

Integrative taxonomy of the Changeable Hawk-Eagle *Nisaetus cirrhatus* complex (Accipitriformes: Accipitridae) in India

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Abstract

The Changeable Hawk-Eagle *Nisaetus cirrhatus* complex is represented by two taxa in mainland India: *N. c. cirrhatus* in the northern plains and peninsula and *N. c. limnaeetus* in the Himalayan foothills. Traditionally these taxa have been regarded as subspecies of one species, but recently they have been proposed to be different species. Here, we use an integrative taxonomic approach based on considerations of plumage, biometrics, genetics and vocalizations. Several plumage characters are significantly different between the two taxa, but crest length was the only one of 56 characters that was diagnostically different, with no overlap. About 30% of the birds had intermediate crest lengths, suggesting that they are hybrids or backcrosses, as also supported by the microsatellite results. PCAs of adult plumage

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show many intermediate individuals, irrespective of whether these birds were collected near a putative contact zone. There is restricted gene flow between the two taxa, presumably as a result of their largely allopatric distributions. On current knowledge, reproductive isolation appears to be weak at best, and we therefore recommend continuing to regard *limnaeetus* and *cirrhatius* as conspecific.

Key words: morphology, genetics, vocalization, integrative taxonomy

Introduction

The Changeable Hawk Eagle *Nisaetus cirrhatus* (Horsfield) has long been treated as two subspecies groups, the Crested Hawk Eagle group and the Changeable Hawk Eagle group (del Hoyo et al. 1994). In the first group, subspecies *N. c. cirrhatus* is distributed in peninsular India and *N. c. ceylanensis* (Gmelin) in Sri Lanka. In the second subspecies group, *N. c. limnaeetus* occurs from north India to western Indonesia and the southern Philippine islands, *N. c. andamanensis* (Tytler) on the Andaman island, *N. c. vanheurni* (Junge) in Simeulue island north-west of Sumatra, and *N. c. floris* (Hartert) on the Lesser Sunda islands from Lombok to Alor (Fig. 1).

Rasmussen & Anderton (2005, 2012) treated *N. c. cirrhatus* and *N. c. limnaeetus* as separate species based on apparently consistent morphological differences and some vocal differences, and this has been followed by several other authors (Ferguson-Lees & Christie 2005; Clements *et al.* 2016; Eaton *et al.* 2016), the first also regarding *N. c. andamanensis* and *N. c. vanheurni* as distinct species. Gjershaug *et al.* (2004) treated *N. c. floris* (Hartert) as a separate species based on consistent morphological differences. Although Gamauf *et al.*

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(2005) found that *N. c. cirrhatus* and *N. c. limnaeetus* were separate lineages based on a short mtDNA sequence (<300 bps), this was weakly supported, and genetic divergence was low, so they considered that their data did not strongly support treatment as separate species.

Dickinson & Remsen (2013) and Gill et al. (2020) treated *N. c. limnaeetus* as a subspecies of *N. cirrhatus*. Lerner *et al.* (2017) could not fully evaluate their species status as there was not enough existing sequence data (i.e. <300 bp mtDNA). They concluded that future work should address the species status of the Changeable Hawk Eagle with more sequence data, both from multiple nuclear loci and a larger amount of mitochondrial data. Under the Tobias *et al.* (2010) criteria, all subspecies groups were regarded as conspecific by del Hoyo & Collar (2014) and Clark et al. (2020).

Due to forest clearance in northern India, *N. c. cirrhatus* and *N. c. limnaeetus* have allopatric distributions today. Delimitation of species limits between some allopatric taxa will always remain arbitrary, no matter what species concept is applied, especially when the taxa are very similar. This is an inevitable consequence of the artificial partitioning of the continuous processes of evolution and speciation into discrete steps. Under the Biological Species Concept (BSC) there have been only vague guidelines as how to treat allopatric populations (Mayr & Ashlock 1991). More recently, Helbig *et al.* (2002) worked out more detailed guidelines for assigning species rank. According to their criteria, allopatric taxa may be assigned species rank if they are fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, e.g. structure, plumage, vocalizations or DNA sequences, and the sum of the character differences matches or exceeds the levels of divergence seen in related species that coexist in sympatry. Under the BSC, indications of reproductive barriers should be present between taxa treated as different species. Small diagnostic differences which may not have any implications for reproductive

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isolation are better regarded as indicators of subspecies rank. In this study we examine species limits in the *Nisaetus cirrhatus* complex in India using an integrative taxonomic approach (Dayrat 2005) based on novel molecular, morphological and vocal data and we interpret the data in light of the BSC.

Methods

Morphological analyses.

Morphological measurements and plumage studies were carried out primarily at the Natural History Museum, Tring (NHMUK). Measurements (all taken at NHMUK) were taken using a calliper and a ruler to the nearest tenth of a mm. A total of 39 adult and subadult specimens representing two taxa (16 *N. c. cirrhatus* and 23 *N. c. limnaeetus*) (see Appendix 1) were measured for 13 variables: crest length; bill length from cere; bill breadth; bill depth; wing length (flattened); Kipp's distance (= primary projection); tarsus length; hind toe; middle toe; hind claw; middle claw; tail length (measured from the emergence point of the central pair of feathers) and number of dark tail bands. We excluded juvenile birds from the data set, since any not fully grown would bias the analysis.

Plumage characters were scored for 206 specimens (49 *cirrhatus*, 30 *ceylanensis*, 120 *limnaeetus*, six *andamanensis*, and one *vanheurni*). These included nearly all specimens from NHMUK, as well as those at the American Museum of Natural History (AMNH), National Museum of Natural History, Smithsonian Institution (USNM), and University of Michigan Museum of Zoology (UMMZ). Dark-morph *limnaeetus* (the only form for which dark-morph specimens were available) were not scored. Plumage characters scored, with a description of each state, differed for different ages classes, and those scored were those previously noted as

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apparently differing between corresponding age classes of *limnaeetus* and *cirrhatius*. For all birds, the following two plumage characters were scored: breadth of fresh upper mantle pale edges (1 = none, 2 = very narrow, 3 = rather narrow, 4 = moderate, 5 = rather broad, 6 = very broad) and uniformity of mid-mantle feathering (1 = entirely uniform, 2 = slight contrast, 3 = moderate contrast, 4 = marked contrast, 5 = extreme contrast). For adults only, the following six plumage characters were scored or measured: breadth of medial throat streak (1 = none, 2 = very narrow, 3 = rather narrow, 4 = moderate, 5 = rather broad, 6 = very broad); percentage of pale lower belly feathering; percentage of pale vent feathering; maximum breadth of pale upper thigh barring; degree of contrast of head streaking (1 = none, 2 = weak, 3 = moderate, 4 = prominent); and rufescence of neck feather edgings (1 = none, 2 = slight, 3 = distinct but weak, 4 = moderate, 4 = strong). Although immatures (defined as being those in transitional plumage between juvenile and adult plumages) were scored, these were not used in analyses owing to the mix of plumage characters they exhibit. For univariate statistics, samples were partitioned by sex and age (birds without label sex being excluded), and significance levels between taxon groups for each sex and age class were determined with Kruskal-Wallis One-way Analysis of Variance. Principal Components Analyses were undertaken separately for adults and juveniles, with sexes combined. To determine whether overlap in plumage characters was stronger where the ranges of the two taxon groups nearly contact, specimens localities from within 100 km of the range of the other group were distinguished in the analysis. Plumage-related statistics were done using MYSTAT (<https://systatsoftware.com/>)

The sex of most of the museum skins was as given on the labels, however we used a discriminant analysis approach (described below) to identify the sex of unsexed individuals. By this method, we also found four individuals that obviously were incorrectly sexed by their

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collectors. The same result, except for one fewer individual, was obtained using a simpler test by plotting bill length versus hind claw from each taxon, similarly to a predictive model used by Bortolotti (1984).

Birds were placed into four age classes based on their rectrices: 1) those with all juvenile rectrices (fully grown) were considered juveniles; 2) those with at least one second generation rectrix and at least one retained juvenile rectrix were considered first stage subadults; 3) those with at least one third generation (adult) rectrix and at least one retained second generation (subadult) rectrix were considered second stage subadults; and 4) those with entirely adult (third generation) rectrices were considered adults.

Discriminant function analysis (DFA) is a multivariate technique that identifies underlying, independent linear discriminators (LDs) that contribute to the correct discrimination between groups of individuals (see e.g. Venables & Ripley 2002). Helbig *et al.* (2002) argued that when there is overlap in the range of several variables between taxa, ‘statistical diagnosis’ can be applied by using discriminant analysis based on two or three ‘functionally independent’ variables. We have here chosen candidate variables having the least range overlap, while assumed to have as little covariance as possible. The discriminant function analysis was performed using the *MASS* package in the free statistical software R (R Core Team 2018).

Vocalizations

Field studies were carried out in two areas in India in January and February 2005. Tape recordings of vocalizations of *N. c. cirrhatus* were made in Nagarahole National Park in Karnataka (South India) (about 11° 45’ N and 76° 5’E) on 7–9 January 2005 and of *N. c. limnaeetus* in Corbett National Park in Uttaranchal in North India (about 29° 25’ N and 78° 5’ E) on February 4–6 and 15–17. This was the start of the breeding season in Corbett with nest

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building and courtship under way. In Nagarahole, it was probably also the beginning of the breeding season, as egg-laying usually takes place in January in the southern part of India (Naoroji 1985).

