Vocal divergence and new species in the Philippine Hawk Owl *Ninox philippensis* complex

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We show, based on morphology and especially vocalisations, that the Philippine Hawk Owl *Ninox philippensis* requires treatment as seven allopatric species and at least one additional subspecies. Morphological distinctions between three groups of taxa are striking, and although taxa within one major group are relatively similar in plumage they vary rather consistently in size and proportions. It has not been possible until now to resolve the species limits in this complex due mainly to the lack of sound recordings of key taxa, a problem now rectified. Vocalisations differ significantly between all seven species, the limits of which are incongruent with all previous taxonomies. Taxa from Mindoro (*mindorensis*), Mindanao (*spilocephala*), Camiguin Sur (named herein), and the Sulu Islands (*reyi*) exhibit especially great vocal differences from all other taxa along with smaller but consistent differences in plumage and morphometrics. Although specimens have been in museum collections for many years, two of these species and one subspecies have heretofore remained undescribed, and we formally name these taxa for science. The recommended species-level treatment and English names of the *N. philippensis* complex are: Luzon Hawk Owl *N. philippensis*; Mindanao Hawk Owl *N. spilocephala*; Mindoro Hawk Owl *N. mindorensis*; Sulu Hawk Owl *Ninox reyi*; Romblon Hawk Owl *N. spilonota*; Camiguin Hawk Owl new species; and Cebu Hawk Owl new species.

INTRODUCTION

During the heyday of ornithological discovery in the Philippines (approximately 1850–1910), as many as seven species were recognised in the islands' endemic hawk owl complex (e.g. McGregor 1909-1910). Since 1945, however, it has been treated as a single polytypic species, Philippine Hawk Owl *Ninox philippensis* (Delacour & Mayr 1945), recently considered to contain eight subspecies (Dickinson 2003). These subspecies group into three distinctive plumage types: one with all-streaked underparts and plain crown (*philippensis*, *proxima*, *ticaoensis* and *centralis* of Luzon and many other islands); one with mottled or barred breast, streaked lower underparts, and spotted crown (*spilocephala* of Mindanao); and one with barred to nearly plain underparts (the 'unstreaked' group: *mindorensis* of Mindoro, *spilonota* of several small islands, and *reyi* of the Sulu Islands) (Collar & Rasmussen 1998; for main islands and distribution of taxa see Figure 1). This last group of three described races is highly disjunct, and the distribution of the race *spilonota* as currently defined in particular is biogeographically peculiar because the Cebu population is surrounded by members of the *philippensis* group, and the Camiguin Sur population is from a small island off northern Mindanao and well away from other taxa in *spilonota*.

Within the unstreaked group there are marked differences in size and proportions, as well as more subtle distinctions in plumage. However, it has not been possible to resolve relationships between these racial groups based on morphology owing to intra-island plumage variation and, for some taxa, small sample size. Sound recordings until recently were available only for taxa from a few islands, and most were incomplete and of poor quality. Given the complexity of the vocal repertoire in this group, the small sample of recordings previously available precluded further analysis of species limits. The sample was, however, adequate to establish that Mindoro *mindorensis* differs profoundly in vocalisations from Luzon nominotypical *philippensis*, prompting the separation of Mindoro Hawk Owl *N. mindorensis* (König *et al*. 1999). However, this cursory treatment left other unstreaked forms united with *N. philippensis*, although in the absence of acoustic data it seemed plausible that they could separate out as a single species for which the name with priority was *Ninox reyi* (Collar & Rasmussen 1998). Within this species, however, there were clearly multiple undescribed taxa based on morphology, although the populations on Cebu and Tablas were feared possibly extinct (Collar & Rasmussen 1998, Collar *et al*. 1999).

There the matter unsatisfactorily rested, in the absence of adequate or sometimes any vocal evidence from all the taxa, including the four insular populations comprising the form *spilonota*. However, recent fieldwork has resulted in nearly complete sampling with extensive, high-quality recordings of the vocal repertoire of the key island populations of *Ninox philippensis sensu lato*. Taxa that differ in plumage also differ in vocalisations, so much so that their treatment as conspecific in a group with innate vocalisations such as owls is untenable. Surprisingly, however, some unstreaked taxa that resemble each other closely are also divergent in vocalisations, and cannot be maintained as taxa below the species level. We propose here that seven vocally well-defined allopatric species are involved in the Philippine Hawk Owl complex, of which two are new species (described herein) with distinctly divergent vocalisations. Because individuals from four islands now known to pertain to four different taxa were included in the description of *N. spilonota*, we designate a lectotype and hence type locality for this ambiguous name. We also describe an additional island taxon here that shows only moderately distinctive vocalisations and morphology, and which we consider better treated at the subspecies level.

METHODS

Acoustic analyses

We analysed sound recordings of all taxa known or suspected to be critical to an analysis of species-level taxonomy of the Philippine Hawk Owl (*sensu lato*). The majority of recordings we used were made by ROH during trips specifically targeting islands that hold morphologically distinctive *Ninox* taxa for which we previously lacked or had poor representation of vocalisations. Several other recordings were made by co-authors and others, and most of these are available in full on AVoCet (avocet.zoology.msu.edu, AV). (To access individual numbered recordings on AVoCet, use e.g. http://avocet.zoology.msu.edu/recordings/14561.) A few recordings were assembled from other sound archives (Macaulay Library, http://macaulaylibrary.org/, ML; National Sound Archive, London, http://www.bl.uk/nsa, NSA; xeno-canto, http://www.xeno-canto.org/, XC).

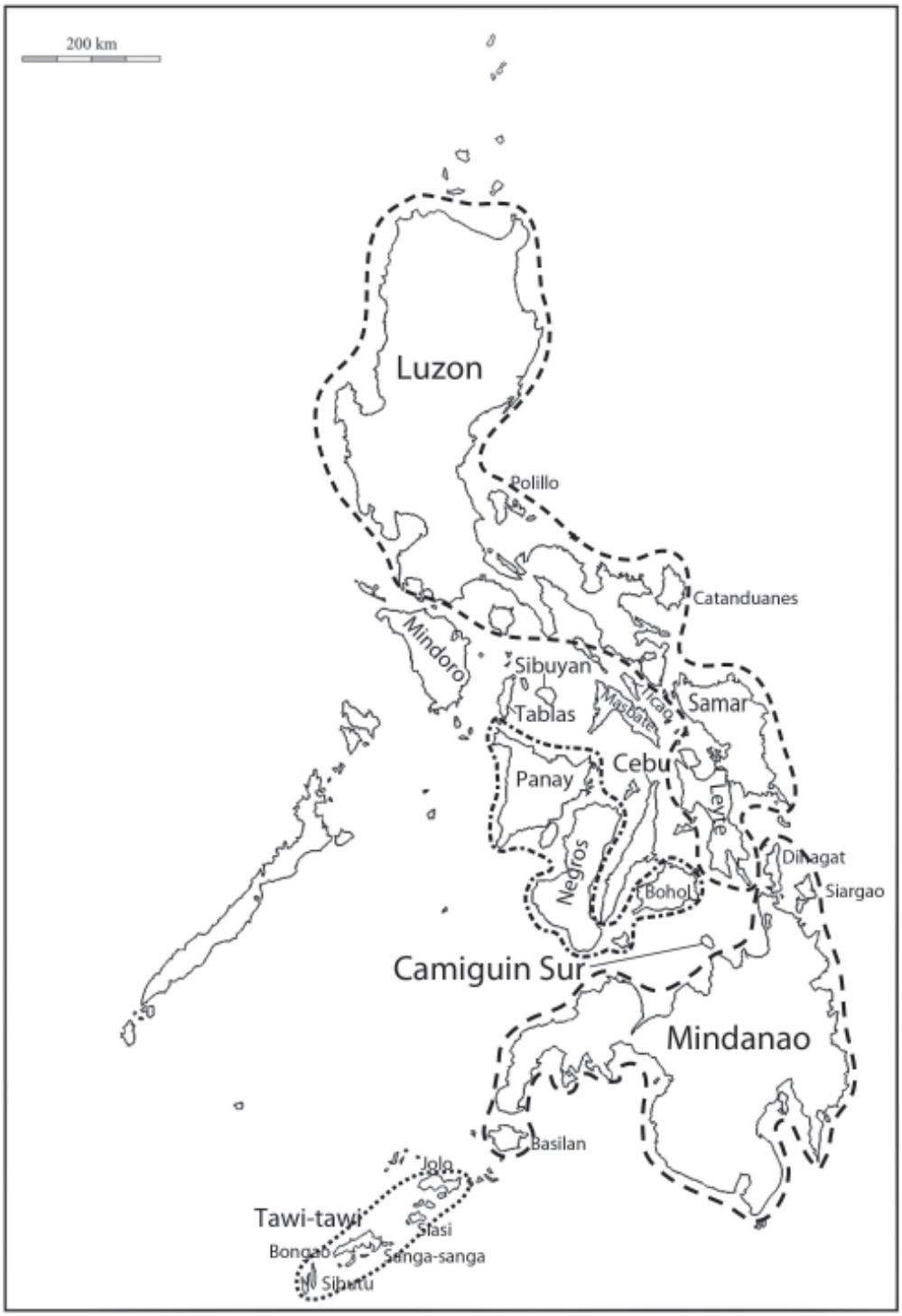


Figure 1. Map of the known distribution of taxa of the Philippine Hawk Owl *Ninox philippensis* (*sensu lato*). Taxa and groups are Philippine Hawk Owl *Ninox philippensis* (*sensu stricto*) nominotypical *philippensis* group, of Luzon, Samar, Leyte, and small surrounding smaller islands; *centralis*, of Panay, Negros, Bohol, Siquijor (unlabelled small island between southern Negros and Bohol) and surrounding smaller islands; *proxima*, of Masbate; and *ticaoensis*, of Ticao; Mindanao Hawk Owl *N. spilocephala*: Mindanao and smaller surrounding islands except Camiguin Sur; Sulu Hawk Owl *N. reyi*: larger islands of Sulu and Tawi Tawi provinces; Camiguin Hawk Owl new species; Mindoro Hawk Owl *N. mindorensis*: Mindoro; Romblon Hawk Owl *N. spilonota*: Tablas and Sibuyan islands, Romblon Province; Cebu Hawk Owl new species.

By island (listed alphabetically), the number of recordings used is listed below, with recordist (initials used for co-authors) and (where applicable) abbreviation for sound archive where recording is held (for recordings by FRL first uploaded to AVoCet but also on xeno-canto, only the AV number is provided here): Biliran, 1 (RSK: ML#38695); Bohol, 2, (F. Verbelen [FV]: AV#8971–8972); Camiguin Sur, 19 (ROH: 13554–13557, AV#13559, AV#13567, AV#13575, AV#13577, AV#13593, AV#13598, AV#13602, AV#13605, AV#13609, AV#13614–13615, AV#13618, AV#13622; LMP: AV#13552–13553); Cebu, 13 (DNSA: XC#79316, AV#11320–11322; LMP: AV#10469–10470, AV#10805; PGCJ: AV#10804, AV#10806; BD: AV#12609–12612); Leyte, 2 (RSK: ML#38671, ML#38674); Luzon, 34 (PCR: AV#2168–2174; FV: AV#8970; FRL: XC#30725–30728; ROH: AV#12420, AV#12450–12454, AV#13551, AV#13648–13554; D. Edwards: XC#35238; P. Noakes: XC#40819, 40821, XC#40823, XC#40825–40826, XC#40828; G. Wagner: XC#23116); Masbate, 1 (LMP: AV#14563); Mindanao, 23 (FRL: AV#8056–8057, AV#8088, AV#8111–8113; ROH: AV#12455–12467; S. Harrap: NSA Wildlife ref. #132605–132606; B. F. King: NSA Wildlife ref. #54931); Mindoro, 6 (ROH: AV#11507, AV#13655; P. Morris: NSA#65216 W1CDR0000309 BD24, NSA#W1CDR0000307 BD1, NSA#W1CDR0000309 BD21, NSA#W1CDR0000309 BD24); Negros, 5 (FRL: AV#10664, AV#10699–10701, AV#10800–10801); Sibuyan, 8 (ROH: AV#13637, AV#13641–13647); Siquijor, 2 (DNSA: AV#14564–14565); Tablas, 15 (DNSA: AV#10803, AV#11323–11324; BD: AV#11325; ROH: AV#11508–11515, AV#12606–12608); Tawi Tawi, 17 (DNSA: AV#10802; ROH AV#14566–14581). Recordings are highly variable in length, quality and documentation, but we have extensive,

good to excellent material from all the above islands except Biliran, Leyte and Masbate; material for Siquijor is rather inadequate.

Sounds were studied, measured and graphed in Raven Pro 1.3 (Raven 2012). Measurements taken (where possible) for each recording were maximum number of notes/strophe, maximum and minimum note length per recording; minimum inter-note spacing; maximum and minimum fundamental frequencies (one each per recording), maximum frequency difference within a single note and between strophes; and maximum note bandwidth at a single point. Principal components analyses (PCAs) were done in SYSTAT 13 (SYSTAT 2012) using these measurements except for maximum note bandwidth (excluded because hisses were difficult to measure precisely). After an initial run that showed that all recordings from islands populated by nominotypical *philippensis* or *centralis* grouped together, these groups were combined in the analysis of all groups. Also, because inclusion of atypical song sequences resulted in much greater variance in early analyses, only songs considered to be typical were included in further analyses. Thus, typical songs of all taxon groups (with *philippensis* and *centralis* combined) were used in the main PCA. However, because of the great vocal differences of Camiguin Sur, *reyi*, *mindorensis* and *spilocephala* from each other and all other ('core') groups (those with non-extreme song characteristics), the core groups (*philippensis* plus *centralis*, Tablas *spilonota*, Sibuyan *spilonota*, and Cebu) were not well resolved. Therefore, a subsequent PCA was undertaken using just the core groups, and for this recordings from the different islands were graphed separately.

For taxa (all but Camiguin Sur, *reyi*, *mindorensis* and *spilocephala*) that typically give lengthy series starting with single notes and building after a few minutes to a multi-note climax, only one of each of the above measurements was taken. It should be noted that many recordings and analyses of this type of strophe are likely to be incomplete, as the recordist may have begun recording only after hearing the bird, or the initial notes may be very soft and cannot be picked up by a recording. For taxa that typically give a series of short strophes each of which climaxes individually, each of the above measurements was taken for each good-quality strophe. It must also be borne in mind that many recordings made by a single recordist on a single night, or even possibly over multiple nights at the same locality, are likely to be of the same individual owls, leading to some potential pseudoreplication in our analyses (a problem we could not avoid but which is unlikely to bear on the outcome). Moreover, many recordings will have been made after playback, and this has not typically been documented by the recordist. Many recordings are duetted between pair members, while others appear to be counter-singing between birds in neighbouring territories; it is not easy on present knowledge to distinguish these. However, the ability to do so is not critical to our analyses, as the differences between taxa here considered species are so marked. We chose the above measurements because they are little affected by such problems. However, given the great variation among taxa in vocalisations, few if any song characteristics are shared among all taxa, so choosing appropriate measurements was challenging.

In the vocal transcriptions presented in Results, notation follows Rasmussen & Anderton (2005). Lower case signifies relatively low volume compared to SMALL CAPITALS then to FULL CAPITALS, which is much louder than lower case. The forward slash / signifies a rise in frequency and the backslash \ a frequency drop between elements. Run-together syllables signify no pause, an apostrophe (') extremely short breaks (e.g. in a trill), a hyphen (-) indicates a very short pause, a comma a mid-length break, and an open underscore _ a still longer pause. Ellipsis (...) is used to indicate the continuation of a vocalisation as previously transcribed, not to indicate pauses or fading out.

