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Taxonomy and distribution of the Pygmy Eagle *Aquila* (*Hieraaetus*) *weiskei* (Accipitriformes: Accipitridae)

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Abstract

We re-evaluated the taxonomic status of the New Guinean subspecies *weiskei* of the Little Eagle *Aquila morphnoides* and confirmed that it differs considerably from the Australian *A. morphnoides* in multiple morphological and plumage characters. Genetic differentiation in published mitochondrial cyt-b and ND2 sequences between the nominate subspecies and *weiskei* is equivalent to that found between other accipitrid taxa at the species level, as are pairwise divergences between each Little Eagle taxon and their sister species, the Booted Eagle *A. pennata*. The available morphological and genetic evidence thus strongly and unambiguously supports the specific distinctness of *A. weiskei*. We propose the English name Pygmy Eagle, as this is the world's smallest known eagle. We show that the distribution of *A. weiskei* includes the western part of New Guinea (Vogelkop) and the Moluccas (Halmahera, Ternate and Seram), based on our new observations.

Key words: morphology, genetics, *pennata*, *morphnoides*, Little Eagle, New Guinea, Moluccas

Introduction

The Little Eagle *Aquila morphnoides* was described by Gould (1841) from Australia. Reichenow (1900) described a similar taxon from New Guinea as *Eutolmaetus weiskei*. The latter taxon was later regarded as a subspecies of *Hieraaetus morphnoides* (Peters 1931; Stresemann & Amadon 1979). Dementiev *et al.* (1966) treated *Hieraaetus* as a synonym of *Aquila*. The genera *Aquila* and *Hieraaetus* (*sensu* Stresemann & Amadon 1979) are now known to be paraphyletic, and most of the species of the latter genus may be included in *Aquila* (Wink & Sauer-Gürth 2004; Helbig *et al.* 2005; Lerner & Mindell 2005; Gjershaug 2006; Haring *et al.* 2007), which has priority (ICZN 1999). The Taxonomic Sub-Committee of the BOU Records Committee (Sangster *et al.* 2005) treats the Booted Eagle *Hieraaetus pennatus* as *Aquila pennata*. The name *Hieraaetus* can be used as a subgenus name for the 'booted eagle' clade (Parry 2001) that includes *A. morphnoides*, Pygmy Eagle *A. weiskei*, *A. pennata*, Ayres's Hawk-Eagle *A. ayresii* Gurney, 1851 and Wahlberg's Eagle *A. wahlbergi* Sundevall, 1851 (Helbig *et al.* 2005). Alternatively, *Aquila* and the revised *Hieraaetus* (*sensu* Helbig *et al.* 2005) may be treated as separate genera, and there is some behavioural, vocal and morphological support for such a distinction (Debus *et al.* 2007), but here we follow Sangster *et al.* (2005).

Brown and Amadon (1968) mentioned that the New Guinea race of *Hieraaetus morphnoides* is sometimes regarded as a separate species, but did not provide a reference. Amadon and Bull (1988) indicated that the diminutive form *weiskei* of New Guinea may be a separate species. Parry (2001) suggested that *A. weiskei* should be treated as a valid biological species based on character differences (in both juvenile and adult plumages) and biometric differences between this taxon and its sister *A. morphnoides*. He (Parry 2001) maintained that these differences are greater than the differences between *A. morphnoides* and *A. pennata*,

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which demonstrates that *A. morphnoides* and *A. weiskei* occupy different fundamental niches. Additionally, the finding that *A. weiskei* differs considerably from *A. morphnoides* in mtDNA and seems to be more closely related to *A. pennata* than to *A. morphnoides* (Bunce *et al.* 2005; Lerner & Mindell 2005), prompted us to re-evaluate morphological differentiation between these three taxa. Some sources (e.g. Gregory 2008a; BirdLife International 2009; Gill *et al.* 2009) already treat *weiskei* as a separate species, based on the limited treatments in Bunce *et al.* (2005) and Lerner and Mindell (2005), but a thorough analysis demonstrating the necessity of this taxonomic change has not previously been published.

Under the Biological Species Concept (BSC), guidelines as to how allopatric populations should be treated taxonomically have long been vague at best (Mayr & Ashlock 1991). Recently, Helbig *et al.* (2002) worked out more detailed guidelines for assigning species rank. According to their criteria, allopatric taxa should be considered species if they are fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, e.g. structural features, plumage colours, vocalizations, or DNA sequences, or some combination of these, and when the sum of the character differences corresponds to or exceeds the level of divergence seen in related species that exist in sympatry.

The distribution of *A. weiskei* has been described as New Guinea except Vogelkop (Marchant & Higgins 1993; Debus 1994; Ferguson-Lees & Christie 2001, 2005). In addition to our observations, *A. weiskei* was recently reported (as Little Eagle) from the Arfak Mountains and Batanta Island (Gregory 2008b). It has been considered as uncommon or rare and presumably resident in Wallacea (Coates & Bishop 1997). A small eagle observed on Halmahera in July 1989 was considered to have been a Little Eagle, and was reported as apparently a vagrant from Australia or New Guinea (King 1990). Because of the confusion in the literature about the geographic range of *A. weiskei*, we present our own observations of the species in the Moluccas and on western New Guinea.

