BEHAVIOR, MORPHOLOGY, AND SYSTEMATICS OF *SIRYSTES SIBILATOR* (TYRANNIDAE)

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ABSTRACT.—Field and laboratory studies support recent hypotheses that *Sirystes sibilator* is closely allied with the myiarchine flycatchers rather than with *Tyrannus* or with the cotingids. The first confirmed nest of this tyrant (located in a natural tree cavity), its foraging behavior, and the derived character states of the nasal septum and of the syrinx argue convincingly for its placement in an assemblage with *Myiarchus, Rhytipterna,* and *Casiornis.* Data, still lacking, on the color of the eggs and nature of the nest lining are needed for *Sirystes* (and for *Rhytipterna* and *Casiornis*) before consideration can be given to the generic relationships within the myiarchine flycatchers. *Received 1 February 1982, accepted 16 July 1982.*

THE systematic position of the Sirystes (*Sirystes sibilator*), traditionally placed in its own monotypic genus, has been enigmatic for decades. Though included in the family Cotingidae by Ridgway (1907), largely on the basis of the scutellation of the tarsal envelope, *Sirystes* has been considered a tyrant flycatcher by Hellmayr (1927) and subsequent authors. Hellmayr allied it with the *Tyrannus* group, but Traylor (1977), influenced by Warter's (1965) study of the tyrannoid skull, placed it in the *Myiarchus* group. On the basis of syringeal characters, Ames (1971) was unable to place it with conviction in any of his "structural groups" of tyrannids.

This paper was prompted by Fitzpatrick's discovery of the first confirmed nest of *Sirystes,* to which description he has added behavioral observations made in recent years. Lanyon has contributed an analysis of cranial and syringeal morphology, part of a more general study of the putative relatives of *Myiarchus.*

BEHAVIOR

Sirystes is a regular but uncommon inhabitant at the Cocha Cashu Biological Station, located in the Manu National Park, dept. Madre de Dios, Peru (11°55'S, 71°18'W, elev. 380 m). It forages almost exclusively in the high canopy of the alluvial plain forest bordering the meandering Manu River (Terborgh et al. in press). Mean foraging heights for 21 independent sightings in 1976 and 1977 was 38 ± 8.5 m in a forest whose average canopy treetop is between 40 and 45 m (unpubl. data). *Sirystes* here appears to prefer primary, dry-ground forest to other, more inundated forest types, and it shows an unusual propensity for foraging in tall, emergent trees adjacent to treefalls.

Sirystes forages in a fashion virtually identical to the unusual style of *Myiarchus,* especially in its frequent use of outward and downward hovergleaning (Fitzpatrick 1980, unpubl. notes). Moreover, while searching the surrounding vegetation, *Sirystes* uses the peculiar posture typically associated only with the genus *Myiarchus.* The head is held out horizontally, stretched away from the body in more exaggerated fashion than in other flycatchers. Perhaps for this reason, the throat and crown feathers are often erected, giving the bird a large headed, "throaty" silhouette. Again in conjunction with these habits, both *Sirystes* and *Myiarchus* peer about and slowly bob the head in more deliberate fashion than any other flycatcher (except in the unrelated genus *Mionectes*). Members of the genus *Myiarchus* are among the few tyrannids that habitually "pop" the bill loudly while being held in the hand after removal from a mist-net. Although the significance of this behavior is obscure at best, it may be worthy of note that a *Sirystes* removed from a mist-net (also at Cocha Cashu) repeatedly popped its bill while being banded and photographed.

The typical daytime vocalization given during active foraging is a clear, ringing "wherpéw." During more intense calling, intrapair displaying, and dawn-singing, this frequently is lengthened into "wher-pe-pep-pep-pew-pew

Fig. 1. View from ground of *Sirystes sibilator* nest site (white arrow near center) in emergent *Calicophyllum* tree, well above nearby forest canopy (dark vegetation to lower right and upper left). Note unusually open surroundings at nest height amidst several old treefall openings.