Sonagrams (spectrograms) prepared in Raven Pro 3.1 are presented for each taxon along with the corresponding waveform (oscillogram, in Raven units, which are unique to Raven software and hence not indicated on the Y axis), which shows power *versus* time, and hence allows visualisation of rhythm better than the sonagram alone. The corresponding spectrum plots power *versus* frequency, hence allowing visualisation of power peaks. The area of the sonagram highlighted in grey is that on which the spectrum is constructed.

Mensural analyses

We studied specimens of *Ninox philippensis* (*sensu lato*) held (in alphabetical order of acronym) in the American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, Tring, UK (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Cincinnati Museum of Natural History, Cincinnati (CMNH); Delaware Museum of Natural History, Greenville (DMNH); Field Museum of Natural History, Chicago (FMNH); Institut Royal des Sciences Naturelles, Brussels (IRSNB); Museum of Comparative Zoology, Boston (MCZ); Bell Museum of Natural History, Minneapolis (MMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Naturalis, Leiden (NCB); Philippine National Museum, Manila (PNM); Royal Ontario Museum, Toronto (ROM); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SFN); Staatliches Museum für Tierkunde, Dresden (SMTD); Staatliches Naturhistorisches Museum, Braunschweig (SNHM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Washington, DC (USNM); Peabody Museum, Yale University, New Haven (YPM); and Museum für Naturkunde, Berlin (ZMB). All specimens of this complex available at the above museums during our visits were studied, and most of them photographed and measured. In total, 177 specimens of the following established taxa were included in mensural analyses: 40 *philippensis* (5 Catanduanes, 5 Leyte, 2 Lubang, 26 Luzon, 1 Marinduque, 1 Polillo); 4 *proxima* (Masbate); 1 *ticaoensis* (Ticao); 36 *centralis* (2 Bohol, 27 Negros, 7 Siquijor); 16 *spilonota* (1 Tablas, 12 Sibuyan, 1 Cebu, 2 Camiguin Sur); 43 *spilocephala* (10 Basilan, 31 Mindanao, 2 Siargao); 25 *mindorensis* (Mindoro); and 12 *reyi* (1 Siasi, 9 Tawi Tawi [8 main island, 1 Bongao], 1 Sibutu, 1 Sulu). Not all measurements were available for all specimens (see below), hence numbers in certain analyses are smaller.

For specimens from most of the above collections, PCR measured a wide array of characters, and then after preliminary analyses chose the following as most useful: culmen from cere; upper mandible height at cere; auriculars maximum length (including filamentous extensions); tail length (measured by inserting ruler between two central rectrices); tarsus length; unfeathered (bristled) portion of tarsus; length of middle claw; wing length (flattened), and maximum width of dark and light bands on central portion of one central rectrix. Broken, heavily worn or incompletely grown feathers were not measured. NJC also measured culmen from skull for specimens from some museums. Univariate statistics and PCAs were run in SYSTAT 12. Sexes were combined for analyses, because most specimens of key taxa were not labelled as to sex. Although it would be possible to examine sexual size dimorphism in the better-represented taxa, and it may be significant, we leave that to future studies and do not consider the interpretation of our results to hinge on the matter.

Colour and pattern analyses

Plumage characters were documented at major collections with holdings of multiple key taxa. Photographs were taken of nearly all specimens examined and were used for later comparisons, but only as a general guide and mnemonic.

In addition to traditional assessment of species limits under the Biological Species Concept, we apply the system proposed by Tobias

et al. (2010) to measure the degree of phenotypic differentiation between taxa. In this system an exceptional difference (a radically different coloration, pattern or vocalisation) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or vocalisation) 3, a medium character (clear difference reflected, e.g., by a distinct hue rather than different colour) 2, and a minor character (weak difference, e.g. a change in shade) 1; a threshold score of 7 is required for taxa to be considered separate species, but only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2 is treated as minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character may be counted (Tobias *et al*. 2010). However, we observe that, in the case of nightbirds where vocalisations are crucial for species recognition, this system may not give enough weight to single key vocalisations and may give too much weight to plumage characteristics, which in owls often show relatively high degrees of individual variability.

Because the original diagnoses of heretofore named taxa placed in *spilonota* and *reyi* were invariably based on inadequate material, often involving single specimens and without reference to the most similar taxa, and because *spilonota* proves to contain four different taxa, we provide new diagnoses based (where possible) on larger samples. We are constrained by the paucity of specimens from Cebu, Tablas and Camiguin Sur, but good photographs now exist of these and other taxa. Photographs often show features no longer existing or never apparent in specimens, so we rely strongly on them to supplement specimen material in these diagnoses. We have few data on immatures, so these are not included in the diagnoses. In general immatures are less well-marked and fluffier than adults.

Owing to the generally small sample sizes and poor labelling of key taxa we were unable to analyse whether sexual dichromatism exists in these owls. However, we suspect that it may, as in some other *Ninox* owls. In photographs that show what is almost certainly a singing pair for each 'unstreaked' taxon, one individual has noticeable whitish streaking on the lower underparts, while the other is plain or barred below. Whether this is a simple sexual difference is, however, unclear, given that the white-streaked birds are in a minority among specimens. Further fieldwork is needed to clarify this issue.

RESULTS

Acoustic analyses

The following are vocal comparisons by taxon or island (see Methods for conventions used). For simplicity, we focus on a few individual recordings and then summarise variations. Overall song patterns and quality are summarised in Table 1, and univariate statistics for measurements of songs in Table 2.

N. p. philippensis (Luzon)

(AV#2168, AV#2171, Luzon).—The non-duetted song of *N. p. philippensis* (Table 1, Figure 2a) begins quietly, with single, short, rather sharp *cuk* notes (each note comprising a short upslurred then rapidly downslurred element, upper frequency limits c.0.9 kHz, frequency range c.0.6 kHz, note duration c.0.11 s) spaced c.2–2.5 s apart (at first slightly more than 2 s, then gradually accelerating slightly to just under 2 s apart). The series becomes louder, and after several single notes the bird then begins to add in soft, lower-pitched (0.66 kHz) preliminary notes, single or doubled, as in *boo,/CUK* and *bu-bu,/CUK*. There are several iterations of this, in which the first element becomes progressively louder, but the main subsequent element is still greatly accented, more strident and yapping, and much broader-band, and the couplets or triplets are separated by pauses of just over 1 s. This then changes into a four-element repeating motif in which the first note is mellow and low as before, and the subsequent three notes are broader-band, louder and sharper, the last slightly softer and tailing off in pitch. In the four-element motif, the second and third notes are farther apart than the third and fourth, hence the rhythm seems halting; in addition the third note is primarily upturned, while the second and third are primarily downturned, and the third note has a slightly lower maximum frequency. The four-note strophes are c.2 s in duration. The series becomes slightly higher-pitched overall towards the end, just exceeding 1 kHz, and the pauses between motifs are c.2 s long. The series lasts 75–95 s and ends suddenly, or becomes intermittent, with longer pauses (up to 8 s) between motifs, e.g.: *cuk_cuk_CUK_CUK_CUK_boo,/CUK_boo,/CUK_bu-bu,/CUK_bu-bu,/CUK_boo,/CUK,CRIK-COOk_boo,/CUK,CRIK-COOk … boo,/CUK,CRIK-COOk…*

Shorter versions and song fragments (SOM 1a.12453) may be given, as may long series of single note types, and excited duets with multiple birds joining in that may appear to have more than four notes per motif (SOM 1b.13551).

N. p. centralis (Bohol, Negros)

(AV#8971, Bohol; AV#10699–10700, Negros).—Song on both islands is similar to that of *N. p. philippensis*. A Bohol recording (SOM 1c.8972) of a duet is similar to duets of *N. p. philippensis*. AV#10699, from Negros, has much longer (c.5 s) pauses between initial notes than similar song strophes studied for nominotypical *philippensis*, while those of AV#10700 (SOM 1d–e.10700) are c.2 s, as in nominotypical *philippensis*, and the strophes last 120–168 s.

N. p. centralis (Siquijor)

Song (SOM 1f.112a) is similar to that of nominotypical *philippensis*, except that it is hoarser and the later strophes contain more (sometimes several more) notes, especially in duets, which have many short hoarse notes (SOM 1g.99).

N. p. spilocephala (Mindanao)

The long song of *spilocephala* (Table 1, Figure 2d, continued as SOM 1j) differs dramatically from all others in consisting of very slow, long, mellow, dove-like notes, singly or in couplets. The strophe starts simple and becomes somewhat more complex, but slows down considerably. The song (e.g. AV#12462) starts with single mellow, slightly slurred *hUUUu* notes that eventually become longer, with the addition of an initial very soft low segment to the note (now *oo/HUUUu*), then adding a short final element after a short pause (now *oo/HUUUu*, *Huu*). The fundamental frequency is 0.37–0.53 kHz, with only the main (*hUUUu*) note reaching the highest frequencies. All notes are slightly slurred and convex (especially the main note) and have the same quality. Early notes in a strophe are 0.4 s and the last couplets are 1.3 kHz. The notes have one strong harmonic. Pauses between early notes are c.2.5 s and between later couplets c.4 s. The entire strophe may last over 190 s. A transcription is: *hUUUu_hUUUu_ … hUUUu_hUUUu_oo/HUUUu_oo/HUUUu_ … oo/HUUUu_oo/HUUUu_oo/HUUUu, Huu_oo/HUUUu, Huu_oo/HUUUu__oo/HUUUu, Huu__ … oo/HUUUu, Huu__oo/HUUUu, Huu__oo/HUUUu, Huu …*

Duets (e.g. AV#14263, Figure 2e) may be much shorter, e.g. 11 s, with the primary singer starting with just a few single notes that quickly lead into *oo/HUUUu*, *Huu* couplets like those described above. The duetting bird sporadically adds in slightly but noticeably higher couplets in which the first, stressed note is mostly upslurred and the second, slightly softer note is mostly downslurred, transliterated as *WAUUUU, WUUUu*. The lowest frequency of this couplet is 0.36 and the highest c.0.73. The couplet length is 1.2 s. The single noticeable harmonic produced by this second individual reaches c.1.3 kHz. These same *WAUUUU, WUUUu* couplets may be given with another distant bird giving this same type instead of the *oo/HUUUu*,

Table 1. Qualitative summary characteristics of songs of each taxon and/or island population of *Ninox philippensis* (*sensu lato*) studied.

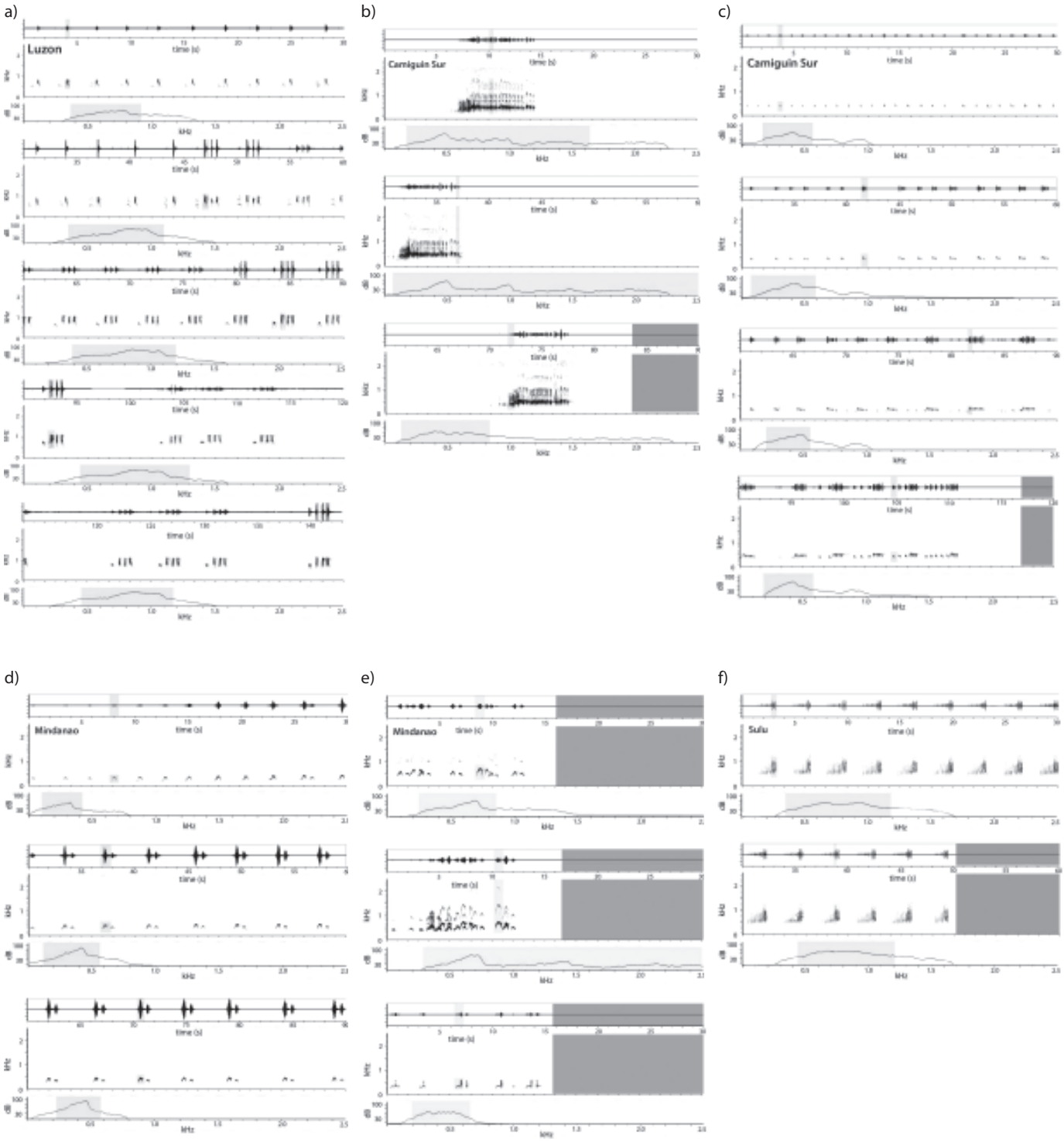
Song characteristic								
Taxon	**Gives long steady series**	**Increasing note number?**	**Maximum note number/ strophe**	**Note pace accelerating (+), even (0), or decreasing (–) within strophes**	**Pause length even (0) or decreasing (–) between strophes**	**1st note of multi-note strophe lowest (–), highest (+), intermediate (i) or no difference (0)**	**1st note of multi-note strophe softest (–), loudest (+),or no difference (0)**	**All notes of multi-note strophe nearly the same length (0) or different (in order from shortest to longest)**
philippensis	Yes	Yes	4	+	0 to –	–	–	3, 2, 4, 1
spilocephala	Yes	Yes	2	+	–	+	+	2, 1
reyi	Yes	Yes	c.20	0	Irregular	0 or –	0 or –	0
Camiguin Sur	Occasionally	Occasionally	22	–	Irregular	–	–	Shortest at start, longest at end
mindorensis	Yes	Occasionally	1 main note, several grace notes	+	0	0	–	1–4, 5
Cebu	Yes	Yes	5 (strophes run-together)	+	0	–	–	1,4,3,2 (frequent; also other patterns)
Tablas *spilonota*	Yes	Yes	4–5 (strophes well separated)	+	–	+	–	1,3,2 (usually)
Sibuyan *spilonota*	Yes	Yes	5 (strophes well separated)	+	–	i	–	2, 1–4, 3

Song characteristic						
Taxon	**Most notes short (|), long (—), or intermediate (0)**	**Most notes near-vertical (|) vs horizontal (–) or slurred (~)**	**Harsh notes present**	**Harmonics prominent**	**Quality of main notes**	**Degree of variability (from 0 to 5, 5 highest)**
philippensis	0	|	As response to playback, not in songs	No	Emphatic but mellow	3
spilocephala	—		Rarely	No	Mellow, clear	2
reyi	|	|	No	No	Hollow, clucking, percussive	2
Camiguin Sur	|	| to ~	Yes, at start of each strophe	Yes	Rapid hooting barks, like mid-sized dog	2
mindorensis	—	~ (slightly)	Yes	No	Thin whistles, peeps, metallic screeches	3
Cebu	0	~ (greatly)	Yes	No	Shrill, slightly croaking	5
Tablas *spilonota*	0	~ to |	Yes	In some note types	Sweet whistles to hoarse plaintive barks	3
Sibuyan *spilonota*	0	~	Slight	Yes	Robust, musical, slightly hoarse, mournful	4

Table 2. Univariate summary statistics [mean±SD (range, *n*)] of measurements of song characteristics of each taxon and/or island population of *Ninox philippensis* (*sensu lato*).