Here we present results from evaluation of 12 morphological characters, published DNA sequences from *A. pennata*, *A. morphnoides* and *A. weiskei*, and over 30 field observations of *A. weiskei*. From these new data and further evaluation of published data, we conclude that *A. morphnoides* and *A. weiskei* should be regarded as distinct species.

Material and methods

Morphological measurements and plumage studies were carried out at The Natural History Museum, Tring (BMNH). Measurements were taken using callipers and a ruler. A total of 25 specimens representing three taxa (12 *A. pennata*, 8 *A. morphnoides*, 5 *A. weiskei*; see Appendix) were measured for 12 variables: flattened wing length, Kipp's distance = primary projection (distance from the tip of longest tertial to the wingtip), tail length (measured from the insertion of the central rectrices), length of hind toe, middle toe, hind claw, middle claw, tarsus length, bill length from cere, bill breadth (measured immediately anterior to the cere), bill depth and number of dark tail bands.

We used principal component analysis (PCA) to help explain mensural variability within and among individuals, sexes, and taxa. This multivariate method uses the correlation structure among variables to identify underlying, independent principal components (PCs), which are linear functions of the original variables that may explain the dimensions associated with high data variability (see e.g. Afifi & Clark 1998). The first few PCs typically explain most of the variation in the original data, and some operational meaning can be attached to the PCs to aid in their interpretation. Our PCA analysis was based on a correlation matrix to allow scaling to unit variance.

The sex of most museum skins was given on the label; however, we also used a PCA to sex individuals. We analyzed the PCA results by plotting bill length versus hind claw of individuals of each taxon, similar to the predictive model used by Bortolotti (1984). No juveniles were measured because birds not fully grown could add an age effect, and juveniles of many raptors have different feather lengths than adults. We distinguished juvenile from adult rectrices by their narrower pale outermost tail bands and more pointed remiges. Because of small sample sizes, no statistical tests were performed to compare the three taxa with respect to different morphological variables. Non-overlapping measurements are indicated in Table 1.

TABLE 1. Biometrics and differences between Pygmy Eagle *Aquila weiskei*, Little Eagle *A. morphnoides* and Booted Eagle *A. pennata*. Non-overlapping measurements are indicated by an asterisk (*).

Morph.	Sex	*A. weiskei*			*A. morphnoides*			*A. pennata*		
		n	min	max	n	min	max	n	min	max
Wing length	M	2*	305	306	3	345	350	7	360	380
	F	2*	315	340	5	384	390	5	385	408
Kipp's dist.	M	2	72	105	3	95	100	7	85	120
	F	2	111	123	5	95	140	5	100	120
Tail length	M	2	163	165	3	163	173	7	190	200
	F	2*	160	183	5	185	208	5	190	210
Hind toe	M	2	17.7	20	3	19.9	25.7	7	20	26.2
	F	2	23.5	25.9	5	23.5	28.7	5	24	29.2
Middle toe	M	2*	37.9	39	3	41	43.6	7	38.5	42.7
	F	2	42.2	42.8	5	42.5	49.8	5	41.7	48.3
Hind claw	M	2	25.8	27.3	3	26.1	27.8	7	23.7	27.4
	F	2	31	31.2	5	28.8	33.6	5	27.3	30.8
Middle claw	M	2*	21.4	21.5	3	20.4	21.1	7	18	21.2
	F	2	23.3	24.3	5	21.4	24.7	5	21.6	24.1
Tarsus length	M	2	58	60	3	50	67	7	55	68
	F	2	58	66	5	61	70	5	58	73
Bill length	M	2*	25.6	28	3	29.8	31	7	28.4	30.9
	F	2	30.3	32.1	5	31.5	34.3	5	30.6	33.6
Bill breadth	M	2	10.8	11.2	3	11.5	12.6	7	9.9	12.5
	F	2	12.6	12.9	5	12.4	14.7	5	11.8	13
Bill depth	M	2	15.6	16.3	3	16.3	16.4	7	15.2	16.9
	F	2	18.2	18.3	5	17.3	19.1	5	17.1	18.5
Tail bands	M	2	7	8	3	7	8	7	0	6
	F	2	8	8	5	7	8	5	0	7

JOG undertook field work for a total of 75 days on Halmahera, Ternate and Tidore in the Moluccas (7–8 Sep 1994, 1–25 Sep 1995, 30 Aug–17 Oct 1996) and 26 field days in the Arfak Mountains, Papua Barat (western New Guinea) (11–15 Sep 1994, 11–16 Oct 1995, 20–24 Mar 1996, 7–16 Jan 1997). Identification criteria used in the field to distinguish *A. weiskei* are provided in the Discussion, under Field Identification.

