

Assessing the geographic range of Black-fronted Ground-Tyrants (*Muscisaxicola frontalis*) using extralimital and winter range occurrence records and ecological niche modeling

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ABSTRACT. Estimating the geographic range of a species can be complicated by insufficient occurrence data and a lack of information about range limit determinants. Accurate estimates of species distributions are needed to assess the impacts of anthropogenic actions and for exploring evolutionary and ecological processes that maintain biological diversity. After documenting several extralimital locations for Black-fronted Ground-Tyrants (*Muscisaxicola frontalis*; Tyrannidae), we questioned the accuracy of the current winter range estimate. We provide specimen and observation records from central and southern Peru that represent new information about the winter distribution of Black-fronted Ground-Tyrants. We used ecological niche models generated from new extralimital records and records from the winter range to assess the current range estimate. We also tested winter and extralimital niche models for model equivalency using a resampling technique available through Maxent and ENM Tools. Niche models developed with locations from the winter range predicted with high probability (>90%) the area of the extralimital records. Reciprocally, niche models developed with the extralimital locations predicted the majority of the winter range locations, although the probability was lower for some locations and the most southerly points were not included in the prediction. The test for model equivalency did not distinguish the two models, suggesting the possibility that the extralimital records were from poorly sampled areas of the true winter range. Smaller scale habitat associations of Black-fronted Ground-Tyrants, such as a preference for sparsely vegetated slopes, were documented that were more specific than published accounts. Finally, we present the first case of frugivory in *Muscisaxicola* with the identification of *Cumulopuntia boliviana ignescens* (Cactaceae) seeds and pericarp in all five stomach samples of Black-fronted Ground-Tyrants collected in southern Peru.

RESUMEN. Evaluación de la distribución geográfica de *Muscisaxicola frontalis* mediante el uso de registros dentro y fuera de los límites conocidos en el invierno y modelos de nicho ecológico

Estimar el rango geográfico de una especie puede ser complicado debido a la insuficiencia de registros y el desconocimiento de los mecanismos que limitan su distribución. Una estimación precisa es necesaria para evaluar los impactos de las acciones antropogénicas y para explorar los mecanismos ecológicos y evolutivos responsables de mantener la diversidad biológica. Además de documentar varios registros que representan una ampliación en el rango de distribución de la dormilona de frente negra (*Muscisaxicola frontalis*, Tyrannidae), evaluamos la precisión del actual estimativo de su rango de distribución. En este estudio, presentamos registros de observaciones y especímenes obtenidos en el centro y sur de Perú que representan nueva información sobre la distribución de la especie durante el invierno. Mediante el desarrollo de modelos de nicho ecológico generados a partir de nuevos registros dentro y fuera del rango de distribución conocido generamos modelos de nicho ecológico (ENM) para estimar el rango de distribución de la especie durante el invierno. Además, evaluamos si los modelos de nicho basados en registros dentro y fuera del rango de distribución son equivalentes usando una técnica de remuestreo disponible a través de Maxent y ENM Tools. Los modelos realizados usando los registros dentro del rango de distribución conocido predijeron con alta probabilidad (>90%) el área donde encontramos los nuevos registros de la especie. De igual forma, los modelos basados en los nuevos registros fuera del rango de distribución predijeron la mayoría de las localidades dentro del rango de distribución, aunque con probabilidades bajas para algunas localidades, especialmente en el sur de la distribución. El test de equivalencia de nicho no pudo distinguir los dos modelos, lo que sugiere que los registros recientes fuera de rango de distribución provienen de áreas pobremente muestreadas del rango real

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de distribución en el invierno. Finalmente, describimos la preferencia de la especie por pendientes con vegetación escasa, y presentamos el primer caso de frugivoría en el género *Muscisaxicola* mediante la identificación de semillas y el pericarpio de *Cumulopuntia boliviana ignescens* (Cactaceae) en los contenidos estomacales de los cinco individuos colectados en el sur de Perú.

