A new subspecies of Tyto owl (Aves: Strigiformes: Tytonidae) from Alor and Pantar islands, Lesser Sundas, Indonesia

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ABSTRACT

We describe a new subspecies of Barn Owl, *Tyto javanica fallens*, from Alor and Pantar islands in the Lesser Sunda islands of eastern Indonesia. This subspecies differs significantly in morphology and colouration from other members of the *Tyto alba* complex, namely the Common or Western Barn Owl *Tyto alba* from Africa and Eurasia; the Eastern or Australian Barn Owl *Tyto javanica* (including *T. j. delicatula*, *T. j. sumbaensis* and the Sulawesi Owl *Tyto j. rosenbergii*) restricted to southern and South-East Asia, Australia, New Zealand, New Guinea and parts of Polynesia; and the American Barn Owl *Tyto furcata* from North to South America. It also differs from the Lesser or Moluccan Masked Owl *Tyto sororcula* and the Australian Masked Owl *Tyto novaehollandiae*. These differences are corroborated by molecular analyses. Four specimens were collected, one from Pantar and 3 from Alor, in April 1991 during joint Western Australian Museum and Museum Zoologicum Bogoriense vertebrate surveys in eastern Indonesia. These are the first *Tyto* specimens recorded from these islands.

Key words: speciation, morphology, DNA sequencing, Wallacea, *Tyto javanica fallens* ssp. nov.

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INTRODUCTION

The Indonesian archipelago, consisting of many thousands of islands, encompasses the Oriental–Australian faunal interface (see Fig. 1). The islands of eastern Indonesia (Wallacea) form a major contact overlap or transition zone between Asia and Australia. Since Alfred Russel Wallace's time this region has attracted the attention of biogeographers who have sought to delineate the Australian–Oriental divide (Simpson 1977). The biogeographic affinities of some of the birds of this region continue to be equivocal. Wallacea contains biogeographic subregions with relatively high levels of endemism and evidence of incipient speciation following changes in sea levels and climate during the Pleistocene. Within southern Wallacea are 2 island chains, the Banda Arcs, of different geological age and composition. The inner Banda Arc islands (including Sumatra and Java, and the islands from Bali through Lombok, Sumbawa, Flores, Pantar, Alor, Wetar to Banda) are principally volcanic, whereas the outer Banda Arc islands (including Sumba, Savu/Sabu, Roti, Timor, Tanimbar, Kai and Seram), are chiefly sedimentary in origin and represent outliers of the Australian Plate (Veevers 1991). The Banda Arcs formed during the collision and subduction of the Australian and Pacific plates beneath the Asian Plate in the mid- to late Pliocene. Sea levels in the region fluctuated because of alternating glacial maxima and minima during the subsequent Pleistocene (Roy *et al.* 1996). The islands also experienced changes in the seasonality of precipitation and fluctuations in mean temperatures (Morley & Flenley 1987). It is highly likely that local extinctions followed volcanic activity (Diamond 1974).

There has been considerable uncertainty about the biogeographic affinities of the Wallacean fauna. Wallace changed the position of his line of demarcation between the Asian and Australasian regions several times between 1859 and 1876 (Wallace 1876). Some assemblages of butterflies, bats and birds from islands within the region show different distributions depending on whether they originated from either Oriental or Australian forms (Holloway & Jardine 1968). There is now abundant evidence indicating Wallacea has a high proportion of endemic species with considerable speciation because the islands have been variously isolated in both space and time (Vane-Wright 1991; Kitchener & Suyanto 1996; How & Kitchener 1997).

Until recently the avifauna of many of the smaller islands in the Lesser Sundas, including Alor and Pantar, was poorly known. The relatively recent descriptions of several taxa (e.g. Mees 1973; Rozendaal 1987; Olsen *et al.* 2002; Sangster & Rozendaal 2004) and a new subspecies of the Sunda Bush Warbler *Cettia vulcania kolichisi* from Alor (Johnstone & Darnell 1997a) indicate higher levels of speciation within the region than previously recognised. Noteworthy among these are 2 taxa of Boobook Owl. That from Roti (Johnstone & Darnell 1997b), recently elevated to species status, and a new species from Sumba (Olsen *et al.* 2002), highlighting that speciation has taken place on both large and small Banda Arc islands. More recently, Jønsson *et al*. (2013) described a new species of owl, *Tyto almae*, from Seram. No endemic bird species are known from Alor or Pantar whereas there are 4 on Flores, 7 on Sumba and 10 on Timor/Semau; however, there are

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Figure 1. a) Wallacea and nearby regions; b) Lesser Sunda Islands showing Alor and Pantar Islands.

some endemic subspecies known from both Alor and Pantar.

Owls in the genus *Tyto* are one of the most secretive and hence poorly studied taxonomic groups in Wallacea. Within this group are several closely related species and subspecies including the 'Barn Owl' *Tyto alba* (Scopoli, 1769) complex, the Sulawesi Masked Owl *Tyto rosenbergii* (Schlegel, 1866), Minahassa Owl *Tyto inexspectata* (Schlegel, 1879), the Taliabu Owl *Tyto nigrobrunnea* Neumann, 1939, the Lesser Masked Owl *Tyto sororcula* (P.L. Sclater, 1883) and the Seram Masked Owl *Tyto almae* Jønsson *et al.*, 2013. The phylogeny and taxonomic status within the genus *Tyto* remains largely unresolved. Konig & Weick (2008) recognised 25 species within *Tyto*; however, many of these have yet to be subjected to molecular phylogenetic analysis, so their taxonomic and

systematic status is unclear. For example, we follow them in treating the Moluccan Masked Owl *Tyto sororcula* as a full species rather than as a subspecies of the Australian Masked Owl *Tyto novaehollandiae* (Stephens, 1826). The islands of eastern Indonesia, which harbour about 11 taxa and exhibit relatively high levels of endemism and speciation, are central to providing insights into the origin, colonisation and genetic differentiation within the genus (Fig. 2). A good example of this problematic taxonomy at the species and subspecies levels is the Common Barn Owl *Tyto alba* complex, which was long recognised as a single, nearly cosmopolitan species with 28 to 46 subspecies (del Hoyo & Collar 2014).

