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Reprising the taxonomy of Cyprus Scops Owl *Otus* (*scops*) *cyprius*, a neglected island endemic

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Abstract

The endemic Cyprus Scops Owl *Otus* (*scops*) *cyprius* has been treated as a subspecies of the widespread Eurasian Scops Owl *O. scops* since at least the 1940s. However, its song is distinct from that of all other subspecies of *O. scops* in being double-noted, rather than single-noted. Its plumage also differs, most obviously in being consistently darker than other subspecies and in lacking a rufous morph. However, it shows no biometric differences from *O. s. cycladum* and southern populations of *O. s. scops*. It is also unusual among *scops* (*s. l.*) populations in being at least partially resident, although two specimens showing characters of this taxon were collected in Israel in early spring, and the numbers of birds that are resident on Cyprus appear to vary, with few recent winter records. It differs from *O. s. scops* by one synapomorphic nucleotide exchange in the analysed mitochondrial marker, indicating a recent separation. Given that large numbers of *O. s. scops* and *O. s. cycladum* pass through Cyprus on spring migration, and that the latter breeds in adjacent countries, it seems probable that *cycladum* would colonize the island, but for the presence of *cyprius*. That it does not do so, and that *cyprius* retains its distinctive song and plumage, suggests that isolating mechanisms exist. We recommend that *cyprius* be considered specifically distinct, as are other distinctively voiced insular *Otus* populations.

Key words: taxonomy, mitochondrial DNA, *Otus*, Cyprus, morphometric analyses

Introduction

Cyprus Scops Owl *Otus* (*scops*) *cyprius* (von Madarász, 1901), which breeds only on Cyprus, was initially afforded specific status, owing to its very dark coloration without buff, perceived larger size, and resident status (von Madarász 1901). The type specimen, a male collected on 8 February 1901 at 'Livadia', Cyprus, and held in Budapest, was destroyed by a fire in 1956 (L. Horváth *in* Flint & Stewart 1983) but another, a female, sent by Madarász and originally labelled 'cotype' is at Manchester University Museum (reg. no. B.10688; H.A. McGhie *in litt*. 2013). However, the latter cannot be considered to have type status, as its original label states that it was collected on 1 March 1902 (at Stavrovouni, Cyprus), and therefore could not have been to hand when Madarász described his new taxon, as the relevant issue of the *Természetrajzi Füzetek* containing his description is dated 10 June 1901. Cyprus Scops Owl was treated subspecifically by Vaurie (1960, 1965) and C.S. Roselaar (*in* Cramp 1985), both of whom considered it a well-defined island endemic because of its distinctive plumage, whereas König *et al*. (1999) initially united it with birds from Turkey (*O. s. cycladum*) but subsequently reinstated the last-named race for populations in Crete, the Cyclades, southern Greece and southern Turkey to Israel and Jordan (König *et al*. 2008). In addition, Eurasian Scops Owl occurs commonly on Cyprus as a passage migrant in Mar–early May and Sep–Oct; most are apparently *O. s. scops*, though *O. s. cycladum* also occurs (Flint & Stewart 1992).

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The song of *cyprius*, a regularly repeated double note, was long believed to be a pair duet, being described as 'a clear single flute-like note uttered first by the male, and answered immediately a few tones lower by the female' (Bannerman & Bannerman 1958); to some extent this belief persists. In 1991, when D.W. & J. Dawes resided at Marathounta, Paphos, western Cyprus, they discovered that the two notes were produced by one bird and realized it was very different from the single-note song of Eurasian Scops Owl and from its duets (Mikkola 1983; Cramp 1985; Voous 1988). Despite a published note (Whaley 1991) and confirmation of the vocal differences in a sound-recording made by J. Gordon, the discovery did not become widely known. Although *cyprius* is rarely seen singing by day and there was an apparently reasonable explanation for its different song (i.e. duetting), in retrospect it is strange that the significance of its two-note song should have gone unremarked for so long.

In 1998 the two-note song and some three-note phrases were independently noted by P. Cant (pers. comm.), who observed a singing owl at close range in daylight. Cant informed P.F., who attracted singing owls closely using playback. These owls almost constantly gave two-note phrases, which P.F. observed were made by individuals, not pairs. One individual included three- and four-note phrases among the two-note phrases.

While living in different parts of Cyprus, D.W. & P.F. started work on separate papers, but in 1999 learnt of their common interest and were later joined by M. Robb, who in Mar–Apr 2000 visited the island to sound-record birds. He confirmed the two-note song of *cyprius*, recording both it and male-female duets. The distinctive song of *cyprius* was briefly reported, and its possible significance discussed, by Ieronymidou (2008), Kirwan *et al*. (2008), Charalambides (2010) and Porter & Aspinall (2010), and was described by Robb & The Sound Approach (2015). The present paper aims: (1) to provide a fuller analysis of the song of *cyprius* compared to that of *scops*[1]; (2) to compare the morphology, molecular phylogenetics, resident status and breeding biology of *cyprius* with those of *scops*; and (3) to re-assess the taxonomic status of *cyprius*.

Material and methods

Vocalizations. Vocal analyses of *cyprius* were based on the songs of 39 different birds from virtually throughout Cyprus. Ten songs were timed in the field for mean phrase length (the interval between consecutive loud notes) over ten phrases using a stopwatch (P.F., C. Richardson), while for the other 29 songs mean phrase length, first and second note frequency, and second note position and relative amplitude were measured by P.F. from recordings (recordists: M.C., 2 recordings; J. Honold, 9; C. Richardson, 9; M. Robb, 6; M. Smith, 1; Robb & The Sound Approach, 2) using Raven Lite 1.0 software (Cornell Lab of Ornithology). The field-timed songs were of solo-singing presumed males; the recordings measured included 15 solo-singing presumed males and seven with two singing birds on each; the latter included at least four duetting male/female pairs, while the remaining three were either duetting pairs and/or two rival males in close proximity.

For consistency, the frequency (kHz) of each recorded song was measured at the point of maximum power (dB) within the main horizontal section of each sonogram (excluding the initial vertical spike present in some notes). Relative amplitude (amplitude of the quieter note/amplitude of the louder note %) was unreadable in three recordings due to high background noise. Three- and four-note phrase timings were determined from the recordings as were the notes (louder or quieter) on which songs begin and end. The phrase composition of three complete songs containing three- and four-note phrases was noted in the field (P.F.). For *scops* we analyzed mean phrase length and frequency and noted the presence/absence of a second note in a total of 108 recordings of solo-singing presumed males where the provenance is known, including presumed *O. s. pulchellus* (n = 11) from China, Pakistan and Kazakhstan; presumed *O. s. turanicus* (n = 1) from Iran, presumed *O. s. scops* (n = 56) from France, Sardinia, Corsica, Italy, Austria, Switzerland, the Czech Republic, Slovakia, Croatia, Bulgaria, Romania, northern Greece, northern Turkey and Russia, presumed vagrant *O. s. scops* (n = 10) from Switzerland, Germany, the Netherlands, Sweden and Finland; presumed *O. s. mallorcae* (n = 20) from Morocco, Portugal, Spain and Mallorca, and presumed *O. s. cycladum* (n = 10) from southern Turkey, Kephalonia, Kos, Lesbos, the Peloponnese, Crete and Israel (hosted on: www.xeno-canto.org, www.ibclynxeds.com, www.avisoft.com, www.birdsofkazakhstan.com,

1. Throughout this paper, we use the following terminology when referring to the *Otus scops* complex: *scops* = *O. scops* excluding *cyprius*; *scops* (*sensu lato*—*s. l.*) = *O. scops* as presently defined, *i. e*. including *cyprius*. Nominate *O. s. scops* is always defined as such.

www.avocet.zoology.msu.edu, www.macaulaylibrary.org, www.youtube.com, www.birdsongs.it, www.ivovicic.bandcamp.com, www.kalerne.net and www.freesound.org, and from M. Strömberg, A.D. Mitchell, the British Library of Wildlife Sounds and Mild 1990). We also examined, but did not include in our main analysis, a recording from France (C. Chappuis *in* Palmér & Boswall 1968–80), and sonograms from Morocco (A.B. van den Berg pers. comm.) and Kazakhstan (M. Robb pers. comm.). Recordings of solo-singing *cyprius* were of regularly singing and apparently territorial birds so are presumed to be males. However, unpaired females of *scops* in the early breeding season sing in a quite similar manner to that of the male (Cramp 1985); this is probably also the case in *cyprius* so we cannot exclude the possibility that our recordings of solo *cyprius* and *scops* include a few females.

