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Two species of *Neopelma* in southeastern Brazil and diversification within the Neopelma/Tyranneutes complex: implications of the subspecies concept for conservation (Passeriformes: Tyrannidae)

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RESUMO. **Duas espécies do gênero *Neopelma* no sudeste do Brasil e diversificação dentro do complexo Neopelma/Tyranneutes: implicações do conceito de subespécie para a conservação (Passeriformes: Tyrannidae).** Duas subespécies admitidas de *Neopelma aurifrons*, a forma típica do norte e *chrysolophum* das montanhas do sul provam ser espécies distintas, com limitada parapatria/simpatria elevacional, com base em evidentes diferenças na vocalização, morfologia externa e hábitat. O exame de padrões de distribuição das aves na Mata Atlântica e na Amazônia conjugado com os dados acima sugere que as duas espécies vieram a se estabilizar no sudeste do Brasil durante períodos distintos e não são parentes próximos um do outro. Postulamos que os membros do gênero *Neopelma* (conforme geralmente admitido) representam populações relictuais de um antigo e bem espalhado complexo, e sugerimos que a segregação dentro desse grupo originou *aurifrons* e os atuais representantes de *Tyranneutes*, provavelmente em concordância, pelo menos em parte, com as alterações paleoclimáticas que interferiram na distribuição e composição dos ambientes florestais. *N. aurifrons*, forma altamente distinta e espécie-tipo do gênero, está entre as mais precariamente protegidas e menos conhecidas das espécies endêmicas da floresta atlântica brasileira. Lembramos que *N. aurifrons stricto sensu* tem sido desconsiderada pelos biologistas de campo, sistematas e conservacionistas devido principalmente ao seu tratamento como subespécie. O caso *Neopelma aurifrons/chrysolophum*, como aqui apresentado, chama a atenção para a proteção, sempre que possível, de populações representativas de formas isoladas, sem considerar o nível hierárquico arbitrado por sistematas na mutável classificação convencional. Tal abordagem deve subsidiar a definição de "áreas prioritárias" para a conservação.

PALAVRAS-CHAVE: Amazônia, biogeografia, Brasil, conservação, especiação, Mata Atlântica, *Neopelma*, padrões de distribuição, taxonomia, Tyrannidae, *Tyranneutes*, vocalizações.

ABSTRACT. Based on clear differences in vocalizations, external morphology, and habitat, the two subspecies of *Neopelma aurifrons*, lowland *aurifrons* in the north and montane *chrysolophum* in the south, are shown to be distinct species in limited elevational parapatry/sympatry. Consideration of avian distribution patterns in the Atlantic Forest and Amazonia coupled with the above data suggests that the two species became established in southeastern Brazil during separate periods and are probably not each others' closest relatives. We postulate that the members of *Neopelma* (as the genus is currently defined) are relicts of an ancient, widespread complex, and we suggest that one isolate of this group gave rise to *aurifrons* and to *Tyranneutes*, probably in concordance with paleoclimatic shifts in the distribution and composition of forest habitats. *N. aurifrons* is the type of the genus and a highly distinctive form, yet is among the least-known and most poorly protected endemic birds of the Brazilian Atlantic Forest. We suggest that it has been neglected by field biologists, systematists, and conservationists owing principally to its status as a subspecies. *N. aurifrons* represents a case in point for the importance of safeguarding, wherever possible, representative populations of isolated forms, regardless of their level of formal classification. Such an approach should inform the definition of "priority areas" for conservation.

KEY WORDS: Amazonia, Atlantic Forest, biogeography, Brazil, conservation, distribution patterns, *Neopelma*, speciation, taxonomy, Tyrannidae, *Tyranneutes*, vocalizations.

The genus *Neopelma* currently comprises four allopatric species regarded as allospecies (Snow 1979, Sibley and Monroe 1990). Within their respective ranges, all of the members of *Neopelma* are patchily distributed and generally inconspicuous birds, and are overall poorly known. The easternmost member of the genus, *N. aurifrons* (Wied's Tyrant-Manakin), is represented by two subspecies occupying the Atlantic Forest region between southern Bahia and southern São Paulo, Brazil. Between 1988 and 1990, Geraldo T. de Mattos and Luiz P. Gonzaga corresponded concerning the possibility that the two subspecies of *N. aurifrons* were separate species, based primarily upon clear vocal differences observed by Mattos in Minas Gerais (L. P. Gonzaga pers.

comm. 1995). Suspecting that two species were involved because of morphological distinctions and their unusual distribution pattern within the Atlantic Forest, we independently documented vocal differences and made other comparisons of *aurifrons* in Espírito Santo and *chrysolophum* from Minas Gerais, Rio de Janeiro, and São Paulo. Most recently, we found nominate *aurifrons* near the city of Rio de Janeiro and gathered further data on vocalizations and behavior. In this paper we provide evidence that these subspecies are distinct species, and discuss their relationships within *Neopelma* and diversification of the Neopelma/Tyranneutes complex.

RESULTS AND DISCUSSION

Taxonomic history. Muscicapa aurifrons (Wied 1831) was described from an unspecified number of specimens collected in southern Bahia. Wied listed two specific localities for his material: "Camamu und Bahiá". The holotype is at the American Museum of Natural History (AMNH), number 5065, with the vague locality designation "Brasilien" (Allen 1889; M. LeCroy *in litt.* 1995), although Allen (1889) designated the type locality as "Vicinity of Bahia". Wied referred to the city of São Salvador da Baía de Todos os Santos (today known simply as Salvador) as "Baía" or "Bahia". This is explicit in several passages of Wied's (1940) "Viagem ao Brasil"; for example, his chapter title on page 421: "Viagem de Conquista à capital da Baía e estadia nessa cidade" and page 449: "O comércio da Baía é muito ativo; essa cidade serve de entreposto para os produtos do Sertão..." Thus, it is acceptable that the type locality for *Neopelma aurifrons* be Salvador, Bahia or, as reasonably designated by Allen (1889), "Vicinity of Bahia" (= vicinity of Salvador). Hellmayr (1929), however, listed the type locality as "Camamu, southern Bahia" (at sea-level about 126 km SSW of Salvador in the southern coastal region of the state [Paynter and Traylor 1991]), despite Allen's earlier designation. Camamu has been perpetuated as the type locality by Pinto (1944) and Snow (1979). As there apparently existed (and yet exists) only one AMNH specimen of *N. aurifrons* taken by Wied (aside from the specimen of "*brevipes*" mentioned below), we accept that the type locality of "Camamu", now in use for more than 60 years, continue as such for *N. aurifrons*, notwithstanding Hellmayr's (1929) apparent invention of the quotation marks around his citation of Camamu, implying that Wied (1831) had designated it the type locality.