There is extensive geographic variation in plumage and body size across the vast range of the *Tyto alba* complex, and recent molecular studies have cast doubt on the validity of many subspecies while elevating others to species rank. Wink *et al.* (2008) identified 3 widely distributed species within this complex: the Common Barn Owl *T. alba*, in which they placed 10 subspecies (*T. a. alba*, *T. a. affinis*, *T. a. erlangeri*, *T. a. ernesti*, *T. a. gracilirostris*, *T. a. guttata*, *T. a. hypermetra*, *T. a. javanica*, *T. a. schmitzi* and *T. a. stertens*) from Africa, Europe and parts of south and South-East Asia; the Western or American Barn Owl *Tyto furcata*, which comprises 5 subspecies (*T. f. furcata*, *T. f. contempta*, *T. f. hellmayri*, *T. f. pratincola* and *T. f. tuidara*) from North, Central and South America; and the Eastern Barn Owl *Tyto delicatula*, which includes at least 4 subspecies (*T. d. delicatula*, *T. d. interposita*, *T. d. meeki* and *T. d. sumbaensis*) restricted to the easternmost part of South-East Asia, Australia, New Zealand, New Guinea and parts of Polynesia. In addition to these taxa, Konig & Weick (2008) considered 6 restricted-range island taxa to be separate monotypic species and mentioned that *Tyto alba sumbaensis* from Sumba in the eastern Lesser Sundas could also be considered a separate species, although they did not formalize this suggestion. Mikkola (2012) treated several subspecies of the Barn Owl (*T. alba*) *sensu lato* complex (including the West Indian taxa *glaucops*, *insularis* and *nigrescens*) as full species (although some with reservations).

Recent phylogenetic analyses (Aliabadian *et al.* 2016) confirmed that the *T. alba* complex contains at least 3 species, with the Old World and New World groups, *T. alba* and *T. furcata* respectively, showing a high degree of genetic divergence and best considered as seperate species. They also showed that *Tyto alba javanica* (from the Malay Peninsula and the Greater and Lesser Sundas), and *Tyto alba stertens* (of South-East Asia) are both more closely related to the *T. a. delicatula* group, and that the name *javanica* (Gmelin, 1788) has nomenclatural priority

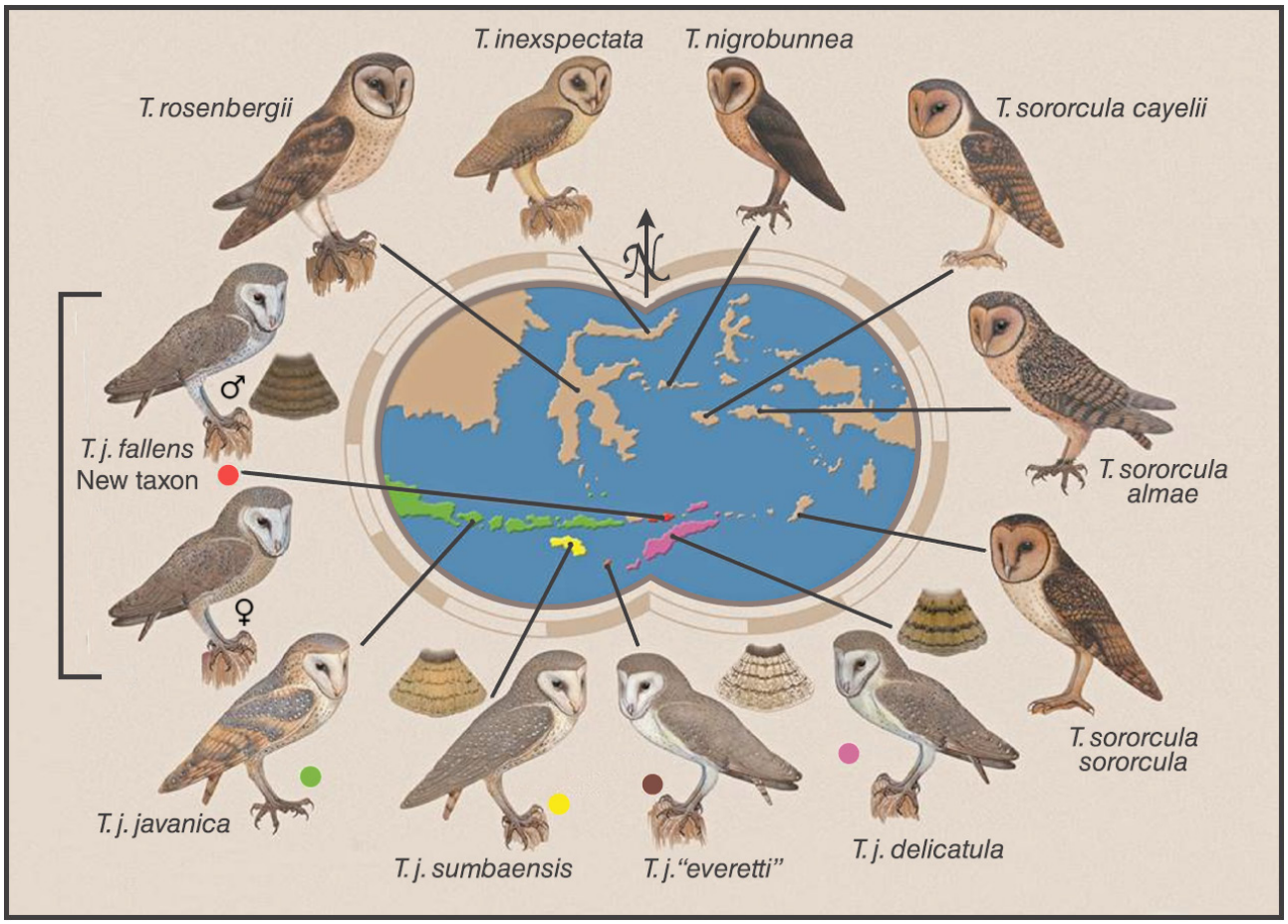

Figure 2. Map showing speciation and subspeciation within the genus *Tyto* in eastern Indonesia (artwork adapted from del Hoyo & Collar 2014).

over *delicatula* (Gould, 1836). Therefore, *T. javanica* (including *delicatula* and *stertens*) is the correct name for the Eastern Barn Owl. Their study confirmed that *Tyto alba sumbaensis* (*sensu lato*) showed high genetic divergence from *T. j. delicatula* and might represent a distinct species, although they did not distinguish it as a full species. We follow this treatment, including the retention of *sumbaensis* as a subspecies of *T. javanica*.

A comprehensive molecular phylogeny of Barn Owls and relatives by Uva *et al.* (2018) confirmed that the Common Barn Owl, *Tyto alba*, may be divided into 3 main evolutionary units: the American Barn Owl, *T. furcata*; the Western Barn Owl, *T. alba*; and the Eastern Barn Owl, *T. javanica*. Noteworthy, however, in this study was the inclusion of the Sulawesi Masked Owl *Tyto rosenbergii* and the Minahassa Owl (Minahassa Masked Owl), *Tyto inexspectata*, within the Eastern Barn Owl *T. javanica.*

Tyto species within Wallacea

Based on del Hoyo & Collar (2014), Aliabadian *et al.* (2016), Uva *et al*. (2018) and Gill *et al*. (2022), we accept that the following *Tyto* species and subspecies occur in eastern Indonesia (Fig. 2).