Morphometric data. According to existing label data, G.M.K. examined specimens of *O. scops* (nominate from the south of its breeding range—northern Turkey, Romania, Yugoslavia and the Volga region of Russia—and *O. s. cycladum* from Israel, Palestine, southern Turkey, Crete, Cephalonia and Greece, $n = 25$) and *O.* (*s.*) *cyprius* ($n = 28$) at the following museums: Natural History Museum, Tring (NHMUK; $n = 8$ *scops*, $n = 10$ *cyprius*); National Museums of Scotland, Edinburgh (NMS; $n = 2$ *scops*, $n = 1$ *cyprius*); Tel Aviv University Museum (TAUM; $n = 7$ *scops*, $n = 5$ *cyprius*); and Naturalis Biodiversity Center, Leiden (RMNH; $n = 8$ *scops*, $n = 12$ *cyprius*). The following measurements were taken according to standard protocols (Svensson 1992) using dial callipers and a metal wing-rule with a perpendicular stop at zero: wing length (from carpal joint to tip applying gentle pressure to the primary-coverts—Svensson's method 2); tail length (from the pygostyle to the tip); tail gradation (from tip of longest to tip of shortest rectrix); tarsus length (from the back of the intertarsal joint to the last complete scute before the toes diverge); bill length (from the tip of the maxilla to skull) and bill depth (at the feathers); as well as the following measurements relating to wing formula: distance of pp1–5 to wingtip (primaries numbered ascendantly, thus p1 = outermost); and the relative positions of p2 and p3 versus the other primaries. G.M.K. also examined (but did not measure) specimens labelled *O. s. cycladum* ($n = 12$) and *O. s. cyprius* ($n = 10$) at the Museum für Naturkunde, Berlin (ZMB), and Zoologisches Forschungsinstitut und Museum Koenig, Bonn (ZFMK).

Morphometric differences between *scops* and *cyprius* were investigated using a multivariate approach. For individuals with all measurements available, we analyzed wing, tail, tarsus and bill lengths, the length of three primaries (pp1, 4 and 5) relative to the wingtip, which was formed by either p2 or p3 (Table 7). The method of Baur & Leuenberger (2011) was applied, which permits interpretation of principal components (PCs) as ratios, enabling a strict separation of differences in size and shape. Such distinction is important in diagnosing taxa as shape can provide more reliable information than size in morphological comparisons (Jolicoeur & Mosimann 1960). This approach uses the geometric mean of original measurements to define an isometric size axis ('isosize') (*cf.* Baur & Leuenberger 2011). Isosize is composed solely of differences in scale, and size-independent shape variables are then obtained by projecting the measurements orthogonal to isosize. A PCA accounting exclusively for differences in proportions is then computed on the covariance matrix of the shape parameters.

Genetic data. For DNA studies, samples were obtained for *cyprius* ($n = 3$), *cycladum* ($n = 4$), nominate *scops* ($n = 2$) and *pulchellus* ($n = 1$) (Table 8). A molecular phylogeny of *O. scops* was reconstructed by maximum likelihood (ML) using nucleotide sequences of mitochondrial cytochrome *b* gene (900 nucleotides). The program MEGA5 (Tamura *et al*. 2013) was used to calculate the ML tree under the following conditions: Substitution model: Tamura-Nei; rates among sites: gamma distributed (G) with five discrete Gamma categories; tree inference option: ML heuristic method with subtree-pruning-regrafting (SPR level 5). DNA isolation, amplification and sequencing of cytochrome *b* were performed as outlined in Wink *et al*. (2009). Cytochrome *b* sequences have been submitted to GenBank with the accession numbers KR181837–KR181846 (Table 9).

Results

Song of Cyprus Scops Owl (*cf.* Table 1). *Two-note song*.—The advertising or territorial song of male *cyprius*, given throughout its breeding season and occasionally all year, is a continuous series of two-note phrases. In each phrase there is clear contrast between a louder, longer, slightly higher-pitched note followed by a longer silence, and a quieter, shorter, slightly lower-pitched note followed by a shorter silence (Fig. 1a). Although the second note is quieter than the first, both are normally clearly audible even in a distant bird. The steady rhythmical alternation of these two notes is very different from the well-known single-note song of *scops* (Fig. 1b) although a few *scops* include a usually faint and sometimes intermittent second note in their song (Fig. 1f and see below).

TABLE 1. Differences in songs of Cyprus *Otus* (*scops*) *cyprius* and Eurasian Scops Owls *O. scops*.

Cyprus Scops Owl *O.* (*s.*) *cyprius*	Eurasian Scops Owl *O. scops*
Mean frequency of louder note at maximum power (dB) = 1.11 kHz (range 1.00–1.36 kHz , *n* = 15)	Mean frequency of single note at maximum power (dB) = 1.33 kHz (range 1.20–1.55 kHz, *n* = 108)
Mean phrase length = 3.34 seconds (range 2.95–3.81 s, *n* = 25)	Mean phrase length = 2.80 seconds (range 2.28–3.37 s, *n* = 108)
Two notes per phrase	Usually a single note per phrase, occasionally two
32–40 notes/minute	18–26 notes/minute in usual single-note phrases
Second note is quieter than the first note but still quite loud and clearly audible at a distance	Second note, if present, is usually faint, often intermittent and inaudible at a distance
Usually isolated three- and four-note 'phrases' occur within a series of two-note song phrases	Not known to produce three-note or four-note phrases
Two-note song differs from *duet* of Eurasian Scops in that the quieter note is usually slightly lower pitched than the louder note and the two notes always maintain the same rhythmic pattern	Duets have the quieter note usually higher pitched than the louder note. Male and female notes are often not synchronised, not maintaining the same rhythmic pattern
Duets involve a cycle of four notes (one two-note phrase from each bird) and can be synchronised or unsynchronised	Duets involve a cycle of two notes (one single-note phrase from each bird) and can be synchronised or unsynchronised

The mean phrase length of *cyprius* is 19% longer than that of *scops* and 20% longer than that of *O. s. cycladum* (Table 2), the latter the closest race to *cyprius* in distribution and plumage. As each *cyprius* phrase contains two notes, *cyprius* gives *c*. 68% more notes/min than *scops* (mean 35.93 vs. 21.43). Phrase length, second note position and first and second note frequencies of *cyprius* are highly consistent individually (Table 3); as suggested by Le Gassick (1993) for phrase length, these consistencies may be used to identify individual birds. Consistent individual phrase lengths and frequencies are also a feature of *scops* (Cramp 1985; Denac & Trilar 2006; Dragonetti 2007). The mean frequency of the louder note of *cyprius* is 17% lower than that of *scops* and 15% lower than that of *O. s. cycladum* (Table 2), supporting the finding by Robb & The Sound Approach (2015) that *cyprius* song is lower-pitched. The mean frequency of the second note of *cyprius* is 96% that of the first note (SD ± 5%, range 88–101%; *n* = 15).

TABLE 2. Song timings and frequencies: *O.* (*s.*) *cyprius*, *O. scops* and *O. s. cycladum*. For each the mean, ± SD and range are given.

Character → Taxon ↓	Phrase length (seconds)	2nd note position (% of phrase length)	Frequency range: 1st note (kHz)	Frequency range: 2nd note (kHz)
O. (*s.*) *cyprius* Solo-singing males	3.34 ± 0.27 2.95–3.81 *n* = 25	57.2 ± 3.5 51.7–63.2 *n* = 15	1.11 ± 0.09 1.00–1.36 *n* = 15	1.07 ± 0.07 0.95–1.26 *n* = 15
O. (*s.*) *cyprius* Two birds singing together (see Methods)	3.34 ± 0.32 2.90–3.70 *n* = 14	55.4 ± 3.2 50.5–61.1 *n* = 14	1.13 ± 0.08 1.03–1.29 *n* = 14	1.09 ± 0.09 0.94–1.31 *n* = 14
O. scops Solo-singing males	2.80 ± 0.26 2.28–3.37 *n* = 108		1.33 ± 0.09 1.20–1.55 n = 108	
O. s. cycladum Solo-singing males	2.78 ± 0.28 2.28–3.12 n = 10		1.31 ± 0.06 1.22–1.38 *n* = 10	