Song characteristics								
Taxon/island	**Max. notes/strophe**	**Max. inter-strophe frequency difference (Hz)**	**Max. frequency in song series (Hz)**	**Min. frequency in song series (Hz)**	**Max. note length (s)**	**Min. note l (s)**	**Min. internote interval (s)**	**Delta frequency within note (Hz)**
philippensis (including *centralis*, *proxima*, *ticaoensis*)	4.2±0.8 (2–7, 34)	303.4±66.3 (177.0–420, 34)	1116.6±90.2 (864–1364, 55)	585.7±90.7 (386–787, 54)	0.3±0.1 (0.1–0.7, 52)	0.1±0.1 (0.0–0.3, 52)	0.6±2.1 (0.1–15.0, 52)	479.0±148.6 (107–1068, 52)
spilocephala	2±0 (2, 11)	82.1±31.8 (55.0–166.0, 11)	693.4±92.2 (549.0–854.0, 22)	402.1±45.5 (325.0–508.0, 22)	0.5±0.1 (0.3–0.6, 22)	0.2±0.04 (0.1–0.3, 22)	0.3±0.1 (0.1–0.4, 20)	271.0±69.7 (178–417, 22)
reyi	18.8±8.1 (6–40, 15)	284.6±85.2 (155–420, 15)	1048.8±90.7 (834–1179, 18)	427.8±64.6 (331–528, 18)	0.1±0.1 (0.0–0.3, 18)	0.01±0.0 (0.01–0.02, 18)	0.08±0.04 (0.01–0.14, 18)	529.0±165.4 (376–1006, 18)
mindorensis	2.4±1.5 (1–5, 11)	365.7±68.7 (221–443, 8)	2364.6±182.7 (2070–2716, 12)	1451.0±208.6 (1282–1840, 12)	0.8±0.2 (0.5–1.0, 12)	0.2±0.1 (0.1–0.6, 12)	0.6±0.5 (0.2–1.6, 12)	648.8±183.5 (351–909, 12)
Camiguin Sur	22.8±5.6 (8–39, 34)	122.9±50.2 (39–221, 34)	631.8±36.8 (568–699, 47)	327.6±53.0 (241–434, 47)	0.2±0.4 (0.1–0.3, 44)	0.1±0.1 (0.0–0.3, 43)	0.3±0.9 (0.1–5.4, 34)	284.0±78.3 (96.4–445.1, 43)
Sibuyan	3.8±0.4 (3–4, 7)	110.6±28.9 (66–133, 7)	1559.6±238.4 (1280–1911, 9)	783.4±95.6 (584–935, 9)	0.3±0.1 (0.2–0.5, 9)	0.1±0.1 (0.1–0.3, 8)	0.8±1.7 (0.2–5.0, 8)	639.2±236.5 (239–935, 8)
Tablas	3.6±0.5 (3–4, 11)	201.4±80.6 (111–332, 11)	1784.1±192.2 (1484–2213, 18)	923.6±190.5 (569–1545, 18)	0.4±0.1 (0.2–0.6, 18)	0.2±0.1 (0.1–0.4, 18)	2.3±3.2 (0.1–8.5, 18)	681.2±229.6 (306–1121, 18)
Cebu	4±0.8 (3–5, 10)	181.5±83.9 (99–376, 10)	1466.7±96.7 (1220–1545, 12)	829.2±73.0 (711–996, 12)	0.4±0.2 (0.2–0.9, 12)	0.1±0.0 (0.03–0.1, 12)	0.2±0.1 (0.05–0.3, 12)	505.6±130.5 (254–734, 12)

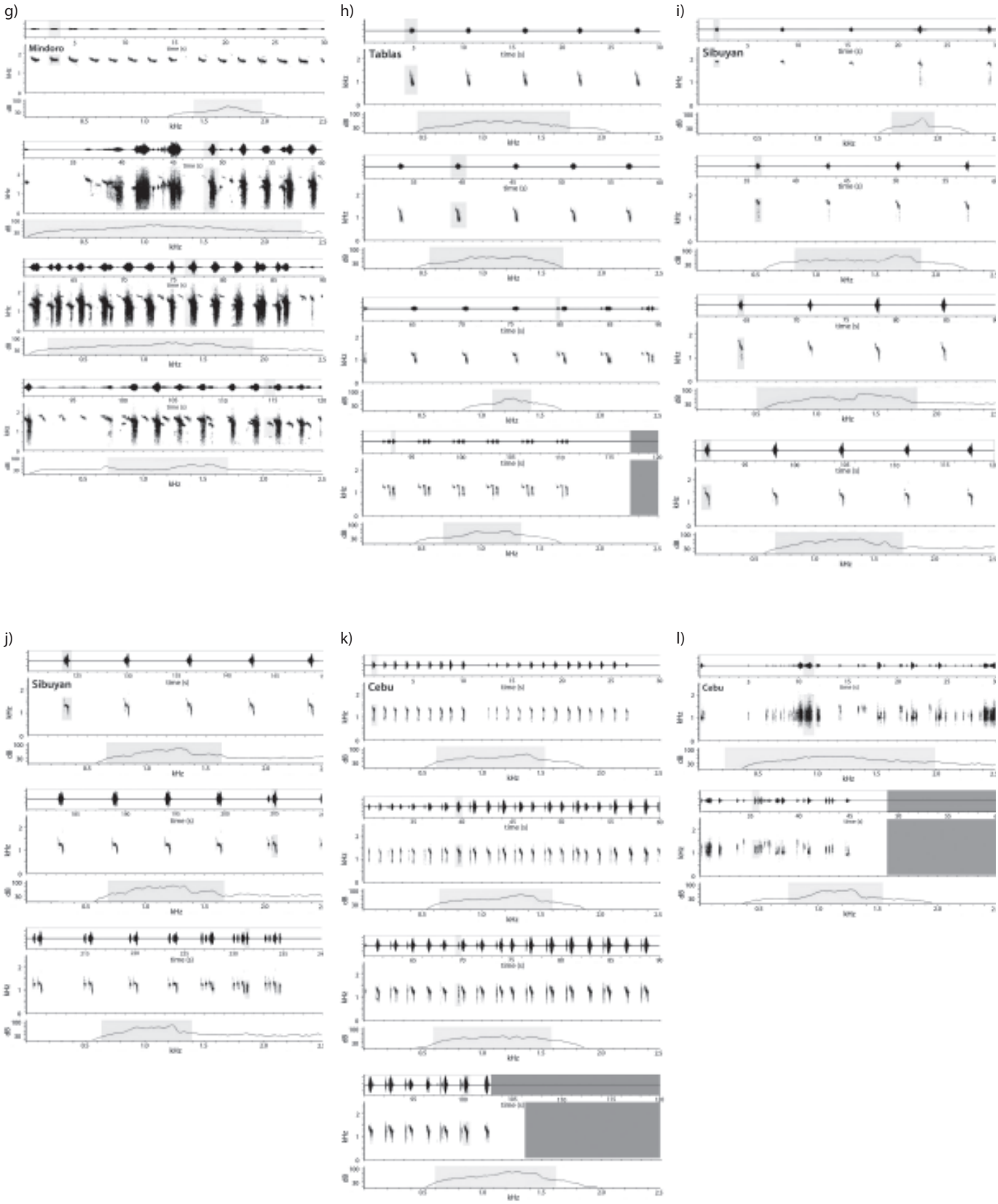
Figure 2. Typical songs of each major taxon in the Philippine Hawk Owl *Ninox philippensis* (*sensu lato*) complex. For each song, the first row is the waveform, the second is the sonagram, and the third is the spectrum: (a): Philippine Hawk Owl *N. p. philippensis*, probably non-duetted long song of single bird singing in different directions, hence the variations in amplitude late in the song series; AV#2171, PCR, Luzon; (b): Camiguin Hawk Owl *Ninox* new species 1, duetted series of short strophes; AV#13554, ROH, Camiguin Sur; (c): Camiguin Hawk Owl *Ninox* new species 1, long song by single bird; AV#13622 ROH, Camiguin Sur; (d): Mindanao Hawk Owl *N. spilocephala*, long song by single bird (series continued in SOM 1j); NSA Wildlife ref. #132605, S. Harrap, Mindanao; (e): Mindanao Hawk Owl *N. spilocephala*, short duetted songs; AV#12461, ROH, Mindanao; (f): Sulu Hawk Owl *N. reyi*, series of short probably non-duetted strophes; AV#14577, ROH, Tawi Tawi; (g): Mindoro Hawk Owl, first half of long duet (continued in SOM 1l); AV#11507, ROH, Mindoro; (h): long song of single Romblon Hawk Owl *Ninox spilonota* new subspecies; AV#10803, DNSA, Tablas; (i–j): long song of single Romblon Hawk Owl *N. spilonota* on Sibuyan, AV#13637, ROH, Sibuyan; (k): long song of single Cebu Hawk Owl *Ninox* new species 2, AV#12612, BD, Cebu; (l): duetted song of Cebu Hawk Owl *Ninox* new species 2; AV#10805, LMP, Cebu.



Huu couplets, or the latter type may grade into the former type (e.g. AV#8088). Other versions include (AV#8056) a series of long dove-like notes ending in a stressed barking upslur, a version in which the first note of each couplet is more accented and staccato (AV#8111), or single short gruff notes. None of the vocalisations of *spilocephala* closely resembles those of any other taxon in the group, although there is some resemblance to the much shorter, sharper, two-note portion of the long song of *philippensis*.

N. p. mindorensis (Mindoro)

The song (Table 1, Figure 2g, continued in SOM 1l) is distinctly high-pitched, and composed of long series of thin, slightly descending squealed whistles *fiiiiew* (each c.0.8 s long) separated by pauses of c.1 s, then gradually changing into descending squealed whistles that become hoarse raspy downslurred screeches, e.g. *fiiikshrew*, the whistle-screeches often preceded by several very short high-sounding tittering toots, 0.1–0.3 s. The screeches and toots



are duetted, both birds often chiming in simultaneously giving both note types, which may overlap closely. Whistled notes may rise slightly at the start before falling again, and others may be entirely screeched. Duetted song may also consist of much longer series almost entirely of long whistled notes, some of them strongly frequency-modulated (SOM 1m–n).

The song of *mindorensis* bears no resemblance to those of *philippensis*, *spilocephala*, *reyi* or Camiguin Sur birds. It somewhat resembles songs of Tablas, Cebu and Sibuyan birds (as noted by Allen [2006], except that no recordings were then available for Sibuyan) in being composed of thin whistles and hoarser rasps, but it is very different in frequency and structure, especially in its much longer-drawn whistles and screeches, the near-constant frequencies of the long whistled notes, presence of high tittering toots, much harsher screeches, and lack of rhythmic repetition of lower notes.

N. p. spilonota (Tablas and Sibuyan)

The song of Tablas birds (Table 1, Figure 2h.10803) consists of long slow series of single short, steeply falling wistful whiny whistles *\FYEW* separated by pauses of several seconds, and later in a strophe often changing into a hoarse version *\FYURSH*, then into two-note and finally three- to (occasionally) four-note versions, e.g. *(tut-)TUT-TIY\IEW-hut* near the end. Hoarser note-types have a few widely spaced harmonics (SOM 1o). The maximum fundamental frequency is 2 kHz, and that only at the start of strongly downslurred notes, while most of the notes are 1–1.7 kHz.

Song in Sibuyan (Table 1, Figs. 2i–j.13637) is similar to that in Tablas, but sounds slightly more croaking and is even slower, with many introductory notes nearly level, barely downslurred, and with strong harmonics. The later notes in a strophe are typically clearly four-noted, and each note is more similar to the others except the longer, stressed, downslurred third note, e.g. *TOOT, TOOT, TIY\IEW, TOOT*.

N. p. spilonota (Cebu)

In Cebu, song (Table 1, Figure 2k) is highly variable in rhythm and note type, although in quality notes are of two main types, gruff staccato chucks and plaintive short downslurs, and (less often) metallic treefrog-like upslurred abrupt *bwick!* notes (several of which may be given in quick succession), low clear abrupt *duit!* bell-tones (sometimes quickly doubled), and hoarse white-noise screeches lasting c.0.6 s (Figure 2l, SOM 1q–r). Overall, compared to Tablas and Sibuyan birds, to which it is most similar, the song in Cebu is much faster (but relatively low-pitched, with notes mostly below 1.5 kHz and even down to 0.8 kHz) and lacks the long pauses between notes within a strophe so characteristic of these other taxa. Non-duetted strophes are long series of short */KYEUr* notes (separated by pauses of only c.0.9 s), running into *djuk*, */KYEUr_djuk*, */KYEUr...* series and even four-noted, more complex versions. Duets are medium-length strophes starting with several low soft *djuk* and *gwick* notes, running into *djuk, \KYEUr-gwuck, djuk, \KYEUr-gwuck*, etc., petering out after c.30 s and then starting again after a pause of a few seconds. Despite similarities to Tablas and Sibuyan birds the numerous notable and consistent differences exhibited by Cebu birds are very striking.

N. p. spilonota (Camiguin Sur)

(AV#13554, 13556–13557).—Duetted strophes (the common type available to us; Table 1, Figure 2b) differ greatly from those of all other known taxa. They begin with a few sporadic, very soft, very low (0.28 kHz) mid-length gruff notes, then turn into a low, very hoarse growl (e.g. 0.9 s) that quickly leads into rapid laughing mellow barks (0.36–0.69 kHz), recalling the chorused yapping of distant mid-sized dogs. The duetted notes typically overlap only partially, so the strophe sounds faster than is each individual's contribution, and the rhythm is non-uniform and jerky. Each note (excepting the growl) is strongly convex (highest part in the middle), and note shape is quite uniform; individual note length is 0.10–0.15 s, and pauses between note-pairs in the first two-thirds of the main strophe can be as long as 0.1 s, then to 0.2 s between this part (signified by *CUR* notes below) and the accented ending (*BOO* notes). Strophes (including introductory grace notes) last 5–11.5 s and are separated from each other by 7–18 s. Strophes slow down slightly near the end, with the final few notes slightly longer, louder and higher-pitched. There are often a few stray loud notes just following the well-defined strophe (SOM 1h.13557). Harmonics are prominent throughout the entire strophe following the growl, which has very broad bandwidth. The highest detectable harmonics on available recordings are at c.2.6 kHz, and there are up to five bands of harmonics above the fundamental frequency, although only the first harmonic (peaking at 1.25 kHz) is very prominent. Growls do not occur elsewhere within the strophe but the introductory growls are duetted, with the second individual joining in just after the first, or they may be shorter growls separated by short pauses, e.g.: *(huk__huk__)burrrrrrrr'CUR,CUR'r,CUR'ur,CUR,CUR'ur, CUR'ur,CUR'ur,CUR,CUR'r,CUR'r,CUR'r, CUR'ur,CUR'CUR-/BOO-BOOR-BU'U__(boo)*

Lone birds (Figure 2c, SOM 1i) also give shorter, low-intensity series of c.6 *boo* notes, the series lasting c.2 s, and the fourth note highest and stressed (e.g. AV#13602), or long series starting with single notes, then two, the first stressed, then three, first still stressed, then grading into strophes of up to seven low hoots followed by up to six higher stressed hoots, the first of the higher notes being most stressed, but all evenly spaced and of approximately the same length (e.g. AV#13622).

