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NESTING, BEHAVIOR, DISTRIBUTION, AND SPECIATION OF PATAGONIAN AND ANDEAN GROUND TYRANTS (*MYIOTHERETES*, *XOLMIS*, *NEOXOLMIS*, *AGRIORNIS*, AND *MUSCISAXICOLA*)

François Vuilleumier

Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street,
New York, NY 10024, U.S.A.

Resumen. La biología, distribución y evolución de los tiránidos de monte o terrestres (Tyrannidae, subfamilia Fluvicolinae) es todavía poco conocida. Nidos de cuatro especies patagónicas (*Xolmis pyrope*, *Neoxolmis rubetra*, *Neoxolmis rufiventris*, y *Muscisaxicola capistrata*) fueron estudiados durante expediciones a la Patagonia en 1988 y 1992 y nidos de dos especies altoandinas (*Myiotheretes rufipennis* y *Agriornis andicola*) fueron observados durante una expedición al Perú en 1975. Los nidos de *Neoxolmis rubetra* y de *Agriornis andicola* son aparentemente los primeros señalados para estas dos especies, y aquellos de *Neoxolmis rufiventris* y *Myiotheretes rufipennis* los segundos para estas especies. Los nidos de *Xolmis pyrope* y *Muscisaxicola capistrata* demuestran la nidificación de la primera especie en matorral patagónico fuera del bosque de *Nothofagus* (Fagaceae), y confirman la nidificación de la segunda en el norte de la Patagonia. Estos datos sobre nidificación son ampliados con observaciones de terreno sobre la conducta, los biotopos, la abundancia relativa y la distribución geográfica de estas seis especies. Además, se analiza de manera comparativa aspectos del comportamiento, de la biogeografía y de la evolución presentados por tiránidos terrestres en los géneros *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Muscisaxicola*, y *Agriornis*. Se discute especialmente patrones de simpatria, alopatría, y parapatria, y de aislamiento reproductivo. La especiación en este grupo de tiránidos se analiza en términos de tres modos de especiación: peripátrico, dichopátrico, y parapátrico. Los fluvicolinos son muy bien representados en varios biotopos de puna y estepa andino-patagónicos, donde constituyen un alto porcentaje de esas faunas, y donde presentan fenómenos de radiación adaptiva. Por esas razones, estos tiránidos merecen amplio análisis, para facilitar el cual se sugieren muchas cuestiones para estudios futuros.

Abstract. The biology, distribution, and evolution of the bush and ground tyrants (Tyrannidae, subfamily Fluvicolinae) remains poorly known. Nests of four Patagonian species (*Xolmis pyrope*, *Neoxolmis rubetra*, *Neoxolmis rufiventris*, and *Muscisaxicola capistrata*) were studied during expeditions to Patagonia in 1988 and 1992 and nests of two high Andean species (*Myiotheretes rufipennis* and *Agriornis andicola*) were observed during an expedition to Perú in 1975. Apparently these are the first reported nests of *Neoxolmis rubetra* and of *Agriornis andicola*, and only the second of *Myiotheretes rufipennis* and of *Neoxolmis rufiventris*. The nesting records of *Xolmis pyrope* and *Muscisaxicola capistrata* show that the first species lives in Patagonian matorral away from *Nothofagus* (Fagaceae) forest, and confirm that the second breeds in northern Patagonia. Besides data on nesting, detailed field observations on behavior, habitat preferences, relative abundance and geographic distribution of these six species are also given. Comparative aspects of the behavior, biogeography, and speciation of bush and ground tyrants of the genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola* are reviewed. Particular attention is paid to patterns of sympatry, parapatry, allopatry, and reproductive isolation, in order to describe and analyze the occurrence of three modes of speciation: peripatric, dichopatric, and parapatric. Fluvicoline flycatchers constitute an important component of Patagonian steppe and high Andean puna habitats, where they make up a high percentage of these faunas and where they show adaptive radiation. For these reasons, these flycatchers deserve further study. To facilitate future work a number of general as well as specific questions are presented. Accepted 11 July 1993.

Key words: *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, *Muscisaxicola*, *Tyrannidae*, *Patagonia*, *Andes*, *nesting*, *behavior*, *distribution*, *speciation*.

INTRODUCTION

Among the bush and ground tyrants discussed by Smith & Vuilleumier (1971), the genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola* collectively show impressive radiations, components of which include parallel patterns of sympatry, parapatry, and allopatry in the high Andes and in Patagonia (Vuilleumier 1971: 203–230), and congruent speciation patterns in the arid diagonal of Brazil and Argentina (Fitzpatrick 1980: 1277–1278). These five genera (listed above according to the sequence and nomenclature of Traylor 1979) belong to what Traylor (1977: 159–166; 1979: 112–186) diagnosed as the subfamily Fluvicolinae, and to what Lanyon (1986: 42–52) called the “*Muscisaxicola* Group.”

Unfortunately, lack of comparative information on many species in the monophyletic assemblage of 31 species in five genera (*sensu* Traylor 1979) that make up the main part of Lanyon’s *Muscisaxicola* Group (including even basic data on breeding biology, behavior, habitat preferences, and geographic distribution) impedes a clear understanding of their phylogenetic relationships and, consequently, of their evolution. To help remedy some of these deficiencies, I report herein new field information, review and synthesize old and recent evidence, and offer speculations designed to fill gaps and to stimulate further research. Because Tyrannidae in general, and bush and ground tyrants of the subfamily Fluvicolinae in particular, are often, together with Furnariidae and Emberizidae, numerically and ecologically dominant among the passerine component of high Andean and Patagonian avifaunas (Vuilleumier 1986: 591–592, 1993, 1994), intensive study of their evolutionary relationships should figure prominently in analyses of Andean-Patagonian biogeography.

During expeditions to Patagonia (5 February – 3 April 1965, 1 November – 13 December 1985, 7 February – 4 March 1987, 1 – 30 October 1987, 15 – 22 January 1988, 2 – 30 November 1988, 5 – 18 November 1991, and 18 October – 15 November 1992) as part of a research program on speciation and evolution in Patagonian birds (Vuilleumier 1985, 1991a, 1991b, 1993), and during expeditions to the Andes of northern

Perú (18 October – 9 December 1975), and of Bolivia (8 October 1967 – 30 January 1968), as part of a research program on the origins of high Andean birds (Vuilleumier & Simberloff 1980, Vuilleumier 1986, 1994), I found nests of, and made other observations on, six species of bush and ground tyrants (*Myiotheretes rufipennis*, *Xolmis pyrope*, *Neoxolmis rubetra*, *Neoxolmis rufiventris*, *Agriornis andicola*, and *Muscisaxicola capistrata*), for which biological and distributional information is scanty (Johnson 1967: 234, 251–252, 264–266; Humphrey *et al.* 1970: 268–270, 271–272; Venegas & Jory 1979: 157–158, 159–160; Clark 1986: 230, 234, 236; Fjeldså & Krabbe 1990: 502–504, 509–510).

For each of these six species, after a review of its systematic position, I describe these nesting observations and report data on behavior, relative abundance, habitat preferences, and geographic distribution. I then discuss comparative aspects of the behavior and biogeography of all bush and ground tyrants in the genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*; analyze their patterns of sympatry, parapatry, and allopatry; and, finally, review speciation patterns in terms of various modes of species formation and of reproductive isolating mechanisms.

Localities mentioned in this paper are shown in Figures 1 (southern South America), 2 (Fuego-Patagonia), 3 (parts of the Andes of Perú), and 4 (Bolivia). The spelling of collecting localities and other geographic names in Figs. 1–4 follows the ornithological gazetteers for Perú (Stephens & Traylor 1983), Bolivia (Paynter 1992), Chile (Paynter 1988), and Argentina (Paynter 1985). In a few instances, however, I have followed what seems to be current or local usage. For example, the well known collecting locality “Huanuluan” in Río Negro, Argentina (e.g., Peters 1923: 276, Wetmore 1926b: 402) is spelled “HUANULUAN” by Paynter (1985: 131). The present owner of this ranch, Mr. J. A. Chuburu, spells it “Huanuluán” and I have retained this spelling in Figure 1.

SPECIES ACCOUNTS

The order, sequence, and nomenclature of species in this section follow the classification proposed by Traylor (1979) in Peters’ check-list.

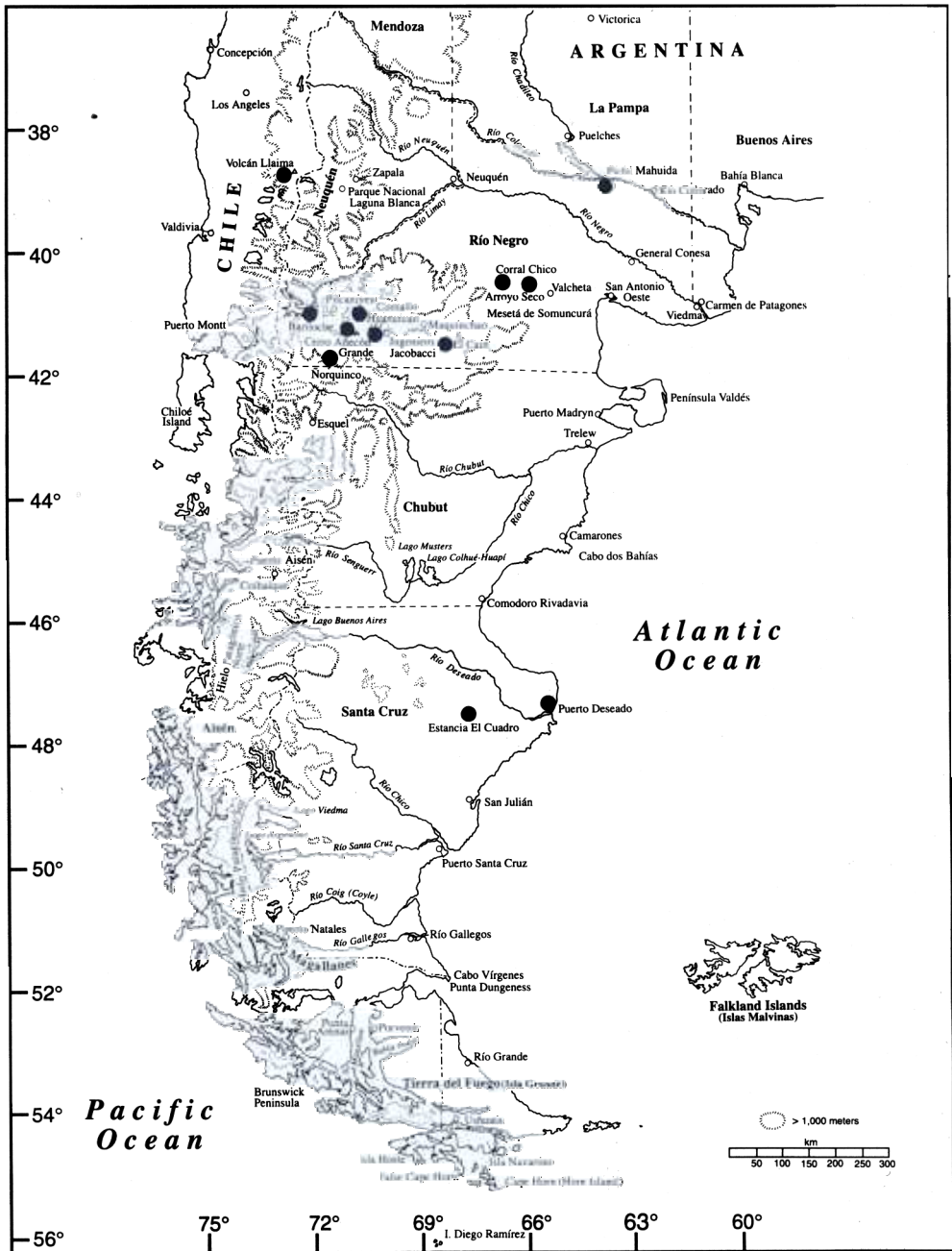


FIG. 1. Schematic map of Patagonia showing collecting localities and study sites mentioned in the text (black dots), except for those in Fuego-Patagonia, illustrated in Fig. 2.

Myiotheretes rufipennis (Taczanowski 1874)

Systematic position

Myiotheretes rufipennis, originally described in *Muscisaxicola* by Taczanowski 1874, was included by Hellmayr (1927: 38) in the genus *Cnemarchus* of Ridgway (1905: 208, for *Taenioptera erythropygia*). Meyer de Schauensee (1966: 335) and Vuilleumier (1971: 195) later put *rufipennis* in *Xolmis*, but recently Lanyon (1986: 49) erected a new, monotypic genus *Polioxolmis* for *rufipennis*, largely on the basis of differences in syringeal morphology. In their book on Andean-Patagonian birds, Fjeldså & Krabbe (1990: 499–500) included *rufipennis* in *Polioxolmis* (see also Fjeldså 1990: 26). Here I follow Traylor's (1977, 1979) treatment, which I feel better expresses the relationships of *rufipennis* than does its inclusion in a monotypic genus.

Nesting behavior

Fjeldså (1990: 27) described a nest of *Polioxolmis* [= *Myiotheretes*] *rufipennis* with two fledglings

found 15 February 1987 (in Perú?, Bolivia?) as "a rather flimsy and open cup of stalks and thin twigs placed just below the top of a 5 m-tall [*Polylepsis*, Rosaceae] tree overhanging [a] stream." However, information on nesting remains scanty (Fjeldså & Krabbe 1990: 500). For example, in his classification of nests of birds in the Peruvian puna, Venero (1990: 5) only briefly described the nest of *Xolmis* [= *Myiotheretes*] *rufipennis* ("on trees, made of twigs, fibers and feathers") without mentioning the species of trees on which it was found.

In 1975 I found two nests of this species in two different stands of the giant bromeliad *Puya Raimondii* Harms, 1928 (Bromeliaceae) in Ancash, northern Perú, in the Cordillera Blanca. The first nest was found on 28 October 1975 in an open stand of *Puya Raimondii*, at 4050 m at Carpa (Vuilleumier & Simberloff 1980: 363). The nest was placed among the hooked leaves below the top of an old *Puya* plant lacking a flowering stalk, about 2.5 m above the ground

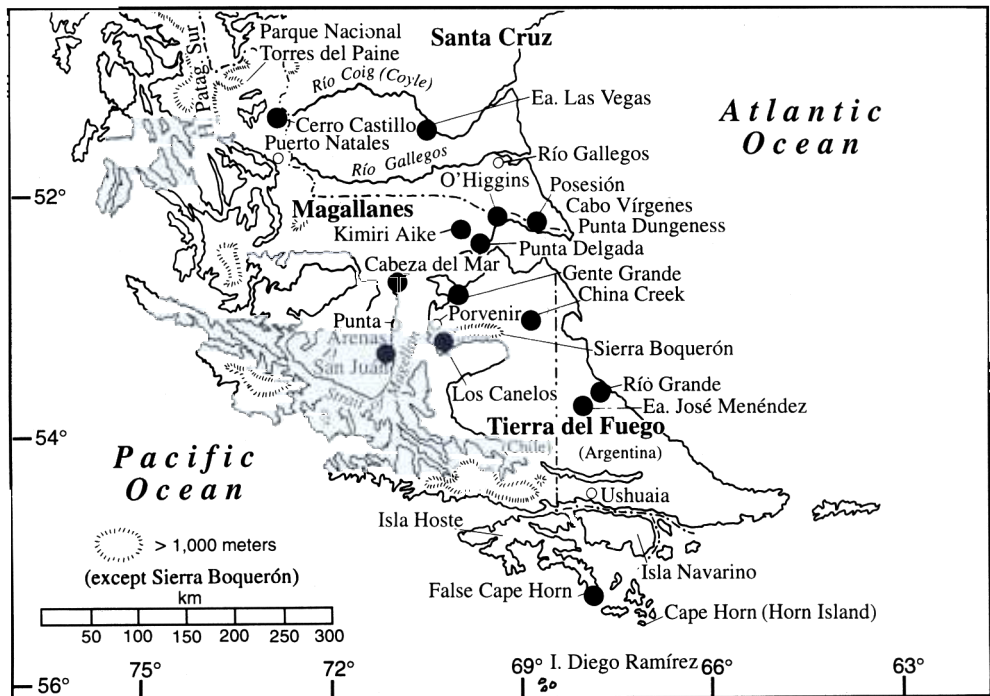


FIG. 2. Schematic map of Fuego-Patagonia showing localities and study sites mentioned in the text (black dots), but not shown in Fig. 1.

(Fig. 5). Both parents fed the two young in the nest frequently. The nest was an open cup, 27 cm in diameter and 16 cm high, rather coarsely built of twigs, grass stems, and pieces of fibrous material from *Puya*. The cup was lined with feathers of *Myiotheretes rufipennis* and of *Colaptes rupicola*. The two young were ready to fledge and flew off when I inspected the nest. Their feathers and down were pale gray and their gape yellow orange.

The second nest was discovered 31 October 1975 at the edge of a dense stand of *Puya Raimondii* at 4080 at Queshque (Vuilleumier & Simberloff 1980: 363). This nest, like the first one, was an open cup made of twigs and was placed among the hooked dry leaves near the top of an old *Puya* plant lacking a flowering stalk, 2.8 m above the ground (Fig. 6). The second nest also contained two young with pale gray feathers and down that were nearly ready to fledge. They were fed at frequent intervals by their parents.

A third stand of *Puya Raimondii* visited in 1975 at Cajamarquilla at 4050 m in the Cordillera Negra (Vuilleumier & Simberloff 1980: 363), had a population of *Myiotheretes rufipennis* (flock of 8 birds observed 6–7 November 1975), but they did not seem to be breeding at the time. One specimen collected from this flock (AMNH 4658, spirit specimen) was a male with small testes, no brood patch, weight 38.0 g, bill and legs black, eyes pale pinkish brown, and gape whitish gray; skull not fully ossified (small unossified window in the occipital).

Display behavior and relative abundance

In an earlier paper (Vuilleumier 1969: 604–605) I had briefly described the behavior of *Myiotheretes rufipennis* in Bolivia. Fjeldså (1990: 28) and Fjeldså & Krabbe (1990: 500) also briefly described the behavior of this species. Because so little is known about this species, I give below a more complete description of my observations in Bolivia in 1967 as well as my observations in Perú in 1975.

In Bolivia, I almost always saw birds perched on the top of *Polylepis* trees or shrubs, where their characteristic upright silhouette reminded me of *Muscisaxicola* spp. From time to time, they would fly rapidly down to the ground where they had presumably found some prey. Unfortunately, because the ground was covered

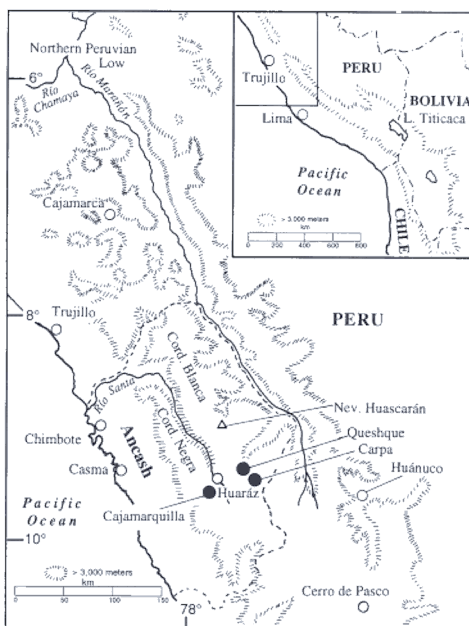


FIG. 3. Schematic map of the Andes of northern Perú showing collecting localities and study sites (black dots) mentioned in the text.

with tussock grass and tola shrubs, I did not actually see them catch prey. Occasionally, while perched, they emitted soft, slightly raspy monosyllabic whistles (transcribed as *tiu*, *tsiup*, *thup* or *tju*) that reminded me of the call notes of *Xolmis pyrope* (see later).

In the early afternoons, a rather strong wind started to blow up from the bottom of the quebrada toward the ridge top, creating a strong updraft, and I observed their hovering display flights. At first one bird, then a second, would take part, flying not close to each other. Each bird would fly up with long and leisurely wing strokes from its perch on a *Polylepis* tree to about 10 to 12 m above the ground, then it would face the wind and spread out both its wings and its tail, thus conspicuously displaying the rufous of its wing and tail feathers. Then the bird would hover with rather irregular, more or less rapid up and down strokes, with its legs dangling. At times the bird would switch from hovering to simply gliding with its wings and tail partly spread out and would remain immobile in the air

current, with little or no movement relative to the ground. After several seconds of hovering and/or immobile gliding, the bird would fly off with deep wing strokes, carried by the wind several meters away from the quebrada, and then it would fly back to the updraft to begin the hovering/gliding display again. This behavior was seen at two different sites, one near Nevado Sajama, Province Oruro, altitude 4250 m, and the second at Mina Isca-Isca north of Tupiza, Province Potosí, 4160 m (Fig. 1). One of the birds seen at the foot of Nevado Sajama was collected (AMNH 793163). It was a male with enlarged gonads, skull fully ossified, weight 34.5 g. No other displaying bird was collected and so I cannot state whether only males display in this fashion. In stands of *Puya Raimondii* in Perú in 1975, I did not see *M. rufipennis* perform hovering/gliding displays in the two sites in the Cordillera Blanca where I found the species nesting or the one site in the Cordillera Negra where it did not appear to nest.

Whereas Fjeldså & Krabbe (1990: 500) stated that this hovering/gliding display permits the birds to see prey on the ground, I only saw them fly down to catch prey from a perch, not during a session of hovering or gliding. These striking hovering/gliding displays were not similar to flight displays I saw performed by individuals of *Muscisaxicola* spp., in which the birds flew actively with rather deep wing strokes, describing a rather broad circle high up in the air (Aerial Displays in Smith 1971). However, Smith (1971: 246) described an Aerial Display of an individual *Muscisaxicola albilora* in which the bird “often simply hovered, sometimes climbed higher, and frequently turned to a new direction, remaining over a limited area”, much as in *Myiotheretes rufipennis*. Sick (1988: 585) described for *Xolmis cinerea* what may be a display similar to that in *M. rufipennis*: “Flies with great skill, frequently with legs dangling, with the digits clenched like a fist, reminding one of a bird of prey like *Elanus*” (translated by F. V. from Portuguese; see also Sick 1993: 473). Thus, the hovering/gliding display of *M. rufipennis* is probably related to the Aerial Display shown by other fluvicoline flycatchers (Smith 1971). Whether or not the hovering/gliding display of *M. rufipennis* is “probably derived from the aerial display seen in related genera (e.g., *Muscisaxicola*

and *Knipolegus*)” (Fjeldså & Krabbe 1990: 500; italics mine) remains to be verified by further comparative studies.