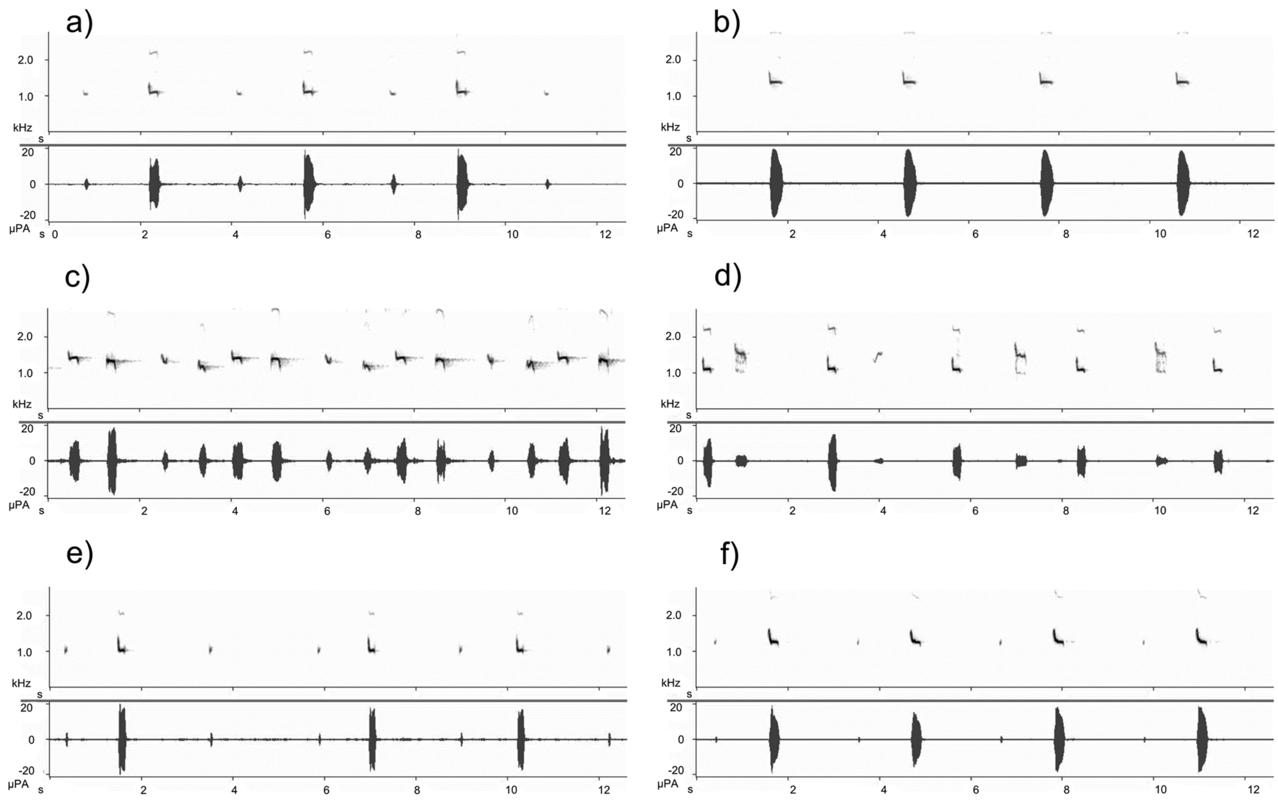

FIGURE 1. (a) Typical two-note song of Cyprus Scops Owl *Otus* (*scops*) *cyprius*, Nikoklia, Paphos District, Cyprus, 7 April 2000 (Magnus Robb / The Sound Approach). **(b)** Typical single-note song of Eurasian Scops Owl *Otus scops*, presumably *O. s. scops*, Ooypolder, Ubbergen, Gelderland, Netherlands, 2 June 1998 (Magnus Robb / The Sound Approach). (**c**) Duetting by presumed female and male Cyprus Scops Owl *Otus* (*scops*) *cyprius*, near Troodos, Cyprus, 26 March 2000 (Magnus Robb / The Sound Approach). The sequence of notes is: female louder note, male louder note, female quieter note, male quieter note, etc. (**d**) Duetting of Eurasian Scops Owl *Otus scops mallorcae*, Mallorca, Spain, April 1990 (Claus König, British Library of Wildlife Sounds, London, UK). (**e**) Example of two quiet notes between loud notes, Cyprus Scops Owl *Otus* (*scops*) *cyprius*, Neokhorio, Akamas, Cyprus, 2 April 2000 (Magnus Robb / The Sound Approach). **(f)** Song of Eurasian Scops Owl *Otus scops cycladum* with faint second note, Crete, Greece, May 1989 (Mats Strömberg, via Krister Mild Bioacoustics).

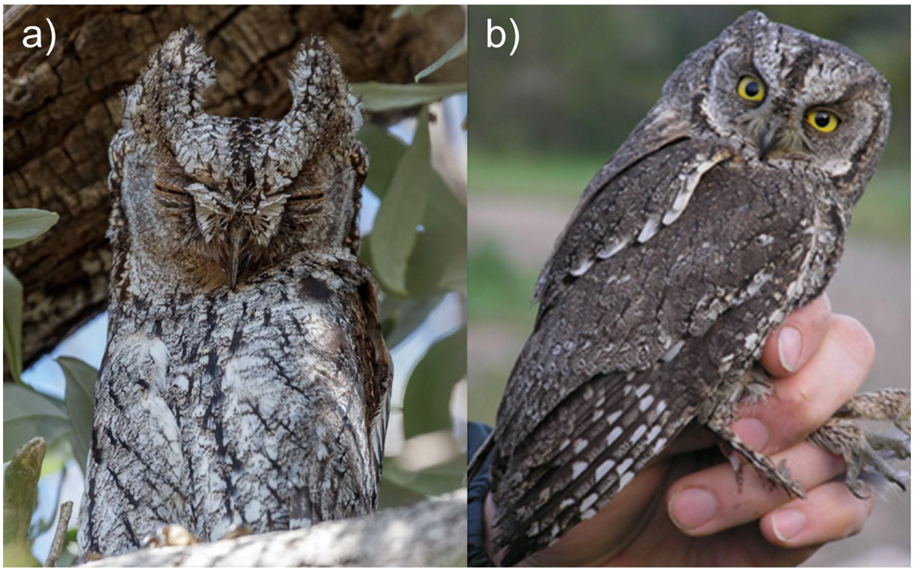

FIGURE 2. (a), Cyprus Scops Owl *Otus* (*scops*) *cyprius*, near Paphos Zoo, between Peyia and Agios Georgios, Paphos District, Cyprus, 25 May 2012. (© Albert Stoecker). **(b)**. Cyprus Scops Owl *Otus* (*scops*) *cyprius*, Ayios Minas, Paphos District, Cyprus, 10 April 2006. (© Geoff Mawson)

FIGURE 3. (a). Comparison (left to right) between two Eurasian Scops Owl taxa: *O. s. mallorcae* from Mallorca and *O. s. cycladum* from Palestine and from Crete, and Cyprus Scops Owl *Otus* (*scops*) *cyprius*. (Guy M. Kirwan / © Natural History Museum, Tring). **(b–e)** Comparison between three typical Cyprus Scops Owls *Otus* (*scops*) *cyprius* (**b**, dorsal; **d**, ventral) and three Eurasian Scops Owls from Turkey (**c**, dorsal; **e**, ventral), the left and right birds from Turkey were collected within the breeding range of *O. s. cycladum*, the centre bird within that of *O. s. scops*. (Guy M. Kirwan / © Natural History Museum, London).

Songs of *cyprius* may begin and end on either note: in our recordings seven songs commence with the quieter note and two with the louder, while five songs end with the quieter note and seven with the louder. As most recordings contain incomplete songs they are unsuitable for calculating mean song duration; the shortest song is one isolated phrase (one louder note, one quieter note). The longest continuous song timed in the field is 18 min 52 sec (P.F.).

Male/female duets.—Four-note duetting by a pair with both birds producing two-note songs (Fig. 1d) occurs commonly in *cyprius*. It has been recorded from a breeding pair at a nest box (M.C.) and often emanates from the same tree, indicating that a pair is involved. In duets, female two-note song is very similar to the male's, but may be slightly higher-pitched, weaker and more modulated (Robb & The Sound Approach 2015).

Duets in *cyprius* may be synchronized (or almost so) or unsynchronized (the song of one bird appears to catch up with then overtake the other); duetting by *scops* is similar in this respect (Mikkola 1983; Cramp 1985) but if the sonogram of *cyprius* duetting (Fig. 1c) is compared to that of *mallorcae* (Fig. 1d), there are striking differences. The duet of *cyprius* involves four different notes (two two-note phrases) whereas that of *mallorcae* involves just two different notes (two one-note phrases).

Of seven recordings of two birds singing together, four appear to be male/female duets: the songs in these were sexed using various combinations of note frequency, loudness, regularity (continuous or not) and the presence of female 'twiu' calls (Robb & The Sound Approach 2015). The three other recordings of 'pairs' could not be reliably sexed; they were male/female duets and/or two rival males in close proximity. In the duets, male and female second notes have a higher relative amplitude (*i.e.* are louder) than those in male solo song (Figs. 1a, c; Table 4). The unsexed 'pairs' also have a higher second note mean relative amplitude than that in male solo song (Table 4). In the seven recordings of two birds singing together, phrase length, second note position and first and second note frequency are similar or close to those of solo males (Table 2).