N. p. reyi (Tawi Tawi)

(AV#10802).—The song of this taxon is extraordinarily different in tone from those of all other known taxa (Table 1, Figure 2f), being a hollow wooden knocking, usually in duetted short strophes of a few to several seconds, separated from other such strophes by short pauses (1–2 s). Each strophe starts with several quiet low clucks at the rate of 1/0.1 s, then gets louder and higher-pitched, although each note has broad bandwidth; the strophe then slows down, often dropping in pitch and becoming more emphatic and higher again. The duet has a stuttering rhythm overall and there are no harmonics. Each note has broad bandwidth, the earlier ones c.45 kHz and the louder, higher ones c.80 kHz, and note length is c.0.01 s for earlier notes and 0.02 s for most others, some perhaps as long as 0.03 s, e.g. *kt-kt-kt-kt-kt-kt-kt-/KRT-KRT-KRT-KRT-KRT\-KLAK-KLAK-KLAK-KRT-KRT-KRT-KRT-KRT-KRT-/TOK!-TOK!*

Strophes may be much shorter, e.g. *kt-kt-kt-KRT-/TOK!-TOK!*, and successive strophes in a series can vary considerably in length (SOM 1k). They can also be more uniform, but still with slightly higher pitch and emphasis near the end, or they can be mostly uniform *kt-* series until a sudden speeding up and more clattery pattern at the end. This clattery effect occurs when clacking notes are introduced by a very short low grace note that increases the hollow knocking quality. The latter notes are evidently responsible for the taxon's local name of 'lukluk' (Allen 1998).

This form also gives a simple song of hollow triplets continued for long periods, e.g. *tluk'tluk'tluk_tluk'tluk'tluk ... tluk'tluk'tluk*. The motifs are c.0.7 s in duration and separated by usually 3–5 s (commonly 4.5 s), and consist of three principal elements, each preceded by a very short, lower, introductory element. The frequency range of the principal elements is about 0.5–0.9 kHz. This song type somewhat resembles in quality the typical song of Cinnabar Hawk Owl *Ninox ios* of Sulawesi, although that species's song is distinctly two-noted (King 2005, Hutchinson *et al.* 2006), and no songs comparable to the other types of *N. reyi* are known.

Very occasionally a longer, very hoarse growl or hoarse hoot is interspersed with the clacking notes.

Principal components analysis

The PCA using all groups (with *philippensis* and *centralis* combined; Table 3, Figure 3a) shows that Tawi Tawi *reyi*, Camiguin Sur *spilonota*, Mindanao *spilocephala* and Mindoro *mindorensis* are highly differentiated from each other and from 'core' groups (those with intermediate characteristics) on the vocal characteristics measured. Factor 1 contrasts mainly frequency and note length with number of notes, so factor scores for individuals of the high-pitched, long-noted *mindorensis* are uniformly higher on this axis than other groups, while those of the short-noted, low-pitched Camiguin Sur *spilonota* and (to a lesser extent) *reyi* are lowest on this axis. Factor 2 is more difficult to interpret, but it contrasts mainly frequency differences within and between notes with length of shortest notes and length of shortest internote pauses; on this axis *reyi* and Camiguin Sur *spilonota* separate out clearly from each other, and *spilocephala* separates out cleanly from the *philippensis* group.

The PCA using only core groups (with all island forms of *philippensis* and *centralis* graphed separately, and including Tablas *spilonota*, Sibuyan *spilonota* and Cebu *spilonota*; Table 3, Figure 3b) shows that all *philippensis/centralis* forms group together, with the two Siquijor recordings somewhat marginal, while Cebu, Tablas and Sibuyan are all fairly similar to each other on vocal measurements, Tablas birds being somewhat intermediate between those of Cebu and Sibuyan. Factor 1 is mainly a contrast between frequency and note length *versus* number of notes/strophe and degree of inter-strophe frequency change, while Factor 2 mainly contrasts number of notes, maximum note length, and frequency change within notes *versus* minimum note length and minimum pause length.

Table 3. Summary results of principal components analyses of measurements of vocal characteristics for all groups and core groups only (*philippensis* and *centralis*, Tablas *spilonota*, Sibuyan *spilonota*, and Cebu).

	All groups		Core groups		
Component loadings	**Factor 1**	**Factor 2**	**Factor 1**	**Factor 2**	**Factor 3**
Max. no. notes/strophe	–0.736	0.189	–0.468	0.461	–0.075
Max. note length/series	0.772	–0.337	0.556	0.461	0.165
Min. note length/series	0.562	–0.629	0.169	–0.507	0.697
Min. inter-note spacing	0.470	–0.537	0.324	–0.598	0.168
Max. fundamental frequency/series	0.883	0.339	0.895	0.249	–0.020
Min. fundamental frequency/series	0.898	0.127	0.759	–0.058	–0.464
Max. intranote frequency difference	0.590	0.587	0.519	0.469	0.607
Max. inter-strophe frequency difference	0.416	0.589	–0.650	0.282	0.376
Variance explained	3.781	1.657	2.733	1.405	1.273
Percent of total variance explained	47.263	20.711	34.157	17.557	15.911

Summary of vocalisations

To summarise the main points of the vocal evidence reviewed above and in Tables 1 and 2, the Camiguin Sur population and *reyi* from Tawi Tawi give many more notes per strophe than do other forms. Tawi Tawi *reyi* is strikingly divergent from all others in giving almost exclusively very short percussive toneless notes in extremely rapid, rhythmic strophes. Camiguin Sur birds and, to a lesser extent, Mindanao *spilocephala* are much lower-pitched than other taxa, while Mindoro *mindorensis* is much higher-pitched than others. The song of Mindanao *spilocephala* is unique in several ways, including the stressed first note in the couplets, low number of notes per strophe, and consistently mellow tone. Songs of nominotypical *philippensis* and *centralis* are similar to each other; they are in the middle of the pitch range for the entire group, and differ from other taxa in the halting, regular rhythm of later notes, strongly convex note shape, without whistles and normally without growls, and mellow barking quality. Recordings from Siquijor appear to show rather more distinctive vocalisations, but further and higher-quality material is required before taxonomic conclusions can be drawn. While Cebu birds are similar in frequency range and number of notes to Tablas and Sibuyan *spilonota*, their songs have several peculiarities including the rapid, continuous series, varied unmatched note types, and often erratic delivery. Tablas and Sibuyan *spilonota*, while by no means identical vocally, do share most characteristics, and on present data appear to represent distinctive races. The other taxa summarised here all show an extraordinary degree of vocal differentiation in a group of birds for which vocal communication is innate and of paramount importance in species recognition.

Mensural analyses

Our sample of *Ninox philippensis sensu lato*, with all island populations kept separate (Table 4), shows that, while we do not have adequate sample sizes of most taxa for significance testing, mensural differences between *philippensis*, *centralis*, *proxima* and *ticaoensis* as currently recognised are not striking. However, in a PCA of nominotypical *philippensis*, *centralis*, *proxima* and *ticaoensis* (Figure 4, Table 6), *centralis* from Siquijor separates out from almost all *centralis* from Negros and Bohol on Factor 1, a size axis, while the sole *ticaoensis* specimen included falls at the extreme small end of this axis. Masbate *proxima* is medium-sized on this axis (Figure 4, Table 6).

Measurements (Table 4) also show that all island populations of *spilocephala* are quite similar in size and proportions. We therefore combine these poorly if at all differentiated forms for subsequent analyses. Table 5, in which only clearly differentiated taxa (named or unnamed) are included, shows that there is considerable size variation, with *philippensis*, *spilocephala* and *mindorensis* all being small, while *reyi* and the four *spilonota* populations from Camiguin

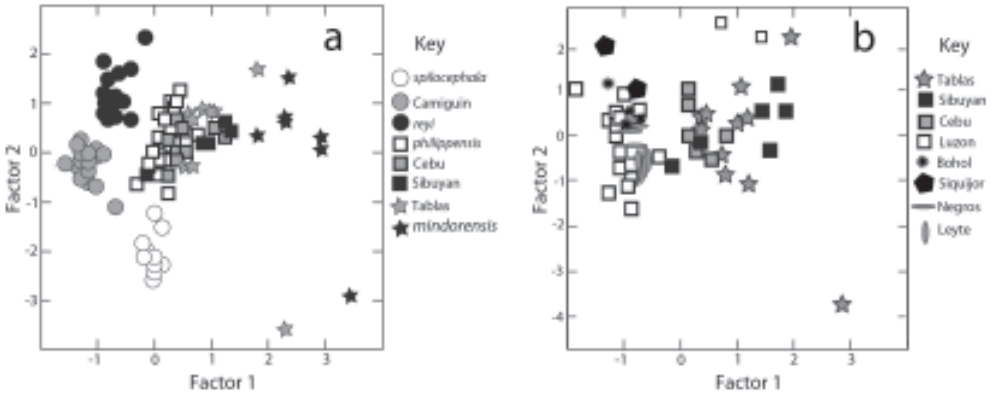


Figure 3. Results of PCAs of measurements of vocal characteristics for (a) all groups (*philippensis* and *centralis* combined) and (b) core groups (*philippensis* and *centralis* from different islands graphed separately; Tablas *spilonota*, Sibuyan *spilonota*, and Cebu).

Sur, Tablas, Sibuyan and Cebu are all large in most measures. PCAs (Figure 5, Table 6) consistently show this same pattern. On Factor 1, which is a strong size axis, taxa are either small or large, although a few individuals in both groups are intermediate in size. On Factor 2, the highest-loading variables are the two tail-banding measurements (Figure 5a, Table 6). On this axis, *philippensis*, with its broadly banded tail and to a lesser extent the Cebu bird, score high, in contrast to narrow tail-banded taxa including *spilocephala*, *mindorensis* and the Camiguin Sur birds. Although *spilocephala* is small, it has the longest (and densest) ear-covert extensions of all taxa (readily visible in photographs of live birds; Figure 6b), with *philippensis* not too different; all the larger taxa have relatively shorter and less prominent ear-covert extensions, which are rarely apparent in photographs. In fact, auricular length is much the highest-loading variable on Factor 3 of the PCA (Figure 5b, Table 6), on which *spilocephala* loads highest, with considerable overlap with *philippensis* and a few Sibuyan birds.

Figure 4. Results of PCAs of skin specimen measurements of *Ninox philippensis philippensis*, *N. p. centralis*, *N. p. proxima* and *N. p. ticaoensis*, with all islands shown with different symbols but previous subspecies groupings within dashed polygons. Summary statistics in Table 6.

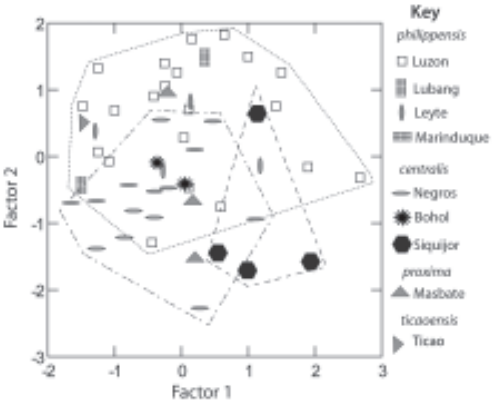


Table 4. Summary statistics for univariate measurements [mean±SD (range, *n*); (in mm)] of island populations of *Ninox philippensis sensu lato*, using previously recognised racial divisions. Not included here are *mindorensis* and taxa formerly united in *spilonota*. Ht = height; L = length.

Variable											
Island	**Culmen from skull**	**Culmen from cere**	**Upper Mandible Ht**	**Auricular extension L**	**Tail L**	**Tarsus L**	**Tarsal feathering**	**Mid-claw L**	**Wing L**	**Dark tail-bands**	**Light tail-bands**
philippensis											
Luzon		12.7±0.7 (11.8–14.4, 25)	7.4±0.4 (6.8–8.7, 26)	27.9±3.6 (18.1–33.6, 26)	82.7±4.5 (72.4–92.2, 24)	31.1±1.8 (26.9–36.0, 25)	15.8±2.2 (12.8–20.8, 25)	11.4±0.6 (10.0–13.1, 26)	173.5±5.7 (164–190, 26)	8.8±1.1 (6.7–10.7, 26)	3.9±0.8 (2.4–5.7, 26)
Polillo		13.4 (1)	7.9 (1)	28.6 (1)	83.2 (1)	30.5 (1)	16.9 (1)	13.0 (1)		8.4 (1)	3.7 (1)
Catanduanes		13.1±0.4 (12.4–13.6, 5)	7.3 (1)	–	79.7±6.8 (74.6–89.6, 4)	29.7±1.8 (27.8–32.4, 5)	–	11.8±0.8 (10.8–12.9, 5)	172±4.2 (169.0–175.0, 2)	9.2±0.9 (8.1–10.3, 4)	3.1±1.4 (2.1–5.1, 4)
Marinduque		13.2 (1)	7.8 (1)	22.9 (1)	84.0 (1)	32.3 (1)	21.5 (1)	12.0 (1)	174.0 (1)	9.8 (1)	2.6 (1)
Lubang		12.7±0.7 (12.2–13.2, 2)	7.1±0.1 (7.1–7.2, 2)	26.3±4.4 (23.2–29.5, 2)	84.3±6.8 (79.5–89.2, 2)	29.0±4.2 (26.0–32.0, 2)	14.2±1.2 (13.4–15.1, 2)	11.1±1.3 (10.1–12.0, 2)	169.5±9.2 (163.0–176, 2)	8.9±0.6 (8.5–9.4, 2)	4.5±0.8 (3.9–5.1, 2)
Leyte		12.9±0.8 (12.4–14.3, 5)	7.4±0.4 (6.8–7.9, 5)	30.1±2.9 (27.9–35.0, 5)	75.6±2.9 (71.4–79.5, 5)	30.3±2.7 (26.8–33.9, 5)	16.6±2.3 (13.8–20.3, 5)	11.4±0.3 (11.0–11.7, 5)	167.2±9.2 (154–175, 4)	9.0±1.0 (7.8–9.8, 5)	3.3±0.4 (3.0–4.0, 5)
centralis											
Negros		12.9±0.7 (11.6–14.6, 25)	7.6±0.3 (7.1–8.8, 25)	25.3±3.3 (19.3–32.7, 20)	78.7±3.0 (73.8–86.4, 24)	28.4±1.7 (25.6–31.1, 25)	14.3±2.4 (9.6–18.8, 17)	11.7±0.6 (10.3–13.1, 25)	167.7±6.1 (158.0–184.0, 21)	8.3±1.1 (6–10.6, 24)	3.7±0.7 (2.5–5.2, 24)
Bohol		13.3±0.1 (13.3–13.4, 2)	7.4±0.3 (7.2–7.7, 2)	25.4±2.1 (23.9–26.9, 2)	80.8±0.8 (80.2–81.4, 2)	30.0±0.4 (29.7–30.3, 2)	15.7±0.5 (15.4–16.1, 2)	10.3±0.5 (10.0–10.7, 2)	187.5±5.0 (184–191, 2)	8.6±1.0 (7.9–9.3, 2)	3.5±0.2 (3.4–3.7, 2)
Siquijor		14.0±0.7 (13.6–15.3, 5)	8.1±0.5 (7.5–8.8, 6)	24.5±4.8 (18.4–91.0, 6)	86.1±4.0 (80.9–91.0, 6)	30.8±2.4 (28.2–34.4, 5)	14.6±1.7 (13.1–17.5, 6)	11.7±0.2 (11.6–12.1, 5)	176±7.3 (166–186, 7)	8.5±1.5 (6.5–10.8, 6)	3.4±0.6 (2.8–4.5, 6)
proxima											
Masbate		13.1±0.5 (12.7–13.6, 4)	7.5±0.3 (7.1–7.9, 4)	25.4±2.9 (21.5–28.5, 4)	80.3±1.1 (78.7–81.3, 4)	28.9±1.9 (26.3–30.6, 4)	14.7±0.9 (14.0–15.9, 4)	12.0±0.7 (11.2–12.9, 4)	173.3±4.9 (170.0–179.0, 3)	9.0±1.1 (8.2–10.6, 4)	3.4±0.3 (3.0–3.8, 4)
ticaoensis											
Ticao		12.0 (1)	7.7 (1)	24.5 (1)	81.0 (1)	29.3 (1)	13.4 (1)	10.1 (1)	173.5 (1)	10.2 (1)	4.5 (1)
spilocephala											
Siargao		15.2±0.3 (15.0–15.4, 2)	8.6±0.3 (8.4–8.8, 2)	33.3±2.2 (31.8–34.9, 2)	81.9±1.4 (80.9–82.9, 2)	31.2±0.3 (31.0–31.4, 2)	15.7±0.3 (15.5–16.0, 2)	12.4±0.7 (11.0–12.9, 2)	178±11.3 (170–186, 2)	7.6±0.7 (7.1–8.1, 2)	3.4±0.5 (3.0–3.9, 2)
Mindanao		13.7±0.7 (12.1–15.0, 29)	7.8±0.4 (7.0–8.5, 30)	29.3±4.0 (23.5–40.2, 30)	74.6±4.4 (68.3–82.7, 24)	29.5±1.8 (25.5–33.2)	16.8±2.2 (13.1–21.0, 25)	11.5±0.6 (10.3–12.7, 29)	170±4.3 (162.0–181, 26)	7.2±0.9 (5.9–9.6, 28)	2.6±0.5 (1.2-–3.7, 28)
Basilan		14.2±0.7 (12.7–15.2, 9)	8.1±0.7 (7.3–9.4, 10)	29.1±3.8 (23.9–37.6, 10)	77.5±6.8 (67.5–87.0, 10)	29.6±1.1 (27.8–31.5, 10)	14.5±1.5 (11.9–16.4, 9)	11.8±1.0 (10.0–13.3, 9)	170.6±9.6 (159–188, 10)	7.6±1.4 (5.7–10.0, 9)	2.7±0.5 (2.0–3.6, 9)
reyi											
Tawi-Tawi	24.3±0.9 (23.0–26.0, 7)	13.7±1.2 (10.7–15.2, 10)	8.1±0.3 (7.7–8.5, 10)	21.0±5.2 (15.7-31.3, 10)	98.5±4.1 (92.9–107.5, 10)	35.7±2.6 (31.9–39.4, 10)	17.7±2.4 (14.4–21.1, 8)	12.5±0.7 (11.5–13.5, 10)	186.7±8.4 (172–195, 10)	6.7±1.2 (5.2–9.2, 10)	3.2±0.8 (2.4–4.3, 10)
Sibutu	25.0 (1)	14.1 (1)	7.8 (1)		88.7 (1)	34.7 (1)		12.7 (1)	173.0 (1)	5.3 (1)	2.7 (1)