Sonagrams from calls of adults and fledged juveniles were obtained on a KAY Elemetrics DSP Sona-Graph model 5500. The analyses were based on 164 sonagrams, representing adult and juvenile birds in three territories in each of the recording sites Nagarahole and Corbett. Due to uncertainty as to how many adult individuals we recorded, we lumped the recordings from each taxon. Measurements are reported as mean \pm standard deviation (SD) and range.

Our vocalization analyses used the following variables: 1) pitch (highest frequency measured to the nearest 0.01 kHz); 2) length of strophe (to the nearest 0.01 s); 3) length of note (measured to the nearest 0.01 s); 4) number of notes in the strophe; 5) strophe rate (number of strophes per s); 6) note rate (number of notes per s).

Genetic analyses

We obtained toepad samples from 40 specimens at the Natural History Museum (NHMUK), Tring (Appendix 2). Of these, five were from *Nisaetus c. ceylanensis* from Sri Lanka, 15 from *N. c. cirrhatus* from southern India, and 20 from *N. c. limnaeetus* from north India and Nepal. Ten of these were from specimens with intermediate crest lengths. These were assumed to be hybrids or backcrosses between *N. c. cirrhatus* and *N. c. limnaeetus*.

Genomic DNA was isolated using the E.Z.N.A. MicroElute Genomic DNA kit (Omega Biotek). All samples were genotyped with 11 microsatellite loci, Bbu42 (Johnsen *et al* 2005),

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BV13 (Gautschi *et al.* 2003), SNMS01, SNMS16, SNMS24, SNMS26, SNMS27, SNMS30, SNMS32 (Hirai & Yamasaki 2010), TG04-061 (Dawson *et al.* 2010) and Tgu06 (Slate *et al.* 2007). As DNA from old museum specimens might be degraded and thus potentially have a negative effect on the genotyping success rate, we selected these 11 loci as they amplified relatively short fragments (<250 base pairs). To amplify the microsatellites and construct a consensus genotype based on three independent PCR-replicates, we followed the same procedure as described by Selås *et al.* (2017). Of the 40 samples, 32 contained a consensus genotype with at least 10 loci and were included in the downstream analyses.

Linkage disequilibrium and deviations from Hardy-Weinberg were tested using Arlequin 3.5.2.2 (Excoffier & Lischer 2010). A Bonferroni correction for multiple statistical tests (Rice 1989) was applied to linkage disequilibrium p-values. Genetic diversity within each group was described by the mean number of alleles per locus, observed and expected heterozygosity, and the inbreeding coefficient using Arlequin 3.5.2.2 (Excoffier & Lischer 2010). Genetic variation within and among groups was analysed with an analysis of molecular variation (AMOVA) using Arlequin 3.5.2.2 (Excoffier & Lischer 2010). Population structure was estimated using principal coordinate analysis (PCoA) implemented GenAlEx ver. 6.5 (Peakall & Smouse 2012).

Results

Biometry and plumage of *Nisaetus cirrhatus*

Among mensural characters, only crest length differed diagnostically (no overlap) between the taxa (Table 1), with *N. c. cirrhatus* having the longer crest. Of the 15 *N. c. limnaeetus* observed in the field, 4 (27%) had an intermediate length crest (Table 2).

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The DFA-plot presented in Fig. 2, based on tail length, tarsus length and bill depth, indicates that the discrimination of the two taxa between individuals of the same sex is not complete. In this DFA, we have excluded crest length as a candidate variable since it had no overlap between ranges for the two taxa. When the DFA was performed for one sex at the time, all females were classified to correct taxa, whereas two *N. c. limnaeetus* males were classified as *N. c. cirrhatus*.

Figure 3 and 4 show one adult and one juvenile *N. c. limnaeetus* with intermediate-length crests in Corbett National Park. In the NHMUK skin collection, 18 *N. c. limnaeetus* specimens (31%) of 58 individuals had more or less intermediate crest length. Most of these had originally been identified as *N. c. cirrhatus* based on the crest but had later been reidentified by one of us (PCR). The plumage of *N. c. cirrhatus* and *N. c. limnaeetus* is very similar both in adults (Fig. 5) and juveniles, but with some consistent differences (Tables 3, 4, 5).

Several plumage characters differed significantly between adults of the two taxa (Table 5), especially those related to degree of darkness of the lower belly, vent, and thighs. Plumage characters between immatures overlapped more broadly and showed lower distinctiveness. In both adults and juveniles, the mantle was significantly more uniform in the *limnaeetus* group than the *cirrhatus* group. However, there was broad overlap between the taxon groups in ranges of all plumage characters. Similarly, a PCA of plumage characters of adults (Figure 6) showed considerable overlap in multivariate space, and specimens from near the range limits of the other taxon group appear no more likely to have intermediate plumage characters than those from areas less likely to constitute a hybrid zone. A PCA of plumage characters of juveniles showed even greater overlap between scores of the two taxon groups and is not presented here.

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Vocalization characteristics

We recognized four categories of adult vocalizations (A–D) and one category of juvenile call (E):

- A. Unmodulated whistle
- B. Double whistle
- C. Glissando whistle with or without cackling
- D. Screaming
- E. Juvenile call

The unmodulated whistle (Fig. 7A, Table 6) was made up of a varying number of similar notes, given in sequences from three or four notes up to bouts of several tens. Maximum recorded number was 64 notes in the same sequence.

The double whistle calls (Fig. 6B, Table 5) were sometimes given in rapid sequences of a varying number and sometimes inserted in sequences of high-frequency unmodulated whistles. Bouts of short notes (cackling) were sometimes inserted between double whistle calls.

The glissando whistle (Fig. 7C, Table 6) differed from the first two types in that the figure described a curved ascending glissando, sometimes differing in pitch between start and end with more than 1 kHz. Bouts of short notes (cackling) were often inserted between the whistles. The typical unmodulated whistle sometimes transitioned gradually to the glissando whistle.

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The screaming call (Fig. 7D, Table 7) was made up of four or five partly overlapping elements. Calls were given in series of one to five in a bout. The call was probably identical to that described by Brown & Amadon (1968) as “kleee-klee-ek” and by Rasmussen & Anderton (2012) as “*FWEE-\fwee(-fwee)*”.

The juvenile call (Fig. 8, Table 8) was described by Brown & Amadon (1968) as “ki-ki-ki-ki-ki-ki-ki-keeee” and by Rasmussen & Anderton (2012) as “*FLEE-/FLEE-/FLEE-/FLEE-/FLEE/FLEe//KEEEeee*”. The latter authors suggested the call was uttered by presumed territorial birds. However, the call appears to be used by begging juvenile birds.

None of the twenty vocal characters described in tables 6–8 are diagnostically different (without overlap) between the two taxa, except the note rate of the double whistle call (Fig. 7B, Table 6). The sample size for this character was, however only two.

Genetic analyses

After correcting for multiple tests, no pairs of loci displayed significant linkage disequilibrium either across all three groups or within each group. Three loci deviated significantly from Hardy-Weinberg equilibrium, but there was no consistent pattern across or within the three groups (Appendix 3). We thus retained all 11 loci in the downstream analyses. All 11 loci were polymorphic with observed heterozygosity ranging from 0.09 to 0.97 (Appendix 3). Within each group the mean observed heterozygosity ranged from 0.57 (no crest) to 0.62 (long crest) (Appendix 3). The inbreeding coefficient ranged from 0.09 (no crest) to 0.21 (long crest) and was not significant for any of the three groups (Table 10). The average number of unique alleles was lowest for birds with intermediate crest length, higher for those with no crest and highest for those with long crest (Table 10). A global AMOVA revealed an overall low but significant genetic differentiation ($F_{ST} = 0.042$) over all loci ($P = 0.0008$).

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Pairwise comparisons revealed the highest genetic differentiation between long and no crested birds ($F_{ST} = 0.06$, $P = 0.0001$), weaker differentiation between long and intermediate crested birds ($F_{ST} = 0.042$, $P = 0.011$), and no significant differentiation between intermediate and no crested birds ($F_{ST} = -0.0009$, $P = 0.64$). The PCoA result revealed no clear pattern of genetic structure, although intermediate crested birds seemed to cluster between the long-crested and uncrested birds (Figure 9).

Discussion

The DFA of biometrics showed that the two taxa are not completely separated. Of all morphological characters compared between the two taxa, 13 biometrical characters (Table 1) and 14 plumage characters (Table 3 and Table 4) only the crest length was diagnostically different (no overlap) between the two taxa. These differences are comparable with what is found between subspecies of some other raptors, e.g. Mountain Hawk Eagle *Nisaetus nipalensis* Hodgson and Oriental Honey Buzzard *Pernis ptilorhynchus* (Temminck), in both of which some subspecies have a long crest while others lack a crest (Ferguson-Lees & Christie 2005).

The difference in crest length was one of the main reasons for splitting them into two different species by Rasmussen & Anderton (2012). As we have seen, there are skins from North India in the collection at the Natural History Museum, Tring (NHMUK) with intermediate crest lengths, and individuals with intermediate crest lengths have also been observed by JOG in Corbett National Park in North India. This is perhaps an indication of some gene flow between *N. c. limnaeetus* and *N. c. cirrhatus*. Today, this is probably restricted by habitat alteration from forest to scrub and cultivation across the northern part of the Indian peninsula south of the Himalayan foothills.