TABLE 3. *O.* (*s.*) *cyprius* individual variation over ten phrases for phrase duration, second note position and first and second note frequency for 15 solo-singing males. For each the mean, ± SD and range are given.

Individual variation in phrase duration (seconds)	Individual variation in 2nd note position (% of phrase length)	Individual variation in 1st note frequency (kHz)	Individual variation in 2nd note frequency (kHz)
0.09 ± 0.04 0.02–0.18, *n* = 15	1.6 ± 0.7 0.6–2.6, *n* = 15	0.03 ± 0.05 0.00–0.14, *n* = 15	0.04 ± 0.05 0.00–0.17, *n* = 15

TABLE 4. *O.* (*s.*) *cyprius* second note relative amplitude (second note amplitude/first note amplitude %) when duetting, singing in 'pairs' and males singing solo. For columns 1, 2, 5 & 6 the mean, ± SD and range are given.

Duetting males	Duetting females	Duetting male, 26 Mar 2000 (M.R.)	Same male, 26 Mar 2000, singing solo (M.R.)	3 unsexed 'pairs' (with at least one male in each)	Solo-singing males
56.2 ± 16.1 43.2–77.1 *n* = 4	58.0 ± 5.0 51.9–64.2 *n* = 4	62.9 (mean of 10 consecutive phrases)	37.9 (mean of 10 consecutive phrases)	40.0 ± 5.2 34.2–46.4 *n* = 6	28.3 ± 9.3 14.2–49.7 *n* = 15

Apparent three- and four-note phrases.—Some *cyprius* song phrases include two consecutive quieter notes between louder notes (apparent three-note phrases, Fig. 1e) while others include three consecutive quieter notes (apparent four-note phrases). Three complete songs (three individuals) containing apparent three- and four-note phrases monitored in the field by P.F. included: (1) 36 two-note and four three-note phrases, (2) 45 two-note, two three-note and three four-note phrases, and (3) 370 two-note and three three-note phrases. In these songs each of the three- and four-note phrases occurred in isolation among normal two-note song, but in one recorded song (C. Richardson, 18 Jun 2013) three consecutive three-note phrases occur and in another (C. Richardson, 3 Jul 2015 #3) two consecutive four-note phrases occur.

The additional quieter notes in three- and four-note phrases are all usually clearly audible in the field, but are easily overlooked unless closely listened for or detected in sonograms. However, they have been heard or recorded at many locations and are apparently common. Nothing similar is known in *scops* (M. Robb pers. comm.) and none of our *scops* recordings include such phrases.

Three-note phrases (n = 11) amongst two-note song are given by five of the 29 *cyprius* in our recordings and four-note phrases (n = 3) by two birds (Table 5). In ten of these three-note phrases the first quiet note is within the normal timing range for the second note of that individual's two-note song, and nine of the second quiet notes lie within the normal timing range for the quiet note preceding the next loud note in two-note song. The gap between the two quiet notes varies, but in no case fits the normal note timings for that individual. This suggests that three-note phrases may represent the end of one song on a quiet note, followed by the almost immediate commencement of a new song, also on a quiet note. The first and last quiet notes in the four-note phrases also fit the normal timings for those individuals, with one additional note between that varies in its timing (Table 5) and appears as a pause or hesitation in normal song.

TABLE 5. *O.* (*s.*) *cyprius* three- and four-note phrase timings in seconds. For columns 1–4 the mean, ± SD and range are given; the last column gives timings for individual notes.

Three-note phrase: duration	Three-note phrase: interval between loud note and first quiet note	Three-note phrase: interval between the two quiet notes	Three-note phrase: interval between second quiet note and following loud note	Four-note phrases (n = 3): intervals between notes
5.67 ± 1.02 4.41–7.06, n = 11	1.81 ± 0.13 1.53–1.95, n = 11	2.42 ± 0.63, 1.72–3.33, n = 11	1.49 ± 0.32 0.92–1.87, n = 11	1st–2nd : 1.90, 1.63, 1.70 2nd–3rd : 2.36, 1.81, 2.75 3rd–4th : 1.43, 2.19, 2.96 4th–next: 1.78, 1.30, 1.27

Single-note songs in Cyprus—Most observers reporting *Otus* song types in Cyprus have never heard single-note songs [e.g., M.C., P.F., G.M.K., C. Richardson (pers. comm.), M. Robb (pers. comm.), D. Pomeroy and F. Walsh (pers. comm.)]. Single-note songs were heard by D.W. only at Marathounta, Paphos District, on 17 and 29 Mar 1991 and 16 Mar 1992; these single-note songs prompted local *cyprius* to respond strongly, and given the dates, they could refer to migrant *scops* en route north. Occasional quiet single-note 'songs' heard in Cyprus in May–Jun 2013 (J. Honold pers. comm.) are believed to represent a female contact/begging call shared in similar form by several Palearctic *Otus* (Robb & The Sound Approach 2015). Occasional single-note song heard in Cyprus by C. Ieronymidou (pers. comm.) and by M. Hellicar (pers. comm.) might also fall into this category.

Individual notes in the single-note song of *scops* sound very similar to the louder note in two-note *cyprius* song, which is also suggested by the strong response of *cyprius* to playback of the single-note song of *scops* (see below). Elsewhere it is not unusual for Eurasian Scops Owls to sing at least briefly on spring migration (M. Robb pers. comm.), but although many *scops* migrate through Cyprus and breed in southern Turkey and the Levant, their single-note song is almost never heard on the island. Perhaps they are inhibited by the high density of singing *cyprius* and by the strong response of existing territory holders to 'interlopers'.

Response to playback.—Song from a recording of a single-note *O. scops* (Roché 1996) was played by P.F. on 6 & 7 Jul 1998 and 15 Mar 2002 at three sites in olive/cypress woodland east of Kyrenia, at each of which several *cyprius* were singing. At all three sites singing owls approached the speaker closely; at the first an owl landed next to it and another approached to an adjacent tree, at the second two more distant owls approached into trees close by and at the third an owl flew into a mist-net above the speaker.

Two-note song phrases of Eurasian Scops Owl. The advertising song of *scops* is single-noted with little geographical variation (Cramp 1985) and all of the 104 recordings on the websites listed in Methods (as of 20 Sep 2015) are of such single-note song. However, occasional two-note song has been noted in Morocco (A.B. van den Berg pers. comm.), France (C. Chappuis *in* Palmér & Boswall 1968–80), Crete (M. Strömberg pers. comm., Fig. 1f; A.D. Mitchell pers. comm.), mainland Greece (M. Strömberg pers. comm.), Israel (Mild 1990), Portugal, Jordan and Kazakhstan (M. Robb pers. comm.) and Pakistan (Roberts & King 1986). Exceptionally, as in the case of one heard in Portugal, the second notes may be as loud as in *cyprius* (M. Robb pers. comm.), but they are usually quieter and shorter, may be intermittent and also tend to occur later in the phrase (Table 6, Fig. 1f).

TABLE 6. Details of two-note songs of individual *scops* from Morocco, Kazakhstan, France, Israel, and Crete ($n = 2$) and of solo-singing male *cyprius* from Cyprus. For *cyprius*, columns 2, 3 & 6 give mean and range. For origins of *scops* recordings see Two-note song phrases of Eurasian Scops Owl.

Location	Phrase length (seconds)	Second note position as % of overall phrase duration	% of phrases where second note audible or visible on sonograms	Second note volume *cf.* second note of *cyprius*	Second note, relative amplitude (%)
Morocco	2.81	67.6	100	much fainter	6.9
Kazakhstan	2.77	75.1	<50	very much fainter	3.5
Camargue, France	3.39	61.0	100	much fainter	10.2
Israel	3.05	61.1	100	much fainter	10.1
Crete, Fig.1f	3.04	62.9	28	much fainter	<10.0
Crete	2.89	67.5	25	much fainter	unreadable
Cyprus	3.34 2.95–3.81 $n = 25$	57.2 51.7–63.2 $n = 15$	100	n/a	28.3 14.2–49.7 $n = 15$

From our sample, songs with a second note are scarce in *O. s. scops*, *mallorcae* and *pulchellus*; two recordings from Mallorca (British Library of Wildlife Sounds) are both single-noted. In *O. s. cycladum* a second note is present in two recordings from Crete and in that from Israel (and in another from there; K. Mild pers. comm.) but on Crete a second note has not been noticed by Y. Kontogeorgos (pers. comm.) or by C. Turvey (pers. comm.) and in Israel H. Shirihai (pers. comm.) has never heard anything other than normal *scops* song. Also, a second note is not present in four *cycladum* recordings from Kephalonia, Kos, Lesbos and the Peloponnese (www.xeno-canto.org, www.avisoft.com, www.avocet.zoology.msu), and importantly, in the *cycladum* population closest to Cyprus, that in southern Turkey, it is inaudible or absent in six of seven recordings by A.B. van den Berg (M. Robb pers. comm.), and four other recordings from there (www.soundcloud.com, www.xeno-canto.org) are also of single-note songs. This supports the statement in Kirwan *et al*. (2008) that vocalizations from southern Turkey are very similar to those of nominate *scops* in northern Turkey and of *turanicus* from the extreme south-east, and are distinct from *cyprius*.