. . . pew." On the morning of 2 October 1981, incessant repetitions of this latter song, in an area known even in previous years to be frequented by a pair of *Sirystes*, attracted JWF's attention to two birds high in a 45-m *Calicophyllum spruceanum* tree (Rubiaceae) adjacent to a slightly overgrown treefall clearing (Fig. 1). Both birds were bobbing and flitting excitedly from perch to perch with their slightly elongated crown feathers raised into vague "crests." One bird was carrying in its bill a large wad of dark material, apparently insects. Several minutes later, the bird carrying prey disappeared into a hole along a major limb high in the tree. It remained out of sight about 1 min, then flew back out, sat briefly a few meters above the hole, then flew off to forage elsewhere. From 0755 to 0941 a total of 12 such nest visits occurred, the intervals between visits averaging 8.6 min (shortest interval 1 min, longest 16 min). Both birds visited the nest with food, frequently calling loudly together in the nest tree. They appeared to be foraging up to 200 m from the nest tree, although they almost invariably continued to sally after prey items high in the nest tree itself, even while carrying large boluses of food. Twice, the birds returned simultaneously to the nest tree; one waited perched on twigs outside the hole, while the other entered and exited. Nest visits varied from just a few seconds up to about 1 min. One fecal sac removal was observed.

The nest site was determined through telephoto lenses to be about 32 m above the ground. In comparison with the birds' body sizes the hole appeared to be at least 15 cm wide, perhaps larger. It was at the base of a nearly perpendicular "elbow" in the tree limb, with the hole running roughly horizontally into the main branch. An old break had rotted out to create the cavity, and it left a 6- to 8-cm long lip rimming the lower edge of the hole. The depth of the hole, penetrating horizontally into the limb, could not be determined, nor could any features of nest construction or contents be seen. *Calicophyllum* trees are known locally as "Palo Calato" ("naked pole") because of their extraordinarily smooth, seemingly barkless appearance (Fig. 1). This makes the trunk and limbs extremely slippery and difficult to climb, presumably for predators as well as for humans.

Judging from the frequency of nest visits and the large size of the food boluses brought in on 2 October, the nest must have contained well-developed nestlings. Fitzpatrick left the study site the following day, but N. Pierpont reported nest visits by both birds on 3, 4, and 5 October. Thereafter, no further activity was observed at the nest. Early on 6 October, at least two *Sirystes* were heard actively calling about 100 m from the nest. They did not come near the nest tree during a 20-min observation period there (1450–1510) nor on two subsequent days. Assuming the nestlings fledged successfully, they apparently did so on 5 or 6 October.

The only previous, published information on the nesting habits of *Sirystes* is Wetmore's (1972: 436) reference to birds in Panama "occasionally examining cavities in tree trunks."