Key words: austral migrant, frugivory, Peru, microhabitat, niche equivalency test

Knowledge of the geographic ranges and basic ecology of some species of birds is limited, and this is especially true in South America. Difficulties in access and a shortage of researchers have limited our ability to obtain ecological information about many Neotropical birds, including most austral migrants that breed in southern South America and migrate north to the Andes for the austral winter (Stotz et al. 1996, Chesser and Levey 1998). Recently, investigators using ecological niche models (ENMs) have taken advantage of museum locality data to develop species distribution estimates (Peterson 2001) and to test ecological (Anciães and Peterson 2006, Cadena and Loiselle 2007) and evolutionary (Peterson et al. 1999, Graham et al. 2004, Kozak et al. 2008) hypotheses. A promising application of ENMs is identifying potential areas of occupancy in unexplored areas (Engler et al. 2004, Overton et al. 2006, Kumar and Stohlgren 2009) and determining if those areas represent an extension of a species' niche breadth (Warren et al. 2008). These models can also be used to explore the relative influence of biotic and abiotic factors that shape distributions (Graham et al. 2010). This can be particularly useful for conservation planning for uncommon species in remote areas of the Neotropics (e.g., Loiselle et al. 2003, Marini et al. 2010).

Black-fronted Ground-Tyrants (*Muscisaxicola frontalis*), one of at least six austral migratory species in the genus *Muscisaxicola* (Chesser and Levey 1998), breed in the Andes from Antofagasta, Chile, south to Río Negro, Argentina, and migrate north in the austral fall to Bolivia, western Argentina, and southwest Peru (Fjeldsá and Krabbe 1990, Jaramillo 2003, Narozky and Yzurieta 2003, Schulenberg et al. 2007). Schulenberg et al. (2007) noted that some individuals rarely stray farther north. Similarly, Ridgely and Tudor (1989) assigned vagrant status to a single northern record in his distribution map. Schulenberg (pers. comm.) and presumably Ridgely and Tudor (1989) comments refer to a specimen (LSUMZ 80625) collected on 22 May 1975 by Ted Parker in dpto. Ancash

at 4267 m. The northernmost previously published record is from the Chuquibamba area of dpto. Arequipa, Peru, at 4150 m (Fjeldsá 1987).

During fieldwork in central and southern Peru, we documented several new occurrence records of Black-fronted Ground-Tyrants beyond their current estimated geographic range. These records suggest that the current range estimate based on few records may need revision. The new records provided an opportunity to address the question of whether the locations of the extralimital records were in niche space similar to those of existing records or, in other words, whether the extralimital records represent an extension of niche space or just geographic space. To address this question, we used a novel application of ENMs to test the equivalency of models derived from extralimital and within-range occurrence records. If the extralimital records represent a geographic range extension as well as an extension in niche space, then we should be able to distinguish statistically the climatic niche spaces of the known range and the extralimital range. Any difference would indicate that the realized niche of Black-fronted Ground-Tyrants is broader than previously estimated. However, if the climatic envelope models are statistically indistinguishable, then the extralimital records would suggest a larger wintering range. In either case, this provides a large-scale starting point from which additional range-limiting variables can be explored (Fig. 1).

METHODS

New and historical records. We compiled historical and new occurrence records using both sight records and specimens (Table 1). Locations were vetted, with questionable data omitted. We obtained six new records (Supplementary Table S1) during fieldwork in June 2007, August 2009, and from 19 September to 10 October 2008, 2–7 and 27–30 April 2009, 16–20 August 2009, 31 January to 8 February 2010, 9–15 March 2010, and 1–4 April 2010 in the Peruvian departments of Ancash, Lima,