Biometrics. The principal component analysis (PCA) performed in isometry-free shape space revealed no separation in shape PC1 and shape PC2 between *O. s. scops*/*cycladum* and *cyprius* (not shown). Moreover, there was a complete overlap in isosize between the two (not shown). Biometric data from specimens and live birds are summarized in Table 7.

Plumage. The Cyprus Scops Owl (Figs. 2 and 3) is the darkest and arguably most distinctive of all six taxa generally recognized within *O. scops*. Compared to *O. s. cycladum* (the most similar taxon), it is consistently even darker grey (Fig. 3), with heavier black streaks on the upperparts that extend laterally as narrow bars, although rarely *cycladum* can be as dark above (e.g. ZFMK 57.703, from Crete). The white spots on the hindneck and mantle are larger and more contrasting, often extending over the crown and scapulars. The underparts have much broader black streaks with coarser black vermiculation and narrow bars, often isolating the white spots on the breast, belly and flanks. The faint buff bars on the inner webs of the primaries of *scops* are usually virtually absent, but the white spots on the inner borders are more extensive. *O.* (*s.*) *cyprius* is remarkably constant in coloration (apparently more so than any other *scops*) and also lacks the rufous morph of *scops* (Vaurie 1965; C.S. Roselaar *in* Cramp 1985), although most *cyprius* possess some rufous feathers scattered across the upperparts. Coloration thus discriminates *cyprius* from populations on other Mediterranean islands, e.g. Crete (*cycladum*) and Mallorca (*mallorcae*: Fig. 3a). In most specimens examined by G.M.K. there was no overlap in plumage characters between *cyprius* and *scops*. However, three specimens labelled as *cyprius* (NHMUK 1909.8.7.25, 1909.11.30.9 and 1909.11.30.10, all collected in Cyprus in Mar 1905 and 1909) are somewhat 'abnormal', being atypically pale and similar to some collected in Turkey in coloration; they are also long-winged (mean 160 mm) compared to *cyprius* (mean 153.3 mm; Table 7, wherein they are treated as *O. s. cycladum*). All three were collected near the southeast coast of Cyprus in spring in an area with little suitable breeding habitat and just one summer record in 1993–2012 (J. Honold pers. comm.; BirdLife Cyprus database *per* C. Richardson). However, many migrants pass through the area; in spring 1968, Horner & Hubbard (1982) found that migrant *scops* outnumbered migrant *cyprius* there 10:1. Thus, it seems probable that these three pale specimens were *scops* on spring passage (and have been treated thus in our analyses). In addition, three other specimens labelled as *cyprius* collected near the south and southeast coasts of Cyprus in spring, autumn and early winter (ZFMK 56.441, ZMB 2000/28676 and 2000/28675, taken 22 Apr 1956, *c*. 25 Sep 1902 and 3 Dec 1902, respectively) do not show characters of that taxon and may be migrants of other taxa. Two additional specimens at ZFMK (A.III.10.a.λλ, A.III.10.a.μμ), labelled *cyprius*, collected in western Turkey (at Solak, 29 May 1934, and Elmali, 4 Jun 1934), are clearly *cycladum*, especially as the second-named was a female on eggs. G.M.K. also examined two specimens labelled as *O. scops* with typical *cyprius* plumage collected in Israel, one from Tel Aviv on 19 Mar 1961 (TAUM 3978), the other at Be'er Ya'aqov in 2013 before Mar (TAUM 17849); both were perhaps returning migrant *cyprius*.

TABLE 7. Comparative biometrics for *O.* (*s.*) *cyprius*, *O. s. scops* and *O. s. cycladum*; all measurements are in mm and mass is in g; for each the mean, ± SD and range are given. For information concerning measuring protocols of specimens and relevant institutions see Materials and Methods. Subspecies broadly assigned according to range and museum label data where given, but see main text for some exceptions (three BMNH specimens originally listed as *cyprius* are here considered to be one or another race of *scops*). All specimens measured by G.M.K. Biometric and mass data from live birds [*O.* (*s.*) *cyprius*] provided by A. Crabtree, G. Mawson, S. Samworth, C. Walton and P.F. Wing lengths of live birds are maximum lengths, *i.e.* flattened and straightened wing; Svensson (1992) method 3.

Character → Taxon/sex ↓	Wing	Tail	Tarsus	Bill length	Bill depth	Mass
O. (*s.*) *cyprius* (specimens)						
Males (*n* = 10)	153.3 ±2.5 150–159	69.5±2.7 65–74	29.2±1.8 26.5–32.8	17.6±0.7 16.5–18.85	7.9±1.0 6.6–9.9	
Females (*n* = 13)	153.5±4.1 145–162	67.3±3.4 62–72	30.9±2.5 27.8–37.6	17.9, *n* = 12 ±0.7 16.5–19.1	8.3±0.7 7.1–10.2	
Sex unknown (*n* = 2)	154.5 154–155	66.5 66–67	28.8 28.6–29	17.65 17.6–17.7	6.67 6.6–6.75	
O. (*s.*) *cyprius* (live birds)						
Males (*n* = 3)	159±3.3 155–163					78, *n* = 2 73–83
Females (*n* = 3)	166±3.3 162–170					106±12.3 89–119
Sex unknown (*n* = 20)	163±6.0 150–172					84, *n* = 18 ± 8.1 72–105
O. s. cycladum (specimens)						
Males (*n* = 6)	153.8±3.7 148–159	68.8±2.8 64–72	28.2±1.4 26.5–30.5	17.8±0.5 17.25–18.5	7.3±0.7 6.4–8.3	
Females (*n* = 8)	156.7±3.6 150–164	68.1±3.4 63–75	27.0, *n* = 7 ±2.0 24.1–30.5	18.2±0.7 16.9–18.9	7.7±1.2 6.2–9.9	
Sex unknown (*n* = 1)	155	70	27.8	17.65	6.7	
O. s. scops (specimens)						
Males (*n* = 5)	154.8±4.1 150–160	70.4±2.2 68–73	29.1±1.75 27.4–31.4	17.5±0.5 17.1–18.4	7.9±0.3 7.4–8.2	
Females (*n* = 3)	157±2.4 154–160	66.6±0.5 66–67	29.2±1.7 27.6–31.6	18.1±0.4 17.6–18.4	7.7±0.5 7.3–8.5	
Sex unknown (*n* = 1)	157	67	27.95	17.75	7.25	

Molecular phylogenetic analysis. Our molecular phylogeny of *O. scops* reveals little structure (Fig. 4), *cyprius* differing from *O. s. scops* by one nucleotide substitution (Table 8). The three birds from Cyprus representing *cyprius* are identical and form a monophylum, which is characterized by a T instead of C in all other subspecies (Table 8) (bootstrap support 63%). Three of the four samples from *O. s. cycladum* also form a clade (bootstrap support 57%), but birds of this subspecies show more differences from *O. s. scops*. In this analysis, *O. s. pulchellus* from Mongolia does not differ from *O. s. scops*. Divergence of mitochondrial DNA is correlated with time (e.g. Weir & Schluter 2008). Thus in very young species no or little sequence divergence occurs. For *cyprius* the uncorrected genetic distance from *O. s. scops* is 0.1%, suggesting that a split occurred quite recently, probably only some tens of thousands of years ago. The uncorrected genetic distance between *O. s. cycladum* and *O. s. scops* is higher: 0.2–0.5%. Again DNA data indicate a recent separation of both *cyprius* and *O. s. cycladum*.