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The large intra-individual variation in the different calls (recorded in the same sequence) seems to be related to differences in the motivation of the birds. Due to the small sample size and uncertainty on which individual was calling, it was not possible to estimate the degree of inter-individual variation.

Observations also indicate that the three types of whistle calls probably are used by the female as solicitation calls. They represent a continuum, as the female usually gave them successively according to her motivation, similarly to what has been described for the Osprey *Pandion haliaetus* Linnaeus (Bretagnolle & Thibault 1993). When cackling (series of very short notes) were inserted between the main whistles, the pair was often seen together, and copulations were seen in such situations.

The screaming call is probably used both as an advertising call in claiming the territory and as a pair-contact call. The call is given both in flight and when perched. When an adult *N. c. cirrhatus* was mobbed by a giant squirrel *Ratufa indica* (probably close to the nest), it also gave series of screaming calls.

The juvenile call is most likely also a solicitation call (begging for food). Juveniles call more frequently when hungry, and the structure of the call probably also changes with the motivation of the bird.

Our results indicate that the different call types are similar in the two study areas. The note rate of the double whistle call was the only character that was diagnostically different (no overlap) between the taxa, but the sample size was very small (N=2).

Some of the variation is probably related to the sex of the birds. We have recorded a difference of about 1 kHz in pitch of the glissando whistle when the male and female in a territory were calling at the same time. A negative relationship between body mass and frequencies of signals has been demonstrated below and above the species level in several

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bird species: larger birds are believed to emit calls with a lower fundamental frequency because of their larger syringes (Ryan & Brenowitz 1985).

The occurrence of about 30% of birds with intermediate crest lengths in the breeding area of *N. c. limnaeetus* in North India (4/15 *N. c. limnaeetus* seen in Corbett NP in 2005, 18/50 *N. c. limnaeetus* in the NHMUK skin collection) suggests hybridization between the two taxa. If we assume that these birds with intermediate crest lengths are hybrids and backcrosses, North India could be considered as a zone of limited hybridization and not part of a cline as the individuals are not phenotypically uniform (Helbig *et al.* 2002).

Our microsatellite DNA analyses revealed that the intermediate-crested birds showed a tendency to cluster between the long-crested and the uncrested birds. The pairwise comparisons revealed a weaker but significant differentiation between long and intermediate crested birds than between long and uncrested birds. This supports the assumption that the intermediate-crested birds are hybrids and backcrosses. However, the lack of concordance of other plumage characters with proximity to the range of the other taxon fails to support this explanation.

Although a small differentiation (0.4-1.2 % in cytochrome *b*) was found between these taxa in mtDNA (Gamauf *et al.* 2005), the sample sizes are small (only three *N. c. cirrhatus* from India and 1 *N. c. limnaeetus* from Nepal). A genetical difference of 0.4 % between the two taxa indicates that they were separated about 200.000 years ago (with a molecular clock of 2% per million years). During the Pleistocene glaciations there were cool and dry periods (e. g. 190,000 years ago), and biogeographical evidence indicates that Asian rainforests were fragmented during these periods (Brandon-Jones 1996). From a Pleistocene refugium somewhere in SE Asia, *N. c. limnaeetus* probably expanded westwards to the Himalayan

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foothills quite recently, indicated by the small genetic difference between the bird from Nepal and birds from the Indonesian islands (Gamauf *et al.* 2005).

Under the criteria of Helbig *et al.* (2002) and Isler *et al.* (1999), diagnosability is a purely practical undertaking of the taxonomist, as whether or not characters are diagnostic may or may not be relevant to the birds themselves, for instance in mate recognition. The fact that they differ between taxa indicates that there has been a period during which genetic differences have accumulated. However, if two taxa are different biological species, there should be differences in characters that contribute to reproductive isolation. This could be related to mate recognition (e.g., plumage and vocalizations) or selection against hybrids with intermediate structure characters (e.g., bills and feet). If there are no such indications, the taxa are better regarded as conspecific. In this specific case, we find no indications of reproductive isolating mechanisms, so we recommend continuing to treat *N. c. limnaeetus* as a subspecies of *N. c. cirrhatus*.

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FIGURE CAPTIONS

Figure 1. Ranges of taxa in the Changeable Hawk Eagle *Nisaetus cirrhatus* complex (after Ferguson-Lees & Christie 2005; Rasmussen & Anderton 2012; Naoroji 2006; Gamauf 2018; own data).

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Fig. 2. Discriminant function analysis (DFA) plot for the two first linear discriminators, based on tail length, tarsus length and bill depth. *Cirrhatus* individuals are indicated by circles, *limnaeetus* by triangles; empty symbols are males and filled symbols females. Groups are enclosed by polygons.

Figure 3. Adult *Nisaetus c. limnaeetus* with intermediate-length crest in Corbett NP.

Figure 4. Juvenile *Nisaetus c. limnaeetus* with intermediate-length crest in Corbett NP.

Figure 5. Adult NHMUK specimens in ventral view, (a) *Nisaetus c. cirrhatus*; (c) *N. c. limnaeetus*. Same specimens on dorsal view: (b) *N. c. cirrhatus*; (d) *N. c. limnaeetus*.

Figure 6. Principal Component Analyses (PCA) of eight plumage characters (Table 5) of adult Changeable Hawk-eagles.

Figure 7. Sonagrams of calls of adult Changeable Hawk-eagle. A. Unmodulated whistle. B. Double whistle. C. Glissando whistle with cackling. D. Screaming.

Figure 8. Sonagram of calls of juvenile Changeable Hawk-eagle.

Figure 9. Principal coordinate analysis (PVoA) of pairwise distance based on microsatellite data of Changeable Hawk-eagles. Indicated are birds with long crest (circle), intermediate-length crest (square) and no crest (triangle).

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Table 1. Biometrics of *N. c. cirrhatus* and *N. c. limnaeetus* and diagnosability. F=female, M=male. Characters with overlap indicated by -, those without overlap by +.

Morph. character	Sex	<i>cirrhatus</i>				<i>Limnaeetus</i>		
		N	mean	min-max	overlap	N	mean	min-max
Crest length	M	5	97	90-110	+	11	42.9	37-60
	F	11	100.9	80-120	+	12	45	40-65

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Bill length	M	5	28.2	26.6–30.1	-	11	30.1	28.3–31.9
	F	10	30.8	27.4–33.5	-	12	33.1	30.4–36.1
Bill breadth	M	5	13.2	13.0–13.4	-	10	13.8	13.0–14.9
	F	11	14.6	13.4–15.7	-	12	14.9	13.4–16.4
Bill depth	M	5	20	19.3–21.6	-	8	20.4	19.3–21.9
	F	11	20.6	18.9–22.1	-	12	22.6	20.3–23.6
Wing length	M	5	407.6	400–425	-	11	389.1	340–420
	F	11	423.7	380–445	-	12	432.5	405–450
Kipp's dist.	M	5	69	55–90	-	9	67	55–80
	F	11	76.4	55–100	-	12	70.4	50–100
Tarsus length	M	5	112.8	109–120	-	11	111.4	100–123
	F	10	110.5	94–118	-	12	114.7	108–120
Hind toe	M	5	27.2	25.6–28.8	-	11	25.5	21.1–29.1
	F	11	28.7	26.6–31.3	-	12	28.6	24.9–32.0
Middle toe	M	5	48.1	45.2–51.1	-	11	47.2	42.1–51.3
	F	11	51.4	46.7–54.6	-	11	51.6	46.7–58.4
Hind claw	M	5	31.8	27.6–35.1	-	11	32.2	28.3–34.3
	F	11	35.4	31.2–37.8	-	11	36.8	30.9–40.4
Middle claw	M	5	25.5	23.8–27.4	-	10	24.7	22.0–26.8
	F	11	26.9	24.2–29.5	-	10	27.7	25.4–29.5
Tail length	M	5	279.6	270–290	-	10	257.7	240–280
	F	11	285	260–300	-	12	277.1	260–290
Tail bands	M	5	4.4	4–5	-	10	4.1	3–5
	F	11	4.5	4–5	-	12	4.7	4–5

Table 2. Presence of crest among individuals in territories of *limnaeetus* in Corbett National Park. I = intermediate-length crest; N = uncrested bird.

Territory Number	Male	Female	Unsexed Adult	Juvenile
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1	N	I	—	I
2	N	I	—	N
3	I	N	—	N
4	N	—	—	N
5	N	N	—	—
6	—	—	N	—
7	—	—	N	—

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Table 3. Principal plumage differences between adult *N. c. cirrhatus* and *N. c. limnaeetus*.
N = number of individuals.

Character	<i>cirrhatus</i>	<i>limnaeetus</i>
Head and neck	Typically darker brown (18/23 birds), so the dark streaks contrast less with the background colour	Less dark brown (all 6 birds)
Belly and vent	Solid dark from mid-belly to vent in all the largest birds (presumed females)	Usually banded; 1/7 full adult birds has a solid dark lower belly, but the vent is strongly banded
Upperparts	Appear slightly more streaked due to the paler feather edgings in 19/23 birds.	Solid dark brown appearance (all 6 birds)
Tarsal feathering	Less extensive, barely extends beyond the tarsal joint. Distance from the midpoint of distalmost tarsal feathering to the base of the furrow between the middle toe and the inner toe 3.5–7.8 mm (N=7).	Extends well beyond the tarsal joint. Distance from the midpoint of distalmost tarsal feathering to the base of the furrow between the middle toe and the inner toe 4.0–9.2 mm (N=11).

