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Geographic distribution analysis of the genus *Xenodacnis* (Birds: Thraupidae) using ecological niche modeling

Análisis de la distribución geográfica del género *Xenodacnis* (Aves: Thraupidae) utilizando el modelado de nicho ecológico

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Trabajos originales

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Palabras clave: Altos Andes; biogeografía; aislamiento; modelos de nicho; Xenodacnis parina.
Keywords: High Andes; biogeography; isolation; niche modeling; Xenodacnis parina.

Abstract

Xenodacnis is a monotypic thraupid genus restricted to the tropical high Andes of Peru and Ecuador. Its only species, *X. parina* has a large discontinuous distribution from central Ecuador to southern Peru. To date, three subspecies are recognized, all separated by geographical barriers that clouded promote allopatric events. The taxonomic affinities of the Ecuadorian population have not been assessed since its discovery in the 1970s at the Cajas National Park in Azuay province. I studied the environmental affinities between the distribution of the described subspecies and the Ecuadorian population bias ecological niche modeling. I found a distinctive ecological niche in the distribution of each of the analyzed populations and also for the southern Arequipa population. These different environmental niche conditions come apart by deep Andean valleys playing a role as geographical barriers for the isolation of these populations that need further taxonomic analysis.

Resumen

Xenodacnis es un género de traupido mono típico restringido a los altos Andes tropicales de Perú y Ecuador. Su única especie, *X. parina* tiene una distribución extensa pero discontinua desde el centro Ecuador hasta el sur de Perú. A la fecha se reconocen tres subespecies, todas separadas por barreras geográficas que pudieron promover eventos alopátricos. Las afinidades taxonómicas de la población de ecuador no se han analizado desde su descubrimiento en los años 70 dentro del Parque Nacional Cajas en la provincia del Azuay. Yo estudié las afinidades ambientales entre las distribuciones de las subespecies descritas y la población en Ecuador mediante modelos de nicho ambiental. Encontré diferentes condiciones ambientales en los nichos de cada una de las poblaciones analizadas y también para la población sureña de Arequipa. Estas diferencias ambientales están separadas por profundos valles Andinos que cumplen el roll de barreras geográficas para el aislamiento de estas poblaciones que necesitan un próximo análisis taxonómico.

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Introduction

The thraupid genus *Xenodacnis* (Cabanis 1873) is a high Andean specialist that occurs from central Ecuador through southern Peru, in elevations between 3,000 and 4,400 m; it has a specialized diet on small insects and extra floral nectar gleaned from beneath the leaves of *Gynoxys* shrubs, mainly within *Polylepis* woodland patches (Ridgely & Greenfield 2001, Aguilar & Iñiguez 2015). It is placed in a clade of montane forest specialists with several genera formerly classified in the 'finch' family Emberizidae, including *Phrygilus*, *Idiopsar*, *Diuca*, *Haplospiza*, and *Acanthidops* (Campagna et al. 2011, Barker et al. 2012, Burns et al. 2014). *Xenodacnis* has a single species, the Tit-like Dacnis, *X. parina*; moreover, some authors consider that the genus is composed by at least two different species (del Hoyo & Collar 2018).

Xenodacnis was described in 1873 by Jean Louis Cabanis, the type locality being "Maraynioc", Junín department, east central Peru (Mlíkovský 2010). Later, Bond y de Schauensee (1939) described a different species from the northern Andes of Peru: *X. petersi*, with two subspecies: *X. p. petersi* (Yánac, Ancash department, west central Peru), and *X. p. bella* (Atuén, Amazonas department, northern Peru). In a revision of the genus, Zimmer (1942) and later Zimmer y Mayr (1943) established size and some plumage characters (i.e., bright streaks in male foreparts) as diagnosable characters, and suggested that *X. petersi* merit species status, but were later lumped under a single species by de Schauensee (1966), a treatment followed by all subsequent authors (Paynter 1970, Ridgely & Tudor 2009, Hilty 2011). Currently, *X. parina* is considered as a single species with three subspecies: *X. parina parina*, *X. p. bella* and *X. p. petersi* by most authorities (Clements et al. 2017, Remsen et al. 2017), but del Hoyo y Collar (2018) recently resurrected species status for the *petersi* group. Yet, the taxonomy of *X. parina* has not been thoroughly revised to date.