We evaluated the levels of genetic differentiation among multiple individuals of *A. morphnoides*, *A. weiskei*, and *A. pennata* and, for comparative purposes, other sister species pairs of booted eagles (subfamily Aquilinae [Gadow 1893; Lerner & Mindell 2005] or tribe Aquilini [Amadon 1982; Helbig *et al*. 2005]), using publicly available homologous DNA sequences from GenBank. Sequences were aligned in BioEdit and trimmed to the shortest complete sequence (Hall 1999). Sister species pairs were selected based on results of published studies (Haring *et al*. 2007; Helbig *et al*. 2005; Lerner & Mindell 2005) and verified by maximum likelihood analysis in RaxML (Stamatakis *et al*. 2008). Uncorrected "p" distances and total base pair differences were calculated in Paup* v. 4.0b10 (Swofford 2004).

Results

Biometry and plumage of *Aquila weiskei*, *A. morphnoides* and *A. pennata*

There was no overlap between *A. weiskei* and *A. morphnoides* in six characters (wing length in both sexes; tail length in females; middle toe, middle claw, bill length and bill breadth in males; Table 1). Between *A. morphnoides* and *A. pennata* there is no overlap in three characters (wing length, tail length and number of tail bands in males; Table 1).

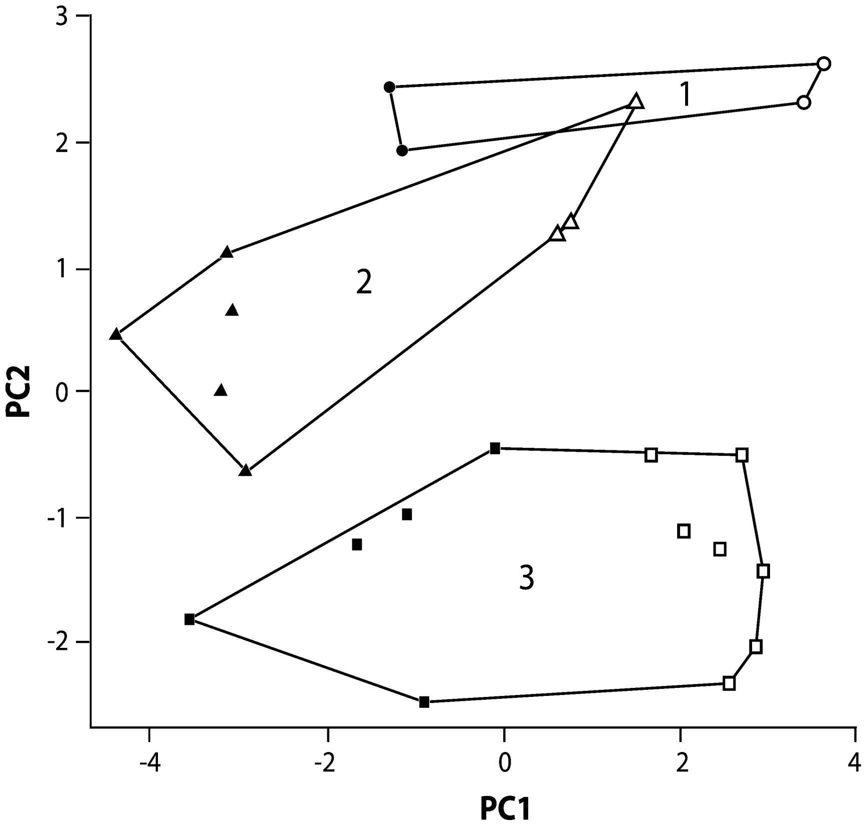

FIGURE 1. Results of a Principal Component Analysis (PCA) of biometrics. 1 = *Aquila weiskei*, 2 = *A. morphnoides*, 3 = *A. pennata*. Filled symbols indicate females; open symbols indicate males.

The PCA plot in Figure 1 indicates a taxon and sex separation of the individuals along the two first principal components. The first principal component (PC1) explains 48% of the total variance, whereas the second component (PC2) explains 19% (Table 2). The sexes segregated without overlap on PC1, whereas the taxa *A. weiskei*, *A. morphnoides* and *A. pennata* separated with very small overlap on PC2.

All three taxa have both a pale morph (most common) and a dark morph, with some intermediate individuals. Major plumage differences between adults of *A. weiskei*, *A. morphnoides* and *A. pennata* are summarized in Table 3 and illustrated in Figure 2. In adult plumage, *Aquila weiskei* has the upperparts darker contrasting less with the paler scapular patch, and darker underparts with broader streaks than in either *A. morphnoides* or *A. pennata*. Compared to *A. morphnoides*, *weiskei* lacks that species' distinctive black crown with a short crest that contrasts sharply to the paler nape. In *A. weiskei* the crown is dark brown streaked with no crest.

Four of the five specimens of *A. weiskei* at BMNH were pale morphs. The fifth was a dark morph immature (shown in Figure 2). Eleven pale morph and one dark morph bird were observed in the field.

All pale morph *A. weiskei* at BMNH had all the underwing coverts whitish with small dark spots, similar to light morph *A. pennata*. This pattern was also observed in eight of 11 pale morph birds observed in the field under conditions allowing study. The other three pale morph individuals had underwing patterns very similar to *A. morphnoides*, with rufous brown lesser underwing coverts (leading edge) that contrast with the white oblique band of the greater underwing coverts. Five of nine *A. morphnoides* at BMNH were pale morphs. These pale morph specimens had all rufous-brown lesser underwing coverts contrasting with the white oblique band of the greater underwing coverts (Figure 3). In the dark morph both *A. weiskei* and *A. morphnoides* have all the underwing coverts dark.