EASTERN BARN OWL

Tyto javanica javanica (J. F. Gmelin, 1788) is present in Burma, south-west China, Thailand, Cambodia, Laos, South Vietnam, Malay Peninsula, Greater and Lesser Sundas (east to Flores). Christidis & Boles (2008) treated birds from southern Asia through Australia and the Pacific as *T. a. javanica*. Alternatively, Mees (2006) showed that birds from Australia are paler on their upper parts than those from Java, and that birds from Flores are similar to those from Java. They concluded that *T. a. delicatula* is a valid subspecies differing from *T. a. javanica* by its smaller size and paler colouration.

Tyto javanica delicatula (Gould, 1837) ranges across the eastern Lesser Sundas (Savu, Roti, Timor, Jaco and Wetar, Kisar and Tanimbar Islands), Australia and Pacific Ocean islands such as New Britain, New Ireland, Bougainville and Solomon Islands, New Caledonia, Loyalty Islands, and east to Fiji, Tonga and Samoa. Specimens in the Western Australian Museum from Savu and Roti are similar in size and colouration to birds from northern Australia.

Tyto javanica sumbaensis (Hartert, 1897) is confined to Sumba in the eastern Lesser Sundas. Few specimens of this subspecies are known and Mees (2006) considered the validity of *sumbaensis* required confirmation; however, a specimen in the Western Australian Museum has the very pale cinnamon-buff tail, marked only with 3 narrow dusky bars (Fig. 2). The tail is the main character of this subspecies and Wink *et al.* 2004 show the distinctiveness of this taxon. Although we retain *sumbaensis* as a subspecies of *javanica*, it may well deserve full specific status.

The form *T. alba everetti* Hartert, 1929 was described from birds collected from Savu. Hartert (1929) commented that in colour, they were inseparable from his *T. a. kuehni* specimens from Kisar, differing only in their slightly smaller size. In his review of the birds of Timor and Sumba, Mayr (1944) treated both *everetti* and *kuehni* as synonyms of *delicatula.* The single specimen A23508 from Savu in the Western Australian Museum is, however, most distinctive. It lacks any buff colouration whatsoever. The tail pattern best resembles that of *T. j. sumbaensis* but the ground colour is whitish, and there are some fine markings between the distinct tail bars. Based on the single specimen A23508, we choose to resurrect the taxon *T. j. everetti*, as this bird lacks buff pigmentation (Fig. 2). Although Hartert (1929) commented that the specimens he named *everetti* were indistinguishable from Timor birds (= *delicatula*), this is definitely not the case with our male specimen A23508. The form *T. a. kuehni* Hartert, 1929 from Kisar (specimens of which were borrowed from the American Museum of Natural History) could not be distinguished from specimens of *Tyto javanica delicatula* from Timor, as noted by Mayr (1944).

Birds collected from Kalao and Kalaotoa (between Sulawesi and Flores) have not been examined by us. Hartert (1929) suggested that they differed from Savu birds (*T. a. everetti*) in being more golden brownish above especially on the tail. They seem to resemble more closely the Indian subspecies *T. j. stertens.* Peters (1940) noted that these birds differ from others but had not (at the time of his writing) been assigned to any taxon. White & Bruce (1986) list them under *T. a. javanica*, but note that they are small, with a wingspan between 265 and 273 mm, and markedly red-brown on the dorsal surface, especially on the tail. It is of interest that these forms come from smaller islands between the *T. j. javanica* and the *T. j. delicatula* interface, as does our new subspecies from Alor and Pantar. To some degree this parallels the situation of *Ninox* owl species in that there are several taxa limited to islands between Sumba and the Moluccas.

SULAWESI MASKED OWL

Tyto rosenbergii (Schlegel, 1866) occurs on the Sangihe Islands, Sulawesi and Butung, and *T. r. pelengensis* Neumann, 1939 is tentatively identified from the Banggai Islands (Peleng).

MINAHASSA MASKED OWL

Tyto inexspectata (Schlegel, 1879), or the Minahassa Masked Owl, is confined to northern Sulawesi.

TALIABU MASKED OWL

Tyto javanica nigrobrunnea Neumann, 1939, is sometimes considered conspecific with *T. inexspectata*. It is found on Taliabu in the Sula Islands.

MOLUCCAN MASKED OWL

Tyto sororcula (P.L. Sclater, 1883), also known as the Lesser Masked Owl, is treated here as a full species, but was recently considered to be a subspecies of *T. novaehollandiae* (Stephens, 1826) by del Hoyo *et al*. (2014). The species includes *T. s. cayelii* (Hartert, 1900), from the south Moluccan island of Buru, and *T. s. sororcula*, from the Tanimbar Islands of Larat and Yamdena. Known only from 4 specimens, the nominate subspecies was collected on Tanimbar in 1882 and 1923 (Sclater 1883; Stresemann 1934), and *T. s. cayelii* is known only from 2 specimens from Buru Island collected in 1898 and 1921 (Hartert 1900; Siebers 1930).

Tyto sororcula almae Jønsson *et al*., 2013, also known as the Seram Masked Owl, comes from Seram Island in the Moluccas. It is known only from a single specimen in the Museum Zoologicum Bogoriense and is sometimes considered a full species: *T. almae*.

EASTERN GRASS OWL

Tyto longimembris (Jerdon, 1839) is known from Sulawesi, Tukangbesi Islands, Flores, Sumba and northern Australia.

Background

Between 1987 and 2006, the Western Australian Museum and the Museum Zoologicum Bogoriense (MZB: Cibinong, Java, Indonesia) conducted 13 surveys of the terrestrial vertebrates on 29 islands of eastern Indonesia—from Bali east through the Lesser Sundas and southern Moluccas to the Aru Islands on the Sunda Shelf. The main purpose of these surveys was to record the distribution and examine the taxonomy of amphibians, birds, mammals and reptiles throughout the region. Extensive observations were made of the birds, and specimens were collected across this zone of complex speciation and taxonomy. Based on these, several island avifaunal checklists have been prepared and new taxa described (Johnstone 1994; Johnstone & Sudaryanti 1995; Johnstone & Jepson 1996; Johnstone *et al.* 1996; Johnstone & Darnell 1997a, 1997b; Johnstone & van Balen 2013; and Johnstone *et al.* 2014).

Recent taxonomic studies on other faunal groups including bats, rodents, skinks and snakes show that several species or subspecies are endemic to Nusa Tenggara (e.g. Auffenberg 1980; Kitchener *et al*. 1991, 1992; Aplin *et al*. 1993) and from these it is obvious that there have been many mammal, bird and reptile speciation events in this region. A good example is the Johnstone's Mastiff Bat *Otomops johnstonei*, Kitchener *et al*., 1992, described from Alor (Kitchener *et al.* 1992), which is distinct from its nearest congeners on Java and in New Guinea. This is an example of a species that, although able to fly, has not extended its distribution beyond these islands. Also noteworthy was the description of a new subspecies of the montane Sunda Bush Warbler *Cettia vulcania kolichisi* from Alor (Johnstone & Darnell 1997a). Trainor (2005) mentions that a revision of the taxonomic status of some restricted-range species on Alor including the Lesser Shortwing *Brachypteryx leucophrys* and Yellow-breasted Warbler *Seicercus montis* is needed.