Table 5. Summary statistics for univariate measurements [mean±SD (range, *n*); (in mm)] of major taxon groups of *Ninox philippensis* (*sensu lato*).

Variable											
Island	Culmen from skull	Culmen from cere	Upper Mandible Ht	Auricular extension L	Tail L	Tarsus L	Unfeathered tarsus	Mid-claw L	Wing L	Dark tail-bands	Light tail-bands
philippensis		13.0±0.7 (11.6–15.3, 75)	7.5±0.4 (6.8–8.8, 73)	26.6±3.7 (18.1–35.0, 67)	80.9±4.6 (71.4–92.2, 73)	29.8±2.2 (25.6–36.0, 75)	15.3±2.3 (9.6–21.5, 63)	11.6±0.7 (10.0–13.1, 76)	171.9±7.2 (154.0–191.0, 68)	8.7±1.1 (6–10.8, 75)	3.6±0.8 (2.1–5.7, 75)
mindorensis	21.2±0.6 (20.0–22.0, 12)	12.6±0.6 (11.7–14.3, 24)	7.2±0.4 (6.4–8.3, 25)	23.5±3.7 (15.5–30.3, 25)	82.6±4.1 (74.1–91.7, 25)	29.3±2.4 (24.2–36.1, 25)	13.0±1.9 (8.4–16.0, 24)	11.2±0.8 (9.6–12.5, 25)	164.4±5.7 (154–176, 25)	5.2±0.8 (4.0–7.1, 24)	2.9±0.6 (2.0–3.9, 24)
Tablas		15.5 (1)	8.5 (1)	24.5 (1)	96.1 (1)	30.2 (1)	15.8 (1)	12.6 (1)	188.0 (1)	8.6 (1)	3.2 (1)
Sibuyan	26.0±1.1 (25.0–28.0, 8)	16.4±0.8 (15.2–17.6, 11)	9.1±0.4 (8.8–9.9, 11)	22.6±3.5 (18.3–30.5, 11)	101.9±4.6 (91.6–107.0, 12)	33.0±1.1 (31.2–34.4, 11)	15.5±1.3 (13.0–17.5, 11)	13.7±0.7 (12.4–14.7, 12)	194.4±5.4 (185–202, 12)	7.5±0.6 (6.4–8.6, 11)	3.4±0.5 (2.5–4.0, 11)
Cebu	22.0 (1)	13.1 (1)	8.4 (1)	23.8 (1)	98.5 (1)	38.4 (1)			195 (1)	5.8 (1)	
Camiguin		16.2±0.1 (16.2–16.3, 2)	9.4±0.1 (9.3–9.4, 2)	25.1±2.0 (23.7–26.6, 2)	97.7±10.9 (90.0–105.4, 2)	35.2±3.7 (32.6–37.8, 2)	19.8±1.5 (18.8–20.9, 2)	13.5±1.1 (12.7–14.3, 2)	184±4.2 (181–187, 2)	6.5±0.5 (6.1–6.8, 2)	2.4±0.8 (1.9–3.0, 2)
spilocephala		13.9±0.8 (12.1–15.4, 40)	7.9±0.5 (7.0-–9.4, 42)	29.4±3.9 (23.5–40.2, 42)	75.8±5.3 (67.5–98.0, 36)	29.6±1.6 (25.5–33.2, 40)	16.2±2.2 (11.9–21.0, 36)	11.6±0.8 (10.0–13.3, 40)	170.3±6.5 (159.0–188.0, 38)	7.3±1.0 (5.7–10.0, 39)	2.7±0.5 (1.2–3.8, 39)
reyi	24.2±1.0 (23.0–26.0, 12)	13.7±1.1 (10.7–15.2, 11)	8.1±0.3 (7.7–8.5, 11)	21.0±5.2 (15.7–31.3, 10)	97.5±4.7 (88.7–107.6 (12)	35.6±2.5 (31.9–39.4 (11)	17.7±2.4 (14.4–21.1, 8)	12.5±0.6 (11.5–13.5, 11)	186.7±8.2 (172–195, 15)	6.6±1.2 (5.2–9.2, 11)	3.2±0.8 (2.4–4.3, 11)

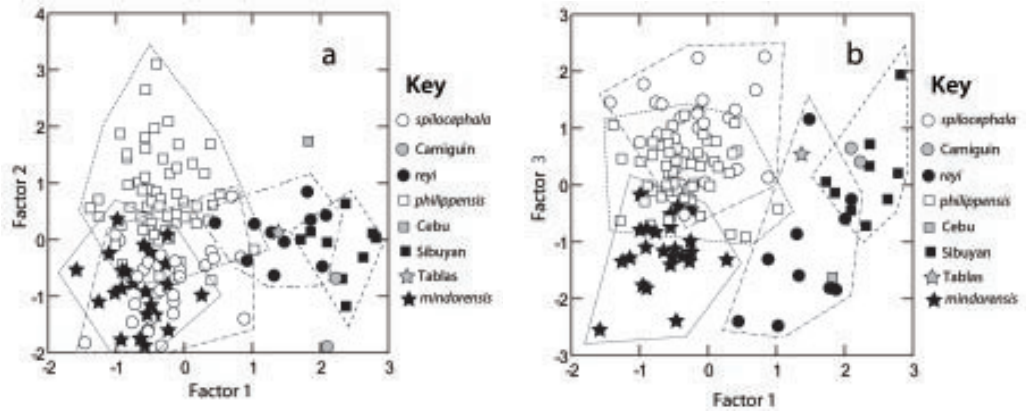


Figure 5. Results of PCAs of skin specimen measurements of *Ninox philippensis* (*sensu lato*), with all major taxa shown with different symbols and those with more than two specimens grouped within dashed polygons. Summary statistics in Table 6.

Unfortunately, sample sizes of all three new taxa formally described in this analysis are very small, and therefore we can only guess at the ranges of their measurements. However, the sample size for Sibuyan is moderate, and while the single Tablas specimen included falls just within the range of measurements for Sibuyan birds (on the small side for all but one measure: Table 4), it consistently falls outside all Sibuyan birds, on the small side of Factor 1 (a size axis), in the PCA (Figure 5). This could either indicate minimal or moderate difference in size between these two morphologically and acoustically fairly similar taxa. There is great plumage variation in photographs of Cebu birds, and we assume they also vary in size as with other taxa. The only Cebu specimen known is as large as the smallest Sibuyan birds but has a proportionately long tarsus, the measurement of which has been independently verified (Table 4, Figure 5). Camiguin Sur birds may vary less in size and plumage than other taxa, based on the two specimens studied and photographs of at least three further individuals.

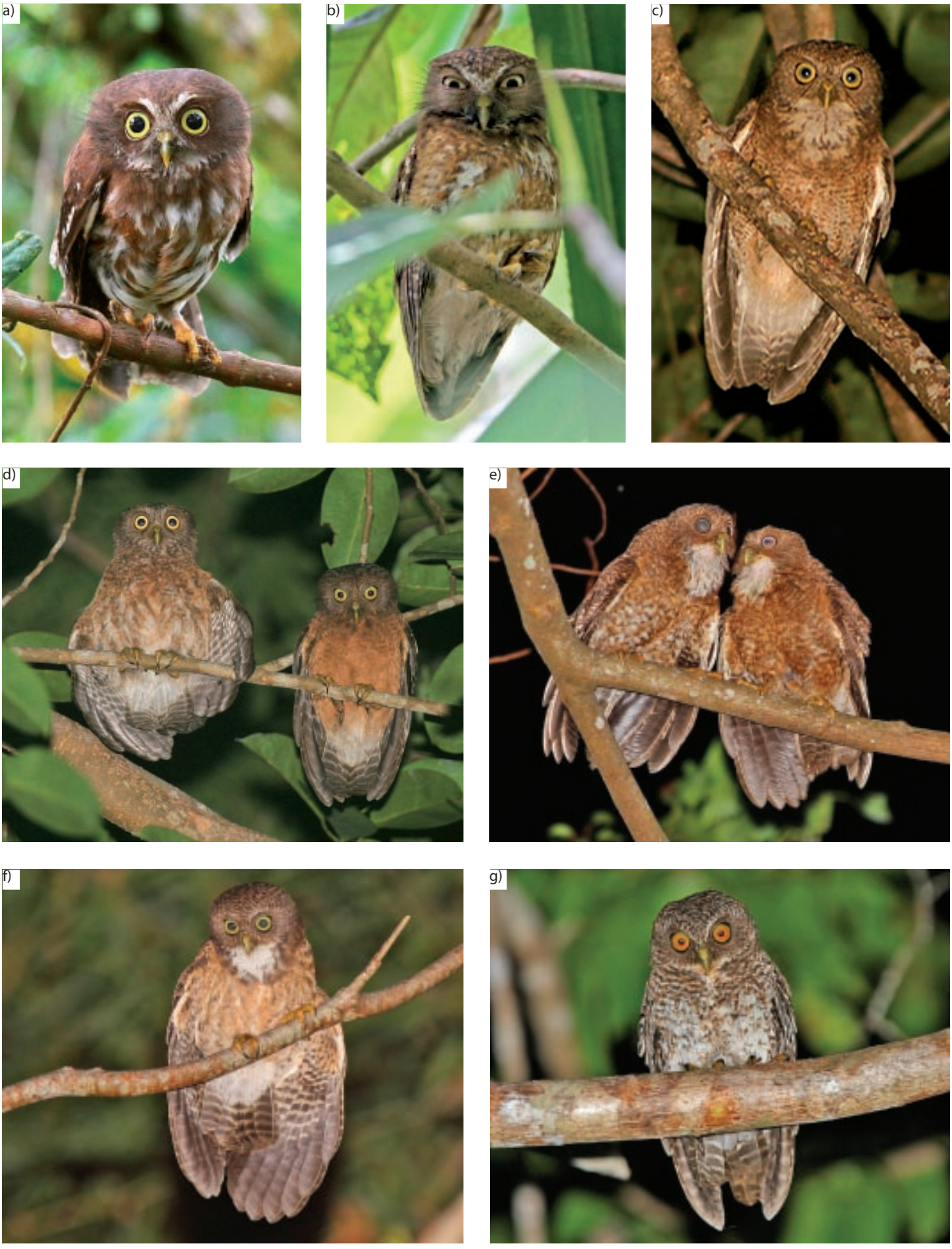
Colour and pattern analyses

Most taxa in the *Ninox philippensis* (*sensu lato*) complex are at least moderately variable in plumage, particularly in the case of most of the small island forms formerly united within *spilonota* or *reyi*. Given the small sample sizes available for most of these taxa, delineating diagnostic plumage characteristics is problematic. Plumage or structural characters that are unique to a single taxon are scarce. It may not even be possible to attribute every individual

Table 6. Summary results of principal components analyses of measurements of morphological characteristics for all groups and *philippensis* (*sensu stricto*) island taxa only (*philippensis*, *centralis, proxima, ticaoensis*). Ht = height; l = length; w = width.

	All groups			*philippensis* only			
Component loadings	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 4
Culmen from cere	0.75	–0.26	0.31	0.68	–0.41	0.13	0.05
Upper mandible ht	0.79	–0.17	0.34	0.62	–0.40	0.24	–0.33
Auricular l	–0.25	–0.06	0.76	0.25	0.64	–0.42	0.18
Tail l	0.83	0.08	–0.28	0.61	0.41	0.24	0.06
Tarsus l	0.73	0.09	–0.09	0.55	0.45	0.29	0.05
Unfeathered tarsus l	––	––	––	0.42	0.33	–0.15	–0.53
Mid-claw l	––	––	––	0.62	–0.02	–0.29	0.43
Wing l	0.84	0.24	0.01	0.14	0.02	0.75	0.03
Dark tail-band w	–0.03	0.70	0.55	–0.43	0.45	0.26	–0.46
Light tail-band w	0.01	0.88	–0.20	–0.37	0.21	0.49	0.54
Variance explained by components	3.17	1.44	0.85	2.49	1.47	1.37	1.13
Percent of total variance explained	39.60	17.99	15.30	24.87	14.72	13.69	11.26

Figure 6. Photographs of (a) Luzon Hawk Owl *N. philippensis*, Dolores, Quezon, Luzon, 16 January 2012 (R. J. Quisumbing); (b) Mindanao Hawk Owl *N. spilocephala*, PICOP, Mindanao, February 2011 (R. O. Hutchinson); (c) Mindoro Hawk Owl *N. mindorensis*, Sablayan, Mindoro, December 2008 (James Eaton); (d) Romblon Hawk Owl *N. spilonota*, Tablas, 4 March 2012 (Marc Thibault); (e) Camiguin Hawk Owl (new species), Camiguin Sur, 8 June 2011 (R. O. Hutchinson); (f) Cebu Hawk Owl (new species), Cebu, 3 January 2012 (Christian Artuso); (g) Sulu Hawk Owl *N. reyi*, Tawi-Tawi, January 2012 (R. O. Hutchinson).



to taxon without recourse to measurements or knowledge of island of origin. However, on a combination of characters, each of the taxa we recognise below can be readily identified.