At Mina Isca-Isca (Bolivia) a pair of *Myiotheretes rufipennis* was seen at 4000 m in a *Polylepis* woodland aggressively and rapidly pursuing one individual *Agriornis andicola*, which could have attempted to rob their nest (although I failed to find a nest). While mobbing *A. andicola*, the two *M. rufipennis* gave rather loud yapping calls, quite different in pitch and in tone from the soft calls I normally heard from this species. I did not hear such yapping calls from *M. rufipennis* elsewhere. I also saw the birds of this pair do some single-wing lifting in a manner quite reminiscent of that of *Muscisaxicola* spp. (Wing Raising display, Smith 1971: Figs. 3a and 3c, page 245). Note that in his review of fluvicoline display behavior Smith (1971: 255–257) did not describe either Wing Raising or Aerial Displays in *Myiotheretes* spp., and only a probable Wing Raising in *Xolmis pyrope* and a probable Aerial Display in *Neoxolmis rubetra*. The wing raising Smith observed in *X. pyrope* was “probably a display similar to the Wing Raising of *Muscisaxicola* species” (Smith 1971: 256). The display in *Neoxolmis rubetra* “may be similar to flight displays in *Knipolegus* and related genera” (Smith 1971: 257).

Relative abundance

On the basis of my experience in Perú and Bolivia, I would judge that *M. rufipennis* is relatively rare and localized. In Perú, I saw only one pair (with nest) at Carpa at about 4050 m, but three to four pairs at Queshque between 4050 and 4170 m (both sites in the Cordillera Blanca) and about eight birds at Cajamarquilla at 4050 m (in the Cordillera Negra). One of the eight birds at Cajamarquilla was collected (AMNH 4658, see above). In Bolivia, in the Nevado Sajama area (Oruro) at about 4250 m, I saw about five birds in total; in the Mina Isca-Isca area (Potosí) between 4000 and 4200 m, I saw two pairs; and above Pongo near Quime (La Paz) at 3800 m I saw only one bird. (Note that this Pongo, near Quime, which I visited on 9 January 1968, is not the same as “Pongo”, near La Paz City, cited in Paynter 1992: 107, that I visited on 28 October 1967.)

Habitat preferences and geographic distribution Fjeldså (1990: 27) noted the species in *Polylepis*

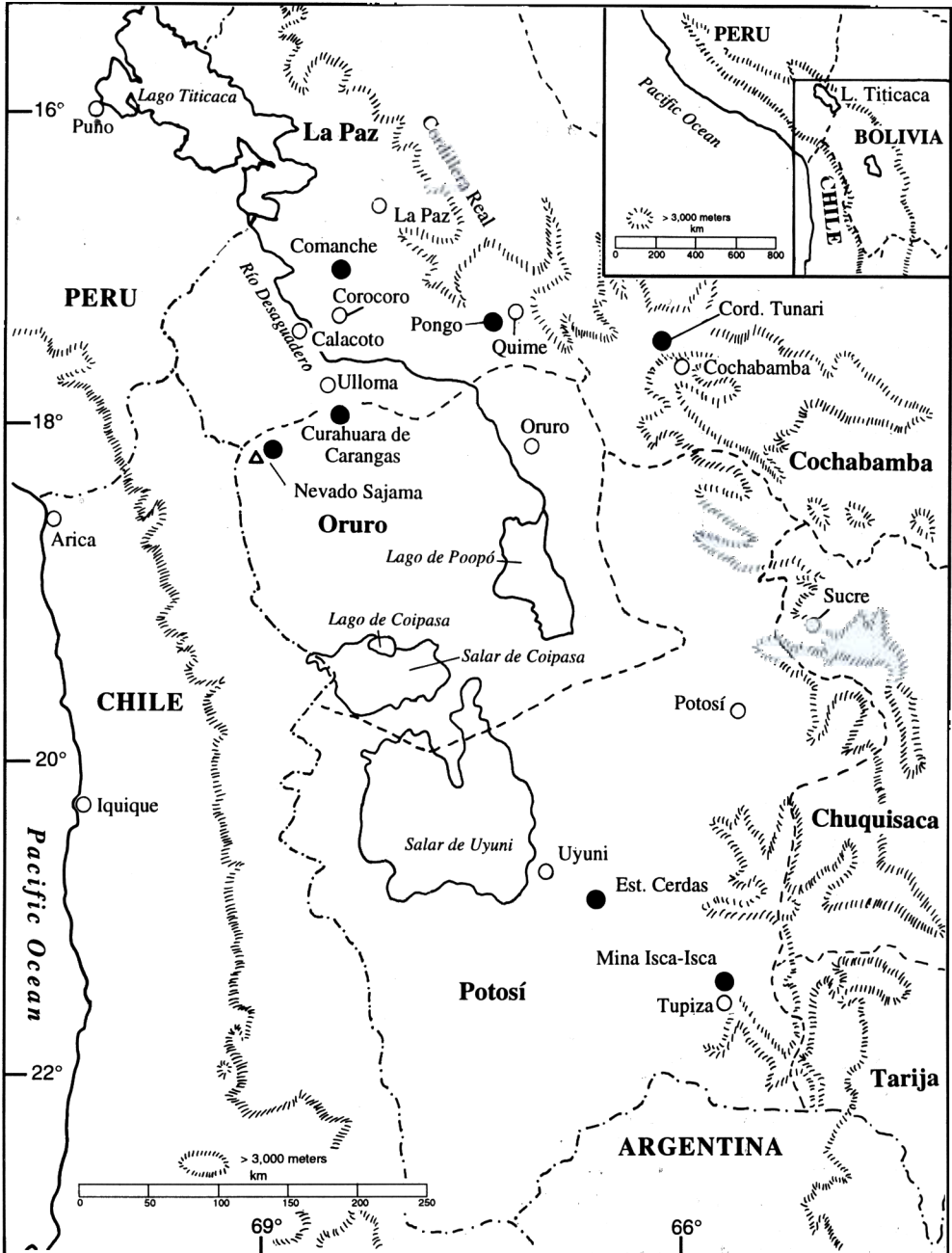


FIG. 4. Schematic map of the Andes of Bolivia showing collecting localities and study sites (black dots) mentioned in the text.

woodlands and *Puya Raimondii* stands, and Fjeldså & Krabbe (1990: 500) noted: "at least in breeding season narrowly associated with *Polylepis* groves." I had earlier (Vuilleumier 1969: 604–605) observed this species in *Polylepis* woodlands and wet brushlands, and can now confirm its nesting in *Puya Raimondii* stands. Fjeldså (1990: 27) wrote that "In the breeding season, the species seems to be narrowly restricted to the edges of *Polylepis* woods or to areas with scattered, park-like *Polylepis* vegetation sometimes with the giant bromeliad *Puya raimondii* admixed (sic)." Fjeldså (1990: 27) also wrote that *Myiotheretes rufipennis* was apparently specialized to *Polylepis* woodlands.

My own experience with this species in Perú in 1975 (Ancash, this report) and Bolivia in 1967 (La Paz, Oruro, Potosí; Vuilleumier 1969: 604–605) indicates that *Myiotheretes rufipennis* occurs in three kinds of high Andean habitats: (1) *Polylepis* woodlands (Fig. 7), (2) wet brushlands with no *Polylepis*, and (3) *Puya Raimondii* stands with no *Polylepis* (Figs. 8, 9). In my 1969 paper I stated (Vuilleumier 1969: 605) that: "All the sites where *X. [Xolmis = Myiotheretes] rufipennis* was observed included two features. The first is the presence of shrubs or trees...because [it] habitually perches on shrubs (even low shrubs) or, more often, on trees, usually on the very top of them." I also noted (loc. cit.) that "The second feature of the habitat ... is the rocky nature of the terrain. Birds of this species were always seen along quebradas, or small rocky bluffs, or near steep slopes with large boulders." My 1975 field work in *Puya Raimondii* stands in Ancash confirmed the presence of these birds in such rocky habitats (see Fig. 9). The nesting of *Myiotheretes rufipennis* in *Polylepis* woodlands (Fjeldså 1990: 27) and in *Puya Raimondii* stands (this report) suggests that it is not so much dependent on a given kind of tree, but on woodland-like or park-like vegetation within the normally treeless, grassy or shrubby puna steppes, irrespective of what actual plant taxon is dominant, and provided that rocks or cliffs are also present.

The distribution of *Myiotheretes rufipennis* is illustrated by maps in Fjeldså & Krabbe (1990: 500) and Fjeldså (1992: 25). The earlier map shows about 22 or 23 isolated patches, only three or four of which are in Bolivia. The later map shows fewer but larger patches, especially in

Perú. Even though these maps are schematic, they do show the patchy distribution of the species and are adequate representations of its range.

To illustrate in more detail the variability in habitats and in avifaunas associated with *Myiotheretes rufipennis* within its range, I describe below four specific sites.

(1) At Nevado Sajama, in the dry puna (Troll 1959: 52) of northwestern Bolivia, in open woodlands of relatively low and spaced out *Polylepis* trees (Figs. 4, 7), neighbors of *M. rufipennis* included one other species of bush and ground tyrants, *Muscisaxicola albifrons*, as well as *Buteo poecilochrous*, *Falco femoralis*, *Caprimulgus longirostris*, *Leptasthenura* sp., *Asthenes modesta*, *Ochthoeca oenanthoides*, *Anairetes* sp., *Mimus dorsalis*, *Carduelis atrata*, *Phrygilus atriceps*, and *P. plebejus*.

(2) At Mina Isca-Isca, in the moist puna area (Troll 1959: 52) of Bolivia, in dense woodlands of tall *Polylepis* trees, neighbors included one other species of bush and ground tyrants, *Agriornis andicola*, and also *Bolborhynchus aurifrons*, *Colaptes rupicola*, *Upucerthia* sp., *Leptasthenura yanacensis*, *Asthenes dorbignyi*, *Ochthoeca oenanthoides*, *O. leucophrys*, *Mimus dorsalis*, *Turdus chiguanco*, *Oreomanes fraseri*, *Carduelis crassirostris*, *Phrygilus atriceps*, and *P. unicolor*.

(3) Above Pongo near Quime (La Paz), in the moist puna area (Troll 1959: 52) of Bolivia (Fig. 4), in a glacial valley without *Polylepis* where the valley floor was covered with numerous shrubs of red, pink and white flowered *Digitalis* (Scrophulariaceae), the neighbors included one other species of ground tyrant, *Agriornis montana*, as well as *Leptasthenura yanacensis*, *Diglossa carbonaria*, *Phrygilus punensis*, *P. plebejus*, and *Zonotrichia capensis*.

(4) At Queshque, in the moist puna (Troll 1959: 52) of north central Perú, in a dense woodland-like stand of *Puya Raimondii* (Fig. 9), the neighbors included one other species of bush and ground tyrants, *Agriornis montana*, as well as *Buteo poecilochrous*, *Phalcoboenus megalopterus*, *Falco femoralis*, *Oreotrochilus estella*, *Colaptes rupicola* (nesting in *Puya*), *Upucerthia serrana*, *U. jelskii*, *Leptasthenura andicola*, *Asthenes humilis*, *A. flammulata*, *Ochthoeca oenanthoides*, *Troglodytes aedon*, *Phrygilus gayi*, *P. fruticeti*, *Carduelis atrata*, and *C. uropygialis*.

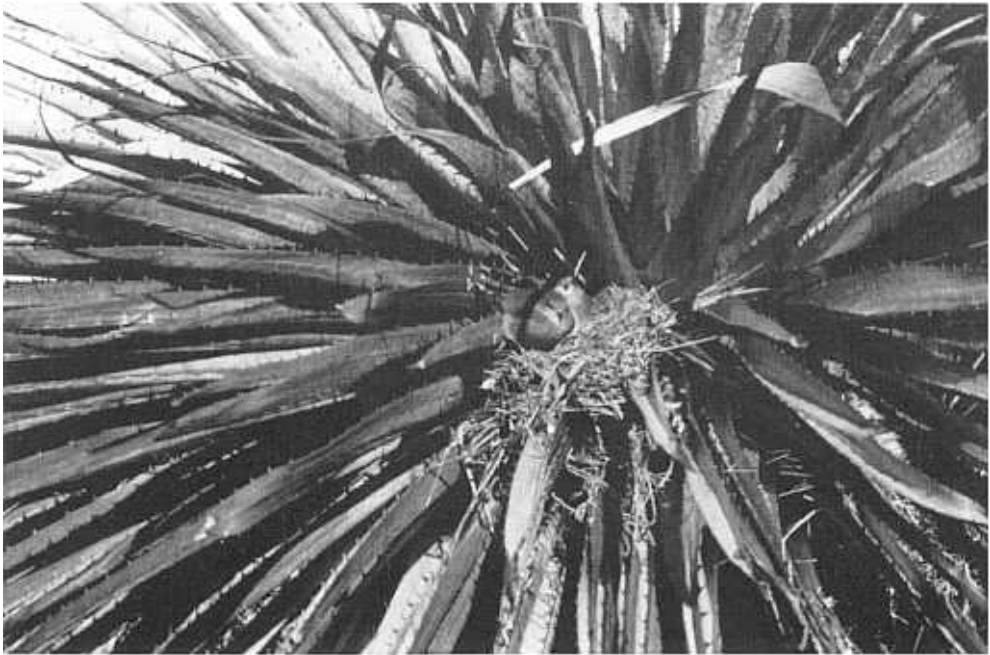
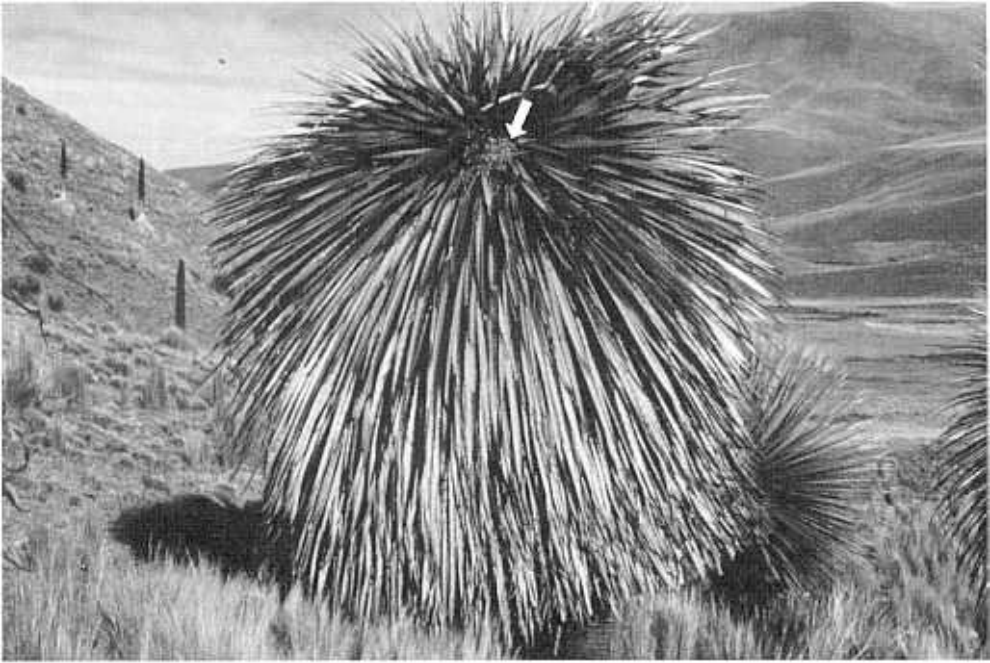


FIG. 5. Top: nesting site of *Myiotheretes rufipennis* in a dead 3 m tall *Puya Raimondii* at Carpa, Ancash, Perú. Arrow shows nest. Bottom: close-up view of same nest, with two young, in cluster of hooked leaves. Photographs F. Vuilleumier, October 1975.

Xolmis pyrope (Kittlitz 1830)

Systematic position

Xolmis pyrope was described by Kittlitz (1830: 191) in the genus *Muscicapa*, and placed in *Pyrope* by Cabanis & Heine 1859, a new name for *Muscicapa pyrope*. This species was later either kept in *Pyrope* (e.g., Meyer de Schauensee 1966: 335) or placed in *Taenioptera* (e.g., Wetmore 1926a: 447, 1926b: 301) or else in *Xolmis* (e.g., Peters 1923: 320; Hellmayr 1927: 19; Vuilleumier 1971: 195). In his revision of the Tyrannidae, Traylor (1977, 1979) kept *pyrope* in *Xolmis*. Lanyon's (1986: 47) recent studies of syringeal morphology suggested to him that *pyrope* is indeed a member of the genus *Xolmis*. I believe the relationships of *pyrope* are best shown by keeping it in *Xolmis*.

Nesting behavior

In spite of this species being relatively common wherever it occurs (see below), few authors have

described its nesting behavior. Pässler (1922: 463–464) wrote that it “prefers to build its nest among the twigs of a small tree or a shrub 2–5 meters above the ground. The outer part consists of thin twigs, plant stems and grass stems, which are interlaced with moss and dried fibers. The inside of the nest is richly lined with cattle and horse hairs, wool and a few feathers.” Johnson (1967: 264) also described the nest of this species in general terms: the “nest is built of dry sticks firmly interlaced with grass stems and well lined with lichens, moss or wool.” He stated further: “Favored locations are 6 to 10 feet [2 to 3 m] from the ground in small pines or flowering shrubs at the edge of or around clearings in the forest or plantations where the sun can penetrate freely, but farther north where the country is more open, bush-covered hillsides or the vegetation bordering the bed of a stream.” Neither Pässler nor Johnson, however, mentioned the nestlings.

On 22 November 1988 I found a nest of *Xolmis pyrope* about 13 km east of Porvenir, NW Tierra del Fuego, Chile, at an altitude of about 300 m in the foothills of the Sierra Boquerón (also called Cordón Baquedano) (Fig. 10). The two adults were feeding large caterpillars to four almost fully feathered, dark gray nestlings, which I judged to be about 2.5 weeks old. The nest was placed about 40 cm above the ground in a 130 cm tall shrub of *Chiliotrichum diffusum* (Compositae), in an area of relatively dense matorral composed almost exclusively of *Chiliotrichum*. The cup measured about 10 cm in diameter and 5 cm in depth. The rather deep and neatly made cup was made of *Chiliotrichum* twigs, the rim of *Usnea* moss, and the inside of the cup was lined almost entirely with hair of *Lepus europaeus* (introduced hare) and a few horse hairs. Both parents fed actively on the two days I observed the nest. The nestlings looked like their parents but lacked the red iris, so conspicuous in adult birds, and had orange gapes. Besides the description of the nestlings, what is of interest in this nesting record is the choice of habitat.

The nesting site described above is in an area of glacial terraces with an open vegetation of shrubsteppe or low matorral composed chiefly of *Chiliotrichum diffusum* and *Berberis buxifolia* (Berberidaceae). The tallest elements of this vege-



FIG. 6. Nesting site of *Myiotheretes rufipennis* in the cluster of leaves of a dead 3.5 m tall *Puya Raimondii* at Queshque, Ancash, Perú. Arrow shows nest. Photograph F. Vuilleumier, October 1975.



FIG. 7. Left: habitat of *Myiotheretes rufipennis* in the dry puna northeast of Nevado Sajama, Oruro, Bolivia. The birds occupied the *Polylepis tarapacana* woodland in the foreground. Right: close-up view of *Polylepis tarapacana* woodland at the same locality; trees are between 2 and 4 m tall. Note rocky soil. Photographs F. Vuilleumier, October 1967.

tation are shrubs or low trees of *Embothrium coccineum* (Proteaceae). This plant association seems to represent an ecotone between *Nothofagus* (Fagaceae) forests and Patagonian steppes (Pisano 1977: 189–191), and is normally encountered farther west where forests dominate the landscape. In northwestern Tierra del Fuego, however, this vegetation type occurs far away from any forest association.

Although no nest was found in the usual forested habitat for *X. pyrope*, a female in breeding condition was collected on 11 November 1988 in disturbed *Nothofagus* forest near the mouth of the Río Santa María, about 2 km south of San Juan, at sea level, in the Brunswick Peninsula across the Strait of Magellan (skeleton number AMNH 17703). This bird had a brood patch, ovary 7 x 4 mm, ovum 1.5 mm in oviduct, skullfully ossified, no body, wing or tail molt; 45 g; iris yellowish-brown, bill black.

Display behavior and relative abundance
Xolmis pyrope is usually encountered alone or in pairs. Birds most often perch in the medium to high levels of trees or shrubs, where they remain immobile for varying periods of time. This spe-

cies seems to feed by pouncing down on prey (presumably insects) on the ground. On two occasions I saw one individual eat hairy caterpillars on the ground (10 November 1985, Brunswick Peninsula, and 24 November 1985, Navarino Island, Fig. 1). On both occasions the bird actively removed hairs from the caterpillar while on the ground, then flew up to a perch to eat it. The specimen collected in 1988 had large insects in her stomach.

Xolmis pyrope is usually silent. Occasionally, however, I have heard birds emit soft and short monosyllabic or bisyllabic calls that can be rendered as *tuk* or *tuk-tuk*. In an earlier publication (Vuilleumier 1967: 402) I mentioned that this species seems to be an occasional member of mixed species flocks dominated by the furnariid *Aphrastura spinicauda*.

On only two occasions did I observe flight displays in this species, on 2 December 1985 on Hoste Island (False Cape Horn) and on 5–7 October 1987 on Tierra del Fuego near Los Canelos, south of Porvenir (Fig. 2). These flight displays were not accompanied by vocalizations. The birds were flying fairly high in the air with slow wing beats, a display reminiscent of the

Aerial Display in *Muscisaxicola* spp. (Smith 1971). Smith (1971), however, did not describe flight displays in *Xolmis pyrope*.

During field trips to Patagonia in 1965, 1985, 1987, and 1988 I encountered *Xolmis pyrope* daily, whenever I worked in areas where forest habitat looked suitable. Thus, in northern Patagonia in 1965 (western Río Negro, Argentina, and adjacent Chile), I saw *Xolmis pyrope* on 11 days from 6 February to 1 March; in Fuego-Patagonia I saw this species on 15 days from 1 November to 12 December 1985, on 10 days in 1987 (25 and 26 February and from 4 October to 25 October) and on 10 days from 6 November to 24 November 1988. Most encounters mentioned above involved one or two birds per sighting. Thus, although I never found *X. pyrope* to be abundant, it was not rare in every area where it would have been expected. By contrast, Philippi *et al.* (1954: 47) found *X. pyrope* scarce ("escaso") on the mainland north of the Strait of Magellan and saw very few ("poquísimos ejemplares") on Tierra del Fuego and Isla Dawson. Pässler (1920: 486), writing about the Coronal area (37¹/₂°S) near Concepción, Chile stated that "in summer, it [*X. pyrope*] is seen in pairs, in winter isolated birds . . ."