Table 4. Principal plumage differences between juvenile *cirrhatius* and *limnaeetus*.

Character	<i>cirrhatius</i>	<i>limnaeetus</i>
Head and nape	Initially has cinnamon tinge; retains buff tint throughout the juvenile stage	Initially has cinnamon tinge, wears off quickly to white
Neck sides	Persistent cinnamon colour	Cinnamon colour wears off quickly; present in the youngest 5/11
Underside	Not snowy white	Snowy white in all but the youngest
Underwing coverts	Moderately speckled in all but two; one was lightly and one heavily speckled	Unmarked white to lightly marked; two moderately speckled
Webs of mantle feathers	Buff triangular edges on both webs	Most have whiter edges, usually only on inner web
Wing coverts	Most (6/9) show much cinnamon. Usually browner, less blackish, and grade from the dull whitish edge into the darkest central portion.	Usually more starkly contrasting, with whiter edges contrasting more sharply against the darker main parts of the feathers. Some birds show much white in the wing coverts, while a single very young bird showed relatively little (1/10).
Undersurface of primaries	More contrastingly banded, with the paler bars paler grey	Less contrastingly banded
Dark tips of mantle feathers	Smaller, with buffier bases	Larger and whiter, giving a more solidly blackish-brown mantle; feathers more round-tipped
Uppertail coverts	Darker, not appearing as a white rump band	Distinctly white in 9/10 individuals, in some cases just the longest central ones, in others most are white
Rump colour	Uniformly warm brown	Variable; some medium brown and others with rump much paler; 2/9 have the longest rump feathers worn to barred whitish

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Table 5. Univariate statistics of plumage scores for *Nisaetus limnaeetus* and *N. cirrhatus* taxa, partitioned by sex and age, stated as mean±SD (range). Unsexed and transitional plumage birds excluded. Significance levels (tested within a sex and age class, between taxon groups only) from Kruskal-Wallis One-way Analyses of Variance: ns = $p > 0.05$; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

Character levels	<i>cirrhatus</i> group		<i>limnaeetus</i> group		Significance	
	Males (n=13)	Females (n=16)	Males (n=34)	Females (n=16)	Males	Females
Adults						
Mantle feather pale edge breadth	2.7±1.1 (1–5)	3.2±1.0 (1–5)	1.6±1.1 (1–4)	1.8±1.1 (1–4)	**	***
Mid-mantle uniformity	2.4±0.8 (1–4)	2.6±0.9 (1–4)	1.5±0.6 (1–3)	1.5±1.3 (1–3)	***	***
Mesial streak breadth	3.5±1.0 (2–5)	4.0±0.6 (3–5)	3.2±1.1 (2–5)	4.1±0.9 (3–6)	ns	ns
% pale in belly	25.4±17.5 (0–60)	4.0±5.5 (0–15)	46.0±23.3 (0–80)	41.2±21.9 (2–80)	**	***
% pale in vent	12.4±14.2 (0–40)	5.7±5.1 (0–15)	36.3±19.2 (0–80)	36.6±17.7 (10–70)	***	***
Max. thigh bar w	1.9±1.3 (0–5)	1.2±1.5 (0–4)	14.2±15.8 (0–5)	11.5±14.7 (1–4)	***	***
Head streak w	3.5±1.0 (2–5)	3.1±0.8 (2–4)	2.2±1.7 (0–5)	2.5±1.7 (0–5)	*	ns
Neck rufescence	3.2±0.7 (2–5)	3.4±0.7 (3–5)	3.1±1.3 (0–5)	2.9±1.0 (1–5)	ns	ns
Juveniles						
Mantle feather pale edge breadth	3.6±1.4 (2–6)	3.8±1.3 (2–6)	2.5±1.0 (1–5)	2.2±1.0 (1–4)	*	**
Mid-mantle uniformity	3.8±0.7 (3–5)	3.8±0.6 (3–5)	2.7±1.0 (1–4)	2.6±1.0 (1–5)	**	***
Underwing covert speckling	3.6±1.1 (2–5)	3.5±1.3 (2–5)	3.0±0.8 (1–4)	3.3±0.8 (2–4)	ns	ns
P3 band contrast	3.4±0.5 (3–4)	3.5±0.5 (3–4)	2.6±1.0 (1–5)	2.7±0.8 (1–4)	*	**
Uppertail covert band whiteness	3.1±0.9 (2–5)	3.0±1.0 (1–4)	3.2±1.3 (1–5)	3.6±1.0 (2–5)	ns	ns

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Wingbar prominence	3.5±0.9 (2–5)	3.8±1.0 (2–5)	3.0±1.0 (1–5)	3.0±0.8 (2–4)	ns	*
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Table 6. Whistle of adult hawk eagles in three territories of each taxon.

		<i>N. c. cirrhatus</i>	<i>N. c. limnaeetus</i>
Unmodulated whistle	pitch	1.93 kHz ± 0.16 (1.8–2.3) (n=13)	1.81 kHz ± 0.25 (1.4–2.6) (n=38)
	note length	0.34 sec ± 0.08 (0.2–0.4) (n=15)	0.41 sec ± 0.21 (0.1–1.1) (n=38)
	note rate	0.95/sec ± 0.07 (0.9–1.0) (n=2)	0.68/sec ± 0.32 (0.2–1.2) (n=8)
Double whistle	pitch	2.65 kHz ± 0.14 (2.3–2.8) (n=9)	2.21 kHz ± 0.29 (1.7–2.6) (n=9)
	note length	0.38 sec ± 0.09 (0.3–0.6) (n=9)	0.63 sec ± 0.11 (0.5–0.8) (n=9)
	note rate	1.53/sec ± 0.08 (1.5–1.6) (n=2)	0.50/sec ± 0.04 (0.5–0.5) (n=2)
Glissando whistle	pitch	1.96 kHz ± 0.09 (1.8–2.0) (n=4)	1.99 kHz ± 0.33 (1.6–2.7) (n=8)
	note length	0.35 sec ± 0.12 (0.2–0.5) (n=5)	0.44 sec ± 0.18 (0.2–0.7) (n=8)
	note rate	0.43/sec (n=1)	1.20/sec ± 1.28 (0.4–2.7) (n=3)

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Table 7. Screaming call of adult hawk eagles in three territories of each taxon.

	<i>N. c. cirrhatus</i>	<i>N. c. limnaeetus</i>
pitch	2.48 kHz \pm 0.10 (2.1–2.6) (n=23)	2.34 kHz \pm 0.04 (2.2–2.4) (n=12)
strophe length	0.75 sec \pm 0.11 (0.5–0.9) (n=25)	0.74 sec \pm 0.15 (0.4–1.0) (n=12)
strophe rate	0.35/sec \pm 0.05 (0.3–0.4) (n=4)	0.39/sec \pm 0.08 (0.3–0.5) (n=4)
strophes/bout	2.83 \pm 1.47 (1–5) (n=6)	2 (n=11)
notes/strophe	2.83 \pm 0.41 (2–3) (n=6)	1.55 \pm 0.52 (1–2) (n=11)

Table 8. Begging call of juvenile hawk eagles in three territories of each taxon.

	<i>N. c. cirrhatus</i>	<i>N. c. limnaeetus</i>
pitch first note	2.20 kHz \pm 0.38 (1.7–2.7) (n=22)	2.04 kHz \pm 0.19 (1.8–2.3) (n=21)
pitch final note	2.72 kHz \pm 0.16 (2.4–2.9) (n=21)	2.69 kHz \pm 0.08 (2.5–2.9) (n=22)
strophe length	1.6 sec \pm 0.31 (1.1–2.3) (n=22)	1.54 sec \pm 0.18 (1.2–1.9) (n=21)
strophe rate	0.17/sec \pm 0.05 (0.1–0.3) (n=4)	0.17/sec \pm 0.11 (0.1–0.3) (n=4)
number of notes	5.86 \pm 1.08 (5–9) (n=22)	6.05 \pm 0.67 (5–7) (n=21)
note rate	3.74/sec \pm 0.62 (2.6–4.9) (n=22)	3.95/sec \pm 0.35 (3.4–4.8) (n=21)

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Table 9. Summary of genetic variability in *N. c. limnaeetus*. Sample size (N), average number of alleles across loci (A), average number of unique alleles (AU), observed (HO) and expected heterozygosity (HE) and inbreeding coefficient (F_{IS}). Genetic variability was based on the average of 11 polymorphic microsatellite loci.

Group	N	A	A _U	H _O	H _E	F _{IS}
Long crest length	15	5.9	1.6	0.62	0.64	0.21
Intermediate crest length	7	4.5	0.2	0.60	0.65	0.11
No crest	10	5.2	0.5	0.57	0.61	0.09

Table 10. Taxonomic decision table with all criteria used for species delimitation. + = character is diagnostic; - = character is non-diagnostic; +/- = character is/is not diagnostic.