Wied (1831) described *N. aurifrons* as having a lemon-yellowish color at the bases of the crown feathers. Together with his description of *aurifrons*, Wied (1831) described from a single specimen a plain-crowned form, *Muscicapa brevipes* (= "*Elaenea brevipes*" of Burmeister [1855]), which Allen (1889) determined to be an immature specimen of *aurifrons*. In 1833, Lafresnaye presented an illustration of a new form, *Muscicapa luteocephala*. Lafresnaye's (1833) type, collected by A. Saint-Hilaire, was examined by Hellmayr (1929) who designated the type locality as "Minas Gerais" and determined that it matched specimens from Rio de Janeiro and São Paulo. In 1860, P. L. Sclater erected the genus *Neopelma* (type *aurifrons*, with *luteocephala* included as a synonym) based upon the cursory description, *"Pedibus debilibus, rostro breviore, latiore, apice non uncinato"* ("feet weak, bill short, broad, without hook on tip").

In one of his earliest ornithological publications, Pinto (1933) described *Neopelma inornata* from five specimens from southern Bahia and one from Espírito Santo on the basis of their lack of bright coronal color (plain crowns) and "much smaller size when adult", in comparison to *N. pallescens* and *N. aurifrons* (which latter comparison must have been based entirely upon Wied's [1831] type description, and apparently having overlooked the description of the plain-crowned *M. brevipes*). Pinto later (1944) synonymized *inornata* with *aurifrons*, and also recognized that the name *luteocephala* (Lafresnaye 1833) was preoccupied by *Muscicapa luteocephala* (Lesson 1830). He applied the new name chrysolophum to Lafresnaye's description, and considered it a southern subspecies of *aurifrons*. This treatment has been followed since.

Distribution. Until very recently, *Neopelma a. aurifrons* was known to occur from southern-coastal Bahia south to the Santa Leopoldina area of Espírito Santo, extending west into the northeastern corner of Minas Gerais north from the rio Doce region (map, figure 1;

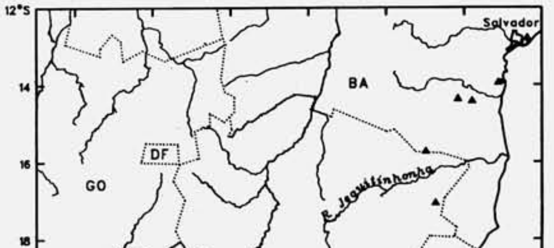

Figure 1. Distribution of *Neopelma aurifrons* (triangles) and *N. chrysolophum* (stars). Localities and sources are provided in the Appendix. There are few modern localities for *N. aurifrons*, which occurs from sea-level to about 1000 m; *N. chrysolophum* inhabits the mountains farther south between about 1150 and 1750 m. The two are in elevational parapatry/sympatry in central Rio de Janeiro state. Dotted lines are state boundaries.

see Appendix for precise localities) between sea-level and, at least locally (Mattos *in litt.* to L. P. Gonzaga 1990), about 1000 m. Its northernmost points of occurrence in Bahia are the vicinity of Salvador, Camamu, and a few kilometers east of Boa Nova, whence came an unpublished specimen in AMNH (No. 244293) collected by E. Kaempfer. In December 1994, its presence near Anil just northeast of the city of Rio de Janeiro was documented with tape recordings by R.P.. This may represent the sole record of *N. a. aurifrons* in Rio de Janeiro state. There is, however, reason to suspect that C. Euler collected *N. a. aurifrons* near Cantagalo (which he placed at 300-400 m), Rio de Janeiro, during the period 1862-66 (Euler 1900:130-1), and that at least one specimen, which he identified as *Elaenia brevipes* apparently because of agreement with Wied's (1831) description of this form having an "olive-grayish crown slightly paler in the center", is held at Humboldt Museum in Berlin (Ihering 1900). This could be confirmed quite easily by examination of any extant Euler specimens there. Euler (1900) provided a fine description of the nest of "*Elainea brevipes*", which would represent to this day the only description of the nest of any *Neopelma* (Portuguese description translated below).

Neopelma a. chrysolophum is known to occur (figure 1) from east-central Minas Gerais (Parque Natural do Caraça, where documented by tape recordings, figure 2D and 2E) south through the serra da Mantiqueira and the serra do Mar of Rio de Janeiro to extreme southern São Paulo at "Fazenda Intervales" (where observed by J. F. P., R. P., and C. Bauer), between about 1150 and 1750 m. It almost certainly occurs farther south, at least into neighboring Paraná.

Habitat and behavior. Neopelma a. aurifrons inhabits the interior of undisturbed and lightly disturbed forest (usually numerous trees greater than about 50 cm DBH nearby), sometimes foraging near forest edges. It forages with short-range (less than about 1.5 m) sally-hovers to pluck small fruits (terminology for foraging behavior follows Remsen and Robinson [1990]), sometimes hovering very rapidly for 1-2 seconds to maintain position as a fruit is grasped in the bill and snapped free from its stipe. Fruits are swallowed whole. An individual was observed to capture and eat a stick insect (suborder Phasmodea) about 3 cm long with a 1 m-range, lateral sally-strike. Most of our foraging observations have been of birds within about 20 m of their regularly used song perches. Singing individuals perch on thin, horizontal limbs in relatively open (vegetation not particularly dense), shaded situations in the understory, usually between 3.5 and 7 m above ground. Song perches are maintained for many minutes at a time as the birds deliver songs monotonously, occasionally reversing orientation 180°. Individuals occasionally change song perches by flying to another perch at similar height, usually within 3-15 m of the previous one. Singing individuals seem to be loosely grouped, often within human earshot of one other individual. In Espírito Santo, a group of about five singing birds has occupied the same area of the forest for at least three years, perhaps forming a loose lek assemblage. We have thus far located only a single singing individual in Rio de Janeiro.

Euler (1900:44) described the nest of "*Elainea brevipes*" from near Cantagalo, Rio de Janeiro (probably *N. a. aurifrons*):

"Also an artist. Its nest is in the form of a bag, always situated beneath banks and under hanging roots where it is protected from rain and wind. It is 22 cm long. The upper part is narrow and about 12 cm long, then widens into a sphere. The entrance is in the lower-middle of the bag; it is rounded, about 3.5 cm in diameter, being protected by an "alpendre" (awning, overhanging piece?) that runs smoothly along the wall for about 2 cm. The chamber is spacious, about 7 to 8 cm deep. The material consists of moss, soft , woolly fiber ["paina", strictly speaking from "paineira" or kapok: derived from endocarp of *Bombax* spp.] and small pieces of cork-like bark material ["cortiça fina"], loosely woven and without soft material ["não feltrado"]. The interior is garnished exclusively with "paina". It lays three snow-white eggs, without lustre or markings, normally shaped with rounded ends. Length 19 mm; width 14 a 15 d."