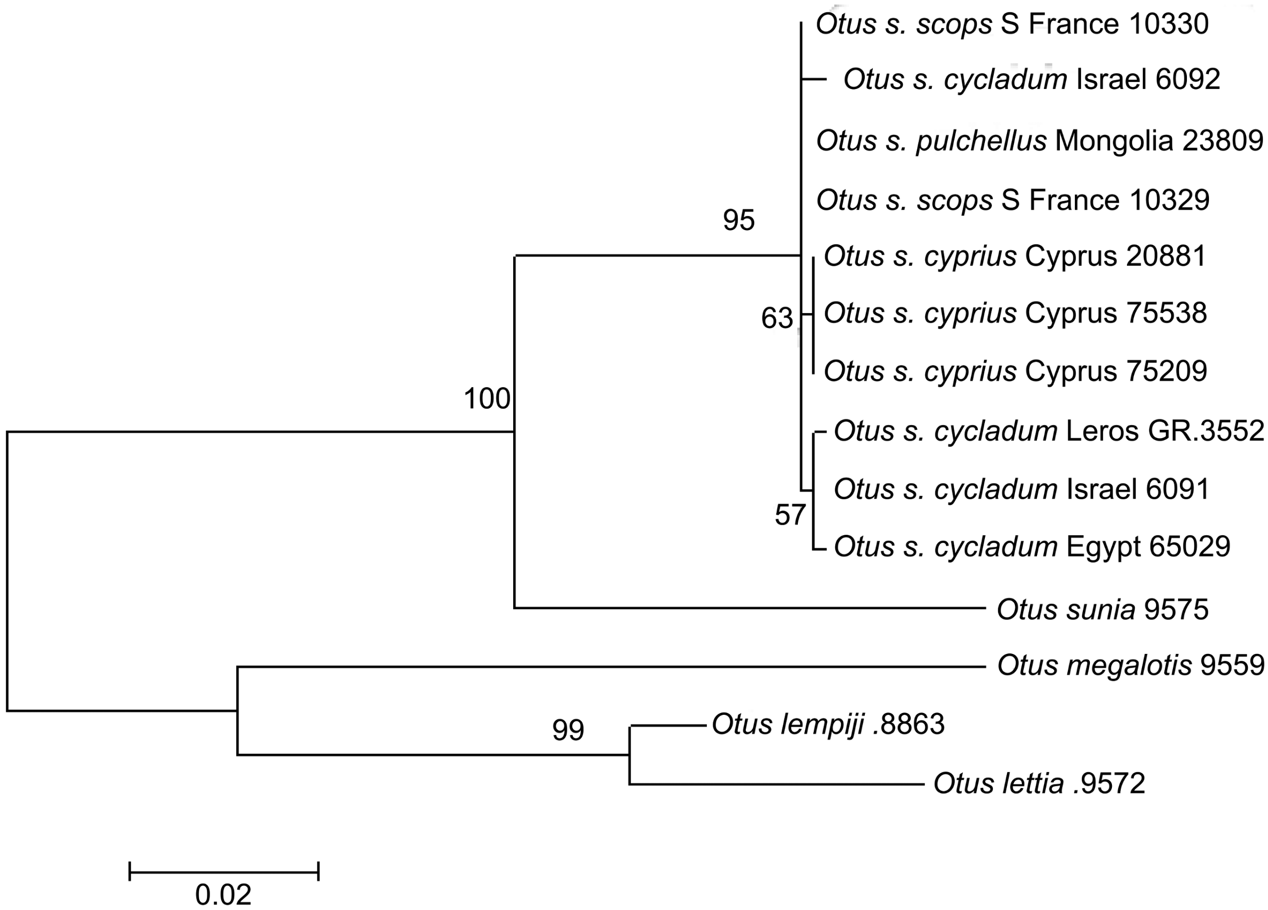

FIGURE 4. Phylogenetic tree of *Otus scops* reconstructed by maximum likelihood (ML) using nucleotide sequences of mitochondrial cytochrome b gene. Numbers represent bootstrap values from 250 replications.

Resident status of Cyprus Scops Owl. Ever since its description (von Madarász, 1901), *O.* (*s.*) *cyprius* has been considered to be the only resident race of *O. scops* (Cramp 1985) but this is now uncertain (Flint in prep.). Although there are few winter records, birds sing much less frequently after Jul, so it is possible that many are silent and unrecorded in winter. There is evidence of at least some returning spring migrants (Flint & Stewart 1992); the increase in records on Cyprus in Feb–Mar (C. Richardson pers. comm.) also suggests this and the presence of two specimens (in TAUM) showing plumage characters of *cyprius* collected in Israel in late winter/ early spring may also be evidence of wintering elsewhere.

Wing length and shape of *cyprius* differ little from those populations of *scops* that are long-distance trans-Saharan migrants (Cramp 1985), whereas if *cyprius* was sedentary a noticeably shorter and more rounded wing might be expected. Our study confirmed the lack of significant differences in wing formula of *cyprius* compared to *O. s. cycladum* and southern *O. s. scops*, populations of which are also migratory or largely so (e.g. Cramp 1985; Shirihai 1996; Eken 1997), suggesting their migration strategies are similar. It appears that *cyprius* is partially migratory, with an unknown proportion leaving the island in winter. To date, there are no recoveries anywhere of 95 Cyprus-ringed birds (A. Crabtree pers. comm.).

TABLE 8. Variable nucleotide positions in cytochrome *b* from *Otus scops*. The synapomorphic nucleotide exchange of *O.* (*s.*) *cyprius* is highlighted in bold as are the substitutions in *O. s. cycladum*, which are shared among different individuals. When nucleotides are identical with those of the first taxon, then the position is marked as ".".

Otus s. scops	
#*Otus s. scops*_S_France_10330	GCCCCTGACA
#*Otus s. scops*_S_France_10329	. . . .
Otus s. pulchellus	
#*Otus s. pulchellus*_Mongolia_23809	. . . .
Otus s. cycladum	
#*Otus s. cycladum*_Israel_6092	C . . . . . C . . .
#*Otus s. cycladum*_Leros_GR.3552	. . . . T**G**
#*Otus s. cycladum*_Israel_6091	. . . . **G**
#*Otus s. cycladum*_Egypt_65029	. . . . . C . . . **G**
Otus* (*s.*) *cyprius	
#*Otus s. cyprius*_Cyprus_20881	. . **T** . . . .
#*Otus s. cyprius*_Cyprus_75538	. . **T** . . . .
#*Otus s. cyprius*_Cyprus_75209	. . **T** . . . .

Breeding season, distribution, habitat and density. The breeding season of *cyprius*, with eggs Apr–May and chicks late Apr–Jul (Flint & Stewart 1992 and subsequent Cyprus Bird Reports) is several weeks earlier than in Turkey (Kirwan *et al*. 2008). Breeding birds are common in towns, villages, lightly wooded areas, and open pine *Pinus brutia* forest to 1,900 m (Flint & Stewart 1992 and subsequent Cyprus Bird Reports; Ieronymidou 2008; Pomeroy & Walsh 2013; J. Honold pers. comm.). Habitats of *cyprius* thus appear generally similar to those of *scops* except that *cyprius* is common in pine forest, whereas *scops* (except *O. s. pulchellus*) infrequently inhabits conifers (Cramp 1985).

TABLE 9. Provenance of specimens used for genetic analysis.

Specimen	Date	GenBank number	Location	Live bird or specimen and details
France_10330	5.6.2000	KR181839	Corbieres, France	Live: captured in mist-net
France_10329	5.6.2000	KR181838	Corbieres, France	Live: captured in mist-net
Mongolia_23809	14.3.2003	KR181837	SW Mongolia	Live
Israel_6092	Jun 1992	KR181842	Ranat Hanadiv Raptor Reproduction Program, Israel	Live: in captivity
Leros_GR.3552	Oct 1997	KR181840	Leros, Greece	Feather sample
Israel_6091	Jun 1992	KR181841	Ranat Hanadiv Raptor Reproduction Program, Israel	Live: in captivity
Egypt_65029	23.5.2012	KR181843	Hamata, Egypt	Live: captured in mist-net
Cyprus_20881	15.3.2002	KR181844	Kazaphani, Cyprus	Live: adult male territorial *cyprius* captured in mist-net
Cyprus_75538	18.8.2013	KR181845	Pelentri, Cyprus	Live: juvenile *cyprius* found injured 14.7.2013; recuperated and sample taken before release
Cyprus_75209	1.6.2013	KR181846	Kalo Khorio Orinis, Cyprus	Live: chick from nest box of *cyprius* pair

The density of singing male *cyprius* is high: 3–4 (exceptionally 8–10, Charalambides & Charalambides 1990) are often heard from one point simultaneously in favoured areas, and counts in and around villages often involve 10–12, exceptionally 20 (e.g. Charalambides & Charalambides 1983; Sanders 2000; Gordon *et al.* 2004; Richardson *et al*. 2012; C. Richardson pers. comm.). High breeding densities have been recorded in *scops* (Cramp 1985), but those for *cyprius* seem to be usually greater, apparently much more so than on Corsica (Thibault & Bonaccorsi 1999). The estimated breeding population of *cyprius* of 10,000–20,000 pairs (BirdLife International 2004) or 5,000–15,000 pairs (BirdLife Cyprus 2013 estimate) is relatively high compared to those in the much larger nearby countries of Greece and Turkey (BirdLife International 2004), suggesting that mean density on Cyprus is higher. However, estimates of densities of singing male *cyprius* across a range of habitats are required to enable more accurate comparisons.