Surveys during April 1991 (by R. E. J.) on Alor were done near Kalabahi (8°14′S, 124°32′E) and Mali (8°08′S, 124°36′E) on its western end and near Apui in the central mountains (at 8°17′39″S, 124°43′17″E). On Pantar the surveys included the north-east at Batu (8°15′16″S, 124°17′59″E) and the north-western side at Kabir (8°15′30″S, 124°13′05″E).

On 20 April 1991, an adult female *Tyto* owl (Western Australian Museum A24588) was collected at Kabir on Pantar from a coconut palm in a small plantation backing a patch of dense low scrub and mangroves. It was listed in field notes as a *Tyto* ?*alba* buff morph. On 25 April 1991, another adult female *Tyto* owl from Apui on Alor Island (WAM A24508) came from a patch of rainforest at the edge of cultivation (kebun, gardens). This bird was collected along with a large pin-feathered chick (WAM A24243) from a large tree hollow. It was noted that this adult was another buff-cinnamon-coloured specimen similar to the bird from Pantar with a much darker mask and back, and heavily marked underparts, compared to typical *Tyto alba* specimens from other adjacent islands.

On 27 April 1991, a third adult *Tyto* owl, a male, was collected at Apui on Alor (WAM A24528) among gardens, trees and palms at the edge of the rainforest. This bird was noted as being dark on its upperparts, but with a white belly rather than a buff-cinnamon one as in the other specimens.

That both females were dark-coloured and heavily marked whilst the male was white and speckled black on its underparts, raises the question whether the plumage differences represented differing colour morphs or they were sexual variation. Because female birds in many of the '*Tyto alba*' complex are more intensely coloured than the males, we have concluded that this is an exceptionally extreme instance of sexual dimorphism. To our knowledge, no other taxon within the '*Tyto alba*' *sensu lato* complex exhibits such marked sexual diversity (Fig. 2).

METHODS

Morphometrics

We compared the 3 *Tyto* specimens collected on Pantar and Alor with *Tyto alba – Tyto javanica* specimens from Indonesia housed in the Western Australian Museum, Museum Zoologicum Bogoriense (MZB), the American Museum of Natural History (AMNH), and the Natural History Museum, Tring (NHMUK), as well as with other *Tyto* specimens including *T. novaehollandiae* from Western Australia.

We also compared our specimens with photos taken of the type specimen (MCZ 270559) of *Tyto rosenbergii pelengensis* from Peleng Island (Banggai Islands, central Sulawesi Province) in the Museum of Comparative Zoology, Harvard University, and with figures of *Tyto sororcula* and *Tyto almae* in Jønsson *et al.* (2013). These photographs demonstrate overall similarities, but also highlight some conspicuous plumage differences. Ridgway (1912) was used as a standard for colour terminology.

Molecular analyses

TAXONOMIC SAMPLING

Toe pad samples from the 4 Western Australian Museum *Tyto* specimens include 3 from Pantar and Alor and one from Sumba Island. Toe pads were also sampled from specimens from the American Natural History Museum, including 3 *Tyto javanica sumbaensis* from Sumba, 2 *Tyto javanica javanica* from Java, and one *Tyto javanica delicatula* from Kisar. Additionally, DNA sequences were downloaded from GenBank (see Appendix A).

MOLECULAR METHODS

DNA was extracted from toe pads using a dedicated cabinet workstation for historical specimens, cleaned with

10% bleach and ultraviolet light. A QIAGEN extraction kit was used but included the addition of 20 µL DTT (1M) in the protein denaturing step and a Qiaquick column in exchange for the DNeasy column. Library preparations were conducted by Kerensa McElroy, ANWC, CSIRO, Canberra and sequenced using standard depth paired-end sequencing at the Garvan Institute of Medical Research. Whole mitochondrial genomes were assembled iteratively using MITObim (Hahn *et al*. 2013) and the *Strix leptogrammica* mitochondrial genome (KC953095) as a reference. Three mitochondrial loci (*Cox1*, *Cytb* and *16s*) were extracted from the whole mtDNA genome for further analysis and comparison with DNA sequences available on GenBank. GenBank numbers are provided in Appendix A.

PHYLOGENETIC ANALYSIS

The 3 mitochondrial loci (*Cox1*, *Cytb* and *16s*) were concatenated and aligned with the same 3 mtDNA loci from representatives of *Phodilus badius*, *Tyto alba* and *Tyto furcata* from Aliabadian *et al*. (2016) (omitting some replicates where possible, particularly those missing data). The nuclear locus *Rag1* was also included from this dataset and *Cytb* and *Rag-1* were included from *Tyto castanops*, *Tyto longimembris* and *Tyto novaehollandiae* (Appendix A). Concatenated sequences were generated in Geneious version 10.2.3 (http://www.geneious.com, Kearse *et al*. 2012) and aligned using MAFFT Multiple Sequence Alignment and the FFT-NS-2 algorithm (Katoh & Standley 2013). Bayesian phylogenetic analyses were done using MRBAYES 3.2.6 (Huelsenbeck & Ronquist 2001); the GTR model on the dataset partitioned as follows: 16S; *Cox1* 1st + 2nd codons; *Cox1* 3rd; *Cytb* 1st + 2nd codons; *Cytb* 3rd; *Rag-1* 1st + 2nd codons; *Rag1* 3rd. Four chains were run for 1.5×10^{-7} generations and a subsampling frequency of 15,000. Burnin length was 3×10^{-6}. Convergence and effective sample sizes were assessed for all parameters using a tracer within Geneious version 10.2.3. (http://www.geneious.com; Kearse *et al*. 2012). A maximum likelihood tree with 10,000 bootstrap replicates was generated in RAxML 8.2.7 (Stamatakis 2014) using the same partitioning scheme as the Bayesian analysis and the GTR+gamma model.

TAXONOMY

Based mainly on plumage patterns and morphology, and to a lesser degree genetic divergence, the *Tyto* specimens from Pantar and Alor fall outside the variation seen in *T. j. javanica* and *T. j. delicatula* of the Lesser Sundas, *T. sororcula* of Buru and Tanimbar, *T. almae* of Seram, *T. j. rosenbergii* from Sulawesi and *T. novaehollandiae* from the Australo-Papuan region. Consequently, we describe them here as a new subspecies: *Tyto javanica fallens* **subsp. nov.**

Etymology

The specific epithet is from Latin *fallens* [deceiving], in allusion to it having been mistaken for the Common Barn Owl *Tyto alba* or the Eastern Barn Owl *Tyto javanica javanica.*

Holotype

The holotype is held at the Western Australian Museum, study skin WAM A24508, adult female; it was collected by R. E. J. at Apui, Alor Island, Indonesia, elevation approximately 1,000 m, 8°17′39″ S, 124°43′17″ E, on 25 April 1991. It was found with a pin-feathered chick in a large hollow 9.5 m up in the main trunk of a partly dead tree in a patch of rainforest backing a small coconut plantation.