N. a. chrysolophum inhabits generally dense regrowth and forest edge or somewhat stunted woody vegetation (few trees greater than about 40 cm DBH, and most less than about 10 cm DBH), often with abundant bamboo and ferns in the vicinity, such as that on old landslides, roadcuts, and at forest borders; it does not frequent closed forest interior. While vocalizing, *N. a. chrysolophum* perches on thin, horizontal limbs in the middle stratum of the vegetation, which usually puts it at about 3-6 m above ground. We have not found more than two singing individuals, which may or may not be within earshot of each other, in proximity. Sick (1993) reported that males (no number specified) remain within hearing range of each other. Discrete territories (i.e., the exact same place) are occupied by one or two singing individuals year after year (pers. observ.). Like *N. a. aurifrons*, *chrysolophum* forages with short-range (usually less than about 1 m) sally-hovers to pluck small fruits, often at the forest edge, and with sally-strikes of similar range to live vegetation for small arthropods.

We have not observed a stereotypical courtship display (as we have several times for *N. chrysocephalum* [Saffron-crested Tyrant-Manakin] and Sick [1985] has described for *N. pallescens* [Pale-bellied Tyrant-Manakin]) for either taxon under discussion here, or for *N. sulphureiventer* (Sulphur-bellied Tyrant-Manakin). Sick (1993: 490) stated that *Neopelma aurifrons* has "simple displays" that are "limited to a call that serves as a song; neighboring males remain in hearing range of each other's voices but do not assemble, remaining alone (as do the *Tyranneutes*) and assuming special poses when they see a female". According to Sick's personal diary index housed in UFRJ, this observation pertains to *N. a. chrysolophum*.

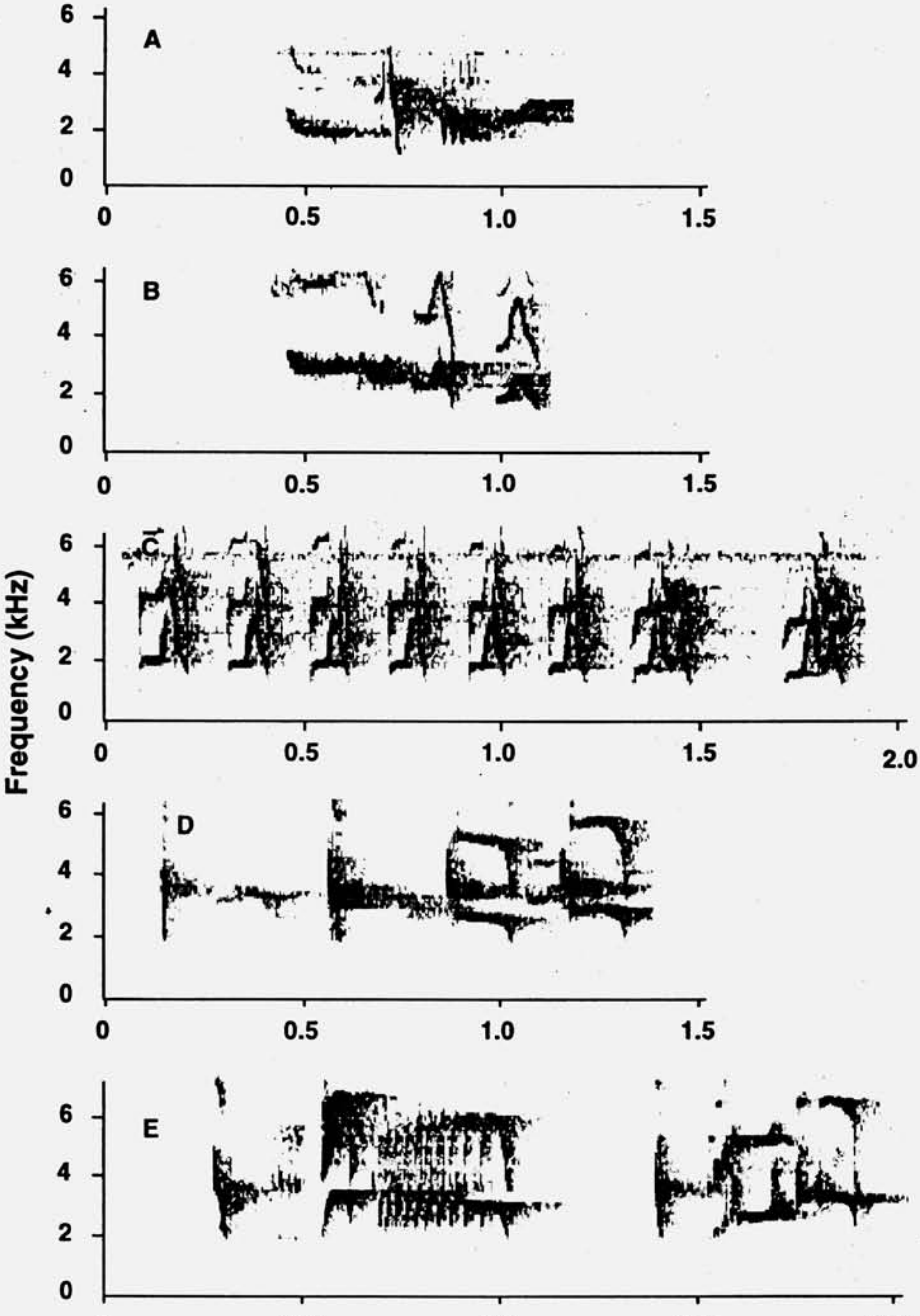

Figure 2. Sound spectrograms of vocalizations of *Neopelma aurifrons* and *N. chrysolophum*. A: *aurifrons*, typical four-syllable song from Reserva Biológica Augusto Ruschi, ES; 770 m elev., 26 Sept. 1992. This song is repeated monotonously throughout the day. Compare final two syllables with typical song of *T. stolzmanni* on left side of figure 3B. B: *aurifrons*, typical four-syllable song from Anil, RJ; 100 m elev., 17 Dec. 1994. C: *aurifrons*, vocalization delivered after playback of song from Res. Biol. A. Ruschi, ES or Anil, RJ (one of at least three variants); Anil, RJ; 17 Dec. 1994. D: *chrysolophum*, first of three elements of typical song, which is often delivered repeatedly apart from the other two elements; number of syllables variable from 3 to 5; Serra do Caraça, MG; 1200 m elev., 26 Sept. 1989. E: *chrysolophum*, second and third elements of song of same individual shown in D. All recordings by B. Whitney. Spectrograms produced with "SoundEdit" of Farallon Computing, Emeryville, California, and "Canary" 1.1 of the Bioacoustics Research Program of the Cornell Laboratory of Ornithology, Ithaca, New York. All recordings have been or will be archived at the Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology, and the Arquivo Sonoro Prof. Elias P. Coelho (ASEC), Universidade Federal do Rio de Janeiro, Rio de Janeiro.