Ridgely (1980) provided the first report of *X. parina* from southern Ecuador, in Cajas National Park, Azuay province. He did not determine the subspecies identity for this population, but suggested that it might represent an undescribed form, resembling the geographically closest *X. p. bella*, but the taxonomic status of the Ecuadorian population is still uncertain (Ridgely & Greenfield 2001, del Hoyo & Collar 2018).

The northern distribution of *X. parina* is interrupted by the dry North Peru Low, a depression of the Andean cordillera that starts at the Jubones River valley in Ecuador and ends at the Huancabamba River valley in Peru (Weigend 2002, 2004). In central Peru the Andean valleys split the described subspecies; the nominal *X. p. parina* from the eastern Andean ridges and *X. p. petersi* from the western cordillera, this last subspecies is separated from the northern Peruvian *X. p. bella* by Marañon River. It has been postulated that these barriers for species dispersal, acted as drivers of allopatric speciation in birds (Vuilleumier 1969, Parker et al. 1985, Gutiérrez-Pinto et al. 2012, Winger & Bates 2015, Hazzi et al. 2018). However, in allopatry, species with specialized diets (e.g. *Xenodacnis*), may have conserved morphological traits that reflect ecological adaptations (Winger & Bates 2015), making it difficult to assess the degree of morphological variation for some taxa. Consequently, morphologically cryptic species are often lumped under a single species with presumed widespread distributions (Cabot & de Vries 2009, Lara et al. 2012, Avendaño et al. 2015), as might be the case for allopatric populations of *Xenodacnis*.

Environmental niche models have been useful to define Andean bird distributions (Jiguet et al. 2010, Tinoco et al. 2009); and have shown non-overlapping distribution in closely related high Andean species with apparently little differences in niches occupied (Jiguet et al. 2010). In order to analyze the distribution of *X. parina*, I performed an environmental analysis to assess the taxonomy of this isolated, cryptic bird species complex (Gill 2014, Sangster 2014).

Material and methods

To explore environmental niche and predict the geographic ranges of *X. parina* described subspecies of Peru and the Ecuadorian population; occurrence localities were obtained from online resources (eBird 2015), published literature, fieldwork and unpublished records. Environmental niche models were based on 19 bioclimatic variables, obtained from WorldClim (http://www.worldclim.org), which included seasonality, averages and extremes in temperature and precipitation across South America at a resolution of 30 sec (Hijmans et al. 2005). To avoid spatial autocorrelation, occurrences in localities closer than 5 km were excluded. Niche models were obtained using the maximum entropy algorithm as implemented in Maxent 3.3.3k (Phillips et al. 2006). For all models, we used default parameter settings. To test model performance, we evaluated if 30% of randomly selected points are predicted by 10 replicate bootstrap models performed with remaining fraction of data, obtaining a maximum possible test value of the area under the ROC curve (Test AUC). Binary maps of presence and absence of suitable habitat conditions were based on the mean values of equal training sensitivity and specificity threshold from models (Phillips et al. 2006). One environmental niche model was obtained for the species as a whole, one for each described subspecies from Peru, and one for the Ecuadorian isolated population.

To analyze differences in environmental conditions between the Ecuadorian population and all Peruvian subspecies, the climate envelope of each group was characterized by extracting the bioclimatic values at each occurrence locality and synthesizing eight non-correlated variables in a principal component analysis (PCA). The first two components of the analysis were plotted to illustrate multivariate space of the environmental niche, with 50% confidence ellipses for each subspecies and the Ecuadorian population. Finally, we analyzed the correlations between environmental distances and geographical distances among subpopulations using a Mantel test.