Habitat preferences and geographic distribution *Xolmis pyrope* is normally found within the area occupied by *Nothofagus* forests of Patagonia (Vuilleumier 1985: 296). In northern Patagonia and Chilean Fuego-Patagonia, I found *X. pyrope* near forests, usually along forest edges or in clearings (Fig. 11). In such situations the avifauna associated with *X. pyrope* includes such typical *Nothofagus* forest species as *Enicognathus ferrugineus*, *Campephilus magellanicus*, *Aphrastura spinicauda*, *Pygarrhichas albogularis*, *Scytalopus magellanicus*, *Elaenia albiceps*, *Curaeus curaeus*, *Phrygilus patagonicus*, and *Carduelis barbata* (this list corresponds to observations made near San Juan, Brunswick Peninsula, Magallanes, Chile, from 6 to 13 November 1988; note that no other species of bush and ground tyrant is sympatric with *X. pyrope*).

I did also, however, observe *Xolmis pyrope* in more open situations. In northern Patagonia, for example, I saw the species on 13, 16 and 19 February 1965 in shrubland a few km west of Bariloche, and on 1 March 1965 at timberline in

open woodland of *Araucaria araucana* and *Nothofagus* on Volcán Llaima (Fig. 1).

In my experience, this species seems to have a broader habitat niche in the Tierra del Fuego archipelago than on the mainland of southern Patagonia. Thus, on Tierra del Fuego I have encountered it not only in *Nothofagus* forest edges and clearings, but also in a relictual woodland of *Drimys winteri* (Winteraceae) and *Maytenus magellanica* (Celastraceae) at Los Canelos near Bahía Inútil (Pisano 1977: 180–181) and in matorral away from forest (this is the nesting habitat reported on here). (Note that in the matorral where the nest was found, neighbors of *X. pyrope* included such nonforest species as *Circus cinereus*, *Leptasthenura aegithaloides*, *Troglodytes aedon*, *Phrygilus gayi*, and *Zonotrichia capensis*.) On Navarino Island I saw the species on 24, 26, 27, and 28 November 1985 in low second growth *Nothofagus* forest and in scrub. Finally, on Isla Hoste (False Cape Horn), at or near the southernmost part of the species' range, I saw it 3 times in open shrubbery on 2 December 1985.

My observation that *X. pyrope* breeds in matorral away from forest in the southern part of its range, and Johnson's (1967: 264) remark that the same is true in the northern part of its range, suggest that although this species occupies forest and its edges in the main part of its distribution, it is able to occupy nonforest in the extreme north or south. In spite of this ecological versatility, *X. pyrope* does not live in the even more open situations found east of the *Nothofagus* forest area, in Patagonian steppes (Hueck & Seibert 1981), where other species of bush and ground tyrants are found, for example *Neoxolmis rubetra*, *N. rufiventris*, *Muscisaxicola capistrata*, and *M. maculirostris*, but no other species of *Xolmis*.

Neoxolmis rubetra (Burmeister, 1860)

Systematic position

This species, originally described in the genus *Taenioptera* by Burmeister (1860) (usage followed by Peters 1923: 320, and Wetmore 1926a: 301), was later moved to the genus *Xolmis* (e.g., Hellmayr, 1927: 18; Meyer de Schauensee 1966: 355; Vuilleumier 1971: 208; Olrog 1979: 204). In my revision of *Xolmis*, I (Vuilleumier 1971: 196–197) suggested that *rubetra* was sufficiently



FIG. 8. Open stand of *Puya Raimondii* with few rocks, nesting habitat of *Myiotheretes rufipennis* in the moist puna grassland at Carpa, Ancash, Perú. Arrow in center tree points to nest illustrated in Fig. 5. Photograph F. Vuilleumier, October 1975.

distinct within the genus *Xolmis* to be placed in its own species-group, but I added (p. 197): "In color, pattern, and habits, *X. rubetra* is intermediate between the other species of *Xolmis* and *Neoxolmis rufiventris*, and may represent an evolutionary transitional 'stage' between arboreal and terrestrial tyrants." On the basis of several characters Traylor (1977: 163), however, believed that *Xolmis rubetra* (Burmeister) and *Neoxolmis rufiventris* (Vieillot) were each other's closest relatives, and placed them both in *Neoxolmis* (Traylor 1979: 165). Lanyon's (1986: 51) studies of syrinx morphology supported Traylor's (1977, 1979) recommendation that they be considered congeneric (in *Neoxolmis*). I accept this view here, thus modifying my earlier conclusion (Vuilleumier 1971: 208). It is interesting to point out that in his original description Burmeister (1860: 247) had remarked that *rubetra* was related to, but smaller than, *Taenioptera variegata* D'Orbigny, which is a synonym of *Neoxolmis rufiventris*. Thus the interrelationships of *rubetra* and *rufiventris* were recognized early on. Fig. 12 compares *Neoxolmis rubetra* (top) with *N. rufiventris* (bottom).

Nesting behavior

On 8 November 1992 I found what may be the first reported nest of *Neoxolmis rubetra*. Thus, Lanyon (1986: 51) had written about the eggs of this species: "the eggs of [*Neoxolmis*] *rubetra* have markings similar to those of [*Neoxolmis*] *rufiventris* (WFVZ [Western Foundation of Vertebrate Zoology, Los Angeles] collection), but noted: "the nest is unreported." More recently, Fjeldså & Krabbe (1990: 503) wrote: "Voice and breeding: No data." Lloyd Kiff (pers. comm.) kindly sent me a copy of the data slip for one egg at the WFVZ collected by J. R. Pemberton on 17 October 1911 "South of Corral Chico, F.C.P. [= Ferrocarril Patagónico], Río Negro." The same data slip describes the nest thus: "Fine cup shaped nest composed of fine grass. Lined with feathers entirely. Placed 1 foot above ground in a very small green bush." Although this data slip is labeled "*Taenioptera rubetra* (Burmeister)," doubt remains about this identification. Under "Identity" the word "Uncertain" has been written, and under "Remarks" the following comment appears: "Supposed to be egg of the Aeroplane flycatcher." Interestingly, in his report

on the Pemberton collection, Wetmore (1926b: 448) did not mention a nest or egg of *Neoxolmis rubetra*, only three specimens, in full breeding plumage, none of which was collected south of Corral Chico.

—The nest site was about 20 km east of El Caín, at the western base of the Mesetá de Somuncurá, Río Negro, Argentina, at an altitude of about 1100 m (Fig. 1). Note that the nest of *Neoxolmis rubetra* was less than 1 km from the nest of *N. rufiventris* found the previous day (see below under that species). These two tyrants were found breeding sympatrically in a flat plain with relatively uniformly distributed, open vegetation of low shrubs and tussock grasses (Fig. 13). Bunch grass (*Festuca* sp., Gramineae) is dominant, with most tussocks about 20–30 cm tall, but shrubs (including *Mulinum spinosum*, Umbelliferae) are also present throughout the grassy steppe. Grass tussocks are spaced about 40 cm apart, leaving bare areas of rather soft, gravelly or sandy soil in between.

Both parents *Neoxolmis rubetra* were seen carrying food in their bills and disappearing in the vegetation toward the ground, a behavior that eventually led me to discover their nest. Each parent had a different food gathering area in the steppe and followed a different pathway toward the nest. I was unable to distinguish the sexes on morphological or behavioral ground. Only once during the approximately one hour I observed feeding behavior of the pair before looking for the nest, did I see removal of the fecal sac, which was dropped on top of a shrub, only about 25 m from the nest.

While I was examining and photographing the nest the two parents remained nearby, within 2–4 m, calling several times. Their calls were soft monosyllabic sounds, audible only at close range, that can be rendered by *tjup*, *tjupp*, or *twitt*. These calls were similar to calls given the day before under similar circumstances by *Neoxolmis rufiventris* (see below).

The nest of *Neoxolmis rubetra* (Fig. 14) was situated much like that of *N. rufiventris* (see Fig. 17), in that it was placed on the ground, exposed, at the base of a 20 cm tall grass tussock. The nest was an open cup, the exterior rather coarsely made of dried twigs and grass stems, the inside of the cup being about 12 cm in diameter and 5 cm

deep, and lined with white feathers of *Pterocnemia pennata*. The nest had two chicks, which were a little less advanced than those of *Neoxolmis rufiventris*, and were covered with brownish gray down and had an orange gape. The two chicks of *N. rufiventris* were also covered with gray down, but the tint was perhaps a little less brownish; their gape was orange also.

Display behavior and relative abundance

At sites other than the nesting locality, *Neoxolmis rubetra* regularly perched on top of shrubs, where it usually remained immobile for relatively long periods of time, up to 3–5 minutes, before pouncing down to catch prey, presumably insects, on the ground. After taking off, individuals of *N. rubetra* characteristically flew rather long distances, low over the vegetation, before perching again. Upon landing, the birds often raised their wings (Wing Raising display, Smith 1971), a behavior that exposed their cinnamon-rufous underwing coverts.

Birds called not infrequently when perched. The calls emitted then were all soft and monosyllabic, similar to the sounds heard near the nest, and transcribed as *ship*, or *shup*, or else *tjip*. Wings are flicked at each *tjip*. Fjeldså & Krabbe (1990: 503) wrote that this species is "Terrestrial, occ. perches on a wire or low bush." My observations suggest, in contrast, that this species spends more time on perches than on the ground.

No other *Neoxolmis rubetra* was seen in the nesting area, but several birds were observed several km away in an open valley west of El Caín. Elsewhere in central and northern Patagonia (Chubut, Río Negro and Neuquén Provinces, and in neighboring southern La Pampa Province) I found *N. rubetra* to be locally quite common in 1991 and 1992 in a variety of steppe and shrubsteppe (monte, Morello 1958) vegetation types. I had 12 sightings in Chubut in 1991 (on 7 days out of 14 field days), from rather open coastal shrubsteppes near Camarones and Península Valdés inland and westward all the way to more open steppes near Esquel (Fig. 1). In 1992 I had 32 sightings of *N. rubetra* (on 13 days out of 23 field days), from coastal and near coastal shrubsteppes of Chubut and eastern Río Negro (6), to denser shrubsteppe and monte of southern La Pampa (20), to open steppes of



FIG. 9. Dense stand of *Puya Raimondii* on rocky slope, nesting habitat of *Myiotheretes rufipennis* in the moist puna grassland at Queshque, Ancash, Perú. *Puya* plant with flowering stalk in foreground is about 8 m tall. Photograph F. Vuilleumier, October 1975.

western Neuquén (1) and of south central Río Negro (5).

Neoxolmis rubetra was thus relatively common in the areas I visited in 1991 and 1992. In the 1870s Durnford (1877: 34) found it "rare" and "saw only two examples" during his first trip. During his second and longer trip Durnford (1878: 394) found it "rarely" in the Chubut Valley but "common in the valley of the Sengel in November." (This is Río Senguerr in Paynter 1985: 380–381, and in Fig. 1.) Peters (1923: 320) called it "locally common in western Río Negro" in 1920–1921. Wetmore (1926a: 301–302) recorded it in 1920 "as fairly common on the plains that bordered the Río Negro," and also noted it near Zapala (Neuquén) and Bahía Blanca (Buenos Aires) (Fig. 1). The observation that *N. rubetra* was relatively common in the 1870s and the 1920s more or less matches my own perception of the relative abundance of this species in the early 1990s and do not seem to support the comments by Fjeldså & Krabbe (1990: 503) that *N. rubetra* is "Declining, being fairly rare now throughout its range."

Habitat preferences and geographic distribution
I found *Neoxolmis rubetra* to be more common in shrubsteppe or monte with relatively well spaced out shrubs or low trees up to 2–3 m tall growing on bare or sparsely vegetated soil (Fig. 15), than in very open Patagonian steppe (Hueck & Seibert 1981) with low shrubs and bunch grass. Therefore, the habitat where I found the nest near El Caín in 1992 (Fig. 13) is more open than most other habitats where I encountered *N. rubetra* elsewhere in Río Negro, Neuquén and La Pampa in 1992, as well as in Chubut in 1991. Most recently, De Lucca & Saggese (1992: 259) mentioned having observed a pair of *N. rubetra* in "a very arid valley with sparse vegetal cover" on 6 October 1987 at Estancia El Cuadro, Deseado Department, Santa Cruz (Fig. 1). This record extends the range of this species about 300 km southward.

Other than the Santa Cruz record just cited, the geographic distribution of *Neoxolmis rubetra* corresponds largely to that of the monte biome (as defined by Morello 1958; see also Hueck & Seibert 1981) and to the transition zones (eco-

tones) between monte and Patagonian steppes and between the monte and the espinal biome (see map in Hueck & Seibert 1981). The distribution map of *N. rubetra* in Fjeldså & Krabbe (1990: 503) is thus incomplete in the southern part of this species' range. Fig. 16 (left) gives a tentative map of the breeding distribution of *N. rubetra*, not including *Xolmis* [= *Neoxolmis*] *rubetra salinarum* Nores & Yzurieta (1979: 7–8, from northeastern Córdoba Province) (outside Fig. 16). The winter range is not shown.

To give more detailed indications about the kinds of habitats within its range, and about the avifaunas associated with *Neoxolmis rubetra*, I describe below four specific sites.

(1) In low and open grassy steppe at 1100 m near El Caín (Río Negro) on 7 and 8 November 1992, in the area where the nest described above was found and in nearby areas (Fig. 13), neighbors included another bush and ground tyrant, its congener *Neoxolmis rufiventris*, and *Pterocnemia pennata*, *Tinamotis ingoufi*, *Thinocorus rumicivorus*, *Asthenes pyrrholeuca*, *Knipolegus aterrimus*, *Anthus bellmayri*, *Mimus patagonicus*, *Phrygilus fruticeti*, and *Zonotrichia capensis*.

(2) In low and open shrubsteppe growing on sand dunes near sealevel in the Península Valdés on 9 November 1991, *Neoxolmis rubetra*'s neighbors included two other species of bush and ground tyrants, *Agriornis murina* and *A. microptera*, as well as *Pterocnemia pennata*, *Eudromia elegans*, *Falco femoralis*, *Falco sparverius*, *Oreopholus ruficollis*, *Athene cunicularia*, *Geositta cunicularia*, *Upucerthia dumetaria*, *Anthus furcatus*, *Notiochelidon cyanoleuca*, *Diuca diuca*, *Sicalis lebruni*, and *Zonotrichia capensis*.

(3) In dense and tall shrubsteppe on gravelly and pebbly soil at about 100 m altitude about 15 km west of Puerto Madryn (Chubut) (Fig. 15), neighbors of *Neoxolmis rubetra* on 5 and 10 November 1991 included one other species of bush and ground tyrant, *Agriornis microptera*, and *Eudromia elegans*, *Cathartes aura*, *Zenaida auriculata*, *Leptasthenura aegithaloides*, *Mimus triurus*, *Mimus patagonicus*, *Diuca diuca*, *Phrygilus carbonarius*, *Phrygilus fruticeti*, *Zonotrichia capensis*, *Sturnella loyca*, and *Molothrus bonariensis*.

(4) In variably dense and rather tall monte or shrubsteppe in northwestern Río Negro Pro-

vince and southern La Pampa Province between Pichi Mahuida and the Río Curacó (Fig. 1), on 26 October 1992, neighbors of *Neoxolmis rubetra* included three other species of brush and ground tyrants, *Xolmis irupero*, *X. coronata*, and *Agriornis murina* (but not *A. microptera*), as well as *Eudromia elegans*, *Cathartes aura*, *Falco sparverius*, *Milvago chimango*, *Leptasthenura platensis*, *Synallaxis albescens*, *Pseudoseisura gutturalis*, *Furnarius rufus*, *Rhinocrypta lanceolata*, *Pyrocephalus rubinus*, *Phytotoma rutila*, *Mimus triurus*, *Mimus patagonicus*, *Sicalis luteola*, *Notiochelidon cyanoleuca*, *Progne modesta*, *Diuca diuca*, and *Zonotrichia capensis*.

Neoxolmis rufiventris (Vieillot, 1823)

Systematic position

The genus *Neoxolmis* was described by Hellmayr (1927: 39) for *Tyrannus rufiventris* Vieillot, 1823, which most authors had included previously in the genus *Myiotheretes* (e.g., Peters 1923: 320; Wetmore 1926: 447), on the basis of structural characters like tarsus length, length of claw of hallux, length and shape of wing, relative length of outermost and second primaries, and rictal bristles. Meyer de Schauensee (1966: 334) maintained *rufiventris* in *Neoxolmis*, and so did I in my revision of the bush and ground tyrants (Vuilleumier 1971: 197), in which I gave a diagnosis. I added: "My reason for maintaining *Neoxolmis rufiventris* in a monotypic genus distinct from an enlarged genus *Xolmis* (to which it is most closely related) is that *N. rufiventris* has gone farther toward the terrestrial adaptive zone (zone *sensu* Simpson, 1953) than any other *Xolmis*, including *X. rubetra*." Traylor (1977: 163; 1979: 165) maintained *rufiventris* in *Neoxolmis* and added *rubetra* to that genus, a decision with which Lanyon (1986: 50–51) agreed, on the basis of his analysis of synringeal morphology. I follow this treatment here, thus modifying my earlier assessment of this species' systematic relationships.

Nesting behavior

Maclean (1969) described the first nest of this species, which he found at Estancia Las Vegas in the Valley of the Coig (Coyle) River in Santa Cruz Province, Argentina, on 3 December 1967 (Fig. 2). I found what appears to be only the second reported nest on 7 November 1992 about



FIG. 10. Top: nesting habitat of *Xolmis pyrope* in about 2 m tall matorral of *Chilietricum diffusum* east of Porvenir, in the foothills of the Sierra Boquerón, Tierra del Fuego, Chile. Adult bird with food in bill is shown perched on shrub in foreground, bringing food to young in nest about 3 m away. Bottom: same nest with two young. Photographs F. Vuilleumier, November 1988.

20 km east of El Caín, at the western base of the Mesetá de Somuncurá, Río Negro, Argentina, at an altitude of about 1100 m (Fig. 1). This nest was less than 1 km from the nest of *Neoxolmis rubetra* reported above, and the habitat of the site was described under that species (Fig. 13). Besides the breeding pair with nest, three other pairs of *Neoxolmis rufiventris* were seen at this site, but their nests could not be found. The open steppe area where these four pairs were seen was about 4 km² or 400 ha.

The nest was discovered after having watched the feeding behavior of one of the two parent birds for nearly an hour. The nest of *Neoxolmis rufiventris*, like the nest of *N. rubetra* described above, was placed on the ground at the base of a grass tussock, and was exposed (Fig. 17). The cup was made largely of dried grass stems. The inside of the cup was about 10 cm in diameter and 4 cm deep. It contained two large young covered with pale gray down and with orange gape. The down color of these young was perhaps a little less tawny than that of the two young of *Neoxolmis rubetra*, but the young of both species had the same orange gape.

Both parents remained nearby while I inspected the nest, and emitted soft alarm calls that can be transcribed as *pukut* or *tuput*, similar in tone and pitch to the calls of *Neoxolmis rubetra* heard near their nest, but bi-syllabic rather than monosyllabic.

Display behavior and relative abundance

Besides the nesting pair and three other pairs of *Neoxolmis rufiventris* at the steppe site east of El Caín, I had six other sightings of this species (total 7 birds, 1 pair plus 5 isolated individuals) along the road from Maquinchao to El Caín (Fig. 1), along the stretch between Laguna Néluan (not indicated on Fig. 1) and El Caín, about 45–60 km southeast of Maquinchao and about 30 km west of El Caín, on 7 and 9 November 1992, at altitudes of 1100 to 1200 m. The landscape of this area consists of a relatively flat to gently undulating basaltic plateau covered with low steppe, where spaced out grass tussocks are dominant over low thorny shrubs. The vegetation is thus rather similar to that where the nest was found farther east, but the soil is much more rocky and includes conspicuous basaltic outcrops.

Individuals of *Neoxolmis rufiventris* were observed while they were perched either on a rock or on the low vegetation for long periods of time, during which they remained almost entirely motionless, in one instance as long as about 8 minutes while I sketched a bird (Fig. 12, bottom). They would then fly off, skimming the top of the vegetation, to a rather distant spot before perching again, a behavior similar to that described earlier for *Neoxolmis rubetra*.

While perched, I regularly heard individuals of *Neoxolmis rufiventris* emit soft monosyllabic calls that can be rendered by *tzup*, *juj*, or *joop*, and that sounded similar to calls of *Neoxolmis rubetra* or *Xolmis pyrope*. None of the seven *N. rufiventris*, two of which appeared to be paired, seen on this basaltic plateau were observed with food in their bills.

Thus in 1992, whereas I had a total of 32 sightings of *Neoxolmis rubetra* in steppes, shrub-steppes and monte shrub, I had only 8 sightings of *Neoxolmis rufiventris* in open steppes. In 1991, I had 7 sightings of *N. rubetra* in steppes and shrubsteppes but none of *N. rufiventris*. Thus I failed to detect *N. rufiventris* in the open steppe areas of the basaltic plateaus that I visited in central Chubut in 1991 (which are less than 100 km to the southwest of the 1992 nesting area in Río Negro, and which look similar), even though I was on the lookout for the species.

Habitat preferences and geographic distribution
The nesting record reported here extends the known breeding range of *Neoxolmis rufiventris* based on actual nests from Santa Cruz (Maclean 1969) north to Río Negro, a distance of about 900 km. It is likely, however, that the breeding range of this species has long included north-central Patagonia. Fjeldså & Krabbe (1990: 504) did not include Chubut in the range of this species, but both Olrog (1979: 203) and Clark (1986: 230) did.