Taxon	morphometrics	plumage	vocalizations	Microsatellite DNA	Proposed taxonomic status
<i>cirrhatu</i> s	+/-	+/-	-	-	<i>Nisaetus c. cirrhatu</i> s
<i>limnaeetu</i> s	+/-	+/-	-	-	<i>N. c. limnaeetu</i> s

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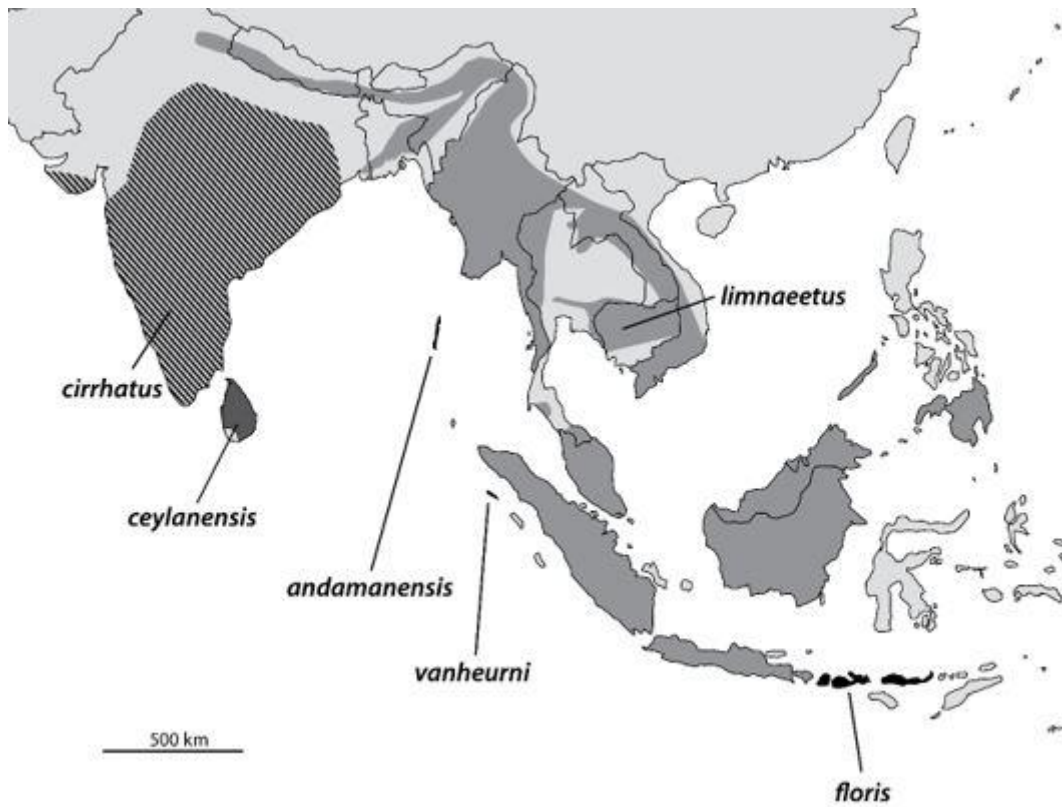


Fig. 1.

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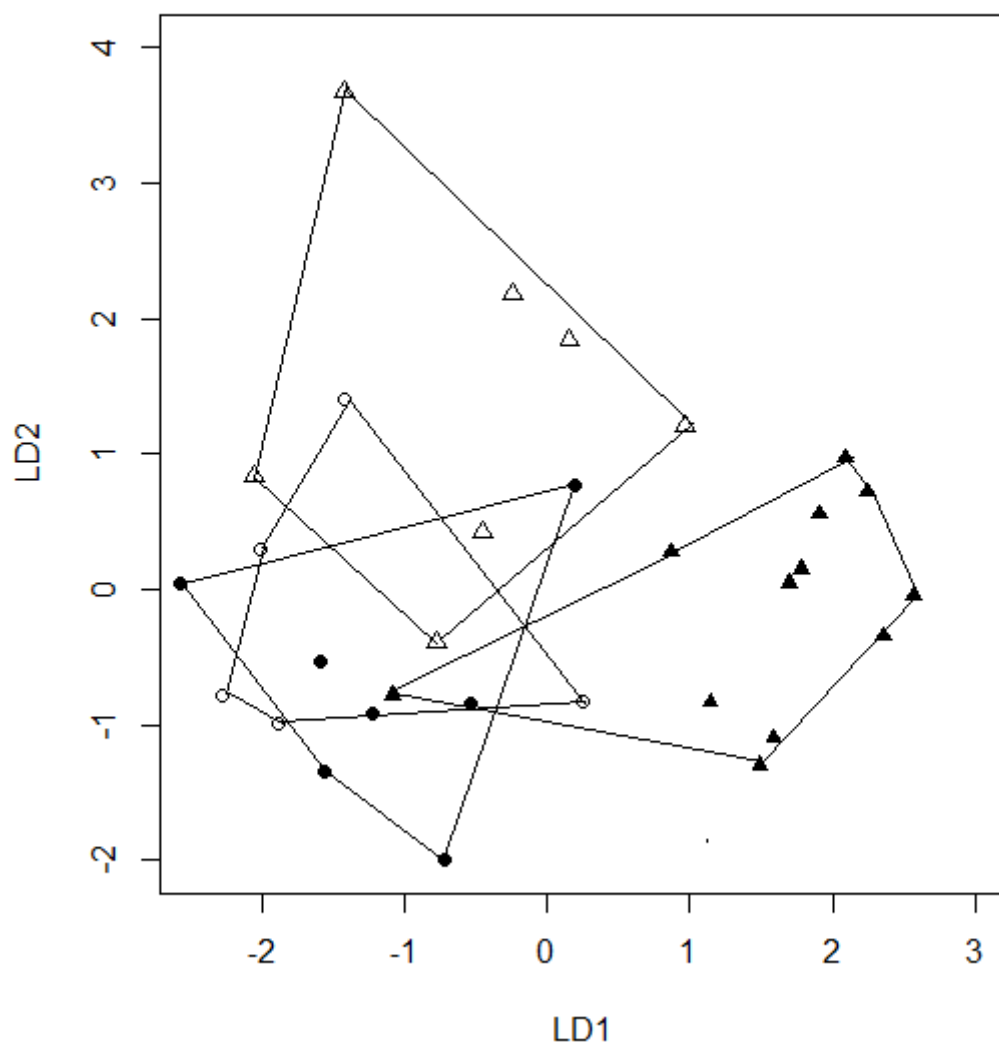


Fig. 2.

Gjershaug, Jan Ove; Diserud, Ola Håvard; Kleven, Oddmund; Rasmussen, P.C.; Espmark, Yngve.
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Fig. 3

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Fig. 4

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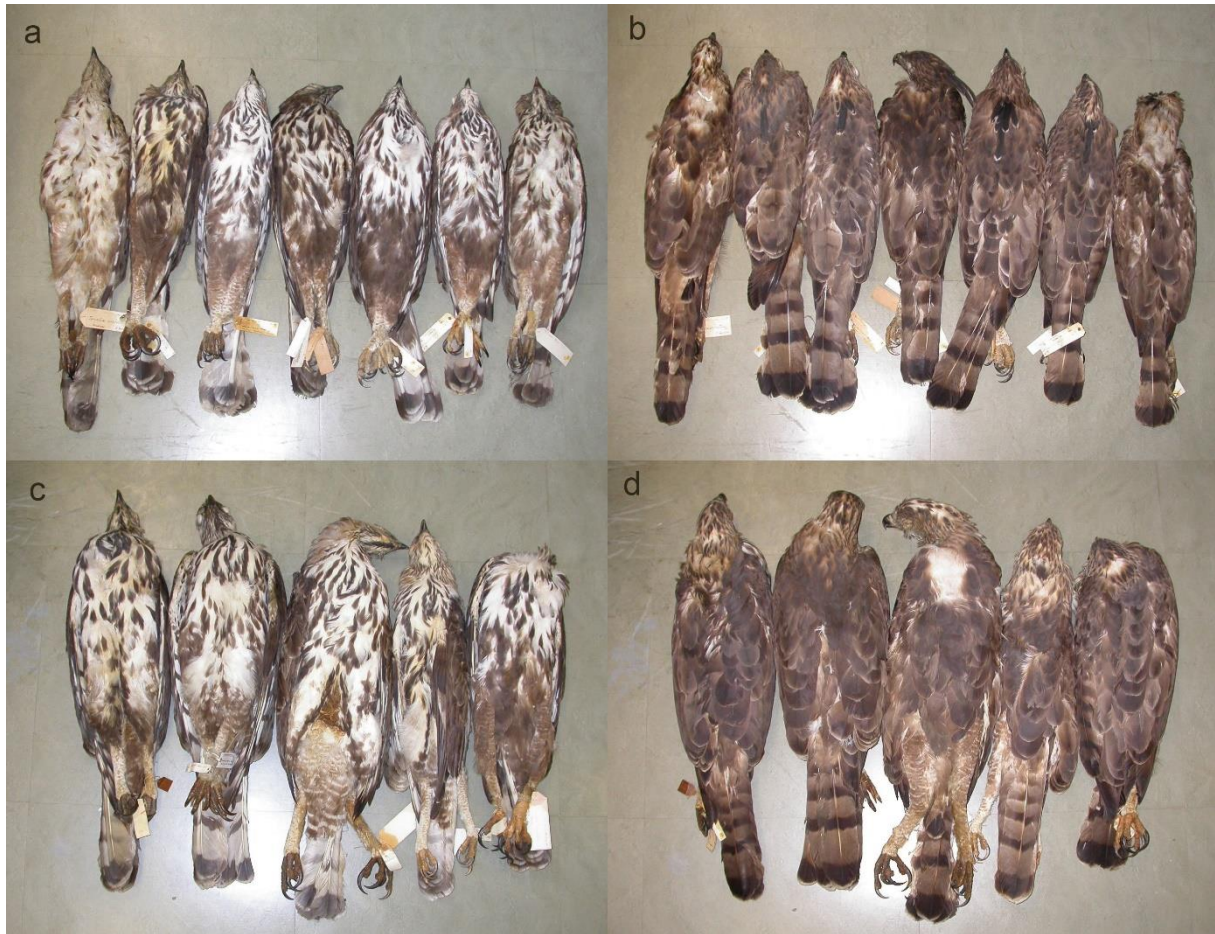


Fig. 5.