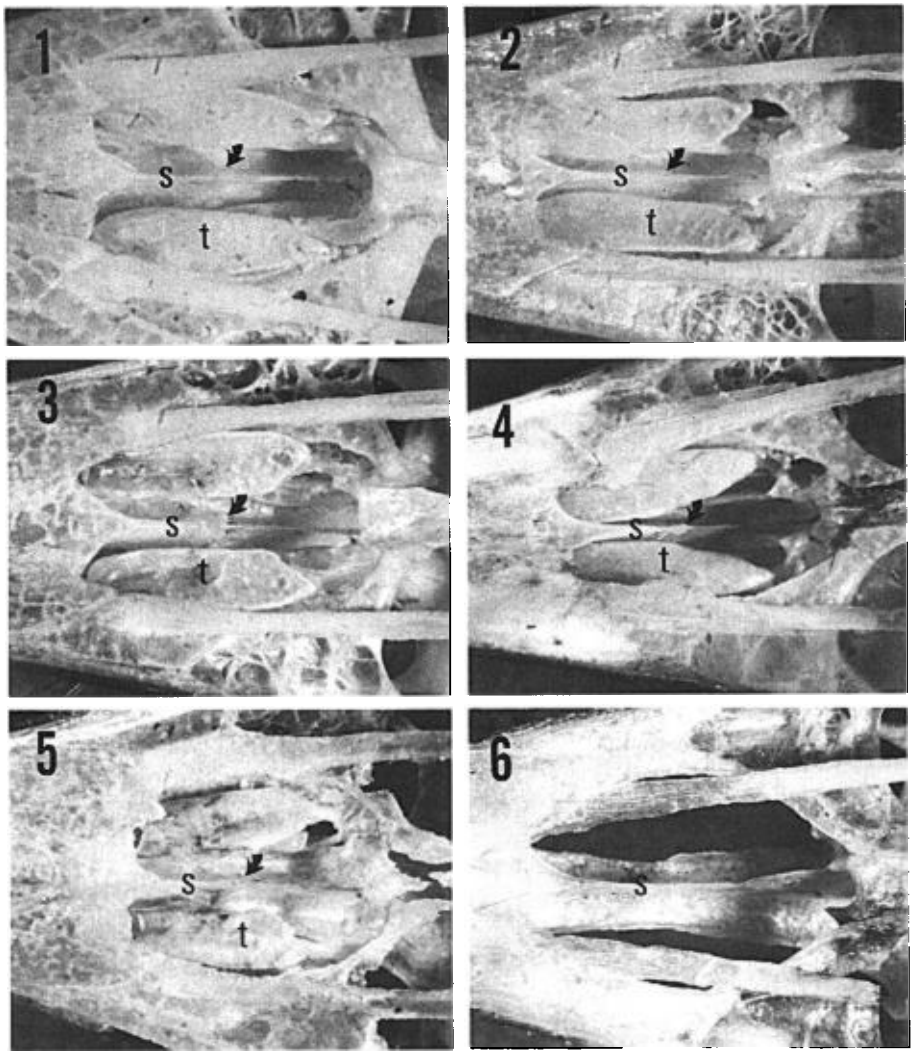

Fig. 2. Photographs, taken through a dissecting microscope, of the ventral aspect of the nasal region of the skulls of some tyrannine flycatchers (anterior end of the skull to the left): 1. *Sirystes sibilator* (USNM 347723); 2. *Myiarchus tuberculifer* (AMNH 7175); 3. *M. cephalotes* (AMNH 9248); 4. *Rhytipterna immunda* (AMNH 11617); 5. *Deltarhynchus flammulatus* (AMNH 11391); 6. *Attila cinnamomeus* (AMNH 11615). Arrows indicate the internal supporting rod present in all skulls except that of *Attila*; the knife-like ventral edge of the ossified nasal septum, s, lacks a trabecular plate; ossification of the nasal capsule includes the alinasal turbinals, t, in all skulls except that of *Attila*. All specimens magnified 16×.

MORPHOLOGY

Sirystes differs from most *Myiarchus* in possessing a complete suture along the outer edge of the tarsus as well as the usual full inner suture (i.e. tarsus holaspidean, not exaspidean). This arrangement of the tarsal envelope was the principal basis for Ridgway's (1907) placement of *Sirystes* in the Cotingidae, but Ridgway admitted that "the bill [of *Sirystes*] is typically tyrannine, resembling closely that of *Tyrannus* and the stouter billed *Myiarchi*." The striking black-and-white plumage pattern of *Sirystes*, with diffuse olive dorsal streaks, also differs from the familiar and remarkably uni-

form plumage pattern of most *Myiarchus*. The rectrices and wing coverts of the juvenal plumage of *Sirystes* are fringed with Antique Brown (Smithe 1975), though this color is lacking in the adult plumage. This is a pattern characteristic of all species of *Myiarchus*, including those species in which Antique Brown is lacking in the adults.

Recent anatomical studies involving the skull (Warter 1965) and the syrinx (Ames 1971) have indicated the effectiveness of these structures in determining relationships within the suboscines. Two complexes in particular have already proven useful in diagnosing *Myiarchus* flycatchers and their relatives: (1) the nasal septum, and specifically the degree to which there is ossification and buttressing with internal supporting structures, and (2) the number, shape, and position of the internal cartilages of the syrinx (Lanyon 1982).