The adult breeding cinnamon-coloured female (ovary 20 × 7 mm), has a total length of 360 mm, weight 475 g, wing length 285 mm, tail 114 mm, tarsus 74 mm, middle toe and claw 44 mm, bill entire (from base of skull) 40 mm, bill exposed (from feathering) 23 mm, bill width 17.7 mm, and bill depth 17.4 mm. Iris brown, orbital ring pinkish, bill bone or whitish, mouth flesh pink, legs grey, tarsus feathered almost to base of toes; sparse, stiff hair-like bristles on tops of toes, claws blackish brown.

Description

Upperparts

Variable, crown, nape, mantle, back, rump and wing coverts greyish brown or hair brown, the feathers tinged and variegated with greyish white and cinnamon buff and with a black or blackish sub-terminal or terminal shaft streak and a white spot at or near the tip. The spots finer on crown than on the back and wings but giving an overall finely spotted appearance. Primaries and secondaries mostly mottled cinnamon and brown, barred with fuscous or dark brown and inner webs broadly margined with white that increases in extent on secondaries. Outer edge of wing white to cinnamon buff spotted with fuscous. Tail mostly dark cinnamon mottled with fuscous or dark brown and with 5 fuscous bars (Fig. 3).

Facial disc

Dull greyish white, more whitish on chin and buffy brown to dusky grey tinge behind the eye (the feathers with pale greyish tips), with a blackish brown or rufous brown spot in front of the eye. Feathers of the thick facial ruff mostly white to dull cinnamon or cinnamon. The gular plumes whitish to cinnamon, the feathers with a broad blackish brown tip forming a distinct black fringe to lower section of the mask.

Underparts

Chin and centre of the throat mostly white. Sides of the neck cinnamon buff, the feathers with white bases and cinnamon tips marked with fuscous spots and bars. Breast and belly cinnamon buff heavily marked with fuscous brown spots, chevrons and vermiculations. Flanks and legs to toes dull to rich cinnamon buff, heavily marked with fuscous or dark brown spots, chevrons and vermiculations (Fig. 3). Undertail dull greyish white with dark grey bars.

PARATYPE WAM A24528

Western Australian Museum, study skin WAM A24528, adult white male, collected by R. E. J. at Apui, Alor Island, Indonesia on 27 April 1991. This specimen was collected in dense palms and gardens at the edge of rainforest.

Adult male (testes 10 × 5 mm) is 350 mm long, weight 340 g, wing length 291 mm, tail 118 mm, tarsus 77 mm,

Figure 3. Dorsal and ventral view of WAM A24508 female Holotype of *Tyto javanica fallens* from Alor Island.

middle toe and claw 46 mm, bill entire 37 mm, bill exposed 22.5 mm, bill width 16.2 mm and bill depth 16.4 mm. Iris brown, orbital ring pinkish, bill pinkish white, mouth flesh pink, legs pinkish grey, tarsus and claws as for holotype.

Upperparts

Variable, crown, nape, mantle, back, rump and wing coverts mouse grey (mostly pale brownish grey), the feathers finely variegated with greyish white, greyish brown, cinnamon buff and buff, and with a black or blackish subterminal shaft streak and a white or dull white spot at the tip (sometimes the white spot edged above and below with black). The spots finer on the crown than on the back and wings, and the cinnamon buff often more extensive on the wing coverts; overall giving a mottled appearance (Fig. 4). Outer edge of wing white, some feathers with a small black central streak at the tip.

Outer web of primaries and secondaries cinnamon buff, barred with dark brown, inner web more broadly margined with dull white that increases in extent on secondaries and with a white spot edged black at the tip. Tertiaries mostly greyish brown mottled with white and cinnamon buff.

Tail mostly cinnamon buff, mottled with greyish brown and dusky white and with 5 fuscous brown or dark brownish olive bars. The inner webs of all but central pair of feathers margined with white.

Facial disc

Dull white with a pale grey tinge on outer feathers and a dark blackish brown spot in the eye pit (front of the eye). Long bristle-like feathers at the base of the bill, mostly white with a rufous tinge.

Feathers of the thick facial ruff mostly white, tinged cinnamon buff, with a blackish shaft streak or Vshaped bar, a wavy subterminal bar and whitish tip. The gular

plumes whitish, all distinctly tipped with a narrow subterminal cinnamon buff bar and broad black tip forming a distinct black fringe to the lower section of the mask (Fig. 4).

Underparts

Breast, belly flanks and thighs white with greyish brown or fuscous spots, streaks and chevron marks that become larger on the belly and flanks (Fig. 4).

Underwing white except for blackish brown subterminal spots on lesser coverts, broad dull grey tips to outer greater coverts, and greyish brown bars and mottling on distal portion of the flight feathers. Undertail mostly dull white with greyish bars and mottling.

PARATYPE WAM A24588

Western Australian Museum, study skin WAM A24588, adult cinnamon-coloured female, collected by R.E. Johnstone at Kabir, Pantar Island on 20 April 1991. This specimen was collected from a coconut palm in a small plantation backing mangroves.

Adult female (ovary 15 × 5 mm), is 345 mm long, with a weight of 470 g, wing length 284 mm, tail 114 mm, tarsus 73 mm, middle toe and claw 39 mm, bill entire 38 mm, bill exposed 24 mm, bill width 18.4 mm, and depth 15.6 mm. Iris brown, orbital ring pink, bill white, mouth flesh pink, legs grey.

Upperparts

Crown, nape, mantle and back greyish brown or hair brown, tinged with cinnamon, the bases of the feathers cinnamon grading to brownish grey and with a black sub-terminal shaft streak and white tip. The wing coverts similar, but with richer cinnamon bases to feathers visible. Primaries and secondaries mostly cinnamon with well-spaced fuscous bars and mottling or stippling between the bars in the cinnamon zones. Tail feathers mostly dark cinnamon with 5 exposed fuscous or sepia

Figure 4. Dorsal and ventral view of WAM A24528 male Paratype of *Tyto javanica fallens* from Alor Island.

brown bars and mottling between the bars within the cinnamon zones (Fig. 5).

Facial disc

Mostly whitish inclining to grey or tinged with grey behind the eye, the feathers in front of the eye with chestnut-rufous bases, dull white distally and with pale grey tips. Feathers of the thick facial ruff mostly white, cinnamon buff and cinnamon, and the gular plumes with blackish tips forming a distinct black fringe to the lower section of the mask.

Underparts

Centre of the throat mostly white. Sides of the neck cinnamon buff, the feathers with white bases and cinnamon tips and with fuscous and sepia brown spots and chevrons. Breast and belly mostly dull white tinged with cinnamon buff, darker on the breast and grading slightly more whitish on the belly, the feathers with whitish bases grading to cinnamon buff distally and with extensive sepia brown and fuscous spots, bars and chevrons giving an overall heavily spotted appearance. Thighs and legs to toes rich cinnamon buff spotted and marked with sepia brown (Fig. 5). Undertail dull greyish white with dark grey bars.