Results

A total of 60 occurrence localities of *Xenodacnis* were obtained after data clean and avoiding spatial autocorrelation: 20 records of *X. p. parina*, 25 of *X. p. petersi*, 5 of *X. p. bella* and 10 from Ecuador (Anexo 1). The predicted distribution for the entire species (n = 60, ETSS = 0.249, Test AUC = 0.984) showed a somewhat continuous distribution in Peru, but an entire isolation for the Ecuadorian population (Fig. 1). The suitable environmental conditions for the Ecuadorian population are also restricted to this country (n =10, ETSS = 0.432, Test AUC = 0.998 sd=0.002), but the model predicts areas extending north where it has not been recorded (Fig 1). Distribution models for the Peruvian subspecies overlap mostly in west-central Peru (Fig 1). Models showed that suitable conditions for *X. p. parina* and *X. p. petersi* are not found in Ecuador (n= 20, ETSS = 0.307, Test AUC = 0.986 sd=0.003), but are widely distributed across the Peruvian Andes, with a large overlap in an area were only *X. p. petersi* has been positively recorded (n = 25, ETSS = 0.302, Test AUC = 0.997 sd= 0.001); the southern Arequipa records have also proven different environmental conditions in the model obtained for the species. Model for *X. p. bella* showed that environmental conditions for this subspecies are marginally predicted in northern Ecuador, in an area were no *Xenodacnis* has been recorded (n = 5, ETSS = 0.587, Test AUC = 0.997 sd=0.001) (Fig. 1).

The first two components from the PCA of bioclimatic variables explained 79% of variance. First component had high loadings on precipitation means and seasonality values. The second component had the highest loadings in temperature variables, especially temperature of coldest quarter (Table 1). Overall, the population of Ecuador occupies a climatic envelope characterized by

Table 1. Eigenvectors of the principal components analysis of the environmental variables of occurrence localities of *Xenodacnis parina*. Only the most influential bioclimatic variables are included.

Variables	PC1	PC2
Bio11 = Temperature of Coldest Quarter	-0.136	-0.561
Bio1 = Mean Annual Temperature	-0.188	-0.544
Bio10 = Temperature of Warmest Quarter	-0.229	-0.523
Bio17 = Precipitation of Driest Quarter	0.439	-0.201
Bio12 = Annual Precipitation	0.471	-0.157
Bio16 = Precipitation of Wettest Quarter	0.266	-0.064
Bio15 = Precipitation Seasonality	-0.509	0.086
Bio4 = Temperature Seasonality	-0.384	0.192