The nasal capsule of *Sirystes* (Fig. 2, number 1) is typically tyrannine (as defined by Traylor 1977), in that the nasal septum is well-developed (ossified) but lacks a trabecular plate along the ventral edge. The nasal septum is buttressed by a well-developed internal supporting rod, identified with an arrow in Fig. 2. This derived state of the nasal septum, found in *Sirystes*, is shared with *Myiarchus* (20 of the 22 species; two still unavailable), *Rhytipterna* (all three species), *Casiornis* (both species), and *Deltarhynchus* and is not found in any of the remaining genera placed in the Tyranninae by Traylor (Lanyon 1982, unpubl. notes). Note the lack of an internal supporting rod in the nasal septum of *Attila* (Fig. 2, number 6).

Sirystes shares a suite of syringeal characters with *Myiarchus* (15 species examined thus far), *Rhytipterna* (all three species), and *Casiornis* (both species examined) that sets these genera apart from all other tyrannids (Lanyon 1982, unpubl. notes). In these four genera there are two pairs of cartilages that lie within the internal tympaniform membranes: (1) a large, dorsal pair, which are J- or L-shaped and are connected anteriorly to the ventral segment of the tracheo-bronchial junction (with no connection to the dorsal ends of the A-2 semirings), and (2) a much smaller, ventral pair, of variable shape and located within the membranous connections that extend between the posterior ends of the large cartilages and the ventral ends of the B-2 bronchial semirings. In Fig. 3 we compare the number, shape, and location of these internal cartilages as seen in *Sirystes*, in three other myiarchine flycatchers (*Myiarchus ferox, M. oberi*, and *Rhytipterna holerythra*), and in two other tyrannines (*Deltarhynchus flammulatus* and *Attila cinnamomeus*).

The large cartilages are J-shaped in *Sirystes* and the other myiarchine flycatchers, and their anterior ends are connected to the ventral segment of the tracheo-bronchial junction, at some distance from the dorsal ends of the A-2 semirings. The large cartilages do not have this characteristic shape in *Deltarhynchus* and *Attila*, where they can be seen to connect to the dorsal segment of the tracheo-bronchial junction and the dorsal ends of the A-2 semirings. The smaller, ventral pair of cartilages is lacking in the syrinx of *Deltarhynchus*.

The method of dissection and terminology follow Ames (1971).

Discussion

The behavioral features described above, even down to the quality of the song, once confused no less capable a field ornithologist than the late Paul Schwartz with regard to birds that he had recorded but not collected along the Rio Masparro, Barinas, Venezuela. The recordings had been deposited with the Library of Natural Sounds at Cornell University's Laboratory of Ornithology and filed as "*Myiarchus ferox*," but Lanyon wrote Schwartz that they could not have been made from any species presently regarded as *Myiarchus*. Six months later Schwartz replied: "The birds from the Rio Masparro I've now definitely identified as *Sirystes sibilator*. I feel embarrassed, but not terribly so. If you already know the bird or if you some day experience it I'm sure you'll know what I mean. In size, shape, attitudes and actions this bird is extremely *Myiarchus*-like rather than like the group with which it is presumed to be related [the *Tyrannus* group] . . . . I recently encountered the bird again down near Burgua, alerted by the voice. Here again I was convinced they were *Myiarchus* for the same reasons, until with playback I finally got them to where the sun was at my back and they were against a foliage background. . . . I collected one just as a clincher." Schwartz's field experience, though anecdotal and unconvincing by itself, was of sufficient importance to alert both of us to the need for further information about this species.