Older records suggest that Chubut and Río Negro have had a breeding population for a long time. Durnford (1878: 394), who remained in the Chubut Valley from 5 September 1877 to 20 April 1878, wrote: "A few [*Neoxolmis rufiventris*] visit Chuput [= Chubut] in the spring, remaining till the end of the summer." This observation suggests summer residency. Peters (1923: 320) collected two males near Huanuluán, Río

Negro, on 2 November 1920, in the breeding season. I visited this locality from 3 to 5 November 1992, but did not see the species there. Huanuluán is about 150 km west of El Cañ (Fig. 1) and has open steppes that look suitable for *Neoxolmis rufiventris*. Wetmore (1926a) did not report it from his own field work in Río Negro or Neuquén, but cited three males collected by Pemberton in Río Negro (Wetmore 1926b: 447). Two of these birds were obtained 2 and 6 September 1911 (early spring) at Arroyo Seco, a locality about 35 miles west of Valcheta (Fig. 1). This area, which I visited on 10 November 1992, is covered with shrubsteppe, a habitat where I saw (and would have expected) *Neoxolmis rubetra*, but where I neither saw nor would have expected *N. rufipennis*. Were Pemberton's birds spring migrants on their way to more open steppes on higher ground? (After all, my nesting area is only about 200 km southwest of Arroyo Seco.) The third male collected by Pemberton was obtained 16 January 1911 (in the breeding season and "very worn" according to Wetmore (1926b: 447) at Cerro Añecón Grande, Río Negro (Fig. 1), "a volcanic peak 20 miles west of Huanuluán" (Wetmore 1926b: 396) (Fig. 1). Unfortunately I did not have a chance to visit this mountain during my stay in the Huanuluán area in November 1992, but I would judge this range to have suitable habitat for *N. rufiventris*. The two birds mentioned by Peters (1923: 320) were collected near Cerro Añecón Grande. I therefore suspect that *N. rufiventris* was breeding locally in small numbers in Chubut in Durnford's time in the late 1870s and in central Río Negro in Pemberton's and Peters' time in the 1910s to 1920s. The occurrence of a breeding population west of the Meseta de Somuncurá (Fig. 1) is thus not that surprising. Note that Bettinelli & Chebez (1986) did not report either *Neoxolmis rufiventris* or *N. rubetra* from the localities that they visited in the Meseta de Somuncurá between 18 and 22 February 1985.

The question remains, whether the distribution of *Neoxolmis rufiventris* in Patagonia is disjunct with a northern breeding population on the basaltic plateaus of Río Negro and Chubut (not mapped in Fjeldså & Krabbe 1990: 504), and a southern breeding population (mapped in Fjeldså & Krabbe 1990: 504) in southern Santa Cruz Province (Argentina), southern Magallanes

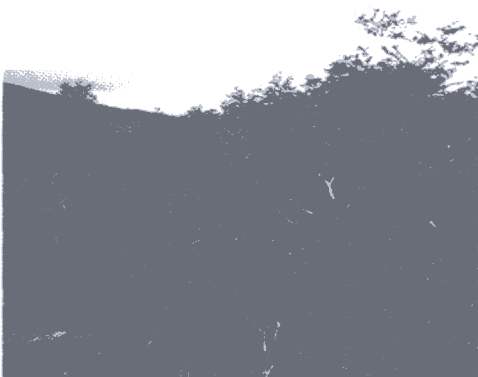
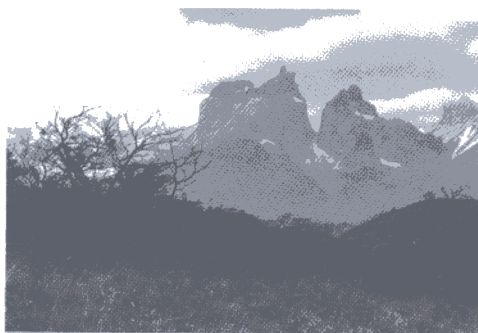


FIG. 11. Three views of *Nothofagus* forest edge and *Nothofagus* forest, usual habitat of *Xolmis pyrope*, in Chilean Patagonia (Magallanes). Top: forest edge in Torres del Paine National Park. Center: forest edge alongside bog-heath in Brunswick Peninsula south of Punta Arenas. Bottom: forest in Brunswick Peninsula south of Punta Arenas. Photographs F. Vuilleumier, February 1987.



(Chile) and northern Tierra del Fuego (Chile and Argentina). There is no obvious reason why these two populations should be disjunct. The apparent gap between them might be due to a lack of sampling in southern Chubut and northern Santa Cruz. Zapata (1967: 376), for example, reported two specimens, a male and female (a pair?), both collected during the breeding season on 24 November 1961 (Museo Argentino de Ciencias Naturales, Buenos Aires No. 41188, Estación de Biología Marina de Puerto Deseado No. 27), a few km northeast of Puerto Deseado, northeastern Santa Cruz, not far from the Atlantic coast (Fig. 1). This collecting date is bracketed by the aforementioned dates of the known nesting records for Río Negro (7 November) and southern Santa Cruz (3 December), and corresponds to the date of the male bird collected with a brood patch in Magallanes (27 November, AMNH 826145). Fig. 16 (right) gives the known breeding distribution of *Neoxolmis rufiventris* (winter range not included).

The southern population of *Neoxolmis rufiventris*

Statements in the literature about the relative abundance and distribution of the southern population of this species seem contradictory. In the most recent review of the status and distribution of *Neoxolmis rufiventris* Fjeldså & Krabbe (1990: 504) wrote: "Numbers fluctuate greatly. Some years abundant at the Strait of Magellan and plateaus of Sta. Cruz, other years almost absent." Clark (1986: 230) called the species not common ("*poco común*") in the northern part of Tierra del Fuego. Venegas & Jory (1979: 157) called it rather common ("*algo común*") in northern Tierra del Fuego. Earlier Johnson (1967: 234) had written that *Neoxolmis rufiventris* was "a rare bird in Chile" (on both sides of the Straits of Magellan) but "in Argentina and especially in [Argentine] Patagonia it is a fairly abundant bird." Johnson (1967: 234) stated further that "According to local residents, in some years it arrives on the grasslands of nor-

thern Tierra del Fuego in considerable numbers and in others it is scarcely seen at all." Johansen (1966: 252) reported that "Mrs. Huntley, a good ornithologist, told Philippi (1957) that the bird can even be common ("*häufig*") on the northern plains [of Tierra del Fuego] in some years in the summer, whereas it is rare ("*selten*") in other years (translated from the German)." This statement, and the one by Johnson quoted above, may be the basis for the aforementioned remarks made by Fjeldså & Krabbe (1990: 504).

Actual data for Tierra del Fuego, however, are scanty. Humphrey *et al.* (1970: 268–269) cited all available information up to that time. On the basis of two observations by Crawshay (1907: 61), one by Mogensen (1930: 293), one by Philippi *et al.* (1954: 50), and only 3 specimens collected in January (summer), April (fall), and November (spring), Humphrey *et al.* (1970: 268) concluded that on Tierra del Fuego *Neoxolmis rufiventris* was "Accidental: This uncommon species is known from only a few records from the northern, nonforested parts of Isla Grande." Jehl & Rumboll (1976: 149) recorded this species near Estancia José Menéndez on 24 October 1973 and at Río Grande on 10 November 1973 (Fig. 2). Judging from the eleven localities north of the Strait of Magellan mentioned for Chilean Patagonia by Venegas & Jory (1979: 157), *Neoxolmis rufiventris* would indeed appear to be more common north than south of the Strait of Magellan. Olrog (1948), a keen observer, did not report *N. rufiventris* during his extensive trips to southern Patagonia in 1939–1941. Other than Fjeldså & Krabbe (1990: 504), who may in fact have used his writings, no author since Johnson (1967: 234) has documented the alleged population fluctuations in northern Tierra del Fuego. The scholarly Humphrey *et al.* (1970: 268–269) and Venegas & Jory (1979: 157) did not mention such fluctuations. Note that Fjeldså & Krabbe (1990: 504) did not state that these abundance fluctuations occur in Tierra del Fuego, but "*at [italics mine] the Strait of Magellan and plateaus of Santa Cruz.*"

FIG. 12, page 20. Top: adult *Neoxolmis rubetra* sketched in the field by F. Vuilleumier at its nesting site near El Caín, Río Negro, Argentina, on 8 November 1992. Bottom: adult *N. rufiventris* drawn in the field by F. Vuilleumier 30 km west of El Caín, Río Negro, Argentina, on 7 November 1992.

Given the paucity of data on the occurrence of *Neoxolmis rufiventris* in Fuego-Patagonia, I cite below my own observations before concluding on the relative abundance of this species on the mainland of southern Patagonia and in northern Tierra del Fuego. During four expeditions to Chilean Fuego-Patagonia in 1985, 1987 and 1988, I had repeated opportunities to travel in areas that might be suitable for *N. rufiventris* on both sides of the Strait of Magellan, from 1 November to 13 December 1985; from 7 February to 4 March 1987; from 1 October to 30 October 1987; and from 6 November to 30 November 1988. Trips were made, sometimes repeatedly, to areas where *N. rufiventris* had been recorded previously (Humphrey *et al.* 1970: 268–269; Venegas & Jory 1979: 157) on both sides of the Strait of Magellan.

Neoxolmis rufiventris was encountered on only six occasions, two on Tierra del Fuego and four on the mainland. On 7 November 1985 a single bird was seen briefly by Claudio Venegas in our field party, about 15 km S of Porvenir, Tierra del Fuego, on a grassy knoll with a large "town" of burrowing rodents (*Ctenomys* sp.) gently sloping toward Bahía Inútil, about 500 m from the sea. The species was never seen again at this site, even though it was repeatedly visited later in 1985, in February 1987, in October 1987, and in October 1988. Other species found in this habitat included one other species of ground tyrant, *Muscisaxicola capistrata* (thus I was wrong to state that *N. rufiventris* does not share its habitat with other bush and ground tyrants; Vuilleumier 1971: 192), as well as *Buteo polyosoma*, *Circus cinereus*, *Geositta antarctica*, *Cinclus fuscus*, *Lessonia rufa*, *Sturnella loyca*, *Anthus correndera*, and *Zonotrichia capensis*. The other sighting on Tierra del Fuego was of two birds near China Creek on 26 October 1987 (Fig. 2). They appeared to be paired and were found in open, rolling, grazed grassy steppe with *Poa* sp. (Gramineae), perching on low shrubs or on the ground. They disappeared from sight after a period of observation of only about 10 minutes. In the same area I recorded *Geositta cucularia*, *G. antarctica*, *Lessonia rufa*, and *Zonotrichia capensis*.

On the mainland north of the Strait of Magellan on 9 February 1987, I observed two *Neoxolmis rufiventris* off and on for about two

hours along the road from Kimiri Aike and O'Higgins to Posesión and Punta Dungeness (Fig. 2), in gently rolling and very open steppes with short, grazed grass and scattered low *Berberis* shrubs. These birds appeared to be paired. They ran on the ground, looking like *Turdus* thrushes. Prey (insects?) were caught near or on the ground, after a quick run and characteristic wing flicks. Often they disappeared out of sight for several minutes at a time, simply "vanishing" in the short grass on the other side of a low hill. Other birds seen nearby included *Pterocnemia pennata*, *Polyborus plancus*, *Thinocorus rumicivorus*, *Geositta antarctica*, *Lessonia rufa*, and *Zonotrichia capensis*.

On 26 November 1988, 4 individuals were observed in flat, open grassy steppe dominated by *Festuca* sp. a few km north of O'Higgins (Fig. 2). One individual was holding a large lizard (*Liolaemus* sp.) in its bill when first seen. He flew to the ground among the grass tussocks and when he reappeared a few minutes later the lizard was gone. (Jehl & Rumboll 1976: 149 observed one *N. rufiventris* "carrying a small lizard [*Liolaemus* sp.]; lizards may be a regular part of the diet of this species; Fjeldså's Pl. XLIII in Fjeldså & Krabbe 1990: 789 shows this species holding a green lizard in its bill, see also text p. 503). The four birds emitted soft calls that sounded similar to those given by *Xolmis pyrope*. Other birds seen in these grassy steppes were *Theristicus caudatus*, *Chloephaga picta*, *Haematopus leucopodus*, *Gallinago gallinago*, *Thinocorus rumicivorus*, *Lessonia rufa*, *Anthus correndera*, *Melanodera melanodera*, and *Zonotrichia capensis*.

On 27 November 1988, one *Neoxolmis rufiventris* was seen and collected along the road from Kimiri Aike and O'Higgins to Posesión and Punta Dungeness, at a site less than 1 km from where I had seen a pair on 9 February 1987. The bird (skin, AMNH 826145), was a male, left testis 10 x 6 mm, right testis 9 x 5.5 mm, with fully ossified skull, no fat, weight 80 g, no molt, and a brood patch. The stomach contained beetle remains. Iris dark brown, bill black, legs and feet black. The bird was collected in grassy steppe with sparse, low *Berberis* shrubs, while perched on a shrub. Other birds seen nearby included *Polyborus plancus*, *Thinocorus rumicivorus*, *Lessonia rufa*, *Anthus correndera*, *Sturnella loyca*, and *Sicalis lebruni*.



FIG. 13. Two views of steppe with 20 to 30 cm tall shrubs and tussock grass near El Caín, Río Negro, Argentina. This is the resting habitat of *Neoxolmis rubetra* and *N. rufiventris*. Photographs F. Vuilleumier, November 1992.

On 29 November 1988, one bird was seen and collected (skeleton, AMNH 17702) about 3 km southeast of O'Higgins. The bird was a male, left testis 13 x 5.5 mm, right testis 8 x 6.5 mm, with fully ossified skull, light fat in the furculum area, body mass 80 g, no molt; iris dark brown, bill black, legs and feet black. No brood patch was noted. The stomach contained insect remains. The bird was collected in flat grassy steppe with only scattered, low and small *Berberis* shrubs. The bird perched on the shrubs and on the ground. Nearby were seen *Pterocnemia pennata*, *Thinocorus rumicivorus*, *Haematopus leucopodus*, *Vanellus chilensis*, and *Lessonia rufa*. The specimen of *Eremobius phoenicurus* mentioned in Vuilleumier *et al.* (1993) was collected only about 1 km away the previous day.

On the basis of records summarized by Humphrey *et al.* (1970: 268–269) and Venegas & Jory (1979: 157), and of my own field observations of *Neoxolmis rufiventris* in Chilean Fuego-Patagonia, I conclude that this species is rare and localized in this area. Even though I did not obtain actual proof of breeding, indicative is the brood patch of the male specimen collected on 27 November 1988. The habitats favored by the species in Chilean Fuego-Patagonia include open, grazed, grassy steppe with scattered low shrubs (*Berberis*) both north and south of the Strait of Magellan, a grassy knoll with a *Ctenomys* colony on Tierra del Fuego, and grassy steppes with tussock grass north of, and a few km inland from, the Strait of Magellan. These habitats are generally more open and more disturbed by sheep-grazing than those where I saw the species in Río Negro in 1992. Other than Johnson's (1967: 234) report from "local residents" in northern Tierra del Fuego that numbers there vary widely from year to year (see above), there is apparently no reliable documentation of such fluctuations. Indeed, Philippi *et al.* (1954: 50) saw and collected only one bird in Tierra del Fuego and "saw no other" during two expeditions, and were told by a Mr. Spooner that he had only seen a few individuals ("*solo unos pocos ejemplares*") in the many years that he had lived there. Philippi *et al.* (1954: 50) wrote: "There is no doubt that it is a very scarce bird on Tierra del Fuego and we did not have an opportunity to study it in the field" (translated from Spanish). Since Johnson was a member of

the Fuego-Patagonian expeditions of 1945/46 and 1952, upon which the Philippi *et al.* (1954) report was based, is it possible that his memory of the "local residents'" observations was faulty when years later he wrote his 1967 book? Perhaps *Neoxolmis rufiventris* is more common in Santa Cruz Province, where I have no field experience. Thus Maclean (1969: 144), who worked in Santa Cruz, called it "a common bird of Argentine Patagonia." This qualification of "common," however, clearly does not apply to areas where I have studied the species farther north in Río Negro, or farther south in Chilean Fuego-Patagonia. Consequently, until clear cut evidence to the contrary is presented, I consider the abundance fluctuations, at least in Chilean Fuego-Patagonia, to be unfounded.

Agriornis andicola Sclater, 1860

Systematic position

This species was described as *Agriornis andicola* by Sclater (1860: 78), but the name *albicauda* Philippi & Landbeck (1863: 132; who had placed the species in the genus *Dasycephala*) was used by Hellmayr (1927: 9) because *andicola* was thought to be a homonym of *andecola* d'Orbigny. Two other species names, *pollens* and *insolens*, have also been used (see synonymy in Hellmayr 1927: 9). Meyer de Schauensee (1966: 333) and Vuilleumier (1971: 211) used *albicauda*, following Hellmayr (1927). Traylor (1979: 166, footnote), however, stated that, according to the International Code of Zoological Nomenclature, *andicola* Sclater, 1860 is not a homonym of *andecola* d'Orbigny, 1839 and should be used instead of *albicauda*. Collar *et al.* (1992: 790) recently reviewed the history of the name of this species.

Nesting behavior

The nest of *Agriornis andicola* seems not to have been described previously. Thus, Johnson (1967: 233) wrote: "we were not successful in finding a nest which, as far as we are aware, remains undescribed." Fjeldså & Krabbe (1990: 505), under "Breeding," wrote only "Large gonads June (nw Ecu)." Most recently, Collar *et al.* (1992: 789) wrote: "No nest has been described."

On 30 October 1975 I discovered a nest of *Agriornis andicola* at Carpa, Ancash, Cordillera Blanca (Vuilleumier & Simberloff 1980: 363) at 4060 m in a stand of the giant bromeliad *Puya*



FIG. 14. Two views of nest of *Neoxolmis rubetra* near El Caín, Río Negro, Argentina. Note coarse platform of twigs in front of nest. Photographs F. Vuilleumier, November 1992.

Raimondii, in the same area and habitat where *Myiotheretes rufipennis* was also nesting (see above) (Fig. 18). The nest was located after watching two parents bring what looked like insects to their concealed young. The parents' feeding behavior was so discreet, however, that it took me two days of careful watching before I found the nest.

The nest of *A. andicola* was placed on the ground near the base of a largely collapsed old *Puya* plant and was only partially sheltered by a large clump of grass (Fig. 19). The base of the nest was coarsely made of twigs. The nest was a large cup made of dried grass stems and some moss. The inside of the cup was lined with horsehairs, dried pieces of membranous material from *Puya*, a piece of shed snake skin, and some feathers. The outside diameter of the nest was 50 cm; the outside diameter of the cup was 20 cm; the inside diameter of the cup was 11 cm; and the cup was 7 cm deep. The nest was occupied by two different sized young (weights 79 and 61 g). Both young had bright yellow gapes. The larger young (Fig. 20) had 6 mm-long feathers on the wings and tail, but the smaller one had no feathers yet. Both young had pink skin, covered with fluffy gray down on the head, scapulars, wing, back and sides of the lower back. Both young were regularly fed by the parents. While I examined the nest the young emitted occasional squeaky calls and the parents, short bisyllabic chirps.

The nesting area is the same, but at a lower altitude, than the site where Fjeldså (1987: locality 15b, page 15, 58; see also Collar *et al.* 1992: 787) have seen *Agriornis andicola* on 15 February 1987.

Display behavior and relative abundance

Since very little seems to have been published on the behavior of *Agriornis andicola* I describe below two observations concerning this species. On 3 December 1967 at Mina Isca-Isca north of Tupiza, Potosí, Bolivia, at about 4000 m (Fig. 4), I saw one individual being pursued by a pair of *Myiotheretes rufipennis* (see above). The mobbed bird disappeared in the dense vegetation of a *Polylepis* woodland, then flew up to the top of a tree where I collected it. I thought that the *Agriornis* might have been robbing a nest of *Myiotheretes*, but its stomach was full of insect debris and did not contain either egg or young birds.

The second observation concerns an Aerial Display (Smith 1971: 259) that I witnessed on 1 November 1967 at Comanche, La Paz, Bolivia at about 4100 m (Fig. 4). The entire display lasted about 10 minutes and was silent. The bird flew very high over a rocky hill covered with *Puya Raimondii* describing a broad circle about 150 m in diameter. During its display the bird flew up with its tail half outstretched showing the white on its outer rectrices, then stalled and closed its wings half way, dropping down forward before opening its wings again to fly up for a new stall and drop. This display was similar to an Aerial Display I saw performed by *Agriornis microptera* in Chubut, northern Patagonia in 1991 (Vuilleumier 1993a: 26-27). Other than the vocalization heard from the two parent birds at their nest in Ancash, I did not hear calls emitted by *A. andicola*.

Fjeldså & Krabbe (1990: 506) wrote that *A. andicola* was "generally local and rare, may be declining and outnumbered by Black-billed S-t. [*A. montana*] (in Bol. by 1 : 10)." I agree with them that *A. andicola* is rare and local. For example, in Ancash in 1975, I found only one pair of *A. andicola* (in one of three stands of *Puya Raimondii*), but at least two pairs of *A. montana* (one in each of two stands). The information about the 1 : 10 ratio in Bolivia in Fjeldså & Krabbe (1990: 506) and in Collar *et al.* (1992: 788) comes from my own observations there in 1967–1968 (Vuilleumier 1971: 213). After checking my field notes from my 1967–68 trip to Bolivia, I found that I had had three sightings of *A. andicola* from 19 October to 3 December 1967 (two birds were collected, AMNH 793161 and 793162), and 14 sightings of *A. montana* from 15 October 1967 to 11 January 1968 (5 birds were collected, AMNH 793198, 793199, 793200, 793201, and 793202). The ratio thus is not about 1 in 10 as I erroneously reported (Vuilleumier 1971: 213) but closer to 1 in 5. There is no question, however, that *A. montana*, even though nowhere abundant, is not a rare species, whereas *A. andicola* is definitely rare. Collar *et al.* (1992: 788-789) gave additional information on the localization and rarity of *A. andicola* and considered it a threatened species.

I have no personal information that would suggest a decline in the period 1964-1975 when I regularly visited areas of the high Andes occu-

pied by *A. andicola*. I did not observe this species in Ecuador in 1964, and saw it only at one site in Perú in 1975 (Carpa, see above), where it was breeding, and at three sites in Bolivia in 1967. Collar *et al.* (1992: 789) wrote that "If the species has truly declined, the cause of this is not apparent."

It may be worthwhile to comment briefly about the relative abundance of other *Agriornis* species. Two other species besides *montana* and *andicola*, while never common, can be observed regularly where the habitat is suitable (*A. microptera* and *A. murina*, Vuilleumier 1993a: 26–27 and 1992 unpublished observations). By contrast, like *A. andicola*, I found *A. livida* to be rare and saw it only twice in Patagonia, one bird at about 1200 m in a ravine near Refugio Llaima, on the slopes of Volcán Llaima, Chile, on 2 March 1965 (Fig. 1) and one bird near Cerro Castillo, south of the Torres del Paine National Park, Magallanes, Chile, on 26 February 1987 (Fig. 2). Olrog (1948: 513) saw isolated individuals of *livida* in Porvenir (Tierra del Fuego) and Cabeza del Mar (mainland; Fig. 2). Smith (1971: 234) also found *A. livida* rarer than he had expected. Finally, Johnson (1967: 226) qualified this species as "far from common" yet "fairly frequently" seen. It might have been more common in the past. Thus, Peters (1923: 319) found it "not uncommon in the open clearings about Bariloche", where I did not see a single bird between 6 February and 23 February 1965. Has there been a decline in *A. livida*?