Gjershaug, Jan Ove; Diserud, Ola Håvard; Kleven, Oddmund; Rasmussen, P.C.; Espmark, Yngve.
Integrative taxonomy of the Changeable Hawk-Eagle *Nisaetus cirrhatus* complex (Accipitriformes: Accipitridae) in India. *Zootaxa* 2020 s. -

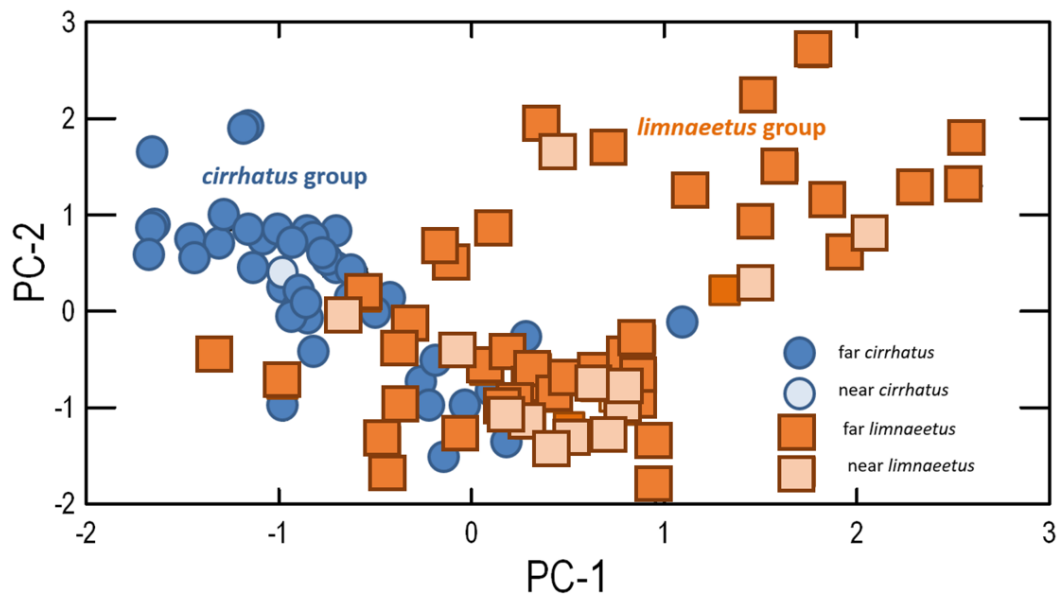
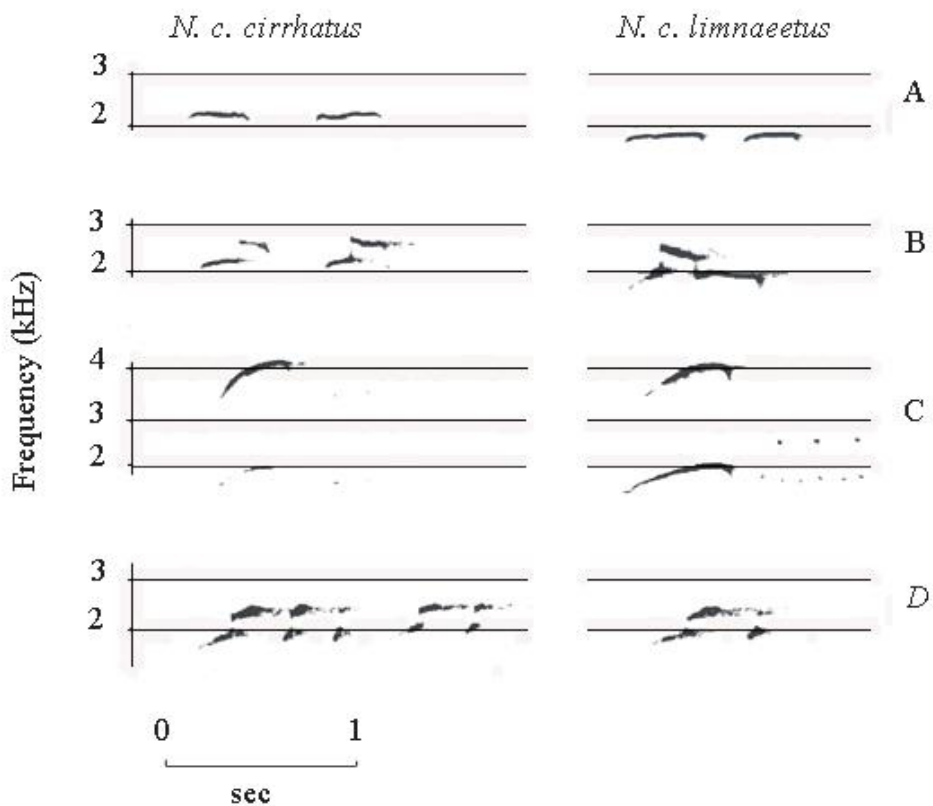


Fig. 6.



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Fig. 7.