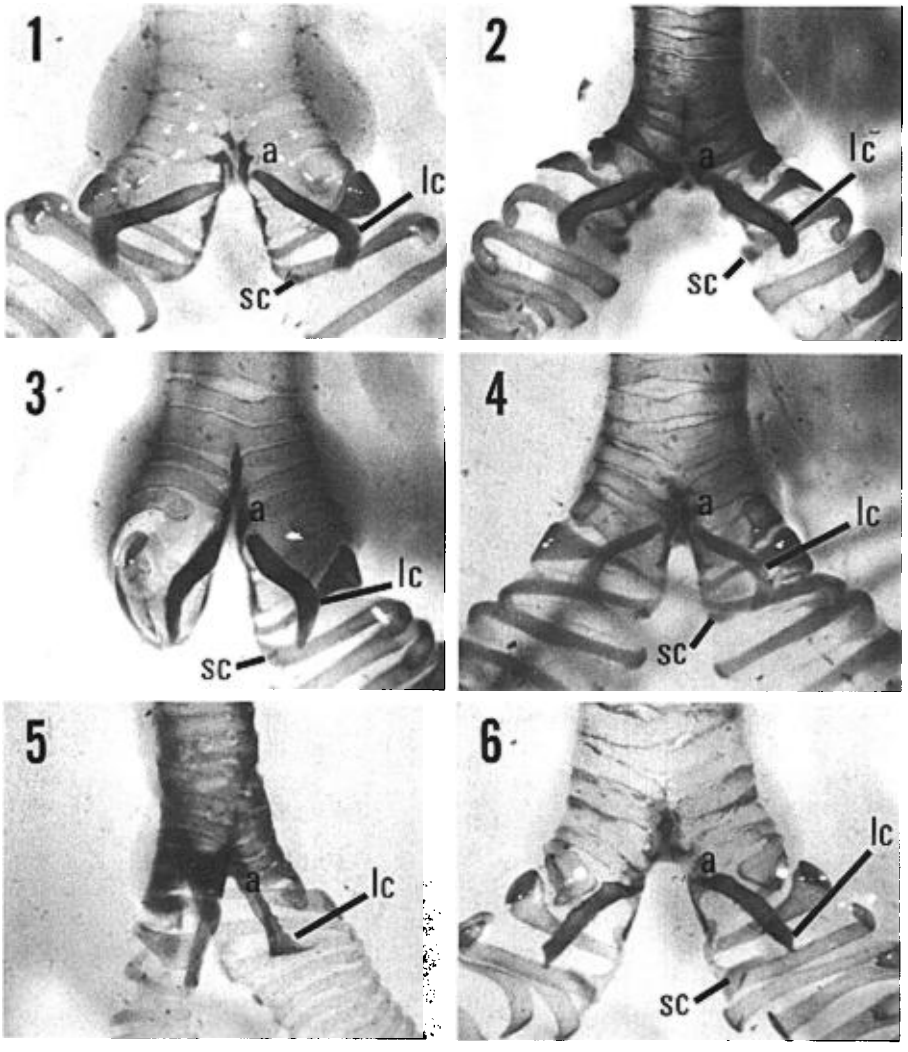

Fig. 3. Photographs, taken through a dissecting microscope, of the dorsal aspect of the syringes of some tyrannine flycatchers: 1. *Sirystes sibilator* (YPM 2791); 2. *Myiarchus ferox* (AMNH 8112); 3. *M. oberi* (AMNH 6677); 4. *Rhytipterna holerythra* (AMNH 8260); 5. *Deltarhynchus flammulatus* (AMNH 8128); 6. *Attila cinnamomeus* (AMNH 8126). Large cartilages, lc; small cartilages, sc; dorsal end of A-2 semirings, a. All specimens magnified 19×.

Cavity-nesting is a rare and almost certainly derived condition in the Tyrannidae, being most prevalent in the genus *Myiarchus* and its close relatives (Lanyon 1978, 1982). *Casiornis* has been reported to be a cavity nester, but the eggs and nest lining have not been described (*fide* Helmut Sick pers. comm.). The nesting habits of the three species of *Rhytipterna* are still unknown, but, on the basis of derived morphological and behavioral characters shared with *Myiarchus*, one would hypothesize that they too are cavity-nesters and have eggs like those of *Myiarchus*. That *Sirystes* is now known to be a cavity-nester lends support to the hypothesis (Traylor 1977, Lanyon 1982) that *Sirystes* is a close relative of *Myiarchus*.

