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SEASONAL DISTRIBUTION OF THE SLATY ELAENIA, A LITTLE-KNOWN AUSTRAL MIGRANT OF SOUTH AMERICA

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Abstract.—An analysis of the seasonal and geographic distribution of specimen records of the Slaty Elaenia (*Elaenia strepera*; Tyrannidae) confirms that the breeding range is restricted to a small area of the Andes Mountains in northwestern Argentina (Jujuy, Tucumán) and southern Bolivia (Tarija, Chuquisaca, probably also Santa Cruz), mainly from 800 to 2500 m elevation. Although the winter range is usually assumed to include much of the western Amazon Basin north to northern Venezuela, the only specimens from the core of the austral winter are from hilly areas in northern Venezuela (Bolívar, Carabobo, and Sucre), approximately 3000 km north of the breeding range; other records from Colombia, Peru, and central Bolivia are from periods when transients would be expected. Therefore, the data so far indicate that the true winter range might be as small as the breeding range and, like the breeding range, is not in the Amazonian lowlands. It is suspected that the true winter distributions of many migratory bird species that winter in the tropics are as imprecisely known as that of the Slaty Elaenia.

DISTRIBUCIÓN ESTACIONAL DE *ELAENIA STREPERA*, MIGRATORIO AUSTRAL SURAMERICANO

Sinopsis.—La utilización de registros de individuos para el análisis de la distribución geográfica y estacional del tiránido *Elaenia strepera* confirma que su área de reproducción está restringida a una pequeña área en los Andes en el noroeste de Argentina (Jujuy, Tucumán) y el sur de Bolivia (Tarija, Chuquisaca y probablemente Santa Cruz), particularmente a elevaciones entre 800 y 2500 m. Aunque se asume que el área invernal incluye gran parte del oeste de la Cuenca del Amazonas, al norte del norte de Venezuela, los únicos individuos del núcleo invernal austral son de las áreas montañosas del norte de Venezuela (Bolivar, Carabobo y Sucre), apróximadamente a 3000 km al norte de las áreas de reproducción. Otros registros de Colombia, Perú y la parte central de Bolivia son de periodos en donde deben esperarse aves de paso. Por lo tanto, los datos hasta el momento indican que la verdadera área en donde pasa el invierno este tiránido, podría ser tan pequeña como el área en donde se reproduce, y que al igual que esta última, no se encuentra en las partes bajas de la región Amazónica. Se sospecha que la verdadera distribución de muchos migratorios en los trópicos podría ser tan imprecisa como el de *E. strepera*.

Numerous bird species that breed in southern South America migrate northward into tropical South America during the austral winter. At least 250 species are involved (R. T. Chesser, unpubl. data). Although widely recognized by South American ornithologists (e.g., Sick 1968), the extent and even the existence of this major migration system has gone largely unnoticed by all but a few other ornithologists (e.g., Hilty and Brown 1986, Parker et al. 1982, Ridgely and Tudor 1989, Zimmer 1938). For example, austral migrants were scarcely mentioned in a major symposium "Migrant Birds in the Neotropics" (Keast and Morton 1980).

One of the least-known of all the austral migrants is the Slaty Elaenia (*Elaenia strepera*; Tyrannidae), the only dark-gray-plumaged member of

a genus with 17 species (Traylor 1979), many of which are migratory (Zimmer 1941). The breeding range of the Slaty Elaenia is remarkably small (Andes of northwestern Argentina and southern Bolivia) given that its wintering distribution allegedly includes a vast area of northern Amazonia from central Peru to northern Venezuela (Fjeldså and Krabbe 1990; Meyer de Schauensee 1966, 1970; Traylor 1979).