TABLE 2. Loadings and total variance of the two first principal components for morphological characters of Pygmy Eagle *Aquila weiskei*, Little Eagle *A. morphnoides* and Booted Eagle *A. pennata*.

Character	PC1	PC2
Wing length	-0.24	-0.44
Kipp’s dist.	-0.21	
Tail length	-0.16	-0.52
Hind toe	-0.29	-0.27
Middle toe	-0.30	-0.17
Hind claw	-0.35	0.22
Middle claw	-0.31	0.23
Tarsus length	-0.22	
Bill length	-0.37	
Bill breadth	-0.32	0.15
Bill depth	-0.35	
Tail bands	-0.18	0.48
Crest	-0.20	0.23
Total variance	48%	19%

Genetic differentiation

Homologous DNA sequences were available for 965 bps of cytochrome b (cyt-b) for two *A. weiskei* individuals (AY987291.1, AY754045.1) and three individuals each of *A. morphnoides* (AY754044.1, EU345503.1, AJ604499.1, AY987290.1), *A. pennata pennata* (EU345502.1, Y15760.1, AY987289.1) and *A. pennata dubia* (AY987288.1, stored in GenBank under the synonym *Hieraaetus pennatus minisculus* Y15761.1). Suspected contamination in the first ~240 bps of an additional *A. pennata* sequence, AJ604500.1, precluded its use. Homologous sequence from 1041 bps of ND2 was available from a single representative of each taxon (*A. weiskei*, AY987113.1; *A. morphnoides*, AY987112.1; *A. p. pennata* AY987111.1; *A. p. dubia* AY987110.1). The highest values for pairwise divergence were found between *A. weiskei* and *A. morphnoides* and between *A. weiskei* and *A. p. dubia* (0.026, cyt-b; Table 4). Pairwise numbers of base pair differences ranged from a minimum of three differences between the two subspecies of booted eagle to a maximum of 28 differences between *A. morphnoides* and *A. weiskei* (cyt-b, Table 4).

Cytochrome b sequences were available for 214 booted eagle individuals and seven outgroup individuals (Harpy Eagle *Harpia harpyja*, Crested Eagle *Morphnus guianensis* and Papuan Eagle *Harpyopsis novaeguineae*). Sequences of length 965 bases were retained (n=128, including 6 outgroup sequences) and three sequences of >924 bases or longer were included to increase taxon sampling (dataset available upon request). The topology of the maximum likelihood tree generated by these sequences corresponded to previously published phylogenies, albeit with lower support values at deeper nodes (Helbig *et al.* 2005; Lerner & Mindell 2005; and Haring *et al.* 2007; tree is available upon request). Sister species pairs discussed here were all recovered with bootstrap support values of >90. Genetic divergence among sister species pairs ranged from 1.7% between four individuals of Eastern Imperial Eagle *Aquila heliaca* and two individuals of Spanish Imperial Eagle *Aquila adalberti*, to 4.7% between two individuals of Ornate Hawk-Eagle *Spizaetus ornatus* and one Black and Chestnut Eagle *Spizaetus isidori*, with an average divergence of 2.7% (Table 5).

FIGURE 2. BMNH specimens in dorsal and ventral view. From left to right, pale-morph male and dark-morph female *Aquila pennata*, dark-morph male and light-morph female *A. morphnoides*, and dark-morph and pale-morph female *A. weiskei*.

FIGURE 3. Underside pattern of pale morph *Aquila pennata* (upper), *A. morphnoides* (middle) and *A. weiskei* (lower). Drawn from photos and field sketches.

TABLE 3. Main plumage differences between adult Pygmy Eagle *Aquila weiskei*, Little Eagle *A. morphnoides* and Booted Eagle *A. pennata*.

Character	*A. weiskei*	*A. morphnoides*	*A. pennata*
Crown	dark brown streaked	Blackish	Pale rufous to cream with fine black-brown shaft-streaks.
Crest	No crest	Short crest	No crest
Cheek	Dark streaked as rest of the head	Dark in contrast to paler nape and neck-side.	Dark in contrast to rest of the head
Nape	Dark streaked as crown	Pale rufous to cream with narrow shaft-streaks in contrast to darker crown and mantle	Pale rufous to cream with narrow shaft-streaks without contrast to crown
Breast markings	Broad dark streaks	Narrow dark streaks	Narrow dark streaks
Upperwing coverts	Lack of distinctive light panels	Distinctive light panels	Distinctive light panels
Underwing pattern in pale morph	Variable, from all coverts white (80%, N=15), to lesser underwing coverts rufous in contrast to white greater coverts	Lesser underwing coverts rufous in contrast to white greater underwing coverts	All underwing coverts white
Mantle	Dark with little contrast to tertials	Lighter than the dark tertials	Lighter than the dark tertials
Uppertail-coverts	Darker with little contrast to rump	Pale buff to pale rufous in contrast to dark rump	Pale buff to pale rufous in contrast to dark rump
Tail pattern	7–8 distinctive dark bars in less contrast to the light bars	7–8 distinctive dark bars in more contrast to the light bars	0–7 less distinctive dark bars

TABLE 4. Mitochondrial genetic divergence among Pygmy Eagles *Aquila weiskei*, Little Eagles *A. morphnoides* and Booted Eagles *A. pennata*. Number of base pair differences followed by uncorrected “p” distances in parentheses for 1041 bps of ND2 above the diagonal for one individual of each taxon and for 965 bps cyt-b for two *A. weiskei* individuals and three individuals of all other taxa below the diagonal.

