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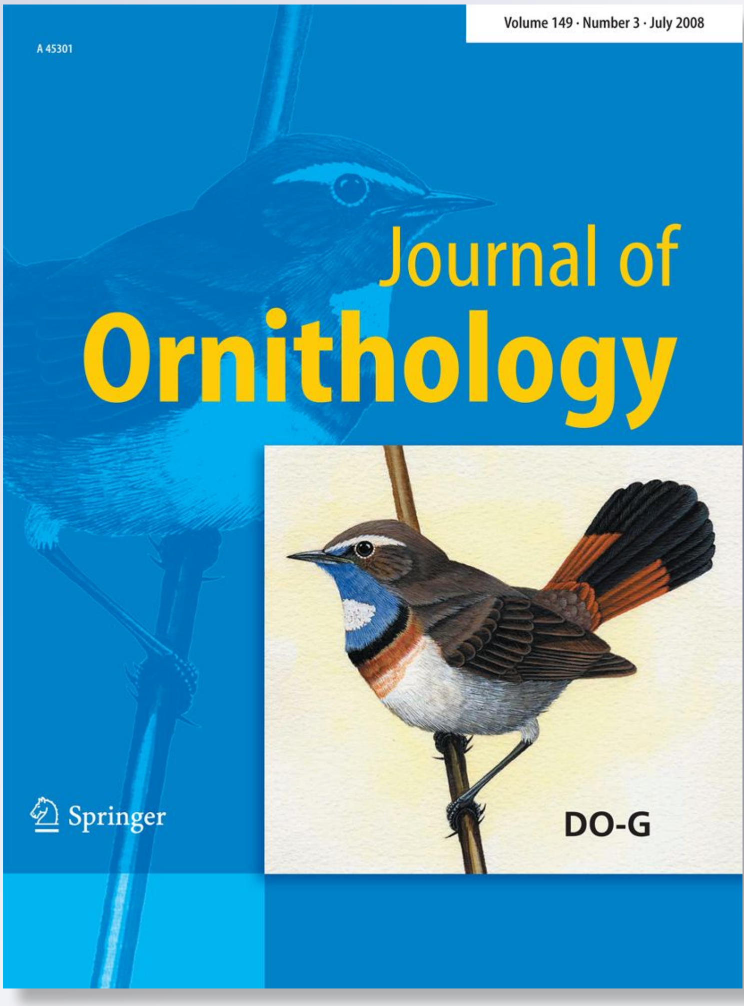

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ORIGINAL ARTICLE

Range size estimates of Bolivian endemic bird species revisited: the importance of environmental data and national expert knowledge

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Abstract Accurate extent of occurrence (EOO) estimates are essential for reliable conservation assessments. Recent studies suggest that current EOO maps often significantly overestimate range sizes of birds, particularly for narrow-ranging, threatened and ecological specialist species. Such species may therefore be at danger of being falsely overlooked by conservation assessments. Using species distribution modeling combined with 'expert' review and according corrections of inductive models, we estimated historic range sizes of 15 Bolivian endemics, which were compared to BirdLife International's 2011 EOO estimates. The same comparisons were made for 65 additional species modeled by Young et al. (Auk 126:554–565, 2009) to corroborate the general validity of our results. Species distributions were modeled deductively for eight, with a hybrid approach for six and inductively for one species. For 67 % of Bolivian endemics, EOO estimates were 1.48–4.22 times larger than our estimates (1.75–4.33 larger for 89 % of the species in Young et al.). Overestimation can largely be attributed to inclusion of areas outside a species' elevational range and of portions of ecoregions or extensive habitat areas uninhabited by a species. For 33 % of Bolivian endemics (all threatened species), EOO estimates were 21.2–75.3 % smaller than our estimates (30.3–72.2 % smaller for 11 % of the species in Young et al.). This can partly be attributed to more sophisticated range size analyses for threatened species by BirdLife, differences between historic versus current range sizes, and overly conservative EOO estimates. EOO definition and estimates are in serious need of improvement. Exclusion of discontinuities within overall distributions of species needs to be applied rigorously at small spatial scales, using spatially explicit environmental data such as digital elevation models and ecosystem classifications. Incorporating national expert knowledge into range size estimation can be similarly important for reducing overestimation. We recommend prioritizing species with EOO estimates of <200,000 km^2 for a revision of these estimates.

Keywords Extent of occurrence · Range size overestimation · Restricted-range species · Species distribution modeling · Threatened species

Zusammenfassung

Arealgrößenschätzungen endemischer Vögel Boliviens neu betrachtet: die Bedeutung von Umweltparametern und nationalem Expertenwissen

Akkurate Schätzungen der Größe von Verbreitungsarealen (*extent of occurrence*, EOO) sind essenziell für eine verlässliche Bewertung des Gefährdungsgrades von Arten. Neueste Studien zeigen, dass derzeitige EOO-Karten die Verbreitungsareale von Vogelarten oft signifikant überschätzen, besonders für geographisch eng verbreitete, bedrohte und ökologisch spezialisierte Arten. Solche Arten

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laufen daher Gefahr, bei Gefährdungsbewertungen fälschlicherweise übersehen zu werden. Mittels Verbreitungsareal-Modellierung kombiniert mit Experteneinschätzung und entsprechender Korrektur induktiver Modelle schätzten wir die historischen Arealgrößen von 15 bolivianischen Endemiten. Diese Werte wurden mit den EOO-Schätzungen von BirdLife International aus dem Jahr 2011 verglichen. Um die generelle Gültigkeit unserer Ergebnisse zu überprüfen, stellten wir denselben Vergleich mit 65 zusätzlichen Arten an, deren Areale von Young et al. (Auk 126:554–565, 2009) modelliert wurden. Artenareale wurden deduktiv modelliert für acht Arten, mit einem Hybridansatz für sechs Arten und induktiv für eine Art. Für 67 % der bolivianischen Endemiten waren EOO-Schätzungen 1,48–4,22 Mal größer als unsere Schätzungen (1,75–4,33 Mal größer für 89 % der Arten aus Young et al.). Diese Überschätzung kann größtenteils zurückgeführt werden auf die Einbegreifung von Gebieten außerhalb der Höhenverbreitung einer Art und von Teilen von Ökoregionen oder ausgedehnter Habitatareale, die von der jeweiligen Art nicht bewohnt werden. Für 33 % der bolivianischen Endemiten (allesamt bedrohte Arten) waren EOO-Schätzungen 21,2–75,3 % kleiner als unsere Schätzungen (30,3–72,2 % kleiner für 11 % der Arten aus Young et al.). Dies liegt zum Teil an der differenzierteren Bestimmung von Verbreitungsarealen für bedrohte Arten durch BirdLife, an Unterschieden zwischen historischen und heutigen Arealgrößen sowie übermäßig konservativen EOO-Schätzungen. Sowohl die Definition von EEOs als auch EOO-Schätzungen sind verbesserungswürdig. Der Ausschluss von durch eine Art nicht bewohnten Gebieten innerhalb ihres gesamten Verbreitungsareals sollte rigoros auf kleinen räumlichen Skalen angewandt werden, unter Einbeziehung räumlich expliziter Umweltdaten wir z.B. digitaler Höhenmodelle und Ökosystemklassifikationen. Die Einbeziehung nationalen Expertenwissens in die Schätzung von Arealgrößen kann ähnlich wichtig für eine Verringerung von Überschätzungen sein. Wir empfehlen, Arten mit EOO-Schätzungen von <200,000 km^2 für eine Überprüfung dieser Werte zu bevorzugen.