At one time, the Slaty Elaenia was believed to have two remarkably disjunct populations, one in Argentina and the other in northern Venezuela. Cory and Hellmayr (1927) scrutinized minor individual differences among the few specimens from the two areas for potential subspecies differences. Then Zimmer (1941), citing earlier reports that indicated that the Slaty Elaenia was present in Argentina only during the breeding season, proposed that the records from Venezuela and Peru pertained to migrants. Bond and Meyer de Schauensee (1941) added southern Bolivia to the breeding range, based on specimens collected there by M. A. Carriker. Three specimen records from Colombia added that country to the nonbreeding range (Hilty and Brown 1986; Appendix 1). Currently, most references give the breeding range as the Andes of northwestern Argentina (provs. Jujuy and Tucumán) and southern Bolivia (dptos. Santa Cruz, Chuquisaca, and Tarija), and give the wintering range as eastern Peru, eastern Colombia, and eastern Venezuela. Distribution maps in bird guides have portrayed the winter range as including most of western Amazonia (Dunning 1987, Fjeldså and Krabbe 1990, Olrog 1984).

Intrigued by the contrast between sizes of breeding and winter ranges and by the scarcity of records away from the breeding range, we analyzed the seasonal distribution of this species in detail. We were also intrigued by the fact that a disproportionate number of the specimens from the nonbreeding season were from that part of the nonbreeding range, northern Venezuela, that is farthest from the breeding range. With this background, we sought to clarify the seasonal distribution of the Slaty Elaenia by examination of specimen records.

METHODS

We solicited most museums that house extensive Neotropical bird collections for information on their specimens of Slaty Elaenia. The following data were requested for each specimen: date, locality, elevation, sex, age, gonad size and fat condition. Based on specimens collected during the time of peak breeding activity, we considered males with testes larger than 6 × 3 mm to be in breeding condition. For some comparisons, a crude gonad area was computed by multiplying length by width measurements. Some older specimen labels had only qualitative data on whether the gonads were "enlarged"; those specimens with enlarged gonads were taken as being in breeding condition. We did not request body weights (as an additional means of detecting subcutaneous fat deposits) because most specimens, particularly from the nonbreeding range, were collected so long ago that weight data were too scanty for analysis. Because many

older specimens also lacked information on subcutaneous fat, we also asked whether a specimen's label was soaked with oil (as a potential indicator of high fat levels.) Latitude, longitude and elevation of the collecting localities were obtained from the appropriate ornithological gazetteers (Paynter 1982, 1985; Paynter et al. 1975; Paynter and Traylor 1981; Stephens and Traylor 1983).

RESULTS

Nearly 100 specimens have been collected from the breeding range in the southern Andes (Fig. 1; Appendix 1). Males with gonad information were mostly in breeding condition (26 of 34 specimens). Eight females in Dpto. Tarija, Bolivia, collected between 4 January and 10 February were noted as having eggs, a brood patch or ova ≥3 mm. In Dpto. Tarija, individuals collected in late February (testis area: $\bar{x}$ = 12.6 mm^2, n = 5; ovary area: $\bar{x}$ = 11.5 mm^2, n = 2) have smaller gonads than do those collected nearby in January (testis area: $\bar{x}$ = 34 mm^2, n = 8; ovary area: $\bar{x}$ = 24 mm^2, n = 7) of the same year. Birds seem to arrive in their breeding range in Argentina in late October, with records as early as 19 October at Palma Sola, Prov. Jujuy, and Tafí Viejo, Prov. Tucumán. However, both these localities, at 800 and 1000 m respectively, are at the lower end of the elevational range for breeding-season specimens, which extends from 800 m to just over 2500 m. Most specimens from Bolivian breeding localities are from later in the season than those collected farther south, presumably a sampling artifact. However, there is one record for Buyuivi (= Boyuibe; Paynter et al. 1975), Dpto. Chuquisaca, from 1 October, but the elevation there, 600 m, is probably too low for breeding. The latest individuals at a presumed breeding locality include five specimens collected on 22–23 February at 108 km ENE of Tarija, Bolivia.

