



The taxonomic status of Palearctic and Nearctic populations of northern goshawk *Accipiter gentilis* (Aves, Accipitridae): New evidence from vocalisations

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Abstract

The taxonomic status of the North American and Eurasian populations of northern goshawk *A. gentilis* has been called into question by recent molecular studies, indicating the need for additional taxonomic study. Vocalisations have long played an important role in diagnosing potentially reproductively isolated groups of birds. The chattering-type call of *A. gentilis* plays a role in advertisement and pair-contact, making this a suitable basis for taxonomic study of vocalisations. The data set consisted of recordings of the calls of 75 individuals of the Eurasian *gentilis*-group of *A. gentilis*, 37 of the North American *atricapillus*-group of *A. gentilis* and, for comparison, seven of Henst's goshawk *A. henstii*. The three groups showed non-overlapping variation in the duration of call-notes and also showed several other highly significant differences. Discriminant Function Analysis resulted in 100% correct classification of recordings into the three groups. It is here argued that the new bioacoustic data, in combination with previous evidence of morphological, mitochondrial DNA and genomic DNA differences between Eurasian and North American *A. gentilis*, suggests that two species are best recognised: northern goshawk *A. gentilis* and American goshawk *A. atricapillus*. *A. gentilis* / *A. atricapillus* add to a growing list of Holarctic temperate zone taxa that have recently been recognised as separate species based on a deep phylogeographic split between Eurasian and North American populations in combination with differences in other characters. This is the first quantitative taxonomic study of vocalisations in Accipitridae.

Keywords

Accipiter gentilis, integrative taxonomy, species limits, systematics, vocalisations

Introduction

Many temperate zone bird species have a Holarctic distribution. Recently, the importance of the Beringia barrier in the diversification of the Holarctic fauna has been demonstrated by phylogeographic analysis of mitochondrial DNA and in some cases nuclear DNA (Zink et al. 1995; Kerr et al. 2009; Johnsen et al. 2010; Humphries and Winker 2011). Deep divergences have been documented

in several species, including *Larus canus* / *L. brachyrhynchus* (Sonsthagen et al. 2012), *Picooides tridactylus* / *P. dorsalis* (Zink et al. 2002), *Lanius excubitor* / *L. borealis* (Olsson et al. 2010), *Pica pica* / *P. hudsonia* (Kryukov et al. 2017; Song et al. 2018), *Nannus troglodytes* / *N. pacificus* (Drovetski et al. 2004), *Hirundo rustica* (Zink et al. 2006; Dor et al. 2010), *Eremophila alpestris* (Drovetski

et al. 2014; Ghorbani et al. 2020) and *Pinicola enucleator* (Drovetski et al. 2010). These findings indicate that the taxonomic status of Palearctic and Nearctic populations of temperate zone birds deserve further study because their unique evolutionary history may also be reflected in other differences. Indeed, in several of these cases additional lines of evidence have resulted in the elevation of Nearctic taxa to species rank (e.g. AOU 2000; Banks et al. 2003; Chesser et al. 2010, 2017, 2021).

Northern goshawk *Accipiter gentilis* has a Holarctic distribution and is widely found in both coniferous and deciduous forests. There is considerable variation in plumage, which has led to the recognition of seven subspecies in the Old World (*A. g. gentilis*, *A. g. buteoides*, *A. g. albidus*, *A. g. schvedowi*, *A. g. fujiyamae*, *A. g. marginatus*, *A. g. arrigonii*) and three subspecies in North America (*A. g. atricapillus*, *A. g. laingi*, *A. g. apache*) (Stresemann and Amadon 1979; Dickinson and Remsen 2013). The North American subspecies *A. g. atricapillus* has a distinct plumage and was formerly treated as a full species (e.g. AOU 1873, 1931; Sharpe 1874). During the era of the ‘polytypic species concept’ in the late 1800s and early 1900s, when morphologically distinct but geographically non-overlapping taxa became treated as representatives (subspecies) of the same species (Haffer 1992; Sangster 2018), *A. g. atricapillus* was lumped with Palearctic subspecies in a single species *A. gentilis* (Peters 1931; AOU 1944), but without any descriptions of plumage similarities and differences. This taxonomic treatment was maintained after the introduction of the Biological Species Concept in the first half of the twentieth century, although there has never been any published evidence that the allopatric Palearctic and Nearctic populations are reproductively compatible.