Introduction

Estimates of range size constitute one of several important criteria that are applied in conjunction to evaluate the conservation status and determine extinction risk of species (IUCN 2001). Range size is most frequently expressed as 'extent of occurrence' (EOO), which is defined as "the area contained within the shortest continuous imaginary boundary that can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy. This measure may exclude discontinuities or disjunctions within the overall distributions of taxa (e.g., large areas of obviously unsuitable habitat)" (IUCN 2001). EOO estimate thresholds for the three globally threatened categories of Critically Endangered, Endangered, and Vulnerable are 100, 5,000 and 20,000 km^2, respectively (criterion B; IUCN 2001). Range size estimates have also been instrumental in determining broad-scale terrestrial priority regions for biodiversity conservation at a global scale through BirdLife International's Endemic Bird Area (EBA) blueprint (Stattersfield et al. 1998). EBAs are based on distribution patterns of terrestrial bird species with historical breeding ranges of 50,000 km^2 or less, so-called restricted-range species.

Accurate EOO estimates are thus essential for reliable conservation assessments. However, recent studies on birds (Hurlbert and White 2005; Jetz et al. 2008) suggest that the currently used EOO maps often significantly overestimate the distributions and range sizes of species, particularly so for narrow-ranging, threatened, and ecological specialist species, which are characterized by comparatively low range occupancy. Specialist species may therefore be in danger of being falsely overlooked by conservation assessments because they fail to meet the EOO threshold (Jetz et al. 2008). In light of these findings, it could be argued that a more sophisticated EOO definition beyond minimum convex polygons is needed, taking into account spatially explicit environmental data such as digital elevation models and other advances in geographic information systems (GIS).

Alternatively, it could be argued that 'area of occupancy' (AOO) should be used in conservation assessments, which is defined as "the area within its 'extent of occurrence' that is occupied by a taxon, excluding cases of vagrancy" (IUCN 2001). AOO estimate thresholds for the three globally threatened categories of Critically Endangered, Endangered, and Vulnerable are 10, 500 and 2,000 km^2, respectively (criterion B; IUCN 2001). Nevertheless, in data-poor tropical regions, AOO estimates are often likely to underestimate a species' true distribution and may lead to false evaluations of species as being threatened. Similarly, our knowledge of the exact distribution limits of many tropical bird species is far from perfect. In South America, which harbors almost one-third of the world's birds (3,070 native breeding species; Remsen et al. 2011), explorations of biologically uncharted or poorly studied areas generally result in numerous new distributional records, often expanding previously known distribution limits of species and thereby increasing their known range sizes (e.g., Alonso and Whitney 2003; Cuervo et al. 2003; Herzog et al. 2008, 2009; Robbins et al. 2011). This underlines the necessity to regularly update EOO (and AOO) estimates.

In the present study, we estimated the historic range sizes of Bolivia's 15 endemic bird species (excluding one additional endemic recently elevated to species rank; Hennessey 2011) using species distribution modeling (inductive method) combined with 'expert' review and, where deemed necessary, GIS-based adjustments and corrections of inductively modeled distributions. Our range size estimates, which can be considered intermediate between EOO and AOO estimates as defined by the IUCN (2001), were then compared to the EOO values specified on BirdLife International's (hereafter BirdLife) species factsheets (BirdLife International 2011a). Our study was restricted to Bolivian endemics because several environmental data layers used in modeling species ranges were exclusive to Bolivia and no equivalent or comparable information was available for entire other South American countries. To compensate for the limited sample of species, and to verify whether the results for Bolivian endemics have more general validity, we also compared BirdLife's EOO estimates with those obtained by a similar, independent species distribution modeling study (Young et al. 2009) for an additional 65 bird species that are endemic to the east Andean slope and adjacent lowlands of Peru and Bolivia (to ~18°S latitude).

For most species (the major exception being threatened species), BirdLife's EOO estimates are based on hand-drawn distribution maps in Ridgely et al. (2007) and can therefore be expected to be prone to range size overestimation (see Hurlbert and White 2005). This may particularly be the case in the topographically complex tropical Andes, where numerous species have small ranges and/or inhabit narrow elevational bands (Herzog and Kattan 2011). We discuss the conservation implications of our findings and argue for the need of a more sophisticated EOO definition that incorporates advances in geographic information systems.

Methods

Occurrence records and species

Occurrence records for 15 bird species endemic to Bolivia (Table 1) were extracted from Asociación Armonía's distributional database for Bolivian birds. This regularly updated database contains over 100,000 occurrence records from approximately 1,400 georeferenced localities for Bolivia's 1,422 bird species. It is drawn from a wide range of sources, including museum specimens (locality coordinates obtained directly from specimen labels or taken from Paynter 1992 with corrections where necessary, see below), the ornithological literature, and unpublished reports, among others. All records of the endemics were scrutinized by S.K.H. and O.M.Z. for accuracy of locality data and reliability of species identifications. For all localities that were not georeferenced with handheld GPS units in the field, we determined or verified coordinates and elevation using Google Earth. For old specimen records, we used the most probable collecting locality based on Paynter (1992) within the currently known range of the species, although some records had to be excluded because they could not be georeferenced with sufficient certainty about the location of the most probable collecting locality. Records were excluded when reasonable doubt existed about the correct identification of a given species.