The main plumage and other external features that differ between taxa in the *Ninox philippensis* (*sensu lato*) complex are summarised in Table 7. While plumage differences between *N. philippensis* (*sensu stricto*) and all other taxa are straightforward and consistent, those between all other taxa are less obvious and are only diagnostic in combination, although the conformation of the streaks of the lower underparts of *spilocephalus* is highly distinct except from a very few individuals of *reyi*. The profound differences in vocalisations demonstrated above are entirely inconsistent with treatment as a single species, but these differences are largely congruent with additional evidence from mensural analyses and plumage and soft-part colours. Under the Biological Species Concept, we consider that *Ninox philippensis* (*sensu lato*) represents seven species, of which two formerly treated under the race *spilonota* are undescribed species and a third is an undescribed subspecies. Under the Tobias criteria (Tobias *et al.* 2010), all unstreaked forms differ from the taxa in *N. philippensis sensu stricto* by their exceptional vocalisations (score 4) and unstreaked *versus* streaked plumage (score 3), plus various other characters not necessary to enumerate here; total at least 7.

Diagnoses

N. p. philippensis

Our evidence indicates clearly that the streak-breasted taxa form a highly consistent group very weakly differentiated in plumage, morphometrics and voice, and without attempting to score these characters, all of which appear to be minor, we propose that the taxa *philippensis*, *proxima*, *centralis* and *ticaoensis* be considered a single species, Luzon Hawk Owl *Ninox philippensis*. Indeed, given the variability in plumage, size and voice we feel that the case for subspecific separation in this widespread northern and central Philippine species is not solid. The Masbate race *proxima* (diagnosed on a sample size of two as 'similar to *philippensis* but larger and with a relatively shorter tail', but also darker above, with less pronounced pale tail-bars, reduced pale spots on wing-coverts and wings, and coarser, darker stripes below: Mayr 1945) is particularly doubtful, and we subsume it here in the nominotypical. The small dark Ticao race *ticaoensis* (diagnosed in a comparison with *proxima* on a sample size of three as having 'the upperparts darker, the ventral streaking sharper and darker, and the light barring on the tail narrower': duPont 1972), is at best marginally distinct. Birds from Siquijor, bearing the name *centralis* (diagnosed as 'much larger than *proxima* and with a long tail', with no rufous or tawny tones in the 'dark earth brown' of the upperparts, much reduced pale spotting on the scapulars and upperwing-coverts, ill-defined streaking below with an ochraceous wash to the white feathers: Mayr 1945), are certainly larger than and, on our sample, vocally distinguishable from other island populations currently placed with *centralis*, so we restrict *centralis* to the Siquijor population (for which the name was established) and place populations from other islands except Ticao in the nominotypical, but further study is needed.

Diagnosis (from large series of specimens and many photos of live birds; see Plate and Figure 6a).—**Size** small, with compact, sleek plumage. **Head** has prominent if small and/or buff-tinged whitish supercilium. Auriculars are uniform plain dark brown, concolorous with or slightly paler than crown, with fairly long, prominent filamentous extensions; facial disk not well defined. **Above**, uniform brown above from crown to rump, lacking barring or speckling. Scapular patch with some largely white to pale buff feathers with dark brown edgings, or large white/buff patch on mid-distal portion of dark brown feather; barring or mottling lacking. Larger outer wing-coverts have large white spots, usually one but sometimes two per feather; barring is lacking. Tail banding is variable in intensity but most have fairly weakly marked pale bands that are much narrower than the dark bands. **Below**, throat narrowly white, with fine dark streaks; underparts prominently streaked dark brown or rufescent-brown, either crisply or indistinctly, on a white or rufous-tinged background. The streaks are not edged with darker colour or intruded by spots or bars. The streaks become more distinct, narrower, and longer on the central lower underparts, where they typically cover the central half to third of the feather, the remainder being white or whitish, and the undertail-coverts are white without markings or with a few faint and/or narrow dark markings. **Bare parts**: irides bright yellow, often appearing slightly paler, more lemon-yellow on outer ring; narrow orbital ring pale tan, not conspicuous; cere and bill pale olive-yellow, the culmen ridge and tip slightly yellower; tarsi and toes bright yellow, claws almost entirely black, the bases paler. **Vocalisations** are long, mid-pitched series of strongly convex barking notes starting with single notes and ending with about four halting notes, the first note softest, without whistles and usually without growls.

Table 7. Main qualitative plumage and soft-part character differences between taxa in the *Ninox philippensis* (*sensu lato*) complex.

Morphological characteristic									
Taxon	**Crown pattern**	**White supercilia**	**Filamentous ear-covert extensions**	**Throat-patch**	**Dark-streaked underparts**	**Barring below**	**Iris colour**	**Bill colour**	**Claw colour**
philippensis	unmarked	well-marked	long	not apparent	yes	no	yellow, paler outer ring		mostly dark
mindorensis	finely barred	small but prominent	shorter, less apparent	intermediate; apparent but not large or bright white	no	yes, narrow and/or broken	yellow, mustard inner, lemon outer	pale dull yellow, sides greener	mostly dark
Tablas *spilonota*	barred		shorter, less apparent	not apparent	no	obsolete	yellow		mostly dark
Sibuyan *spilonota*	speckle-barred	not present	shorter, less apparent	not apparent	no	yes, prominent to obsolete	yellow	mostly mustard yellow	mostly dark
Cebu	speckle-barred	small but prominent	shorter, less apparent	well- marked, bright white	no	at most, broken spotty barring	yellow	pale olive, culmen and tip yellower	mostly dark
Camiguin Sur	coarsely barred	not present	shorter, less apparent	well-marked, bright white	no	yes, strong overall	blue-grey to whitish	mostly mustard-yellow, sides greener	mostly pale
spilocephala	spotted	well-marked	very long, profuse	not apparent	yes	no	yellow		mostly dark
reyi	prominently barred	very small	shorter, less apparent	well- marked, bright white	occasionally	yes, strong at least on breast	mustard-yellow, may show pale greenish-yellow outer ring	dull greenish yellow	mostly dark

N. p. spilocephala

Tweeddale (1879) established this taxon simply on the basis of the 'bright rufous' to 'pale tawny rufous' spotting on the forehead and crown, a feature absent in the otherwise similar form from Luzon with which he compared his extensive (6 males, 13 females) material from Mindanao, noting that this material was variable in coloration above and pattern below. He also observed, without proposing these points as possessing diagnostic force, that male *spilocephala* were longer-winged than male *philippensis*, but that *spilocephala* by his measurements was shorter-legged than R. B. Sharpe's of *philippensis*. However, Mayr (1945) pointed out that *spilocephala* is 'the principal connecting link' between the extremes represented by *philippensis* on the one side and *mindorensis* on the other, and in this he was clearly referring to the fact that *spilocephala* possesses underparts which conflate the streaking of *philippensis* and the barring of *mindorensis*.

Specimen material confirms the apparent intermediacy of plumage for *spilocephala*, which shows brown and white streaking in varying degree on the belly, as in *philippensis* and its Visayan representatives. However, this streaking is only vague on the breast, which is interrupted by a disorganised and inconsistent pattern of bars and mottling in many specimens. In addition, the streaking of the lower underparts differs from *philippensis* in being dark-edged and irregular (see Diagnosis below). The spotting and stippling on the crown (which extends onto the mantle) is similar between *spilocephala* and the bar-breasted forms.

Thus the form *spilocephala* differs significantly from all the others in plumage, morphometrics and voice, and we propose that this also be considered a species under the name Mindanao Hawk Owl. Its main song and other vocalisations are highly distinct from that of any other form (Tobias score 3). Moreover, in its combination of barred breast and streaked belly, it displays what we judge to be a major character difference from any other taxon (score 3). It also has exceptionally long, full auricular extensions (from data in Table 5 effect size *vs philippensis* = 0.74; score 1).

Diagnosis (from large series of specimens and photos of at least three live birds; see Plate and Figure 6b).—**Size** small, with especially short tail. Plumage compact and sleek. **Head** has a very small, indistinct or absent white patch between eye and supercilia. Auriculars appear nearly uniform dark brown but they are in fact vaguely speckled and/or barred; filamentous auricular extensions normally very long, full and profuse, more so than for any other taxon. **Above**, crown, nape and upper mantle of adults is strongly and usually evenly spotted with buff, the spots becoming weak on the upper mantle and disappearing. In an immature, the crown is unspotted brown but there is a collar of weak pale buff spots on the upper mantle. Mid- to lower mantle to rump is uniform dark brown. Uppertail-coverts may have a little vague fine pale barring. Scapular patch similar to those in *philippensis* group. Larger wing-coverts have both large white spots and narrow buff barring. Tail is typically more distinctly banded, with narrower dark bands, than for *philippensis*. **Below**, throat is narrowly white with medium-broad, distinct blackish-brown shaft-streaks, becoming broader on upper breast. Sides of neck and breast are weakly barred and spotted dark brown and buff, and central breast is mostly streaked. Lower underparts have mostly longitudinal dark markings but these are typically somewhat rounded, with dark chevron tips and irregular dark markings edging the paler brown internal markings. Undertail-coverts white, often with tiny dark spots. **Bare parts**: irides pale yellow; narrow bare orbital ring tan-brown, not conspicuous; cere and bill pale olive, more yellow on culmen ridge near tip; feet bright yellow, claws nearly all black, paler at bases. **Vocalisations** are low-pitched, mellow, slow, and two-noted, with first note of each couplet stressed.

N. p. mindorensis

Ogilvie Grant (1896a) characterised this form as 'nearly allied to *N. spilocephala*... in having the top of the head and nape barred [*sic*] with buff' but 'the whole of the underparts... tawny buff, transversely barred with brown, while in... *N. spilocephala*, though the breast is generally like that of the present species, the belly and flanks are always white, with longitudinal reddish-brown shaft-stripes'. He distinguished *mindorensis* from *spilonota* (which the describers had listed as including the Mindoro population) simply by its 'much smaller size'.

Our examination of specimens confirms this basic diagnosis. In addition, as noted above, the barring on the tail is denser in *mindorensis* than in *spilocephala*. König *et al*. (1999) mistakenly suggested that *mindorensis* is larger and that the number of its tail-bars is fewer than the Philippine Hawk Owl *sensu lato*.

Dutson *et al*. (1992) and Brooks *et al*. (1995) were the first in the modern era to realise that the form *mindorensis* is so different from Luzon birds that it appears to represent a separate species. After hearing tapes by P. Morris made in 1999, König *et al*. (1999) concurred and established it as Mindoro Hawk Owl *N. mindorensis*. However, they made this move without knowing the songs of other unstreaked forms, which they retained with *N. philippensis* (*sensu lato*). Only now is it confirmed that *mindorensis* possesses a highly distinctive voice, with few similarities to those of the other unstreaked forms.

Compared to any other unstreaked form, *mindorensis* is distinctly smaller (see Table 5: wing and tail shorter, with effect size *vs reyi* –2.79 and –3.39 respectively; Tobias score 2), with a weaker pale throat than Camiguin Sur and Cebu birds and *reyi* but more prominent than in *spilonota* (score 1), especially narrow underparts barring (score 1), high-pitched song (score 2), and very short toots in climax song (score 2). There are other unique vocal characteristics as well (not scored), such as the unusually long notes.

Diagnosis (from large series of specimens and photos of numerous live individuals; see Plate and Figure 6c).—**Size** small, with small bill, tarsus mostly feathered. **Head** moderately patterned, with small short white supercilia; facial disk rather pale brown, small, with moderately distinct rim, and usually rather short filamentous auricular extensions. **Above**, crown and nape finely barred dark brown and buff to whitish, but bars broken resulting in overall appearance of speckling. Speckling grades out on upper mantle, and rest of central mantle uniform, with vague fine barring at edge of mantle and on rump. Scapular patches are extensively white with irregular dark margins and dark spots. Wing-coverts are extensively and finely barred, with dark bands predominating, and with white spots/bands on outer webs of larger coverts that have tiny dark spots and scrawls within the white portions. Primaries have prominent broad dark brown bands and narrower buff bands on outer webs, and very vaguely banded inner webs. Tertials virtually unbanded and with very fine, weak pale mottling, appearing uniform brown. Tail banding is obscure and both dark and light bands appear narrow. **Below**, throat-patch pale buff, not very clear-cut but more so than for Sibuyan and Tablas birds. Underparts highly variable but typically the most finely barred of any taxon in the *N. philippensis* (*sensu lato*) complex. Underparts vary in tone from pale buff to saturated, and may have fairly prominent white streaking below. **Bare parts**: irides have mustard-yellow inner ring, brighter lemon-yellow outer ring. Bill and cere pale dull yellow, tinged greenish on sides. Tarsi and toes dull olive-yellow, claws black, paler near bases. **Vocalisations** are high-pitched long whistles often ending with a screech, and often starting with tittering high toots.

N. p. spilonota from Tablas and Sibuyan

Bourns & Worcester (1894) gave the name *spilonota* to unstreaked birds from 'Cebu, Sibuyan, Tablas, Mindoro', but their description made no comparison with any other *Ninox* taxon, so the diagnostic features of *spilonota* are not immediately obvious. The description

refers to an overall colour of 'fulvous brown' above, with light rufous speckling from head to mantle and wing-coverts, a tail 'nearly black with nine narrow transverse bands of light rufous brown', underparts 'rufous brown... many feathers of breast and abdomen with fulvous brown spots'. McGregor (1905) noted that the scapulars, normally white in many *Ninox*, are reduced to 'bars of pale fulvous' in the specimen to which he had access. We now verify that this character holds in the far more extensive material we have examined from Sibuyan.

On Sibuyan and Tablas, *spilonota* is diagnosed by its plain head without white supercilia (score 2), lack of notably paler throat (score 3), lack of white spots in scapulars (score 2), and distinctive song pattern and quality (score 3).

Diagnosis (from several Sibuyan specimens and two photos of a live bird, and one Tablas specimen and two photos of a live bird; see Plate and Figure 6d).—**Size** large, with large bill. Plumage rather lax, and general appearance very plain. **Head** plain brown, lacking pale supercilia or any strongly contrasting pattern, and with indistinct facial disk. **Above**, finely speckled buff on dark brown crown and nape, mantle unmarked, scapulars and tertials entirely and distinctly barred dark brown and buff, without large white scapular spots; uppertail rather narrowly but distinctly barred dark, with narrower buff bars. **Below**, no prominent pale throat-patch. Underparts typically have ochraceous background, either lightly and indistinctly marked with large darker brown broken bars and spots, sometimes looking almost plain ochraceous-brown, or completely barred below, with fairly even, dark brown bars on ochraceous background; rarely has fairly prominent white streaking on lower underparts. **Bare parts**: irides bright yellow, not differing between inner and outer rings; narrow bare orbital skin dull tan-brown, not standing out from surrounding feathers; bill and cere pale olive-yellow, yellowest along culmen and at tip. **Vocalisations** are short falling whistles, often hoarse, starting singly then changing into a three-note (Tablas) or four-note (Sibuyan) version.

Populations of both islands are covered by this diagnosis; however, Tablas birds differ from those on Sibuyan and require a name.

Ninox spilonota fisheri subsp. n.
Romblon Hawk Owl

Diagnosis.—Smaller than *N. s. spilonota*. Vocalisations differ from those of *N. s. spilonota* as indicated above.

Holotype.—USNM 314875, female, Badajos [now San Agustin], Tablas, 18 September 1892, collected by D. C. Worcester and F. S. Bourns; Ex. Menage Collection no. 373. Culmen from cere 15.5 mm, wing 188 mm, tarsus 30.2 mm, tail 96.1 mm.