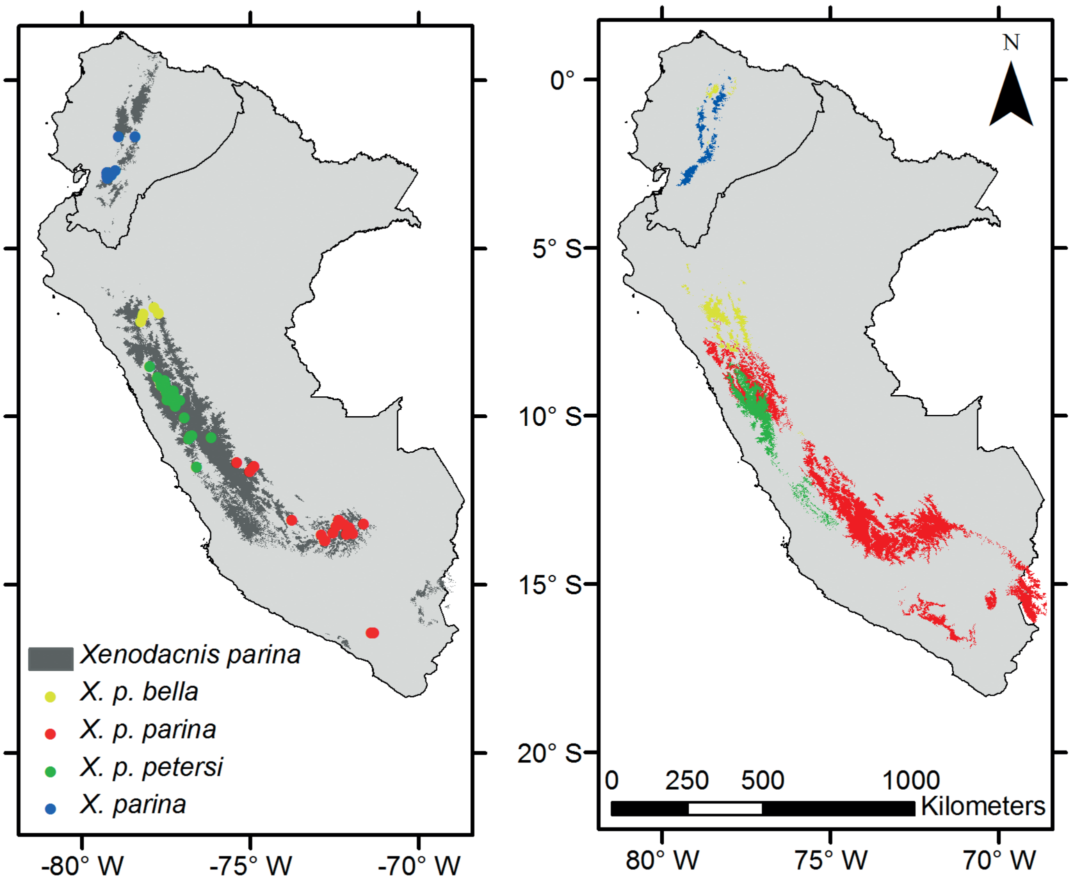

Figure 1. (Left) Occurrence localities of *Xenodacnis parina*, dark grey represents the distribution model for the entire species; (Right) and environmental models of each subspecies and the Ecuadorian population. Colored areas represent presence probability using values under the equal training sensitivity and specificity threshold from distribution models: red (*X. p. parina*), green (*X. p. petersi*), yellow (*X. p. bella*), blue (Ecuadorian population).

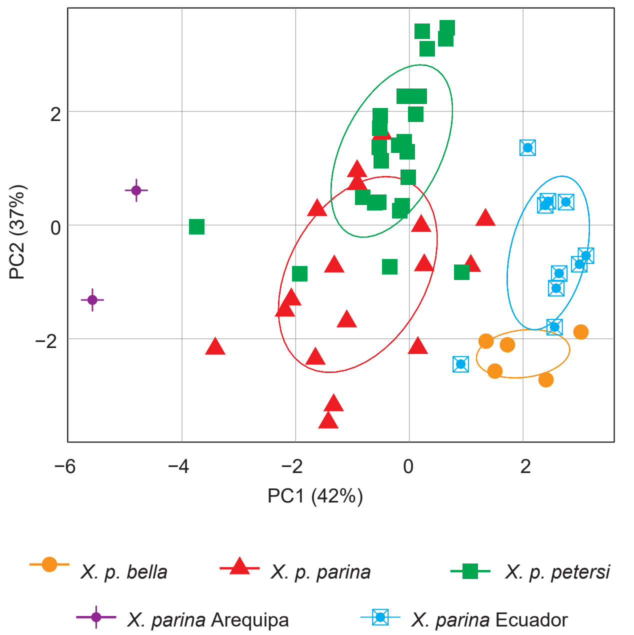

Figure 2. Graphic output of first two components from the bioclimatic PCA based on eight no correlated environmental variables for 60 locations where different populations of *Xenodacnis parina* have been recorded.

higher minimum annuals and less variation in seasonal temperatures, accompanied by higher annual precipitation (Fig. 2). Because data from Arequipa did not occupy the predicted distribution for the entire species, we separated data from this southern *X. p. parina* population for the following PCA. The results of the Mantel test also revealed correlation between environmental and geographical distance (r= 0.35, p= 0.001).

Discussion

These results show isolation accompanied by variation of environmental niche conditions. These environmental differences suggest a reduction in the ability to move across Andean barriers and highlighted the differences between biogeographical regions in the Andes of Peru and Ecuador (Wang & Bradburd 2014, Hazzi et al. 2018), reviling also differences for the Arequipa southern population. The Ecuadorian population inhabits shrubby paramo characterized by higher precipitation and higher temperature, when compared with Peruvian high Andean ecosystems, the *X. p. bella* population in northern Peru is found in the Jalca biome (Ochoa-Tocachi et al. 2018), whereas western and eastern described subspecies from central Peruvian Andes inhabit more xeric puna ecosystem, which is drier, colder, and more seasonal (Luteyn 1999, Tovar et al. 2013); the Arequipa population also inhabits lower precipitation means and different seasonality values (Fig. 2), and is isolated by the Apurimac River Valley (Hazzi et al. 2018). Both, the reduced ability to disperse across a major geographical barrier and isolation by environment are drivers of speciation in the tropical Andes (Wang & Bradburd 2014, Smith et al. 2014, Winger & Bates 2015).