Recently, Bayard de Volo et al. (2013) analysed mitochondrial Control Region sequences and found a large divergence between goshawks sampled in North America and Germany. In an analysis of short mitochondrial COI sequences, Breman et al. (2013) found that *A. g. gentilis* was more closely related to black sparrowhawk *A. melanoleucus* than to *A. g. atricapillus* but with very poor support. Using genomic DNA sequences, Gerald et al. (2019) found a deep divergence between Palearctic and Nearctic populations of *A. gentilis*. In a detailed mitochondrial DNA study, Kunz et al. (2019) showed that Nearctic *A. g. atricapillus*, *A. g. laingi* and *A. g. apache* (hereafter *atricapillus*-group) and the Palearctic subspecies of *A. gentilis* (hereafter *gentilis*-group) formed reciprocally monophyletic groups which were not sister groups because the *gentilis*-group was closer to Meyer’s goshawk *A. meyerianus*, Henst’s goshawk *A. henstii* and *A. melanoleucus* than to the *atricapillus*-group. Kunz et al. (2019) suggested that species status may be appropriate for the *atricapillus*-group but noted that this is best considered in an integrative context, i.e. together with other lines of taxonomic evidence.

Vocalisations have not yet been used in the species-level taxonomy of Accipitridae but may be informative for two major reasons (Sangster et al. 2021). First, vocalisations often play a role in mate choice and pair

bonding, so differences among populations in such vocalisations may be indicative of reproductive barriers (Slabbekoorn and Smith 2002). Second, in most species of non-Passeriformes, vocal differences are not learned, and thus likely reflect inherited differences (Marler and Slabbekoorn 2004). Thus, populations with distinct vocalisations may have unique evolutionary histories. In *A. gentilis*, two main call types have been documented (Schnell 1958; Cramp and Simmons 1980). One of these, the ‘chattering-type’ call, is a series of ‘kek’ notes which are used for advertisement and pair-contact, but also for alarm (Cramp and Simmons 1980; Squires and Reynolds 1997), which makes these a suitable basis for taxonomic study of vocalisations. The call is used by both sexes and is especially given during the period of territory establishment and until egg-laying (Cramp and Simmons 1980).

This study aims to test whether the phylogenetically distinct *atricapillus*-group and *gentilis*-group also differ in vocalisations. The ‘chattering-type’ calls of the *atricapillus*-group are compared with those of the *gentilis*-group using quantitative methods. For comparison, recordings of another member of the [*A. gentilis*] super-species, *A. henstii*, are included.

Materials and Methods

In this study, species are viewed as population lineages whose boundaries our species-level concepts (species taxa) are intended to align with, through an iterative process (de Queiroz 2007; Padiál et al. 2010). Species taxa are hypotheses, and may present themselves in many ways (e.g. through differences in morphology, vocalisations, DNA sequences, intrinsic reproductive isolation, behaviour) but not necessarily in all ways in the same taxa. To increase the reliability and sensitivity of the taxonomic discovery process, species taxa should be documented using as many independent lines of evidence as possible (Sangster 2018). The trend towards using multiple evidence to document species taxa has been underway for several decades (Sangster 2014). In this study, evidence from vocalisations is interpreted in combination with previous evidence from morphology, and mitochondrial and nuclear DNA sequence data.