Two species are currently not treated as Bolivian endemics by BirdLife, but were included here for the following reasons. First, Southern Horned Curassow (*Pauxi unicornis*) consists of two widely disjunct populations: the nominate subspecies in Bolivia and the Peruvian subspecies *koepckeae*, which is restricted to a tiny area (ca. 400 km^2; R. MacLeod, personal communication) in a small, isolated mountain range (Cerros del Sira) in Huánuco department (Herzog and Kessler 1998; MacLeod et al. 2006; BirdLife International 2011d; Gastañaga Corvacho et al. 2011). Gastañaga Corvacho et al. (2011) presented evidence for elevating both subspecies to species rank, which is followed here. Second, the only report of Gray-bellied Flowerpiercer (*Diglossa carbonaria*) outside Bolivia originated from La Quiaca in Jujuy province, extreme northwest Argentina, approximately 450 km south of the nearest Bolivian record, where two individuals were observed once by Moschione and San Cristobal (1993). No tangible evidence was obtained by Moschione and San Cristobal (1993), and it is unknown whether a resident population exists in the La Quiaca area, or whether the observation corresponds to an unusual case of vagrancy. Given that no records of this easily detectable species exist from intervening areas in southern Bolivia despite extensive field work in suitable habitats (e.g., Fjeldså and Kessler 1996; Krabbe et al. 1996), we consider the observation by Moschione and San Cristobal (1993) a likely case of vagrancy and Gray-bellied Flowerpiercer a Bolivian endemic.

Inductive species distribution modeling

We used the MaxEnt algorithm (Maximum Entropy; Phillips et al. 2006; Phillips and Dudík 2008) for modeling potential species distributions (inductive method) with the following environmental data layers: WorldClim climatic layers (Hijmans et al. 2005), NASA's Shuttle Radar Topography Mission (SRTM) 90-m (0.81 ha) digital elevation model (DEM) (http://www2.jpl.nasa.gov/srtm/), Bolivian ecoregions (Ibisch et al. 2003) and ecological system complexes (Josse et al. 2007). All species had >4 occurrence records, which is considered the minimum number of records necessary for obtaining robust modeling results (Pearson et al. 2007; Hernandez et al. 2008). The potential distribution of each species was produced by

Table 1 Comparison of BirdLife International's 2011 species factsheet global range size estimates (http://www.birdlife.org/) with those obtained by the present species distribution modeling study for 15 bird species endemic to Bolivia

Species and conservation status	Range estimate (km^2)		% Overestimation	% Underestimation	Modeling method	Main deductive criteria
	BirdLife	Armonía-FAN				
Gray-bellied Flowerpiercer (*Diglossa carbonaria*) LC	70,100	16,596	322.4	–	Deductive	Vegetation series, elevation (2,500–4,000 m)
Black-throated Thistletail (*Asthenes harterti*) LC	23,800	5,743	314.4	–	Hybrid	Vegetation series, elevation (2,500–3,600 m)
Unicolored Thrush (*Turdus haplochrous*) NT	192,000	48,860	309.7	–	Deductive	Vegetation series
Bolivian Blackbird (*Oreopsar bolivianus*) LC	77,400	33,154	133.5	–	Deductive	Ecoregions, vegetation series, elevation (1,400–3,400 m, to 3,800 m in dpto. Cochabamba)
Berlepsch's Canastero (*Asthenes berlepschi*) NT	2,200	984	123.5	–	Deductive	Vegetation series, elevation (2,300–3,700 m)
Rufous-faced Antpitta (*Grallaria erythrotis*) LC	39,100	20,391	91.7	–	Hybrid	Ecoregions, elevation (1,700–3,300 m)
Black-hooded Sunbeam (*Aglaeactis pamela*) LC	16,500	10,203	61.7	–	Hybrid	Vegetation series, elevation (2,700–4,000 m)
Bolivian Spinetail (*Cranioleuca henricae*) EN	3,000	1,889	58.8	–	Hybrid	Ecoregions, vegetation series
Bolivian Earthcreeper (*Tarphonomus harterti*) LC	61,400	41,244	48.9	–	Deductive	Ecoregions, vegetation series, elevation (1,350–3,100 m, to 3,400 m in dpto. Cochabamba)
Rufous-naped Brush-Finch (*Atlapetes rufinucha*) LC	39,000	26,386	47.8	–	Deductive	Ecoregions, vegetation series, elevation (1,350–3,500 m)
Cochabamba Mountain-Finch (*Compsospiza garleppi*) EN	3,800	4,821	–	21.2	Deductive	Vegetation series
Masked Antpitta (*Hylopezus auricularis*) VU	380	509	–	25.4	Inductive	–
Southern Horned Curassow (*Pauxi unicornis*) EN	4,000[a]	10,244	–	61.0	Hybrid	Elevation (400–1,400 m)
Red-fronted Macaw (*Ara rubrogenys*) EN	10,100	27,349	–	63.1	Deductive	Ecoregions, vegetation series, elevation (1,000–3,000 m)
Blue-throated Macaw (*Ara glaucogularis*) CR	12,900	52,327	–	75.3	Hybrid	Ecoregions, vegetation series

Percent over- and underestimation refer to the degree to which BirdLife International's range size values differ in relation to the estimates obtained by the present study. Conservation status: *LC* least concern; *NT* near threatened; *VU* vulnerable; *EN* endangered; *CR* critically endangered. Species nomenclature follows Remsen et al. (2011)

[a] Excludes the 400 km^2 range size estimate of the Sira Curassow [*Pauxi* (*unicornis*) *koepckeae*]

resampling individual occurrence records, randomly partitioning the records of every species into a training set with 80 % of the records, and a test set with 20 % of the records (e.g., Phillips and Dudík 2008). We determined model accuracy using a receiver operating characteristic (ROC) analysis, which establishes that the area under the curve (AUC) of the resulting plot provides a measure of model performance (Phillips et al. 2006), although the suitability of AUC values for evaluating model performance has been questioned (Soria-Auza et al. 2010). An optimal model has an AUC of 1.0, whereas a model that predicts species occurrences at random has an AUC of 0.5 (Phillips et al. 2006). All species had training and test data AUC values >0.975, well above the commonly accepted minimum threshold of 0.75 (e.g., Fielding and Bell 1997; Pawar et al. 2007). We used Arc View 3.2 to convert MaxEnt models to binary maps (presence = 1; absence = 0) using equal training sensitivity-specificity threshold values. Maps were adjusted using the majority filter tool in order to eliminate isolated grid cells. All environmental data layers were scaled to and all distribution maps were produced at a spatial resolution of $1' \times 1'$ latitude-longitude grid cells (1.855×1.855 km).

'Expert' review and deductive model adjustments

All inductively modeled maps were subject to a detailed 'expert' review by S.K.H. and O.M.Z. using Arc View 3.2. For most species, adjustments or corrections were deemed necessary, and in cases where MaxEnt model outputs were considered unsatisfactory, species distributions were modeled entirely deductively. For most Andean species, we used NASA's 90-m DEM to eliminate grid cells above and below the known or expected upper and lower elevational limit, respectively. Additional environmental data used to add or eliminate potential distribution areas included vegetation series (Navarro and Ferreira 2007) and ecoregions (Ibisch et al. 2003). In most cases, we also used reliable absence data (well-surveyed areas without records of a given species) to determine latitudinal range limits or to eliminate disjunct areas without records of a given species.