It seems plausible that an ancient *Xenodacnis* spread north from the older central Andes from Peru as other high Andean birds (Chesser 2000, Gutiérrez-Pinto et al. 2012, Valderrama 2014, Benham et al. 2015), colonizing new high Andean ecosystems reaching north of the North Peru Low (Weir 2009, Tobias et al. 2014, Winger & Bates 2015), during the Miocene (3.4 Ma; Weir & Schluter 2008). This colonization event might have been followed by allopatry 2.7 Ma, when the northern Andes in Ecuador had already reached modern elevations (Gregory-Wodzicki 2000), and active Andean drainage systems had already shaped the North Peru Low (Garzione et al. 2008). The colonization of *Xenodacnis* may have followed a high Andean common fashion of expansion and isolation with deep Andean valleys playing an important role in the differentiation of populations (Gutiérrez-Pinto et al. 2012, Valderrama 2014, Benham et al. 2015, Hazzi et al. 2018).

All information presented is a contribution to assess the distribution and taxonomy of *Xenodacnis*; results obtained from environmental niche analysis indicates that *X. parina* as a hole species occupy different environmental conditions across a large tropical high Andean distribution, supporting the current taxonomy of the genus, in which *X. p. petersi* in a polytypic group and *X. p. parina* is monotypic (Clements et al. 2018); however, the northern and southern populations, from Ecuador and Arequipa, are not yet described lineages, geographically isolated with particular environmental conditions that need further taxonomic analysis.

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JMA conceived the idea, collected the data, conducted the analyses, and prepared the manuscript. The author read and approved the final manuscript.

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Ethics / legal considerations:
Not applicable.

Anexo 1. Occurrence localities of *Xenodacnis parina*.

	Country	State/Province	Subspecies	Altitude	Latitude	Longitude
1	Ecuador	Morona-Santiago	X. p. bella	4089	1° 40' 20'' S	78° 25' 58'' W
2	Ecuador	Chimborazo	X. p. bella	3210	1° 40' 24'' S	78° 55' 57'' W
3	Ecuador	Cañar	*X. p. bella*	3603	2° 40' 55'' S	79° 02' 00'' W
4	Ecuador	Azuay	*X. p. bella*	4297	2° 44' 16'' S	79° 16' 30'' W
5	Ecuador	Azuay	*X. p. bella*	3736	2° 46' 11'' S	79° 12' 19'' W
6	Ecuador	Azuay	*X. p. bella*	4001	2° 48' 13'' S	79° 15' 16'' W
7	Ecuador	Azuay	*X. p. bella*	3327	2° 49' 18'' S	79° 08' 29'' W
8	Ecuador	Azuay	*X. p. bella*	3799	2° 50' 00'' S	79° 13' 00'' W
9	Ecuador	Azuay	*X. p. bella*	4032	2° 51' 27'' S	79° 16' 22'' W
10	Ecuador	Azuay	*X. p. bella*	3636	2° 54' 33'' S	79° 15' 19'' W
11	Peru	Amazonas	*X. p. bella*	3341	6° 45' 00'' S	77° 52' 00'' W
12	Peru	Amazonas	*X. p. bella*	3695	6° 55' 00'' S	77° 43' 50'' W
13	Peru	Cajamarca	*X. p. bella*	3239	6° 57' 02'' S	78° 11' 17'' W
14	Peru	Cajamarca	*X. p. bella*	3401	7° 01' 32'' S	78° 12' 46'' W
15	Peru	Cajamarca	*X. p. bella*	3372	7° 10' 37'' S	78° 15' 57'' W
16	Peru	Ancash	*X. p. petersi*	3932	8° 30' 00'' S	78° 00' 00'' W
17	Peru	Ancash	*X. p. petersi*	3555	8° 50' 03'' S	77° 45' 33'' W
18	Peru	Ancash	*X. p. petersi*	4405	8° 55' 09'' S	77° 33' 59'' W
19	Peru	Ancash	*X. p. petersi*	4243	8° 58' 19'' S	77° 33' 20'' W
20	Peru	Ancash	*X. p. petersi*	4703	8° 59' 15'' S	77° 40' 06'' W
21	Peru	Ancash	*X. p. petersi*	3973	9° 01' 40'' S	77° 32' 44'' W
22	Peru	Ancash	X. p. petersi	4861	9° 02' 15'' S	77° 36' 29'' W
23	Peru	Ancash	*X. p. petersi*	3949	9° 04' 48'' S	77° 39' 11'' W
24	Peru	Ancash	*X. p. petersi*	4454	9° 06' 40'' S	77° 31' 47'' W
25	Peru	Ancash	*X. p. petersi*	4127	9° 09' 24'' S	77° 33' 16'' W
26	Peru	Ancash	*X. p. petersi*	4234	9° 13' 07'' S	77° 18' 05'' W
27	Peru	Ancash	*X. p. petersi*	4793	9° 17' 12'' S	77° 30' 12'' W
28	Peru	Ancash	*X. p. petersi*	3978	9° 21' 50'' S	77° 16' 22'' W
29	Peru	Ancash	*X. p. petersi*	4165	9° 22' 46'' S	77° 27' 38'' W
30	Peru	Ancash	*X. p. petersi*	3940	9° 25' 26'' S	77° 16' 02'' W
31	Peru	Ancash	*X. p. petersi*	3655	9° 29' 48'' S	77° 28' 45'' W
32	Peru	Ancash	*X. p. petersi*	4246	9° 30' 27'' S	77° 23' 23'' W
33	Peru	Ancash	*X. p. petersi*	4112	9° 30' 46'' S	77° 05' 45'' W
34	Peru	Ancash	*X. p. petersi*	4295	9° 41' 00'' S	77° 14' 00'' W
35	Peru	Huánuco	*X. p. petersi*	4838	10° 01' 55'' S	76° 58' 18'' W
36	Peru	Lima	*X. p. petersi*	4203	10° 33' 44'' S	76° 44' 49'' W
37	Peru	Lima	*X. p. petersi*	4468	10° 35' 00'' S	76° 48' 00'' W
38	Peru	Pasco	*X. p. petersi*	3727	10° 37' 06'' S	76° 10' 21'' W
39	Peru	Lima	*X. p. petersi*	4400	10° 39' 00'' S	76° 50' 00'' W
40	Peru	Junin	*X. p. parina*	3933	11° 22' 00'' S	75° 24' 00'' W
41	Peru	Junin	*X. p. parina*	3983	11° 27' 54'' S	74° 53' 53'' W
42	Peru	Lima	X. p. petersi	3144	11° 29' 40'' S	76° 36' 39'' W
43	Peru	Junin	*X. p. parina*	4205	11° 31' 52'' S	74° 56' 35'' W
44	Peru	Junin	*X. p. parina*	3501	11° 37' 25'' S	75° 01' 04'' W
45	Peru	Ayacucho	*X. p. parina*	3912	13° 04' 25'' S	73° 46' 35'' W
46	Peru	Cuzco	*X. p. parina*	2946	13° 04' 42'' S	72° 23' 09'' W