Recordings were obtained from the Xeno-Canto (<http://www.xeno-canto.org>) data base and the bird sound collections of the Macaulay Library at the Cornell Lab of Ornithology (<https://www.macaulaylibrary.org>) and the Florida Museum of Natural History (<https://www.floridamuseum.ufl.edu/bird-sounds>). The data set was supplemented by published recordings (Brigham 1992; Sander 1996; Elliott 1997; Colver 1999; Peyton 1999; Huguet and Chappuis 2003; Keller 2003). In total, calls of 75 individuals of Palearctic *A. gentilis* (*gentilis*-group), 37 of Nearctic *A. gentilis* (*atricapillus*-group) and seven of *A. henstii* were included in the analysis. A list of recordings with localities and recordists is provided in Appendix 1. The *A. [gentilis]* superspecies (sensu Kunz et al. 2019)

includes two additional species, *A. meyerianus* and *A. melanoleucus*. However, no recordings of the ‘chattering-type’ calls of the *A. meyerianus* and too few ($n=2$) of *A. melanoleucus* were available for study.

In statistical analysis, the recordings of the Palearctic *gentilis*-group, which comprise multiple subspecies, were treated as a single operational taxonomic unit (OTU) because there were no major subdivisions in a mitochondrial Control Region phylogeny (Kunz et al. 2019). The Nearctic recordings represented three subspecies, *A. g. atricapillus*, *A. g. laingi* and *A. g. apache*, which were treated as a single OTU based on the results of Gerald et al. (2019) and Kunz et al. (2019).

Seven variables were defined on the basis of sonagrams. The following measurements were recorded: (1) call duration, (2) number of notes, (3) note rate (notes per second), (4) duration of the median note, (5) maximum frequency of the second harmonic of the median note, (6) minimum frequency of the second harmonic of the median note, and (7) frequency range of the median note. All measurements were made using Raven Pro 1.5 (Bioacoustics Research Program, 2014) using a window size of 256. Care was taken to avoid pseudoreplication; therefore, when multiple recordings were available from the same recordist at the same locality, only one was used in the analyses. Univariate statistical differences between OTUs were calculated using ANOVA with Bonferroni correction. If the assumptions of homogeneity of variances (as shown by Levene’s test) or normal distribution (as shown by the Kolmogorov-Smirnov test) were violated, Mann-Whitney U test was used and significance determined using Holm’s sequential Bonferroni test (Holm 1979).

Canonical discriminant function analysis (DFA) was applied to the acoustic variables of individuals to test whether the individuals could be correctly assigned to the three groups. DFA generates a set of criteria to assign individuals to groups that are defined prior to the analysis. Prior to DFA analysis, a tolerance test was conducted to assess the independence of each variable. Variables that fail the tolerance test, i.e. which are an almost linear combination of other variables, were excluded from the analyses. Two DFAs were performed: (i) a ‘descriptive’ DFA, in which the observations used to develop the criteria are then subjected to these criteria; (ii) a ‘predictive’ DFA, which uses a jackknife procedure to obtain a more accurate test of the predictive performance of the DFA. In the jackknife procedure, the DFA is recalculated using the combination of variables of the initial DFA with one individual removed from the data set. The criteria are then used to classify the removed individual. This process was repeated for all individuals of the data set.

The effect size, expressed as Cohen’s d , was calculated to show the strength of the acoustic differences between taxa. For interpretation of effect size data, we used the classification of Cohen (1992), which was updated and expanded by Sawilowsky (2009). Thus, we regard an effect size of $d < 0.1$ as ‘negligible’, $d \geq 0.1$ as ‘very small’, $d \geq 0.2$ as ‘small’, $d \geq 0.5$ as ‘medium’, $d \geq 0.8$ as ‘large’, $d \geq 1.2$ as ‘very large’ and $d \geq 2.0$ as ‘huge’. All statistical analyses were performed with SPSS 28.0 (IBM Corp.,

Table 1 Standardized canonical discriminant function coefficients examining trends in variance of six acoustic variables¹ measured for calls of the *A. g. gentilis*-group, *A. g. atricapillus*-group and *A. henstii*. Eigenvalues and percentage of variance accounted for by DF1 and DF2 are given at the bottom of the table.