Habitat at the breeding localities has been recorded as humid or semihumid montane forest and forest edge. The best descriptions of the breeding habitat come from the specimen labels and field notes of Richard Crossin, who collected an extensive series of Slaty Elaenias in southern Bolivia (Appendix 1). Crossin's specimens came from pockets of moist forest with substantial epiphytic growth in canyons and ravines (n = 18); heavy, undisturbed forest (n = 5); and brushy hillsides adjacent to forest (n = 7). M. A. Carriker, Jr., collected another extensive series from a breeding locality (Tomina) in Bolivia that also included a heavily wooded canyon (Bond and Meyer de Schauensee 1941:317). Fjeldså and Krabbe (1990: 461) described the breeding habitat as "bushes or trees along streams in wooded valleys."

Although southern Dpto. Santa Cruz, Bolivia, is now considered the northern limit of the breeding range (Fjeldså and Krabbe 1990, Traylor 1979), the specimen evidence for breeding there is not as strong as it is for areas farther south. This evidence consists solely of birds with enlarged gonads, rather than records of nests, laying individuals, or juvenals. All four specimens from Dpto. Santa Cruz with gonad information had enlarged gonads, but only one (LSUMZ 124626) was taken in the middle

FIGURE 1. Distribution of the Slaty Elaenia. Small dots indicate a single specimen, medium dots represent between two and ten specimens from that locality, and large dots show localities, and groups of adjacent localities, with more than ten specimens. Note the large concentration of records around breeding localities in comparison to the paucity of non-breeding records.

of the breeding season, 20 January 1984. This specimen, however, was the only individual noted at that locality in many weeks of fieldwork (C. G. Schmitt and D. C. Schmitt, pers. comm.). If the Slaty Elaenia breeds in southern Dpto. Santa Cruz, then the records from Samaipata, 1700 m, on 17 March 1920, and from west of Comarapa, 2550 m, on 25 March 1973, would represent the latest records, by a month, from any presumed breeding locality (Fig. 2).

Only one specimen has been collected in Dpto. Cochabamba, the next Departamento north of Santa Cruz; it was collected at Duraznillo on 27 March 1920. Because Cochabamba is one of the most thoroughly sampled regions in Bolivia, and because the date is later than any record from a known breeding locality, we believe that the Duraznillo specimen represents a transient.

The small number of specimens collected away from probable breeding localities makes conclusions concerning the nonbreeding distribution tentative. With this cautionary preamble, we note that all specimens from the core of the austral winter (May–August) are from a rather small section of northern Venezuela, most near the Coastal Range (Figs. 1–2). Furthermore, the little information available on these localities in northern Venezuela leads us to suspect that most are in hilly areas. Two specimens are from the Sierra de Carabobo, in the Coastal Range; one is presumably from the vicinity of Cerro Azul in the mountains of the Paria Peninsula; two are from separate localities in the Serranía Imataca in extreme northern Edo. Bolívar; and one is from the Guiana highlands in extreme eastern Venezuela. At least three of these localities, those in Edo. Bolívar, are in regions of deciduous forest (T. A. Parker, pers. comm.) rather than in rainforest. Therefore, this species might not winter in Amazonian lowland habitats, but in areas more similar to the breeding areas in their topography and proximity to drier habitats.

The 10 specimen records from Peru and Colombia are from the austral spring or fall, the period when transients would be expected (Fig. 2). Presumed post-breeding, north-bound transients have been collected in central Bolivia, on 27 March; in Peru between 16 and 20 March; and in Colombia, on 2 and 25 April. Individuals presumably returning to their breeding localities have been recorded in Colombia on 13 October, in Peru between 15 September and 13 November, and in the lowlands of Dpto. Santa Cruz, Bolivia, at Buena Vista on 19 September, 18 October and 16 November. The majority of presumed transients have been collected along the western edge of Amazonia near the Andes (Fig. 1).