Diagnosis

The head is large and round with a well-defined heart-shaped facial disc; the tail is moderately long; legs are long, as is typical of masked-owls in the genus *Tyto*. It is generally similar in size and colouration to *Tyto j. javanica*. It differs strikingly, however, from nominate *javanica* and for that matter all other Indonesian *Tyto* species in having 2 conspicuously different colour morphs—one cinnamon (females) and the other white (male), in being considerably darker on upperparts (in both morphs), more heavily marked on underparts (especially the cinnamon females), and in having a more well-defined facial disc. Overall the rich dorsal pattern, the facial disc outlined in black or blackish brown (in both phases)

Figure 5. Dorsal and ventral view of WAM A24588 female Paratype of *Tyto javanica fallens* from Pantar Island.

and the more heavily marked underparts (again in both phases) are the most significant differences between *fallens* and other members of the *T. alba* and *T. javanica* group making these unique characteristics.

RESULTS AND DISCUSSION

Variation among type specimens

The holotype and both paratypes were breeding adults. The holotype A24508 is a cinnamon female, as is paratype A24588, and the holotype was selected because it is a breeding adult and showing the distinctive colour characteristics of this sex. The 2 paratypes differ markedly, one being another cinnamon female and the other a more typical white adult male of *Tyto j. javanica*. Overall, paratype A24588 is more richly cinnamon than the holotype and has more extensive dark fuscous markings on underparts. The white male, paratype A24528, highlights the marked sexual variation–dimorphism in colour found in this subspecies. It has upperparts more mouse-grey rather than brownish grey with larger white terminal spots, the wings more greyish lacking cinnamon, and the throat, breast and belly are more pure white with fuscous spots and marks. While its general appearance is much like that of *Tyto j. javanica*, it differs in being considerably darker in dorsal coloration to typical *T. j. delicatula* specimens from the nearby islands of Savu, Sumba, Kisar (see Figs 6–8) and Timor, and it has a more boldly defined facial mask and a longer wing and tarsus. Being generally similar in size and colouration to *Tyto j. javanica* along with its geographical location, this initially led us to believe that it belonged within that subspecies.

Breeding information

Judging from these 3 specimens, breeding was in progress during the period from late March to early

Figure 6. Dorsal and ventral view of WAM A23508 *Tyto javanica delicatula* from Savu Island.

May. The female holotype was collected from a hollow with a pin-feathered chick and had an enlarged ovary and worn plumage. The male from Apui had enlarged testes measuring 10 × 5 mm. The female from Kabir also had an enlarged ovary measuring 15 × 5 mm and was in breeding condition.

Systematic relationships

Phenotypically, the closest relatives of *Tyto j. fallens* appear to be the historic *Tyto alba* complex (worldwide distribution), *Tyto j. rosenbergii* (of the Sulawesi region) and *Tyto novaehollandiae* (from the Australian region).

We have considered whether the new form might be a well-differentiated species or a geographic representative of the *Tyto alba–javanica* complex and, based on the recent genetic studies by Uva *et al*. (2018), thought that it is best treated as subspecifically distinct. The sub-species most resembles *T. j. javanica* in general morphology, size and partly in colouration. The 2 subspecies differ, however, in some important respects: *Tyto j. fallens* has 2 conspicuously different colour morphs, one white (male), and the other rich cinnamon buff with grey and white markings (female). Extreme sexual dimorphism is not known in the Asian *Tyto javanica* complex, including specimens typical of this subspecies, were collected on the Lesser Sunda islands of Savu (Fig. 6), Sumba (Fig. 7), Kisar (Fig. 8), Timor and Roti. Based mainly on morphology we treat *fallens* as a distinct subspecies.

Comparison with *T. javanica* populations within the region

Rensch (1931) placed the Barn Owls from Java, Lombok, Flores and Timor in the subspecies *javanica* and accepted the subspecies *sumbaensis* from Sumba, *everetti* from Savu, and *kuehni* from Kisar that were described by Hartert (1897, 1929). White & Bruce (1986) included birds from Lombok, Flores and Alor as *javanica,* birds from Savu, Timor and Kisar in *delicatula,* and noted that *javanica* is larger and darker than *delicatula.* We compared specimens

Figure 7. Dorsal and ventral view of WAM A22855 *Tyto javanica sumbaensis* from Sumba Island.

Figure 8. Dorsal and ventral view of AMNH 629341 *Tyto javanica 'kuehni'* from Kisar Island.

and photographs of birds from neighbouring islands Kisar and Timor (Figs 6–9); in size and colouration they matched typical *T. j. delicatula.*

A specimen from Kisar (*T. j. kuehni* AMNH 629341; Figs 8, 9) is close in colouration to birds from Timor and Roti as well as birds from northwestern Australia. Specimens in the Western Australian Museum from Sumba (*T. j. sumbaensis* A22855) and Savu (*T. j. everetti* A23508) are also similar to Timor birds but differ in that *sumbaensis* has a mainly pale buff tail and *everetti* has a greyish white tail (Fig. 2), although overall they match well with *T. j. delicatula* populations in the region. Mayr (1944) pointed out that Hartert's *everetti* from Savu and *kuehni* from Kisar are synonyms of *delicatula*. This is a little surprising considering our single specimen from Savu appears to differ significantly from the birds examined by Mayr in that it lacks any buff pigmentation and, from a plumage aspect, is most similar to the birds from Sumba (not Timor). Further observations are needed to determine the plumage characteristics of birds from Savu. The Kisar birds (= *T. a. kuehni* of Hartert) clearly resemble *delicatula* and we agree with Mayr's findings.

Throughout its distribution *T. javanica* shows little intra-island differentiation, which is expected from a vagile species with island populations that are effectively a single population. Potential must have existed recently for ready exchange of genes between populations throughout these geographically close islands.

The Alor and Pantar *T. j. fallens* specimens on the other hand are conspicuously different to both the nominate *T. j. javanica* and *T. j. delicatula* from neighbouring islands and differ mainly in having a much darker dorsal pattern, a darker tail and a darker, more distinct blackish facial disc (Figs 2 & 5). Additionally, the females exhibit patterning of dark chevron feather edges to the underparts, a feature somewhat similar to the *T. j. rosenbergii* forms but absent in most other *javanica* taxa. The male, however, has underparts close to those of other *T. javanica* taxa. Noteworthy is that its occurrence on 2 islands in a region that has given rise to endemic *Tyto* species, most of which are confined to one or only a few islands, highlights Wallacea as a region of speciation in this genus. It is therefore not surprising to find that the form of *Tyto* on Alor and Pantar is a distinct subspecies.