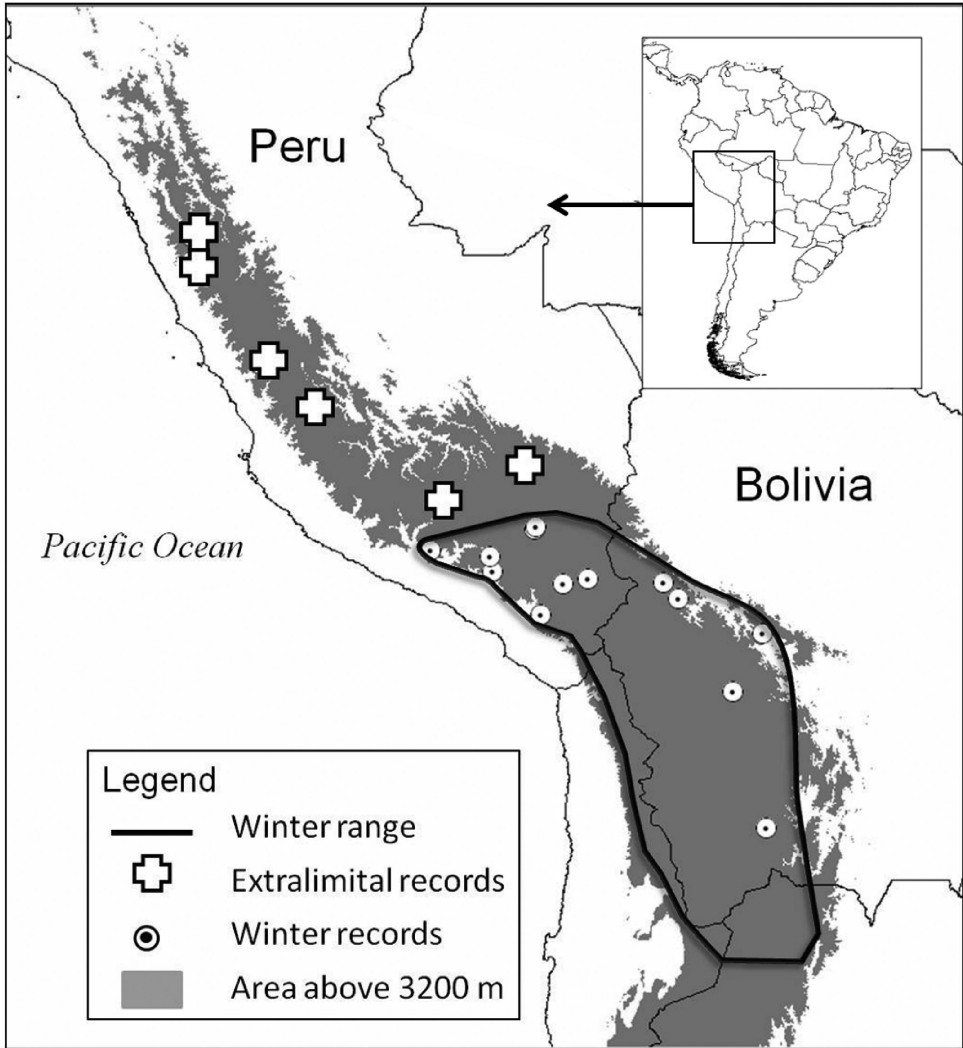


Fig. 1. The study area is shown with the occurrence records used to develop ecological niche models. The models were restricted to the area (shown in gray) above 3200 m. The current geographic wintering range estimated from Fjeldså and Krabbe (1990) and Schulenberg et al. (2007) is circumscribed with a bold black line, and dark-centered white circles represent winter range localities. Extralimital records are represented with white plus signs.

Junín, Huancavelica, Arequipa, Moquegua, and Puno. Fieldwork by REG included surveys along line transects ($N = 38$; mean = 1.2 km, range = 0.5–1.75 km) for a study of puna bofedales and surrounding habitats located in the departments mentioned above. Transects were surveyed during the wet (December–February) and dry (June–August) seasons.

Additional records were obtained during opportunistic collecting, most often within a few kilometers of transects or when traveling between transects. Specimen preparation included a thorough necropsy, collection of tissue samples, and preservation of stomachs and contents. Specimens collected by REG were deposited in either the Centro de Ornitología y Biodiversidad (Lima, Peru) or the Louisiana State University

Table 1. Occurrence records of Black-fronted Ground-Tyrants used in ecological niche models.