We had hoped to use seasonality in subcutaneous fat deposits as an indicator of migratory condition; however, specimens with fat data from the nonbreeding season were nearly nonexistent, and our attempt to use the degree to which specimen labels were greasy (as an index for fat deposits) showed no seasonal pattern. Unfortunately, only three specimens collected north of the breeding range had gonad data; all were in nonbreeding condition.

Approximately equal numbers of each sex (7 males, 9 females) have

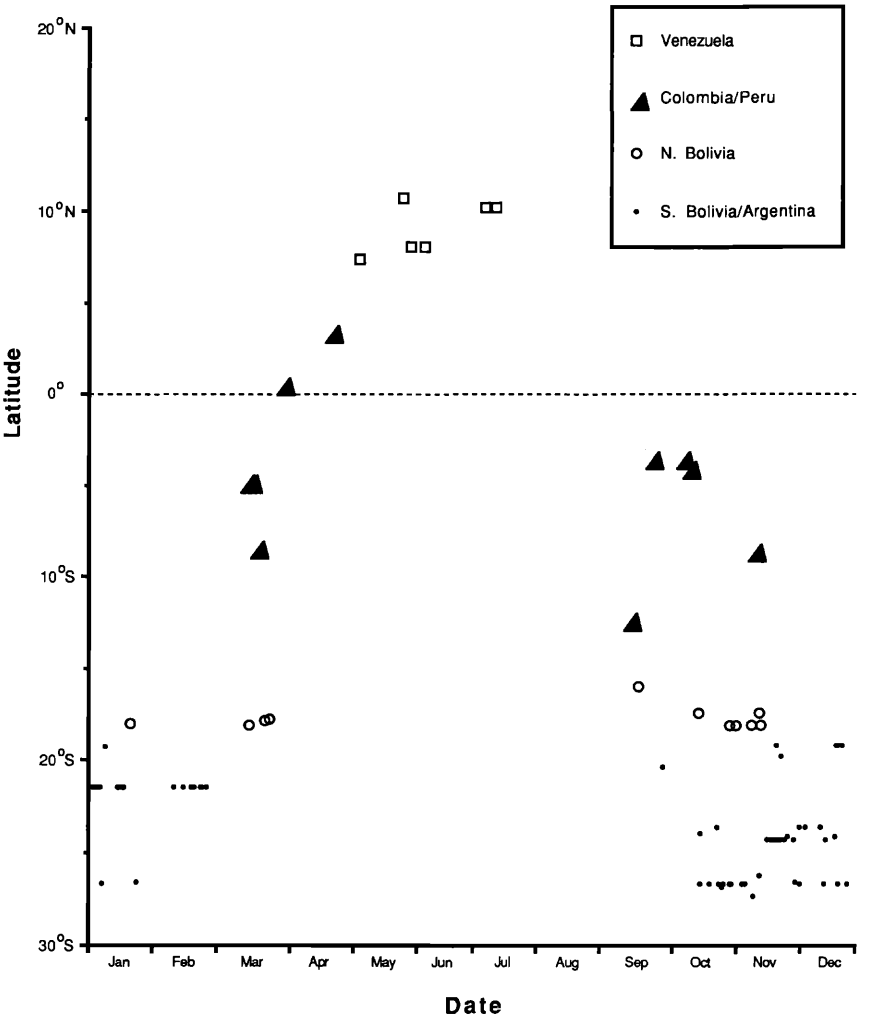

FIGURE 2. Plot of Slaty Elaenia records by latitude. A pronounced seasonal distribution of records is clearly evident with breeding birds found farthest south and records during the austral winter at the northern extreme of the range.

been collected during the non-breeding season. The small sample sizes preclude any quantitative examination of potential sexual differences in wintering range, but we see no obvious pattern. There is almost a 2:1 bias for males collected in the breeding range. Eleven of the 12 specimens with skull data had completely pneumatized skulls; one individual with a nonpneumatized skull was collected on 14 February 1973 at a known breeding locality south of Tarija, Bolivia.