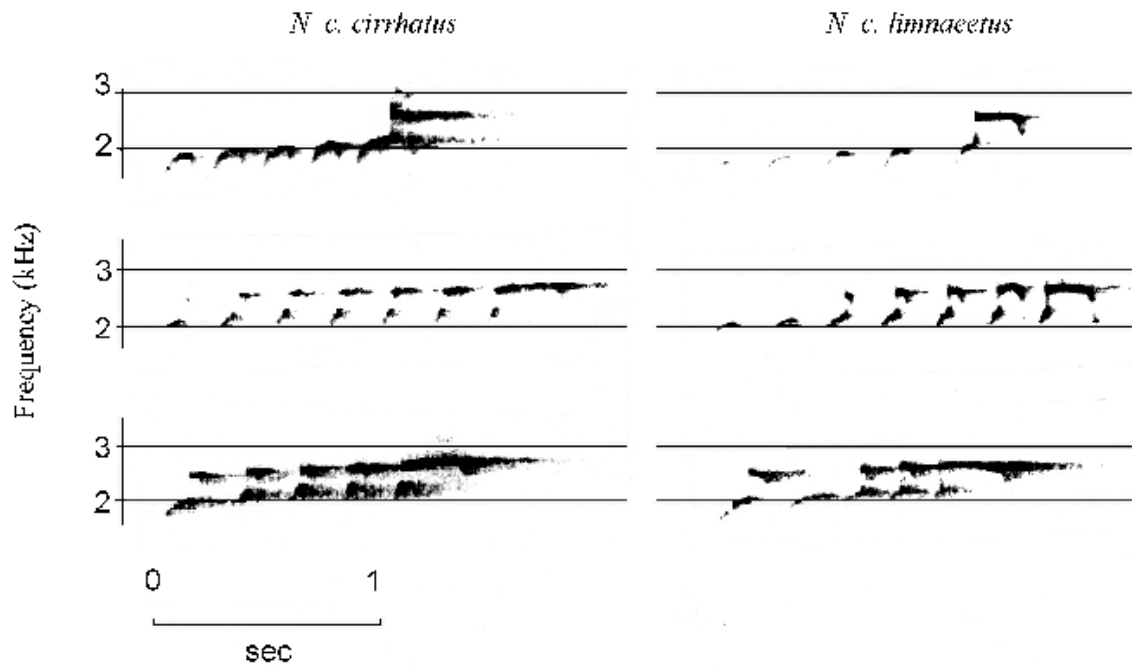


Fig. 8

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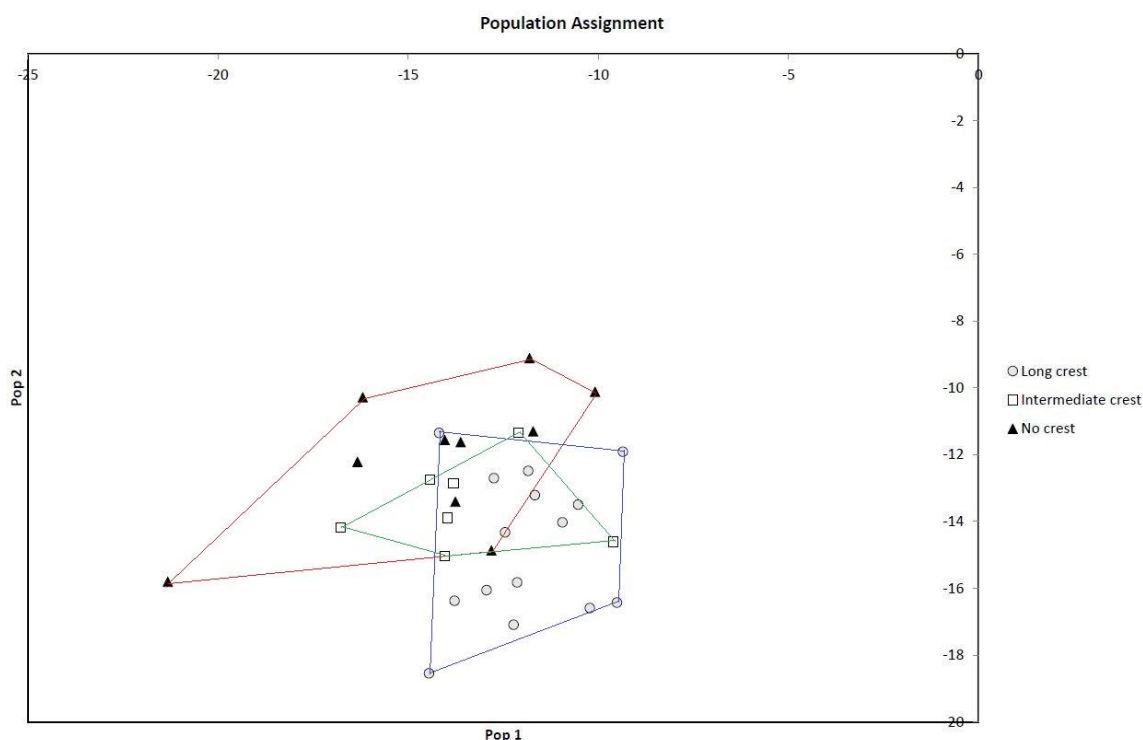


Figure 9.

Appendix 1. Specimens of *Nisaetus* examined for plumage analyses in this study.

Nisaetus c. cirrhatus

India: AMNH 461933, Londa, Karnataka; AMNH 534911, Deorukh, Maharashtra; NHMUK 1845.5.19.3, Behar; NHMUK 1845.8.18.5, Madras; NHMUK 1846.11.9.16, Madras; NHMUK 1846.11.9.20, Madras; NHMUK 1873.6.6.7, Wargaon, W Ghats; NHMUK 1880.1.1.1707, Madras; NHMUK 1885.8.19.1406, Sambhur; NHMUK 1885.8.19.1410, Abu; NHMUK 1885.8.19.1415, Buralokpur; NHMUK 1885.8.19.1424, Seoni, CP; NHMUK 1885.8.19.1425, Seoni, CP; NHMUK 1885.8.19.1426, Mundla, CP; NHMUK 1885.8.19.1428, Raipur; NHMUK 1885.8.19.1429, Raipur; NHMUK 1885.8.19.1430, Raipur; NHMUK 1885.8.19.1431, Raipur; NHMUK 1885.8.19.1432, S of Godavery; NHMUK 1885.8.19.1433, Khandesh; NHMUK 1885.8.19.1434, Naggiri, Shada, Khandesh; NHMUK 1885.8.19.1435, S Konkan; NHMUK 1885.8.19.1436, S Konkan; NHMUK 1885.8.19.1437, S Konkan; NHMUK 1885.8.19.1438, S Konkan; NHMUK 1885.8.19.1439, Nilgiris; NHMUK 1885.8.19.1445, S Konkan; NHMUK 1885.8.19.1446, S Konkan; NHMUK 1885.8.19.2090, Raipur District; NHMUK 1887.11.1.354, Khandesh; NHMUK 1887.11.1.355, Khandesh; NHMUK 1887.11.1.357, Mahabaleshwar; NHMUK 1898.12.9.1, S India; NHMUK 1898.12.12.26, S of Godavery near Bhadrachallam; NHMUK 1898.12.12.27, Godavery Valley near Bhadrachallam; NHMUK 1925.12.23.40, Kutyl, N Kanara; NHMUK 1925.12.23.41, Shada, Khandesh; NHMUK 1937.12.21.167, Nallamalai Range, S Kurnool; NHMUK 1937.12.21.168, Palkonda Hills, S Cuddapah; NHMUK 1949.Whi.1.52, Gwalior; NHMUK

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1949.Whi.1.53, Chettiri Range, Salem District; NHMUK 1949.Whi.1.54, Uttoor, Asifabad District; NHMUK 1949.Whi.1.55, Nelipaka;
NHMUK 1952.19.4, Deccan; NHMUK 1955.6.N.20.393, no locality; NHMUK 1966.6.N.20.394, no locality; USNM 390860, Anaikatti, N base of Nilgiris; USNM 399826, Dediapada, Rajpipla State, Gujarat, USNM 608814, Honnametti Estate, Biligirirangan Hills, S Mysore.

Nisaetus c. ceylanensis

Sri Lanka: AMNH 534871, Ceylon; AMNH 534913, Ceylon; AMNH 534914, Ceylon; AMNH 534915, Ceylon; AMNH 534916, Ceylon; AMNH 534917, Ceylon; AMNH 534918, Ceylon; NHMUK 1875.11.24.1, NE Ceylon; NHMUK 1885.8.19.1442, Ceylon; NHMUK 1885.8.19.1443, Colombo; NHMUK 1878.10.4.30, Knuckles; NHMUK 1887.11.1.349, Ceylon; NHMUK 1887.11.1.351, Puswella; NHMUK 1887.11.1.351, Ceylon; NHMUK 1887.11.1.352, Ceylon; NHMUK 1887.11.1.353, Ceylon; NHMUK 1920.4.29.1, Matugama, WP; NHMUK 1924.11.10.5, Ratnapura District; NHMUK 1928.6.25.2, Tellula; NHMUK 1940.12.3.221, Vidataltivu, NP; NHMUK 1947.46.12, Galapitakande Estate, Namunukala, Uva Province; NHMUK 1955.6.N.20.415, Ceylon; NHMUK 1955.6.N.20.416, Ceylon; NHMUK 1955.6.N.20.417, Ceylon; NHMUK 1955.6.N.20.418, Ceylon; NHMUK 1955.6.N.20.419, Ceylon; USNM 375846, Ceylon.

Nisaetus c. limnaeetus

India: AMNH 228796, Kalnahi, Uttar Pradesh; AMNH 461932, Kalnahi, Uttar Pradesh; NHMUK 1842.11.8.7, India; NHMUK 1876.10.20.45, N Bengal; NHMUK 1876.10.20.46, N Bengal; NHMUK 1879.11.28.71, Kumaon; NHMUK 1885.8.19.1409, Bijnur, near Hardwar; NHMUK 1885.8.19.1411, Dehra; NHMUK 1885.8.19.1412, Kumaon; NHMUK 1885.8.19.1413, Kumaon; NHMUK 1885.8.19.1414, Oudh; NHMUK 1885.8.19.1416, Sikkim terai; NHMUK 1885.8.19.1418, Buxa duars; NHMUK 1885.8.19.1419, Buxa duars; NHMUK 1885.8.19.1421, Bhutan duars; NHMUK 1885.8.19.1444, Cachar; NHMUK 1885.8.19.1447, Garhwal; NHMUK 1885.8.19.1448, Garhwal; NHMUK 1885.8.19.1449, Sikkim terai; NHMUK 1885.8.19.1450, Buxa duars; NHMUK 1885.8.19.1469, Tipperah; NHMUK 1885.8.19.1470, Tipperah; NHMUK 1887.11.1.361, Kamroop, Assam; NHMUK 1895.7.14.69, Mussoorie; NHMUK 1898.12.12.25, Calcutta; NHMUK 1949.Whi.1.49, Jalpaiguri District, Bengal; NHMUK 1949.Whi.1.50, Haldibari Tea Estate duars; NHMUK 1949.Whi.1.51, Dharakoh, Betul District, CP; NHMUK 1949.Whi.1.56, Surbar, Gorakhpur; NHMUK 1955.6.N.20.391, Kashmir; NHMUK 1955.6.N.20.392, Singhai, Kheree, NW India; UMMZ 78297, Bhadwar, Kangra, Punjab; UMMZ 140516, Bamanigaon, Assam; UMMZ 140517, Bamanigaon, Assam.

Nepal: AMNH 776685, Hetora, Nepal; NHMUK 1859.3.4.603, Nepal; NHMUK 1879.11.28.70, Nepal; NHMUK 1880.1.1.1709, Nepal.

Bangladesh: NHMUK 1885.8.19.1423, Faridpore; NHMUK 1885.8.19.1453, Dacca; NHMUK 1885.8.19.1454, Dacca; NHMUK 1885.8.19.1455, Dacca.

Myanmar: AMNH 534881, Fort Mandalay; AMNH 535369, Kaukaryit, Myanmar; NHMUK 1882.1.9.20, Lower Pegu; NHMUK 1882.1.9.21, E of Thayetmyo, Pegu; NHMUK 1885.8.19.1436, Yeaboo; NHMUK 1885.8.19.1457, Bankasoon; NHMUK 1885.8.19.1458, Bankasoon; NHMUK 1885.8.19.1459, Tavoy; NHMUK 1887.11.1.359, Tonghoo; NHMUK

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1887.11.1.360, Tonghoo; NHMUK 1948.80.3609, Shwebo District, Myanmar; NHMUK 1948.80.3610, Shwebo District, Myanmar; NHMUK 1955.6.N.20.403, near Thayetmyo; NHMUK unregistered, Kyabin Chaung, Maymyo Forest District; USNM 89897, Tenasserim; USNM 95915, Prome, Pegu, Myanmar; USNM 172952, Malewoon, Tenasserim.