	A. weiskei	*A. morphnoides*	*A. p. pennata*	*A. p. dubia*
A. weiskei	*	22 (0.022)	21 (0.021)	26 (0.026)
A. morphnoides	25–28 (0.026)	*	20 (0.019)	23 (0.022)
A. p. pennata	23 (0.023)	22–25 (0.022)	*	5 (0.005)
A. p. dubia	22 (0.024)	21–24 (0.023)	3 (0.003)	*

Distribution

In the period 1994–1997, JOG observed *Aquila weiskei* 19 times in the Arfak Mountains, Vogelkop, New Guinea, and 17 times in the North Moluccas (16 times on Halmahera and once on Ternate) (Table 6). Twelve of 36 total observations were under conditions that allowed descriptions of plumage. Observations of pairs and territory display indicate that they are breeding in these areas, and are not vagrants as earlier suggested. Figure 4 indicates the distribution of *Aquila weiskei*, *A. morphnoides*, *A. pennata* and the extinct giant Haast's Eagle *A. moorei* (based on Marchant & Higgins 1993; Ferguson-Lees & Christie 2005; Rasmussen & Anderton 2005; Naoroji 2006; own data).

TABLE 5. Pairwise genetic divergence between species of booted eagles. Uncorrected "p" distances for 965 bps cyt-b calculated from all published sequences of booted eagle species pairs.

Sister species comparison (# of sequences)	Uncorrected "p" distance	Reference
Nisaetus alboniger[1] *(3)* vs. *N. nipalensis (2)*	0.035	Lerner and Mindell (2005)
Nisaetus cirrhatus (3) vs. *N. philippensis*[2] *(1)*	0.023	Helbig *et al*. (2005)
Spizaetus ornatus (2) vs. *S. isidori (1)*	0.047	Lerner and Mindell (2005); Helbig *et al*. (2005); Haring *et al*. (2007)
Aquila clanga (1) vs. *A. pomarina (3)*	0.019	Lerner and Mindell (2005); Helbig *et al*. (2005)
Aquila audax (4) vs. *A. gurneyi (1)*	0.028	Lerner and Mindell (2005); Haring *et al*. (2007)
Aquila fasciata (29) vs. *A. spilogaster (5)*	0.018	Lerner and Mindell (2005); Helbig *et al*. (2005)
Aquila heliaca (4) vs. *A. adalberti* (1)	0.017	Helbig *et al*. (2005)
Average distance	0.027	

[1] may be more closely related to Javan Hawk-Eagle *Nisaetus bartelsi* (Haring *et al*. 2007), a taxon not included in Lerner and Mindell (2005) or here.

[2] may be more closely related to Southern Philippine Hawk-Eagle *Nisaetus pinskeri* (Haring *et al*. 2007), a taxon not included in Helbig *et al*. (2005) or here.

Discussion

Taxonomy

On the basis of the large number of diagnostic differences between *Aquila weiskei* and *A. morphnoides*, we recommend that *A. weiskei* should be treated as a distinct species, and propose to use the English name 'Pygmy Eagle' because it is the smallest eagle in the world, males being smaller even than the Little Eagle. Parry (2001) used the alternative name 'Weiske's Eagle' after the collector Emil Weiske, who collected the type specimen in Astrolabe Mountains in Jun 1898, but we prefer to use the more descriptive 'Pygmy Eagle'. Other English names in use for *weiskei* include 'Papuan Booted Eagle' (Debus *et al.* 2007), 'Papuan Little Eagle' (Gregory 2008a), and 'New Guinea Hawk-Eagle' (Gill *et al.* 2009), but we prefer the less cumbersome 'Pygmy Eagle', which is now used by the Global Raptor Information Network (2009). Also, use of either of 'Papuan Booted Eagle' or 'Papuan Little Eagle' would likely require modification of existing, well-established English names.

In regard to proposed assignment of species rank to allopatric taxa, Helbig *et al.* (2002) recommended that taxa be considered species if they are fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, e.g. structural features, plumage colours and DNA sequences. We find that the Pygmy Eagle is diagnosable from the Little Eagle in several structural features (wing, tail, middle toe, middle claw and bill length; Table 1), 10 adult plumage differences (Table 3) and in DNA sequences (Table 4; Bunce *et al*. 2005; Lerner & Mindell 2005).

We did not study the Pygmy Eagle in juvenile plumage. In the Little Eagle juveniles are similar to adult birds, except for being richer rufous on the head and underparts, lacking black patches on the crown, and having thinner dark streaks on the underparts. In fresh plumage, the upperparts are darker than in adults, with less contrasting pale scapular patch and diagonal band across inner wing coverts. Juvenile Little Eagles are therefore probably more similar to *A. weiskei* than are adults. Differences between juvenile and adult Little Eagles are negligible in worn plumage (Marchant & Higgins 1993).