Variable ¹	DF1	DF2
Call duration	0.588	-2.328
Number of notes	-0.481	3.018
Note rate	0.134	-1.142
Duration median note	0.956	0.152
Max. freq median note	-0.153	-0.251
Min. freq. median note	0.221	0.816
Eigenvalue	11.311	0.485
Variance explained	96.1%	3.9%

¹ The variable ‘Frequency range of the median note’ was excluded because it failed the tolerance test.

Armonk, NY, USA), except Holm’s sequential Bonferroni test, which was carried out by hand using uncorrected significance data from SPSS 28.0.

Results

Discriminant Function Analysis

Most variables passed the tolerance test, except frequency range of the median note which was excluded from the test. The descriptive DFA was highly significant (Wilks’ $\lambda = 0.056$; Chi Square₁₂ = 327.7; $P < 0.001$). The variables most important in the discrimination were duration of the median note, song duration and number of notes (Table 1). Both the initial and jackknife DFA led to a 100% correct classification of the individuals into the three groups. A scatterplot of the first two discriminant functions illustrates the three groups (Fig. 1).

Univariate analysis

Call characteristics of the three groups are given in Table 2 and illustrated in Figure 2. Four variables differed significantly in comparisons of the *gentilis*-group with the *atricapillus*-group. Five variables differed significantly in comparisons of the *gentilis*-group with *A. henstii*. Comparisons of the *atricapillus*-group with *A. henstii* revealed five significant differences.

The effect size of the differences between the three groups is given in Table 2. The three groups showed multiple ‘very large’ (Cohen’s $d > 1.2$) or ‘huge’ (Cohen’s $d > 2.0$) differences. The difference between the *gentilis*-group and the *atricapillus*-group in the duration of the median note was ‘huge’, and the differences in call duration and note rate were ‘very large’. The differences between *Accipiter henstii* and the *gentilis*-group in call

Table 2. Descriptive statistics of seven variables measured for calls of two groups of *A. gentilis* and *A. henstii* (mean \pm SD, range). The right three columns present significance levels of ANOVA or Mann Whitney *U*-tests, the effect size (expressed as Cohen's *d*) and the interpretation of effect size by Cohen (1988) and Sawilowsky (2009). All significant differences, except three (marked with an asterisk), remained significant after Holm's sequential Bonferroni test (Holm 1979).

Variable	<i>gentilis</i> -group (n=75)	<i>atricapillus</i> - group (n=37)	<i>A. henstii</i> (n=7)	<i>gentilis</i> -group vs. <i>atricapillus</i> -group Significance Cohen's <i>d</i> (interpretation)	<i>gentilis</i> -group vs. <i>A. henstii</i> Signifi- cance Cohen's <i>d</i> (interpretation)	<i>atricapillus</i> -group vs. <i>A. henstii</i> Signifi- cance Cohen's <i>d</i> (interpretation)
Call duration	4.320 \pm 1.710 (1.285–8.908)	7.294 \pm 2.392 (2.219–15.567)	8.101 \pm 1.367 (6.339–10.332)	P<0.001 ^b 1.53 (very large) ^c	P<0.001 ^b 2.27 (huge) ^d	n.s. ^a 0.36 (small) ^c
Number of notes	22.9 \pm 9.4 (6.0–47.0)	28.9 \pm 10.6 (11.0–67.0)	15.6 \pm 3.3 (10.0–19.0)	P<0.01 ^{b*} 0.61 (medium) ^c	P<0.05 ^{b*} 0.81 (large) ^c	P<0.001 ^b 1.38 (very large) ^c
Note rate	5.32 \pm 0.91 (3.59–8.03)	3.97 \pm 0.48 (2.78–4.96)	1.92 \pm 0.28 (1.52–2.32)	P<0.001 ^b 1.70 (very large) ^c	P<0.001 ^b 3.90 (huge) ^d	P<0.001 ^b 4.61 (huge) ^d
Duration median note	0.046 \pm 0.009 (0.021–0.069)	0.116 \pm 0.018 (0.092–0.158)	0.238 \pm 0.043 (0.196–0.312)	P<0.001 ^b 5.49 (huge) ^d	P<0.001 ^b 13.33 (huge) ^d	P<0.001 ^b 5.32 (huge) ^d
Max. freq median note	3060 \pm 317 (2581–4191)	2899 \pm 294 (2357–3520)	2281 \pm 487 (1763–3022)	P<0.05 ^{a*} 0.52 (medium) ^c	P<0.001 ^b 2.37 (huge) ^d	P<0.005 ^b 1.92 (very large) ^c
Min. freq. median note	1945 \pm 250 (1484–2748)	1960 \pm 231 (1355–2468)	1323 \pm 347 (837–1776)	n.s. ^a 0.06 (negligible)	P<0.001 ^b 2.43 (huge) ^d	P<0.001 ^b 2.60 (huge) ^d
Freq. range medi- an note	1115 \pm 240 (579–1716)	939 \pm 281 (486–1603)	958 \pm 180 (709–1246)	P<0.001 ^b 0.70 (medium) ^c	n.s. ^a 0.67 (medium) ^c	n.s. ^a 0.07 (negligible)