Record type	Institution ^a	ID #	Collector/ observer ^b	Location	Latitude	Longitude	Elevation (m)	Date	Extralimital (E) or winter (W)
Sight record Specimen	AUDCLO	OBS95010983	REG	Peru: dpto. Ancashi; 14 km ENE Oileros	-9.65	-77.35	4200	5 June 2007	E
	LSUMNS	LSUMZ80625	TAP	Peru: dpto. Ancashi; 8 km W Laguna Conococha	-10.13	-77.35	4300	22 May 1975	E
Sight record Sight record	CORBIDI	OBS88266852	JB	Peru: dpto. Lima; 1.75 km SSE Tanta	-12.16	-76.02	4500	19 August 2009	E
	-	None	REG	Peru: dpto. Huancavelica; 6 km NE Astobamba	-12.91	-75.05	4720	23 June 2009	E
Sight record Sight record	AUDCLO	OBS95037287	SH	Peru: dpto. Cusco; near Laguna Sibinacocha	-13.9	-70.92	5100	29 June 2009	E
	-	None	JU	Peru: dpto. Arequipa; 0.7 km W Laguna Huanoso	-14.71	-72.55	4740	1 July 1998	E
Sight record Sight record	-	None	REG	Peru: dpto. Puno; 12.5 km SW Vila-Vila	-15.21	-70.74	4570	26 July 2009	W
	-	None	REG	Peru: dpto. Puno; 9 km WSW Vila-Vila	-15.26	-70.75	4575	26 July 2009	W
Specimen Specimen	ZMUC	None	JF	Peru: dpto. Arequipa; on road to Cotahuasi	-15.67	-72.75	4150	6 May 1987	W
	LSUMNS	LSUMZ ^c	REG	Peru: dpto. Arequipa; 15.5 km SSE Chirway	-15.76	-71.62	4500	15 July 2009	W
Sight record Specimen	-	None	REG	Peru: dpto. Arequipa; 12 km S Chirway	-15.79	-71.62	4580	15 July 2009	W
	MVZ	MVZ-158797	ATS	Peru: dpto. Puno; Rio Huanque, 50 km S Ilave	-16.2	-69.73	3900	19 July 1968	W
Specimen	LSUMNS	LSUMZ102460	JVR	Bolivia: dpto. La Paz; 5.4 km W dam Zongo Rd.	-16.28	-68.28	4365	19 July 1981	W
Sight record	-	None	REG	Peru: dpto. Puno; along Interoceanica Sur Hwy.	-16.31	-70.22	4440	23 July 2009	W
Specimen	LSUMNS	LSUMZ101480	TSS	Bolivia: dpto. La Paz; Rio Choquekkota Valley	-16.59	-68	4150	15 August 1981	W
	-	None	JB	Peru: dpto. Moquegua; 44 km NE Moquegua	-16.91	-70.64	4550	18 August 1996	W
Sight record Specimen	AUDCLO	OBS96898344	RH	Bolivia: dpto. Cochabamba; Cerro Tunari	-17.27	-66.38	4575	28 August 2009	W
	ANSP	135333	MAC	Bolivia: dpto. Oruro; Callipampa	-18.37	-66.95	4100	5 June 1936	W
Specimen	ANSP	135330	MAC	Bolivia: dpto. Potosí; Chocaya	-20.98	-66.32	4100	14 June 1936	W

^aInstitutional codes: AUDCLO, Cornell Laboratory of Ornithology, IUSUMNS, Louisiana State University Museum of Natural Science, CORBIDI, Centro de Ornitología y Biodiversidad, ZMUC, Zoological Museum of the University of Copenhagen, MVZ, Museum of Vertebrate Zoology Harvard University, and ANSP, Academy of Natural Sciences Philadelphia.

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^cNo institution accession number was assigned.

Museum of Natural Science (Baton Rouge, LA). JB and LA also gathered Black-fronted Ground-Tyrant records opportunistically during surveys for White-bellied Cinclodes (*Cinclodes palliatus*), a rare inhabitant of the central Peruvian puna.

We used global positioning system units (Models Colorado 300 or 60Csx, Garmin, Olathe, KS; GPS 315, Magellan, Santa Clara, CA) to determine elevations and geographic coordinates of transects and collecting localities. Coordinates and elevations were verified using 1:100,000 topographic maps obtained from Peru's Instituto Geográfico Nacional.