The nest lining of *Myiarchus* is unique among the 12 genera of tyrants in which nesting in tree cavities has been reported, bearing in mind that we still lack complete data for

Rhytipterna, Casiornis, and *Sirystes.* Invariably, the lining consists of quantities of fur and feathers, in addition to vegetable fibers, and frequently there are fragments of shed reptilian skin or plastic and paper substitutes (Lanyon 1978, unpubl. notes). These unique contents of the nest lining form an important part of the generic diagnosis of *Myiarchus,* for they help to embrace three of the more "aberrant" species formerly placed in monotypic genera: *semirufus, validus,* and *magnirostris.* Because no details could be obtained regarding the nest lining or the color pattern of the eggs in the single nest record reported here, the generic relationship of *Sirystes* and *Myiarchus* remains uncertain. Indeed, on its own, the cavity-nesting behavior of *Sirystes* could be a simple case of convergence, as it most certainly is in the case of *Colonia* (subfamily Fluvicolinae).

The scutellation of the tarsal envelope, once given considerable weight in the classification of the suboscines, has been shown to be more variable within genera and families than even Ridgway (1907: 328–329, 336) would admit, and several workers have cautioned against placing undue reliance on this character (Lanyon 1967, Ames et al. 1968, Snow 1973, Zimmer unpubl. notes). We are reminded that *Myiarchus validus* was at one time placed in a monotypic genus and transferred to the Cotingidae because the tarsal envelope was nonexaspidean (Ridgway 1906). Indeed, the suggestion by Warter (1965) and Ames (1971) that *Rhytipterna, Casiornis,* and *Attila* be transferred from the Cotingidae to the Tyrannidae has been followed for Peters' Checklist (Snow 1973, Traylor 1977), even though the tarsal scutellation of these genera is nonexaspidean.

Virtually every feature of the plumage color and pattern of *Sirystes* can be found within the genus *Myiarchus*: the dark cap and contrasting pale back characterizes the Andean populations of *tuberculifer,* the pale-tipped rectrices are found in *apicalis,* and the gray and white underparts distinguish *sagrae* and *antillarum.* Even the white rump patch and extensive white in the wings, so conspicuous in northern *Sirystes,* virtually disappear in the southernmost populations of the species. With full cognizance of the range of variation within the 22 species of *Myiarchus,* it becomes difficult to argue against merger of *Sirystes* and *Myiarchus* on the basis of plumage color and pattern.

Ames (1971) concluded that "the syrinx of *Sirystes* is typically tyrannid in cartilages and musculature with little similarity to the simple syringes of the Cotingidae," but questioned Hellmayr's (1927) placement of the species with the *Tyrannus* group, because it lacks almost all of the syringeal features of that assemblage. Lanyon agrees with Ames on both of these points but has difficulty reconciling Ames' failure to recognize the syrinx of *Sirystes* as typically myiarchine. The single specimen initially available to Lanyon agrees in all respects with the syringes of *Myiarchus, Rhytipterna,* and *Casiornis;* it could not with certainty be separated from a series of syringes taken from those three genera. Ames did not stain his specimens for bone and cartilage and consequently may have overlooked some of the critical myiarchine characters. He kindly loaned his two specimens of *Sirystes* to Lanyon and gave permission for them to be stained with alcian blue and alizarin red (after Dingerkus and Uhler 1977). These two specimens were found to share the same derived complex of syringeal characters that distinguishes the myiarchine assemblage from all other tyrannids.

Although we believe the affinities of *Sirystes* with the myiarchine group of tyrannines to be unequivocal now, we recommend caution in any revisionary consideration of the generic relationships among *Sirystes, Myiarchus, Rhytipterna,* and *Casiornis.* Descriptions of the color and markings of the eggs and of the nature of the nest lining, still lacking for all but *Myiarchus,* are needed before we can adequately address the problem of generic limits and devise a meaningful phylogeny for this group.

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