Discussion

Evolution of Cyprus Scops Owl and its song. Although occasional song with a faint and often intermittent second note is not typical of Eurasian Scops Owl, it occurs throughout most (if not all) of the species' range, suggesting that it is widespread and long-established. This agrees with the statement by König *et al*. (1999) that owls do not possess distinct regional dialects.

Colonizations between islands and the mainland normally occur from the latter to the former; this combined with the different environmental conditions on islands means that differences between an island taxon and its mainland counterpart are usually the result of change in the former rather than the latter (Newton 2003). Evolutionary divergence on islands tends to be rapid (Grant 1998). Thus when *cyprius* separated from *scops*, its distinctive song may have evolved by selection for individuals that sang the occasional faint second note both more regularly and louder.

During spring migration on Cyprus, southerly breeding taxa typically pass earlier than northerly breeders (Flint & Stewart 1992). *O. s. cyprius*, being a southerly and insular breeder, would be expected to return before the main passage of the more northerly breeding, continental *scops*. The Feb–Mar arrival (if the increase of records at this time indicates arrival) of *cyprius* compared to the late Mar–Apr arrival of *scops* in southern Turkey (Kirwan *et al*. 2008) appears to support this, as does a survey of spring migrants at Paralimni in southeast Cyprus in 1968 (Horner & Hubbard 1982): apparent migrant *cyprius* (n = 14) occurred 12 Mar–3 Apr (Flint in prep.), whereas *scops* (n = 136) occurred 16 Mar–8 May, with the main arrival in mid-Apr. As rival males seldom encroach on a resident's territory (Cramp 1985) and *cyprius* responds strongly to intruders, the earlier arrival, territory occupation, and breeding of *cyprius* has probably acted as a prezygotic isolation mechanism, and also prevented *scops* from breeding in significant numbers. This may have been sufficient to permit the separate evolution of *cyprius*, even with substantial numbers of *scops* passing through.

Notably, all six Cypriot endemic avian taxa [*O.* (*s.*) *cyprius*, *Oenanthe cypriaca*, *Sylvia melanothorax*, *Parus ater cypriotes*, *Certhia brachydactyla dorotheae* and *Garrulus glandarius glaszneri*] are darker, drabber and/or greyer than their mainland counterparts (Flint & Stewart 1992), suggesting that these plumage differences have evolved in response to the insular conditions, rather than being due to founder effects. Other factors influencing the evolution of *cyprius* may have been the absence of native mammalian predators (Kryštufek & Vohralík 2001) and Tawny Owls *Strix aluco* (Flint & Stewart 1992), the latter elsewhere a significant predator of *O. s. scops* (Sergio *et al*. 2009), probably resulting in reduced predation and higher breeding densities compared to the mainland.

Lack of a type specimen The type specimen of *cyprius* is no longer extant, so we considered whether to designate a neotype for *cyprius* under Art. 75 of the Code (ICZN 1999). However, given that the Code states 'A neotype is validly designated when there is an exceptional need…' (Art. 75.3), we consider that the need is not 'exceptional' because the distinct morphological features of the *cyprius* type specimen were described by Madarász (1901), they correspond with those of the taxon breeding on the island and distinguish it from other *scops* taxa. Also, another specimen from the same source as the type (namely MANCH B.10688) and labeled co-type is extant, shows the morphological features of *cyprius* and can be considered confirmatory of the lost type's features, but (as discussed above) cannot be considered to have type status.

Taxonomic status of *cyprius*. No sharing of mtDNA haplotypes was revealed between *cyprius* and *scops*. However, more samples should preferably be analyzed to corroborate that the haplotype found in *cyprius* is diagnostic and that *cyprius* has indeed reached monophyly in its mtDNA. In any case, the weak genetic difference of *cyprius* from *O. s. scops* and *O. s. cycladum* indicates a very recent separation and could be taken as an argument against species status for *cyprius*. However, it is difficult to translate genetic divergence into species limits and its relationship to reproductive isolation is not straightforward (*cf*. Tobias *et al*. 2010). By contrast, Fuchs *et al*. (2008) found that in *Otus* species vocal and morphological differences are indeed associated with distinct evolutionary lineages, but may not obviously relate to the genetic distances between these lineages, and suggested they be used with caution for taxonomic conclusions.

In addition to its distinctive plumage Cyprus Scops Owl has a distinctive song that clearly differs from *scops*; it may also differ in its ecology and behaviour, in particular it appears to breed at higher densities and more frequently in pine forest, and to be less migratory, but detailed studies are needed to confirm these differences.

König *et al*. (1999, 2008) claimed to have applied the traditional Biological Species Concept (BSC) to owls and concluded that where species are sympatric, allopatric or parapatric, clearly distinguishable vocal patterns suggest different species, although it might be argued that their test of species status is based more obviously on diagnosability than proven reproductive isolation. [See Sangster (2014) for discussion of how many authors claiming to apply BSC in avian taxonomy have in fact used other criteria to delimit species.] In Strigidae, species are most frequently differentiated vocally and, as owls lack distinct regional dialects and vocalizations are inherited, bioacoustics represents the most important taxonomic criterion, especially in particularly complex genera like *Glaucidium* and *Otus* (e.g. Howell & Robbins 1995). Although several authors have claimed that some species possess different voices in different parts of their range, König *et al*. (1999) found that either different parts of the vocabulary had been compared or that separate species were involved. Similarly, Wink & Heidrich (1999) stated that morphology varies little in many owls, but that distinctive songs are of considerable taxonomic value.

Referring to *O. scops*, König *et al*. (1999) found that it overlaps geographically with several other *Otus* species similar in size and plumage, all of which are best distinguished vocally. In the past, several of these were lumped as subspecies (for example, many Southeast Asian *Otus* were treated within *O. scops*), but are now known to possess different vocalizations (e.g. Fuchs *et al*. 2008; Pons *et al*. 2013). It is especially noteworthy that *Otus* is so prone to island speciation: of 51 species recognised by König *et al*. (2008), 36 are endemic to islands or archipelagos, and three others to small continental areas.

The most important factor in BSC is reproductive isolation. For insular endemics, which are not in contact during the breeding season with their closest relatives this is impossible to prove and decisions must be based on other characters, as with many endemic island *Otus* species (e.g. König *et al*. 2008; Sangster *et al*. 2013; Pons *et al*. 2013). In the case of *cyprius*, however, large numbers of *scops* (probably mainly *O. s. scops* and *O. s. cycladum*) pass through Cyprus on migration during its breeding season, and as *scops* breeds in all adjacent countries, it seems likely that migrants would quickly colonize but for the presence of *cyprius* on the island. The recent discovery of presumed *cycladum* wintering locally in southwest Turkey (Eken 1997) suggests that this race might also occur on the island in winter. Because of the presence of *scops* and the fact that *cyprius* responds strongly to playback of a single-note song, hybridization is a possibility; this would seem most likely to occur if singing unpaired male *cyprius* attracted female *scops* and bred with them. That *cyprius* duets involve two-note songs by both the male and female, and that the second notes of both are relatively loud in duets (compared with male solo song), suggests that the two-note song of both sexes may be important in establishing and maintaining pair bonds; the different song of *cyprius* may therefore act as an isolating mechanism preventing significant male *cyprius*/female *scops* hybridisation. Other isolating mechanisms appear to be the residence or earlier arrival of *cyprius*, its early establishment of territories, earlier breeding season and strong reaction to territorial intruders; its dense population may also inhibit male *scops* from singing. Because *cyprius* retains its distinctive song and plumage, and because migrant *scops* has not colonized despite breeding in adjacent countries, we conclude that effective isolating mechanisms are in place and that significant gene flow between the two does not seem to occur; therefore we recommend that *cyprius* be considered specifically distinct, as are other distinctively voiced insular *Otus* populations.

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References

Bannerman, D.A. & Bannerman, W.M. (1958) *Birds of Cyprus*. Oliver & Boyd, Edinburgh, 384 pp.

Baur, H. & Leuenberger, C. (2011) Analysis of ratios in multivariate morphometry. *Systematic Biology*, 60, 813–825. http://dx.doi.org/10.1093/sysbio/syr061

BirdLife International (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status.* BirdLife International, Cambridge, 374 pp.

Charalambides, M. (2010) Cyprus Scops Owl *Otus scops cyprius* breeding at Kalo Khorio Orinis, in spring 2009. *Cyprus Bird Report*, 2009, 153–154.

Charalambides, M.A. & Charalambides, C.A. (1983) Sightings 1978. *Cyprus Ornithological Society (1970) 9th Bird Report*, 1978, 1–44.

Charalambides, M.A. & Charalambides, C.A. (1990) Sightings 1988. *Cyprus Ornithological Society (1970) Bird Report*, 19, 1–45.

Cramp, S. (Ed.) (1985) *The Birds of the Western Palearctic. Vol. 4*. Oxford University Press, Oxford, 960 pp.