TABLE 6. Observations of Pygmy Eagle by JOG in the Arfak Mts, western New Guinea (1°13'S 134°03'E), and Halmahera (1°05'N 127°32'E) and Ternate (0°50'N 127°22'E) in North Moluccas in 1994–1997. S = soaring, D = undulating display flight, H = hunting.

Locality	Altitude (m)	Date	Time	Number of individuals	Behaviour
Arfak Mts	1600-1700	14.09. 1994		1	S
Arfak Mts	100-200	11.10. 1995	12.40	1	S
Arfak Mts	100-200	11.10. 1995	13.50	1	S
Arfak Mts	200-300	12.10. 1995	08.20	1	S
Arfak Mts	400-500	13.10. 1995	06.40	1	H
Arfak Mts	700-800	15.10. 1995	11.50	1	S
Arfak Mts	700-800	16.10. 1995	07.39	1	S
Arfak Mts	700-800	16.10. 1995	08.15	2	S
Arfak Mts	700-800	16.10. 1995	08.39	1	S
Arfak Mts	700-800	16.10. 1995	08.47	1	S
Arfak Mts	700-800	16.10. 1995	08.59	1	S
Arfak Mts	100-200	20.03. 1996		2	S
Arfak Mts	300-400	24.03. 1996		1	S
Arfak Mts	1850-1950	11.01. 1997		1	S
Arfak Mts	1600-1700	13.01. 1997		1	S
Arfak Mts	1600-1700	13.01. 1997	09.35	1	S
Arfak Mts	1750-1850	13.01. 1997	11.00	1	S
Halmahera	200-300	30.08. 1996		1	S
Halmahera	200-300	01.09. 1996		1	S
Halmahera	200-300	02.09. 1996		1	S
Halmahera	300-400	03.09. 1996	10.23	1	S
Halmahera	200-300	03.09. 1996	12.00	1	D
Halmahera	300-400	03.09. 1996	14.30	1	S
Halmahera	300-400	08.09. 1996	11.20	1	S
Halmahera	300-400	08.09. 1996	11.48	1	D
Halmahera	300-400	09.09. 1996	10.17	1	S
Halmahera	300-400	13.09. 1996	14.50	1	D
Halmahera	100-200	16.09. 1996	09.00	1	S
Halmahera	200-300	30.09. 1996	10.10	1	S
Halmahera	200-300	30.09. 1996	11.54	1	D
Halmahera	100-200	02.10. 1996	12.35	1	H
Halmahera	300-400	02.10. 1996	15.52	1	S
Halmahera	200-300	04.10. 1996	12.20	1	H
Ternate	100-200	11.10. 1996	12.30	1	S

Dark morph Pygmy Eagles seem to be much rarer than pale morphs (Ferguson-Lees & Christie 2005; this study). It is unknown if the ratio of the two morphs shows geographic variation. In the Little Eagle the pale morph is generally more common than the dark morph but the ratio varies. The dark morph predominates or is equally common to the pale morph in south-eastern Queensland, whereas in West Australia the pale morph is 15 times as common as the dark morph (Marchant & Higgins 1993). In the Booted Eagle, the pale morph is more common than the dark morph, with 80% light morphs in Spain and South Africa (n=648) and 60% pale morphs in Greece and the Middle East (n=362; Forsman 1999; Ferguson-Lees & Christie 2001).

The plumage differences between the Pygmy and Little eagles are greater than those between the Little and Booted eagles, which are widely recognized as distinct species. We therefore consider that the large number of diagnosable characters indicates that Pygmy Eagle is a distinct species, regardless of which species concept is used. The large size difference between Pygmy and Little eagles (female Pygmy Eagles being similar in size to Little Eagle males) would probably function as a reproductive barrier should they meet. In addition, the size difference between the two taxa may function as an ecological isolation mechanism, as intermediate-sized hybrids could be less well-adapted.

Pygmy and Little eagles diverged from Booted Eagle or a common ancestor about one million years ago (2.2–2.6% divergence in mitochondrial cyt-b and ND2). Western Palearctic populations of Booted Eagle are migratory, wintering in Africa. In South Africa the resident subspecies *dubia* has evolved (Brooke & Vernon 1981). Eastern Palearctic populations of Booted Eagle are also migratory and winter in peninsular India. Vagrants have been observed southeast to peninsular Malaysia, Sumatra, Java and Bali (Ferguson-Lees & Christie 2001). Such vagrants of Booted Eagle or a common ancestor may have reached New Guinea and Australia historically and diverged over time, leading to the present-day Pygmy Eagle and Little Eagle. Interestingly, a third closely related species evolved at approximately the same time, the extinct giant Haast's Eagle *Aquila* (*Harpagornis*) *moorei* in New Zealand, as it has a similar level of genetic divergence from the Booted Eagle as from the other two taxa (Bunce *et al*. 2005).