Description of holotype.—Medium-large, weakly marked round-headed owl, largely barred above and nearly plain ochraceous below. **Head**.—Small, with short, inconspicuous partially concealed whitish supercilium extending to about half-way over eye; auriculars appear rather dark brown with inconspicuous buff spotting, their filamentous extensions fairly weak and short; forehead and crown dark brown moderately narrowly and distinctly barred and spotted. Forehead to hindcrown and sides of neck profusely covered with small, closely spaced buff spots and short buff bars. Throat pale buff overall (appearing Munsell 2.5Y 8/4), each larger throat feather with a narrow darker brown shaft-streak and often with narrow whitish outer webs and/or bases. Rictal bristles largely pale buff, with black rachis that extend well beyond the barbs, some exceeding the bill tip in length. **Upperparts**.—Barring/spotting on crown becomes less regular and less conspicuous on sides of neck and nape and grades into a rather vague pattern on upper mantle of broad dark brown and narrower buff (Munsell 10YR 7/6) banding. Scapulars lack any white but have bold, broad but irregular rich buff (Munsell 10YR 8/6) and dark brown banding, the dark brown banding with narrow blackish edgings. Lower mantle and rump are essentially unstreaked warm dark brown (Munsell 10YR 3/4). There is a single all-white abnormal-appearing, badly worn feather in the upper mantle. **Wings**.—Small external coverts of carpal area nearly uniform warm dark brown, with very vague lighter buff speckling. Median wing-coverts fairly distinctly barred with narrow buff bars and broad dark brown; greater coverts yet more distinctly and broadly banded. Tertials very broadly and evenly banded rather dark brown with narrow, widely spaced, moderately distinct dull buff bars. Primaries have broad dark and narrower dull buff banding with narrower, irregular dull buff uniform dark brown inner webs. **Underparts**.—Pale buff throat becomes darker, richer buff on lower throat and grades into rich ochre underparts (Munsell 7.5YR 6/8). Medium brown shaft-streaks on lower throat grade into rather indistinct, broken but fairly broad medium brown bars on upper breast, which break up and fade out on lower breast. Except for flank feathers overlying thighs, which are indistinctly banded medium brown, lower underparts are nearly solid rich ochre 6/8, with a few tiny darker spots and vague mottling. Lower centre of belly has some feathers with a few broad whitish tips, and undertail-coverts are buffy-white with narrow buff tips. Tibial and tarsal feathering is ochre-buff mottled whitish, and extends more than half-way to distal end of tarsus. **Tail**.—Uppertail-coverts are dark brown with a few narrow ill-marked dull buff bars. Uppertail has moderately prominent broad dark brown and rather narrow pale dull buff bands. Counting from base of feather (with uppertail-coverts moved aside), there are 9 clearly discernible pale bands and 10 dark ones. **Bare parts**.—In the dried specimen cere and bill are fairly dark horn, with a paler, more orange-yellow culmen ridge. Distal end of tarsus and toes have sparse, stiff, pale bristles. Toes and claws on dried specimen are medium horn, tips of claws slightly darker.

Remarks.—Appears to be quite closely related to the nominotypical form on Sibuyan, but differences at least in size and vocalisations dictate recognition as a new subspecies.

Etymology.—We name this form in honour of the late Tim Fisher, dedicated Philippine ornithologist and co-author of Kennedy *et al*. (2000).

N. p. spilonota from Camiguin Sur

Birds on Camiguin Sur are unique in their boldly, broadly barred underparts (Tobias score 2), the combination of no white supercilium with an extensive white throat (score 2), grey to whitish eyes (score 3), and mostly pale claws (no score available; would be 1). Vocally they are highly distinctive as well, with their low-pitched, rapid, multi-noted hooting duets (score 3 or 4). This taxon has always been treated within the race *spilonota*, but clearly under both the traditional Biological Species Concept and the scoring system employed here it requires a name and recognition at the level of species.

Ninox leventisi sp. n.
Camiguin Hawk Owl

Diagnosis (from FMNH 284397 and 399384 and photographs of at least three living birds; see Plate, Figure 6e, and journal front cover).—**Size** large, with long, deep bill. Plumage appears full and lax compared to other members of the *N. philippensis* complex, except that ear-coverts have only short filamentous extensions visible only at very close range. **Face** drab warm brown, the auriculars barred but appearing plain at a distance; lacks pale supercilium but may have small white patch above bill extending just over eye; face shows no contrast with rest of head, and facial disk border is not well marked. **Above**, crown very distinctly and regularly barred buff and dark brown, more narrowly and obscurely barred on upper mantle, the barring becoming vague and irregular on lower mantle to rump. Wing-coverts are entirely boldly barred dark brown, buff and white. Scapular patch includes feathers with

large unbarred white areas on outer web, just tip and base being barred. Primaries are dark brown, the outer webs mainly dark buff edged darker brown, with narrow pale buff bars. Tertials are mottled and incompletely but prominently banded. Uppertail has rather narrow dark and pale bars. **Below**, large bright white throat-patch with a few narrow dark streaks extends to top of breast, with some largely white feathers in uppermost central breast; white throat-patch normally mostly hidden, but shown to be extensively white in song display. Sides of neck and entire underparts heavily and distinctly banded dark brown and buff. Underparts from breast to abdomen have some irregular white or light buff banding; banding below is heavier, broader and more distinct, with generally darker, warmer brown tone on underparts than other taxa. Undertail-coverts white with extensive dark barring and spotting. Undertail irregularly banded with broad dark and narrow buffy bands, banding sometimes obsolete. **Bare parts**: irides grey to whitish or very pale yellow-green (*versus* yellow in all other taxa); narrow but distinct bare eye-ring mustard-yellow; bill and cere mustard-yellow, more olive-green at base of bill; legs and feet mustard-yellow, tarsi less extensively feathered than in most other taxa in complex, mostly thinly bristle-covered; claws mostly pale, only the tips fairly dark (claws mostly dark in other taxa, judging from photos of live birds). **Vocalisations** are very low-pitched, typically short strophes repeated after brief pauses, with many rapid, irregular, barking notes per strophe.

Holotype.—FMNH 284397, female, Catarman Mountain, Catarman, Camiguin province, Camiguin Sur Island, 17 June 1968, D. S. Rabor/W. S. Anguila; edge of second-growth, approx. 1,5002 (2,000–4,0002 on label; Balete *et al.* [2006] state 1,5002 , c.450 m). 'Irish [*sic*] dark white'. Culmen from cere 16.2 mm, wing 187 mm, tarsus 37.8 mm, tail 90 mm.

Paratype.—FMNH 399384, female, Mt Timpong, Matugnao, Mahinog, 13 June 1969, D. S. Rabor. Specimens of other species taken on 13 June 1969 on Mt. Timpong were from 3,1502 or c.950 m (Balete *et al.* 2006). Culmen from cere 16.3 mm, wing 181 mm, tarsus 32.6 mm, tail 105.4 mm.

Description of holotype.—Crown dark brown, distinctly and regularly barred with buff from forehead to nape and sides of neck, the barring becoming less distinct on upper mantle and obsolete on lower mantle. Scapulars moderately distinctly barred, outer scapulars largely white with dark brown tips and bases. Wing-coverts heavily barred with buff, the greater coverts barred mostly white. Tertials moderately barred buff on dark brown. Uppertail has broad dark and narrow dull buff bands. No pale supercilium, and facial disk dark brown, weakly barred, and weakly defined. Throat extensively bright white, the white extending well onto the upper central breast. Rest of underparts heavily and distinctly but irregularly banded dark brown on buff, with some short broad white bars on central and lower underparts. Tarsal feathering dull brown with narrow darker bars.

Remarks.—This is evidently the first known owl with grey or whitish eyes. It is vocally highly distinct, normally giving a rapid, low-pitched duet, the two birds facing and leaning towards each other while very close together, with white throat puffed out and pulsating, wings drooped.

Etymology.—We name this new species for Anastasios P. Leventis, whose generous long-term commitment to BirdLife International has been crucial in the stable development of the organisation, and whose particular support for NJC has allowed him to work extensively on Philippine birds and conservation issues over the past decade.

N. p. spilonota from Cebu

The Cebu population of *N. p. spilonota* is diagnosed from Tablas and Sibuyan birds, to which it is in vocal, morphological and geographical terms most closely related, by its combination of fairly prominent white supercilium and barred wing-coverts (Tobias score 1), barred back (score 1), prominent (when singing) white throat strongly edged dark (score 3), relatively small bill (score at least 1), long tarsus (score at least 1), and fast-paced song (score 2) with multiple unmatched note types(score 2). Because n=1 in the morphometric sample (Table 4) we cannot generate an effect size but the differences in bill and leg length are striking. We consider that, under both the traditional Biological Species Concept and the scoring system utilised here, this heretofore unnamed taxon is a new species.

Ninox rumseyi sp. n.
Cebu Hawk Owl

Diagnosis (based on holotype, BMNH 1955.6.N30.4747, and photographs of at least nine living birds; see Plate and Figure 6f).—**Size** medium-large, with long tarsi (based on type specimen), but relatively small-billed for its size class. Prominently marked round-headed owl, mostly barred above, weakly marked or uniform below, with white or near-white vent. Plumage compact and sleek, as with most other taxa in complex; ear-coverts have only short filamentous extensions. **Head** shows prominent short white or whitish supercilia; plain dark ear-coverts contrast with prominent well-marked white throat-patch bordered below and on sides by conspicuous dark markings (apparent in life, especially when singing); crown strongly marked with rows of pale, almost contiguous speckles between dark bars. **Above**, including wing-coverts and tertials, strongly and narrowly barred dark brown and buff, the barring varying from strong to obscure on lower mantle. Scapular spots are mostly white, with narrow dark brown edgings and warm buff between the white and brown areas. **Below**, weakly and irregularly speckled or marked with short broken bars on pinkish-buff to fulvous background, usually heaviest on breast; sometimes with broad white streaking on lower underparts and/or flanks, or virtually unmarked pinkish-buff to rich fulvous below, with or without indistinct white streaking on lower underparts. Undertail-coverts white (rarely pale buff), usually with very narrow dark fringes to longest feathers. Central rectrices have relatively broad, distinct dark bands. **Bare parts**: irides pale to bright lemon-yellow, the inner and outer rings not differing; narrow eye-ring indistinct and dull brown, not standing out from adjacent feathers; bill and cere dull pale olive, tip and culmenridge yellower; legs and feet bright yellow, tarsi about half-feathered, otherwise thinly bristle-covered; claws mostly black, only the proximal portions paler. **Vocalisations** are mid-pitched, irregular strophes delivered rapidly and irregularly with multiple note types.

Holotype.—BMNH 1955.6.N.20.4747, female, Cebu, 17 March 1888, collected F. S. Bourns and D. C. Worcester. Ex. Norwich Castle Museum. Culmen from cere 13.1 mm, wing 195 mm, tarsus 38.4 mm, tail 98.5 mm.

Description of holotype.—Crown very dark brown, heavily speckled with buff in rows that resemble bars; weak short pale supercilium; dark brown auriculars. Rear crown and nape heavily speckled with rows of pale buff spots, becoming more barred on upper mantle, then weaker and more mottled on central mantle, which is nearly uniformly dark brown; inner scapulars are more distinctly barred dark brown and buff, and outer scapulars are largely white with very dark brown edgings, golden-buff between the edgings and white inner portions; wing-coverts lightly barred, more prominently so on greater coverts and tertials; uppertail broadly barred very dark brown and narrowly barred dull buff. Throat white, but mostly hidden due to preparation style. Breast pale ochraceous, moderately barred and mottled dark brown, the bars breaking up into small dull brown speckles on lower breast, flanks, and even smaller, fewer speckles on central lower underparts. Tarsal feathering and undertail-coverts buffy white, with a few irregular dull brown speckles.

Remarks.—The holotype is the sole known specimen in existence. Photographs show this species to be highly variable in underparts colour and pattern, less so in other characters. In plumage closest to the much smaller *N. mindorensis*, from which it most obviously differs in the more widely spaced bars below (where these exist). Vocally fairly distinctive, although recognisably closer to *N. spilonota* and *N. mindorensis* than to other taxa in song characteristics and quality. Thought possibly extinct (Brooks *et al*. 1995b) until its rediscovery in 1998 (Pagantalan & Jakosalem 2008).

Etymology.—We name this new species for Stephen J. Rumsey, dedicated conservationist and ornithologist who has given great support of BirdLife International but who has also helped promote research and conservation on the island of Cebu.

N. p. reyi

This was the third form of resident *Ninox* to be described from the Philippines; but Tweeddale's ('1878' = 1879 *fide* Dickinson *et al*. 1991) description of *spilocephala* apparently was too recent for Oustalet (1880) to be aware of it. Thus Oustalet (1880) only had *philippensis* for comparison, finding that *reyi* is immediately distinguished by its larger size, longer wings (reaching beyond the tail-tip), and russet ('*roux*') plumage with transverse brown bars on head and shoulders. Mayr (1945), having no specimens to hand and evidently misreading or ignoring Oustalet as well as Sharpe's (1897) Latin account of *Ninox everetti* (a synonym of *reyi*), misattributed Sulu birds to the *spilocephala* group, and duPont & Rabor (1973) mysteriously failed to remark on this, despite having eight *reyi* to hand by 1972 (material in DMNH).

The form *reyi* is distinguished from all other taxa by its very pronounced, even barring on head and breast (Tobias score 2), combination of tiny white supercilia with large bright white throat (score 2), and its extraordinarily distinct song (4) as well as other unscored song pattern characters.

Diagnosis (from numerous specimens and photos of three live individuals; see Plate and Figure 6g).—**Size** large, with large, broad bill. **Head** shows tiny white patch in supercilium, concentrically dark-barred ear-coverts, and relatively well-defined facial disk. **Above**, usually distinctly, regularly and rather narrowly barred dark brown on whitish or buffy background; barring becomes muted on upper mantle, and mantle vaguely barred, mottled and vermiculated. Outer scapulars largely or at least partly white, with intricate dark patterning intruding to vane on some; wing-coverts prominently banded, the banding on tertials more muted. Uppertail with prominent dark bands of medium width. **Below**, throat-patch bright white and very well defined, visible even in perched birds looking down. Breast distinctly and evenly dark-barred, but lower underparts highly variable, often being broadly white-streaked or even irregularly dark-mottled on white background; equally the lower underparts can be fulvous, either fairly plain or regularly dark-barred. Some individuals appear almost black-and-white barred overall, lacking warm tones; others (especially young birds) resemble *spilocephala* in underparts pattern, but the dark-streaking pattern on the lower underparts is not as distinct or regular as in *spilocephala*. **Bare parts**: irides bright yellow, often paler on outer ring; bill dull greenish-yellow; feet and toes mustard-yellow, claws black except for paler bases. **Vocalisations** are very short rhythmic strophes of rapid toneless clucks, accented at the end.

Lectotype designation

The description of *Ninox spilonotus* (spelling thus) Bourns & Worcester 1894 was explicitly based on specimens from Cebu, Sibuyan, Tablas and Mindoro. The description does not indicate how many specimens were available, but the only specimens of the last three of these taxa at the NMNH (formerly USNM) are now considered the syntypes. We consider that Bourns & Worcester's (1894) *spilonotus* was based on four diagnosable taxa, and hence designation of a lectotype is necessary. The first specimen listed, from Cebu, is now BMNH 1955.6.N.20.4747, and is not currently considered a syntype (it does not bear a type label, and is not listed in Warren & Harrison 1973). However, Recommendation 74D in the current code (ICZN 2000; http://www.nhm.ac.uk/hosted-sites/iczn/code/index.jsp?nfv=true&article=74) states that the lectotype should be '...preferably of the institution containing the largest number of syntypes of the nominal species-group taxon...'. On this basis we exclude the BMNH Cebu specimen from further consideration as the lectotype, because NMNH has three syntypes. Subsequent to the description of *spilonota*, *Ninox mindorensis* Ogilvie Grant 1896 was described as a new species, based on a BMNH specimen (97.6.14.51) collected by J. Whitehead. This excludes the NMNH Mindoro specimen (USNM 314876) from further consideration as the lectotype of *spilonotus*. Therefore, we are left to choose between the two NMNH specimens, USNM 314877 from Sibuyan and USNM 314875 from Tablas. Neither specimen was figured at the time, and both agree approximately equally well with the description. We therefore arbitrarily fix USNM 314877 from Sibuyan, which precedes Tablas in the 'Habitat' list on the original description, as the lectotype of *Ninox spilonotus*. This furthermore implies that BMNH 1955.6.N.20.4747, USNM 314876, and USNM 314875 are paralectotypes of the name *Ninox spilonotus*. Note, however, that the first and last of these specimens are herein designated as types of a new species and a new subspecies, respectively.