We supplemented our records with museum specimen locations and observations of other investigators (Table 1) to increase the number of model development points. Locations ranged from 3900 to 5100 m elevation in puna habitats (*sensu* Fjeldså and Krabbe 1990), i.e., seasonal dry grasslands ranging from central Peru to northern Argentina and Chile. We used 13 records for the typical winter range model and six records for the extralimital range model (Table 1 and Fig. 1).

Seasonal restriction. Developing distribution predictions for migratory species is complicated by seasonal variation of climatic variables (e.g., Marini et al. 2010). Using data appropriate for the desired time frame is one way to refine model signal. In addition, determining the true winter range of a species can be complicated by dispersal and migration. For example, Marantz and Remsen (1991) and Remsen (2001) showed that winter ranges can be overestimated by inclusion of seasonally inappropriate records. We selected occurrence records within a range of dates to refine model signal. We defined the winter period arbitrarily as May through August.

Spatial restriction. To assess whether extralimital winter records represented an extension in niche space or geographic space, we defined extralimital winter records as those north of the wintering range described by Schulenberg et al. (2007) and Fjeldså and Krabbe (1990). Locations within those limits were considered typical winter records. To minimize spatial autocorrelation, we only used records >5 km from the nearest known location.

Ecological niche modeling and environmental layers. To create winter distribution models for the Black-fronted

Ground-Tyrant, we used a maximum entropy algorithm implemented in the software Maxent 3.3.3e. This program uses species' presence records in combination with the distribution of environmental variables over the study area to estimate a probability distribution for the species (see details in Phillips et al. 2006). Barve et al. (2011) provided suggestions for spatially restricting model analyses following the framework of Soberón and Peterson (2005) based on the earlier work of Hutchinson (1978). We limited our models to a long-term estimate of accessible area to include the last glacial maximum (LGM), following the rationale and recommendation of Barve et al. (2011), because these areas would have been available. To summarize the rationale, inclusion of the potential historical range permits the modeling algorithm to run within connected modeling space in a biogeographically relevant context. This permits the inclusion of potential dispersal pathways that may have resulted in present-day isolated populations. Considerable debate persists regarding the puna's precipitation regime during the LGM (between 20,000 and 26,000 years ago), but there is agreement that it was 2–9 °C cooler and this cooling was accompanied by a downslope vegetation shift of 800–900 m (Flenley 1998). Our environmental layers were clipped to include pixels above 3200 m, 800 m below the current puna boundary, to include the probable historical puna extent for the reasons given above.

ENMs were developed for both winter and extralimital winter ranges using climatic variables related to temperature and precipitation at 1-km² resolution obtained from WorldClim (Hijmans et al. 2005) and two topographic variables (slope and aspect) calculated with the Spatial Analyst from ArcGIS v. 9.3. We minimized our set of variables by conducting analysis implemented in the software ENM Tools 1.1 (Warren et al. 2009). Using the correlation coefficients, we created a pair-wise matrix including all environmental and topographical layers. We identified clusters of variables that were highly correlated. Then, we chose six dissimilar climatic variables from the correlated groups and two topographic variables (slope and aspect) with correlation coefficients lower than 0.85. Climatic variables used were: (1) mean diurnal temperature range (mean of monthly

[maximum temperature – minimum temperature]), (2) isothermality (variable 1/variable 6) ($\times 100$), (3) temperature seasonality (standard deviation $\times 100$), (4) maximum temperature of the warmest month, (5) precipitation during the wettest quarter, and (6) precipitation during the driest quarter (Hijmans et al. 2005).

Assessing the effects of sample size on ecological niche models. To determine if a small sample size affected the validity of our models, we performed two separate tests. First, we evaluated the predictive ability of our winter and extralimital datasets using the jackknifing (leave-one-out) technique presented by Pearson et al. (2007). This allowed us to determine the contribution of each location in our models and to know if our models were primarily driven by a subset of our locations. To perform this test, we used the lowest presence threshold (LPT) value provided by Maxent to threshold our models. LPT provides a conservative estimation of the potential distribution of a species, enhancing the results of our jackknifing and low- N tests. The commission rates, i.e., how many occurrence points were in pixels predicted above our threshold, were 85% and 67% for the winter and extralimital models, respectively. Pearson's pValueCompute program provided P -values (<0.0001) for these results, showing that our dataset had a good predictive ability and that no particular location biased the models.

