A new species of *Megascops* (Strigidae) from the Sierra Nevada de Santa Marta, Colombia, with notes on voices of New World screech-owls

Una nueva especie de *Megascops* (Strigidae) de la Sierra Nevada de Santa Marta, Colombia, con notas sobre las vocalizaciones de los currucutúes del Nuevo Mundo

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Abstract

I describe a new species of screech-owl from the humid tropical montane forest of the Sierra Nevada de Santa Marta in northern Colombia. A genetic comparison indicated that it belongs in the genus *Megascops,* and that it has no close relative. I provide an overall assessment of the vocalizations of the New World screech-owls.

Key words: Colombia, *Margarobyas*, *Megascops gilesi,* new species, *Psiloscops,* taxonomy, voice

Resumen

Describo una especie nueva de búho que habita el bosque húmedo de la zona premontana de la Sierra Nevada de Santa Marta, Colombia. Una comparación genética indicó que la nueva especie pertenece al género *Megascops,* y que no tiene pariente cercano. Proveo una comparación descriptiva de las vocalizaciones de todas las especies de *Megascops* y de otros géneros afines del Nuevo Mundo.

Palabras clave: Colombia, *Margarobyas*, *Megascops gilesi*, nueva especie, *Psiloscops,* vocalizaciones

Introduction

The Sierra Nevada de Santa Marta (heretofore referred to as Santa Marta) is a mountain massif in northern Colombia. Nearly 100 by 100 km wide it rises from the Caribbean coast to its highest peak at over 5,700 m asl. Isolated to the east from a northern spur of the Andes (Serranía de Perijá) by elevations of no more than 200 m, the massif exhibits a strikingly high degree of floral and faunal endemism. Of the nearly 200 bird taxa breeding in Santa Marta no less than 70 are endemic, 20 of them presently ranked as species (Gill & Donsker 2016, Cadena *et al.* 2016). The Santa Marta avifauna is relatively well known. Main bird collectors in the region include F. Simons (in 1878), W. W. Brown, Jr. (1897-1899), H. H. Smith (1898-1899) and M. A. Carriker, Jr. (1911-1919), whose specimens are now mostly deposited in the British Museum of Natural History (BMNH), United States National Museum (USNM), American Museum of Natural History (AMNH), and Carnegie Museum of Natural History, Pittsburg (CM), respectively (Todd & Carriker 1922). No new bird taxon has been found there since these collections were made, but the taxonomic ranks of several of the endemic taxa have been subject to revision (*e.g.,* Krabbe & Schulenberg 1997, Krabbe 2008, Cadena & Cuervo 2010, Bonaccorso *et al.* 2011, Collar & Salaman 2013, and Cadena *et al.* 2016). In 1919, M. A. Carriker, Jr. collected a screech-owl in the Santa Marta, which he believed to represent a new species. He sent the specimen to

W. E. Todd in the Carnegie Museum, who lent it to W. W. Miller of AMNH for a comparison with other screech-owls. Miller found nothing very closely resembling it, the nearest being a specimen of *Megascops choliba* from Matto Grosso, Brazil. Todd then published the specimen as "*Otus choliba* subsp." and noted "...it may very well represent a distinct form, but until more specimens have been collected it would be unwise to formally characterize it" (Todd & Carriker 1922).

During field work in 2007 aimed at documenting the vocalizations of the birds of the Sierra Nevada de Santa Marta, I recorded a screech-owl song that did not match any known species. Upon investigation, it turned out that its song had been recorded earlier but remained unpublished (now XC25823 and XC25824). A specimen with tissue sample was subsequently collected and was found to be phenotypically nearly identical to Carriker's specimen. Phylogenetic analyses including the 2007 specimen and samples of nearly all New World screech-owls, based on sequences of the Cytochrome B mitochondrial gene by Dantas *et al.* (2016), showed that the Santa Marta specimens was as genetically divergent as most major clades in the genus are. However, the phylogenetic placement of the Santa Marta sample with respect to other clades received weak statistical support, except that it is not part of the *choliba* or *nudipes* clades. When comparing the sequences used in Dantas' study and omitting the first 11 bases, the uncorrected genetic distance from the Santa Marta bird is smallest with *M. roboratus* (5.8%), and with

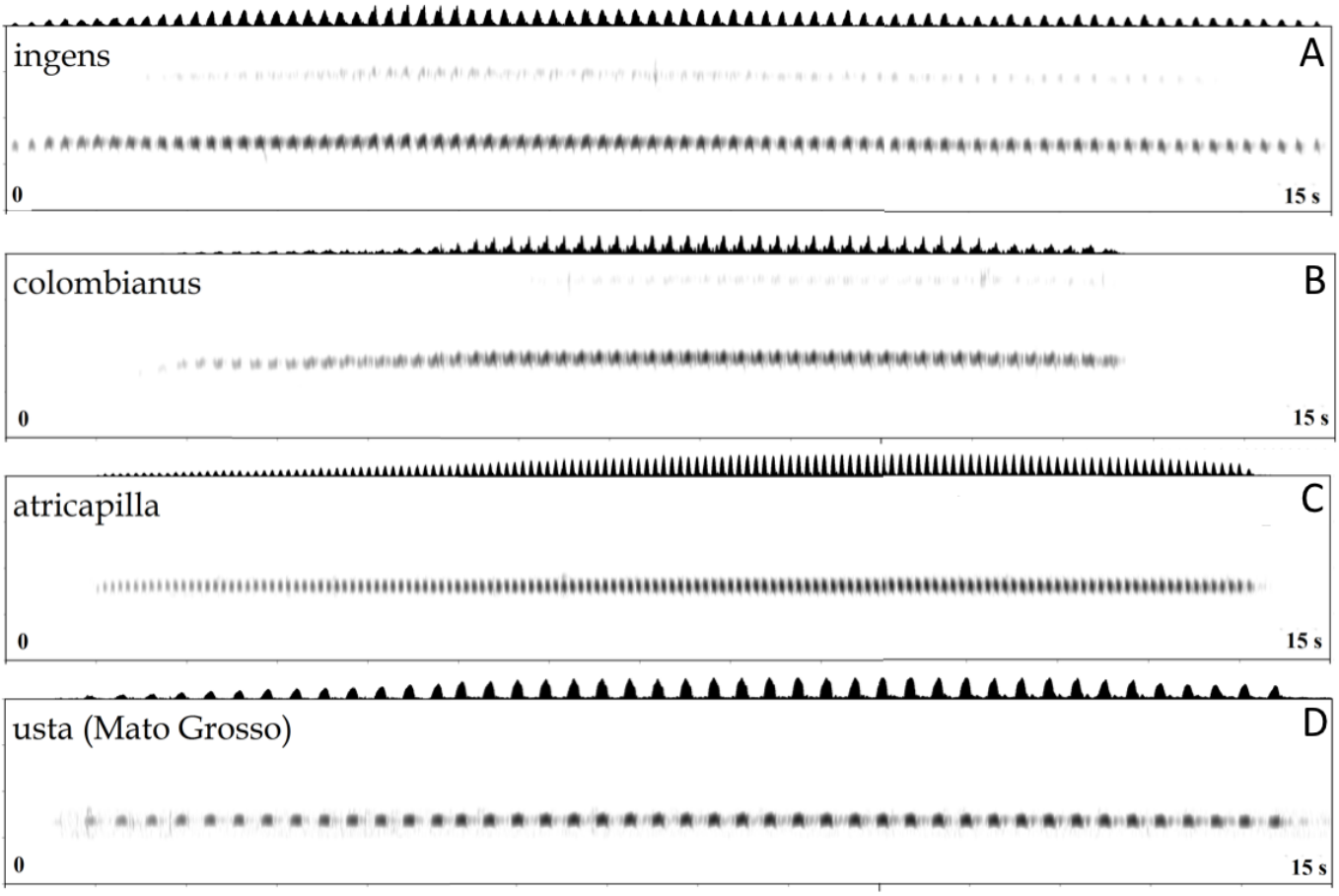


Figure 1. Oscillograms and sonograms of songs of forms of *Megascops*. Vertical scale 0-2 kHz. Catalogue numbers of recordings are: (A): *ingens* XC251093; (B): [*ingens*] *colombianus* ML139095; (C): *atricapilla* ML127980; (D): *watsonii usta* ML48098 (see cont. 1 and 2).

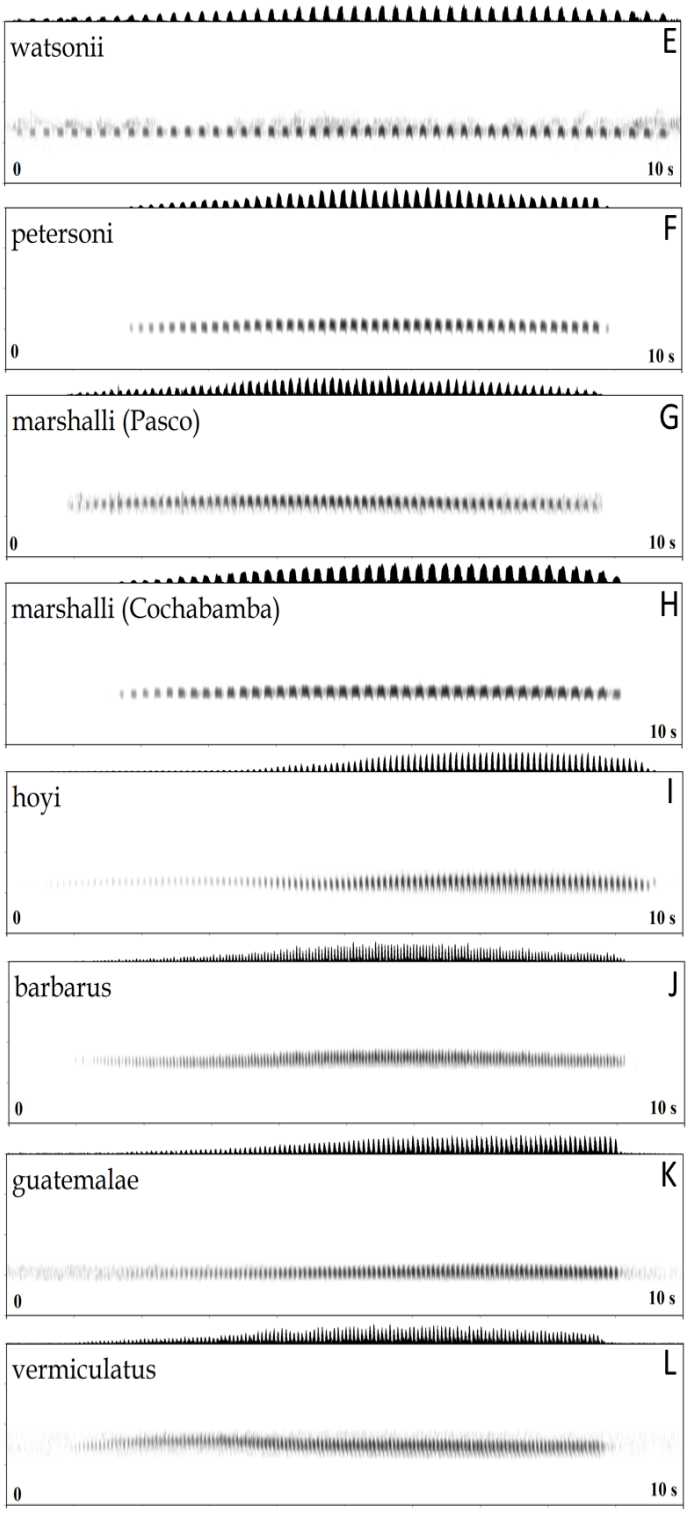
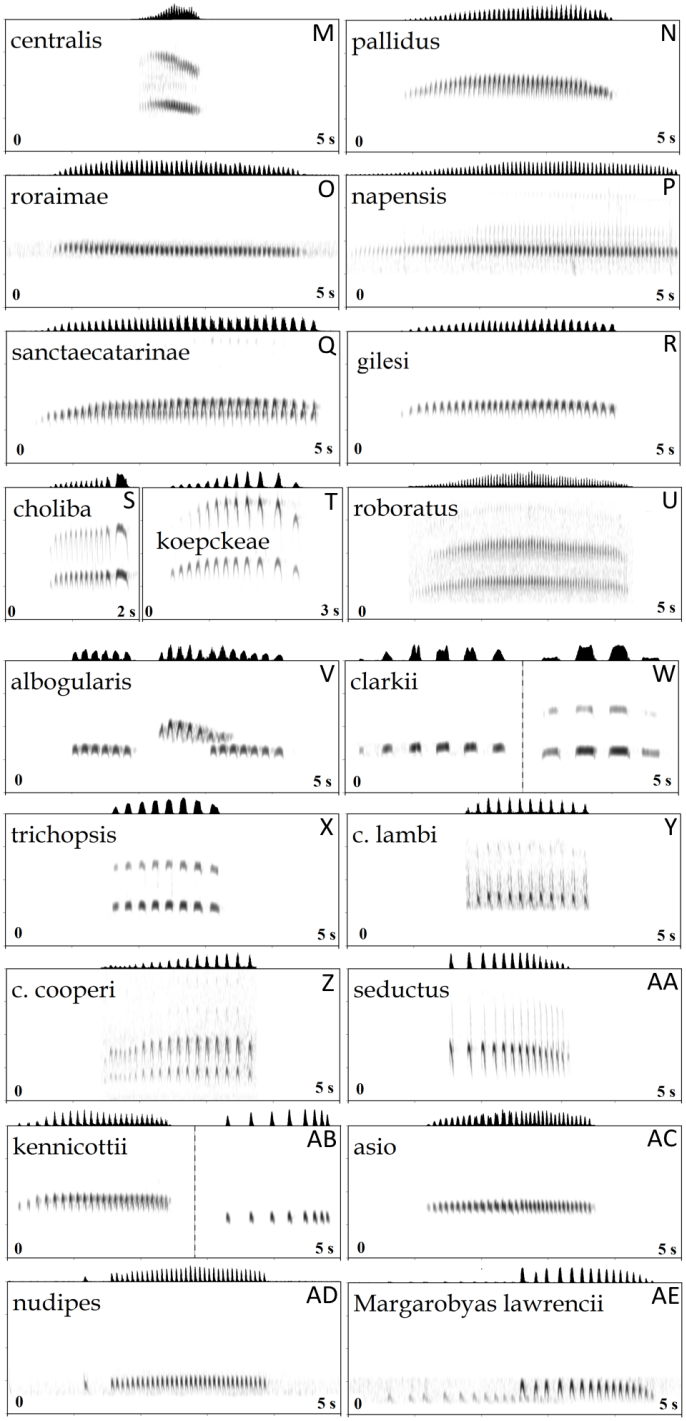


Figure 1 (*cont.* 1) . Oscillograms and sonograms of songs of forms of *Megascops.* Vertical scale 0-2 kHz. Catalogue numbers of recordings are: **(E)**: *watsonii watsonii* XC257742; **(F)**: *petersoni* XC274951; **(G)**: *marshalli* (Pasco) XC105090; **(H)**: *marshalli* (Cochabamba) Mayer (2006 cut 3); **(I)**: *hoyi* XC48743; **(J)**: *barbarus* ML53444; **(K)**: *guatemalae* XC3320; **(L)**: *vermiculatus* XC65705 (see cont. 2).

respect to *M. watsonii, M. atricapilla, M. sanctaecatarinae,* and *M. guatemalae* (6%). Genetic distance of the Santa Marta samples is larger (7.5-8.0%) with respect to *M. cooperi, M. barbarus* and *M. ingens*. Evidently, the lineage leading to Santa Marta taxon has evolved in isolation for millions of years.