Vocalizations. The song of *N. a. aurifrons* is a simple, four-syllable phrase repeated at a regular interval, with inter-song intervals of shorter duration early in the morning than in the afternoon. We have recordings from two localities: Reserva Biológica Augusto Ruschi (formerly Nova Lombardia) near Santa Teresa, Espírito Santo (4-5 individuals); and Anil, Rio de Janeiro (3; probably a single individual recorded on three occasions). Recordings from the two sites are of similar four-syllable structure and frequency and are of the same cadence and duration, but individual syllables have a conspicuously different shape and overall quality (figure 2A and 2B, respectively). We have not yet determined whether this variation is geographic or individual.

To test the reaction of the Rio de Janeiro bird to the song from Espírito Santo, we performed some simple playback experiments. On 17 December 1994, we approached the song perch of a singing *N. a. aurifrons*. After observing the bird from a position below the tree in which it was perched for several minutes, we presented it with playback of a song from Espírito Santo. After falling silent for about 1 min, during which we continued to play the tape, it responded aggressively by flying closer to us and calling repeatedly with an agitated vocalization quite different from the natural song (figure 2C, one of three variations). We ceased tape playback and, after several minutes of calling, the bird resumed singing its normal song. Following 10-15 min of further observation, we presented the bird with playback of a tape recording of *N. a. chrysolophum* from Parque Nacional do Itatiaia, Rio de Janeiro. The bird displayed no interest in this recording, and did not even pause in its song bout or look down toward the tape recorder although we played the tape for more than 1 min. We then presented it with a recording of its own song, to which it responded vigorously in the manner described above for the Espírito Santo experiment.

We returned to the site on 22 February 1995 to find no sign of the *N. a. aurifrons* at the tree in which it had been singing consistently in December (in fact, the entire avifauna was relatively quiet, as by mid-February active song periods for most local birds had passed). Standing in the same place as before, we played the same recording of *N. a. aurifrons* from Espírito Santo. Within 5 seconds the bird flew in to perch on the same limbs on which it had been singing consistently earlier in the season, and delivered the same agitated vocalizations recorded in mid-December. It fell silent within 3 min, and thereafter responded weakly only to playback of a recording of its own song. We have not had an opportunity to perform reciprocal playback experiments with *N. a. chrysolophum.* It is difficult to interpret playback experiments such as these, especially when reciprocal playbacks have not been tested, but we do believe that these limited results underscore the significance of the structurally dissimilar voices of *N. a. aurifrons* and *N. a. chrysolophum*, and indicate that similarities in the overall structure and cadence of the different-sounding songs of *N. a. aurifrons* from Espírito Santo and Rio de Janeiro effectively communicate conspecificity.

The song of *N. a. chrysolophum* is more complex than that of *aurifrons*, and also displays some variation. We have recordings from Minas Gerais (3 from serra do Caraça), Rio de Janeiro (3 from Itatiaia and 1 from serra do Tinguá), and São Paulo (2 from serra da Cantareira). The song comprises three basic elements. The first consists of 1-4 sharp notes (figure 2D); this element may be repeated several times before delivery of the remaining two parts, which are given more closely together (figure 2E). The second element is of 3 or 4 syllables, the final two of which are quieter, drawn-out (especially the second one), and warbled (i.e., they show marked frequency modulation), ending with an emphatic, sharp note. The third element also comprises 3 or 4 syllables, one of which is quieter and warbled, and the final of which is most emphatic. A series of irregularly spaced, sharp, single notes on one frequency is sometimes delivered repeatedly for minutes. Homologous vocalizations are given by *N. sulphureiventer* and *N. chrysocephalum*, at least (B. M. W. pers. observ.). We have not observed this vocalization from *N. a. aurifrons*.

Morphology. Standard measurements (bill length from anterior edge of nares, wing chord, tarsus from last undivided scute) for *Neopelma a. aurifrons* and *N. a. chrysolophum* are presented in table 1. The two taxa differ appreciably in various respects. The nominate form is shorter overall, primarily owing to its much shorter tail: 50.7 mm vs 56.5 mm for *chrysolophum*, with no overlap (males only; females of *chrysolophum* average slightly more than 3 mm shorter than males; sample of female *aurifrons* too small to compare). Length of the tarsus (again, males only) also appears to be consistently shorter in *aurifrons* (15.4 mm vs 17.3 mm), but we have much less confidence in our ability to accurately measure tarsal length than in any of the other measurements. It was often difficult to access the tarsus clearly because of tibial feathering, irregular position of the dried legs, and multiple museum tags.

Although it possesses a much shorter tail and tarsus, *aurifrons* has an appreciably longer bill and wing, and is thus proportioned quite differently from *chrysolophum.* As bill measurements do not appear to vary between the sexes, a larger sample size is permitted, which shows that bill width overlaps almost completely between the taxa; bill depth averages greater for *aurifrons*, with little overlap; and bill length is greater for *aurifrons*, with no overlap among the 15 *aurifrons* and 16 *chrysolophum* measured. Wing length averages about 5% longer for male than female *chrysolophum*, so a comparison of male wing lengths only shows that *aurifrons* averages almost 5 mm longer than *chrysolophum*, with no overlap among the 11 *aurifrons* and 8 *chrysolophum* measured (although a few measurements fell within 1 mm, and we expect that a very large series would demonstrate limited overlap). We did not attempt to establish wing formulae for the taxa, but a cursory inspection seemed to reveal some differences, which merits further study.

Aside from the conspicuous, bright-yellow vertex of *N. a. chrysolophum*, which is absent or only very weakly indicated in a minority of specimens of *aurifrons*, and in these only on the feather bases of the anterior portion of the central crown, the two taxa are outwardly quite similar in plumage. However, even juvenile or immature *chrysolophum* show significantly more yellow in the crown than the most strongly marked *aurifrons*. Additionally, the crown and sometimes nape of *aurifrons* is overall of a more slaty cast, contrasting with the back more than does the essentially concolor feathering of *chrysolophum*. Iris color may also differ between the taxa (with possibly even greater age- or sex-related intraspecific variation), but appears to be yellowish or grayish or pale-brownish most of the time, and requires further study to establish.