Denac, K. & Trilar, T. (2006) Individual recognition of Scops Owls (*Otus scops*) by spectrographic analysis of their calls: a preliminary study. *Razprave IV. Razreda SAZU*, XLVII–3, 87–97.

Dragonetti, M. (2007) Individuality in Scops Owl *Otus scops* vocalisations. *Bioacoustics*, 16, 147–172. http://dx.doi.org/10.1080/09524622.2007.9753573

Eken, G. (1997) Regular wintering by Scops Owl *Otus scops* in Turkey, at Havran Delta. *Sandgrouse*, 19, 147.

Flint, P.R. & Stewart, P.F. (1992) *The Birds of Cyprus: An Annotated Check-list. BOU Check-list No. 6. 2nd Edition.* British Ornithologists' Union, Tring, 234 pp.

Fuchs, J., Pons, J.-M., Goodman, S.M., Bretagnolle, V., Melo, M., Bowie, R.C.K., Currie, D., Safford, D., Virani, M.Z., Thomsett, S., Hija, A., Cruaud, C. & Pasquet, E. (2008) Tracing the colonization history of the Indian Ocean scops-owls (Strigiformes: *Otus*) with further insight into the spatio-temporal origin of the Malagasy avifauna. *BMC Evolutionary Biology*, 8, 197–211. http://dx.doi.org/10.1186/1471-2148-8-197.

Gordon, J., Holgarth, B., Nye, D., Moore, J., Roberts, O. & Mason, R. (2004) Systematic list. *Annual Report*, 2003, 1–112. [BirdLife Cyprus, Nicosia]

Grant, P.R. (Ed.) (1998) *Evolution on Islands*. Oxford University Press, Oxford, 495 pp.

Horner, K.O. & Hubbard, J.P. (1982) An analysis of birds limed in spring at Paralimni, Cyprus. *Cyprus Ornithological Society (1970) Bird Report*, 7, 54–104.

Howell, S.N.G. & Robbins, M.B. (1995) Species limits of the Least Pygmy-owl (*Glaucidium minutissimum*) complex. *Wilson Bulletin*, 107, 7–25.

Ieronymidou, C. (2008) *Habitat preferences of the Cyprus Scops Owl (Otus scops cyprius).* M.Sc. thesis, Institute of Zoology & Royal Veterinary College, University of London, London,

International Commission on Zoological Nomenclature (ICZN) (1999) *International Code of Zoological Nomenclature. 4th Edition*. International Trust for Zoological Nomenclature, London, 306 pp.
http://dx.doi.org/10.5962/bhl.title.50608

Jolicoeur, P. & Mosimann, J.E. (1960) Size and shape variation in the painted turtle. A principal component analysis. *Growth*, 24, 339–354.

Kirwan, G.M., Boyla, K., Castell, P., Demirci, B., Özen, M., Welch, H. & Marlow, T. (2008) *The Birds of Turkey.* Christopher Helm, London, 512 pp.

König, C., Weick, F. & Becking, J.-H. (1999) *Owls: A Guide to the Owls of the World*. Pica Press, Robertsbridge, 462 pp.
http://dx.doi.org/10.2307/4089953

König, C., Weick, F. & Becking, J.-H. 2008. *Owls of the World. 2nd Edition*. Christopher Helm, London, 528 pp.

Kryštufek, B. & Vohralík, V. (2001) *Mammals of Turkey and Cyprus*. Knjižnica Annales Majora, Slovenia, 140 pp.

Le Gassick, J.C. (1993) Call patterns of Eurasian Scops Owl. *British Birds*, 86, 271.

Madarász, J. von (1901) Descriptions of probably two new European birds (*Scops cypria* and *Parus aphrodite*). *Termés. Füzetek*, 24, 272.

Mikkola, H. (1983) *Owls of Europe*. T. & A.D. Poyser, Calton, 400 pp.
http://dx.doi.org/10.1017/s0030605300019141

Mild, K. (1990) *Bird Songs of Israel and the Middle East*. Privately published, Stockholm, Two cassettes.

Newton, I. (2003) *The Speciation and Biogeography of Birds*. Academic Press, London, 682 pp.

Palmér, S. & Boswall, J. (1968–1980) *A Field Guide to the Bird Songs of Britain and Europe.* Privately published, Stockholm, 16 records/cassettes.

Pomeroy, D. & Walsh, F. (2013) Numbers of three small predators in western Cyprus. *Cyprus Bird Report*, 2012, 166–172.

Pons, J.-M., Kirwan, G.M., Porter, R.F. & Fuchs, J. (2013) A reappraisal of the systematic affinities of Socotran, Arabian and East African scops owls (*Otus*, Strigidae) using a combination of molecular, biometric and acoustic data. *Ibis*, 155, 518–533.
http://dx.doi.org/10.1111/ibi.12041

Porter, R. & Aspinall, S. (2010) *Birds of the Middle East. 2nd edition.* Christopher Helm, London, 384 pp.

Richardson, C., Cottle, N. & Christodoulides, S. (2012) Systematic list 2011. *Cyprus Bird Report*, 2011, 14–137. [BirdLife Cyprus]

Robb, M. & The Sound Approach (2015) *Undiscovered Owls*. The Sound Approach, Poole, 300 pp. [Book with audio CDs]

Roberts, T.J. & King, B. (1986) Vocalizations of the owls of the genus *Otus* in Pakistan. *Ornis Scandinavica*, 17, 299–305.
http://dx.doi.org/10.2307/3676817

Roché, J.C. (1996) *Bird Songs and Calls of Britain and Europe*. Four CDs. WildSounds, Salthouse.

Sanders, J.D. (2000) Systematic list. *Cyprus Ornithological Society (1957) Annual Report*, 1999, 13–86.

Sangster, G. (2014) The application of species criteria in avian taxonomy and its implications for the debate over species concepts. *Biological Review*, 89, 199–214.
http://dx.doi.org/10.1111/brv.12051

Sangster, G., King, B.F., Verbelen, P. & Trainor C.R. (2013) A new owl species of the genus *Otus* (Aves: Strigidae) from Lombok, Indonesia. *PLoS ONE*, 8 (2), e53712.
http://dx.doi.org/10.1371/journal.pone.0053712

Sergio, F., Marchesi, L. & Pedrini, P. (2009) Conservation of Scops Owl *Otus scops* in the Alps: relationships with grassland management, predation risk and wider biodiversity. *Ibis*, 151, 40–50.
http://dx.doi.org/10.1111/j.1474-919x.2008.00865.x

Shirihai, H. (1996) *The Birds of Israel*. Academic Press, London, 692 pp.

Svensson, L. (1992) *Identification Guide to European Passerines. 4th Edition*. Privately published, Stockholm, 368 pp.

Tamura, K., Stecher G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
http://dx.doi.org/10.1093/molbev/mst197

Thibault, J.-C. & Bonaccorsi, G. (1999) *The Birds of Corsica: An Annotated Checklist. BOU Checklist No. 17*. British Ornithologists' Union, Tring, 172 pp.

Tobias, J.A., Seddon, N., Spottiswoode, C.N., Pilgrim, J.D., Fishpool, L.D.C. & Collar, N.J. (2010) Quantitative criteria for species delimitation. *Ibis*, 152, 724–746.
http://dx.doi.org/10.1111/j.1474-919x.2010.01051.x

Vaurie, C. (1960) Systematic notes on Palearctic birds. No. 43 Strigidae: the genera *Otus*, *Aegolius*, *Ninox* and *Tyto*. *American Museum Novitates*, 2021, 1–19.

Vaurie, C. (1965) *The Birds of the Palaearctic Fauna: Non-Passeriformes*. H.F. & G. Witherby, London, 763 pp.
http://dx.doi.org/10.1017/s0030605300004671

Voous, K.H. (1988) *Owls of the Northern Hemisphere*. Collins, London, 320 pp.

Weir, J.T. & Schluter, D. (2008) Calibrating the avian molecular clock. *Molecular Ecology*, 17, 2321–2328.
http://dx.doi.org/10.1111/j.1365-294x.2008.03742.x

Whaley, D. (1991) Scops Owl. *Cyprus Ornithological Society (1957) Newsletter*, 91, 3.

Wink, M. & Heidrich, P. (1999) Molecular evolution and systematics of the owls (Strigiformes). *In*: König, C, Weick, F. & Becking, J.-H. (Eds.), *Owls: A Guide to the Owls of the World*. Pica Press, Robertsbridge, pp. 39–58.

Wink, M., El-Sayed, A.-A., Sauer-Gürth, H. & Gonzalez, J. (2009) Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome b and the nuclear RAG-1 gene. *Ardea*, 97, 209–219.
http://dx.doi.org/10.5253/078.097.0425