The New World screech-owls were previously referred to the genus *Otus* (*e.g.,* Cory 1918, Peters 1940) but were recently shown to constitute a distinct clade (König *et al.* 1999, Dantas *et al.* 2016, Enriquez *et al.* 2017). No single morphological character that describes this clade has been found, but all but one species differs from *Otus* by singing multi-noted songs, and were therefore separated in the genus *Megascops,* while a monotypic genus was resurrected for the last New World species, Flammulated Owl (*Psiloscops flammeolus*). Based on genetic data by Dantas *et al.* (2016) the *Megascops* species most distantly related to the others is the Caribbean *M. nudipes,* which is sometimes placed in the genus *Gymnoglaux*. No genetic data exist for the Cuban *M. lawrencii*, so the affinities of that screech-owl are still unsolved, although Hardy *et al.* (1999) suggested that it might be sister to *M. nudipes*. The remainder of *Megascops* encompasses some 60 taxa ranked as 19-24 species (Marshall 1967, Hekstra 1982a,b, Marshall & King 1988, Sibley 1996, Howell & Webb 1995, Hardy *et al.* 1999, Ridgely & Greenfield 2001, Dickinson & Remsen 2013, Gill & Donsker 2016, Dantas *et al.* 2016). All taxa were described on morphological grounds, yet, apart from the large and virtually "hornless" *M. albogularis,* the plumages of most look so confusingly similar, that individual specimens often cannot be safely identified. Nearly all species differ from each other by combinations of characters rather than by any particular morphological trait, and distinguishing features often only become apparent in large series.



Additionally, atypically plumaged specimens occur in most or all species, especially among rufous morphs. Morphometrics, eye colour, facial pattern, and length of the "horns" (Hekstra 1982a, del Hoyo *et al.* 1999; also label data on specimens examined) show little correlation with the phylogenetic tree outlined by Dantas *et al.* (2016). Not surprisingly, given that all taxa are nocturnal, species recognition appears to rest almost entirely on vocal signalling (König 1994).

Hardy *et al.* (1988, 1989) published audio cassettes of the voices of the New World owls, the first to cover songs and calls of the majority of species. In a review of the 1989 publication Marshall *et al.* (1991) commented about *Megascops* (then referred to *Otus*) "most species have two territorial songs, an A and a B song, used in ritual duets of the pair. The female's voice is a third to a fifth higher in pitch than the male's and in some species is naturally harsh." In that same review, they commented on audio recordings of each of the species, and it was apparent that there are many exceptions to this simple model and a few species were poorly known. Since then, much information has been added, most summarized by Marks *et al.* (1999), and numerous additional sound recordings have been obtained and archived in online sources (xeno-canto, Macaulay Library of Natural Sounds). Some forms, however, such as *M. seductus, M. cooperi lambi,* and *M. barbarus* remain poorly represented.

Figure 1 (*cont.* 2) . Oscillograms and sonograms of songs of forms of *Megascops* and *Margarobyas lawrencii*. The taxa *centralis* and *pallidus,* often omitted in taxonomic lists were described by Hekstra (1982b). Songs from two different individuals are included for *clarkii* (both from Costa Rica) and *kennicottii* (from Baja California and Arizona). Song of *albogularis* in duet, song of *Margarobyas lawrencii* in duet or by two differently pitched males. Vertical scale 0-2 kHz. Catalogue numbers of recordings are: **(M)**: *centralis* Hardy (1989 example 3); **(N)**: [*roraimae*] *pallidus* ML59336; **(O)**: [r.] *roraimae* - ML134292; **(P)**: [*roraimae*] *napensis* XC23482; **(Q)**: *sanctaecatarinae* ML18817; **(R)**: *gilesi* XC235877; **(S)**: *choliba* ML59304; **(T)**: *koepckeae* G. Engblom (unpublished from La Libertad); **(U)**: *roboratus* XC33939; **(V)**: *albogularis* XC2021; **(W)**: *clarkii* Hardy (1989) and XC65665; **(X)**: *trichopsis* XC227087; **(Y)**: *cooperi lambi* XC31495; **(Z)**: Hardy (1989 example 2); **(AA)**: *seducus* Hardy (1989 example 1); **(AB)**: *kennicottii* XC11555 and XC48223; **(AC)**: *asio* XC77270; **(AD)**: *nudipes* ML129734; **(AE)**: *Margarobyas lawrencii* ML133244.

Megascops species regularly duetting with two song types include *M. trichopsis, M. asio, M. kennicottii, M. seductus, M. cooperi, M. koepckeae* and *M. sanctaecatarinae*, but only the latter two and *M. albogularis* seem to duet all year round. Only about half of all the species have two territorial song types. Some disagreement persists about what is the primary song type for some species. For example, the "bouncing-ball" song of *M. kennicottii* (Fig. 1AB) has been variously labelled as primary (Sibley 2003) or secondary (Marks *et al.* 1999), as has the "whinny" of *M. asio* (Fig. 2D). The term "aggressive song" as used by D. F. Lane (in Schulenberg *et al.* 2007) is generally homologous with "secondary song" (*sensu* Marshall 1967, Weyden 1974, 1975, Ritchison *et al.* 1988, Klatt and Ritchison 1993), but is also used for some less commonly heard vocalizations given only in aggressive contexts. In this paper the term "shortsong" is generally used for the secondary song type, and "aggressive song" for the rarer vocalizations, but only for *M. asio, M. atricapilla*, and *M. marshalli* are both terms used.

This said, all species of *Megascops* do have at least one territorial song composed of several notes, which sets the genus apart from *Psiloscops* and Old World *Otus* (Hekstra 1982a, Wink & Heidrich 1999). They all differ from each other vocally in any region, but some have dialects (*e.g.,* Tripp 2004, Fjeldså *et al.* 2012). Herzog *et al.* (2009) suggested that vocal character displacement might have influenced the dialects of *M. ingens* and *M. marshalli* and coincidentally driven one population of *M. marshalli* to sing much like *M. petersoni*. However, these authors did not clarify if their large sample sizes represented different individuals or simply the number of songs recorded.

Within the genus, voice is generally very poorly correlated with phylogeny (see Appendix B and Dantas *et al.* 2016). For example, the long songs of *M. atricapilla, M. hoyi,* and *M. guatemalae* sound very similar to each other (Fig. 2C, 2I, 2K) although these taxa belong in widely different clades (Dantas *et al.* 2016). This suggests that the range in diversification of vocalizations is limited. Nonetheless, the discovery of the close relationship (Dantas *et al.* 2016) of *M. marshalli* to the vocally very different *M. hoyi* illustrates the vocal variability that exists within this small range. Several species do show some vocal similarities with their closest relatives, such as the "Morse-code" ("telegraphic trill") songs of *M. trichopsis* and *M. clarkii,* and the "bouncy-ball" songs of *M. asio* and *M. kennicottii* (the closely related *M. cooperi* usually decelerates in pace but at times gives a "bouncy-ball" song). The phylogenetically unsampled *M. seductus* also gives a "bouncy-ball" song, supporting its suggested close relationship to these forms (Marshall 1967).

In general, *Megascops* species do not live in actual sympatry. Some replace each other altitudinally, with up to five species replacing each other along an altitudinal gradient. Others are segregated ecologically, and their vocalizations differ distinctly from those of adjacent forms in pitch, pace, pattern, quality, or duration. The only notable exception is *M. marshalli* and *M. petersoni,* which overlap considerably in altitudinal range with (the much larger) *M. ingens* in humid forest along the East Andean slope. Oddly, their songs can also be confused. How they manage to coexist remains unstudied. At least one species, *M. choliba* takes advantage of forest clearance and now more frequently comes into contact with species of closed forest.

The present study primarily aims at describing and naming the intriguing screech-owl from Sierra Nevada de Santa Marta and at giving a uniform presentation of the vocalizations of the entire genus. Hence, here I attempt to provide a

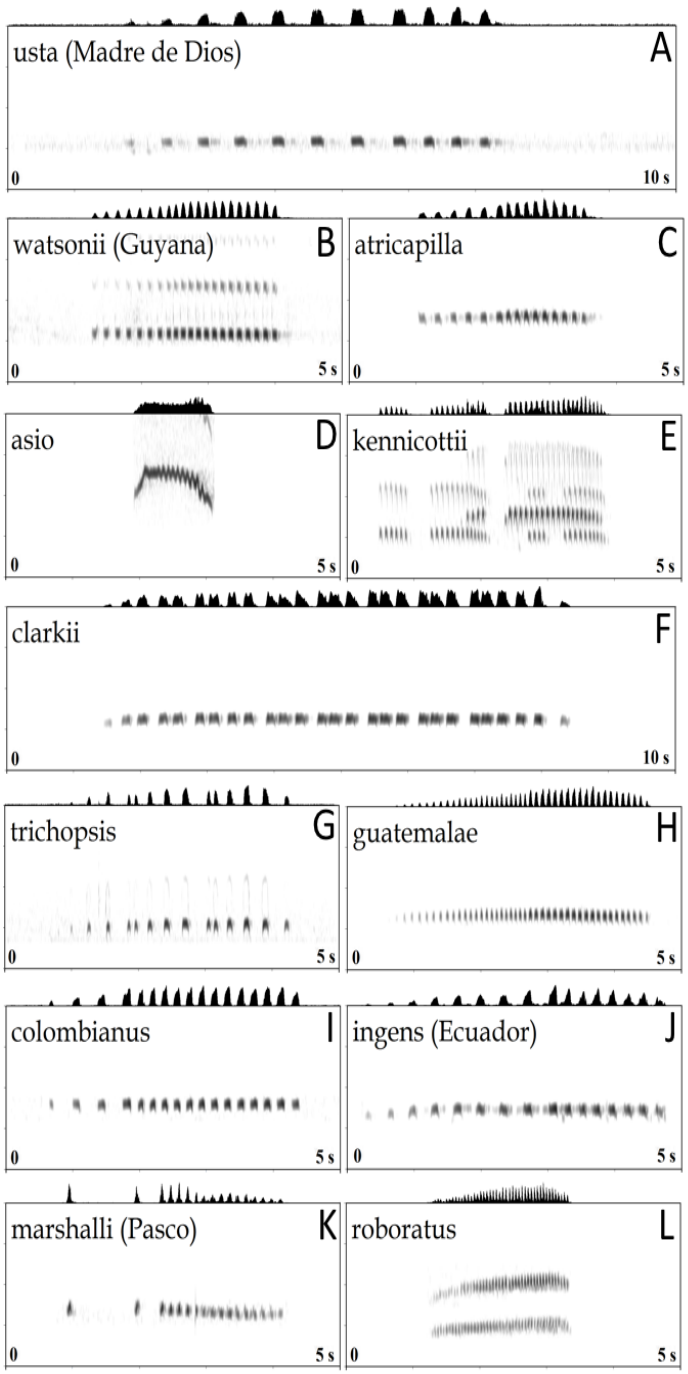


Figure 2. Oscillograms and sonograms of shortsongs of some species of *Megascops*, in *kennicottii* duet. Vertical scale 0-2 kHz. Catalogue numbers of recordings are: **(A)**: *watsonii usta* ML135176; **(B)**: *watsonii watsonii* ML87589; **(C)**: *atricapilla* ML127911; **(D)**: *asio* Hardy (1989 example 3); **(E)**: *kennicottii* XC21274; **(F)**: *clarkii* ML25772; **(G)**: t*richopsis* Hardy (1989); **(H)**: *guatemalae* Hardy (1989); **(I)**: *colombianus* XC80939; **(J)**: *ingens* XC238475; **(K)**: *marshalli* Mayer (2006 cut 1); **(L)**: *roboratus* ML130459.

basis for the use of vocal characters in the identification and ranking of the many *Megascops* taxa. I also indicate for which forms additional vocal material is particularly desirable.

Methods

I collected *Megascops* specimens and voice recordings in the Andes of Argentina, Bolivia, Peru, Ecuador and Colombia between 1983 and 2015. Voice recordings are publicly available in xeno-canto and most specimens are deposited in the Zoological Museum, University of Copenhagen (ZMUC), Museo Ecuatoriano de Ciencias Naturales, Quito (MECN), and Colección Boliviana de Fauna, La Paz (CBF). The birds of Sierra Nevada de Santa Marta, northern Colombia, were investigated from 1 to 25 February 2007, primarily at elevations between 1,100 and 2,550 m on the San Lorenzo ridge in the north-western part of the massif, where as many recordings as possible of the vocally distinct screech-owl were obtained, and where visiting tourists were urged to take photographs and video-tapes of this owl and share them (some now available under Santa Marta Screech-Owl in the photo galleries of http://surfbirds.com). Alonso Quevedo collected a specimen (ICN 38833) of the new screech-owl, took photographs of it while fresh, and provided tissue which was used in the genetic comparisons by Dantas *et al.* (2016). The other Santa Marta specimen, collected by Carriker in 1919, was kindly sent from CM to the Field Museum of Natural History, Chicago (FMNH) for me to compare with the large collection of congeners housed there. In addition, collections of *Megascops* specimens were examined in MECN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá, and ZMUC.