(continue..)

	Country	State/Province	Subspecies	Altitude	Latitude	Longitude
47	Peru	Cuzco	*X. p. parina*	3725	13° 06' 54'' S	72° 20' 57'' W
48	Peru	Cuzco	*X. p. parina*	4432	13° 09' 49'' S	72° 16' 42'' W
49	Peru	Cuzco	*X. p. parina*	3026	13° 11' 05'' S	71° 38' 34'' W
50	Peru	Cuzco	*X. p. parina*	4195	13° 11' 51'' S	72° 13' 00'' W
51	Peru	Cuzco	*X. p. parina*	3237	13° 15' 30'' S	72° 27' 44'' W
52	Peru	Cuzco	*X. p. parina*	3438	13° 17' 35'' S	72° 03' 03'' W
53	Peru	Cuzco	*X. p. parina*	3020	13° 26' 50'' S	72° 32' 59'' W
54	Peru	Cuzco	*X. p. parina*	3880	13° 28' 53'' S	71° 57' 49'' W
55	Peru	Cuzco	*X. p. parina*	3362	13° 29' 00'' S	72° 09' 00'' W
56	Peru	Apurimac	*X. p. parina*	3473	13° 31' 05'' S	72° 53' 12'' W
57	Peru	Apurimac	*X. p. parina*	4114	13° 40' 33'' S	72° 47' 10'' W
58	Peru	Apurimac	*X. p. parina*	4114	13° 40' 39'' S	72° 47' 42'' W
59	Peru	Arequipa	*X. p. parina*	3511	16° 25' 05'' S	71° 19' 39'' W
60	Peru	Arequipa	*X. p. parina*	2898	16° 25' 12'' S	71° 25' 12'' W