To assess the potential impact of our small sample size, we performed a slightly modified version of the low- N test presented by Pearson et al. (2007). This test examines changes in model performance as sample size is reduced by one for each subsequent model, making a power assessment of analyses. Changes in predictive performance were evaluated with additional models developed with a random subsample of all locations. By developing models with a step-wise reduction of one location, we were able to determine where model performance collapsed, i.e., a rapid decrease in commission rate. The percentage of locations from the complete set that were included in the models developed with the subset of locations provided an estimate of model performance. We performed three different random sequences of location removals using the LPT value and found that, for both the extralimital and winter range models, predictive performance was affected negatively as sample size decreased (Fig. 2). Also, all three replicate

chains for both models approached asymptotes at high values of predictive abilities at smaller sample sizes than the one we used, suggesting that the predictive performance of our models were not affected by the sample size.

Niche equivalency test. After determining that our models were performing well despite the small sample size, we constructed final ENMs for winter and extralimital datasets using Maxent 3.3.3e (Phillips et al. 2006). Each model was run with 100 cross-validated replicates using all locations. Then, using the unthresholded logistic output of our models, we performed a niche equivalency test (Warren et al. 2008) using the software ENM Tools 1.1 (Warren et al. 2009). This test follows a permutation approach to estimate whether differences between the climatic envelopes of two species are statistically significant. A significant difference suggests that the niches of the winter and extralimital locations are not equivalent. On the other hand, if differences are not significant, equivalency between models cannot be rejected. We performed our test using 50 replicates.

RESULTS

Both winter and extralimital models predicted the presence of the remaining occurrence records with high probability (Fig. 3). The winter model predicted an area from the higher elevations of dpto. Ancash, Peru, south to northern Argentina, and Chile. The model developed with extralimital points was mostly restricted to upper elevations in Peru, with a few nearby areas in Bolivia. The model developed with all points included the upper elevations of dpto. Ancash, Peru, south through the Andes to central Bolivia, an area significantly reduced in size from the winter model.

We failed to reject the null hypothesis that the two models were distinguishable. Observed values of niche overlap ($I = 0.82$, and $D = 0.71$) fell within the 5–95 percentiles of a null distribution (I_5 0.755– I_{95} 0.93, D_5 0.624– D_{95} 0.899) estimated after 50 randomizations using all locations. Although we did not detect a significant difference between the modeled niche spaces, contributions of the variables differed. The winter model was driven primarily by precipitation during the wettest month (33%) and secondarily by the maximum temperature of the warmest month (30%). The extralimital model

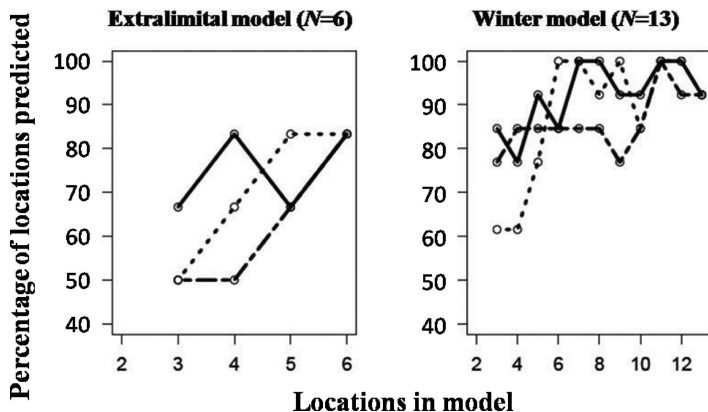


Fig. 2. Models were developed with winter range and extralimital occurrence records. The percentage of occurrence points predicted by the model to have a presence probability higher than the lowest presence threshold (LPT) is shown for each model. Three replicates were performed to account for random removal effect. Both models performed moderately well (80–100%) with only six locations in the models.

primarily was driven by temperature seasonality (50%) followed by the maximum temperature in the warmest month (35%).

DISCUSSION

The current wintering geographic range of Black-fronted Ground-Tyrants was developed with few records, and Schulenberg et al.