Voice recordings of all recognized species and vocally distinct subspecies of *Megascops* were

obtained from published media (Boesman 2006, Coopmans *et al.* 2004, Hardy *et al.* 1988, 1989 (1999), Jahn *et al.* 2008, Krabbe & Nilsson 2003, Lysinger *et al.* 2005, Mayer 2006), from the Macaulay Library and xeno-canto. Additionally, several unpublished recordings of the new species from Santa Marta were kindly forwarded to me by David Bradley and Alonso Quevedo. The number of recordings examined of each taxon is listed in Appendix B. The sound program CoolEdit Pro (Syntrillium Software) was used for measuring vocalizations, including pitch (frequency) of the first harmonic with most volume, change of pitch, pace during first and last quarter of song, number of notes, and duration of the vocalizations, and for the taking of qualitative annotations on relative volume of harmonics and change in volume. Behavioural information, where this was provided, was noted for each recording. In Table 1 *n* is the number of individuals recorded, *i.e.* when there was more than one recording of the same individual available, only one was included. The measurements taken varied little for each individual except for length of song, for which the mean was calculated. Mean song length for the species is thus the mean of means, but the absolute range given includes the length of all songs in the recordings. Because most published accounts of New World screech-owl vocalizations are difficult to interpret, it was deemed necessary to give a brief, but homogeneous and unambiguous representation of them all presentation of them all (Appendix B).

Vocal measurements of all species and some subspecies and populations were compared to those of the Santa Marta form. If absolute ranges of measurements overlapped in all four major variables of song (length, pace during first and last quarter, pitch), a more detailed comparison was made, partly by calculating probabilities that means were the same (two-tailed t-tests), partly by comparing other aspects of song (change of pace and pitch).

Results

Measurements of four variables in male songs and shortsongs are presented in Table 1. A comparison of pace and duration of song indicated that the fastest paced songs were short, and the longest songs slow-paced (Fig. 3). Pitch was uncorrelated with other variables. Absolute ranges of all four measurements overlapped with the Santa Marta form in only five taxa. Three of these differed markedly in change of pace. Means of the remaining two differed from the Santa Marta taxon with over 99.9% probability (two-tailed t-test) in nearly all measurements. Sonograms of songs, shortsongs and aggressive songs of all species are shown in figures 2, 4 and 5.

A comparison of the specimen collected by Carriker in Santa Marta in 1919 (CM 70857) with

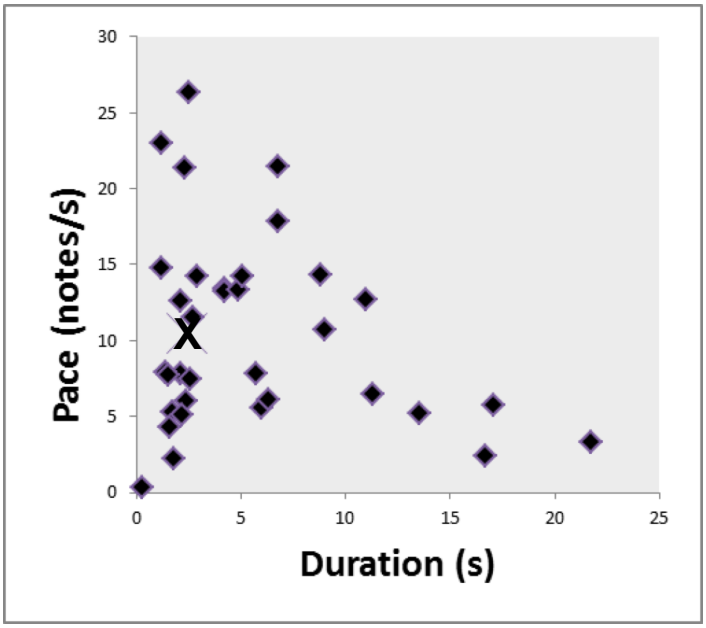


Figure 3. Relationship between pace and duration of the song in New World screech-owls showing a tendency of fast-paced songs to be short and long songs to be slow-paced. Neither duration nor pace showed any correlation with the pitch. The Santa Marta taxon is marked with an X.

Table 1. Some properties (duration, pace during 1st and last quarter of song, pitch of 1st harmonic with most volume) of male songs and shortsongs of New World screech-owls (mean ± standard deviation, range, sample size). *Psiloscops flammeolus* gives a single-noted song and is not included. All included taxa are referred to *Megascops* (abbreviated with an "*M.*") except *Margarobyas lawrencii*, which is ranked in a different genus from *Megascops nudipes* by some. Sequence follows clades outlined by Dantas *et al.* (2016). Ranks of several taxa are subject to debate.

Taxon	Duration (s)	Start pace (s^{-1})	End pace (s^{-1})	Loudest pitch (Hz)
Margarobyas lawrencii	2.2 ±0.2 (2.1-2.5)	5.1 ±0.4 (4.6-5.6)	9.0 ±1.0 (7.7-9.9)	344 ±88 (242-400)
	n = 3	*n = 3*	*n = 3*	*n = 3*
Megascops nudipes	2.9 ±0.4 (2.2-3.5)	14.2 ±0.6 (13.2-15.4)	14.8 ±0.7 (13.4-15.8)	471 ±49 (435-614)
	n = 12	*n = 12*	*n = 12*	*n = 12*
M. albogularis	1.4 ±0.5 (0.6-2.8)	7.9 ±1.0 (5.5-10.0)	7.7 ±1.4 (4.0-10.0)	708 ±70 (570-975)
	n =39	*n = 39*	*n = 39*	*n = 39*
M. koepckeae hockingi	2.6 ±0.3 (2.0-3.2)	7.5 ±0.8 (5.4-8.5)	6.1 ±1.7 (3.3-8.3)	1149 ±128 (879-1360)
	n = 31	*n = 31*	*n = 31*	*n = 31*
M. k. koepckeae	2.1 ±0.5 (1.5-3.0)	7.8 ±1.1 (5.6-9.0)	5.2 ±2.2 (3.5-8.8)	874 ±89 (727-1016)
	n = 7	*n = 7*	*n = 7*	*n = 7*
M. choliba	1.2 ±0.2 (0.8-1.6)	14.8 ±1.5 (11-18)	14.6 ±1.7 (9-18)	688 ±87 (489-968)
	n = 125	*n = 125*	*n = 125*	*n = 125*
M. clarkii	1.8 ±0.3 (1.3-2.5)	2.2 ±0.5 (1.7-3.7)	2.3 ±0.6 (1.7-3.6)	655 ±41 (600-750)
	n = 15	*n = 15*	*n = 15*	*n = 15*
M. trichopsis	1.7 ±0.3 (1.4-2.1)	5.3 ±1.1 (3.0-6.0)	5.1 ±1.2 (3.0-6.0)	658 ±46 (607-740)
	n = 7	*n = 7*	*n = 7*	*n = 7*
M. barbarus	6.8 ±2.0 (4.5-9.1)	21.5 ±1.3 (20.0-22.5)	21.3 ±1.0 (20-22)	812 ±17 (789-827)
	n = 4	*n = 4*	*n = 4*	*n = 4*
M. sanctaecatarinae	4.2 ±0.8 (2.9-5.9)	13.4 ±2.7 (8.7-17.5)	10.7 ±2.7 (6.9-15.1)	731 ±72 (620-900)
	n = 23	*n = 23*	*n = 23*	*n = 23*
M. r. roboratus	2.5 ±0.6 (1.7-3.2)	26.3 ±1.8 (23.4-28.2)	24.1 ±2.7 (19.9-26.8)	582 ±26 (532-620)
	n = 8	*n = 8*	*n = 8*	*n = 8*
M. roboratus pacificus	2.3 ±0.7 (1.5-4.1)	21.4 ±1.7 (18.1-24.1)	24.3 ±1.8 (20.5-28.1)	559 ±75 (450-715)
	n = 22	*n = 22*	*n = 21*	*n = 22*
Megascops sp. nov. Sierra Nevada de Santa Marta	2.4 ±0.4 (1.7-3.1)	10.5 ±1.7 (7.4-13.0)	9.2 ±1.5 (6.4-11.5)	873 ±48 (816-995)
	n = 13	*n = 13*	*n = 14*	*n = 15*
M. w. watsonii S Ecuador	21.7 ±8.5 (12.4-35.1)	3.3 ±0.3 (2.9-3.5)	3.3 ±0.2 (3.0-3.5)	622 ±42 (574-660)
	n = 5	*n = 5*	*n = 5*	*n = 5*
M. w. watsonii N Ecuador, Peru	17.1 ±5.9 (10-27)	5.7 ±0.9 (4.1-7.7)	5.5 ±0.9 (3.6-7.7)	614 ±33 (564-700)
	n = 20	*n = 25*	*n = 25*	*n = 25*
M. w. watsonii N of Amazon	14.9 ±5.1 (5.6-28)	9.9 ±1.3 (8.0-14.0)	9.6 ±1.2 (7.7-13.0)	626 ±60 (524-850)
	n = 30	*n = 34*	*n = 33*	*n = 34*
M. watsonii usta Peru	16.7 ±4.9 (7.8-26.0)	2.4 ±0.2 (2.0-2.7)	2.3 ±0.2 (1.9-2.8)	609 ±55 (507-700)
	n = 24	*n = 28*	*n = 28*	*n = 28*
M. watsonii usta shortsongs Peru	5.1 ±0.9 (4.0-6.8)	1.8 ±0.2 (1.4-2.1)	2.2 ±0.2 (1.9-2.4)	624 ±39 (554-680)
	n = 9	*n = 9*	*n = 9*	*n = 9*
M. w. watsonii shortsongs N Ecuador, Peru	4.2 ±0.9 (3.2-5.8)	3.7 ±0.7 (2.2-4.6)	4.6 ±0.8 (2.5-5.4)	637 ±32 (588-697)
	n = 13	*n = 13*	*n = 13*	*n = 12*
M. w. watsonii shortsongs N of Amazon	3.2 ±0.6 (2.5-4.3)	6.3 ±1.1 (3.4-8.4)	7.4 ±1.1 (4.9-9.3)	634 ±45 (577-700)
	n = 13	*n = 13*	*n = 13*	*n = 13*

Taxon	Duration (s)	Start pace (s^{-1})	End pace (s^{-1})	Loudest pitch (Hz)
M. atricapilla	11.0 ±5.6 (4.1-25.4)	12.7 ±1.5 (10.5-15.9)	12.2 ±1.4 (9.6-14.5)	767 ±38 (700-850)
	n = 19	*n = 19*	*n = 19*	*n = 18*
M. atricapilla shortsong	2.9 ±0.5 (2.6-3.4)	5.9 ±1.4 (4.3-6.8)	9.2 ±2.9 (6.8-12.4)	833 ±28 (800-851)
	n = 3	*n = 3*	*n = 3*	*n = 3*
M. g. guatemalae	8.8 ±1.7 (6.6-11.4)	14.3 ±1.0 (13.3-16.1)	14.2 ±0.9 (13.3-16.0)	586 ±56 (520-660)
	n = 6	*n = 6*	*n = 6*	*n = 6*
M. vermiculatus	6.8 ±1.3 (5.2-8.3)	17.8 ±1.5 (16.2-20.2)	17.6 ±1.2 (16.1-19.1)	676 ±52 (631-760)
	n = 7	*n = 7*	*n = 7*	n=7
M. centralis [Hekstra]	1.2 ±0.2 (0.7-1.6)	23.0 ±1.9 (20.3-27.0)	23.5 ±2.1 (20.4-28.0)	845 ±62 (687-953)
	n = 24	*n = 23*	*n = 23*	*n = 24*
M. [*roraimae*] *pallidus* [Hekstra]	4.2 ±0.7 (2.8-5.6)	13.2 ±0.7 (11.7-13.9)	14.1 ±0.8 (13.0-15.4)	955 ±68 (855-1083)
	n = 16	*n = 16*	*n = 16*	*n = 16*
M. [*roraimae*] *napensis*	5.1 ±1.0 (3.6-6.7)	14.2 ±1.3 (12.6-17.0)	14.0 ±1.5 (11.0-17.0)	843 ±57 (760-960)
	n = 13	*n = 13*	*n = 14*	*n = 14*
M. [*r.*] *roraimae*	4.9 ±1.2 (3.5-6.4)	13.3 ±1.1 (10.7-14.6)	13.6 ±1.0 (11.1-15.1)	884 ±81 (760-1058)
	n = 11	*n = 12*	*n = 12*	*n = 12*
M. c. cooperi	2.1 ±0.3 (1.5-2.5)	12.6 ±2.6 (9.0-18.0)	6.2 ±1.7 (5.0-11.0)	481 ±60 (400-600)
	n = 13	*n = 13*	*n = 13*	*n = 13*
M. cooperi lambi	1.5 ±0.3(1.2-1.7)	7.7 ±0.7 (7.0-8.3)	8.1 ±2.3 (6.0-10.5)	772 ±64 (730-845)
	n = 3	*n = 3*	*n = 3*	*n = 3*
M. seductus	2.4 ±1.0 (1.6-3.7)	6.0 ±2.9 (3.5-10.0)	11.1 ±2.4 (7.0-13.0)	783 ±60 (700-850)
	n = 5	*n = 5*	*n = 5*	*n = 5*
M. kennicottii	1.6 ±0.4 (0.9-3.0)	4.3 ±1.6 (1.5-9.0)	10.2 ±2.5 (4.9-16.0)	615 ±63 (430-737)
	n = 60	*n = 60*	*n = 60*	*n = 60*
M. asio	2.7 ±0.3 (2.4-3.2)	11.5 ±1.7 (9.8-15.0)	15.3 ±1.1 (14.0-17.0)	773 ±104 (620-878)
	n = 7	*n = 7*	*n = 7*	*n = 7*
M. petersoni	6.3 ±1.2 (4.7-8.9)	6.1 ±0.6 (5.0-7.0)	5.8 ±0.8 (4.0-7.0)	606 ±42 (540-700)
	n = 20	*n = 20*	*n = 20*	*n = 20*
M. marshalli SE Peru, Bolivia	6.0 ±1.4 (3.6-7.4)	5.6 ±0.3 (5.0-6.0)	5.5 ±0.3 (5.0-6.0)	673 ±37 (636-742)
	n = 7	*n = 7*	*n = 8*	*n = 8*
M. marshalli C Peru	5.7 ±1.6 (1.8-7.8)	7.8 ±0.5 (7.4-8.4)	7.4 ±0.5 (6.8-7.8)	661 ±22 (636-676)
	n = 3	*n = 3*	*n = 3*	*n = 3*
M. hoyi	9.0 ±0.9 (7.3-9.9)	10.7 ±0.6 (9.9-11.9)	10.6 ±0.7 (9.6-11.8)	672 ±47 (563-726)
	n = 11	*n = 12*	*n = 12*	*n = 12*
M. hoyi shortsong	2.4 ±0.4 (2.0-3.0)	8.0 ±1.1 (6.4-9.1)	9.4 ±0.4 (8.8-9.8)	725 ±58 (659-780)
	n = 5	*n = 5*	*n = 5*	*n = 5*
M. [*ingens*] *colombianus*	13.5 ±5.2 (7.4-21.0)	5.2 ±1.0 (4.3-6.3)	5.3 ±0.7 (4.3-6.3)	808 ±51 (724-868)
	n = 6	*n = 6*	*n = 6*	*n = 6*
M. ingens	11.3 ±2.8 (6.0-17.3)	6.5 ±1.2 (4.1-8.8)	6.5 ±1.3 (4.7-9.6)	826 ±80 (707-975)
	n = 37	*n = 36*	*n = 37*	*n = 35*
M. ingens (*Aragua*) *n=1*	9.0 (7.4-10.1)	10.3	9.4	993
M. [*ingens*] *colombianus* shortsong	4.3 ±1.0 (3.0-5.4)	2.9 ±0.4 (2.4-3.4)	4.6 ±0.3 (4.3-4.9)	820 ±34 (780-850)
	n = 6	*n = 6*	*n = 6*	*n = 6*
M. ingens shortsong	3.4 ±0.7 (2.2-4.9)	4.0 ±1.1 (2.6-7.6)	5.9 ±1.6 (3.8-9.1)	853 ±67 (726-950)
	n = 21	*n = 19*	*n = 19*	*n = 17*