Thailand: AMNH 211076, Petchaburi; AMNH 211077, Petchaburi; NHMUK 1936.4.12.885, Siam; NHMUK 1936.4.12.888, Koh Naka, Siam; NHMUK 1955.6.N.20.331, Khan Thuli, Peninsular Siam; NHMUK 1955.6.N.20.332, Klong Rangsit, Samkok, C Siam; USNM 153668, Tyching, Trong, Lower Siam; USNM 153669, Tyching, Trong, Lower Siam; USNM 153670, Tyching, Trong, Lower Siam; USNM 159402, Lay Song Hong, Trong, Lower Siam; USNM 451579, Thailand, Kamphaeng Phet, Amphoe Khanu; USNM 484017, Thailand, Satun, Thungnui; USNM 484018, Thailand, Phattalung, Pakphayuyun, Kofai; USNM 484019, Thailand, Phattalung, Pakphayuyun, Kofai; USNM 534545, Thailand, Chiang Mai, Chiang Dao.

Cambodia: NHMUK 1928.6.26.220, Sambar.

Vietnam: NHMUK 1878.6.19.150, Cochin China; NHMUK 1935.10.23.162, Kontoum, S Annam.

Malaysia: AMNH 155168, Upper Perak, Lenggong; AMNH 534883, Malay Peninsula, Rantau Panjang; AMNH 534899, North Borneo, Labuan; AMNH 534900, North Borneo, Labuan; AMNH 534901, North Borneo, Labuan; NHMUK 1878.5.4.2, Lawas River; NHMUK 1878.5.12.1721, Penang; NHMUK 1885.8.19.1460, Malacca; NHMUK 1885.8.19.1464, Johore; NHMUK 1887.11.1.365, Malacca; NHMUK 1887.11.1.367, Malacca; NHMUK 1889.7.31.1, Baram, NW Borneo; NHMUK 1894.8.6.165, Labuan; NHMUK 1898.11.24.16, Kinabatangan; NHMUK 1904.5.30.7, Baram District, Sarawak; NHMUK 1936.4.12.890, SW Koh Penang, NE Malay Peninsula; NHMUK 1949.34.1, Repok Ro, Sarawak; NHMUK 1955.6.N.20.413, Baram, Borneo.

Singapore: NHMUK 1885.8.19.1465, Singapore; NHMUK 1949.Whi.1.57, Singapore; NHMUK 1955.6.N.20.400, Singapore; NHMUK 1955.6.N.20.401, Singapore.

Indonesia: AMNH 448453, SW Borneo; AMNH 534885, Sumatra, Deli; AMNH 534890, Sumatra, Deli; AMNH 534891, Sumatra, Deli; NHMUK 1873.5.28.21, Java; NHMUK 1887.11.1.368, S Java; NHMUK 1955.6.N.20.395, Java; NHMUK 1955.6.N.20.397, Batavia, Java; NHMUK 1955.6.N.20.399, Batavia, Java; USNM 181207, mouth of Siak R, E Sumatra; USNM 219263, Tembong, Java.

Brunei: AMNH 534898, Brunei, Tutong R.

Philippines: AMNH 96141, Palawan; AMNH 96142, Palawan; AMNH 534907, Palawan; AMNH 784046, Mindoro; USNM 314846, Culion.

No or ambiguous locality: NHMUK 1955.6.N.20.390, no locality; NHMUK 1955.6.N.20.402, Borneo.

N. c. andamanensis

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India: AMNH 534880, Port Blair; AMNH 534919, Goplakabung, S Andamans; NHMUK 1885.8.19.1466, Andamans; NHMUK 1885.8.19.1467, Andamans; NHMUK 1885.8.19.1468, Andamans; NHMUK 1887.11.1.331, S Andamans.

N. c. vanheurni

Indonesia: USNM 179073, Simalur Island, off W Sumatra.

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Appendix 2. Specimens of the *Nisaetus cirrhatus* species complex sampled for DNA analyses.

Nisaetus c. ceylanensis (from Sri Lanka):

NHMUK 1885.8.19.1442, Sri Lanka; NHMUK 1887.11.1.351, Sri Lanka; NHMUK 1924.11.10.5, Ratnapura District, Sri Lanka; NHMUK 1928.6.25.2, Tellula, Sri Lanka; NHMUK 1955.6.N.20.419, Sri Lanka.

Nisaetus c. cirrhatus (from South and Central India):

NHMUK 1845.8.18.5, Madras, S India; NHMUK 1880.1.1.1707, Madras, S India; NHMUK 1885.8.19.1410, Mt. Aboo, C India; NHMUK 1885.8.19.1427, Raipur, C India; NHMUK 1885.8.19.1428, Raipur, C India; NHMUK 1885.8.19.1429, Raipur, C India; NHMUK 1885.8.19.1431, Raipur, C India; NHMUK 1885.8.19.1433, Khandesh, C India; NHMUK 1885.8.19.1434, Shada, Khandesh, C India; NHMUK 1885.8.19.1439, Nilgiris, S India; NHMUK 1887.11.1.354, Khandesh, C India; NHMUK 1887.11.1.355, Khandesh, C India; NHMUK 1887.11.1.358, Madras, S India; NHMUK 1925.12.23.41, Shada, Khandesh, C India;
NHMUK 1937.12.21.167, Nallamalai Range, S India.

Nisaetus c. limnaeetus (from North and north-eastern India and Nepal, without crest):

NHMUK 1859.3.4.602, Nepal; NHMUK 1879.11.28.71, Kumaon, N India; NHMUK 1885.8.19.1409, Bijnur, near Hardwar, N India; NHMUK 1886.8.19.1412, Kumaon, N India; NHMUK 1885.8.19.1414, Oudh, N India; NHMUK 1885.8.19.1444, Cachar, NE India; NHMUK 1885.8.19.1447, Garhwal, N India; NHMUK 1885.8.19.1448, Garwhal, N India; NHMUK 1895.7.14.67, Mussoorie, N India; NHMUK 1895.7.14.69, Mussoorie, N India.

Nisaetus c. limnaeetus (from North and Central India and Myanmar, with intermediate crest lengths):

NHMUK 1876.10.20.44, N Bengal, N India; NHMUK 1876.10.20.45, N Bengal, N India; NHMUK 1882.1.9.21, east of Thayetmyo, Pegu, Myanmar; NHMUK 1885.8.19.1411, Dehra, N India; NHMUK 1885.8.19.1413, Kumaon, N India; NHMUK 1885.8.19.1449, Sikkim terai, N India;
NHMUK 1887.11.1.360, Tonghoo, Myanmar; NHMUK 1949.Whi.1.51, Dharakoh, Betul District, Madhya Pradesh, India; NHMUK 1949.Whi.1.56, Surbhar, Gorakhpur, N India; NHMUK 1955.6.N.20.392, Kheree, NW India.

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Appendix 3. Summary of allelic variability at 11 microsatellite loci in the Changeable Hawk-eagle.

Crest length	Locus	BV13		Bbu2		SNMS27		Tgu06		SNMS01		SNMS24		SNMS30		SNMS32		SNMS16		SNMS26		TG04-061		Mean
		N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	
Long	N	15	14	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
	N_A	14	5	10	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	H_O	0.80	0.79	0.87	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
	H_E	0.92	0.76	0.89	0.70	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70	0.86	0.70
	P	0.140	0.700	0.823	0.368	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368	0.823	0.368
Intermediate	N	7	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	A	6	5	7	5	5	7	5	7	5	5	7	5	5	7	5	5	7	5	5	7	5	5	7
	H_O	0.57	0.83	0.86	0.71	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71	0.86	0.71
	H_E	0.74	0.80	0.89	0.67	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67	0.89	0.67
	P	0.099	0.311	0.800	1.000	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000	0.800	1.000
No	N	10	8	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
	A	6	6	9	5	5	9	5	9	5	5	9	5	5	9	5	5	9	5	5	9	5	5	9
	H_O	0.60	0.75	0.80	0.50	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50	0.80	0.50
	H_E	0.73	0.78	0.86	0.57	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57	0.86	0.57
	P	0.394	0.378	0.487	0.267	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267	0.487	0.267
Mean	H_O	0.69	0.79	0.84	0.69	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69	0.84	0.69
	H_E	0.85	0.79	0.90	0.65	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65	0.90	0.65
	P	0.019	0.500	0.862	0.844	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844	0.862	0.844
Total	N	32	28	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32
	N_A	16	6	13	8	8	11	10	11	10	10	11	10	10	10	10	10	10	10	10	10	10	10	10

Sample size (N), number of alleles (N_A), observed heterozygosity (H_O), expected heterozygosity (H_E) and test for deviation from Hardy-Weinberg equilibrium (P) for each population and locus. Exact P-values were estimated with Arlequin v3.5.2.2. Bold indicates significant deviation from Hardy-Weinberg equilibrium.

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