(2007) and Fjelds  and Krabbe (1990) were understandably conservative with their estimates. Our ecological niche model developed using the current winter range predicted with high probability all extralimital points, suggesting that the “extralimital” records may be within the true wintering range. Reciprocally, the model developed with the extralimital locations predicted many of the winter range locations, but

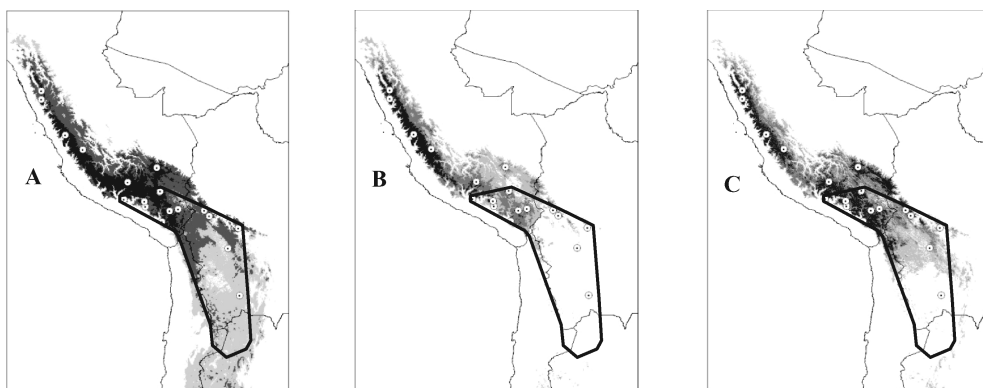


Fig. 3. Occurrence records of Black-fronted Ground-Tyrants are shown as dark-centered white circles. Environmental niche models were developed using occurrence records within the (A) current estimated winter range, (B) extralimital occurrence records, and (C) all occurrence points. The thick-lined polygon approximates the winter range using range maps from Fjelds  and Krabbe (1990) and Schulenberg et al. (2007). Model prediction probability is shown in five colors corresponding to 10% probability intervals ranging from light gray (50%) to dark gray (90%).

did not perform as well as the winter model development. When all locations were used for model development, the niche model predicted an area smaller than the two areas combined, with a southern contraction accounting for most of the difference.

A benefit discovered in the resampling and jackknifing of model locations was our ability to assess the influence of individual locations on model performance. This is similar to a method Chapman (2005) discussed in describing principles and methods for cleaning bioinformatics data. For example, the Chocaya location in southern Bolivia was excluded from several resampled model predictions, essentially identifying it as an outlier. This was one of the two 1936 records from M. A. Carriker, and our resampling may have detected the imprecision of locations often associated with specimen data gathered prior to the late 20th century. We vetted this particular record with S. Herzog, who investigated many historical records and the areas worked by Carriker. Whether this record is at the limit of the winter range, an outlier, or was imprecisely recorded by Carriker is unknown, but the ability of our method to identify outliers that could be caused by misidentified taxa or data entry mistakes is nonetheless illustrated.

Winter and extralimital models were driven primarily by different variables, namely, precipitation during the wettest month (January, onset of wet season) for the winter model and temperature seasonality for the extralimital model. Secondly, both models were driven by maximum temperature of the warmest month (October and November, depending on location). These three variables are definitive characteristics of the *puna*, a highly seasonal grassland maintained by freezing overnight temperatures that prevent expansion of freeze-susceptible vegetation. The difference in model contribution may reflect spatial variation of these variables. That the models were driven by a variable associated with the wet season (maximum temperature during the warmest month) when Black-fronted Ground-Tyrants have migrated from south to their breeding range is perhaps counterintuitive *prima facie*, but climatic features such as precipitation or temperature associated with the wet season with warmer overnight temperatures (i.e., growing season) would be the expected driver of *puna* habitats that Black-fronted Ground-Tyrants may be selecting during the dry season.