For one species, the Critically Endangered Blue-throated Macaw (*Ara glaucogularis*), we also estimated its historic AOO deductively using vegetation series (Navarro and Ferreira 2007). The species occurs in the Beni savannas (Llanos de Moxos), a region dominated by seasonally flooded grassland that is crisscrossed with gallery and seasonally flooded (*várzea*) forests and speckled with evergreen to semi-deciduous forest islands (Ibisch et al. 2003; Larrea-Alcázar et al. 2011). Rather than grassland itself, the Blue-throated Macaw utilizes forest islands, gallery forest and narrow strips of *várzea* forest for feeding, roosting, and breeding (BirdLife International 2011b). Thus, we determined the area covered by these forest types within the species' overall modeled distribution as a measure of its AOO.

Additional range size estimate comparisons based on Young et al. (2009)

Young et al. (2009) modeled the ranges of 115 species that are endemic to the east Andean slope and adjacent lowlands of Peru and Bolivia (to ~18°S latitude) at a spatial resolution of 1×1 km grid cells. A brief outline of the methods used is included below; see Young et al. (2009) for details. MaxEnt inductive models were used for species known from multiple localities and a deductive method for species known from single localities and for those in which inductive methods failed to produce a realistic model. Environmental variables included several WorldClim climate layers and three variables each derived from NASA's SRTM digital elevation model and the Moderate Resolution Imaging Spectroradiometer (MODIS) dataset. For each species modeled with Maxent, four models were run varying in the use of MODIS data. Models were evaluated by 'experts' familiar with the species, who identified the model and threshold (from the 0–1 scale of Maxent output) that produced the most reasonable map for each species and made deductive adjustments or corrections where deemed necessary.

For comparison with BirdLife's EOO estimates, we considered only those species of Young et al. (2009) that had >10 unique localities to minimize potential negative biases in ranges size estimates of poorly known and difficult-to-detect species. Of those, we further excluded five Bolivian endemics, one species whose Young et al.'s (2009) range size estimate was adopted by BirdLife International (2011a), and one taxon not recognized as a species by BirdLife. Range size estimates for the remaining 65 species were compared to EOO estimates of BirdLife International (2011a).

Results

Species distributions of Bolivian endemics were modeled entirely deductively in eight cases (53 %), whereas for six species (40 %), a hybrid approach was used, applying corrections and adjustments to the inductively modeled map (Table 1). The inductive method provided satisfactory results for only one species (7 %) (Table 1). Modeled distributions of all species are shown in Fig. 1.

For ten species, BirdLife's EOO estimates were 47.8–322.4 % larger than the respective range size estimates of the present study (Table 1) (mean ± SD: 151.2 ± 117.1 %); absolute overestimation ranged from 1,111 km^2

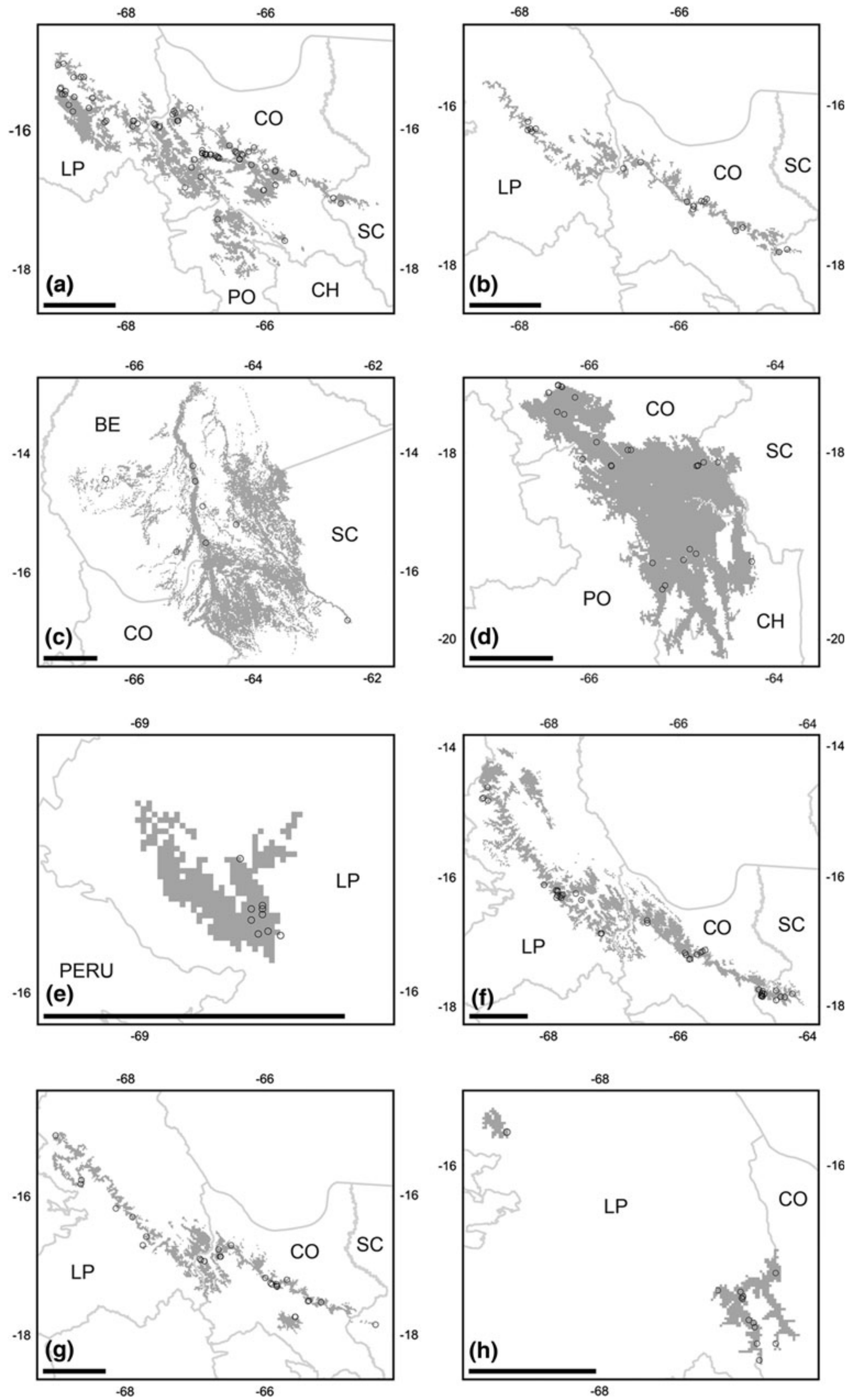
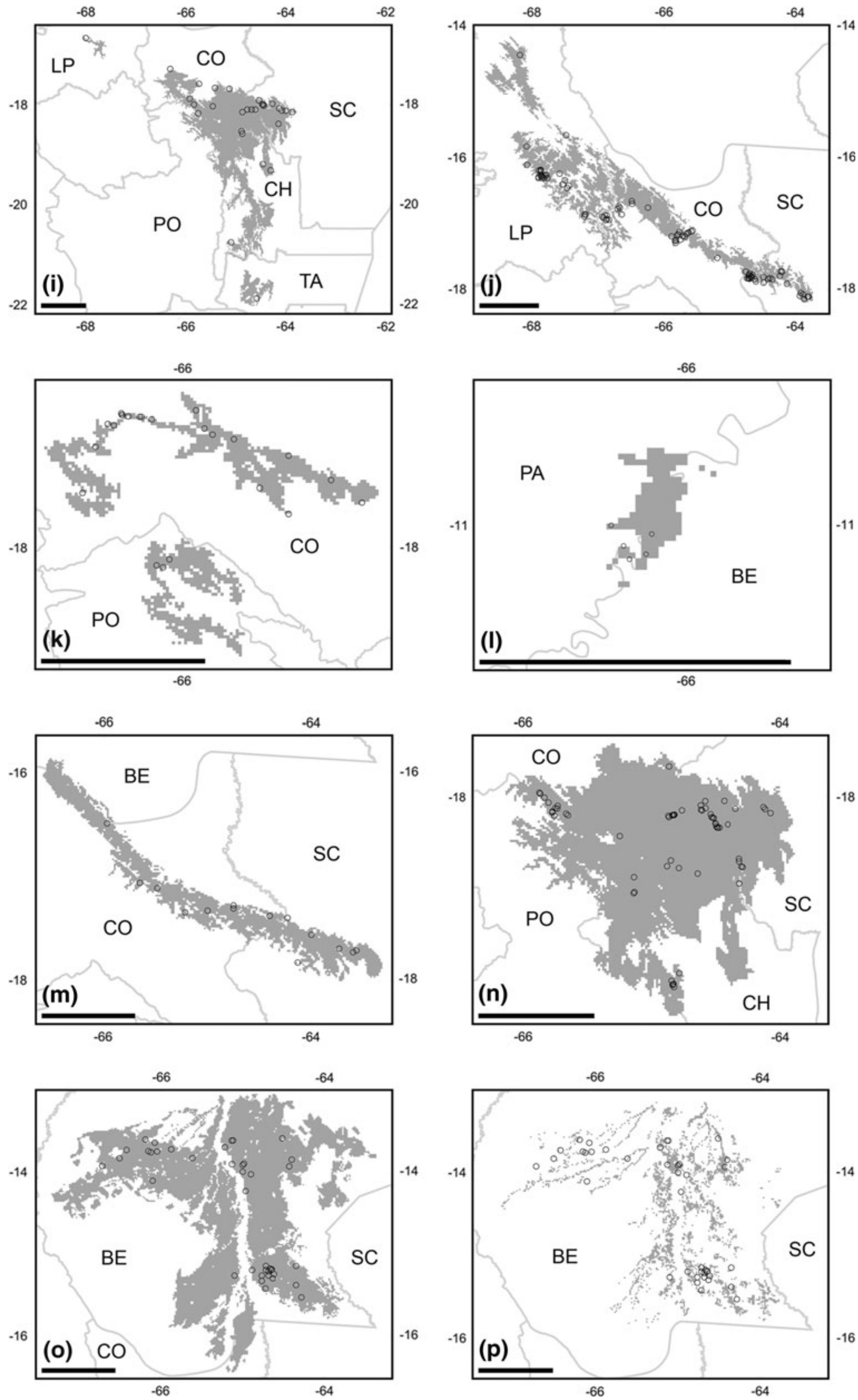