DISCUSSION

The seasonal and geographic distribution of specimen records supports the restriction of the breeding range of the Slaty Elaenia to the Andes of northwestern Argentina and southern Bolivia (Fig. 1), mainly between 800 and 2500 m. Although it is likely that the species breeds as far north as southern Dpto. Santa Cruz, Bolivia, we cannot be certain that this is so.

The limits of the winter range, however, may be dramatically more restricted (Fig. 1) than currently given in reference works. The approximate area of the region of Amazonia in which the Slaty Elaenia is supposed to winter is roughly 2 million km^2, yet the only records from the core of the austral winter are from hilly areas in northern Venezuela, an area of roughly 200,000 km^2. Thus, the winter range may be as small as the breeding range, and may be more similar ecologically to the breeding range than to the lowland tropics of Amazonia, usually also considered as part of the winter range. The few records from Amazonia are from the time of year when transients would be expected. Whether the concentration of records near the foothills of the Andes reflects a sampling artifact or a curved migration route following the Andes (instead of a straight-line, shortest-distance route over Amazonia from the breeding to winter grounds) cannot yet be determined. The scarcity of records from Amazonia, particularly western Brazil, may be a sampling artifact: with a small population crossing a huge expanse (ca. 3000 km straight-line distance) that is relatively undersampled, few specimen records would be expected.

If indeed the wintering range of Slaty Elaenia is restricted to the hilly areas and mountains of northern Venezuela, then the locations of the breeding and winter ranges resemble the remarkably disjunct distributions of a few taxa of resident birds. The Brown-capped Redstart (*Myioborus brunniceps*) is known from the Tepui highlands of northern South America and from the southern Andes from Dpto. La Paz, Bolivia, to Prov. La Rioja, Argentina. The Two-banded Warbler (*Basileuterus bivittatus*) is known from the Tepuis and from the southern Andes from Dpto. Cuzco, Peru, through Bolivia to Prov. Salta, Argentina. Two allospecies of guans also show a similar pattern: Helmeted Curassow (*Pauxi pauxi*) of the Coastal Range of Venezuela and the foothills of the extreme northeastern Andes of Colombia, and Horned Curassow (*P. unicornis*) of the foothills and outlying ridges of the Andes in southern Peru and central Bolivia. The similarity in distribution pattern between these resident species and the migratory Slaty Elaenia might tempt one to propose that the disjunct distributions of these residents could have arisen by long-distance dispersal (see Leck (1980) for examples of resident populations possibly founded by migratory populations). However, we believe that this is highly unlikely in the cases of the warblers above, both of which are members of genera in which long-distance migration is rare or unknown, and is unthinkable in the case of the cracids, no species of which

is known to undergo latitudinal migration (Remsen and Cardiff 1990). (We assume that such disjunct distributions are caused by extinctions of populations from intervening areas.) Furthermore, as pointed out to us by T. A. Parker, these three examples of disjunct distributions of resident birds are just three extremes in a continuum of distribution patterns of several species and allospecies found in foothills around the periphery of Amazonia with varying degrees of disjunction (e.g., Sharpbill *Oxyruncus cristatus,* Rufous-brown Solitaire *Cichlopsis leucogenys,* and Blackish Pewee *Contopus nigrescens*). Finally, we cannot even be absolutely certain that the Venezuelan records do not represent a local breeding population that may even be resident there, as originally assumed by Cory and Hellmayr (1927).

Because the winter distributions of most species that winter in the tropics have not been analyzed by careful plotting of dates and localities, we suspect that the winter distributions given in reference works for many of these species are inaccurate or exaggerated in areal extent. The source of the errors will most likely be the same as that for the case of the Slaty Elaenia, namely the erroneous assumption that records taken outside the breeding distribution refer to wintering individuals without accounting for regions in which a species is only a transient. Therefore, we urge that mapping of true winter distributions of tropical migrants be given high priority, and that projects such as those of Pashley (1988a,b,c) and Pashley and Hamilton (1990) with wood-warblers be extended to other taxa and regions.