Habitat preferences and geographic distribution Vuilleumier (1971: 211–213) described the habitats occupied by *Agriornis andicola* as "open slopes and valley floors of high Andean valleys, and areas having sparse and xeric vegetation of low shrubs, with scattered rocks and boulders used as observation posts." Collar *et al.* (1992: 789) suggested that this species is dependent on the presence of *Polylepis* and/or *Puya* within at least the puna zone of Perú and Bolivia. My observations only partially confirm their suggestion. Thus in Bolivia, I found *A. andicola* at 3900 m 4 km west of Curahuara de Carangas, La Paz (Fig. 4), on 19 October 1967 in a sparsely vegetated, boulder-strewn valley with bunch grass, composite shrubs, and thorny leguminous shrubs with no *Polylepis* or *Puya* (AMNH



FIG. 15. Shrubsteppe about 1.5 m tall near Puerto Madryn, Chubut, Argentina, usual habitat of *Neoxolmis rubetra*. Photograph F. Vuilleumier, November 1991.

793161). Elsewhere in Bolivia, I observed it in woodlands of *Polylepis* on rocky soil (2 sites: 1 November 1967 at 4020 m at Comanche, La Paz; 3 December 1967 at 4000 m at Mina Isca-Isca, Potosí, AMNH 793162); and in Perú, I found it at Carpa, in a stand of the giant *Puya Raimondii* (nesting site, above).

According to Collar *et al.* (1992: 789), "B. M. Whitney (*in litt.* 1991) suggested that *andicola* occurs on average slightly higher than *montana*." I saw both species together in Ancash, Perú at about 4100 m in October 1975 in a *Puya Raimondii* stand, and in La Paz, Bolivia at 3900 m (rocky valley without *Polylepis* or *Puya*) and 4170 m in October 1967 (in a *Polylepis* woodland). Elsewhere, in the area of sympatry in Bolivia between these two species, I have observed and collected *A. montana* from 3070 m in Chuquisaca Department (AMNH 793200, female with largest follicle 4 mm in diameter, skull fully ossified, body mass 56.0 g) to 4620 m in La Paz Department (AMNH 793202, sex unknown, body mass 58.4 g). Collar *et al.* (1992: 787–788) gave altitudes for *A. andicola* between 2440 m (a straggler from higher elevations?) or 3000 m and 4314 m in Perú, and between 2700 m (a straggler from higher elevations?) or 3900 m and 4200 m in Bolivia. At face value it would seem to me that *A. andicola* and *A. montana* are not only broadly geographically sympa-

tric but also occur in the same general elevational range (from about 3000 m to about 4300 m) within which, locally at least, both species co-occur in the same localities.

The geographic distribution of *Agriornis andicola* has recently been described and mapped by Fjeldså & Krabbe (1990: 505) and discussed in detail by Collar *et al.* (1992: 787–788). The map in Fjeldså & Krabbe accurately reflects the patchiness in distribution of this tyrant flycatcher.

Muscisaxicola capistrata (Burmeister, 1860)

Systematic position

This species was originally described by Burmeister (1860: 248) in the genus *Ptyonura*, but all authors since then have included *capistrata* in the genus *Muscisaxicola* Lafresnaye & d'Orbigny, 1837. In my revision of the genus *Muscisaxicola* (Vuilleumier 1971: 203, 218) I placed *capistrata* in the *macloviana* species-group including only the two species *macloviana* and *capistrata*. This decision was made because I concluded that these “two southern South American species are very close to each other in size and proportions and also in head pattern” (Vuilleumier 1971: 203). In his revision of the fluvicoline flycatchers for Peters' *Check-list of Birds of the World*, Traylor (1979: 169) placed *macloviana* and *capistrata* next to each other, although he did not subdivide the genus. Further study is needed to ascertain the position of *M. capistrata* within *Muscisaxicola*.

Nesting behavior

On 30 October 1992 I discovered a nest of this species near Laguna Verde in Parque Nacional Laguna Blanca, Neuquén, Argentina, about 35 km southwest of Zapala, at an altitude of about 1250 m (Fig. 1). The nest was an open cup of dried grass stems lined with feathers, and was placed in a relatively shallow (10–15 cm wide) vertical crevice of a nearly vertical rocky escarpment rising to about 30 m above the valley floor (Fig. 21). One bird, sex unknown, was incubating 2 or 3 eggs. The bird was removed from the cavity, examined, and placed back on its nest. The eggs were left in the nest and could not be counted or examined. Since this site is located in a National Park, neither nest, eggs, or bird could be collected. The bird on the nest had worn (and loose) feathers and a conspicuously large and densely vascularized brood patch.

I was quite surprised to find *M. capistrata* breeding in a rock crevice. Johnson (1967: 252) stated that nests “were in holes beneath stones or other situations similar to those described for other members of this genus.” Although elsewhere Johnson (1967: 235) had stated that *Muscisaxicola* spp. nest “on the ground under stones or clefts among rocks”, there was no reason to expect cleft-nesting in *M. capistrata*. Indeed, Johnson's (1967: 252) own field experience of nesting of this species was from northwestern Tierra del Fuego, an area where rock clefts are probably nonexistent, the landscape being either that of glacial terraces or of moraines made of large deposits of fluvio-glacial till. In the actual expedition report coauthored by Johnson 13 years earlier (Philippi *et al.* 1954: 48), the following statement is found: “At Estancia Gente Grande at our surprise we found a nest at the end of a rabbit burrow. This burrow was in a soft slope covered with short grass” (translated from Spanish). The Gente Grande area of northwestern Tierra del Fuego (Fig. 2), which I have visited repeatedly between 1985 and 1988, is flat or gently rolling and glacial in origin, and to the best of my knowledge has no rocks with clefts. Smith (1971: 242–248) also mentioned a nest of *M. capistrata* in a rabbit burrow in Chilean Tierra del Fuego.

Display behavior and relative abundance

Earlier on the day that I found the nest at Parque Nacional Laguna Blanca, Neuquén, I observed a mixed flock of ground tyrants including 5–6 *Muscisaxicola capistrata*, 4–5 *M. albilora*, at least 2 *M. maculirostris*, and 1 male *Lessonia rufa* on the valley floor in a flat area near a small lake (Laguna Verde) covered with grazed, sparse and low herbaceous vegetation. The foraging site of this mixed flock was about 1 km linear distance from the nest site. At the nesting area of *M. capistrata* one pair of *M. albilora* and one *M. macloviana* were also observed along the rocky escarpment, and might well have been breeding nearby. The two *M. albilora* showed apparent territorial behavior and the one *M. macloviana* was aggressive toward them. But nests of these two other species were not found. [Another ground tyrant, however, *Agriornis montana*, was breeding near or on the top of the escarpment. One bird was seen carrying food (worms?) in its bill from the

grassy valley floor, climbing up the escarpment in a series of flights that led it to the top, before it disappeared out of sight.]

Given the presence of a mixed flock of three species of *Muscisaxicola*, which is suggestive of non-breeding behavior, I was surprised to find an active nest of *M. capistrata* and to observe the (apparent) territorial behavior of two other *Muscisaxicola* species (*macloviana* and *albilora*) in the area. One of these, however (*macloviana*), was not present in the mixed flock.

On several other occasions I have found *Muscisaxicola* spp. (but not *M. capistrata*) in breeding condition on the basis of gonad size of collected specimens, and yet have observed several birds near each other, behaving as if they were members of a mono- or polyspecific flock. Do indivi-

duals of *Muscisaxicola* spp. breed at the same time as they participate in mono- or polyspecific flocks, as seems to be the case in some species of Formicariidae, Vireonidae, and Thraupidae in Amazonian Perú (Munn & Terborgh 1979: 341–343)? The presence in mixed flocks of individuals of *Muscisaxicola* spp. with enlarged gonads during the breeding season is, in my opinion, suggestive of simultaneous breeding and flocking. I give below three examples of apparent mono- or multi-species flocking behavior in this genus during the breeding season.

Thus on 29 November 1967 in Bolivia, Department Potosí, near Estación Cerdas, at 3960 m (Fig. 4), I observed about 6 *Muscisaxicola rufivertex* in an open valley with gravelly or sandy soil and sparse cover of tola shrubs. All

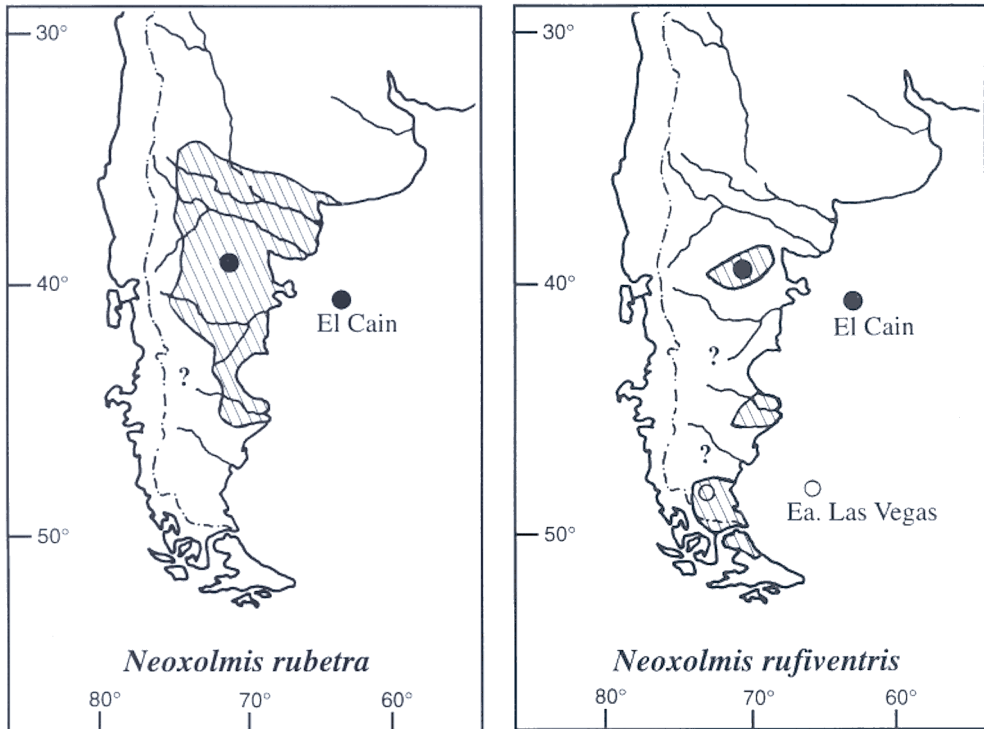


FIG. 16. Left: schematic distribution map of *Neoxolmis rubetra* showing known breeding range in northern and central Patagonia (hatched area). The only known nesting record (El Cain) is indicated by a black dot. Question mark indicates area in west central Patagonia where breeding may occur. See text for further details. Right: schematic distribution map of *Neoxolmis rufiventris* showing known breeding range in northern, central, and southern Patagonia (hatched area). The only known nesting records are indicated by a black dot (El Cain) and an open circle (Estancia Las Vegas). Question marks indicate areas in central and southern Patagonia where breeding may occur. See text for further details.

these birds were wary and flew away at a great distance when I tried to approach them. They behaved like a migratory flock rather than a breeding population. I managed to collect one bird (AMNH 793168), a ♂ with fully ossified skull, weight 18.9 g, with enlarged (7.0 x 6.0 mm) and slightly vascularized testes, suggesting a breeding individual. No nest was found, however.

On another occasion, on 3 December 1967 in Bolivia, Department Potosí, at Mina Isca-Isca north of Tupiza (Fig. 4), on a steep slope between 4140 and 4200 m, I observed a group of 2 *Muscisaxicola rufivertex* and 6–7 *M. cinerea* in a radius of about 1 km. The slope was rocky and covered with sparse bunch grass, sparser tola shrubs, but many *Azorella* (Umbelliferae) cushions above the *Polylepis* belt. These birds were not wary, appeared territorial and paired. Five of the *M. cinerea* were collected, but unfortunately none of the *M. rufivertex*. Two of the apparently paired *cinerea* were males (AMNH 793224, AMNH 793225), weighed respectively 19.0 and 18.9 g, had fully ossified skulls and enlarged testes (respectively 10.0 x 5.0 and 8.0 x 6.0 mm). A third male (AMNH 793223) weighed 20.0 g, had a fully ossified skull and enlarged testes (9.5 x 5.0 mm). Both females had fully ossified skulls but in contrast to the males had small gonads (one, AMNH 793222, weighed 23.3 g and was close to one of the two *M. rufivertex*; the second female, AMNH 793226, weighed 18.5 g). Again, unfortunately, no nest was discovered.

On a third occasion, on 5 January 1968, in Bolivia, Department Cochabamba, at 4040 m in the Cordillera Tunari about 49 km northwest of Cochabamba City along the road to Morochata (Fig. 4), I saw about 10 *Muscisaxicola alpina/cinerea* and one *juninensis* foraging close to each other on a grassy slope cut by rivulets and with scattered rocks. (This site is in the area of parapatry between *M. alpina* and *M. cinerea*.) All of these birds were quite wary and I could not tell whether they were paired or in a loose flock. I collected five *alpina/cinerea*, all males (were the females incubating?). Three of these males had fully ossified skulls and enlarged testes (AMNH 793233, *alpina*, 26.9 g, testes 6.0 x 3.0 mm; AMNH 793228, *cinerea*, 22.1 g, testes 9.0 x 4.0 mm; AMNH 793229, *cinerea*, 22.3 g, testes 9.0 x

4.5 mm). The other two males, both *alpina*, had incompletely ossified skulls and moderately large testes (AMNH 793234, 27.9 g, skull 90% ossified, testes 5.0 x 3.0 mm; AMNH 793235, 26.3 g, skull 50% ossified, testes 4.0 x 2.5 mm).

What exactly is the biological significance of these apparent associations of one or more species of *Muscisaxicola*, some of which had enlarged gonads? In the absence of evidence on actual nesting at the time of my observations or of concrete evidence of territorial behavior or else of data on pairing behavior, it is difficult to speculate about whether these birds, which appeared in reproductive condition, were also in migratory or wandering flocks. Are there helpers at the nest in the genus *Muscisaxicola*?

In two recent overviews of helpers at the nest in birds of the world (Brown 1987: Table 2.2, pp. 18–24; Skutch 1987), only two species of Tyrannidae are mentioned as exhibiting helping behavior toward conspecifics: *Conopias inornata* and *Myiozetetes cayanensis*. Neither species belongs to the bush and ground tyrants (subfamily Fluvicolinae); both belong to the subfamily Tyranninae (*sensu* Traylor 1979). Field workers who have an opportunity to study bush and ground tyrants, especially perhaps *Muscisaxicola* spp., during the breeding season should pay special attention to the possibility of communal or cooperative breeding as reviewed in Brown (1987) and Skutch (1987).

In several publications, Cody (1970: 461, 1974:250–257, 1985: 217–219) discussed interspecific interactions, including interspecific territoriality, among several species of *Muscisaxicola* in Chile but his data are apparently not based on examination of gonads of collected specimens, actual nesting records, plots of nesting territories, or behavior of marked individuals occupying known nests. Cody, Smith, and I all observed interspecific interactions among several species of *Muscisaxicola* in the Andes of central Chile during the breeding season, but only Cody interpreted these observations in terms of interspecific territoriality.

As an example of the kind of difficulty inherent in such interpretations, I quote Smith's (1971: 234) observations: "In early spring [in the Andes of central Chile], several species were grouped into loose flocks at accessible altitudes,



FIG. 17. Two views of nest of *Neoxolmis rufiventris* near El Caín, Río Negro, Argentina. Note coarse platform of dried grass stems in front of nest. Knife in top photograph is 9 cm long. Photographs F. Vuilleumier, November 1992.



FIG. 18. Stand of *Puya Raimondii* on rocky slope, nesting habitat of *Agriornis andicola* at Carpa, Ancash, Perú. *Puya* plants with flowering stalks are 8 to 10 m tall. Photograph F. Vuilleumier, October 1975.

frequenting widely scattered good foraging sites where meltwater collected and where a carpet of green vegetation was present. When higher slopes became more open, they moved up in pairs and scattered. In these sparse populations there was relatively little display behavior ... For my second spring in Chile I found better sites, but had less time available and lost most of that to an unseasonably late snowstorm that closed access to higher altitudes and brought the birds back down into their loose flocks." Some of these birds might well have been breeding. Only a resident ornithologist working on a population of marked birds can hope to determine the evolutionary significance of interspecific interactions among sympatric *Muscisaxicola* spp. living in the same habitat.

The only display I have seen in *M. capistrata* was by one bird observed 11 November 1985 about 30 km south of Porvenir, at Estancia Dalmacia, northwestern Tierra del Fuego (not in Fig. 2). This individual performed an Aerial Display (Smith 1971: 249).

In northern Patagonia, other than the observation of a nest and flock in Parque Nacional Laguna Blanca, Neuquén Province, I saw *M. capistrata* only a few times: at 3 localities in western Chubut in 1991 (Vuilleumier 1993: 28) and 3 individuals at one locality 4 km east of Comallo, between Pilcaniyeu and Ingeniero Jacobacci, Río Negro, in 1992 (Fig. 1).

Published information about the relative abundance of the southern Fuego-Patagonian populations suggests that the species is locally common to abundant there: "quite common on breeding grounds" (Fjeldså & Krabbe 1990: 510); "has been seen quite commonly" (Humphrey *et al.* 1970: 271–272); the second most common *Muscisaxicola*, after *M. macloviana* (Venegas & Jory 1979: 160); "common" (Clark 1986: 234); without doubt the most common flycatcher on the island of Tierra del Fuego, although not seen on the mainland (Philippi *et al.* 1954: 48); "quite abundant" in northern Tierra del Fuego (Johnson 1967: 252); "abundant" in pastures north of Porvenir, Tierra del Fuego (Olrog 1948: 515).

By contrast, my own field observations of this species in Fuego-Patagonia in November 1985, February 1987, October 1987, and October 1988 suggest that *Muscisaxicola capistrata* is not common there. In 1985 this species was sighted on only 4 occasions during 3 days. On 7 November about 15 km south of Porvenir, northwestern Tierra del Fuego, two birds presumed to be a pair were seen in a large rodent (*Ctenomys*) "town" in a gently sloping grassy area facing Bahía Inútil. One of the two birds was collected (AMNH 8968, spirit specimen). It was a female with a well-developed brood patch, small ovary, weight 25 g, iris dark brown, stomach contents small insects (beetles) and one worm. Several rodent burrows were dug out, but no nest was found. This is the same date and area where a *Neoxolmis rufiventris* was also seen (see above), the only site in southern or northern Patagonia where I found these two species together. *Muscisaxicola capistrata* was not seen again at this site later in 1985, in 1987, or in 1988, in spite of repeated visits. On 11 November 1985, 2 *M. capistrata* were seen about 22 km south of Porvenir, and 1 bird about 30 km south of Porvenir at Estancia Dalmacia. On 13 November 1985, 1 bird was seen south of Bahía Inútil, north of Estancia Flórida (not indicated in Fig. 2).

In 1987 I saw the species only 4 times. On 9 February one bird was observed on a slope covered with grazed grassland and *Chilodactylopus* scrub in a shallow valley above O'Higgins, on the mainland north of the Strait of Magellan. On 11 February 1 bird was seen 43 km north of Porvenir in northwestern Tierra del Fuego. On 8 October I saw 2 birds (pair?) near Porvenir, and another pair about 45 km south of Porvenir. The species was not seen in 1988 in any of the areas where it had been observed in 1985 or 1987, in spite of diligent searches for it. For example, I searched for, but failed to find, *M. capistrata* at the *Ctenomys* colony south of Porvenir on 15 and 24 November 1988 where a bird had been collected on 7 November 1985.

Thus, my overall impression is that *Muscisaxicola capistrata* is rare and localized in Chilean Fuego-Patagonia. If it was common in past years, it has certainly decreased markedly in the last few decades. Note that this species may always have been rare in the Argentine part of Tierra del

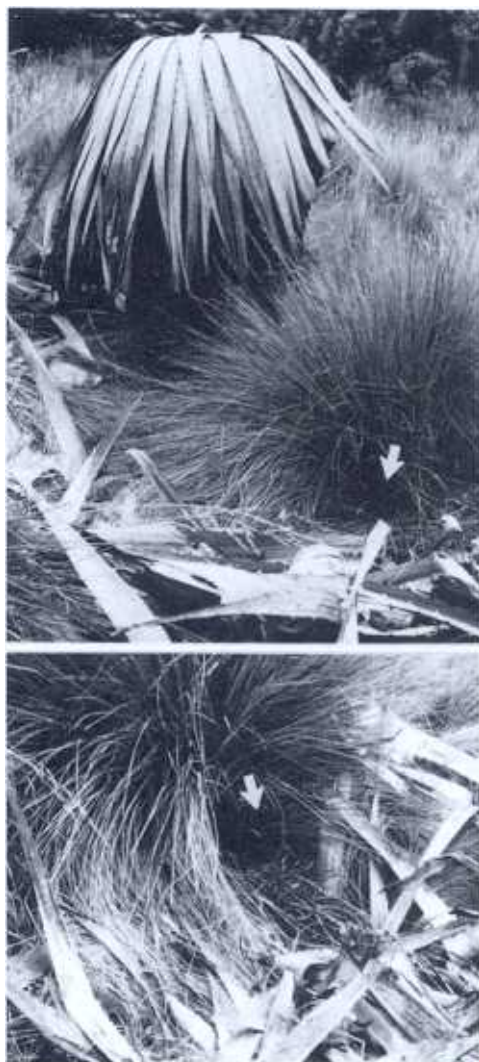


FIG. 19. Two views of nest site of *Agriornis andicola* at Carpa, Ancash, Perú. Top: at base of grass tussock. Bottom: at base of grass tussock in center of figure. Photograph F. Vuilleumier, October 1975.