Fig. 1 Modeled historic distribution of 15 Bolivian endemics. **a** Grey-bellied Flowerpiercer. **b** Black-throated Thistletail. **c** Unicolored Thrush. **d** Bolivian Blackbird. **e** Berlepsch's Canastero; **f** Rufous-faced Antpitta. **g** Black-hooded Sunbeam. **h** Bolivian Spinetail. **i** Bolivian Earthcreeper. **j** Rufous-naped Brush-Finch. **k** Cochabamba Mountain-Finch. **l** Masked Antpitta. **m** Southern Horned Curassow. **n** Red-fronted Macaw. **o** Blue-throated Macaw, overall distribution. **p** Blue-throated Macaw, area of occupancy (AOO) estimate. *Open circles* indicate locality records, *light gray lines* political divisions (departmental limits). Departments: *BE* Beni; *CH* Chuquisaca; *CO* Cochabamba; *LP* La Paz; *PA* Pando; *PO* Potosí; *SC* Santa Cruz; *TA* Tarija. *Scale bars at the bottom of each panel* correspond to 100 km in all cases

(58.8 %) for Bolivian Spinetail (*Cranioleuca henricae*) to 145,140 km^2 (309.7 %) for Unicolored Thrush (*Turdus haplochrous*) (Table 1). For the remaining five species, all of which are threatened species, BirdLife's EOO estimates were 21.2–75.3 % smaller than the respective range size estimates of the present study (Table 1) (49.2 ± 24.3 %); absolute

Fig. 1 continued



underestimation ranged from 129 km^2 (25.4 %) for Masked Antpitta (*Hylopezus auricularis*) to 39,427 km^2 (75.3 %) for Blue-throated Macaw (*Ara glaucogularis*) (Table 1). For Blue-throated Macaw, we estimated an AOO (Fig. 1p) of 9,236 km^2, which corresponds to 17.7 % of its overall modeled distribution area and 71.6 % of BirdLife's EOO estimate.

For 58 (89 %) of the 65 additional species modeled by Young et al. (2009), BirdLife's EOO estimates were 7.5–330.3 % larger (Table 2) (mean ± SD: 97.7 ± 52.7 %); absolute overestimation ranged from 1,176 km^2 (40.2 %) for White-cheeked Tody-Flycatcher (*Poecilotriccus albifacies*) to 127,097 km^2 (161.1 %) for Hooded Tinamou (*Nothocercus nigrocapillus*) (Table 2). For the remaining seven species (11 %), six of which are threatened species, BirdLife's EOO estimates were 30.3–72.2 % smaller than the respective range size estimates of Young et al. (2009) (Table 2) (50.3 ± 17.4 %); absolute underestimation ranged from 2,276 km^2 (52.1 %) for Rusty-tinged Antpitta (*Grallaria przewalskii*) to 30,921 km^2 (72.2 %) for Ash-breasted Tit-Tyrant (*Anairetes alpinus*) (Table 2).