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APPENDIX 1. Specimens of the Slaty Elaenia. The sequence of localities is approximately north to south and, secondarily, by increasing elevation. Elevation in parentheses are those determined from the gazetteers for specimens without an elevation recorded on the label. "Source" refers to the museum housing the specimen; see acknowledgments for museum names.

Country	Dpto.	Locality	Elevation	Date(s)	No./Sex	Source
Venezuela	Carabobo	Sierra de Carabobo		8–13 Jul. 1914	2 ♂	CM[a]
Venezuela	Bolívar	Altagracia	(340 m)	9 Jun. 1910	♀	CM
Venezuela	Bolívar	San Germán de Upata	(340 m)	2 Jun. 1910	♀	CM
Venezuela	Bolívar	El Perú Mine	(200 m)	9 May 1910[b]	♂	CM
Venezuela	Sucre	Cristóbal Colón		30 May	♂	[c]
Colombia	Meta	San Juan de Arama	(400 m)	25 Apr. 1957	♀	FMNH
Colombia	Putumayo	San Antonio, Río Guamués	(250 m)	2 Apr. 1971	♀	FMNH
Colombia	Amazonas	Isla de Santa Sofía II	(100 m)	13 Oct. 1974	♀	MVZ
Peru	Loreto	Río Pichana, rt. bank of Amazon		25 Sep.–10 Oct. 1968	♂, ♀	FMNH
Peru	Loreto	Quebrada Pushaga, Río Morona	(220 m)	16–17 Mar. 1957	♂, ♀	FMNH
Peru	Loreto	Pucallpa	(150 m)	20 Mar. 1947	♀	FMNH
Peru	Loreto	Alto Ucayali, Santa Rosa		13 Nov. 1927	♀	AMNH
Peru	Madre de Dios	Río Manu, 40 km from mouth	(400 m)	15 Sep. 1979	♂	FMNH
Bolivia	Cochabamba	Duraznillo	(2643 m)	27 Mar. 1920	♂	CM
Bolivia	Santa Cruz	Buena Vista (Río Yapacaní)		19 Sep. 1914	♂	CM
Bolivia	Santa Cruz	Buena Vista (Río Surutú)	(350 m)	18 Oct.–16 Nov. 1917	♂, ♀	CM
Bolivia	Santa Cruz	28 km W of Comarapa	(2550 m)	25 Mar. 1973	♀	FMNH
Bolivia	Santa Cruz	2.5 km N Tambo	1500 m	20 Jan. 1984	♂	LSUMZ
Bolivia	Santa Cruz	Samaipata	(5500 ft)	17 Mar. 1920	♀	CM
Bolivia	Santa Cruz	Samaipata	5500 ft	2–17 Nov.[d]	5 ♂	ANSP, CM
Bolivia	Chuquisaca	Tomina	6700 ft	23–26 Dec. 1937	10 ♂, ♀	ANSP
Bolivia	Chuquisaca	Río Azero	4000 ft	24 Nov. 1936	♀	ANSP
Bolivia	Chuquisaca	25 km E of Padilla	8200 ft	8 Jan. 1938	2 ♂	ANSP
Bolivia	Chuquisaca	16 km N of Monteagudo	(1500 m)	26 Nov. 1972	♂	FMNH
Bolivia	Chuquisaca	Buyuivi	(2000 ft)	1 Oct. 1915	♂	CM
Bolivia	Tarija	80 km S Tarija	(1950 m)	14–17 Jan. 1973	6 ♂, 8 ♀	FMNH
Bolivia	Tarija	80 km S Tarija	(1950 m)	10–14 Feb. 1973	♂, ♀	FMNH
Bolivia	Tarija	67 km E Tarija	(2250 m)	18–19 Feb. 1973	♂, ♀	FMNH
Bolivia	Tarija	108 km ENE Tarija	(1950 m)	22–25 Feb. 1973	4 ♂, ♀	FMNH
Bolivia	Tarija	25 km NW Entre Ríos	(1650 m)	2–6 Jan. 1973	2 ♂, 5 ♀	FMNH
Argentina	Jujuy	Santa Barbara		5–16 Dec.[d]	3 ♂	MACN, AMNH

APPENDIX 1. Continued.