Intrageneric and intergeneric relationships. As Hellmayr (1929) recognized more than 60 years ago, *N. a. aurifrons* and *N. a. chrysolophum* are morphologically distinctive taxa, although he did not attach even subspecific rank to the striking structural differences between the two. The different habitats, elevational and latitudinal ranges, and vocalizations of these taxa have come to light only recently. The discovery of *Neopelma a. aurifrons* at the foot of the serra do Mar in Rio de Janeiro, which at higher elevations at the same latitude is occupied by *N. a. chrysolophum*, establishes elevational parapatry, if not actual sympatry, of the two forms. We therefore recommend that *Neopelma aurifrons* and *N. chrysolophum* be recognized henceforth as species. We suggest that *N. aurifrons* continue to be known as Wied's Tyrant-Manakin, and that the name Serra do Mar Tyrant-Manakin would be appropriate for *N. chrysolophum*. Willis and Oniki (1991) provided the Portuguese name "fruchu-serrano" for *N. aurifrons*. This name is appropriate for montane *chrysolophum*; we suggest the name "fruchu-baiano" for *aurifrons*.

Despite their seemingly continuous latitudinal and elevational ranges and outwardly similar appearances, we suspect that *N. aurifrons* and *N. chrysolophum* are not each other's closest relatives, and probably became established in southeastern Brazil during separate speciation periods. If we were to continue under the assumption that they are sister taxa, and if we adopt the conservative stance that their divergence could not have taken place in elevational parapatry, as demonstrated by Patton and Smith (1992) for Andean rodents and Arctander and Fjeldså (1994) for *Scytalopus* tapaculos, then we must assume that these two morphologically and vocally divergent populations have achieved secondary contact, in the meantime also having evolved to occupy different habitats and elevations. Although this is a possible speciation scenario, we believe a more reasonable explanation is informed through examination of present avian distribution/speciation patterns in Amazonia and southeastern Brazil, together with selected intra- and intergeneric comparisons.

The distribution of *aurifrons* lies in the rather restricted north-central portion of the lowland Atlantic Forest domain (i.e., southern Bahia to northern Rio de Janeiro). This basic distribution is shared by a small subset of the lowland Atlantic Forest avifauna (examples include *Crax blumenbachii*, *Neomorphus geoffroyi*, *Pyrrhura cruentata*, *Thripophaga macroura*, *Myrmotherula urosticta*, *Pipra pipra*, *Machaeropterus regulus*, and *Cotinga maculata*), all of which have obvious close (congeneric and morphologically and vocally similar) relatives that are of primarily forested-Amazonian distribution. However, the genus *Neopelma* at this point in its evolutionary history is represented only peripherally in forested Amazonia, where it is restricted to patchily distributed, relictual or even successional habitats (i.e.,

Table 1. Measurements of *Neopelma aurifrons*, *N. chrysolophum*, *Tyranneutes stolzmanni*, and *T. virescens*. All bill measurements from anterior edge of nares. Sexes combined for bill measurements of *Neopelma*, other measurements for males only. *Tyranneutes stolzmanni* sample includes males only from Amazonas (upper rio Negro, rio Branco, rio Juruá) and Pará (Belém region), Brazil. *T. virescens*, upper line, represents our measurement of the single individual (male) held at MZUSP; measurements of tail and wing on lower line are from Hellmayr (1929), n = about 14 from Manaus (type) and British Guiana.

	Bill width $\underline{x}$ (range)	Bill depth $\underline{x}$ (range)	Bill length $\underline{x}$ (range)	Tarsus $\underline{x}$ (range)	Tail $\underline{x}$ (range)	Wing chord $\underline{x}$ (range)
Neopelma aurifrons	4.3 (3.7-4.7) n = 17	3.8 (3.7-4.3) n = 13	7.5 (7.0-7.8) n = 15	15.4 (14.8-16.0) n = 8	50.7 (48.3-53.4) n = 11	68.7 (66.8-71.3) n = 11
Neopelma chrysolophum	3.9 (3.6-4.3) n = 16	3.5 (3.3-3.8) n = 13	6.3 (6.0-6.8) n = 16	17.3 (16.8-17.8) n = 8	56.5 (53.7-60.6) n = 8	64.1 (62.8-66.1) n = 8
Tyranneutes stolzmanni	3.6 (3.3-3.9) n = 12	3.2 (3.0-3.6) n = 11	7.1 (6.7-7.5) n = 11	not measured	21.4 (20.1-22.7) n = 12	48.5 (47.7-52.0) n = 12
Tyranneutes virescens	3.5	2.8	6.1	not measured	22.6 19-23 (n = ~ 14)	47.1 47-51 (n = ~ 14)

not present inside tall, closed forest as inhabits *N. aurifrons* and most of the other taxa above) that in some cases may be maintained by edaphic or local hydrologic conditions (B. M. W. pers. observ.). In his discussion of the origins of the avifauna of eastern Brazil, Willis (1992) included *Neopelma aurifrons* (*sensu* Pinto 1944) in a list of east-Brazilian endemic species "without obvious relatives... with seemingly Amazonian links". We suggest, however, that an overlay of vocal, behavioral, and morphological data with pattern-based distributional analysis (as discussed above) reveals the probable Amazonian relative of *N. a. aurifrons*: *Tyranneutes stolzmanni* (Dwarf Tyrant-Manakin). *T. stolzmanni* inhabits tall, closed Amazonian forests extensively south of the Amazon/Solimões and north of the river west of the rios Negro and Branco (replaced east of the rios Negro and Branco by its sister taxon, *T. virescens* [Tiny Tyrant-Manakin]). Notwithstanding its smaller size (and proportionately much shorter tail; table 1), *T. stolzmanni* is much like *N. a. aurifrons* in behavior of maintaining song perches in the upper understory/midstory of the shady forest interior (but may forage up to canopy height), in its song and vocal delivery (monotonous repetition of a two-syllable song at regular intervals), and in its basically uniform plumage. The crown of *T. stolzmanni* bears a striking resemblance to that of *N. aurifrons*, being a brighter shade of olive in the center and marked on roughly one-third of 30 specimens examined with a trace of yellow at the bases of 1 or more feathers. The bill of *T. stolzmanni* is actually closer to the size of the bill of *N. aurifrons* than is that of *N. chrysolophum* (table 1). *T. virescens* is very much like *stolzmanni*, but sings a three- or four-syllable song, and has a yellow vertex.