Discussion

Range size overestimation by EOO maps

For two-thirds of Bolivian endemics, BirdLife's EOO estimates were on average 2.5 times larger than the respective range size estimates of the present analysis. This trend was even more pronounced among 65 additional bird species endemic to the east Andean slope and adjacent lowlands of Peru and Bolivia: for 89 % of them, BirdLife's EOO estimates were on average twice as large as the respective range size estimates of Young et al. (2009). For 85 % of all 80 species combined, BirdLife's EOO estimates were on average 106 % larger. This confirms the results of Hurlbert and White (2005) and Jetz et al. (2008), who showed that currently used EOO maps often significantly overestimate the distributions and range sizes of birds. The methodological approach of these studies was quite different from that of our and Young et al.'s (2009) analysis, as they determined proportional EOO range occupancy using field survey data. The fact that two fundamentally different methodological approaches consistently yield very similar results reinforces the conclusion that EOO maps and estimates as well as the EOO definition itself are in serious need of improvement.

Naturally, this raises the question as to which specific factors contributed most strongly to the observed range size overestimation of EOO maps of Bolivian endemics. For the Andean species, Gray-bellied Flowerpiercer (*Diglossa carbonaria*), Black-throated Thistletail (*Asthenes harterti*), Bolivian Blackbird (*Oreopsar bolivianus*), Berlepsch's Canastero (*Asthenes berlepschi*), Rufous-faced Antpitta (*Grallaria erythrotis*), Black-hooded Sunbeam (*Aglaeactis pamela*), Bolivian Spinetail (*Cranioleuca henricae*), Bolivian Earthcreeper (*Tarphonomus harterti*), and Rufous-naped Brush-Finch (*Atlapetes rufinucha*) (Fig. 1a, b, d–j), overestimation can largely be attributed to three main factors: (1) the nearly inevitable inclusion of areas outside the elevational range of a given species in minimum convex polygon range maps; (2) the inclusion of portions of ecoregions or extensive areas of habitat uninhabited by a given species (e.g., the inclusion of Inter-Andean Dry Forest ecoregion areas in the range of a Yungas ecoregion species, and vice versa); and (3) imprecise or overly 'generous' range limits (e.g., the EOO maps of Gray-bellied Flowerpiercer and Bolivian Earthcreeper extend too far northeast, including areas of Amazonian lowland and humid montane Yungas forests, where neither species occurs).

For the lowland species, Unicolored Thrush (*Turdus haplochrous*) range size overestimation is attributable to two main factors. First, our deductive range size estimate is based exclusively on vegetation series (seasonally flooded and gallery forest), excluding intersecting grassland areas of the Llanos de Moxos and other forest types in the southeastern portion of its range (Fig. 1c), which the species is not known to inhabit. Our range size estimate may therefore be more of an AOO than an EOO estimate, and it illustrates the proportional range occupancy problem of EOO maps pointed out by Hurlbert and White (2005) and Jetz et al. (2008). Second, the EOO map of Unicolored Thrush extends much farther east than our range estimate, reaching Noel Kempff Mercado National Park in far eastern Bolivia (see BirdLife International 2011e). This eastern limit is based on an isolated record, an alleged sound recording and observation of a single bird in semideciduous forest in September 1989 by T.A. Parker III cited in White et al. (1995) as a personal communication by J.M. Bates. The avifauna of Noel Kempff Mercado National Park has been surveyed extensively (e.g., Bates et al. 1989, 1992; Killeen and Schulenberg 1998), and Unicolored Thrush was not mentioned by these studies. In addition, all of Parker's Neotropical sound recordings are archived at the Macaulay Library, Cornell Lab of Ornithology, and after recent completion of digitization all recordings are searchable and playable on the Macaulay Library web site (http://macaulaylibrary.org/; K.V. Rosenberg and J.V. Remsen Jr, in litt.). This collection does not include a recording of Unicolored Thrush. It therefore appears that Parker's initial identification of the above recording was provisional and later revised or considered uncertain. Until the species' occurrence in Noel Kempff Mercado National Park or adjacent areas can be confirmed by tangible evidence, the doubtful Parker record cited by White et al. (1995) should be excluded from range size estimates.

Range size 'underestimation' by EOO maps

For one-third of Bolivian endemics, all of which are threatened species, BirdLife's EOO estimates were on

Table 2 Comparison of BirdLife International's 2011 species factsheet global range size estimates (http://www.birdlife.org/) with those obtained by the species distribution modeling study of Young et al. (2009) for 65 bird species with >10 unique localities each that are endemic to the east Andean slope and adjacent lowlands of Peru and Bolivia (to ~18°S latitude)

Species and conservation status	Range estimate (km^2)		% Overestimation	% Underestimation
	BirdLife	Young et al. (2009)		
Ancient Antwren (*Herpsilochmus gentryi*) NT	9,500	2,208	330.3	–
Diademed Tapaculo (*Scytalopus schulenbergi*) LC	38,200	12,922	195.6	–
Unadorned Flycatcher (*Myiophobus inornatus*) LC	63,300	21,416	195.6	–
White-browed Hermit (*Phaethornis stuarti*) LC	148,000	52,064	184.3	–
Koepcke's Hermit (*Phaethornis koepckeae*) NT	113,000	42,113	168.3	–
Hooded Tinamou (*Nothocercus nigrocapillus*) LC	206,000	78,903	161.1	–
White-tufted Sunbeam (*Aglaeactis castelnaudii*) LC	23,300	9,102	156.0	–
Upland Antshrike (*Thamnophilus aroyae*) LC	62,500	24,723	152.8	–
Fire-throated Metaltail (*Metallura eupogon*) LC	35,500	14,306	148.1	–
Cabanis's Spinetail (*Synallaxis cabanisi*) LC	190,000	77,703	144.5	–
Rufous-bellied Bush-Tyrant (*Myiotheretes fuscorufus*) LC	110,000	45,346	142.6	–
Large-footed Tapaculo (*Scytalopus macropus*) LC	24,500	10,129	141.9	–
Slaty Tanager (*Creurgops dentatus*) LC	110,000	46,287	137.6	–
Band-tailed Fruiteater (*Pipreola intermedia*) LC	121,000	52,226	131.7	–
Inca Flycatcher (*Leptopogon taczanowskii*) LC	86,300	38,206	125.9	–
Marcapata Spinetail (*Cranioleuca marcapatae*) LC	29,500	13,220	123.1	–
Yellow-scarfed Tanager (*Iridosornis reinhardti*) LC	73,900	34,933	111.5	–
Three-striped Hemispingus (*Hemispingus trifasciatus*) LC	82,200	39,400	108.6	–
Black-faced Brush-Finch (*Atlapetes melanolaemus*) LC	40,400	19,466	107.5	–
Unstreaked Tit-Tyrant (*Anairetes agraphia*) LC	76,900	38,401	100.3	–
Bolivian Tyrannulet (*Zimmerius bolivianus*) LC	112,000	56,428	98.5	–
Chestnut-bellied Mountain-Tanager (*Delothraupis castaneoventris*) LC	131,000	66,053	98.3	–
White-bellied Pygmy-Tyrant (*Myiornis albiventris*) LC	133,000	67,211	97.9	–
Stripe-faced Woodquail (*Odontophorus balliviani*) LC	90,700	46,443	95.3	–
Dusky-green Oropendola (*Psarocolius atrovirens*) LC	139,000	71,706	93.8	–
Pardusco (*Nephelornis oneilli*) LC	30,500	15,913	91.7	–
Masked Fruiteater (*Pipreola pulchra*) LC	78,200	41,514	88.4	–
Black-winged Parrot (*Hapalopsittaca melanotis*) LC	37,900	20,210	87.5	–
Red-and-white Antpitta (*Grallaria erythroleuca*) LC	32,700	17,462	87.3	–
White-browed Conebill (*Conirostrum ferrugineiventre*) LC	147,000	79,553	84.8	–
Peruvian Piedtail (*Phlogophilus harterti*) NT	33,300	18,036	84.6	–
Black-bellied Tanager (*Ramphocelus melanogaster*) LC	76,700	41,659	84.1	–