^a = ANOVA; ^b = MW-U test; ^c = sensu Cohen (1988); ^d = sensu Sawilowsky (2009)

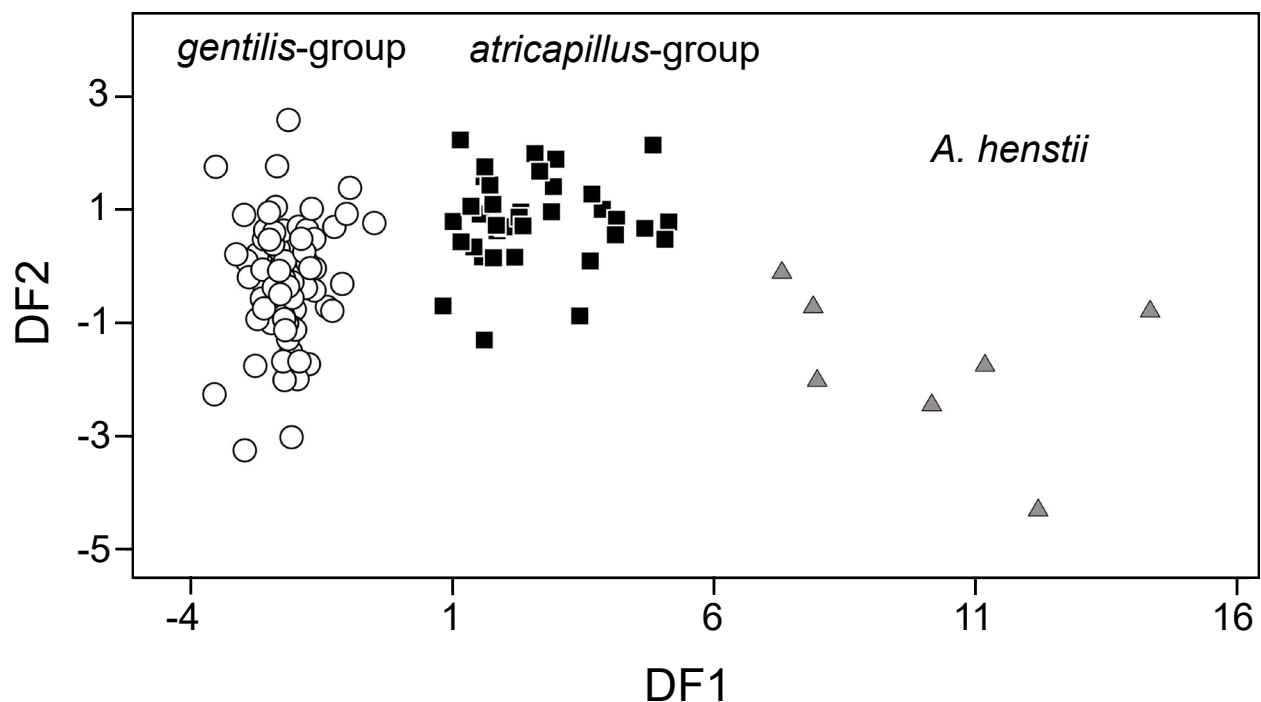


Figure 1. DFA scatterplot of six acoustic variables measured for calls of the *A. g. gentilis*-group, *A. g. atricapillus*-group and *A. henstii* (n=119).

duration, note rate, duration of the median note, and the maximum and minimum frequency of the median note were 'huge'. *Accipiter henstii* and the *atricapillus*-group showed 'very large' differences in the number of notes and the maximum frequency of the median note and 'huge' differences in the note rate, duration of the median note, and the minimum frequency of the median note.

The differences between the three groups are visible on sonagrams (Fig. 2). The calls of the *atricapillus*-group differ from those of the *gentilis*-group by their slower delivery (lower note rate) and longer note duration. The calls of *A. henstii* are even slower than those of the *atricapillus*-group and differ further in their lower frequency and longer note duration.