the large collection of screech-owls held in FMNH confirmed the conclusion made by W. W. Miller after he had compared it with the large collection in AMNH (in Todd & Carriker 1922), that it does not match any other screech-owl. Additionally, the specimen collected by Quevedo in 2007 (ICN 38833) from Santa Marta was found to be a nearly perfect match to Carriker's specimen. The vocal and morphological distinctness of this form, as well as its large genetic distance from other members of the genus (Dantas *et al.* 2016) is evidence that it represents a new species, which I name:

Megascops gilesi species novum
Santa Marta Screech-Owl

Holotype. - Carnegie Museum catalogue no. CM 70857, adult female in breeding condition collected at Las Taguas, Cuchilla San Lorenzo, Santa Marta, Magdalena department, Colombia, at an elevation of 6,000 feet [2,088 m], by M. A. Carriker, Jr. on 13 March 1919.

Diagnosis. - A yellow-eyed, medium-sized screech-owl. Facial disk with a relatively indistinct narrow dark brown rim. Crown and back regularly barred with relatively straight and wide dark bars. Semi-concealed pale nuchal collar separated from back by a contrasting dark band, blackish shaft streaks of underparts relatively sparse and narrow, contrasting with light brown cross bars that are evenly and widely spaced on the belly, not in groups of two, and fairly straight rather than wavy. Tarsi, but not toes feathered, these feathers golden buff, contrasting with white of belly.

Description of holotype. — Plumage coloration (capitalized names and numbers of colours follow Munsell Soil Color Chart (Kollmorgen Instruments Corp., 1994 edition)): Underplumes (down and bases of contour feathers) buffy (10YR8/7), this colour showing through when feathers disturbed. Forehead and faint brow connecting to nuchal collar buffy white, mottled with blackish brown bars connected by thin, about half as wide shaft streaks. Crown buffy brown densely barred blackish, dark bars narrow, 1.6 mm wide, pale bars 1.1 mm, the dark bars only connected by very narrow shaft streaks. Feathers of nape mostly whitish with 1 mm wide, brown bars every 3-4 mm, but tips densely barred blackish brown, creating a pale and lightly barred nuchal collar separated from the back by a dark and densely barred band, the pale nuchal collar continuing around the facial disk to the throat. Back rather uniform brown (7.5YR5/8-4/6) with dense, indistinct blackish brown bars, mostly straight rather than vermiculated, brown and dark bars about equal in width, ranging from less than 1 to over 3 mm, creating a regular overall barring much more extensive than in adults of most species of *Megascops.* Rump and upper tail coverts buffy brown barred blackish brown, dark bars 1 mm wide, pale bars 2 mm. Tail 92 mm, blackish brown with nine buffy grey, 2 mm wide bars that are bordered on each side by a 1-2 mm wide blackish bar, the brown between bars 3-4 mm wide. The pale bars on the inner webs widen to 5 mm towards the edge. The outer 12 mm of outer web and outer 4 mm of inner web of tail feathers densely vermiculated. On upper wing some scapular feathers and outer middle primary coverts with a large whitish spot on outer web, vermiculated brown and blackish on 3-4 mm tip and on entire inner webs, some inner webs with some whitish to buffy white parts. Lesser and middle wing coverts barred reddish brown and black, bars *ca.* 1 mm wide. Greater wing coverts vermiculated grey-brown, buffy-white and blackish. Outer web of two outer alula feathers with large, black-bordered, whitish spot, vermiculated tip, and buffy base. Outer web of primaries barred, the pale bars buffy and 3 mm wide at shaft broadening to 4 mm and whitish at edge, the dark bars blackish brown, 8 mm at shaft

narrowing to 6 mm at edge, some dark bars suffused with grey-brown. Outer web of secondaries blackish brown with some brown vermiculations and with 5-6 mm wide, blackish-bordered, buff bars, some of which are vermiculated with blackish. Tertials wholly vermiculated grey, blackish brown and greyish white. Under wing: Lesser under wing coverts buff with 15-18 mm wide, blackish tips, median under wing coverts buff, a few of the median under primary coverts with a 1 mm blackish dot, greater under wing coverts buffy-white with sharply demarcated blackish tips, forming a contrasting blackish band widening from about 1 cm on the secondary- and inner primary coverts, to about 2 cm on the outer greater under primary coverts. Outer five primaries virtually uniform greyish black on inner web, barring nearly indistinguishable, rest of remiges with broad buffy white bars basally, increasingly extensive towards body. Wing formula as given by distance in mm to wing tip (5th) of each of the ten primaries, beginning with the outer is: 40, 13, 7, 1, (0), 4, 7, 16, 21, 29. Wing chord 162 mm, wing flat 167 mm. Facial disk and throat buffy white, disk with 9 concentric blackish bars (evenly dark and pale) and a poorly defined blackish brown rim (1-3 mm) behind ear coverts to sides of throat. Breast buffy white with narrow, less than 1 mm wide blackish brown shaft streaks and dense brown bars, 1.5 mm wide and 1.3-2.5 mm apart. This grades into the white belly, where the streaks are narrower (0.3-0.7 mm), dark brown, and sparser, and where the brown bars are narrower (0.8-0.9 mm), less distinct, and more widely spaced (2-3.5 mm), bars relatively regularly spaced rather than in groups of two. Tarsi 31 mm, feathered to base of toes, buffy (10YR8/7), feathering sparse and easily coming off on lower tarsus. Middle toe 23.3 mm. Whiskers black, up to 23 mm long. Label data on soft part colours: Iris yellow, bill leaden blue with pale tip, toes bluish flesh.

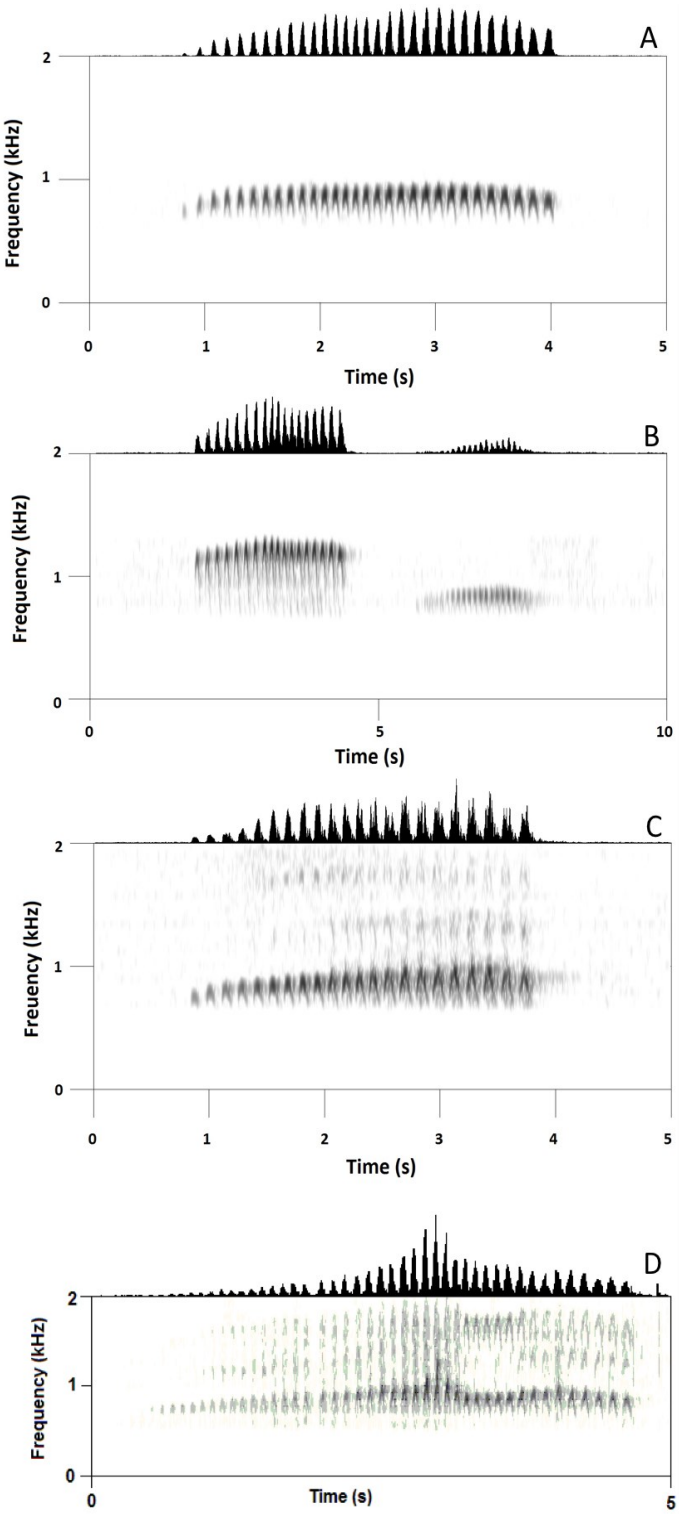


Figure 4. Oscillograms and sonograms of songs of *Megascops gilesi.* (A): Natural song XC235877 (B): presumed duet XC59672 (note time scale). (C): Aggressive song, presumably a male XC59672 (D): Aggressive song, presumably a male D. Bradley5.

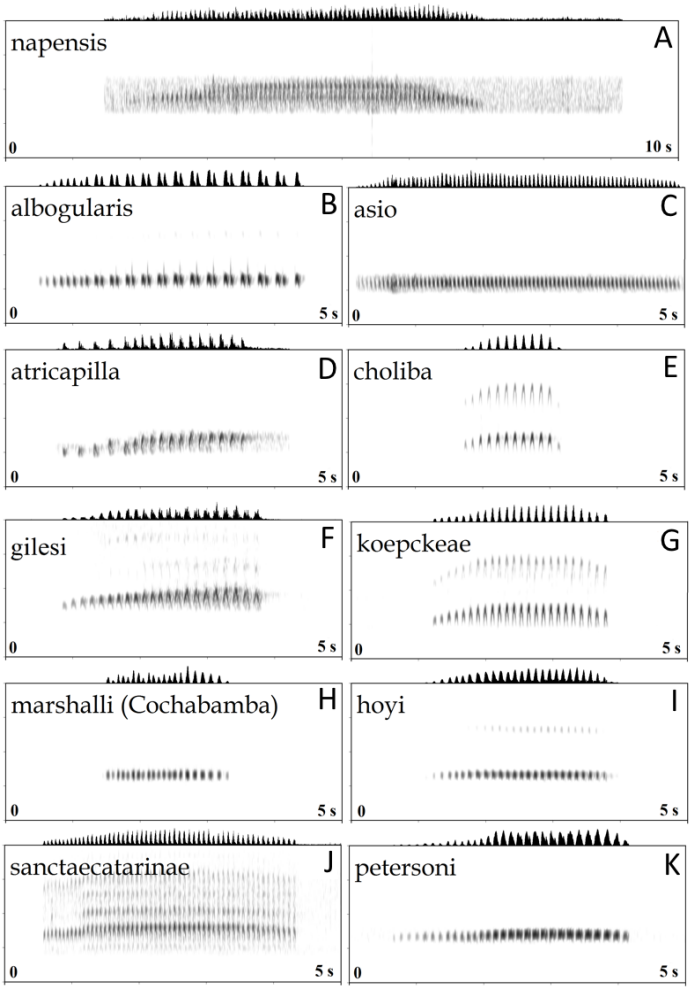


Figure 5. Oscillograms and sonograms of aggressive songs of some species of *Megascops*. Vertical scale 0-2 kHz. Catalogue numbers of recordings are: (A): [*roraimae*] *M. napensis* XC20791; (B): *M. albogularis* ML21912; (C): *M. asio* XC75829; (D): *M. atricapilla* ML127911; (E): *M. choliba* ML4477; (F): *M. gilesi* XC59672; (G): *M. koepckeae* XC67487; (H): *M. marshalli* (Cochabamba) XC3429; (I): *M. hoyi* ML129337; (J): *M. sanctaecatarinae* ML18821; (K): *M. petersoni* ML39962.

Additional material. — The 2007 specimen collected by Alonso Quevedo (ICN 38833) with tissue (Universidad de los Andes ANDES-T 351) near the type-locality had dirty flesh toes and greyish horn claws when fresh. Unfortunately, this specimen was nearly entirely destroyed by insects, but photographs of the fresh specimen (Fig. 6) shows it to be very similar to the type in most ways, differing only in its browner general coloration and broader blackish streaks along the shafts on the crown. Like the type, it has a narrow dark facial rim, a regularly barred back separated from a pale nuchal collar by a darker area, and broadly and regularly spaced, narrow, brown, straight, transverse bars on the belly and flanks, denser on breast, the character of the bars on the lower underparts also exhibited in all individuals photographed. Photographs taken of additional individuals in the wild (Fig. 7; see photo gallery on surfbird.com under Santa Marta Screech-Owl) include both redder and greyer individuals, many showing a distinct contrast in darkness between breast or upper breast and belly. The reddest individual (Fig. 7D) has entirely reddish facial disk without any concentric bars.