Typical songs of *Tyranneutes virescens* and *T. stolzmanni* from near their respective type localities are shown in figures 3A and 3B. Throughout the range of *stolzmanni* the song sounds remarkably like the terminal two notes of the song of *N. aurifrons* from Espírito Santo (figure 2A), differing mainly in the more rapid frequency modulation of the first of its two syllables. The song of *T. virescens* throughout its distribution is also strongly reminiscent (in cadence, overall duration, and frequency) of that of *N. aurifrons*. Both species of *Tyranneutes* also sing a quite different-sounding, evenly paced series of 3-5 short, whistled syllables (the whole lasting 1-2 sec) similar to (and quite possibly homologous to) some vocalizations of *Neopelma* species (B. M. W. pers. observ.). These poorly known "songs" seem to be delivered from somewhat higher perches than the more commonly heard ones described above. Other conspicuous general similarities between *Neopelma* and *Tyranneutes* are their overall olive-green plumage with paler underparts, and lack of sexual dichromatism. Comparison of courtship displays within this complex must await more detailed documentation from the field.

Having reached the conclusion that *Neopelma* and *Tyranneutes* are derived from the same stock, and during the course of research for the writing of this paper, we discovered that the phenetic analysis of allelic frequencies (from protein electrophoresis) within the superfamily Tyrannoidea performed by Lanyon (1985) had suggested a decade earlier that among the 29 genera presented in his table 1, *Neopelma* and *Tyranneutes* were among the most closely related. Thus, our ignorance of Lanyon's (1985) indication that these two genera are closely related allowed an informative "back-test" of biochemical data against data from the field coupled with analysis of modern avian distributional patterns.

Ideas on the origins and diversification within the Neopelma/Tyranneutes complex. Neopelma is a widespread genus that persists in remnants of habitats that long ago must have been dominant over much of lowland South America. Isler *et al.* (in press) documented a similar distributional pattern for the *Thamnophilus*

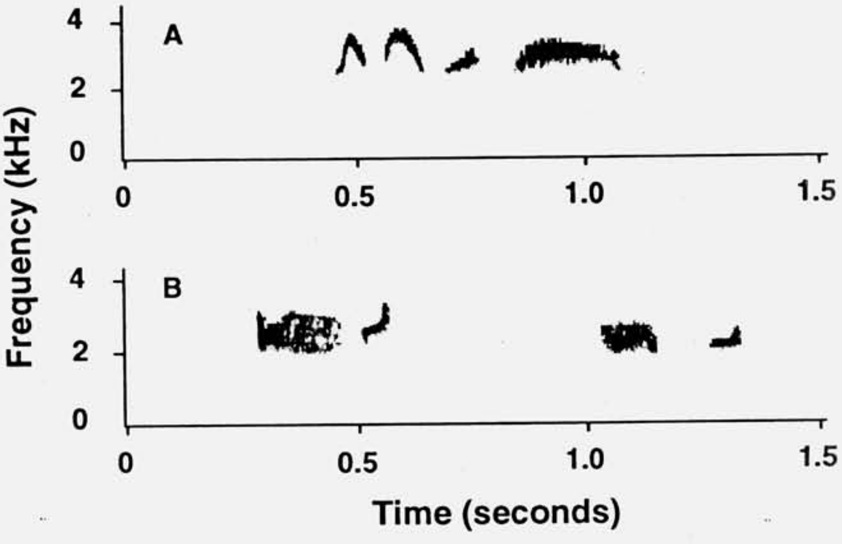

Figure 3. Sound spectrograms of vocalizations of *Tyranneutes* species. A: *virescens*, typical four-syllable song from approximately 60 km north of Manaus, Amazonas; 3 Oct. 1993. B: *stolzmanni*, 2 twosyllable songs delivered sequentially by one bird (intersong interval shortened to show both on a single spectrogram). The song on the left is the most typical (compare with final two syllables of the song of *N. aurifrons* in figure 2A), and is repeated monotonously for hours, occasionally varied slightly, as shown in the example on the right. Rio Cauaburi, AM; 23 Dec. 1994. Recordings by B. Whitney.

punctatus complex of the Thamnophilidae. The four species of *Neopelma*, so far as known, are allopatric, although B. M. W. has found *sulphureiventer* and *pallescens* in different habitats within about 6 km of each other in eastern Santa Cruz, Bolivia, near the edges of the ranges of both species. Carnevalli (1980) reported *N. pallescens* from Parque Natural do Caraça, Minas Gerais, but we and others have found only *N. chrysolophum* there. *Tyranneutes stolzmanni* and *T. virescens* are likewise allopatric or parapatric (replacing each other across rivers), but each of them is sympatric with a member of *Neopelma* over an extensive area. In both cases there seems to be fairly clear habitat segregation between the genera, with the *Neopelma* species in scrubbier woodland ("campinarana", "caatinga forest", second-growth, bamboo-dominated woodland, etc.) and the *Tyranneutes* species more in the interior of tall forest. Where suitable habitats are in close proximity, the two genera may sometimes be heard from the same place.

In an attempt to understand the divergence from a common ancestor of *Neopelma* and *Tyranneutes*, their overlap today, and the origins of the two species of *Neopelma* in southeastern Brazil, we assume that present-day *Neopelma* species are most like the ancestral stock, which was widespread at a time when dry or "low-stature" woodland (habitats mentioned above) dominated most of the South American continent. Subsequent paleoclimatic cycles, which promoted the evolution and variable expansion/contraction of closed forest (e.g., Haffer 1974), eventually resulted in at least four or five increasingly isolated populations of the ancestral *Neopelma* stock. The easternmost of these survived in scrubby forest, patchy successional habitats (landslips?) and perhaps bamboo in the serra do Mar of Brazil: *N. chrysolophum*. We postulate that *Tyranneutes* evolved in isolation somewhere in central Amazonia, having adapted to inhabit tall, closed forest. From its Amazonian base, and early in its divergence from ancestral stock, proto-*Tyranneutes* (or "post-*Neopelma*") first expanded eastward to invade (probably along with many other Amazonian forms) the Atlantic Forest region (perhaps via the "central-middle" or "Januária bridge" route of Willis [1992]), where it subsequently became isolated in tall, humid lowland forest by the "arid diagonal" of Ab'Sáber (1977). This isolate, evolutionarily intermediate between contemporary *Neopelma* and *Tyranneutes*, is proto-*Tyranneutes*, or *N. aurifrons*. It is now in limited altitudinal parapatry with *N. chrysolophum*. We considered the possibility that *N. aurifrons* was an original isolate (that managed to survive in humid forest) of the *Neopelma* ancestral stock which, after a period of diversification that led to its peculiarities (plain crown, different proportions), invaded west into Amazonia. The Amazonian population was then cut off by the "arid diagonal", allowing the independent divergence of *Tyranneutes*, and so forth. Such a mechanism seems weakly plausible in this case, but we believe it is much less likely than the above hypothesis because the overwhelming majority (perhaps all?) of the lowland Atlantic Forest avifauna (especially those members sharing the distribution of *N. aurifrons*) appear to us to be unequivocally derived from Amazonian stock; to suggest differently for this example requires special pleading.