Table 2 continued

Species and conservation status	Range estimate (km^2)		% Overestimation	% Underestimation
	BirdLife	Young et al. (2009)		
Line-fronted Canastero (*Asthenes urubambensis*) NT	63,400	35,023	81.0	–
Fulvous Wren (*Cinnycerthia fulva*) LC	108,000	59,861	80.4	–
Drab Hemispingus (*Hemispingus xanthophthalmus*) LC	92,200	52,308	76.3	–
Orange-browed Hemispingus (*Hemispingus calophrys*) LC	23,100	13,246	74.4	–
Scaled Metaltail (*Metallura aeneocauda*) LC	49,700	28,690	73.2	–
Rufous-faced Antpitta (*Grallaria erythrotis*) LC	39,100	22,754	71.8	–
White-eared Solitaire (*Entomodestes leucotis*) LC	207,000	121,073	71.0	–
Rufous-vented Tapaculo (*Scytalopus femoralis*) LC	83,400	49,171	69.6	–
Coppery Metaltail (*Metallura theresiae*) LC	34,900	20,699	68.6	–
Peruvian Wren (*Cinnycerthia peruana*) LC	75,800	45,002	68.4	–
Striped Treehunter (*Thripadectes scrutator*) LC	116,000	69,519	66.9	–
Peruvian Tyrannulet (*Zimmerius viridiflavus*) LC	68,800	41,361	66.3	–
Yungas Tody-Tyrant (*Hemitriccus spodiops*) LC	67,600	41,720	62.0	–
Hazel-fronted Pygmy-Tyrant (*Pseudotriccus simplex*) LC	69,000	43,356	59.1	–
Versicolored Barbet (Eubucco versicolor) LC	270,000	170,959	57.9	–
Hooded Mountain-Toucan (*Andigena cucullata*) LC	48,700	31,107	56.6	–
Trilling Tapaculo (*Scytalopus parvirostris*) LC	117,000	78,423	49.2	–
White-collared Jay (*Cyanolyca viridicyanus*) LC	198,000	133,484	48.3	–
Cerulean-capped Manakin (*Lepidothrix coeruleocapilla*) LC	140,000	95,078	47.2	–
Light-crowned Spinetail (*Cranioleuca albiceps*) LC	42,300	28,748	47.1	–
Rufous-webbed Brilliant (*Heliodoxa branickii*) LC	127,000	86,582	46.7	–
Golden-collared Tanager (*Iridosornis jelskii*) LC	98,600	68,438	44.1	–
Mountain Cacique (*Cacicus chrysonotus*) LC	83,600	58,121	43.8	–
White-cheeked Tody-Flycatcher (*Poecilotriccus albifacies*) LC	4,100	2,924	40.2	–
Amazonian Parrotlet (*Nannopsittaca dachilleae*) NT	134,000	101,517	32.0	–
Ashy Antwren (*Myrmotherula grisea*) NT	32,000	29,755	7.5	–
Allpahuayo Antbird (*Percnostola arenarum*) VU	7,700	11,045	–	30.3
Bay-vented Cotinga (*Doliornis sclateri*) VU	13,100	19,922	–	34.2
Rusty-tinged Antpitta (*Grallaria przewalskii*) LC	4,100	6,376	–	35.7
Royal Cinclodes (*Cinclodes aricomae*) CR	2,700	5,641	–	52.1
Scimitar-winged Piha (*Lipaugus uropygialis*) VU	6,700	15,436	–	56.6
Superciliaried Hemispingus (*Hemispingus rufosuperciliaris*) VU	6,700	23,017	–	70.9
Ash-breasted Tit-Tyrant (*Anairetes alpinus*) EN	11,900	42,821	–	72.2

Percent over- and underestimation refer to the degree to which BirdLife International's range size values differ in relation to the estimates obtained by Young et al. (2009). Conservation status: *LC* least concern; *NT* near threatened; *VU* vulnerable; *EN* endangered; *CR* critically endangered. Species nomenclature follows Remsen et al. (2011)

average 49 % smaller than the respective range size estimates of the present analysis. Of the 65 additional Bolivian and Peruvian species modeled by Young et al. (2009), only 11 %, all but one of which are threatened species, had EOO estimates that were on average 50 % smaller than the respective range size estimates of Young et al. (2009). This can partly be attributed to a more sophisticated range size analysis for threatened species by BirdLife not based on simple minimum convex polygons. Additional reasons for this 'underestimation' in the five Bolivian endemics are less straightforward than in the cases of overestimation discussed above; it is not attributable to new distributional data included here but not taken into account in BirdLife's EOO estimates.

For the Endangered Cochabamba Mountain-Finch (*Compsospiza garleppi*) (Fig. 1k) and the Vulnerable Masked Antpitta (*Hylopezus auricularis*) (Fig. 1l), the difference between BirdLife's EOO estimate and our estimate is relatively small (<35 %), and it is difficult to pinpoint underlying systematic factors, particularly for the inductively modeled Masked Antpitta. For Cochabamba Mountain-Finch, it should be noted here that, even though our deductive range size estimate is based exclusively on vegetation series (*Polylepis* woodlands), it is not an AOO estimate. *Polylepis* woodlands are characterized by a highly fragmented, relict distribution due to centuries of human impact (e.g., Ellenberg 1958; Fjeldså and Kessler 1996; Fjeldså 2002; Hensen 2002), which is also the case in the range of Cochabamba Mountain-Finch (Hensen 2002). Fjeldså and Kessler (1996) estimated that *Polylepis* woodlands in Bolivia have been reduced by about 90 %, and the species' AOO may therefore be <500 km^2.