Voice. — 29 recordings were examined. Song (Fig. 4) a 2-3 s long trill, pace *ca.* 10/s, rising in pitch and volume through first 1-8 evenly spaced notes, then increasing to full volume at a first more rapid, but decelerating pace, at end dropping slightly and fairly abruptly in pitch and volume. The pitch at loudest volume in natural song averaged 874 Hz in presumed males (n=14), 1,172 Hz in presumed females (n=4) (Fig. 4A). Aggressive song apparently also given by both sexes, similar, but longer, fast part harsh in quality and rising and falling once (Figs. 4C, 5F) or twice (Fig. 4D) in pitch. Sonograms comparing the song to other species of *Megascops* are shown in the figures 1, 2 and 5.

Distribution. — The Santa Marta Screech-Owl is so far only known from humid forest between 1,800 and 2,500 m elevation on the San Lorenzo ridge, in the north-western part of the Sierra Nevada de Santa Marta. Here it was found to be fairly common in February 2007. It probably occurs in similar forest throughout the massif but is unlikely to occur in the surrounding Andean regions, where *M. ingens, M. colombianus* and *M. petersoni* inhabit similar elevations. Considering the absence of *M. albogularis* from Santa Marta it might also occur in humid forest higher than

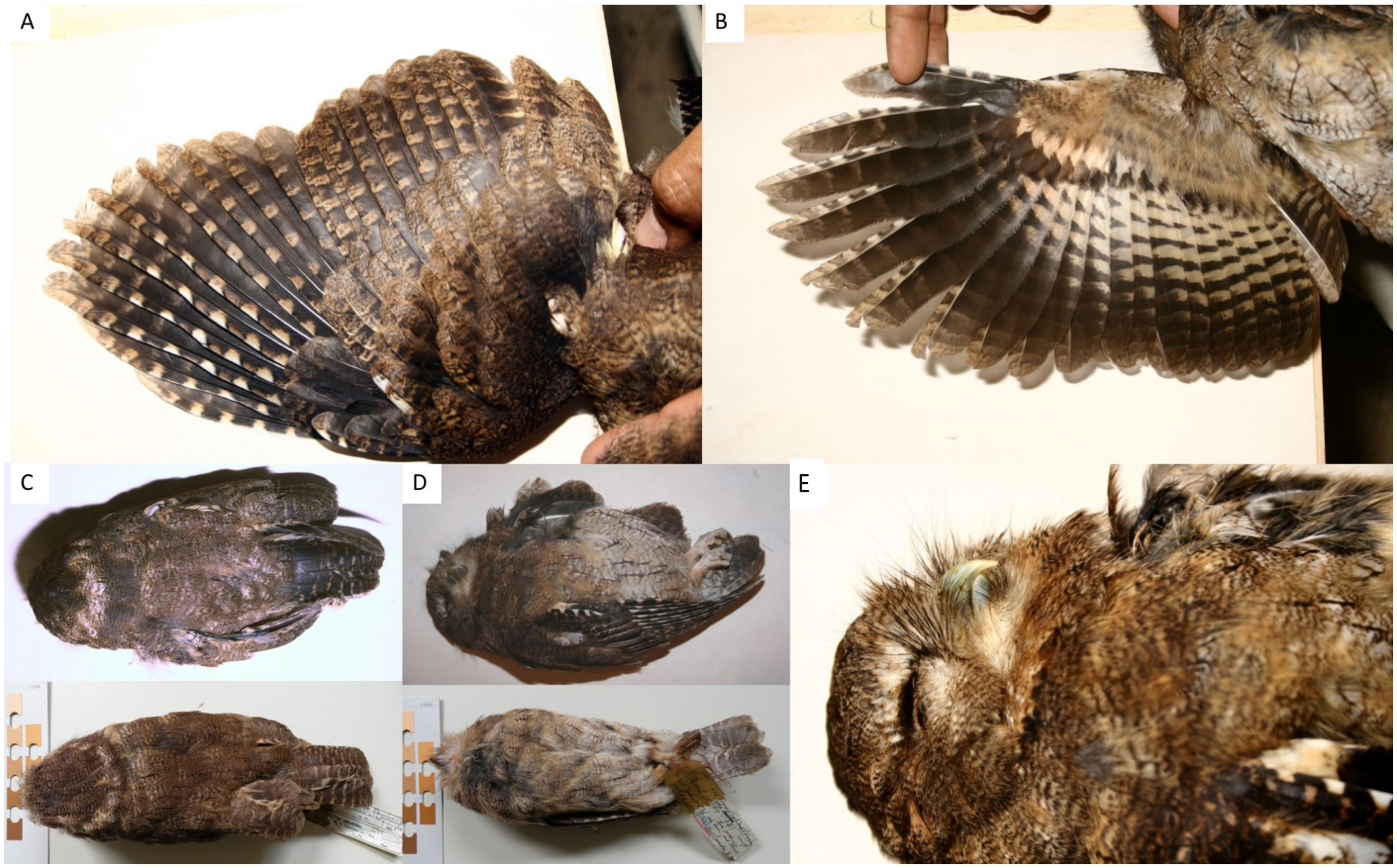


Figure 6. *Megascops gilesi.* **(A)**-**(B)**: Spread upper and underwing of a fresh specimen (ICN38833). **(C)**: Dorsal view of the fresh specimen and the holotype (below). Note conspicuous nuchal collar and barring on crown and back. **(D)**: Ventral view of the fresh specimen and the holotype (below). Note the brown, evenly and rather widely spaced and fairly straight bars on the belly. **(E)**: Bill color of the fresh specimen. ICN38833 by A. Quevedo, holotype by NKK.

2,500 m. On the San Lorenzo ridge, it is replaced below and in drier habitat by *M. choliba*, the only other *Megascops* species recorded in the massif and known to occur up to *ca.* 1,425 m (XC45400) but possibly ranging higher in the drier valleys, as it occurs to at least 2,800 m in the East Andes of Colombia (XC54283, XC54284) and to 3,000 m in the Central Andes (Fjeldså & Krabbe 1990).

Etymology — I name the species after Robert Giles, who funded and took an active part in establishing a bird reserve near the type locality.

Discussion

Nearly all the bird taxa endemic to the Santa Marta region are hypothesized to have originated from Andean ancestors (Todd & Carriker 1922, Caro *et al.* 2013) and have sister populations in the adjacent parts of the Andes (Fjeldså & Krabbe 1990). The lack of known close relatives in the adjacent regions for *Megascops gilesi* is thus remarkable.

The voice descriptions in Appendix B serve to distinguish *M. gilesi,* but are also of interest in the assessment of some forms of disputed taxonomic ranks. Although slight vocal differences of *M.* [*guatemalae*] *vermiculatus* in pitch and pace from *M. g. guatemalae* and *M. guatemalae hastatus* are suggested, sample sizes are small and no recording of the N Nicaraguan form *M. guatemalae dacrysistactus* was included in the comparison. Additional material is needed to assess the rank of *vermiculatus*. The data indicate distinct vocal differences in all measurements

Figure 7. *Megascops gilesi* photographed near the type locality. **(A)**: Intermediate morph. **(B)**: Intermediate morph. **(C)**: Grey morph. **(D)**: Rufous morph. Photographs by A. Quevedo (A), Diego Calderón-Franco (B) and D. Brinkhuizen (C-D).

between *M.* [*guatemalae*] *centralis* (Hekstra) and geographically adjacent forms in the clade (*vermiculatus, pallidus, napensis*), strongly supporting the suggested species rank of *M. centralis* (Ridgely & Greenfield 2001, Gill and Donsker 2016). *M.* [*guatemalae*] *pallidus* (Hekstra) has been overlooked by most authors and deserves mention. The similarity in plumage pattern, tarsal feathering, size and proportions to Mexican *guatemalae* of a specimen (AMNH120332) from the Paria Peninsula, coastal mountains of Venezuela, led Chapman (1931) to

conclude that it was specifically distinct from *roraimae*. Hekstra (1982b) named birds from the coastal mountains of Venezuela *pallidus* (including in that form AMNH476699 [type], FMNH91892, FMNH91893, and four additional specimens in AMNH [2], British Museum and Frankfurt Museum) and also described them as being very similar in plumage and tarsal feathering to *guatemalae*. It would appear that *pallidus* is a valid taxon. Birds from the coastal mountains vocalize similarly to birds from the eastern slope of the Serranía de Perijá, and usually differ in both pitch and change of pitch from *M.* [*guatemalae*] *roraimae*. However, some recordings of the two are indistinguishable, suggesting that despite the morphological differences, *pallidus* may have been correctly referred to *roraimae* by König *et al.* (1999).

Analyses of the material indicate no consistent vocal difference between *M.* [*guatemalae*] napensis and *M.* [*guatemalae*] *roraimae*. Differences between them in plumage and slightly in proportions and tarsal feathering (Chapman (1931) support the validity of the taxon *napensis,* but their similar vocalizations suggest that *napensis* was correctly ranked as a subspecies of *roraimae* by Ridgely and Greenfield (2001). Likewise, there do not appear to be vocal differences between *M.* [*ingens*] *colombianus* and *M. i. ingens*. Differences between them in size, general hue, tail/tarsus proportions and tarsal feathering (Fitzpatrick & O'Neill 1986) leave little doubt as to the validity of the taxon *colombianus,* but vocally there is no support for ranking it as a species.

Fitzpatrick & O'Neill also reported a geographically isolated and vocally distinct population of *M. ingens* from the coastal mountains of Venezuela. A recording of this population with male song and female shortsong was kindly made available to me recently through the joint efforts of John W. Fitzpatrick, Gregory Budney and Miguel Lentino: The shortsong is very short (1.9 s vs. 2.7-3.1 s in three other recordings), lacking the distinction between a slow first part and a fast second part. It is rather fast-paced (6.2-6.4 notes/s) throughout, rather faster than females from Táchira (3.6 notes/s) (ML 59615 and 59616 - possibly the same individual). The male song is very fast-paced and rather high-pitched (see Table 1). In other aspects, the vocalizations of this population are typical of *M. ingens.* Finally, there are regional vocal differences in *M. watsonii*, but those do not help clarify the surprising genetic relationships of *M. atricapilla, M. watsonii* and *M. usta* reported by Dantas *et al.* (2016).

Thus, several taxonomic issues in the genus remain to be solved, but this study sums up present knowledge of *Megascops* vocalizations besides describing the heretofore unnamed taxon from the Sierra Nevada de Santa Marta, *Megascops gilesi.*

Acknowledgments

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type specimen to me at the Field Museum, Chicago and for subsequent information on the specimen; Jason Weckstein, John Bates, Mary Hennen, Shannon Hackett, and Dave Willard of the Field Museum for kind assistance and use of the collection; Marco Altamirano of MECN, and F. G. Stiles of ICN for use of the collections in these museums. Mark B. Robbins and Jon Fjeldså kindly commented on early drafts of the manuscript.

Literature cited

BONACCORSO, E., J. M. GUAYASAMIN, A. T. PETERSON. & A. G. NAVARRO-SIGÜENZA. 2011. Molecular phylogeny and systematics of Neotropical toucanets in the genus *Aulacorhynchus* (Aves, Ramphastidae). Zoologica Scripta 40:336–349.

BOND, J. 1971. Birds of the West Indies. 2nd ed. Collins, London.

CADENA, C. D., & A. M. CUERVO. 2010. Molecules, ecology, morphology, and songs in concert: how many species is *Arremon torquatus* (Aves: Emberizidae)? Biological Journal of the Linnean Society 99(1):152-176

CADENA, C. D., L. M. CARO, P. C. CAYCEDO, A. M. CUERVO, R. C. BOWIE & H. SLABBEKOORN. 2016. *Henicorhina anachoreta* (Troglodytidae), another endemic bird species for the Sierra Nevada de Santa Marta, Colombia. Ornitología Colombiana 15:82-89.

CAMPBELL, W. (ed.) 1994. Know your birds of prey. Vol. 1. Axia NetMedia Corporation, Calgary, Alberta, Canada.

CARO, L. M., P. C. CAYCEDO-ROSALES, R. C. K. BOWIE, H. SLABBEKOORN & C. D. CADENA. 2013. Ecological speciation along an elevational gradient in a tropical passerine bird. Journal of Evolutionary Biology 26:1420-9101.

CAVANAGH, P. M. & G. RITCHISON. 1987. Variation in the bounce and whinny songs of the eastern screech-owl. The Wilson Bulletin 99:620-627.

CHAPMAN, F. M. 1931. The upper zonal bird-life of Mts. *Roraimae* and *Duida*. Bulletin of the American Museum of Natural History 63 (135 pp.).

COLLAR, N. J. & P. SALAMAN. 2013. The taxonomic and conservation status of the *Oxypogon helmetcrests*. Conservación Colombiana 19:31-38.

CORY, C. B. 1918. Catalogue of Birds of the Americas. Field Museum of Natural History Publications 197. Zool. Ser. 13, pt. 2 no. 1.

DANTAS, S. M., J. D. WECKSTEIN, J. BATES, N. K. KRABBE, C. D. CADENA, M. B. ROBBINS, E. VALDERRAMA & A. ALEIXO. 2016. Molecular systematics of the new world screech-owls (Megascops: Aves, Strigidae): Biogeographic and taxonomic implications. Molecular Phylogenetics and Evolution 94:626-634.

DICKINSON, E. C., & J. V. REMSEN, JR. (eds.) 2013. The Howard and Moore complete checklist of the birds of the World. Vol. 2. Non-passerines. Aves Press, Eastbourne, U.K.

ENRIQUEZ, P. L. K. EISERMANN, H. MIKKOLA & J. C. MOTTA-JUNIOR. 2017. A review of the systematics of Neotropical Owls (Strigiformes). Chapter 2 (pp. 7-19) in P. L. Enriquez, ed., Neotropical Owls. Springer International Publishing: ISBN 978-3-319-57107-2.