After separation from its Atlantic Forest counterpart, Amazonian proto-*Tyranneutes* evolved the morphological, vocal and, with respect to *Neopelma*, limited (Lanyon 1985) genetic distinctions that today characterize *Tyranneutes* and set it apart from related genera. Modified for a new environment free of close relatives (which is not to imply free of competitors), *Tyranneutes* greatly expanded its distribution. It first spread across the mouth of the Amazon (probably on shifting channels and ephemeral islands in the river) to colonize the Guianas, extending through forest west to the rio Branco and Negro region to diverge from southern stock into the present-day *T. virescens*. Importantly, it also geographically overlapped *N. chrysocephalum* (as opposed to having evolved in sympatry with that form), which was resticted to scattered patches of scrubby woodland that today seem to be maintained largely by edaphic conditions (B. M. W. pers. observ.). The yellow vertex of *T. virescens* we suspect is a secondary expression of the primitive (in this complex) character state. *Tyranneutes* also made secondary contact to the west with *N. sulphureiventer*, which persisted in scrubby forest, gallery woodland, and bamboo in upper Amazonia. Probably most recently (because differentiation in this group across the Solimões is morphologically and vocally appreciably less than across the Amazon), the expansion of *Tyranneutes* took it north of the Solimões to the west of the rio Negro (the mechanism for crossing is hard to supply, but seems to be part of a general distributional pattern that could be explained by a single change in the course of the major rivers here. In the rio Negro region, *T. stolzmanni* now overlaps extensively with *N. chrysocephalum*.

In sum, the operative mechanism of speciation within the Neopelma/Tyranneutes complex may have been the successful, and perhaps fairly rapid adaptation of proto-*Tyranneutes* for survival and expansion in tall, closed forest. The other members of the complex, which had been "habitat generalists" in dryer, low-stature woodland probably for a very long time (having radiated widely on the continent with limited morphological variation), appear to have undergone much less change during paleoclimatic shifts, and are today viewed as relictual "habitat specialists".

Generic limits within the Neopelma/Tyranneutes complex. Hellmayr (1929) was the first to combine all of the current members of *Neopelma* in that genus, which treatment has been followed since. The type of the genus *Neopelma* Sclater 1860 is *aurifrons*, and *virescens* is the type of *Tyranneutes* Sclater and Salvin 1881. However, Lanyon's (1985) biochemical analysis of *Neopelma* included only *sulphureiventer*, and *Tyranneutes* was represented only by *stolzmanni* from

Loreto, Peru (the type is from Marabitanas, Amazonas, Brazil) (Lanyon pers. comm.1995).

We look forward to a directed biochemical analysis of the Neopelma/Tyranneutes complex that includes as much topotypical material as possible, but we predict that at present it would continue to indicate gross monophyly because we suspect that full expression of diversity would be limited by the current low resolution of biochemical analysis at the species and "subspecies" level, compounded by the problems of determining appropriate outgroups and evolutionary rates. Regardless, we feel that treatment of the group as monophyletic or in any combination of taxa in two genera obscures important evolutionary history that might inform similar investigations of speciation in birds and other organisms. For the same reason, we are also inherently unsatisfied with allocation of any other taxa to *Neopelma* with *aurifrons* under an empty hypothesis that *aurifrons* might be "aberrant"; it more probably represents an evolutionary unit intermediate between "*Neopelma*" and *Tyranneutes*, almost certainly closest to *Tyranneutes*.

From a field and conservation perspective, we urge that discrete groups of related species that are unambiguous in life, as are the three in the Neopelma/Tyranneutes complex, be treated as separate entities. The genus category of classification provides an ideal mechanism for recognition of such groups. However, in the absence of a well-corroborated phylogeny for the entire complex, which at this point lacks any biochemical analysis, we see no advantage to recommending generic rearrangement. As a guide for future biochemical investigation, we suggest that the genus *Neopelma* may include only the species *aurifrons*, and that *Tyranneutes* should stand for *virescens* and *stolzmanni*. Under this arrangement, a new genus would have to be erected for the (apparent) allospecies *chrysolophum*, *pallescens*, *chrysocephalum*, and *sulphureiventer*. If our assumption that this assemblage is closer to the ancestral stock of the group is eventually corroborated by genetic data, the name *Protoneopelma* would be particularly illustrative of the evolutionary history of the complex.

Conservation and the subspecies concept. Neopelma aurifrons is among the most poorly known of all Atlantic Forest endemic birds. We suggest this is owing primarily to its classification as a subspecies, some consequences of which were discussed by Willis and Oniki (1982) more than a decade ago with regard to taxonomic status of the antbird *Pyriglena atra* (Fringe-backed Fire-eye). Further contributing to the paucity of data on *N. aurifrons*, it is not present or is apparently rare in the few protected areas that are visited regularly by ornithologists and bird observers. Its status as a distinctive, threatened taxon, subspecies or no, has been completely overlooked, apparently because the visually similar *Neopelma* (*aurifrons*) *chrysolophum*, which inhabits scrubby woodland and forest edge/bamboo at higher elevations that have suffered relatively much less habitat disturbance, is frequently encountered. There are few modern records of *N. aurifrons* anywhere, and none from Bahia for more than 60 years despite recent field work east of Boa Nova (Gonzaga *et al.* 1995) where Kaempfer collected it in the late 1920s. (We expect now that it has been elevated to species status and its voice has been described, greatly heightened attention will result in its rediscovery in southern Bahia). It is apparently absent (or at best very rare; there are no records) from the Floresta Rio Doce ("Linhares Reserve") of the Companhia Vale do Rio Doce in Espírito Santo, and was listed as "uncommon" at Reserva Biológica Sooretama during field work in early 1981 (Scott and Brooke 1985, who did not distinguish the two species). Subsequent to the records of Scott and Brooke (1985), a single sighting by J. F. P. and C. E. S. Carvalho is the only one we know of from Sooretama. The Reserva Biológica Augusto Ruschi near Santa Teresa, Espírito Santo is the only other officially protected area in which *N. aurifrons* is known to occur, and it seems to be quite local within the reserve (B. M. W. pers. observ.). As an inhabitant of the interior of lowland Atlantic Forest (below about 1000 m elevation), *N. aurifrons* is truly a threatened species, subject to the same conservation considerations discussed by Whitney and Pacheco (1995) for lowland species of *Myrmotherula* antwrens endemic to the Atlantic Forest.