Fuego. For example, Olrog (1948: 515) had found it scarce there in the late 1930s where Keith (1970: 363) observed only 1 bird during several days in the late 1960s. No change appears to have taken place there. My observations of 1991 and 1992 in Chubut, Río Negro, and Neuquén, at the northern extremity of the breeding range of the species, also suggest a rare



FIG. 20. Larger of two young of *Agriornis andicola* from the nest illustrated in Fig. 19 at Carpa, Ancash, Perú. Photograph F. Vuilleumier, October 1975.

and localized species. Finally, I must mention the fact that I have seen *M. capistrata* only twice during migration. Thus I saw 4 birds on 19 March 1965 at 1800 m in open, rocky slopes near Refugio Alemán Lo Valdéz in the Maipo Valley of central Chile, and 1 bird on 25 April 1965 in an open meadow near Abra Pampa, Jujuy, Argentina, at 3600 m (outside range of Fig. 1). After having had field experience with all 12 species of *Muscisaxicola* (*sensu* Traylor 1979), I would state that *M. capistrata* may be, with *M. frontalis*, the rarest and most localized species of this genus. According to my observations only four species can be called common, or even abundant, at least locally: *M. maculirostris* (e.g., in parts of Chubut, Vuilleumier 1993: 28), *M. albilora* (e.g., in the Andes near Santiago, Chile and in the Patagonian Andes in Río Negro), *M. macloviana* (e.g., on Navarino Island and the islands of the Cape Horn archipelago), and *M. flavinucha* (e.g., in the Andes of northern Patagonia and on Navarino Island). Other species, while not "common," are nevertheless not rare: *M. alpina*, *M. cinerea*, *M. rufivertex*, *M. fluviatilis*, and *M. juninensis*. Of the 3 remaining species, one, *M. albifrons*, is ecologically specialized but not rare in its preferred high altitude puna habitat, usually boggy meadows, but the remaining two, *M. frontalis* and *M. capistrata*, have never seemed common anywhere to me.

Habitat preferences and geographic distribution
The nesting record in Neuquén mentioned above confirms the fact that *Muscisaxicola capistrata* breeds in northern Patagonia about 1200 km north of the usually recognized range of the species. For example, Olrog (1979: 206–207) gave as the breeding range for this species only northern Tierra del Fuego and Magallanes in southern Chile, information that matches the indications given earlier by Johnson (1967: 251). Venegas & Jory (1979: 160) gave a series of localities in southern Magallanes and Humphrey *et al.* (1970: 271–272) localities for northwestern Tierra del Fuego. Clark (1986: 234) included Santa Cruz in the breeding range. Fjeldså & Krabbe (1990: 510) stated: "Breeds in unforested n part of Isla Grande...and neighboring Magallanes, Chile, and Sta Cruz and maybe further n along the Andes, and rec. on Somuncurá plateau of Río Negro, Arg." The Somuncurá indication is probably based on Bettinelli & Chebez (1986: 233), who observed "a group of 5 individuals along the shore of Laguna Blanca (1200 m) on 21 February [1985]," a locality within the Somuncurá Plateau (Fig. 1) of Río Negro (and not the same Laguna Blanca in Neuquén, where I found the nest). Whether the Somuncurá birds were breeders may be open to question, since a late February date could correspond to early fall migrants (see Vuilleumier 1993: 30).

Philippi (1938: 10) wrote that *Muscisaxicola capistrata* breeds in Río Negro and Chubut, but did not cite any specific data. Breeding of *M. capistrata* in Río Negro could have been inferred from the report (Wetmore 1926b: 450) of a female "in breeding plumage" collected by Pemberton on 25 September 1911 at Corral Chico, about 60 miles west of Valcheta (Fig. 1). I visited the area of Corral Chico on 10 November 1992, but found the habitat there, a shrubsteppe, to be unsuitable for this species. Thus I am not quite sure where Pemberton collected his specimen. More convincing, however, are the data published by Peters (1923: 323), who collected near Huanuluán, Río Negro, an area with suitable habitat for *M. capistrata*, although I did not observe it there in November 1992. Peters (1923: 323) wrote that he "shot a mated pair in breeding condition, carrying nesting material" on 25 October 1920, and that on 9 November 1920 "a female with an incubation patch was



FIG. 21. Two views of nesting site of *Muscisaxicola capistrata* in rock crevice in Parque Nacional Laguna Blanca, Neuquén, Argentina. Photographs F. Vuilleumier, October 1992.

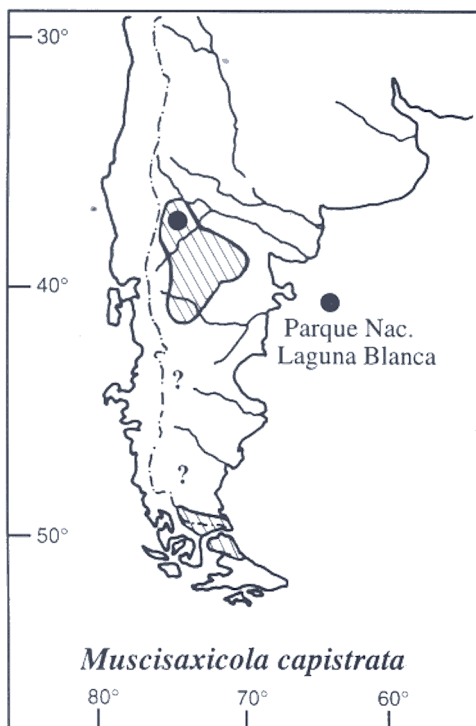


FIG. 22. Schematic distribution map of *Muscisaxicola capistrata* in Patagonia showing known breeding range (hatched areas). The only nesting known record, in the northern part of the range (Parque Nacional Laguna Blanca), is indicated by a black dot. Question marks indicate the possibility of breeding in central Patagonia. See text for further details.

killed in a rocky situation similar to that in which the pair of October 25 was killed." Horváth & Topál (1963: 538) reported a female shot near Ñorquinco, southwestern Río Negro (Fig. 1), on 21 January 1961, thus allowing "the inference of its nesting in this area." Ñorquinco is about 100 km southwest of Huanuluán, and about 300 km south of the breeding site in Neuquén. I observed this species in western Chubut in November 1991 (locality data in Vuilleumier 1993: 28). My Chubut sites are about 200 km southwest of Huanuluán, about 100 km south of Ñorquinco, and about 400 km southwest of Corral Chico. Although I did not observe nesting behavior in Chubut, there is no reason to think that the Chubut birds I saw were not breeding at that time (November, austral

spring). Interestingly, Durnford (1877, 1878) did not report *M. capistrata* from Chubut in his two papers on the birds of the Chubut Valley. Is it possible that this species did not breed in Chubut in Durnford's time about 100 years ago?

At present there are thus two documented breeding populations in Patagonia, the first in west-central Neuquén, central and western Río Negro, and northwestern Chubut (not mapped in Fjeldså & Krabbe 1990: 510), and the second in western Santa Cruz, southern Magallanes, and Tierra del Fuego (mapped in Fjeldså & Krabbe 1990: 510). As in the case of *Neoxolmis rufiventris*, there is no obvious reason why the two populations of *M. capistrata* should be disjunct. The range disjunction may be due to a lack of sampling. Zapata (1967: 375) observed a bird during several days in early November 1961 near Puerto Deseado, northeastern Santa Cruz (Fig. 1), and on 28 November 1961 collected a male (Museo Argentino de Ciencias Naturales, Buenos Aires, No. 41187) and observed other individuals 300 m from the collecting site. Although Zapata gave no information on breeding, these November dates correspond to breeding records elsewhere cited earlier in this report (breeding pair, 25 October, Río Negro; nest, 30 October, Neuquén; specimen, AMNH 8968 [spirit], with brood patch, 7 November; specimen with incubation patch, Río Negro, 9 November). Figure 21 summarizes the known breeding range of *Muscisaxicola capistrata* (winter range not given), thus modifying the map in Fjeldså & Krabbe (1990: 510).

DISCUSSION

The observations reported in this paper give additional information about breeding, behavior, habitat preferences, and spatiotemporal distribution of several fluvicoline tyrants in Traylor's (1979: 160–172) genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*. These five genera belong to what Lanyon (1986: 42–43) called the *Muscisaxicola* Group (the bush and ground tyrants). Note that Lanyon (1986: 42–53) erected the genera *Heteroxolmis* for *Xolmis dominicana* and *Polioxolmis* for *Myiotheretes rufipennis* and retained the genus *Cnemarchus* for *Myiotheretes erythropygius*. In spite of the difference in generic treatment between Traylor and

Lanyon, Lanyon (1986) showed on the basis of syringeal morphology that all these taxa constituted a monophyletic assemblage, thus confirming the earlier conclusions of Vuilleumier (1971) based largely on external morphology, and of Traylor (1977: 159–166) based on a variety of taxonomic characters.

In addition to the eight genera (including 31 species) mentioned above, Lanyon (1986: 43, 51–52) included the monotypic *Gubernetes yetapa* and *Muscipipra vetula* as sister taxa in his *Muscisaxicola* Group, largely on the basis of syringeal morphology. Earlier, however, Traylor (1977: 166) had written that “*Muscipipra* may well prove to be a Tyrannine, but in the absence of more concrete evidence, I leave it in the Fluvicolines” and had written that “While I accept the near relationship of *Colonia*, *Gubernetes* and *Alectrurus* as shown by the cranial characters, I do not consider them more distinct than the other groups of Fluvicoline genera.” Lanyon (1986: 26) placed *Alectrurus* (with two species, *tricolor* and *risora*) in another group that he called the *Ochthoeca* Group, and he excluded the monotypic *Colonia colonus* from his *Empidonax* assemblage that includes the *Ochthoeca* and *Muscisaxicola* Groups on the basis of the condition of its nasal septum.

The above four genera (*Colonia*, *Alectrurus*, *Gubernetes*, and *Muscipipra*), the affinities of which are still uncertain, and 10 others as well (*Sayornis*, *Pyrocephalus*, *Ochthoeca*, *Colorhamphus*, *Ochthornis*, *Lessonia*, *Knipolegus*, *Hymenops*, *Fluvicola*, and *Tumbezia*), can all be considered bush and ground tyrants (Vuilleumier 1971: 183) on ecological grounds and are usually included in the Fluvicolinae (Traylor 1977: 159–166). These aforementioned 14 genera are not dealt with any further in this discussion, although it is worth pointing out that they, like the 5 genera treated in this report, have intriguing and as yet little known evolutionary radiations, especially *Ochthoeca* and allies and *Knipolegus* and allies.

Below I make comparisons of behavior (nesting, foraging, and display behavior) among these five genera before expanding upon some comments made in earlier publications (Vuilleumier 1971: 224–230, 1993a: 36–39) on distribution patterns (sympatry, parapatry, allopatry), modes of speciation, and isolating mechanisms.

Behavior

Nesting behavior

The nests of bush and ground tyrants are rather untidy cups, usually made of twigs and/or grass stems. Apart from size variation, these nests vary little in structure among genera and species. Some genera show constancy, and others, variability in nest site.

There is no known nest site variability in *Myiotheretes* (*sensu* Traylor 1979). *M. rufipennis* (Fjeldså 1990; this report) and *M. erythropygius* (Fjeldså & Krabbe 1990: 501) place their nests in trees or shrubs. No information regarding nest site is available for *M. pernix* or *M. fusciorufus* (Fjeldså & Krabbe 1990: 501–502). According to data reviewed in this report, there is no known variability in nest site in the two species of *Neoxolmis*; both place their cups on the ground.

In *Xolmis*, *Agriornis*, and *Muscisaxicola*, in contrast with *Myiotheretes* and *Neoxolmis*, some species select one kind of nest site but others choose a variety of sites. Below, I list a series of nest site situations which illustrate this point.

Xolmis

Within five of the six species of *Xolmis* (*sensu* Traylor 1979) for which the nest is known (Smith 1971: 242, Lanyon 1986: 47, Dubs 1992: 99), nest sites can be in one or more of seven situations (Table 1): bushes or trees, clump of grass, holes in banks, inside a picid nest, holes in trees, in nests of several furnariid species, or on top of nests of the furnariid *Anumbius annumbi*.

Agriornis

Within the five species of *Agriornis*, the cup-shaped nests can be placed in bushes or trees, in rock crevices or under eaves in churches or houses, in mineshafts, or on the ground (Table 2).

Muscisaxicola

Most species of *Muscisaxicola* hide their cup-shaped nests underground (Johnson 1965: 238–252): in crevices, under rocks in screes (as in *M. flavinucha*, pers. obs.), or in burrows (as in *M. rufivertex*, see Dorst 1962: 11–13). One species, however, *M. maculirostris*, “unlike all other members of the genus...nests on the ground in the open or with the nest partially concealed by a small bush, tuft of grass or a depression among stones” (Johnson 1965: 249).

In one species, *Muscisaxicola capistrata*, nests have been found in three kinds of situations: (1) in rabbit or rodent burrows (Philippi *et al.* 1954: 48–49; pers. obs., this report), (2) in “holes beneath stones” (Johnson 1965: 252), or (3) in a crevice of a rock face (this report).

In a pioneering early paper, von Ihering (1904) used nest shape and nest site as a taxonomic character in his subdivision of the Tyrannidae into subfamilies. More recently, Lanyon (1986) has used nest site as a taxonomic character at the genus and species levels in his phylogenetic analysis of the *Empidonax* and *Knipolegus* Groups, but not of the *Muscisaxicola* Group, to which the genera discussed in this paper belong. Given the variability in nest site described above, his decision appears to be wise. However, knowledge about nest site in these birds remains fragmentary and anecdotal. Particularly desirable would be a population study of any species of bush and ground tyrants, during which many nests would be discovered, thus revealing the full range of potential nest site variability alluded to above. Such detailed information might still reveal that nest site could be used in the future as a taxonomic character, together with other characters.

Foraging behavior

The most complete discussion of foraging behavior in South American tyrant flycatchers is that of Fitzpatrick (1980), who based his analysis on data he obtained in the field on 167 species. Of the bush and ground tyrants placed in the *Muscisaxicola* Group by Lanyon (1986), Fitzpatrick (1981: 56) gave detailed “foraging mode profiles” only for *Xolmis velata* and *Muscisaxicola fluviatilis*, however. *Xolmis velata* spent two-thirds of its time in the subcategory “Perch-ground” of the category “Ground” and about one-third of its time in aerial hawking. By contrast, *Muscisaxicola fluviatilis* spent only 1 per cent of its foraging time in “Perch-ground” feeding and 5 per cent in aerial hawking, but 92 per cent of its foraging time was on the ground.

In a subsequent paper Fitzpatrick (1981) described search strategies of South American flycatchers, an analysis based on quantitative field work on 90 species. Unfortunately, Fitzpatrick (1980) did not give a list of the species he studied and did not discuss any of the species in Lanyon’s (1986) *Muscisaxicola* Group. Some of Fitzpatrick’s (1980, 1981) observations were included in the comprehensive survey of the family by Traylor & Fitzpatrick (1982). In their

TABLE 1. Nest site variability in the genus *Xolmis*.

Species	Nest site						
	Bush or tree	Clump of grass	Hole in bank	pidicid nest	Hole or crevice in tree	Inside furnariid nest	On top of furnariid nest
	+(1)	—	—	—	—	—	—
	+(2)	—	+(3)	—	—	—	+(4)
	+(5)	+(5)	—	—	—	—	—
	—	—	—	+(6)	+(7)	+(8)	—
	—	—	—	+(9)	+(10)	+(11)	—

- (1) Pässler (1922: 463–464); Johnson (1965: 265); F. Vuilleumier (this report).
- (2) Hartert & Venturi (1909: 189); Hudson (1920: 141); Belton (1985: 53).
- (3) Hudson (1920: 141: “Azara found this species breeding in a hole in a bank”).
- (4) Sick (1993: 456: “*Xolmis cinerea*, a savana species, sometimes places its saucer on top of the nest of a Firewood Gatherer, *Anumbius annumbi*, a good solution in open country where there are few trees on which to build.”).
- (5) Hudson (1920: 142: “somewhat shallow nest in a bush or large clump of grass”).
- (6) Sick (1993: 457: “in a hole in a terrestrial termite nest made by a Field Flicker, *Colaptes campestris* [Minas Gerais]”).
- (7) Dubs (1992: 99).
- (8) Sick (1993: 457: “in the nest antechamber of a Common Thornbird, *Phacellodomus rufifrons*”).
- (9) Belton (1985: 56: “nest in woodpecker hole about 4 m up in dead snag in open field”).
- (10) Hudson (1920: 146); Wetmore (1926a: 300); Mogensen (1930: 294); Belton (1985: 56); Dubs (1992: 99); Sick (1993: 457).
- (11) Hartert & Venturi (1909: 190, inside nests of *Anumbius annumbi*, *Furnarius* sp., and *Phacellodomus* sp.); Hudson (1920: 146, inside nest of *Furnarius* sp.); Belton (1985: 56, inside nests of *Furnarius rufus*; Sick (1993: 457, inside nests of *Synallaxis phryganophila* and *Anumbius annumbi*).

Table 1, Traylor & Fitzpatrick (1982: 22) listed the following foraging modes: "near-ground generalist" for *Myiotheretes*, "perch-to-ground" for *Xolmis*, *Neoxolmis*, and *Agriornis*, and "ground picking, sallying" for *Muscisaxicola*. Earlier, Traylor (1977) had used some behavioral information in his classification of the Tyrannidae. To date, the most detailed behavioral information published on the flycatchers belonging to Lanyon's (1986) *Muscisaxicola* Group remains that in Smith (1971).

Smith (1971) had little information on *Myiotheretes*, *Xolmis*, *Neoxolmis*, and *Agriornis* (these genera *sensu* Traylor 1979), but a reasonable amount of information on *Muscisaxicola*. My observations on these birds since Smith's (1971) review largely confirm what Smith described. Similarly, my observations only slightly modify the discussion of foraging modes by Traylor & Fitzpatrick (1982: 22). Thus I agree with Traylor & Fitzpatrick's (1982) generalization that species of *Xolmis* and of *Agriornis* use chiefly the "perch-to-ground" mode and that species of *Muscisaxicola* use mostly "ground picking." The *Elanus leucurus*- and *Falco sparverius*-like hovering behavior of *Xolmis irupero* reported by Belton (1985: 56) and the *Elanus leucurus*-like flying behavior of *X. cinerea* described by Sick (1993: 473) should be noted. *Myiotheretes rufipennis* and *M. striaticollis* (pers. observ.) seem to me to fall in the category "perch-to-ground" rather than "near-ground generalist" in which Traylor & Fitzpatrick (1982: 22) had placed all species of *Myiotheretes*. Fjelds  & Krabbe (1990: 501–502) also mention aerial sallies and sally-gleaning in *M. pennix*, ground foraging and sally-gleaning in *M. fumigatus*, and aerial sallies and sally-gleaning in *M. fusciorufus*. Traylor & Fitzpatrick (1982) gave the foraging mode of the two species of *Neoxolmis* as "perch-to-ground." This may apply more to *Neoxolmis rubetra*, which forages thus more like species of *Xolmis*, than to *N. rufiventris*, which does a fair amount of "ground picking" (pers. observ.). Finally, in my experience the species of *Muscisaxicola* may do more "ground picking" than "sallying" (as illustrated by Fitzpatrick 1980: 56, for *M. fluviatilis*).

The analysis of foraging behavior initiated by Smith (1971) for the bush and ground tyrants has not progressed much in the last 25 years. Detailed comparative studies of the behavior of

TABLE 2. Nest site variability in the genus *Agriornis*.

Species	Nest site		
	Bushes or trees	manmade crevices	On the ground
<i>Agriornis montana</i>	+(1)	+(2)	—
<i>andicola</i>	—	—	+(3)
<i>livida</i>	+(4)	—	—
<i>microptera</i>	+(5)	—	—
<i>murina</i>	+(6)	—	—

(1) F. Vuilleumier (unpublished obs.; one nest in *Puya Raimondii*, Carpa, Ancash, Per , 1975).

(2) Johnson (1965: 229–231: rock crevices or clefts, abandoned mining excavations, halls in walls of houses or churches); F. Vuilleumier (unpublished obs.; rock crevices).

(3) F. Vuilleumier (this report).

(4) Johnson (1965: 226: "placed low down among thick bushes, cacti or small trees of dense foliage").

(5) Johnson (1965: 232).

(6) Nores & Salvador (1990).

these birds in Patagonia and the Andes are therefore needed before we can fully understand the evolutionary significance of the observed variability.

Display behavior

The most detailed comparative analysis of both nonvocal and vocal displays in the bush and ground tyrants is that published by Smith (1971). My observations add some information on the nonvocal displays of *Myiotheretes rufipennis* (see also Fjelds  1990), *Xolmis pyrope*, *Neoxolmis rubetra*, *Muscisaxicola capistrata* and *Agriornis andicola* (see also Vuilleumier 1993: 26–27 for *Agriornis microptera*).

All of these species appear to have displays similar to what Smith (1971) called Aerial Display and Wing Raising. The behavior Sick (1988: 585, 1993: 473) described in *Xolmis cinerea* where birds fly with dangling legs and digits flexed like a clenched fist, resembling a raptor like *Elanus*, may correspond to an Aerial Display (and may resemble similar flights in *Myiotheretes rufipennis* described in detail earlier). Recently, Davis (1993: 23) described courtship behavior in two individuals of *X. cinerea* in Bolivia, during which the birds first performed wing flaps and tail spreading while perched on the top of a bare tree and later engaged in an "aerial display of twisting,

turning, tumbling flight performed directly above the tree." Davis (1993: 23) did not mention vocalizations during the displays she observed. This sequence of perched and flight displays was observed twice. It is likely that the displays observed by Davis in *X. cinerea* correspond to Smith's (1971) Aerial Display and Wing Raising.

Since the full context and message value of these displays (W. J. Smith 1965, 1969) has not been studied, little can be said as yet about the potential phylogenetic significance of these non-vocal displays. Although Miller (1988: 355–356) did not discuss the potential significance of wing raising displays, he made suggestions about how to analyze such motor patterns in terms of characters and character states. Future workers interested in unravelling the phylogenetic meaning of displays in these flycatchers might find Miller's proposed approach to character analysis useful.

The vocalizations described in this paper for *Myiotheretes rufipennis*, *Xolmis pyrope*, *Neoxolmis rubetra*, and *N. rufiventris* are all similar in that they are mono- or bisyllabic soft calls that seem to correspond to what Smith (1971: 262) called Simple Vocalization. Smith (1971: 256–257) described some vocalizations in *Xolmis irupero*, which may also correspond to the Simple Vocalization. More recently, Sick (1988: 585, 1993: 473–474) and Belton (1985: 53–56) described the vocalizations of *X. cinerea*, *X. velata*, *X. dominicana*, and *X. irupero*. Some of these vocalizations may be more complex than Smith's Simple Vocalization, but the available information is presently insufficient to attempt unequivocal assignment to one or more of Smith's (1971: 264–265) other vocal display categories. The repeated whistles described by Sick (1988: 585, 1993: 473) for *X. velata* may correspond to Smith's (1971: 464–465) "Regularly Repeated Vocalization." Once again, however, since the message, meaning, and context value (*sensu* W. J. Smith 1965, 1969) of these vocalizations were not studied, little more can be added to what Smith (1971) wrote almost 25 years ago.