FITZPATRICK, J. W. & J. P. O'NEILL. 1986. *Otus petersoni*, a new screech-owl from the eastern Andes, with systematic notes on *O. colombianus* and *O. ingens*. The Wilson Bulletin 98:1-14.

FJELDSÅ, J. & N. KRABBE. 1990. Birds of the high Andes. Apollo Books, Svendborg, Denmark.

FJELDSÅ, J., J. BAIKER, G. ENGBLOM, I. FRANKE, D. GEALE, N. K. KRABBE, D. E. LANE, M. LEZAMA, F. SCHMITT, R. S. R. WILLIAMS, J. UGARTE-NÚÑEZ, V. YÁBAR & R. YÁBAR. 2012. Reappraisal of Koepcke's Screech Owl *Megascops koepckeae* and description of a new subspecies. Bulletin of the British Ornithologists' Club 132:180-193.

GILL, F, & D. DONSKER (eds.) 2016. IOC World Bird List (v 6.2). doi : 10.14344/IOC.ML.6.2

HEKSTRA, G. P. 1982a. "I don't give a hoot…" A revision of the American screech-owls (Otus; Strigidae). PhD diss. Vrije Universiteit te Amsterdam, Netherlands.

HEKSTRA, G. P. 1982b. Description of twenty-four new subspecies of American Otus (Aves, Strigidae). Univ. Amsterdam Bull. Zool. Museum 9:49-63.

HERZOG, S. K., S. R. EWING, K. L. EVANS, A. MACCORMICK, T. VALQUI, R. BRYCE, M. KESSLER & R. MACLEOD. 2009. Vocalizations, distribution, and ecology of the Cloud-Forest Screech Owl *(Megascops marshalli).* The Wilson Journal of Ornithology 121:240-252.

HOWELL, S. N. G. & S. WEBB. 1995. The birds of Mexico and northern Central America. Oxford University Press.

KLATT, P. H. & G. RITCHISON. 1993. The duetting behavior of Eastern Screech-Owls. The Wilson Bulletin 105:483-489.

KÖNIG, C. 1994 Lautäußerungen als interspezifische Isolationsmechanismen bei Eulen der Gattung Otus (Aves: Strigidae) aus dem südlichen Südamerika. - Stuttg. Beitr. Naturkde. Ser. A. Nr. 511:1-1-35.

KÖNIG, C., F. WEICK & J. H. BECKING. 1999. Owls: A guide to the owls of the world. Yale University Press, New Haven.

KRABBE, N. 2008. Vocal evidence for restitution of species rank to a Santa Marta endemic: *Automolus rufipectus* Bangs (Furnariidae), with comments on its generic affinities. Bulletin of the British Ornithologists' Club 128: 219-227.

KRABBE, N. & T. S. SCHULENBERG. 1997. Species limits and natural history of *Scytalopus tapaculos* (Rhinocryptidae),

with descriptions of the Ecuadorian taxa, including three new species. Pp. 46-88 in Remsen, J. V. (ed.) Studies in Neotropical ornithology honoring Ted Parker. Ornithological Monographs 48.

MARKS, J. S., R. J. CANNINGS & H. MIKKOLA. 1999. Family Strigidae (typical owls). Pp. 76-242 in J. del Hoyo, A. Elliott and J. Sargatal, eds. Handbook of the Birds of the World, vol. 5. Lynx Edicions, Barcelona.

MARSHALL, J. T. 1967. Parallel variation in North and Middle American screech-owls. Monographs No. 1. Western Foundation of Vertebrate Zoology, Los Angeles.

MARSHALL, J. T. & B. KING. 1988. Genus Otus. In: Amadon, Dean & Bull, J: Hawks and owls of the world: A distributional and taxonomic list. Proceedings of the Western Foundation of Vertebrate Zoology 3:296–357.

MARSHALL, J. T., R. A. BEHRSTOCK & C. KÖNIG. 1991. Special review: Voices of the New World Owls (Strigiformes: Tytonidae, Strigidae). The Wilson Bulletin 103:311-338.

PETERS, J. L. 1940. Check-list of birds of the World. Vol. 4. Harvard University Press, Cambridge, Massachussets.

RIDGELY, R. S. & P. J. GREENFIELD. 2001. The birds of Ecuador. Ithaca, NY: Cornell University Press.

RITCHISON, G., P. M. CAVANAGH, J. R. BELTHOFF & E. J. SPARKS. 1988. The singing behavior of Eastern Screech-Owls: seasonal timing and response to playback of conspecifics song. Condor 90: 648-652.

SCHULENBERG, T. S., D. F. STOTZ, D. F. LANE, J. P. O'NEILL & T. A. PARKER III. 2007. Birds of Peru. Princeton University Press, Princeton, NJ and Oxford, UK.

SIBLEY, C. G. 1996. Distribution and taxonomy of birds of the World. CD-ROM, ver. 2.0. Thayer Birding Software, Cincinnati, Ohio.

SIBLEY, D. A. 2003. The Sibley field guide to birds of western North America. Alfred A. Knopf, New York.

TODD, W. E. & M. A. CARRIKER. 1922. The birds of the Santa Marta region of Colombia: a study in altitudinal distribution. Annals of the Carnegie Museum 14 (611 pp.).

TRIPP, T. 2004. Use of bioacoustics for population monitoring in the Western Screech-Owl *(Megascops kennicottii).* M.A. thesis, University of Northern British Colombia.

WEYDEN, W. J. VAN DER. 1974. Vocal affinities of the Puerto Rican and Vermiculated Screech Owls (*Otus nudipes* and *O. guatemalae*). Ibis 116:369-372.

WEYDEN, W. J. VAN DER. 1975. Scops and screech-owls: Vocal evidence for a basic subdivision in the genus *Otus* (Strigidae). Ardea 63:65-77.

WINK, M. & P. HEIDRICH. 1999. Molecular evolution and systematics of owls (Strigiformes). Pp. 39-57 In: C. König, F. Weick & J. H. Becking (eds.): Owls: A guide to the owls of the world. Yale University Press, New Haven.

Sound publication references

BOESMAN, P. 2006a. Birds of Brazil: MP3 Sound Collection. The Netherlands: Birdsounds.

BOESMAN, P. 2006b. Birds of Mexico: MP3 Sound Collection. The Netherlands: Birdsounds.

COOPMANS, P., J. V. MOORE, N. KRABBE, O. JAHN, K. S. BERG, M. LYSINGER, L. NAVARRETE & R. S. RIDGELY. 2004. The birds of southwest Ecuador. [5 Audio CDs with booklet]. John V. Moore Nature Recordings, San José, California, U.S.A.

HARDY, J. W., B. B. COFFEY, JR. & G. B. REYNARD. 1988. Voices of the New World Nightbirds (Owls, nightjars and their allies). 3rd ed. ARA Records, Gainesville, Florida.

HARDY, J. W., B. B. COFFEY, JR. & G. B. REYNARD. 1989 (1999). Voices of the New World owls (Strigiformes: Tytonidae, Strigidae). (Rev. ed. 1999). ARA Records, Gainesville, Florida.

JAHN, O., J. V. MOORE, N. KRABBE, P. M. VALENZUELA, N. KRABBE, P. COOPMANS, M. LYSINGER, L. NAVARRETE, J. NILSSON & R. S. RIDGELY. 2008. The birds of northwest Ecuador. Vol I. Revised and expanded edition. [MP3 CD and data DVD with booklet]. John V. Moore Nature Recordings, San José, California.

KRABBE, N. & J. NILSSON. 2003. Birds of Ecuador. Sounds and Photographs. [DVD-ROM]. Bird Songs International, Westernieland, The Netherlands.

LYSINGER, M., J. V. MOORE, N. KRABBE, P. COOPMANS, D. F. LANE, L. NAVARRETE, J. NILSSON & R. S. RIDGELY. 2005. The birds of eastern Ecuador: the foothills and lower subtropics. [5 Audio CDs with booklet]. John V. Moore Nature Recordings, San José, California.

MAYER, S. 2006. Birds of Peru, Bolivia and Paraguay. Sounds and photographs. Vers. 3.0. [CD-ROM]. Bird Song International, Westernieland, The Netherlands.

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Appendix A. Specimens examined

Museums cited are Carnegie Museum of Natural History, Pittsburg (CM), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN), Museo Ecuatoriano de Ciencias Naturales, Quito (MECN), Field Museum of Natural History, Chicago (FMNH), Colección Boliviana de Fauna, La Paz (CBF). Catalogue numbers are given in brackets.

Psiloscops flammeolus FMNH 12 mm, 3 ff [459505, 470498, 470499, 37663, 37664, 37665, 137726, 137727, 159294, 159295, 159296, 159297, 159298, 159299, 160795] (USA, Mexico, Guatemala)

Megascops (*Gymnoglaux*) *nudipes* FMNH 2 uns [37660, 37661] (Puerto Rico)

M. albogularis albogularis FMNH 5 mm, 10 ff, 2 uns [13709, 13710, 101070, 101071, 101640, 101987, 101988, 101989, 101990, 101991, 249560, 249561, 287979, 287980, 100449, 100450, 102528], MECN 1 m, 4 ff [8514, 772,7755, 6150, 7760] (Colombia, Ecuador); *meridensis* FMNH 1 m [100780] (Venezuela); *remotus* FMNH 2 mm, 1 f, 1 uns [296607, 296608, 296609, 433064] (Peru)

M. choliba luctisonus FMNH 8 mm, 8 ff, 1 uns [101072, 101073, 101292, 101293, 101294, 101643, 101644, 101645, 101790, 101791, 101792, 102444, 248553, 249558, 249559, 6981, 100321, 100322], ICN 13 mmff, 1 juv (Costa Rica, Colombia); *margaritae* FMNH 1 m, 2 ff [38806, 38807, 38808] (Venezuela); *duidae* FMNH 2 mm [318672, 318673] (Venezuela); *crucigerus* FMNH 26 mm, 19 ff, 9 uns, ICN 25 mmff (incl. 1 odd red morph), 3 juv, MECN 1 m, 1 f [770, 3994] (Colombia, Ecuador, Venezuela, Guyana, Brazil, Peru); *alticola* FMNH 1 m [111699] (Colombia)

M. clarkii FMNH 3 mm, 2 ff [372110, 6982, 73409, 73410, 73411] (Costa Rica)

M. trichopsis (aspersus, mesamericanus, trichopsis) FMNH 17 mmff (incl. 1 odd, small, red morph) [97578, 16234, 137851, 137852, 159408, 159410, 159411, 159412, 160834, 111318, 30392, 93611, 185946, 185947, 185948, 185949, 102793] (USA, Mexico, Guatemala, El Salvador)

M. cooperi lambi FMNH 1 f [15415] (Mexico)

M. c. cooperi FMNH 2 mm [111319,100320] (El Salvador, Costa Rica)

M. kennicottii (aikeni, bendirei, cardonensis, kennicottii, macfarlanei, xantusi) FMNH 92 mm, 103 ff, 5 uns (Canada, USA, Mexico)

M. asio (asio, floridanus, mccallii, hasbroucki, maxwelliae) FMNH 259 mm, 245 ff, 52 uns (Canada, USA)

M. g. guatemalae FMNH 1 m [119428] (Mexico)

M. centralis [Hekstra] FMNH 1 m [372109], ICN 1 f, 1 uns [28443, 31177], MECN 1m, 1 f [5994, 7062] (Colombia, Ecuador)

M. [*roraimae*] *pallidus* [Hekstra] FMNH 2 mm [91892, 91893], CM 1f [35307] (Venezuela)

M. [*roraimae*] *roraimae* FMNH 1f (odd grey morph) [339624] (Venezuela)

M. [*roraimae*] *napensis* FMNH 4 mm, 7 ff [311175, 320449, 320450, 311174, 320445, 299043, 283660, 299042, 299044, 102964, 296606], MECN 4 mm [7004, 7636, 8183, 7772] (Ecuador, Peru)

M. sanctaecatarinae FMNH 1 m [69278] (Brazil)

M. gilesi CM 1 f [70857], ICN 1 m [38833] (Colombia).

M. roboratus FMNH 1f [299447], MECN 2 mm [771, 6301] (Peru)

M. atricapilla FMNH 1 f [356565] (Brazil)

M. watsonii watsonii FMNH 8 mm, 3ff [260181, 247144, 277679, 247145, 101573, 102527, 248551, 101084, 248550, 102979, 248552], ICN 2 mm, 4 uns [8831, 8834, 13014, 22633, 32007, 32886], MECN 3 mm, 1 f [776, 6958, 6960, 6959] (Peru, Ecuador, Colombia, Surinam, Brazil); *usta* FMNH 6mm, 3 ff [208178,208177,297889,320434,285081,397727,293363,299045,297888] (Peru)

M. petersoni FMNH 1 m [317314], ICN 1 m [34377], MECN 6 mm, 1 f [774, 775, 7866, 7867, 7762, 7752, 8179] (Colombia, Ecuador, Peru)

M. marshalli FMNH 1 m [324127] (Peru)

M. hoyi FMNH 3 mm, 1 f [255979,101867,255973,293618], ZMUC 1 m [91964] (Bolivia, Argentina)

M. [*ingens*] *colombianus* FMNH 1 m, 3 ff [102108,101642,101641,101992], MECN 1 m [uncatalogued] (Colombia, Ecuador)

M. ingens ingens FMNH 8 mm, 4 ff [364257, 311176, 320263, 320452, 310522, 287769, 287768, 283661, 320451, 102965, 292534, 292533], MECN 5 mm, 1 uns [773, 2498, 7288, 7773, 7758, 7763] (Colombia, Ecuador, Peru); *venezuelanus* FMNH 1 f [317315], ICN 1 m [34994] (Colombia, Venezuela)

Appendix B. A short characterization of vocalizations of New World screech-owls

Number following taxon name indicates number of recordings examined. Catalogue numbers are given in brackets. Sequence as in Table 1.

Psiloscops flammeolus (9) [Hardy1989, XC5835, 13605, 61475, 61476, 61477, 61478, 61480, 67056]: Song a single short (0.3 s) soft hoot at 420-550 Hz repeated every 2-3 s, sometimes preceded or followed immediately by a weaker, shorter and lower-pitched note or double note. Calls include single hoots up to 0.5 s long at varying pitch. Begging calls of juvenile include a wheezy, 0.6 s long note around 900 Hz repeated at 3 s intervals and wheezy calls with some chirping parts at 2.5 kHz.

