern taxonomic survey of the distribution of species with 10 rectrices does not yet exist. Nor does there seem to be an explanation for this reduction. It is not well known (indeed, I have not yet seen it recorded) that 10 rectrices are the norm in several species of wrens (Troglodytidae). Here I investigate the taxonomic distribution of this condition at the genus level in the Troglodytidae and consider possible reasons for its occurrence.

I examined specimens and counted rectrices. Sample sizes were three or more individuals per species except where indicated. I was unable to sample all species of wrens, but I endeavored to sample all of the genera. The genus *Thryothorus* as historically configured is paraphyletic, and generic limits for the taxa that no longer belong in that genus (all but *T. ludovicianus*) are neither statistically nor phenotypically clear (Mann et al. 2006). Resurrection of the genus *Pheugopedius* is the simplest taxonomic solution at present, although future molecular and phenotypic research is likely to change generic limits as relationships become clearer (both through increased genomic and taxonomic sampling). Mann et al. (2006) proposed a three-genus solution (*Pheugopedius*, *Thryophilus*, and *Cantorchilus*), but this required naming a new genus (*Cantorchilus*) based entirely on mtDNA characters because no phenotypic characters are yet known to define this molecular clade of nine species. Because I am

not comfortable using molecular characters exclusively to define the limits of a genus (any well-supported multi-species molecular clade could thus be a genus), I use the genus *Pheugopedius* with subgenera *Thryophilus* and *Cantorchilus* here, sampling each of these three mtDNA clades reported by Mann et al. (2006).

The following 16 taxa have 12 rectrices: *Odontorchilus branickii* (Gray-mantled Wren, *n* = 1), *Campylorhynchus b. brunneicapillus* (Cactus Wren), *Troglodytes hiemalis* (Winter Wren), *Cistothorus platensis stellaris* (Sedge Wren), *C. palustris* (Marsh Wren), *Ferminia cerverai* (Zapata Wren, *n* = 2), *Salpinctes obsoletus* (Rock Wren), *Catherpes mexicanus conspersus* (Canyon Wren), *Thryomanes b. bewickii* (Bewick's Wren), *Thryothorus l. ludovicianus* (Carolina Wren), *Uropsila leucogastra* (White-bellied Wren), *Pheugopedius fasciatoventris albigularis* (Black-bellied Wren), *P.* (subgenus *Thryophilus*) *rufalbus castanonotus* (Rufous-and-white Wren), *P.* (subgenus *Cantorchilus*) *thoracicus* (Stripe-breasted Wren), *P.* (*C.*) *m. modestus* (Plain Wren), and *P.* (*C.*) *nigricapillus costaricensis* (Bay Wren).

These seven taxa have 10 rectrices: *Thryorchilus browni* (Timberline Wren), *Microcerculus marginatus luscinia* (Scaly-breasted Wren), *Cinnycerthia unirufa chakei* (Rufous Wren), *Henicorhina leucosticta prostheleuca* (White-breasted Wood Wren), *Cyphorhinus phaeocephalus* (Song Wren), *Pheugopedius atrogularis* (Black-throated Wren), and *P. coraya ridgwayi* (Coraya Wren). I was not able to access adequate material of *Hylorchilus* (Sumichrast's and Nava's wrens).

I mapped the distribution of 12 and 10 rectrices onto a phylogenetic tree of the family (Figure 1) based on the molecular phylogeny of Mann et al. (2006: their figure 2 and text), collapsing nodes with weak support (<54% nonparametric bootstrap support). It is clear that the reduction to 10 rectrices represents a derived condition and that it arose multiple times. The genus *Pheugopedius* (*sensu stricto*) comprises some species with 12 rectrices and others with 10, so the number of rectrices is not a reliable indicator of generic limits.

Because I did not sample all species, and the phylogeny of the wrens remains uncertain at key nodes, elucidation of the full evolutionary history of 10 rectrices in the family will require further study. For example, the large, unresolved clade of *Pheugopedius* and its allies has a particularly complex and unresolved history of rectrix number. From these data, it is possible that the ancestor of this clade had 10 rectrices and that there were four reversions to 12 rectrices (see Figure 1). However, a great deal more genetic and morphological study will be required to resolve this. Two key results will not change, though: the reduction to 10 rectrices arose independently at least three times, and this character can occur within a genus in which some species have 12 rectrices.

Newton (1896) provided additional examples of intrageneric variation in rectrix number in *Oreocincla* (thrushes now in *Zoothera*), *Phalacrocorax* (cormorants), and *Gallinago* (snipe). Vaurie (1971) gave the furnariids *Synallaxis* and *Certhiaxis* as two more examples of intrageneric variation. Hanmer's (1985) results imply another example in *Colius*, *C. striatus* (Speckled Mousebird) having 12 rather than the 10 given for the genus by Nitzsch (1867).

I cannot figure out any evolutionary hypothesis other than stochasticity that might explain the distribution of this trait within the Troglodytidae. Thus there may be no answer to the titular riddle. (The riddle is why some wrens have reduced rectrices—a conundrum form of the literary device whose answer is yet to be determined.) Simple potential explanations such as tail length or habitat fail to explain 10 rectrices in this family. Newton (1896:770) commented, "Indeed, the number of Rectrices seems to have but little signification, very nearly-allied species differing in this respect." Vaurie (1971:20) wrote that "The number of tail feathers is therefore very clearly not of generic importance."