Field identification

In the Moluccas the possibility of misidentification of Pygmy Eagles with vagrant Booted Eagles exists. Of the 15 pale morph Pygmy Eagles studied in the field and at BMNH, 12 (80%) had all underwing coverts white, lacking the contrasting white band between the rufous lesser underwing coverts and the dark secondaries found in all pale morph Little Eagles. All of the several hundred pale morph Little Eagles seen (in photos, museums and in the field) were all of this normal pale morph (Stephen Debus pers. comm.). The different underwing pattern of the Pygmy Eagle in the field is what first caught JOG's attention, as this plumage has not previously been described. Although the Pygmy Eagle's underwing pattern is broadly similar to that of pale morph Booted Eagle, it is easily distinguished under good observation conditions from the pattern in the Booted Eagle by the much paler inner parts of the outer primaries and very pale inner primaries. This produces a large pale patch on the hand that contrasts with the dark barred outer primaries and secondaries of the Booted Eagle. The Booted Eagle has black unbarred tips of the outer flight feathers (Figure 3). The dark morph Pygmy Eagle is more similar to the Booted Eagle in underwing pattern, but can be distinguished by the less contrasting upperwing pattern and the lack of pale-coloured contrasting uppertail coverts. Booted Eagles also have characteristic white shoulder-patches visible both in flight and when perched, lacking in Pygmy Eagle.

Juvenile Brahminy Kites *Haliastur indus* (Boddaert, 1783) have a similar plumage to the pale morph Pygmy Eagle both on the upperside and underside. However, under good observation conditions the kite is readily distinguished by its broader wings with an S-curved trailing-edge, shorter unbarred tail, bare tarsi and black unbarred primary-fingers.

In New Guinea the Pygmy Eagle may be confused with the Whistling Kite *Haliastur sphenurus* (Vieillot, 1818). Under good observation conditions the kite should easily be distinguished by its more slender body and longer rounded tail. Dark morph Pygmy Eagles can also be confused with Black Kites *Milvus migrans* (Boddaert, 1783); however, the kite's deeply forked tail shape is normally diagnostic.

Genetic differentiation

The level of mitochondrial sequence divergence between *A. morphnoides* and *A. weiskei* (2.2–2.6%; Table 4) lies within the range of that seen for seven other sister species of booted eagles, falling just below the average value of 2.7% (Table 5). Evidence of multiple fixed nucleotide differences between *A. weiskei* and *A. morphnoides* further supports a history of genetic isolation for these taxa.