Margarobyas (*Gymnoglaux*) *lawrencii* (6) [Hardy1989a,b, ML133237, 133244, 133244, 133244]: Song (Fig. 1AE) 2 s long, of 15-17 notes at 200-400 Hz (the lowest pitched New World screech-owl), an accentuated hoot followed by an accelerating trill falling in pitch and volume. The introductory hoot may be repeated two to several times at 2 s intervals before ending in song. Presumed female may answer with a chirpy series of 5-10 notes at 2-3 kHz at a pace of 2.4/s. Calls include a short single hoot, a double hoot with higher pitched second note, a descending series of four hoots, and guttural clicks given in alarm near the nest. The young give high-pitched wheezy notes.

Megascops (*Gymnoglaux*) *nudipes* (*nudipes*) (19) [Hardy1989a,b, ML4491, 4491, 4491, 4491, 4490, 4490, 129734, 51002, 51000, 43413, 53822, 53870, 53821, XC33683 33690, 33705, 46630]: Song (Fig. 1AD) a *ca.* 3 s long series of notes at *ca.* 500 Hz given at a pace of 14-15/s, waxing in volume and pitch at first, waning at end, often given in duet, sometimes synchronously, the female song *ca.* 2 s long and nearly an octave higher. Both sexes occasionally give shorter songs. Also (Bond 1971) a loud *coo-coo* like *Athene cunicularia,* and on occasion a hoarse croaking. A handheld female (ML53870) clicked bill and gave squeaky *qeeooee* calls at 1.2 kHz in alarm.

Megascops albogularis (*meridensis, macabrus, albogularis, remotus*) (52) [Krabbe & Nilsson 2003,1,2,3,4,5, Hardy 1989, Paul Coopmans unpublished (OTUHUBPC), ML148800, 17357, 21782, 21911, 21912, 21930, 21958, 26947, 4448, 4449, 59601, 59602, 59603, 59604, 59605, 59606, 59607, 59608, 59609, 59610, 92153, 92288, 92615, XC11308, 12930, , 5238, 153649, 153650, 153674, 153676, 179, 2021, 2022, 23228, 23231, 23626, 25416, 29389, 32385, 35960, 38917, 39524, 47114, 8015, 8359]: Song (Fig. 1B) usually in duets repeated every 5-6 s, a series of 5-15 hoots at a slightly slowing pace of 8-7/s, on average 1.4 s long in male, 1.5 s in female, but sometimes longest in male. The pitch in 27 duets averaged 708 Hz in males, 959 Hz in females, first 1-2 notes slightly lower, the rest descending gradually and slightly (male) or more distinctly (female), volume fairly constant except first and last note often weaker. Each duet frequently composed of three songs, the first and last by the male. At high excitement, such as after playback (aggressive song, Fig. 5B), song may start with a rapid, sometimes ascending series and the following notes may be doubled and the song be longer, up to 4 s long or more, in female sometimes given as a long descending series. Rarely heard calls include a single-noted, 0.6 s long, rising and falling wail and a sharp, 0.4 s long, 6-noted series of descending screeches. Vocalizations do not seem to vary geographically except for a north-south cline in pitch, decreasing in males, increasing in females.

Megascops koepckeae (*koepckeae* 12, *hockingi* 30, including several unpublished recordings cited in Fjeldså *et al.* (2012)): Song, often given in duet, in female slightly shorter and slower paced and 5-40% higher pitched than male, consists of a rising and falling series of "hysterical" shrill notes that slows down, especially towards the end, with accentuated second- or third-last note. Song in northern part of range (nominate form; Fig. 1T) *ca.* 2 s long, pace beginning at *ca.* 7.6/s, pitch *ca.* 968 Hz. Song in southern part of range (*hockingi*) longer, *ca.* 2.6 s, pace averaging slower, beginning at *ca.* 6.9/s, and pitch decidedly higher, *ca.* 1,246 Hz. In response to playback, songs of both sexes become slightly higher pitched and longer (pitch of an excited male thus much like a relaxed female), or sometimes hoarser. After repeated playback (female only?) may give a high-pitched long series of notes, up to 1,700 Hz and 9 s long. Early in bouts of male song (during "warming up"), songs may be given with notes at constant pace and without any accentuation. The aggressive song (Fig. 5G) is similar, but slightly longer and faster paced, and is much like aggressive song of *M. choliba* and to some degree *M. hoyi,* with a slower pace than songs of *M. roboratus, M. centralis* and *M. napensis.* Other vocalizations (Schulenberg *et al.* 2007) include a hiss (female only?) given in response to male song.

Megascops choliba (*luctisonus, margaritae, crucigerus, decussatus, choliba, uruguaiensis, suturutus, wetmorei*) (164): Song (Fig. 1S) 0.8-1.6 s long, a trill at constant pace of 11-17/s and pitch at 489-968 Hz, followed by 1-2, hesitant, loud, and higher pitched 568-968 Hz notes. The trill often begins with a weak lower note and then usually rises in volume and slightly (8%) in pitch. Bouts of song are often started with a series of trills ("aggressive songs", Fig. 5E) that rise and fall in pitch and volume and are very similar to aggressive songs of *M. koepckeae* and to some degree *M. hoyi*. At high excitement the trill may become harsh in quality, or may turn into typical song. Calls, particularly from agitated birds, include a hoarse screech, single or rapid series of barks, and a variety of cackles (high-pitched in females) that rise quickly and fall slowly, often at slowing pace. Song is fairly similar throughout the large range of the species, but with a southward cline of increasing tendency to two or three rather than one accentuated note at end. In 3 of 125 recordings a song is answered by a similar, but higher-pitched and slightly shorter song. These were believed by the recordists to be duets.

Megascops clarkii (19) [Hardy 1989a,b, ML25772, 25772, 53966, 53966, 53964, 165317, 53965, 144076, 144076, 25811, 54200, 54200, 165332, 165332, 165332, 165332, 108875, 108875, 108875, XC17880, 31765, 36717, 65665, 70710, 70711, 70711, 70712]: Song (Fig. 1W) a 1.3-2.5 s long series of 3-6 notes, 600-750 Hz, pace 2.3/s, the middle one to three notes louder and slightly longer. After playback longer and (at least sometimes) lower pitched (ML144076). Female similar, but higher pitched (640-896 Hz). Also gives a 600-740 Hz, 7-15 s long, syncopated ("Morse-code") series of repeated groups of one, two, or three notes, if three, then two together followed by one (Fig. 2F), in female over six half-notes higher pitched. Call a 0.6-1.0 s long, up-down mew at 930-1,030 Hz, repeated at 3-5 s intervals.

Megascops trichopsis (*aspersus* 22 [Boesman 2006b, Hardy1989a,b, ML109097, 112621, 140238, 18709, 197168, 197829, 197954, 203271, 25146, 25175, 28330, 28331, 40588, 61818, 61822, XC17925, 21757, 21758, 58066], *trichopsis* 4 [ML169956, 17197, XC5251, 67057], *mesamericanus* 2 [ML185721, 185728]): Song (Fig. 1X) 0.8-2.6 s long, a series of 5-19 notes, first, and especially last one or two notes slightly hesitant, general pace 3-10/s, songs repeated for minutes with 2-5 s pauses. Pitch 490-750 Hz and level or slightly rising and falling. The volume fades in and out, variably peaking in the first, mid, or last third

of the song. Also gives a syncopated ("Morse-code") series of 2 short, closely spaced notes, usually followed by 2-5 longer notes (Fig. 2G). Both song types, but mostly the syncopated series may be given in duet, the female higher pitched. Duetting is not common. Other calls include a long rapid series of barks, a trill similar to the female alarm of *Glaucidium gnoma* but shorter (0.7-0.8 s) and at lower and more even pitch (1.3 kHz), and (Marks *et al.* 1999) *chang,* and *shee.*

Megascops barbarus (8) [Hardy1989a,b, ML53444, 55409, 127263, XC259237, 259243, 259244]: Song (Fig. 1J) a fast trill at an even pace of 20-22/s, in presumed male 5-9 s long, at 700-850 Hz, volume and pitch increasing through the first half or two thirds of the song, then decreasing slightly, more abruptly at end. During 'warming-up' trills may be shorter (2-3 s). Song of presumed female shorter (3.1-3.2 s) and higher pitched (1,130-1,150 Hz), variably harsh, introduced by a series of 5-10, single-noted, ventriloquial, high-pitched *hu* calls (1,090-1,300 Hz) 2-3 s apart.

Megascops sanctaecatarinae (33 (44 individuals)): Song (Fig. 1Q) 3-5 s long, of 30-75 notes at 600-800 Hz, growing slowly to a steady crescendo in pitch and volume, dropping more abruptly at the end. The pace, 7-18/s may be steady or slow down over the last few notes but more typically accelerates during the first fifth to half of the song, then decelerates, especially at the end. After playback may shift to a lower-pitched, slightly harsh song (Fig. 5J). The female may give a slightly higher-pitched and shorter version of this song, but all or last few notes with harsh quality, producing a rattled sound. During frequently heard duets, the female gives a harsh song, while the male gives a harsh or a normal song or one intermediate in quality. Harsh songs may be interspersed with single harsh notes, or may be given at double pace ('rattle') or be intermediate, with some notes tending to split into two. Calls include a harsh hissing *rao.*

Megascops roboratus (*pacificus* 29 [Coopmans *et al.* 2004,1,2,3, unpublished recording ©Ginkgo, Hardy1989a,b, Krabbe & Nilsson 2003,1,2,3, XC5627, 8298, 8660, 9822, 17435, 33939, 41265, 41266, 41268, 41276, 41277, 41288, 41289, 45851, 50639, ML13275, 43188, 49430, 130459, 80179], *roboratus* 11 [Hardy1989, XC262874, 276176, 251095, 251096, 251097, 25109, 36580, 36580, 36581, 36585]): Song (Fig. 1U) fairly quiet, a trill rising and falling in volume and pitch, pace constant at 19-24/s, pitch at peak ca. 514 Hz (*pacificus*). The second harmonic is usually prominent and sometimes louder than first. Often, especially during territorial disputes, a third harmonic is added to give a more growling quality. Early in bouts of song the trill may be long (3-4 s) and loudest in the middle ("relaxed song") but more often (shortsong or aggressive song, Fig. 2L) it is shorter (1.5-2.5 s) and peaks three quarters into the trill, and may be higher pitched (to 715 Hz). Frequently duets. Female song similar but higher pitched, at *ca.* 800 (760-856) Hz. There might be a slight vocal difference between the two subspecies, the pitch seemingly highest (surprisingly) in the larger nominate form (average 582 Hz). Calls include a wail at *ca.* 650 Hz, a bark at *ca.* 750 Hz, and, by both sexes, a slightly rising series of 3-5 notes.

Megascops gilesi (30) [6 unpublished cuts by A. Quevedo, 9 by D. Bradley, 1 by NKK, XC235875, 235877, 235878, 235880, 235881, 25823, 25824, 295369, 56768, 56769, 56826, 59670, 59671, 59672]: Song (Figs. 4 and 1R) a 2-3 s long trill, pace about 10/s,, rising in pitch and volume through first 1-8 evenly spaced notes, then increasing to full volume at a more rapid, decelerating pace, at end dropping abruptly in pitch and volume. The pitch averages 874 Hz in presumed males, 1,172 Hz (n=4) in

presumed females. Aggressive song (Figs. 4 and 5F), apparently also given by both sexes, similar, but longer, fast part sometimes harsh in quality.

Megascops watsonii (*watsonii* 112, *usta* 63): Song (Fig. 1D, and 1E) usually 10-20 s long, occasionally up to 45 s or more, a rapidly repeated hoot, sometimes at low volume for prolonged periods before becoming loud, and dying out at the end. The pace increases slightly during the song. Pace at end of song in Guianas and Venezuela 9-11/s, in N Ecuador and N Peru 5-6/s, in S Ecuador 3-4/s (all *watsonii*), and in *usta* 2-3/s. At higher excitement may change suddenly in pitch and volume and notes may become more explosive. Shortsong 3-5 s long in *watsonii* (Fig. 2B), 4-6 s in *usta* (Fig. 2A), composed of 12-26 notes, at first slow-paced and increasing in pitch and volume, then suddenly more rapid, but slowing, and usually fading in volume and descending slightly in pitch. Higher pitched short songs might be given by females. Calls, apparently by both sexes, include a short whoa given singly or in series of up to 7 notes, and a single wail.

Megascops atricapilla (19) [Hardy 1989, ML113381, 127829, 127911, 127980, 128031, XC25671, 25674, 26129, 46306, 55841, 60831, 60832, 60833, 60834, 68691, 7159, 75524, 75526]: Song (Fig. 1C) an 11 (5 -25) s long trill at 700-850 Hz, increasing in volume over first half, usually beginning with a slight rise and fall in pitch and with more rapid pace before becoming steady or rising and falling gradually and slightly in pitch at constant pace of 10-15/s. A single recording (Hardy 1989) is decidedly higher pitched (1082 Hz). A duetting bird, possibly a female (XC46306), similar, 5.5 s long, at 870 Hz. Shortsong (Fig. 2C) 2.6-3.4 s long, of 15-25 notes at 800-850 Hz, in the middle changing pace abruptly, from 4-7/s to a faster, decelerating pace beginning at 7-12/s, volume peaking in middle or three quarters into song. At higher excitement (aggressive song, Fig. 5D) may become harsh in quality and irregular in pitch (slow notes lower pitched). Calls include a rising and falling series of 7 shrill notes, each 0.4 s long and composed of a mew at 1,150-1,400 Hz and terminated with a chuckle at 900-1,000 Hz, first overtone nearly as loud as the fundamental.

Megascops guatemalae (*hastatus, guatemalae*) (9) [Hardy 1989a, ML4484, 4485, 4486, 86661, 55408, XC3320, 5938, 5939]: Song (Fig. 1K) a 6-11 s (during territorial disputes to 20 s) long trill given at a constant pace (13-16/s) and pitch (520-660 Hz), volume rising during first half or three quarters, then constant and ending abruptly. Shortsong or aggressive song (Fig. 2H) a 3-4 s long trill increasing in pace to mid song, much like a 'bouncy-ball' song of *M. kennicottii,* but then suddenly shifts to a slower and constant pace; the volume rises through first half to three quarters of the trill and then drops to the end; the pitch rises and falls similarly, but only slightly.