DISCUSSION

Earlier treatments of taxa in the complex

Treatments of the Philippine *Ninox philippensis* complex have inevitably varied over time, and separate into two periods of activity, 1940–1945 and 1990–2000. First, Peters (1940) grouped the taxa into three species, (1) monotypic *N. philippensis* from Luzon, Marinduque, Masbate, Ticao, Guimaras, Negros, Leyte and Siquijor; (2) monotypic *N. spilonota* from Mindoro, Tablas, Sibuyan and Cebu; and (3) polytypic *N. spilocephala*, consisting of *N. s. mindorensis* from Mindoro, nominotypical *spilocephala* from Mindanao and Basilan, *N. s. reyi* from Sulu and Bongao (Sulu Islands), and *N. s. everetti* from Siasi (Sulu Islands). Shortly afterwards, Delacour & Mayr (1945) united these six forms (plus two, *proxima* and *centralis*, added by Mayr) as races of one species, *Ninox philippensis*, falling into three groups based on simple shared plumage characters (some of which were mistaken): (1) *philippensis* group ('upperparts plain, underparts boldly striped')—*N. p. philippensis* (Luzon, possibly also Marinduque, Samar and Leyte), *N. p. proxima* (Ticao and Masbate) and *N. p. centralis* (Siquijor; apparently also Panay, Guimaras, Negros); (2) *spilocephala* group ('head and neck spotted or barred, underparts striped or variegated')—*N. p. spilocephala* (Mindanao, Basilan), *N. p. reyi* (Sulu, Tawi Tawi, Bongao) and *N. p. everetti* (Siasi); and (3) *mindorensis* group ('head and neck spotted or barred; underparts entirely vermiculated or barred')—*N. p. mindorensis* (Mindoro) and *N. p. spilonota* (Tablas, Sibuyan, Cebu).

Sibley & Monroe (1990) accepted these groupings but rationalised them geographically north–south, making the *mindorensis* group (which, owing to chronological precedent, they called the *spilonota* group) second and *spilocephala* third. However, Dickinson *et al.* (1991) recast the arrangement (adding *ticaoensis*, described in 1972) rather more radically to give: *N. p. philippensis* (Luzon, Polillo, Catanduanes, Marinduque, Samar, Buad, Biliran and Leyte); *N. p. spilocephala* (Dinagat, Siargao, Mindanao and Basilan); *N. p. reyi* (Sulu, Siasi, Tawi Tawi and the adjacent Sanga

Sanga and Bongao, and Sibutu); *N. p. centralis* (Semirara, Carabao, Boracay, Panay, Guimaras, Negros, Siquijor and Bohol); *N. p. spilonota* (Tablas, Sibuyan, Cebu and Camiguin Sur); *N. p. proxima* (Masbate); *N. p. ticaoensis* (Ticao); and *N. p. mindorensis* (Mindoro). Kennedy *et al*. (2000) retained this treatment in spite of the queries by Collar & Rasmussen (1998) and the split of *mindorensis* by König *et al*. (1999).

On the basis of our data (and reiterating our doubt about the validity of *ticaoensis*) we propose the following arrangement (ranges derived from Dickinson *et al*. 1991, Dickinson 2003):

Luzon Hawk Owl *Ninox philippensis*
N. p. philippensis Biliran, Bohol, Boracay, Buad, Carabao, Catanduanes, Guimaras, Leyte, Lubang, Luzon, Marinduque, Masbate, Negros, Panay, Polillo, Samar, Semirara
N. p. ticaoensis Ticao
N. p. centralis Siquijor
Mindanao Hawk Owl *Ninox spilocephala*
Mindanao, Dinagat, Siargao, Basilan
Mindoro Hawk Owl *Ninox mindorensis*
Mindoro
Romblon Hawk Owl *Ninox spilonota*
N. s. spilonota Sibuyan
N. s. fisheri Tablas
Cebu Hawk Owl *Ninox rumseyi*
Cebu
Camiguin Hawk Owl *Ninox leventisi*
Camiguin Sur
Sulu Hawk Owl *Ninox reyi*
Sulu, Siasi, Tawi Tawi and the adjacent Sanga Sanga and Bongao, Sibutu

Figure 7 maps the newly defined species limits of the *N. philippensis* (*sensu lato*) complex. We use 'Luzon' rather than 'Philippine' as the common name for *N. philippensis* (*sensu stricto*) to avoid confusion with *N. philippensis* (*sensu lato*). For *N. spilonota* (*sensu stricto*) we use 'Romblon' because, although no member of this taxon is definitely known to occur on Romblon Island proper (there are unconfirmed reports), both Sibuyan and Tablas are part of Romblon province, so this seems the most appropriate geographical name for this species.

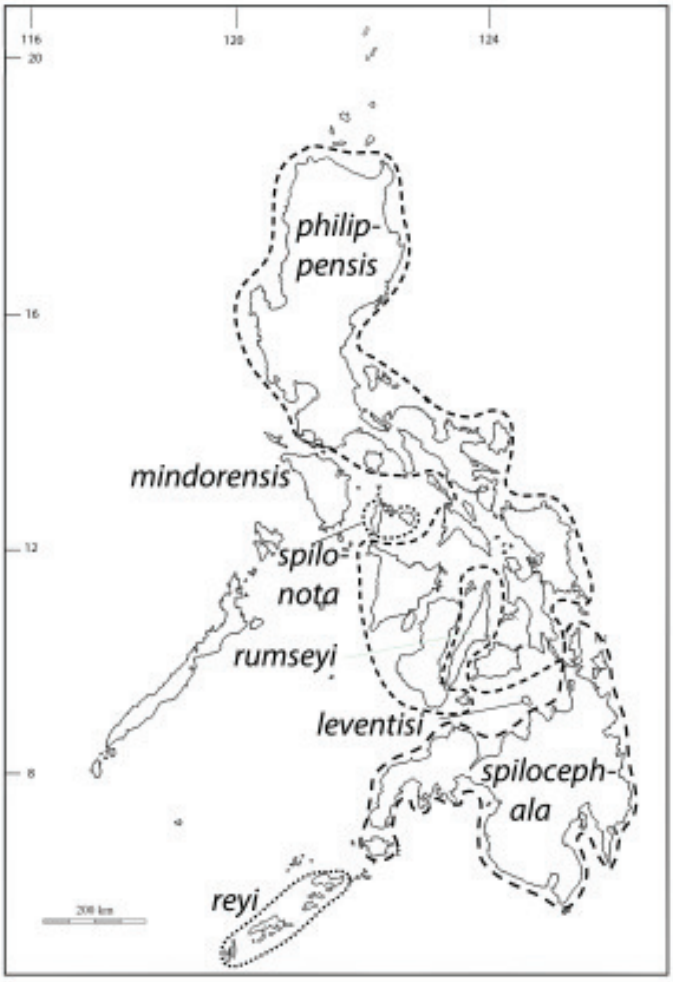


Figure 7. Map of species of the *Ninox philippensis sensu lato* species complex as recognised herein.

Relationships

How can we explain the curious circumstance in which rather similar-plumaged unstreaked *Ninox* populations are scattered on six well-separated islands or island groups within the Philippine archipelago while streak-breasted (or part-streak-breasted) populations occupy the largest islands? One possibility, consistent with the speculation in Collar & Rasmussen (1998) that all unstreaked forms are monophyletic, is that they represent the remnants of an earlier stock of *Ninox* which occupied the archipelago before being displaced from almost all islands which had a Pleistocene land-bridge by a later invasion of streak-breasted birds. Militating against this notion is the fact that the streak-breasted birds are generally smaller than the unstreaked forms.

Even so, *Ninox spilonota* of Tablas and Sibuyan, *N. rumseyi* of Cebu and *N. mindorensis* of Mindoro seem to form a monophyletic group. Their distribution mirrors that of some Philippine *Hypsipetes* bulbuls, of which the forms on Mindoro, Tablas, Romblon and Cebu are more closely related to each other than to the bulbuls of Negros, Panay, Greater Luzon and Greater Mindanao (Oliveros & Moyle 2010). Vocally *spilonota*, *rumseyi* and *mindorensis* all share certain characteristics including descending thin, squealed whistles and croaky hisses, and all are at least relatively high-pitched. *Ninox mindorensis* often particularly resembles the much larger *rumseyi* of Cebu in plumage pattern, although it is typically more narrowly and clearly barred below, and has the throat-patch duller and less conspicuous. *Ninox rumseyi*, which is geographically surrounded by *Ninox philippensis*, can only be diagnosed morphologically from *mindorensis* and *spilonota* on a combination of characters, although its song is moderately autapomorphic. Both forms of *Ninox spilonota* lack both strong head pattern and markedly paler throat-patch, but one specimen of *N. s. spilonota* from Sibuyan (FMNH 358295) shows a white-streaked underparts pattern similar to many *N. reyi* specimens, and thus recalls a weakly marked *N. spilocephala*.

The relationships of Mindanao's *spilocephala* remain unclear. Its different voice and certain other features (e.g. well-developed auriculars) are inconsistent with its being the link (Mayr 1945) between the plain-headed, streak-breasted *philippensis* and the unstreaked taxa. On the other hand its Sulu replacement *reyi*, although completely different from any other Philippine taxon in voice, shows plumage characters in some individuals (dark teardrop-shaped streaking on lower underparts) reminiscent of *spilocephala*, hinting at a shared ancestry. Given *reyi*'s geographical isolation from all taxa except *spilocephala*, this inference is more parsimonious than the notion that *reyi* is more closely related to a more widespread unstreaked form. (The possibility that *reyi* is more closely related to *Ninox ios* of Sulawesi, based on the similarity noted above in the quality if not the pattern of their songs, is not supported by their very dissimilar morphologies; see Rasmussen 1999.)

The derivation of *Ninox leventisi* of Camiguin Sur, despite the fact that this island lies just off Mindanao, is no less problematic. Although at least superficially similar in plumage to other unstreaked taxa, *leventisi* is the most highly autapomorphic of all taxa (although vocally *N. reyi* is even more so). In fact, *leventisi*

and *spilocephala* are strikingly dissimilar to each other, in size, plumage texture and fullness, development of filamentous auricular extensions, pattern of lower underparts, and soft-part colours. The only character that links *leventisi* with *spilocephala* to the exclusion of other taxa is the low pitch of their songs, albeit these are very different in other ways. Indeed, the long solo song of *leventisi* (SOM) has closer resemblances to that of *philippensis* than to any other taxon, and it may well be more closely related to *philippensis* than to the geographically closer *spilocephala* or the morphologically closer *spilonota*.

Resolution will have to await molecular analysis. For the moment, we note a high level of concordance between the species limits proposed here and zones of turnover proposed by Peterson (2006). A separate issue is that of generic limits of *Ninox*, which at least on morphology is probably a non-monophyletic group (Rasmussen 1999). A recent molecular phylogeny (Wink *et al*. 2009) shows a monophyletic *Ninox* but taxon sampling therein was not dense. Although we think that all the species formerly united under *Ninox philippensis* are indeed fairly closely related, this remains to be established, most likely by molecular analyses.

The conservation status of these various forms needs full evaluation elsewhere. However, it should be noted at once that five species—*mindorensis*, *spilonota*, *rumseyi*, *leventisi* and *reyi*—are likely to be at risk. On Mindoro, the Sablayan Penal Colony holds the largest remaining area of lowland forest on Mindoro, and is critically important for populations of lowland bird species endemic to Mindoro (Brooks *et al*. 1995a, Mallari *et al*. 2001). The Mindoro Hawk Owl is also known from forest in Mts Iglit-Baco National Park (Gonzalez & Dans 1998), Naujan Lake National Park (Ticsay & Ledesma 1998), and Mt Halcon between 1,150–1,250 m (ROH). Satellite images taken in the late 1980s suggested Tablas then held two forest parcels together covering under 0.5 km^2 (Goodman & Ingle 1993) and recent visits confirm that the amount of habitat there is tiny, although the species occurs in tall secondary as well as primary forest on the island (Allen 2006, DNSA, ROH). Meanwhile, although forest covered over half of Sibuyan's 233 km^2 land surface at the start of the 1990s, logging was proceeding apace and, in the absence of intervention, all lowland areas were predicted to be cleared within a few years (Goodman & Ingle 1993); illegal logging inside Mt Guiting-guiting Natural Park continues (M. Wallbank verbally 2009 to DNSA). On Cebu, where it was rediscovered in 1998 after a gap of 110 years, the total population of Cebu Hawk Owls may be just 192 pairs (and possibly many fewer) scattered among 11 forest patches (Jakosalem *et al*. in press). On Camiguin Sur forest covers just the centre of the small island, and numbers of the species cannot be high (Heaney & Tabaranza 2006). Finally, of the six islands in the Sulu archipelago from which the owl has been recorded, the current status of forest on Siasi appears on satellite photos to show that almost the entire island's forest has been replaced by orchards; Sulu (Jolo) has apparently also been largely converted except around the volcanic cones; Sanga-Sanga's last forest patch was cleared in 1992–1993; and Bongao retains only a small patch of forest on its sacred mountain (DNSA, ROH). Sibutu may have significant areas of secondary forest, although that seen by DNSA in 1995 was of low stature. The main island of Tawi Tawi still has much secondary and some primary forest (Dutson *et al*. 1996, DNSA, ROH). However, on Tawi Tawi *N. reyi* is also found in forest edge, mature mangroves and large trees in the vicinity of villages.

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Supplementary online material

To be found under *Forktail* 28 page on www.orientalbirdclub.org.

SOM 1. Additional songs of taxa in the Philippine Hawk Owl *Ninox philippensis* (*sensu lato*) complex. SOM 1a.12453: short isolated duetted segment of song of Philippine Hawk Owl *N. p. philippensis*, AV#12453, ROH, Luzon; SOM 1b.13551: long song by a single bird, joined near the end with another in a presumed duet; Philippine Hawk Owl *N. p. philippensis*, AV#13551, ROH, Luzon. SOM 1c.8972: series of short duetted strophes by Philippine Hawk Owl *N. p. centralis*, F. Verbelen, Bohol; SOM 1d–e.10700: long series by Philippine Hawk Owl *N. p. centralis*, FRL, Negros; SOM 1f.112a: long series by Philippine Hawk Owl *N. p. centralis*, DNSA, Siquijor; SOM 1g.99: three short duetted strophes by Philippine Hawk Owl *N. p. centralis*, DNSA, Siquijor, with many hoarse notes. SOM 1h.13557: duetted series of short strophes with stray notes between main strophes; Camiguin Hawk Owl *Ninox* sp. 1. SOM 1i: single Camiguin Hawk Owl *Ninox* sp. 1 singing, giving several more notes/strophe than in Figure 2c. SOM 1j: continuation of long song of Mindanao Hawk Owl *N. spilocephala*, starting where Figure 2d ends. SOM 1k: duet by Sulu Hawk Owl *N. reyi*, series of short variable strophes. SOM 1l: continuation of duet of Mindoro Hawk Owl *N. mindorensis*, starting where Figure 2g ends; SOM 1m–n: whistled duet of Mindoro Hawk Owl *N. mindorensis*, with many highly frequency-modulated notes. SOM 1o: Variant song and note-types of Romblon Hawk Owl *Ninox spilonota* new ssp. on Tablas; SOM 1p.11510: duetted song type of Romblon Hawk Owl *Ninox spilonota* on Sibuyan. SOM 1q–r: various alternate song types of Cebu Hawk Owl *Ninox* new sp. 2.