I was struck, as were other observers earlier (e.g., Smith 1971, Belton 1985: 53, 56), by the fact that the species of bush and ground tyrants described in this paper are either silent or vocally undemonstrative. A conspicuous exception to this rule of silence is *Muscisaxicola maculirostris*

which is quite loudly vocal during its Aerial Display, as I witnessed in Patagonia in 1991 (Vuilleumier 1993: 28) and in 1992 (unpubl. obs.). It is possible that other species of bush and ground tyrants are less vocal or less loud than *M. maculirostris*. It is also possible that these other seemingly silent species actually vocalize during their Aerial Displays, but that their vocalizations are inaudible to the observer because of wind or distance.

One particular kind of vocalization, the dawn song, seems to be rare in the bush and ground tyrants. I have never witnessed it in *Myiotheretes striaticollis* and *M. rufipennis*, in the three species of *Xolmis* I am familiar with, in *Neoxolmis* (both species), in *Agriornis* (all 5 species), or in *Muscisaxicola* (all 12 species). However, dawn songs have been described in a few species. For example, Fjeldså & Krabbe (1990: 501, 502) described dawn songs in *Myiotheretes fumigatus* and *M. fuscus*, Sick (1988: 585, 1993: 452, 473) described a dawn song in *Xolmis cinerea* and an "intense dawn song" in *X. velata* (Sick 1993: 452, 473), and Belton (1985: 53) mentioned a 15 minute-long dawn song in *X. cinerea* and wrote (Belton 1985: 56): "Voss (pers. commun.) reports loud whistles at dawn and dusk on May 16, 1980 near Viamão [near Porto Alegre, Rio Grande do Sul, Brazil]."

Concerning dawn song, Traylor & Fitzpatrick (1982: 12–13) had written that: "Flycatchers are notably undistinguished songsters" but that "One particular vocal feature — the dawn song — sets the Tyrannidae apart from most other tropical birds." Because "Dawn songs are so stereotyped and species-specific" (Traylor & Fitzpatrick 1982: 13), they are probably an important isolating mechanism in some genera (see also Sick 1993: 452). Lanyon (1978: 441–442, 447–448), for example, described dawn songs in South American species of *Myiarchus* but did not comment on their significance as isolating mechanisms. In his 1978 paper, as well as his 1963 paper, Lanyon did not mention the term reproductive isolation but instead stated (1978: 432) "that differences in species-specific vocalizations function as the primary basis for species discrimination among these flycatchers."

If true dawn songs exist, although they have remained unreported in the other species of bush and ground tyrants, they might constitute an

important taxonomic character at the species level. Other workers should make an effort to document dawn songs in Lanyon's (1986) *Muscisaxicola* Group and check whether they are species-specific in this group as they are in *Myiarchus*. Are the vocalizations named by Smith (1971: 264–265) Regularly Repeated Vocalization the kind of calls that one would expect in the dawn song of bush and ground tyrants?

Distribution patterns

Several kinds of distribution patterns can be recognized in the bush and ground tyrants and are discussed below (for a preliminary analysis see Vuilleumier 1971: 224–230; also Vuilleumier 1993: 36–39).

Sympatry

In my review of bush and ground tyrants I considered that 14 out of 31 species (45%) were broadly sympatric with their closest relative (Vuilleumier 1971: Table 4, page 225, 229–230). Note that Table 4 of Vuilleumier (1971: 225) listed 33, not 31, species. One, *Xolmis signata* (originally described as *Ochthodiaeta signatus* Taczanowski, 1874), which I stated “may or may not belong in *Xolmis*,” is in fact a member of the genus *Knipolegus* (Traylor 1982: 18–20). The other, *Muscigralla brevicauda*, which I placed in a monotypic subgenus of *Muscisaxicola*, was found to be so unlike other fluvicolines by Traylor (1977: 165) and Lanyon (1986: 20) that they did not include it in the bush and ground tyrants. Of the five genera discussed here, four (*Xolmis*, *Neoxolmis*, *Muscisaxicola*, and *Agriornis*) have more or less closely related species that show various kinds of interspecific range overlaps (sympatry).

These instances of overlap include: (1) Substantial geographic overlap accompanied with ecological overlap between two *Xolmis* species in northern Patagonia. Thus, in southern La Pampa and Río Negro in 1992 I observed *X. coronata* and *X. irupero* in monte shrubsteppe on several occasions. *X. irupero* was usually perched higher up in the vegetation (often on top of shrubs or trees) than *X. coronata*. (2) Narrow geographic overlap accompanied with ecological overlap between *Neoxolmis rubetra* and *N. rufiventris* in open grass steppe in Río Negro. Elsewhere (but not, at least locally in Departamento Deseado,

Santa Cruz Province; see De Lucca & Saggese 1992) these two species appear to be fully allopatric. (3) Substantial geographic overlap and ecologic overlap between/among various species of *Muscisaxicola* (e.g., *M. flavinucha*, *M. macloviana*, and *M. albilora* in the Andes of northern Patagonia). (4) Substantial geographic overlap and habitat overlap between Andean *Agriornis montana* and *A. andicola*, and between Patagonian *A. murina* and *A. microptera* (for the latter pair see Vuilleumier 1993: 27; also Vuilleumier 1992, unpubl. observ.).

In none of the instances listed above is there sufficient information about the interrelationships between or among the sympatric congeners. Cody (1970: 461, 1974: 250–257, 1985: 217–219) mentioned having observed interspecific territoriality among combinations of species of *Muscisaxicola* (including such species as *M. flavinucha*, *M. frontalis*, *M. alpina* [= *M. cinerea*], *M. albilora*, and *M. maculirostris*) in the Andes of central Chile but his conclusions were challenged by Vuilleumier & Simberloff (1980: 339–342) on observational and methodological grounds. Species of *Muscisaxicola* spp. that are easy to identify as museum skins can be difficult to tell apart under certain field conditions, unless voucher specimens are collected. The further inference of interspecific territoriality in this genus may be tenuous without the identification of nests and without the plotting of territorial boundaries, which may fluctuate throughout the breeding season. Cody's (1970: 461) conclusion that from his observations “it seems that interspecific territoriality is the rule among *Muscisaxicola* species” may need substantiation. There is little doubt, however, first, that in four genera (*Xolmis*, *Neoxolmis*, *Muscisaxicola*, and *Agriornis*) there is considerable sharing of breeding habitat by congeners and, second, that in three genera (*Xolmis*, *Muscisaxicola*, and *Agriornis*) sympatry is geographically extensive.

The evolutionary origins and the detailed ecological circumstances of these patterns of intrageneric overlap are largely unknown. How does geographic sympatry originate and develop? How do geographically sympatric and ecologically overlapping congeneric species partition the habitat in which they coexist? Can patterns of parapatry help one understand the origin of sympatry?

Parapatry

Patterns of parapatry in the bush and ground tyrants involving species in the genera *Myiotheretes* (sensu Traylor 1979) and *Muscisaxicola* were discussed in Vuilleumier (1971: 224–228). Of the 31 species discussed in that paper, only 4 (2 in *Muscisaxicola* and 2 in *Agriornis*) or 13 per cent were found to be parapatric. *Muscisaxicola alpina* and *M. cinerea* were considered to be parapatric members of a superspecies (as defined by Amadon 1966; Vuilleumier 1971: 218–223). The zone of parapatric contact between these two species, called “semispecies” in Vuilleumier (1971), was identified to be “along the eastern wall of the Andes of Bolivia (Department Cochabamba)” (Vuilleumier 1971: 223). *Agriornis livida* and *A. microptera* appeared to be parapatric in Patagonia (Vuilleumier 1971: 212). These two species were placed in the same species group but were not treated as members of a superspecies. In both instances the two species in the pair are probably sister species.

In another paper (Vuilleumier 1993: 28) I described parapatry in Patagonia between other species of *Muscisaxicola* (*M. maculirostris* and *M. capistrata*) and *Agriornis* (*A. montana* and *A. microptera*) to illustrate instances in which congeneric species that are probably not each others' closest relatives nevertheless show parapatry, thus suggesting that competitive exclusion between non-sister species may regulate their respective distributions. Note that *Agriornis montana* and *A. microptera*, which are parapatric in Patagonia, are widely sympatric in the high Andes. Thus parapatry is not an all-or-none phenomenon: a pair of species can be parapatric in part of their range and sympatric elsewhere.

The few cases of parapatry mentioned above contrast with the much larger number of cases of sympatry. Much more needs to be known about parapatry in bush and ground tyrants before one can draw inferences about the origin of habitat separation between closely related (as well as less closely related) species in these birds.

Allopatry

Two kinds of allopatric patterns are found in bush and ground tyrants: (1) between closely related congeners, and (2) absolute allopatry (the species in question is the only one of its genus in its range). Allopatry of the first kind was

described in 7 out of the 31 species (23 per cent) analyzed by Vuilleumier (1971: 225). None of these species included those treated in this report.

Absolute allopatry is found in four of the species discussed in this paper: (1) *Myiotheretes rufipennis* is the only species of *Myiotheretes* in *Polylepis* woodlands, *Puya Raimondii* stands, and other brushlands of the high Andes, although parapatry with *M. erythropterygius* could be expected locally; (2) *Xolmis pyrope* is the only member of its genus in the *Nothofagus* forest zone of Patagonia; (3) *Muscisaxicola capistrata* is the only species of its genus in the southern part of its range and appears to be narrowly parapatric with *M. maculirostris* in northern Patagonia; (4) *Muscisaxicola maculirostris* is the only species of its genus in large areas of Patagonia but is sympatric with other species in the Andes.

At face value it would appear that the cases of absolute allopatry are found in ecologically and/or geographically peripheral areas. Thus, *Myiotheretes rufipennis* lives within the isolated and relatively depauperate high Andean puna, whereas its congeners are found in the much richer habitats of montane forest below the puna. *Xolmis pyrope* is found in the isolated and geographically peripheral *Nothofagus* forest region in western Patagonia, whereas its congeners occur in shrubsteppe and other vegetation types to the northeast, separated from the forest zone by Patagonian steppes. Finally, the two allopatric or largely allopatric *Muscisaxicola capistrata* and *M. maculirostris* occur in Patagonian steppes, to the south or to the east of the main range of the genus in the high Andes.

Significance of distribution patterns

Of the taxa discussed here, those having extensively or exclusively allopatric distributions appear to have no close relative(s) within their respective genus. Thus high Andean *Myiotheretes rufipennis* was taken out of *Myiotheretes* and placed in a monotypic genus, *Polioxolmis*, by Lanyon (1986: 49). Patagonian *Xolmis pyrope* had been isolated by some authors (e.g., Meyer de Schauensee 1966: 335) in the monotypic genus *Pyrope*, and Patagonian *Muscisaxicola capistrata* may not be as closely related to *M. macloviana* as I once thought (Vuilleumier 1971: 203). Finally, note that Patagonian *Neoxolmis rufiventris*,

which breeds sympatrically with *N. rubetra* but may do so only marginally, was long the only member of the genus *Neoxolmis* until Traylor (1977: 163) and Lanyon (1986: 50–51) removed *rubetra* from *Xolmis* and placed it, together with *rufiventris*, in *Neoxolmis*.

Clear-cut pairs of allopatric or parapatric sister species in the bush and ground tyrants include *Muscisaxicola alpina/cinerea* in the Andes (Vuilleumier 1971: 201), probably *M. juninensis/albilora* in the Andes (Vuilleumier 1971: 203), and probably *M. albifrons/flavinucha* in the Andes and in Patagonia (Vuilleumier 1971: 203).

Although in the bush and ground tyrants one finds the gamut of distribution patterns, from isolated and largely allopatric species to allopatric/parapatric pairs of sister species to fully sympatric species, actual instances of truly intermediate situations between allopatry and sympatry are few. This situation makes it rather difficult for one to infer speciation pathways in the bush and ground tyrants on geographical grounds alone. To retrieve more fully the possible historical pathways that have led to differentiation and a complex hierarchy of ecogeographic distribution patterns in the bush and ground tyrants (*Muscisaxicola* Group, Lanyon 1986), I suggest that renewed interest be paid to the phylogenetic relationships of these birds (e.g., Cracraft 1988: 230–233). A research program ought to include a more complete study of behavioral characters such as those used by Smith (1971), morphological characters like those employed by Vuilleumier (1971), Traylor (1977), and Lanyon (1986), as well as new characters, especially biochemical ones.

Modes of speciation

Information concerning distribution patterns in the bush and ground tyrants can be organized in a different way from the one above. Below I analyze patterns of overlap versus non-overlap in terms of modes of speciation (Table 3), examining especially sister-taxa or putative sister-taxa.

Peripatric speciation

This term (Mayr 1982: 3) designates allopatric speciation taking place after establishment and subsequent differentiation of a founder population (Mayr 1954). In the bush and ground tyrants 11 small, peripherally isolated popu-

lations (taxa) have been identified by Vuilleumier (1971: 226–228) (see Table 3) in the genera *Myiotheretes* (*M. fumigatus lugubris*, Mérida Andes, Venezuela; *M. pernix* of the *M. fumigatus* superspecies, Santa Marta Mountains, Colombia; *M. erythropygius orinomus*, Santa Marta Mountains, Colombia), *Xolmis* (*X. pyrope fortis*, Chiloé Island, Chile), *Agriornis* (*A. montana solitaria*, Andes of southern Colombia and Ecuador), and *Muscisaxicola* (*M. maculirostris: m. niceforoi*, Eastern Andes, Colombia, *m. rufescens*, Ecuadorian Andes [indicated by “2” in Table 3]; *M. macloviana macloviana*, Falkland [Malvinas] Islands; *M. alpina: a. columbiana*, Central Andes, Colombia, *a. quesadae*, Eastern Andes, Colombia [indicated by “2” in Table 3]; *M. flavinucha brevirostris*, Tierra del Fuego Archipelago, including Navarino Island). Note that a twelfth peripheral isolate, the Santa Marta population of *Myiotheretes striaticollis*, appears to be undifferentiated morphologically (Vuilleumier 1971: 205) (“?” in Table 3). Of the 11 differentiated peripheral isolates, only 1 (*Myiotheretes pernix*) is considered to be at the species level (allopecies in Vuilleumier 1971, full species in Traylor 1979), whereas the 10 others are considered to be subspecies.

Some authors who advocate the phylogenetic species concept (e.g., Cracraft 1983, McKittrick & Zink 1988) would probably argue that the 10 peripherally isolated taxa listed above and now considered subspecies are in fact species, since they are all clearly diagnosable population units. Regardless of whether these 10 taxa are to be ranked as species rather than subspecies, the fact remains that each of the 12 peripherally distributed populations (now considered 10 subspecies, 1 full species, and 1 apparently undifferentiated population) occupies a small range and is isolated by a clear cut geographical barrier from the larger range of its sister taxon. Ten geographic barriers are involved here and were discussed in Vuilleumier (1971: 226–228); two of these barriers, the Táchira Depression in Venezuela and the Northern Peruvian Low between southern Ecuador and northern Perú (Fig. 3), were analyzed in detail by Vuilleumier (1984).

From a speciation viewpoint 9–10 (29–32%) of the 31 species of bush and ground tyrants show 11–12 examples of incipient peripatric speciation, if each of the isolates men-

tioned above represents a population at or near the species level (Table 3). At face value, therefore, peripatric speciation may be important in the geographical diversification of the bush and ground tyrants. Further research should, first assess whether morphological differentiation is congruent with biochemical differentiation between each isolate and the remainder of its sister taxon, then should attempt to determine the time since original divergence, and finally, should attempt to establish whether each peripheral isolate did indeed originate from a founder event.

Dichopatric speciation

Using a term coined by H. M. Smith (1965: 57) for fully allopatric sister taxa, Cracraft (1984: 115) proposed that allopatric speciation resulting from the splitting of a wide-ranging ancestral species into two or more large descendant species by a vicariance event should be called dichopatric speciation, to clearly demarcate this mode from Mayr's (1982) peripatric mode. In the bush and ground tyrants, dichopatric patterns (including both the fully allopatric and partially or completely parapatric patterns reviewed earlier in this discussion) can be found in the genera *Myiotheretes* (*M. fumigatus* and *M. fusciorufus*, both considered species), *Xolmis* (*X. irupero*, two differentiated populations, both considered subspecies), *Agriornis* (*A. microptera*, two differentiated populations considered subspecies; *A. livida* and *A. microptera*, both species and assuming that they are sister species), and *Muscisaxicola* (*M. juninensis* and *M. albilora*, both species; *M. alpina* and *M. cinerea*, both species; and *M. albifrons* and *M. flavinucha*, both species). Thus, 11 out of 31 species (35%) of bush and ground tyrants show dichopatric speciation with full allopatry (Table 3).

In addition, in 2 species (*Myiotheretes striatocollis* and *Agriornis montana*) patterns of geographic variation suggested to Vuilleumier (1971: 205, 210–211) the possibility of secondary hybridization, also a consequence of dichopatric but incomplete speciation (Table 3). These instances would bring to 13 (42%) the number of cases of dichopatric speciation in the 31 species of bush and ground tyrants analyzed here. Judging from the fact that more species pairs are involved in dichopatric than in peripatric spe-

ciation, it would appear that dichopatric patterns are older than peripatric ones. Once again, however, evidence from biochemical research should illuminate the question of whether the greater morphological differentiation associated with cases of dichopatric speciation reflect a longer period of time since original divergence.

Partial (secondary?) sympatry

Fitzpatrick (1980: 1278, Fig. 4) mapped two instances of partial sympatry in *Xolmis* (between *X. velata* and *X. dominicana* and between *X. cinerea* and *X. coronata*, the latter pair considered members of a superspecies by Short (1975: 268) and I documented (this report) one instance in *Neoxolmis* (between *N. rubetra* and *N. rufiventris*) (Table 3). The amount of geographic overlap between the two species in each of these three pairs of species remains to be fully documented by further field work. For example, information in Short (1975: 268) and Olog (1979: 204–205) suggests that *Xolmis cinerea* and *X. coronata* are in fact parapatric, or even allopatric, rather than partially sympatric, contra Fitzpatrick (1980: 1278). Furthermore, the degree of ecological overlap in the zone of sympatry remains to be studied in all these instances.

The two species in each of these three pairs are morphologically quite distinct and one could question whether they are indeed sister species. The case of the two species of *Neoxolmis*, analyzed in detail by Traylor (1977) and Lanyon (1986), and considered to be each other's closest relative, was mentioned earlier in this paper. If the species pairs in *Xolmis* are sister species and show at least some overlap, one can postulate that these patterns originated by dichopatric speciation, later followed by range expansion by one or both of the vicariant taxa. Much work remains to be done to establish the phylogenetic relationships of the two species in each of the three pairs and the possible barrier(s) that may have led to the present distribution patterns.

Complete (or nearly complete) sympatry

Agriornis andicola and *A. montana* are extensively sympatric and occupy the same or very similar habitats, as discussed earlier. Assuming that these two are sister species, the extent of their sympatry makes it difficult to ascertain the localization of the original speciation (vicari-

TABLE 3: Speciation and distribution patterns in five genera of bush and ground tyrants.

Taxon*	Speciation mode				Parapatric
	Peripatric	Fully allopatric	Second. hybrid.		
<i>Myiotheretes striaticollis</i>		—	—	+	?
<i>M. erythropygus</i>	+	—	—	—	—
<i>M. rufipennis</i> ***	—	—	—	—	—
<i>M. pennix</i>	+	—	—	—	—
<i>M. fumigatus</i>	+	+	—	—	—
<i>M. fuscocorufus</i>	—	+	—	—	—
<i>Xolmis pyrope</i>	+	—	—	—	—
<i>X. cinerea</i>	—	—	+	—	?
<i>X. coronata</i>	—	—	+	—	—
<i>X. velata</i>	—	—	+	—	—
<i>X. dominicana</i>	—	—	+	—	—
<i>X. irupero</i>	—	+	—	—	—
<i>Neoxolmis rubetra</i>	—	—	+	—	—
<i>N. rufiventris</i>	—	—	+	—	?
<i>Agriornis montana</i>	+	—	—	+	?
<i>A. andicola</i> ***	—	—	—	—	—
<i>A. livida</i>	—	+	—	—	—
<i>A. microptera</i>	—	+	—	—	—
<i>A. murina</i> ***	—	—	—	—	—
<i>Muscisaxicola maculirostris</i>	+(2)**	—	—	—	—
<i>M. fluviatilis</i> ***	—	—	—	—	—
<i>M. macloviana</i>	+	—	—	—	—
<i>M. capistrata</i> ***	—	—	—	—	—
<i>M. rufivertex</i> ***	—	—	—	—	—
<i>M. juninensis</i>	—	+	—	—	—
<i>M. albilora</i>	—	+	—	—	—
<i>M. alpina</i>	+(2)**	+	—	—	?
<i>M. cinerea</i>	—	+	—	—	?
<i>M. albifrons</i>	—	+	—	—	—
<i>M. flavinucha</i>	+	+	—	—	—
<i>M. frontalis</i> ***	—	—	—	—	—
Number of instances:	11-(?12)	11	6	2	10?

* Sequence and nomenclature follow Traylor (1979: 160–172).

** "(2)" indicates that 2 instances of peripatric speciation can be detected in *Muscisaxicola maculirostris* and in *M. alpina* (see text).

*** Species not participating in any clear cut instance of speciation (see text).

ance) event as well as the mode of speciation (whether peripatric or dichopatric). Further fine-grained morphological analysis, coupled with fresh insight provided by an analysis of biochemical differentiation, might yield information concerning the exact relationships of these two species and the possible timing of their divergence from a common ancestor. Should the information on timing suggest that the original vicariance event took place one to two million years ago or earlier, then it is unlikely that geographic barriers in the high Andes due to Pleisto-

cene glaciation and deglaciation cycles as postulated by Vuilleumier & Simberloff (1980: 322–326) have been responsible for the evolution of this species pair, since vicariant events predated these glacial fluctuations. Because other species of the genus *Agriornis* occur entirely (*A. livida*) or in part (*A. microptera*) in Patagonia, the ancestral vicariance event need not have taken place in the high Andes, where these two species are now sympatric.