Megascops vermiculatus (10) [ML72676, 76629, 184212, 184177, 184093, 184068, 211131, XC190370, 190369, 65705]: Song (Fig. 1L) very similar to that of *M. guatemalae*, but faster and higher pitched, a 5-8 s long trill of *ca.* 100 notes given at constant pace of 16-20/s. Pitch 630-760 Hz, usually falling (or rising and falling) over the first 2-3 s, then constant or falling slightly until the end. Volume increases gradually through first 1-2/3 of song, then decreases. The female may answer with shorter, higher trill (Stiles *et al.* 1989). Calls include a sibilant wail at 850 Hz and a series of wails at 1,150 Hz. A continuous bubbling series of irregularly paced double notes (*ca.* 5/s) at 600 Hz (ML184068) may be an alarm song. Begging call of juvenile a *whoa* at 700 Hz.

Megascops centralis [Hekstra] (32) [Hardy 1989c, O. Jahn unpublished (OTUVEROJ), Jahn *et al.* 2008, ML108861, 30236, 60254, 83181, 83182, 83183, 83184, XC104127, 104129, 10835, 12952, 163780, 238456, 238457, 251091, 254508, 261632, 261633, 275238, 276167, 293699, 3232, 47011, 60677, 71402, 80928, 80930, 9861, 9902]: Song (Fig. 1M) a short (0.8-1.6 s) trill with a rapid pace of 20-27/s. At start the pitch is level or rises some, and then it falls distinctly, loudest pitch at *ca.* 850 Hz (687-920). The volume fades in and out, loudest when the pitch has just begun to fall. Song during territorial disputes sometimes initiated with a few stuttering notes. No definite calls recorded, but a 1.2 s long wail at *ca.* 1,100 Hz may be of this species.

Megascops [*roraimae*] *pallidus* [Hekstra] (14 from the coastal Mts [ML59327, 59327, 59328, 59326, 59331, 59325, 59322, 59323, 59324, 59333, 59334, 59336, 59339, XC66072], 1 from Perijá Mts [ML59341], Venezuela): Song (Fig. 1N) a trill 4.2 (2.8-5.6) s long, pace 13-14/s, slightly accelerating at first, volume increasing to middle or near end of song, then fading out. Much like *M. roraimae*, but pitch higher*, ca.* 950 Hz, and rising some at first, then falling distinctly. During territorial disputes sometimes lower pitched (ML59336 third song) and with drawn-out beginning. A single recording (ML59333) known to be of a female is like male song, but slightly longer (5.8 s) and much higher pitched than any recording of other forms of *M.* [*roraimae*] (1,385 Hz). A wail at 1,300 Hz (ML59328) may be a call of this form.

Megascops [*roraimae*] *napensis* (17) [Hardy1989, Krabbe & Nilsson 2003,2, ML132737, 135276, 138716, XC20791, 23482, 238472, 238473, 238475, 238476, 238476, 262873, 364158, 4161, 7060, 80927]: Song (Fig. 1P) much like that of *M. roraimae,* a trill 5 (3.6-6.7) s long, pace 11-17/s, pitch *ca.* 850 Hz (760-960), usually rising at first, dropping slightly at end or slightly and evenly throughout, sometimes also suddenly dropping a quartertone in mid song. The volume fades in slowly at start and fades out more quickly at end, or trill ends abruptly with little or no fade out. One recording (ML132737) from Beni, Bolivia, 1,000 m is much longer (15-20 s), slower paced (8-9/s), and fairly constant in pitch (900 Hz) and may represent a different taxon. Aggressive song (Fig. 8A), highest pitched in female, is of similar length and pace, but quality harsh, pitch rising and falling distinctly (5-6 half-notes), and volume fading in slowly and out more rapidly. Gives a mewing call when aggravated (female only?) (Schulenberg *et al.* 2007).

Megascops [*r.*] *roraimae* (11) [ML131078, 134218, 134289, 134292, 134293, 134487, 134865, 134873, XC66386, 6915, 75050]: Song (Fig. 1O) 5 s long (3.5-6.4s), a trill at a pace of 12-15/s, pitch *ca.* 900 (760-975 Hz, once 1,050 Hz, female?), usually rising and falling slightly at start, then level or falling very slightly until the end, or sometimes suddenly dropping a quartertone in mid song. The volume usually fades in and out quickly at start and end. No calls recorded.

Megascops cooperi cooperi 14 [Boesman 2006b, Hardy1989, ML103264, 105978, 105985, 39175, 4479, XC11706, 333, 61150, 61151, 9716, 9717, 9718], *lambi* 4 [Hardy1989, ML4478, XC31494, 31495]): Song of *cooperi* (Fig. 1Z), repeated up to several minutes with 6-10 s pauses, a 1.5-2.5 s long trill at rising and falling pitch, pace gradually decelerating, beginning at 7-12/s, ending at 4-6/s. The song is often preceded by a short chuckle. The volume usually increases for the first third or half of song, then remains constant or drops at end. The fundamental pitch (1st harmonic) averages 400-500 Hz in male

and 500-750 Hz in female, but first overtone (2nd harmonic) is often loudest. During duets songs are more irregular, shorter or longer (up to 4 s) and sometimes harsher in quality, the last 3-6 notes occasionally (at least in female) given at a slightly faster pace, almost with "bouncing ball" effect. Song of *lambi* (Fig. 1Y) (recordings of 2 pairs) similar, but higher pitched (male 713, female 1034 Hz) and with constant or only slightly slowing pace, lacking the rapid introduction; during duets, both sexes may give harsher song with accelerated end. Calls (*cooperi*) include a single harsh note.

Megascops seductus (7) [Boesman 2006b, Hardy1989a,b, ML4468, 4469, 4470, XC181486]: Song (Fig. 1AA) a 1.6-1.8 s long trill, pace accelerating evenly from 4 to 12 or 13/s (as a bouncing ball), volume constant for the first third or two thirds of song (first note sometimes slightly weaker), then fading gradually, pitch falling gradually from 800 to 650 Hz from start to end. During duet, song may be given with a harsher quality and with an introductory note that may be tripled, almost as a whinny, at least in female, and with the trill beginning at faster pace. After playback may give a series similar to the song, but twice as long, beginning at faster pace (8/s), or, after repeated playback, a much longer (8-9 s) series, either level (male only?) or rising and falling in pitch and volume (female only?), at an even pace of 13/s. Calls include a rising and falling, 0.6 s long mew at *ca.* 800 Hz.

Megascops kennicottii (*aikeni, xantusi, bendirei, kennicottii, yumanensis, macfarlanei, suttoni, vinaceus*) (166): Song (Fig. 1AB) given by male alone or during duets, a 1.1-2.9 s long ('bouncing ball') trill of 6 to 24 notes (most in *xantusi*), pace 2-9/s at start, 11-15/s at end, accelerating gradually or with fairly sudden change to fast pace three quarters into song. Female song similar, 3-10 half notes higher pitched. The pitch for both sexes ranges from 430 to 985 Hz. Pitch and volume usually grow for first half or three quarters of song, then drop some, most at end. At high excitement during duets (Fig. 2E), the female or sometimes both sexes will shift to another song type, a double trill, second trill longest, loudest and highest pitched, each trill usually with lower first one and last one or two notes, the male giving a shorter version (1.2-1.7 s) than the female (2.1-2.8 s). Also (Campbell 1994) a soft *cr-r-oo-oo-oo-oo* given as a greeting call and a sharp bark given when excited.

Megascops asio (*asio, maxwelliae, maccallii*) (24): Song (Fig. 1AC) a low-pitched trill that may be given in duet, the female 3 half notes higher, 2.4-3.2 s long, usually with a sudden increase in pace half or three quarters through the song, from 10-15 to 14-17/s. The volume fades in at first, and out slightly faster at end, and often rises suddenly with the change from slow to fast pace. Pitch *ca.* 750 Hz, usually dropping slightly at end, sometimes rising and falling in the fast-paced part of the song. Occasionally the quality may be harsh. Possibly an alarm type song is lower pitched (600 Hz), longer (4.4 s) with constant pace (16/s). Shortsong ("whinny") (Fig. 2D) sometimes in duet (female nearly six half notes higher), 0.8-1.5 s long of a sustained note that first rises steeply then falls gradually as it quavers 10-13 times per s, pitch ranging up to 1,450 Hz just after start of song, down to 550 at end. Aggressive song ("alarm trill") (Fig. 5C) at 600 Hz, 2.4-5 s long, pace constant, 16-22/s, dropping slightly in pitch at end, volume gradually increasing through first third, and then decreasing. Gives various grating rasping hisses near the nest. See also Cavanagh, & Ritchison (1987) and Ritchison *et al.* (1988).

Megascops petersoni (27) [P. Greenfield unpublished (OTUHUB01), ML18048, 39962, XC13436, 16419, 16684, 16685, 238478, 238479, 238480, 238481, 238482, 238483, 274951, 276173, 276174, 364159,

36615, 39348, 39349, 45217, 45219, 57503-4, 62543, 7637, 81866, 85950]: Natural song (Fig. 1F) pitched around 540-640 Hz and 5-10 s long, volume and pitch typically increasing over the first third of song and decreasing over the last third, often ending abruptly. The pace is 5-7/s, constant or slowing slightly. After playback, song may be shorter (3 s), or higher pitched (to 700 Hz). Aggressive song (Fig. 5K) faster paced, 8-11/s, and may either remain fast, slow abruptly with a change in pitch and also be harsh in quality, or slow more gradually while notes become longer. Apparently does not duet. Calls include a 6 s long series of seven short notes at 700-800 Hz, and (male only?) a single mew at 750-850 Hz. Whining notes (female only?) have also been reported (Schulenberg *et al.* 2007).

Megascops marshalli (19 (11 individuals)) [Mayer 2006 (4 cuts), ML120966, 148255, 18287, XC105088, 105089, 105090, 3429, 92487, 92495, 92496, 92497, 92498, 92499, 92500, 92518]: Song *ca.* 3.5-8 s long, a trill at fairly constant pace of *ca.* 7-8/s (Pasco) (Fig. 1G) or 5-6/s (Puno, La Paz, Cochabamba) (Fig. 1H), volume increasing to mid song, then fading out, in two individuals recorded in La Paz, Bolivia only fading out near end or ending abruptly (due to playback?). The pitch is at *ca.* 650-700 Hz, usually rising about a half note or less until mid-song then falling again, but sometimes fairly constant throughout. Aggressive song (Fig. 5H) is of similar quality, a 1.8 s long rapid trill with pace slowing at end (from 13 to 8/s). Also, perhaps a shortsong (Fig. 2K) may give single notes followed by a rapid (8/s) series of notes falling in volume and 3 half notes in pitch. Female may give a soft cooing (M.B. Robbins unpublished data).

Megascops hoyi (18) [Hardy 1989, ML129337, 129354, 116110, 116111, XC3500, 3624, 3626, 3632, 4380, 16181, 19532, 19533, 29128, 29129, 29130, 48743, 51901]: Song (Fig. 1I) about 9 s long, after playback up to 17 s, a series of over 100 notes, given at constant pace of 11/s, pitch about 670 Hz, beginning softly, then swelling, tapering off at end. Shortsong or aggressive song (Fig. 5I) 2-3 s long, pitch *ca.* 725 Hz, pace *ca.* 9/s but slightly slower at start, growing in volume then fading gradually or more abruptly at end. At higher excitement may become harsh in quality and irregular in pitch. Shortsong of presumed female during duets similar, but higher pitched (950 Hz). Call recorded from presumed female during duet, a single-noted, and 0.5 s long mew around 1,350 Hz.

Megascops [*ingens*] *colombianus* (14) [Jahn *et al.* 2008,5, ML135782, 139095, 43399, XC12988, 238459, 238460, 238461, 261634, 264432, 264433, 3847, 80934, 80939]: Vocalizations very similar to *M. ingens*. Song (Fig. 1B) a 7-21 s long trill, pace *ca.* 5/s, pitch *ca.* 800 Hz, rising at start, then level for most of the song, sometimes dropping some at end, volume increasing first half to three quarters of song, then constant or fading out some, often ending fairly abruptly. Shortsong (Fig. 2I) 3-5 s long, a slow series of 2-5 notes at a pace of 2.8-3.4/s (n=6), rising in volume and pitch, followed by a fast, slightly slowing, loud or fading series of 7-17 notes, usually falling in pitch, but sometimes ending fairly abruptly, occasionally given at fairly even pitch or during rarely heard duets with barking, harsh quality. Calls include a wail at *ca.* 1,300 Hz (female?).

Megascops ingens (*venezuelanus, ingens*) (62) [ML101831, 101840, 103993, 103997, 110613, 110793, 120892, 120919, 121711, 126917, 138188, 138654, 13878, 140524, 179784, 36028, 36035, 59611, 59612, 59613, 59614, 59615, 59616, 59617, 59618, 59619, 59620, 59621, 79062, 85083, 92657, 92658, 92847, XC1853, 22992, 238462, 238463, 238464, 238465, 238466, 238467, 238468, 238469, 238470,

257035, 276170, 276171, 3178, 32111, 3367, 3559, 36469, 39766, 4203, 6172, 63824, 65297, 7141, 81865, 85449, 85951]: Song (Fig. 1A) a 10-13 s long trill, slowly and evenly increasing in pitch and volume, at end fading, at times somewhat abruptly, notes given at fairly constant pace of 5-8/s, slowest in Colombia and Ecuador, increasing through Peru to Bolivia. Pitch averages 750-800 Hz in most of range (n=26), 900 Hz in SE Peru and Bolivia (n=19). Rarely duets, female 3-4 half notes higher pitched. Shortsong (Fig. 2J) 3-4 s long, composed of a slow series of 4-7 notes (in Ecuador at a pace of 2.6-3.2/s, n=5) increasing in volume, followed by a fast paced, slightly slowing, loud (or loud then fading) series of 9-15 notes; the number of notes in the shortsong increases s-wards, from *ca.* 12 in Táchira, Venezuela to *ca.* 22 in Bolivia. The pitch averages 820 Hz in Táchira, 780 Hz in Ecuador and northern Peru, 900 Hz in southern Peru and Bolivia. Call much like *M. petersoni,* but higher pitched, a 0.6-1.1 s long mew at 950-1,080 (male?) or 1,300 Hz (female?). Recently, a single uncatalogued ML recording from the coastal mountains of Venezuela (Aragua) became available (see Discussion and Table 1). The female shortsong is very short and rather fast-paced, and the song very fast-paced and rather high-pitched.