We used the niche equivalency test in ENM Tools to determine if the winter and extralimital models could be statistically distinguished, i.e., more dissimilar than expected by chance. This test creates a random distribution of models from all points and then compares the test models (winter and extralimital) to the distribution. If the test models were more dissimilar than expected by chance, they would occur at either end of the randomized distribution tails. Our results show that the extralimital winter records of Black-fronted Ground-Tyrants were in niche space no more different than expected by chance. In fact, some differences are present as shown by the different variable contributions. This result supports the hypothesis that the niche models are no more different from each other than we would expect by chance. In other words, the extralimital model did not represent an extension of the wintering range niche breadth *per se*, but a geographical extension of the wintering range with similar niche space. Our approach represents a useful complementary tool for better understanding distribution patterns of species in remote areas. Pearson et al. (2007) emphasized the ramifications of this technique by showing how the ranges of many additional species in Mexico's bird atlas could be modeled. Peterson et al. (1998) showed that there are few location records for many species in the Neotropics, and this corresponds directly with the difficulty in accessing these areas. With our approach, a few records might provide enough information to identify additional areas where a species might occur and to pursue relevant ecological and evolutionary questions.

Although relying heavily on modeling and computer work, our approach highlights the importance of continuing fieldwork in poorly known areas. With more field-based information, models will be more robust and analyses based on more robust datasets will be more reliable. In addition, our models generate information that must be corroborated in the field. Our approach for comparing the environmental niche space of ranges could also be applied to other types of studies. We believe that this type of assessment could be applied in fields such as evolutionary ecology, migration ecology, conservation biology, and systematics. The field of phylogeography, in particular, may benefit from niche-space comparisons (Peterson 2009).

Although we were unable to reject similarity of niche space using models based on eight environmental variables, the area north of the current winter range of Black-fronted Ground-Tyrants could be unsuitable in finer ecological dimensions not captured in ENMs. Field observations of Black-fronted Ground-Tyrants offer clues concerning factors that might influence their winter range. Published accounts of their habitat use during the winter are general and somewhat conflicting. Suitable habitat has been described as open grassland near wetlands (Schulenberg et al. 2007), rocky slopes (Fjeldså and Krabbe 1990), open habitats near water (Ridgely and Tudor 1989), and rocky habitat with little vegetation (Jaramillo 2003). Our observations in central and southern Peru suggest a preference for rocky slopes with *Baccharis* shrubs, *Cumulopuntia* cacti, and *Festuca* and *Parastrephia* grasses. If Black-fronted Ground-Tyrants have a preference for xeric microhabitats, we predict they would occur in higher numbers at the drier end of the precipitation gradient that spans the *puna* from the wetter north to the drier south. The necessary microhabitat spatial data and survey effort in respective microhabitats needed to test this hypothesis are lacking, but recent progress using remotely sensed data in the high Andes offers hope for these types of inquiries (Otto 2011).

Another potential range-limiting factor is a dietary requirement. We found numerous seeds and pericarp of the cactus *Cumulopuntia boliviana ignescens* in the stomachs of all five Black-fronted Ground-Tyrants collected in dpto. Arequipa. This cactus occurs above 4400 m in southern Peru in dptos. Arequipa, Moquegua, and Puno, whereas other species of *Cactaceae* with palatable fruit occur in the northern *puna* (D. Montesinos, pers. comm.). Whether they consume the fruit of these northern species is unknown, but Black-fronted Ground-Tyrants appear to be at least facultative frugivores. Although frugivory in the genus *Muscisaxicola* is, to our knowledge, undocumented, it is well known for many species in the family Tyrannidae (Fitzpatrick 1980). The diets of most birds in the Neotropics are poorly known, and studying interdependencies across a geographic mosaic (*sensu* Thompson 2005) will likely provide new insights to the study of range limits.

In conclusion, we failed to reject dissimilarity between our two models based on extralimital

and winter-range records, suggesting that the winter range of Black-fronted Ground-Tyrants may be larger than previously thought and gaps in current range estimates are sampling artifacts. Additional field observations are needed to determine the significance of potential range limit drivers, including demography, trophic interactions, and interspecific interactions (Holt and Barfield 2009, Price and Kirkpatrick 2009).

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Supporting Information

The following supporting information is available for this article online:

Table S1. New occurrence records of Black-fronted Ground-Tyrants (*Muscisaxicola frontalis*) for Peru.

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