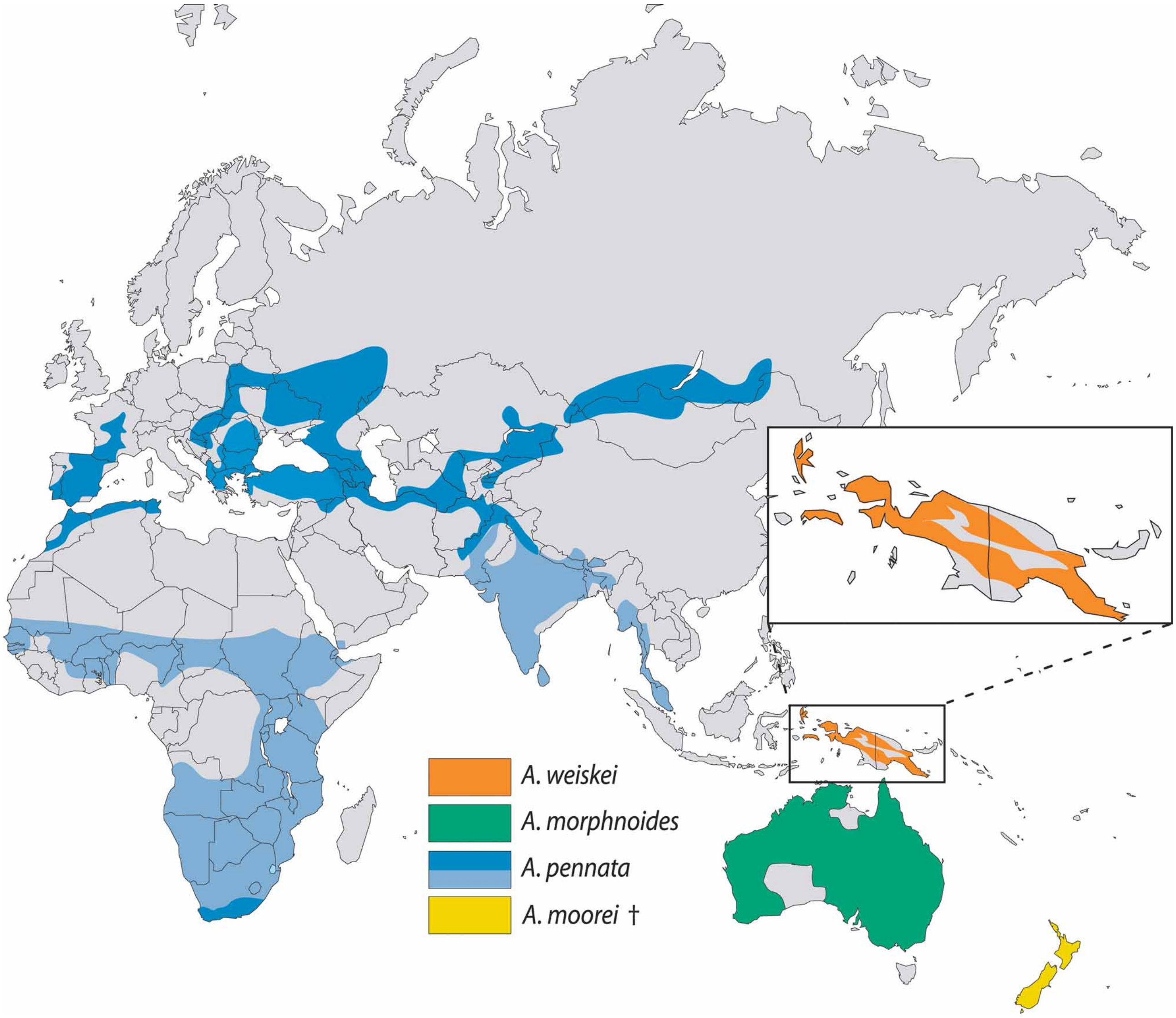

FIGURE 4. Distributions of *Aquila weiskei*, *A. morphnoides* and *A. pennata* (modified after Marchant & Higgins 1993; Ferguson-Lees & Christie 2005; Rasmussen & Anderton 2005; Naoroji 2006; own data). Light blue indicates the winter range of *A. pennata*. The probable distribution of the extinct Haast's Eagle *Aquila moorei* is also illustrated.

Distribution

The distribution of the Pygmy Eagle has been described as the mountain forests of central and eastern New Guinea (Condon & Amadon 1954); as sparsely distributed throughout New Guinea (no records from Vogelkop), but also as common but rather inconspicuous, from sea level to 1950 m (Beehler *et al.* 1986); and as uncommon or rare in Wallacea; presumably resident (Coates & Bishop 1997). A small eagle observed on Halmahera on 27–28 Jul 1989 was considered to have been a Little Eagle, and was regarded as apparently a vagrant from Australia or New Guinea (King 1990). Another small eagle, considered to be a juvenile Little Eagle, was observed in flight over primary forest at c. 700 m in Feb 1996 on Seram (Coates & Bishop 1997).

Neither of these was distinguished (sub)specifically at the time, but would surely have been *weiskei* rather than *morphnoides*. The distribution of *weiskei* was described as New Guinea except Vogelkop in Debus (1994). Elsewhere (Marchant & Higgins 1993; Ferguson-Lees & Christie 2001, 2005), the distribution is described as a more restricted range across New Guinea on each side of the central ridge, up to 2100 m except Vogelkop. In addition to our observations, *weiskei* was recently reported (as Little Eagle) from the Arfak Mountains and Batanta Island (Gregory 2008b). This species may have been previously overlooked because of similarities with Whistling Kites and juvenile Brahminy Kites. Our observations from Vogelkop and the Moluccas indicate that the Pygmy Eagle is resident in these areas.

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Appendix. Specimens of *Aquila* (*Hieraaetus*) examined in this study

Aquila weiskei: BMNH 1901.4.28.5, adult female, Astrolabe Mts., SE New Guinea (type specimen, collected by Emil Weiske); BMNH 1911.12.20.434, unsexed immature, Utakura river, Dutch New Guinea; BMNH 1955.6.N.20.357, adult female, Astrolabe Mts., SE New Guinea; BMNH 1913.3.6.35, female, Moroka Mts., British New Guinea; BMNH 1882.3.8.45, unsexed adult, Astrolabe Mts., SE New Guinea.

Aquila morphnoides: BMNH 1955.6.N.20.353, adult female, Swan River, Australia; BMNH 1955.6.N.20.354, adult female, Queensland, Australia; BMNH 1955.6.N.20.355, adult male, NSW, Australia; BMNH 1955.6.N.20.356, unsexed pullus, NSW, Australia; BMNH 1874.1.12.18, unsexed adult, Queensland, Australia; BMNH 1875.4.20.11, unsexed adult, Queensland, Australia; BMNH 1925.11.1.276, adult male, Queensland, Australia; BMNH 1969.4.22, adult female, Grant range, NE Australia; BMNH 1906.12.20.11, adult male, W. Australia.

Aquila pennata: BMNH 1885.8.19.1308, female, India; BMNH 1894.6.16.295, male, Egypt; BMNH 1875.11.22.17, female, Granada, Italy; BMNH 1885.8.19.1300, juvenile female, India; BMNH 1885.8.19.1297, male, India; BMNH 1887.11.1.319, female, India; BMNH 1885.8.19.1299, adult male, India; BMNH 1885.8.19.1302, male, India; BMNH 1885.8.19.1295, female, India; BMNH 1940.12.1.57, female, Beograd, Serbia; BMNH 1875.11.22.18, adult male, Granada, Italy; BMNH 1901.7.17.6, unsexed adult, Sevilla, Spain; BMNH 1875.11.22.21, adult male, Sevilla, Spain; BMNH 1955.6.N.20.338, adult male, France; BMNH 1945.20.5, adult male, Crete, Greece; BMNH 1886.3.25.125, male, India.