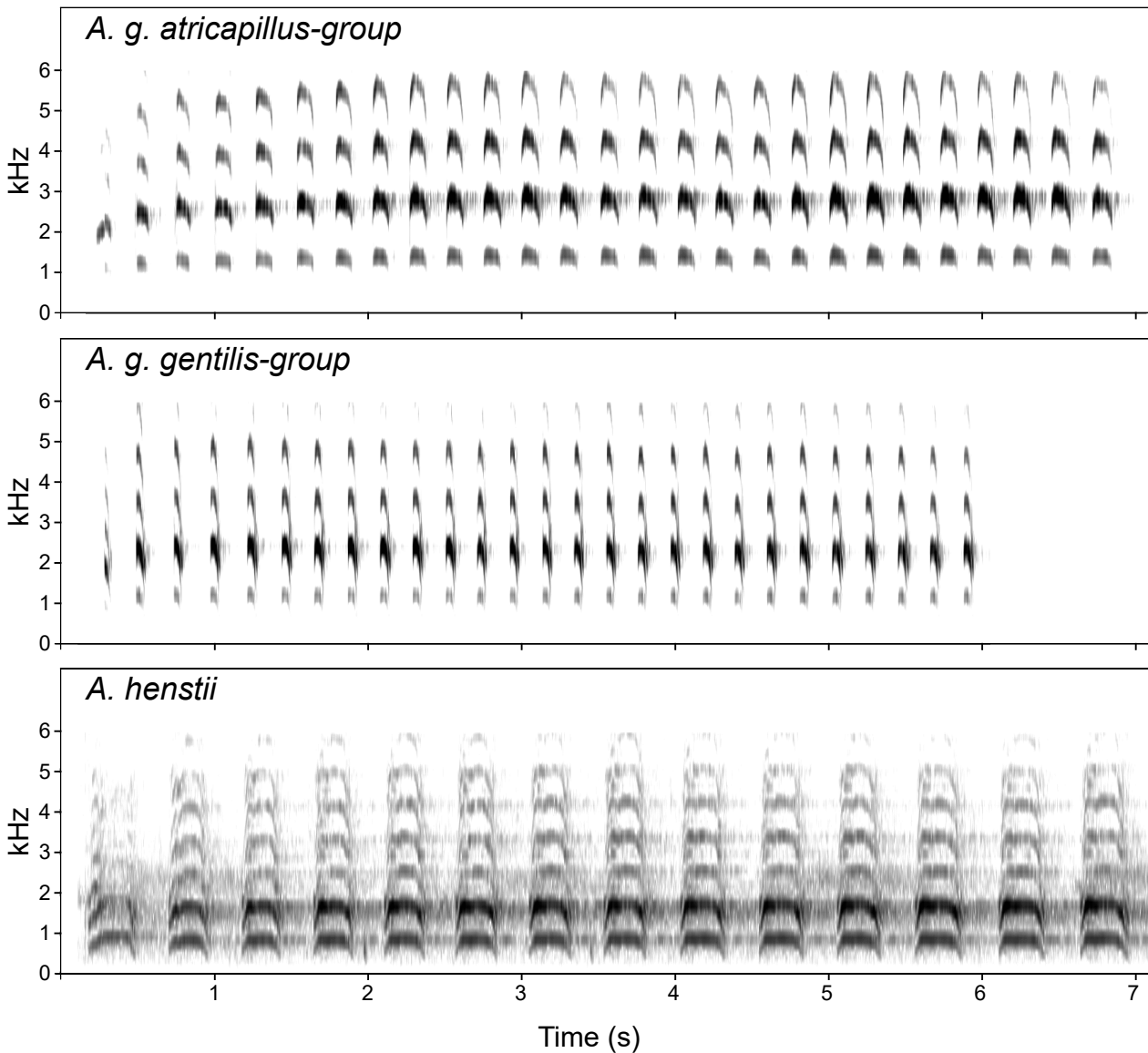


Figure 2. Sonagrams of calls of the *A. g. atricapillus*-group, the *A. g. gentilis*-group and part of an 18-note call of *A. henstii*, illustrating the differences among the three groups.

Discussion

The results of this study show that recordings of the *gentilis*-group differ consistently from both the *atricapillus*-group and *A. henstii* and can be classified correctly at a very high proportion in Discriminant Function Analysis. The three groups show significant differences in several variables and there are ‘very large’ to ‘huge’ differences in effect size between the groups. The lack of evidence for vocal learning in Accipitriformes implies that vocal differences are innate and likely have a genetic basis. The population-level differences in vocalisations between the three groups suggest that these groups have been subjected to long periods of genetic isolation, and may represent full species. Three other lines of evidence provide further evidence of a major split between the *gentilis*-group and *atricapillus*-group.

First, there are multiple differences in the adult plumages of goshawks of the *gentilis*-group and the *atricapillus*-group (Fig. 3). The coloration of the upperparts and upper wings is brownish-grey in males of the *gentilis*-group but pure grey or blue-grey in males of the *atricapillus*-group. The head pattern is more contrasting