The frequency of individual variation within species is sufficiently high that rectrix variation could be considered in the context of a rare, largely neutral allele subject

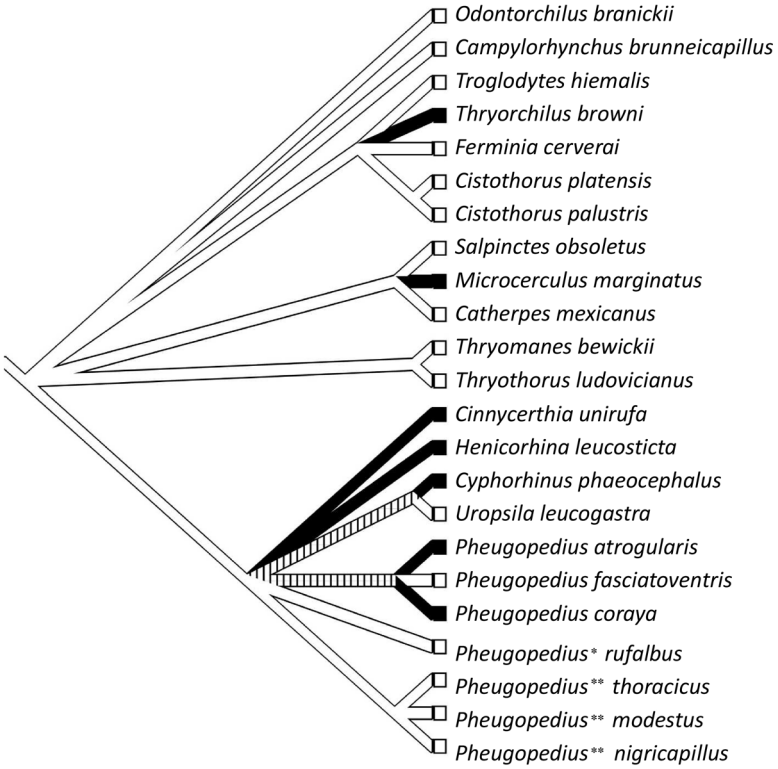

Figure 1. The distribution of 12 rectrices (white bars) and 10 rectrices (black bars) among the species of wrens examined, mapped onto the molecular phylogenetic tree of Mann et al. (2006: figure 2 and text). Uncertain ancestral conditions are indicated by barred bars. The genus *Pheugopedius* includes the subgenera *Thryophilus* (one asterisk) and *Cantorchilus* (two asterisks).

to the stochastic processes of genetic drift. For example, Hanmer (1985) reported that among ~22,800 birds sampled in Mozambique and Malawi, 126 individuals of 45 species had an abnormal number of rectrices, and he reported the frequency of abnormality within a species to range from 0.13 to 12.5%. Zwickel et al. (1991) summarized evidence for variable numbers of rectrices in nine species of North American grouse and found frequencies of intraspecific variation of 0–14%. Interestingly, in the Dusky Grouse (*Dendragapus obscurus*) these authors found rectrix number to vary with subspecies (modal values of 18 versus 20).

Across the class Aves, some of the more extreme variations on the usual 12 rectrices occur among species in which tails are used in courtship displays (Van Tyne and Berger 1976). Thus rectrix number can apparently at times be under strong sexual selection. However, it is possible that single-pair variation in rectrix number, especially in taxa that do not use their tails in courtship displays, represents effectively neutral phenotypic evolution and that stochasticity is responsible for its occurrence and distribution among lineages. This seems at present to be a reasonable null hypothesis.

NOTES

I dedicate this paper to my good friend Bob Dickerman, whose works with variation in birds (including wrens), links between science and poetry, museum specimens, and other endeavors have been an inspiration to many. Deyanira Etain Varona Graniel stimulated my examination of wren tails through her careful field work and by reporting in her *tesis profesional* at the Universidad Nacional Autónoma de México (UNAM) that *Henicorhina leucosticta* has only 10 rectrices. I thank Daniel Gibson, Philip Unitt, and an anonymous reviewer for helpful comments and staff at the U. S. National Museum of Natural History for allowing me access to their wrens. Additional material was examined from the University of Alaska Museum.

LITERATURE CITED

Audubon, J. J. 1831. Ornithological Biography: Or an Account of the Habits of the Birds of the United States of America. Judah Dobson and H. H. Porter, Philadelphia.

Hanmer, D. B. 1985. Abnormal numbers of tail feathers. Bull. Br. Ornithol. Club 105:91–95.

Mann, N. I., Barker, F. K., Graves, J. A., Dingess-Mann, K. A., and Slater, P. J. B. 2006. Molecular data delineate four genera of "*Thryothorus*" wrens. Mol. Phylogen. Evol. 40:750–759.

Melville, D. S. 1985. Further examples of abnormal rectrices and a case of an extra primary. Bull. Br. Ornithol. Club 105:95–96.

Newton, A. 1896. A Dictionary of Birds. Adam and Charles Black, London.

Nitzsch, C. L. 1867. Nitzsch's Pterlyography, translated from the German. Ray Society, London.

Somadikarta, S. 1984. Polyrectricyly. Bull. Br. Ornithol. Club 104:60–61.

Van Tyne, J., and Berger, A. J. 1976. Fundamentals of Ornithology, 2nd ed. Wiley, New York.

Vaurie, C. 1971. Classification of the Ovenbirds (Furnariidae). H. F. & G. Witherby, London.

Wells, J. E. 1907. The Owl and the Nightingale. D. C. Heath and Co., Boston.

Zwickel, F. C., Degner, M. A., McKinnon, D. T., and Boag, D. A. 1991. Sexual and subspecific variation in the numbers of rectrices of Blue Grouse. Can. J. Zool. 69:134–140.

Accepted 7 May 2012