Molecular analyses

There were no premature stop codons found within *Cox1* and *Cytb* DNA sequences. The complete dataset consisted of 2,776 base pairs. There was a total of 229 polymorphic sites and 178 parsimony informative sites. For Bayesian

Figure 9. Dorsal and ventral views of A24528 *Tyto javanica fallens* and AMNH 629341 *Tyto javanica 'kuehni'*.

analyses, ESS for all parameters were above or close to 900. Multiple analyses in both RAxML and Bayesian analyses converged on identical tree topology of all lineages discussed here (Fig. 10).

Our analyses confirm that the *Tyto alba* complex is divided into 3 major lineages: *Tyto alba* (Africa, Europe), *Tyto furcata* (the Americas), and *Tyto javanica* (Australasia) (Aliabadian *et al.* 2016). These 3 lineages are well supported (all have Bayesian posteriors of 1.0; Maximum Likelihood, ML bootstrap support of 79, 80 and 96, respectively). Tree topology suggests *T. furcata* and *T. alba* are sister lineages (similar to the analyses of the concatenated dataset in Aliabadian *et al*. 2016) with high support (Bayesian posterior of 1.0, ML bootstrap of 80).

Within the *Tyto javanica* lineage, *T. j. javanica*, *T. j. delicatula* and *T. j. sumbaensis* all form monophyletic lineages with strong support (see Fig. 10). However, their relationships could not be resolved, which suggests either a lack of statistical power in our data or a period of recent and rapid evolution. Our specimens from Alor and

Table 1 Measurements of *T. javanica* subspecies.

***Tyto javanica* subspecies**	**Wing (mm)**	**Tail (mm)**	**Tarsus (mm)**	**Culmen from** cere **(mm)**
T. j. javanica 15 males	295–324 (308.1)	114–132 (121.5)	68–77 (71.6)	22–24 (23.1)
T. j. javanica 17 females	286–321 (305.4)	110–126 (119.5)	65–74 (70.1)	22–24 (23.5)
T. j. delicatula 15 males from Western Australia	275–290 (281)	101–117 (112.6)	61–70 (64.5)	20–34 (21.4)
T. j. delicatula 21 females from Western Australia	274–289 (281)	99–117 (112.5)	54–68 (62.5)	18–23 (21)
T. j. sumbaensis	274–287 (281)	114	66	23

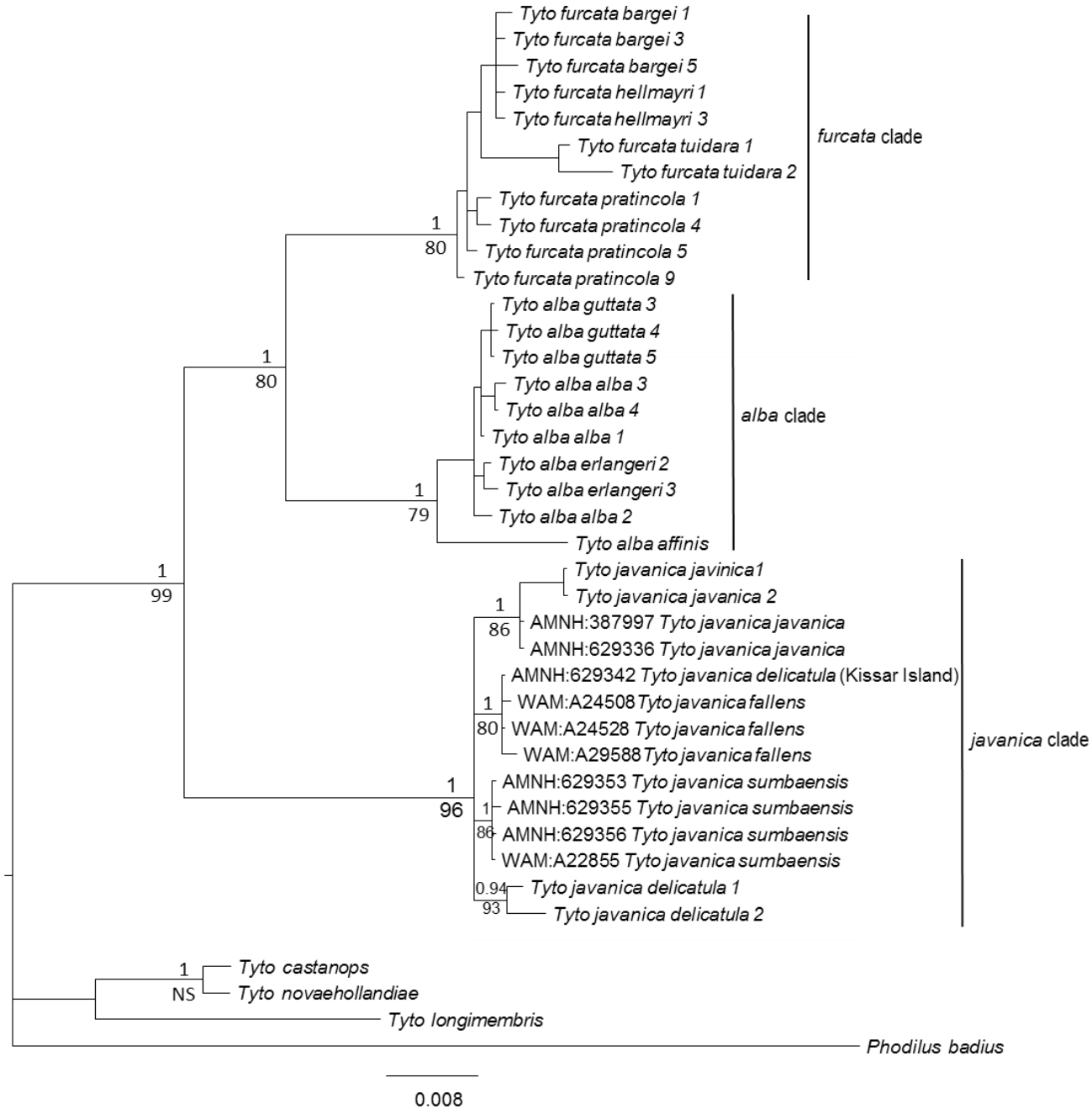

Figure 10. Phylogeny of *Tyto alba* complex represented by a Bayesian summary tree based on 2,776 base pairs of *16s*, *Cox1*, *Cytb*, and *Rag1*. Posterior probability values from Bayesian analyses are indicated on top of the branch and maximum likelihood bootstrap values from RAxML analyses are indicated below the branch.

Pantar form a fourth lineage within the *T. javanica* clade, but this lineage also includes a specimen of *T. j. delicatula* from Kisar (AMNH 629342), collected in 1901 and held at the American Museum of Natural History. Further whole mitochondrial genome analysis, not presented here, separates this specimen from *T. j. fallens*.