If one considers that the allopatric pair of species *Muscisaxicola juninensis/albilora* make up

a single "zoogeographical species" (*sensu* Mayr & Short 1970: 3) then it overlaps considerably with its putative sister taxon, *M. rufivertex*. Again, if *M. albifrons/flavinucha* are counted as one zoogeographical species then its putative sister taxon *M. frontalis* is extensively sympatric with *flavinucha*. In these two instances geographical overlap is accompanied by at least some habitat co-occupation (pers. obs.). As in the case of *Agriornis* just mentioned, both the original vicariance event and the mode of speciation remain to be discovered.

One can hypothesize that the one instance in *Agriornis* and the two instances in *Muscisaxicola* involving substantial amounts of sympatry between what are now believed to be sister taxa represent relatively old speciation patterns, whether the mode was peripatric or dichopatric. These three cases involve 8 species out of 31 (26%) and thus suggest the possibility of active speciation in the past. Other than the verification of the sister taxon relationships of the different species involved, analysis of biochemical characters might reveal the time elapsed since the ancestral taxa split into two or more descendant ones.

Parapatric speciation

According to Endler (1977: 12–16) this mode of speciation can be expected when certain genotypes or phenotypes are eliminated by natural selection in the area of an ecological gradient, thus leaving a parapatric pattern that "mimics" allopatric speciation and could be mistakenly interpreted as dichopatric speciation. The occurrence of parapatric speciation in birds was suggested by Endler (1977: 170–175) as an alternative mode for the dichopatric model (refuge theory) proposed by Haffer (1969, 1974) for a large number of parapatric groups of bird species in Amazonia. Whether parapatric speciation as proposed by Endler (1977) does indeed take place in birds remains uncertain, although in a recent paper Ripley and Beehler (1990: 643) listed six instances of probable parapatric speciation in birds in the Indian subcontinent. Haffer (1992) reviewed parapatric species of birds on a worldwide basis and listed many instances, but unfortunately none from the Andean-Patagonian region. Haffer (1992: 257), correctly pointing out that "Only few parapatric contact zones of birds have been studied in sufficient

detail to be certain about the cause of geographic replacement," hoped to stimulate much needed further research into parapatric species pairs. (The possibility of sympatric speciation in birds has been reexamined by Grant & Grant 1989 for some Galapagos finches and found not to apply.)

Parapatric speciation has recently been evoked as a possibility for some high Andean birds by Fjeldså (1992: 42–43), in view of the apparent importance of ecotones in speciation of many Andean birds. But Fjeldså (1992: 42) rejected parapatric speciation as a likely mode, chiefly because "the taxa inhabiting these adjacent zones [across an ecotone] are in no case each other's sister taxa." The case of parapatry across a forest/steppe ecotone in *Phrygilus patagonicus/gayi*, which are likely to be sister taxa and was mentioned by Vuilleumier (1991: 14–18), will be dealt with more fully in a later publication (Vuilleumier, in prep.). Whether speciation in this instance was parapatric or dichopatric remains to be determined.

In the bush and ground tyrants discussed in this paper, the possibility of parapatric speciation can be entertained in *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*. All cases have been indicated by "?" in Table 3. In *Myiotheretes striaticollis*, the area indicated as a possible instance of secondary hybridization could conceivably correspond to parapatric speciation. In *Xolmis*, *X. velata/dominicana* and *X. cinerea/coronata* meet (and partially overlap according to the maps in Fitzpatrick 1980: 1278) in what appear to be the ecotone areas between chaco and cerrado and between espinal and chaco, respectively (see vegetation map of Hueck & Seibert 1981). The original speciation event could have been vicariant (dichopatric mode), although the barriers involved are unknown, or parapatric. In *Neoxolmis*, *N. rubetra* is a species living largely in the monte, whereas *N. rufiventris* lives in Patagonian steppes, and the area of sympatry corresponds roughly to the ecotone between monte and steppes (Hueck & Seibert 1981). In *Agriornis montana* the area identified by Vuilleumier (1971: 210–211) as either a stepped cline or a zone of secondary hybridization corresponds roughly to the ecotone between the moist puna and the dry puna of Troll (1959). Finally, in *Muscisaxicola*, as in *Agriornis*, the area of contact between the parapatric species

alpina and *cinerea* may correspond to the transition between moist and dry puna (Vuilleumier 1971: 221–223).

Much more field, museum, and biochemical work will be necessary before the instances summarized above can be documented to the point where they can be interpreted unequivocally in terms of given modes of speciation, especially since it may be extremely difficult to distinguish allopatric (dichopatric) from parapatric speciation (Endler 1977: 152–175). If one assumes, for the sake of argument, that the cases reviewed above do represent parapatric speciation, then 10 species of bush and ground tyrants out of 31 (32%) might have originated by this mode (Table 3). This is a high rate. However, even the better documented cases, those of *Agriornis montana* and of *Muscisaxicola alpina/cinerea*, are still far from offering anywhere near enough evidence either pro or con parapatric speciation.

In their paper on speciation in Indian birds, Ripley & Beehler (1990: 644) wrote: "We believe that in six instances our data show a good fit to [the model of parapatric speciation], specifically because the distribution of the two species [in each species pair] coincides so agreeably with the distribution of the two abutting habitats, and the species' range boundaries meet at the ecotone." They further stated (page 644) that: "The relationship of the species' distribution with respect to the two discrete habitats agrees with the parapatry model but no other, mainly because no physical barrier to dispersal is evident (e.g. no river, no gorge, no mountain chain)." I believe that caution should be exercised here because the fact that no barrier can be detected *at present* does not mean that none occurred in the past and has since been removed, or else that the original vicariance event (dichopatry) took place far from the area of present-day parapatry. In the cases of *Agriornis montana* and *Muscisaxicola alpina/cinerea* there is no clear-cut barrier today in the stepped cline or hybridization area within *A. montana*, nor is there a clear-cut barrier between parapatric *M. alpina* and *M. cinerea*. Nevertheless, there is reason to believe that Pleistocene events involving one or more barriers that are no longer evident in the high Andes may have been responsible for some of the speciation patterns detectable today (Vuilleumier 1971: 228–229; Vuilleumier & Simberloff 1980: 321–328).

Overview of speciation

Whatever mode of speciation (peripatric, dichopatric, or parapatric) is taking place now or has taken place in the past in bush and ground tyrants of the monophyletic group of genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*, the previous discussion makes it clear that speciation is and has been active in these birds (Table 3). Thus, of 31 species 9 (29%) show evidence of peripatric (or incipient peripatric) speciation and 11 (or perhaps 13) species (35 or 42%) show evidence of dichopatric speciation. Another six species (19%) show what may represent former dichopatric speciation. If all possible instances of dichopatric speciation are considered together, then a total of 18 out of 31 species (or 58%) have participated or are participating in speciation of the dichopatric mode. Finally, it seems possible that parapatric speciation can be detected in 10 species (32%), although this speciation mode is rather unlikely on theoretical grounds and much more evidence is needed before it can be firmly established.

Within some species-level taxa of bush and ground tyrants there is evidence that more than one speciation mode is operating (or has operated in the past). These taxa are: (1) *Myiotheretes fumigatus* (peripatry: one isolate; dichopatry: allopatric species pair *fumigatus* and *fuscocorufus*); (2) *Agriornis montana* (peripatry: one isolate; dichopatry/parapatry: incomplete speciation and possible secondary hybridization within what is currently considered to be a single species, *montana*); (3) *Muscisaxicola alpina* (peripatry: two isolates; dichopatry/parapatry: *alpina* and *cinerea*); and (4) *Muscisaxicola flavinucha* (peripatry: one isolate; dichopatry: *flavinucha* and *albifrons*).

The seven species not participating in any clear cut instance of speciation (identified by *** in Table 3) are *Myiotheretes rufipennis* (taxonomically isolated), *Agriornis andicola* (extensively sympatric with *A. montana*), *A. murina* (isolated within its genus), *Muscisaxicola fluviatilis* (only tropical lowland species, perhaps isolated within its genus), *M. capistrata* (?isolated within its genus; and with a peripheral distribution in Patagonia), *M. rufivertex*, and *M. frontalis*. Table 3 summarizes the information on speciation reviewed in this section. Of the total of 31 species listed in this table, 23 (74%) show at least some

evidence of active speciation in the more or less recent past.

In my earlier overview of speciation patterns in bush and ground tyrants (Vuilleumier 1971: see Table 4 on p. 225) I did not quantify speciation phenomenon in the same way, in part because I did not analyze speciation in terms of peripatric, dichopatric, or parapatric modes as in the present paper. Although I described several cases of active speciation in that earlier paper, I now believe, after further study in the museum and in the field, that I may have underestimated the number of detectable speciation events in the bush and ground tyrants. This renewed analysis, even more than my earlier one, reveals a group of Andean and Patagonian birds in full evolutionary radiation.

In my earlier paper (Vuilleumier 1971: 230) I concluded that because patterns of sympatry were extensive in the bush and ground tyrants, especially in *Xolmis*, *Agriornis*, and *Muscisaxicola*, "it would therefore seem that [the ground tyrants] have been present in the high Andes and the extra-Andean open regions of central South America for a long time, so long, in fact, that the early stages of their adaptive radiation have been obliterated by complex patterns of secondary sympatry." I may have been overly conservative in my assessment.

Now that Lanyon (1986: 43) has proposed a formal phylogeny of these birds at the genus level, the challenge for future work is twofold: (1) To attack again the problem of the early stages of this radiation by means of appropriate phylogenetic analyses based on novel characters and novel methodologies, in order to test Lanyon's hierarchy of higher taxa; and (2) To identify sister species especially perhaps within speciose genera, in order to document details of the branching sequence of this phylogeny at lower taxonomic levels not treated by Lanyon. This program of research could be accomplished by a concerted effort involving studies of a variety of features of the living birds (behavior, ecology, interspecific interactions), and of characters that can be studied on specimens (reanalysis of external morphology, analysis of new anatomical characters) or on the basis of tissue samples (electrophoresis of enzymes, DNA sequencing).

Reproductive isolation

Given the observation that both vocal and non-vocal displays are (apparently, on present evidence at least) quite similar across many species of bush and ground tyrants in the genera *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*, it seems unlikely that display behaviors act in a major way as reproductive isolating mechanisms (defined in Futuyma 1986: 112–114, 553) in this monophyletic group of tyrant flycatchers. More likely, reproductive isolation between closely related species may be correlated with size or body mass and/or color patterns, although conceivably both size and color pattern differences could be enhanced during some of the vocal and/or non-vocal displays. Table 4 lists differences and similarities between sister taxa of fluvicoline flycatchers (see also Table 1 in Vuilleumier 1993: 36–37). Table 4 lists, first, sympatric sister taxa and next, parapatric ones.

Thus, among the six species of the *Myiotheretes fumigatus* group (*sensu* Vuilleumier 1971: 195) the three allospecies of the *fumigatus* superspecies vary more or less conspicuously from one another in color and pattern and are different as a group, in color and in size, from their partly sympatric congener and probable sister taxon *striaticollis* (Table 4). Interspecific relationships between *striaticollis* and members of the *fumigatus* superspecies should be investigated where these taxa overlap geographically and where color and pattern differences might provide reproductive isolation.

In *Xolmis*, color, pattern and/or size vary among species. Thus, each member of the parapatric or partly sympatric and putative sister species pairs *X. velata/dominicana* and *X. cinerea/coronata* mapped by Fitzpatrick (1980: 1278) differs more or less markedly from its sister species in relative extent of black, white, and gray in its plumage (Table 4).

Similarly, in *Neoxolmis*, color and pattern (as well as body mass) vary between the two parapatric or partly sympatric sister species *N. rubetra* and *N. rufiventris* (Table 4).

In *Agriornis*, color differences that are quite detectable on study skins (for example, number and relative thickness of throat streaks; relative grayness of body plumage, irrespective of the darkening through time to which these skins appear to be prone, Vuilleumier 1971: 210) are

not that marked in the field, at least to the human eye. Bill size differences which are marked in some species pairs with otherwise comparable plumage morphologies including color pattern (sympatric pairs *A. montana/andicola* and *A. livida/microptera*) again are not always that conspicuous to the human eye in the field. In the *A. montana/andicola* species pair the base of the lower mandible is pale in large-billed *andicola* and black in smaller-billed *montana*, a color difference that is more visible in the field (to a human observer) than bill size and that might be a reproductive isolating mechanism (Table 4). A bill size difference in these two species might also act together with the color difference as a reproductive isolating mechanism. Bill size differences are usually thought of as representing trophic differences where bigger-billed birds consume bigger food items (Schoener 1965, Ashmole 1968: 297–300).

The major character that differentiates *A. montana* from *A. andicola* is body mass (Table 4). Thus, 5 Bolivian specimens of *montana* that I collected weigh 54.0 g (♀ AMNH 793201), 56.0 g (♀ AMNH 793200), 58.4 g (sex?, AMNH 793202), 60.9 g (♂ AMNH 793199), and 67.0 g (♀ AMNH 793198) (mean 59.3 g), and 1 Peruvian specimen 74.0 g (♂ AMNH 824145) (overall mean 61.7 g; Vuilleumier 1971: 211 gave a mean of 60.7 g for a slightly different sample). Two Bolivian specimens of *andicola* that I collected weigh 80.0 g (♂ AMNH 793161) and 82.0 g (♂ AMNH 793162) (mean 81.0 g; Vuilleumier 1971: 211 gave a mean of 82.3 g for a slightly different sample). On present evidence there is no overlap in body mass between these two species. Note that the two nestlings of *A. andicola* mentioned earlier had weights of 61 g and 79 g, respectively close to the mean of *A. montana* and 5 g higher than the heaviest specimen of *A. montana* reported above. Note also that in Bolivia these two species have similar tail patterns, whereas in other parts of the range *A. montana* has a different tail pattern from *A. andicola*. Fjeldså (1992: 60) considered the extensively white tail of high Andean *A. montana* and *A. andicola* to be a synapomorphy, but did not elaborate on this comment. The possible significance of tail pattern as an isolating mechanism in *Agriornis* remains to be studied. The variation in tail pattern discussed by Vuilleumier (1971:

210–211) for *A. montana* in southern Perú and northwestern Bolivia was interpreted in terms of secondary hybridization between formerly isolated populations.

In *Muscisaxicola*, there is a clear cut size gradient. Vuilleumier (1971: Fig. 11 p. 202) illustrated this variability in a bivariate plot of wing length against tail length of seven species and Cody (1985: 217–218) commented on bill length differences among several species of *Muscisaxicola*. Most species seem to exhibit little overlap in size. In the parapatric pair of sister species *M. alpina* and *cinerea* in Bolivia (Table 4), there seems to be no overlap in body mass, *alpina* ranging from 24.9 g to 27.9 g (mean 26.6 g), and *cinerea* from 17.5 g to 23.3 g (mean 20.6 g) (see Vuilleumier 1971: Table 3, p. 222).

Other species of *Muscisaxicola* exhibit differences in crest, nuchal, or facial color and pattern (see color plate of heads in Johnson 1967: 236; also Fjeldså & Krabbe 1990: Pl. XLIII, p. 789), which show no apparent intraspecific variability and might serve as reproductive isolating mechanisms. Cody (1970: 461) correctly stated that “cap or head markings ... show all the signs of species-specific recognition cues.” Note, however, that in the field some of these color or pattern differences, no matter how clearly seen on museum skins, are not always very obvious to the observer. Finally, although crest/nuchal patch colors do not appear to be used in display by *Muscisaxicola* spp., more field work is needed to establish conclusively whether this is true or not.

PROSPECT

In spite of much scattered, largely anecdotal, evidence in the ornithological literature, we know remarkably little more in the mid-1990s about many aspects of the reproductive biology, behavior, distribution, systematics, and evolution of bush and ground tyrants than we did about 25 years ago, when W. John Smith and I were preparing our behavioral and systematic reviews of these birds (Smith 1971, Vuilleumier 1971). Hopefully the present paper will spur ornithologists to start paying more attention to these fascinating but often shy, retiring and elusive birds. To help in this endeavor, I have suggested in the preceding sections a number of

TABLE 4. Differences and similarities between sympatric or parapatric sister taxa of bush and ground tyrants in Patagonia and the high Andes.

Sympatric sister taxa	Size	Color and pattern	Habitat
<i>Myiobberetes striaticollis</i>	Much larger than <i>fumigatus</i> supersp.	Throat streaks well marked, tail largely rufous at base, primaries with rufous patch	Variable, forest edge to dry open slopes
<i>fumigatus</i> supersp. (<i>pernix</i> , <i>fumigatus</i> , <i>fusciorufus</i>)	Much smaller than <i>striaticollis</i>	Throat streaks less well marked, tail largely dark, primaries with rufous patch	Cloud forest, forest edge
	Smaller than <i>andicola</i>	Plumage similar to <i>andicola</i> , throat streaks thinner than <i>andicola</i> , bill thinner than <i>andicola</i> and entirely black	Usually dry and rocky mountain slopes
<i>andicola</i>	Larger than <i>montana</i>	Plumage similar to <i>montana</i> , throat streaks thicker than <i>montana</i> , bill thicker than <i>montana</i> , base of lower mandible pale	Usually dry and rocky mountain slopes
Parapatric sister taxa	Size	Color and pattern	Habitat
<i>Xolmis velata</i>	Slightly larger than <i>dominicana</i> , tail shorter than <i>dominicana</i>	Underparts white, outer primaries dark, tail black and white	Caatinga, campos, cerrados, open woodlands
<i>dominicana</i>	Slightly smaller than <i>velata</i> , tail longer than <i>velata</i>	Underparts white, outer primaries with white subterminal band, tail all black	Grasslands, campos, espinal, open woodlands, edges of gallery forest
<i>Xolmis cinerea</i>	Slightly larger than <i>coronata</i>	Forehead, crown and back gray, postocular streak absent, breast gray, outermost primaries with white basal patch, tail with wide terminal gray band	Caatinga, campos, cerrados, chaco, grasslands, open woodlands
	Slightly smaller than <i>cinerea</i>	Forehead white, crown black, back gray, postocular streak white, breast white, outermost primaries without white basal patch, tail with narrow terminal gray band	Grasslands, espinal, monte, chaco transition
<i>Neoxolmis rubetra</i>	Smaller than <i>rufiventris</i>	Back brown, chest white streaked, eyebrow white, secondaries dark brown; underwing coverts rufous	Monte, steppes
<i>rufiventris</i>	Larger than <i>rubetra</i>	Back grayish brown, chest gray unstreaked, no eyebrow, secondaries rufous at base, white at tip; underwing coverts rufous	Patagonian steppes

Sympatric sister taxa	Size	Color and pattern	Habitat
<i>Agriornis montana insolens</i>	Slightly larger than <i>m. montana</i> + <i>m. maritima</i>	Body plumage similar to <i>m. montana</i> + <i>m. maritima</i> , outer rectrices white	Páramo, puna, dry mountain slopes
<i>montana montana</i> + <i>montana maritima</i>	Slightly smaller than <i>m. insolens</i>	Body plumage similar to <i>m. insolens</i> , outer rectrices white-tipped with white outer web	Puna, dry mountain slopes
<i>Agriornis livida</i>	Larger than <i>microptera</i>	Plumage and tail similar to <i>microptera</i> , lower abdomen and undertail coverts brownish rufous; outer rectrices thinly edged with white	Matorral, thorn scrub, Patagonian steppe
<i>microptera</i>	Smaller than <i>livida</i>	Plumage and tail similar to <i>livida</i> , lower abdomen grayish brown, outer rectrices with white outer vane	Monte, Patagonian steppe
<i>Muscisaxicola alpina</i>	Larger than <i>cinerea</i>	Plumage similar to <i>cinerea</i> , breast darker gray than <i>cinerea</i> , wing coverts more grayish than <i>cinerea</i> , lores more conspic. white than <i>cinerea</i>	Páramo, moist puna
	Smaller than <i>alpina</i>	Plumage similar to <i>alpina</i> , breast whitish gray, paler than <i>alpina</i> , wing coverts more brownish than <i>alpina</i> , lores less conspic. white than <i>alpina</i>	Dry puna

general evolutionary questions. Many specific questions need answers as well. I list below a sample of such questions that can best be answered by resident students in South America.

(1) What is the taxonomic and evolutionary significance of variability in nest site at the species and genus levels among the bush and ground tyrants? What is needed is systematic information on the breeding of many species.

(2) What is the taxonomic and evolutionary significance of foraging and display behavior in the bush and ground tyrants (de Queiroz & Wimberger 1993 have recently compared morphological and behavioral characters in phylogenetic reconstruction, including some data from tyrant flycatchers)? What is needed is detailed field studies and descriptions of behavioral traits, even in the more common or widespread species. In a recent paper Miller (1988) made many suggestions about ways to describe bird behavior

that would permit cross-taxonomic comparisons.

(3) What is the closest relative of the high Andean endemic *Myiotheretes (Polioxolmis) rufipennis*? Is *Agriornis montana* the sister species of *A. andicola*, another high Andean endemic, as suggested by Vuilleumier (1971)? What is the closest relative of the Patagonian endemic *Xolmis (Pyrope) pyrope*? Is *Neoxolmis rubetra* really the sister species of another Patagonian endemic *N. rufiventris*, as suggested by Traylor (1977) and by Lanyon (1986)? Finally, what is the sister species of yet another Patagonian endemic, *Muscisaxicola capistrata*? What is needed here is more material for anatomical and biochemical studies.

(4) Do *Neoxolmis rufiventris* (Fig. 16, right) and *Muscisaxicola capistrata* (Fig. 22) have disjunct breeding distributions in Patagonia, as present evidence suggests, or do they have more or less continuous distributions from southern

to northern Patagonia in appropriate steppe habitats? What is needed is a systematic search for these species in areas where they have not been reported ("?" in Figs. 16 and 22).

(5) What are the ecological and behavioral interrelationships of *Neoxolmis rufiventris* (essentially a Patagonian steppe species) and *N. rubetra* (essentially a monte shrubsteppe species) in their narrow area of geographical overlap where they breed side by side? For example, do they have interspecific territoriality?

(6) Is there any concrete evidence that *Muscisaxicola capistrata* has declined in number in the Chilean Tierra del Fuego part of its range since the 1930s and 1940s?

(7) Is *M. capistrata* more common in the Chilean than the Argentine part of northern Tierra del Fuego, and, if so, why? Are there significant habitat differences between northwestern and northeastern Tierra del Fuego? If *M. capistrata* breeds regularly in *Ctenomys* burrows in Tierra del Fuego, what is the distribution of the mammals there?

(8) Is there any concrete evidence of abundance fluctuations in the southern Patagonian population of *Neoxolmis rufiventris*? Resident ornithologists alone can hope to answer this question.

(9) *Xolmis pyrope* seems to favor more open habitats at the northern and southern extremities of its range than in the center; does this species use different features in habitat selection in different parts of its range?

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