BirdLife's 4,000 km^2 EOO estimate for the Endangered Southern Horned Curassow (*Pauxi unicornis*), which inhabits a narrow elevational band (400–1,400 m) of Andean foothill forest in Cochabamba and Santa Cruz departments (Herzog and Kessler 1998; MacLeod et al. 2006; Maillard Z. 2006; Fig. 1m), was based on an approximate calculation of a potential 400-km-long distribution with a width of suitable habitat (excluding deforested and degraded areas) of about 10 km on average (R. MacLeod, personal communication). In addition to this being a current rather than historic range size estimate, it also considered a somewhat narrower elevational range of 500–1,100 m as being regularly inhabited by Southern Horned Curassow (R. MacLeod, personal communication), which explains the difference between BirdLife's EOO and our range size estimate. Conservation status evaluations of the species should therefore use the current EOO estimate of 4,000 km^2 rather than our historic range size estimate.

For the Endangered Red-fronted Macaw, BirdLife's EOO map is largely restricted to the Caine, Mizque, and upper Grande river valleys with a small, disjunct area in the Pilcomayo valley, excluding much of the intervening area (see BirdLife International 2011c). Although most of the species' locality records originate from these four river valleys, overall records are fairly evenly distributed throughout most of the species' predicted range (Fig. 1n). Many areas in the Inter-Andean Dry Forest ecoregion are of difficult access due to complex topography and few roads, and the Red-fronted Macaw Conservation Program of Asociación Armonía continues to discover new breeding cliffs or roost sites on occasion. Some of the predicted area may on the other hand have been used only historically and may currently be too degraded and barren due to centuries of unsustainable human activities, but the size of this area is unknown.

The historic range estimate of the Critically Endangered Blue-throated Macaw is currently divided into a northern subpopulation and a smaller, disjunct southern subpopulation (see locality dots in Fig. 1o; the east–west separation of the species' range is due to the Mamoré River and associated extensive *várzea* forest). The capital of Beni department, Trinidad, is situated in the intervening area, and we suspect that the species was extirpated in the Trinidad area by illegal exploitation for the cage-bird trade, which caused rapid population declines during the 1970s and 1980s (BirdLife International 2011b). The species' current EOO estimate of 12,900 km^2 excludes this area and is based on two disjunct polygons, which explains the difference between BirdLife's EOO and our range size estimate. Nonetheless, the former still underestimates the species' current EOO. Based on known current locality records (Fig. 1o), the northern subpopulation extends over an area of about 260 km (east–west) by 65 km (north–south) and the southern subpopulation over an area of about 95 km (east–west) by 35 km (north–south), which combines to a total area of about 20,000 km^2. In addition, areas without records in the southwest and northeast of our historic range map (Fig. 1o) are very poorly surveyed due to difficult access. We expect that the species may eventually be discovered here, especially in the southwest, given that there already is one record west of the Mamoré River in this area.

Improving the EOO definition and range size estimates

The use of range maps that are much more sophisticated than minimum convex polygons for most threatened species by BirdLife (see BirdLife International 2011a) implicitly recognizes the shortcomings of the EOO definition. The exclusion of discontinuities or disjunctions within the overall distributions of species needs to be applied more rigorously and at smaller spatial scales, not just for threatened species. For example, the availability of global high-resolution digital elevation models makes the exclusion of areas outside the known elevational ranges of species a straightforward task. Other spatially explicit environmental data layers such as regional ecosystem classifications (e.g., Josse et al. 2009) are becoming increasingly available and should also be used to eliminate discontinuities within the overall distributions of species. Further, as exemplified by the case of the Unicolored Thrush discussed above, incorporating national expertise into the process of range size estimation can be similarly important for reducing overestimation and for separating doubtful or vagrant records from those of resident populations.

In light of limited financial resources available for conservation planning, it will be important to prioritize species for a revision of EOO estimates. The currently largest range-size threshold for conservation planning is that of restricted-range species, i.e. 50,000 km^2. Jetz et al. (2008) found that most species occurred in only 40–70 % of the range indicated by their EOO maps. Thus, many species with EOO estimates of up to 125,000 km^2 may qualify for restricted-range status. As in the case of the Unicolored Thrush, a number of species with EOO estimates of up to about 200,000 km^2 may also qualify for restricted-range status. We therefore recommend prioritizing species with EOO estimates of <200,000 km^2 for a thorough revision of these estimates.

Conservation implications

Based on our range size estimates, four Bolivian endemics (Gray-bellied Flowerpiercer, Unicolored Thrush, Bolivian Blackbird, and Bolivian Earthcreeper), whose BirdLife EOO estimates well exceed 50,000 km^2, qualify for restricted-range species status (a similar case can be made for 18 species modeled by Young et al. 2009; see Table 2). Except for Unicolored Thrush, they occur in EBA 056 (Bolivian and Argentine High Andes; Stattersfield et al. 1998). Unicolored Thrush partly overlaps with the Beni Lowlands secondary EBA (s027) of Blue-throated Macaw, and the combined distribution area of the two species could be declared an EBA. Our historic range size estimate for Blue-throated Macaw slightly exceeds the restricted-range species threshold, but given the inclusion of several marginal areas without records, the species should retain its restricted-range species status until there is proof of its occurrence in these areas.

Our range size estimate for Gray-bellied Flowerpiercer is also below the 20,000 km^2 threshold of the Vulnerable category. The same applies to Black-throated Thistletail, which almost meets the Endangered threshold of 5,000 km^2. In contrast, for both Red-fronted and Blue-throated macaws, our range size estimates are greater than the Vulnerable threshold of 20,000 km^2. Naturally, this does not automatically imply a change in threat category, as range size is used in conjunction with rate of population decline, population size, and degree of population and distribution fragmentation to evaluate a species' conservation status (IUCN 2001). For Gray-bellied Flowerpiercer and Black-throated Thistletail, there is no evidence of a population decline, their ranges are not particularly fragmented, and both species are fairly common in their preferred habitats, suggesting a fairly large population size. Thus, their listing as Least Concern species is not affected by the new, smaller range size estimates.

Blue-throated Macaw is listed as Critically Endangered primarily due to its very small population size (<250 mature individuals) and a drastic population decline as a result of illegal exploitation for the cage-bird trade (BirdLife International 2011b). Thus, a current range size estimate of just over 20,000 km^2 does not directly affect its threat category, although it could lead to an upward adjustment of the estimated population size, particularly so if the species is found in new areas such as the southwestern extreme of its predicted historic range (see Fig. 1o). Red-fronted Macaw is listed as Endangered for very similar reasons, i.e., small population size (<2,500 mature individuals) and a continuing population decline due to illegal exploitation for the cage-bird trade, habitat loss, and persecution as a crop pest combined with very small subpopulations (BirdLife International 2011c). Thus, our higher range size estimate does not affect its threat category.

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