Neopelma aurifrons has probably always had a restricted distribution. That it survived until the early 1990s, when it could be studied, is a twist of fate. It could have gone extinct without a trace long ago, as have many passerine birds over the course of time. Or it could have disappeared in the past fifty years as has virtually all of its humid Atlantic Forest habitat. But it has persisted in small numbers in some isolated patches, which has provided the key for an interpretation of diversification within the Neopelma/Tyranneutes complex as it stands at this point in history. Indeed, speciation is a never-ending process, but this natural speciation story is sadly over. Extensive, artificial range fragmentation of *Neopelma aurifrons* has removed it as an informative link in the chain: genetic integrity of the isolate is, without a doubt, forever severed. But like a planarian chopped up in a Petri dish, evolution will plod along with whatever pieces it has without batting an eye.

The complete loss through extinction or the long-term loss of identity through extensive genetic fragmentation of a *single population* of any "species" represents an unreconcilable gap in the evolutionary future of an ecosystem. Realization of this requires acknowledgement of how very little we know about natural ecosystems, even the oldest, most stable ones on the planet. Populations naturally isolated from other possibly related populations deserve protection despite the fact that they often are not morphologically dissimilar from each other, and thus are not named taxa or are recognized only at the subspecies or "variety" level. Unfortunately, governmental agencies of even the countries producing the most active and insightful ecologists and systematists generally base conservation legislation and definition of "priority areas" for conservation on a straight-jacketed species concept that increasingly seems inappropriately constrained.

Examination of the Neopelma/Tyranneutes radiation, which stemmed from investigation of a neglected "subspecies" now threatened by habitat loss, has provided a small-scale model for one evolutionary pathway that may have contributed many times over to the unequaled avian diversity of the richest ecosystems on earth.

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APPENDIX

Localities are listed by species and lati/long from north to south, and are shown on the map (figure 1). A few localities in close proximity are mapped as a single point. An * indicates a sight record; occurrence at all other localities is documented with a specimen or tape recording. Abbreviations are: AMNH (American Museum of Natural History, New York); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo): MNRJ (Museu Nacional do Rio de Janeiro, Rio de Janeiro); B. M. W., J. F. P., and R. P. (authors); BA (Bahia); MG (Minas Gerais); ES (Espírito Santo); RJ (Rio de Janeiro); SP (São Paulo).

Neopelma aurifrons (Wied's Tyrant-Manakin)

"Vicinity of Salvador", BA	1259 / 3831	Wied 1831
Camamu, BA	1357 / 3907	Wied 1831
Boa Nova, BA	1422 / 4010	AMNH
Serra do Palhão, Jequié, BA	1426 / 3948	Pinto 1933
Faz. Sta Maria, Rio Gongogy, BA	1427 / 3950	Pinto 1933
Divisópolis, MG	1544 / 4100	G.T. Mattos
Machacalis, MG	1705 / 4045	MZUSP
Rio Itaúnas, ES	1825 / 3942	MZUSP
Baixo Suassuhy, Rio Doce, MG	1850 / 4146	Pinto 1944
Res. Biol. Sooretama, ES	1910 / 4015	Scott and Brooke1985
Baixo Guandu, ES	1931 / 4101	AMNH
Baixo Piracicaba, Rio Doce, MG	1931 / 4238	Pinto 1944
São José da Lagoa, MG	1945 / 4303	Pinto 1944
Res. Biol. A. Ruschi, ES	1946 / 4030	B.M.W.
Santa Cruz, ES	1956 / 4009	MZUSP
Chaves, Sta Leopoldina, ES	2002 / 4039	Pinto 1944
Porto Cachoeiro, ES	2006 / 4032	Ihering and Ihering 1907
Anil, RJ	2228 / 4239	R.P.

Neopelma chrysolophum (Serra do Mar Tyrant-Manakin)

Serra do Caraça, MG	2008 / 4330	Forrester 1993
Itabirito, MG*	2015 / 4348	R.P.
P. E. Desengano, RJ*	2149 / 4139	J.F.P.
Sumidouro, RJ*	2203 / 4241	J.F.P.
Nova Friburgo, RJ	2216 / 4232	Pelzeln 1874
Maria da Fé, MG	2218 / 4523	Pinto 1944
P. E. Ibitipoca, MG	2142 / 4354	L. P. Gonzaga
P. N. do Itatiaia, RJ	2223 / 4438	Holt,1928
Faz. Boa Fé, Teresópolis, RJ	2226 / 4259	Davis 1945
Petrópolis, RJ	2231 / 4310	MNRJ
Serra do Tinguá, RJ	2236 / 4327	B.M.W. and J.F.P.
Serra da Bocaina, SP	2245 / 4445	J.F.P.
Vitoriana, SP	2247 / 4824	Hellmayr 1929
Itatiba, SP	2300 / 4651	Ihering and Ihering 1907
above Parati, RJ	2313 / 4446	B.M.W. and J.F.P.
Serra do Japi, SP*	2313 / 4702	Willis and Oniki 1981
Serra da Cantareira, São Paulo, SP	2325 / 4639	MZUSP
Ipanema, SP	2326 / 4736	Pelzeln 1868
Mogy das Cruzes, SP	2331 / 4611	Pinto 1944
Ipiranga, SP	2332 / 4637	Ihering 1899
Itapetininga, SP	2336 / 4803	MZUSP
Casa Grande, Salesópolis, SP	2337 / 4557	MZUSP
Boracéia, SP	2339 / 4554	Willis and Oniki 1981; MZUSP
Santo Amaro, SP	2339 / 4642	Ihering 1899
Interlagos, São Paulo, SP	2343 / 4642	MZUSP
Alto da Serra, SP	2347 / 4619	Ihering and Ihering 1907
Pilar, SP	2355 / 4628	Pinto 1944
P. E. Carlos Botelho, SP*	2404 / 4758	Willis and Oniki 1981
Intervales, SP*	2411 / 4812	J.F.P. and R.P.

Neopelma sp. (probably *aurifrons*, but requires confirmation; Euler specimen apparently in Humboldt Museum, Berlin)

Cantagalo, RJ	2158 / 4222	Ihering 1900