The morphology of the Kisar specimen (AMNH 629341) of *T. j. delicatula* was compared directly with *fallens*, and it is typical of *T. j. delicatula*. In light of the strong morphological evidence presented here suggesting *Tyto fallens* may well be a distinct subspecies, the molecular alignment of this specimen with *fallens* suggests either incomplete lineage sorting or a hybridisation event. Lineage sorting as part of the coalescent process is known to go through various stages before lineages become reciprocally monophyletic (Omland *et al*. 2006; Joseph & Omland 2009). Recent evolution of *T. j. fallens* is congruous with the *T. javanica* group being polyphyletic because of a period of rapid evolution. This understanding of population genetic processes, together with clear morphological differentiation, contributes to a multi-criteria approach

to species delimitation (de Queiroz 1998) and suggests that *fallens* represents a recently divergent subspecies within *javanica*. See also Uva *et al*. (2018) on the haplotype network of mitochondrial cytochrome b gene, in which shared haplotypes are common within the Australasian group.

Conservation

The Alor Barn Owl *Tyto javanica fallens* ssp. nov. is an endemic restricted to Alor and Pantar, both small islands in eastern Wallacea. It represents the first *Tyto* specimens recorded from these islands. Almost nothing is known about this owl's local distribution, relative abundance and ecology, and judging from currently limited knowledge, the taxon could be considered endangered. Further studies should be a priority to inform the conservation management of this subspecies.

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APPENDIX A

Specimens of the Barn Owl *Tyto alba* complex: collection and GenBank accession numbers for the 4 genes sampled from the Aliabadian *et al*. (2016) study and 3 genes in the current study.

Taxon	(*sensu lato*)	GenBank accession numbers				Collection no.	Locality	Reference
		Cytb	Cox1	16s	Rag-1			
Tyto alba guttata 3		KX440453	KF432220	KX440413	KX440475	ZMA58962	Netherlands	Aliabadian *et al*. (2016)
Tyto alba guttata 4		KX440454	KF432219	KX440414	KX440476	ZMA58963	Netherlands	
Tyto alba guttata 5		KX440455	KF432218	KX440415	KX440477	ZMA58964	Netherlands	
Tyto alba alba 1		KX440449	KF432226	KX440409	KX440471	NHMC80.4.108.8	Greece	
Tyto alba alba 2		KX440450	KF432223	KX440410	KX440472	NHMC80.4.108.9	Greece	
Tyto alba alba 3		KX440451	KF432225	KX440411	KX440473	NHMC80.4.108.7	Greece	
Tyto alba alba 4		KX440452	KF432224	KX440412	KX440474	NHMC80.4.108.6	Greece	
Tyto alba affinis		–	–	KX440425	–	ZMA19883	Ethiopia	
Tyto javanica javanica 1	*Tyto alba javanica* 1	KX440459	KX440429	KX440419	–	ZMA334	Indonesia	
Tyto javanica javanica 2	*Tyto alba javanica* 2	KX440460	KX440430	KX440420	–	ZMA335	Indonesia	
Tyto alba erlangeri 2		KX440447	KF432227	KX440407	KX440469	MFUM800002	Iran	
Tyto alba erlangeri 3		KX440448	KX440428	KX440408	KX440470	MFUM800003	Iran	
Tyto furcata bargei 1	*Tyto alba bargei* 1	KX440432	KX440426	KX440394	–	ZMA55930	Netherlands Antilles	
Tyto furcata bargei 3	*Tyto alba bargei* 3	KX440434	FJ465379	FJ465285	–	ZMA55941	Netherlands Antilles	
Tyto furcata bargei 5	*Tyto alba bargei* 5	KX440436	KF432207	KX440395	–	ZMA58966	Netherlands Antilles	
Tyto furcata hellmayri 1	*Tyto alba hellmayri* 1	KX440437	FJ465375	FJ465281	–	ZMA55945	Netherlands Antilles	
Tyto furcata hellmayri 3	*Tyto alba hellmayri* 3	KX440438	FJ465377	FJ465283	–	ZMA58259	Netherlands Antilles	
Tyto furcata pratincola 1	*Tyto alba pratincola* 1	KX440439	KF432212	KX440396	KX440461	LSUMZ16306	USA	
Tyto furcata pratincola 4	*Tyto alba pratincola* 4	KX440441	KF432210	KX440399	KX440463	LSUMZ20485	USA	
Tyto furcata pratincola 5	*Tyto alba pratincola* 5	KX440442	KF432215	KX440400	KX440464	LSUMZ49512	USA	
Tyto furcata pratincola 9	*Tyto alba pratincola* 9	KX440445	KF432211	KX440404	KX440467	LSUMZ21784	USA	
Tyto javanica delicatula 1	*Tyto alba delicatula* 1	–	KX440431	KX440421	–	ZMA21.978	Australia	
Tyto javanica delicatula 2	*Tyto alba delicatula* 2	–	–	KX440422	–	ZMA21.979	Australia	
Tyto furcata tuidara 1	*Tyto alba tuidara* 1	–	–	KX440423	–	ZMA22.100	Argentina	
Tyto furcata tuidara 2	*Tyto alba tuidara* 2	–	–	KX440424	–	ZMA22.101	Argentina	
Tyto javanica fallens		TBA	TBA	TBA	–	WAM:A24508	Apui, Alor Is, Indonesia	this paper
Tyto javanica fallens		TBA	TBA	TBA	–	WAM:A24528	Apui, Alor Is, Indonesia	
Tyto javanica fallens		TBA	TBA	TBA	–	WAM:A29588	Pantar Is, Indonesia	
Tyto javanica javanica	*Tyto alba javanica*	TBA	TBA	TBA	–	AMNH:629336	Java - Cheribon	
Tyto javanica delicatula	*Tyto alba delicatula*	TBA	TBA	TBA	–	AMNH:629342	South-west Kissar Is	
Tyto javanica javanica	*Tyto alba javanica*	TBA	TBA	TBA	–	AMNH:387997	Java - Buitenzorg	
Tyto javanica sumbaensis	*Tyto alba sumbaensis*	TBA	TBA	TBA	–	WAM:A22855	Sumba - Waitabula Forest Reserve	
Tyto javanica sumbaensis	*Tyto alba sumbaensis*	TBA	TBA	TBA	–	AMNH:629353	Sumba - Waingapo	
Tyto javanica sumbaensis	*Tyto alba sumbaensis*	TBA	TBA	TBA	–	AMNH:629355	West Sumba	
Tyto javanica sumbaensis	*Tyto alba sumbaensis*	TBA	TBA	TBA	–	AMNH:629356	Sumba - Waingopo	
Tyto castanops		EU349007	–	–	EU348954	IPMB 20995		Wink *et al*. (2009)
Tyto longimembris		EU349008	–	–	EU348955	IPMB 9579		
Tyto novaehollandiae		EU349009	–	–	EU348956	IPMB 20990		
Phodilus badius		KF961183	KF961183	KF961183	–	IPMB		Mahmood *et al*. (2014)