Country	Dpto.	Locality	Elevation	Date(s)	No./Sex	Source
Argentina	Jujuy	Yuto		27 Oct. 1965	♂	IML
Argentina	Jujuy	Palma Sola, Santa Barbara	800 m	19 Oct. 1976	♂	IML
Argentina	Jujuy	Cerro Santa Barbara	2000 m	29 Nov.–22 Dec. 1967	2 ♀	IML
Argentina	Jujuy	Arenal, Santa Barbara	2000 m	20 Nov.–2 Dec.[d]	2 ♀, ♂, ?	IML
Argentina	Jujuy	Arenal, Santa Barbara	2600 m	23 Nov. 1966	♂	IML
Argentina	Jujuy	Arenal, Santa Barbara		21 Nov.–18 Dec.[d]	8 ♂, 5 ♀	IML, MLP
Argentina	Jujuy	Arenales, Santa Barbara	2000 m	25 Nov. 1966	♂	IML
Argentina	Jujuy	El Fuerte, Santa Barbara	1800 m	8 Dec. 1963	?	IML
Argentina	Jujuy	El Fuerte, Santa Barbara	2000 m	8 Dec. 1963	♂	IML
Argentina	Tucumán	San Pedro de Colalao	(1000 m)	16 Nov. 1959	♀	MLP
Argentina	Tucumán	Las Cuchillas		unknown	2?	[e]
Argentina	Tucumán	Amaichá del Valle	(2500 m)	3 Dec. 1958	?	IML
Argentina	Tucumán	La Criolla	1500 m	23 Jan. 1903	♂	AMNH
Argentina	Tucumán	La Hoyada	1300 m	24–28 Dec. 1901	2 ♂	AMNH, IML
Argentina	Tucumán	Tafí Viejo	900 m	7 Jan. 1915	♂	MACN
Argentina	Tucumán	Tafí Viejo	(950 m)	3 Nov. 1900	♂	IML
Argentina	Tucumán	Tafí Viejo	1000 m	23 Oct.–17 Dec.[d]	4 ♂, ♀	MACN
Argentina	Tucumán	Tafí Viejo		19 Oct.–5 Dec. [d]	3 ♂	MACN
Argentina	Tucumán	Tafí (Viejo?)	illegible	28 Oct. 1900	♂	AMNH
Argentina	Tucumán	Tafí Viejo, Cerro de Tucumán		2 Nov. 1900	♀	IML
Argentina	Tucumán	near Camino Tafí del Valle	850 m	29 Oct. 1984	?	IML
Argentina	Tucumán	Concepción		13 Nov. 1918	♂, 2 ♀, ?	MACN, FMNH
Argentina	Tucumán	Cerro Franco		26 Dec. 1957	♀	LSUMZ
Argentina	Tucumán	location unknown		4 Jan. 1902	♀	MZSP
Argentina	Tucumán	location unknown		unknown	?	AMNH

[a] FMNH = Field Museum of Natural History; IML = Instituto Miguel Lillo; ANSP = Academy of Natural Sciences, Philadelphia; MLP = Universidad Nacional de la Plata; MACN = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; CM = Carnegie Museum of Natural History; AMNH = American Museum of Natural History; LSUMZ = Museum of Natural Science, Louisiana State University; MVZ = Museum of Vertebrate Zoology; MZSP = Museu de Zoologia, Universidade de São Paulo.

[b] Specimen date is 9 May 1910, not 10 May 1910 as published in Cory and Hellmayr (1927) and Zimmer (1941).

[c] Zimmer (1941).

[d] Specimens collected during various years.

[e] Cory and Hellmayr (1927).