in the *atricapillus*-group than in the *gentilis*-group. This is because in the *gentilis*-group crown and ear-coverts are dark grey which are barely darker than the upperparts, whereas in the *atricapillus*-group crown and ear-coverts are blackish and much darker than the upperparts. Adult eye colour also differs: Orange-yellow to orange-red in the *gentilis*-group (Clark 1999) and deep red to mahogany (but orange in Basic II birds) in the *atricapillus*-group (Squires and Reynolds 1997). Yet the juvenile plumages of both are almost identical and both are nearly identical to the juvenile plumage of black sparrowhawk. The most striking difference is the pattern of the underparts and un-



Figure 3. **A** *Accipiter atricapillus apache* Arizona, USA, James Wittke/iNaturalist. Note the indistinctly barred underparts, the black crown and ear-coverts which are much darker than the pure grey wings, and the deep orange eye. **B** *Accipiter gentilis gentilis* Flåtanger, Norway, Markus Varesvuo/Agami. Note the distinctly barred underparts, dark grey crown and ear-coverts which are barely darker than the brownish-grey upperparts and wings, and the orange-yellow eye.

derwing coverts, which are distinctly and contrastingly barred dark brown in the *gentilis*-group, but indistinctly vermiculated pale grey in the *atricapillus*-group resulting in much paler underparts (Wattel 1973; Cramp and Simmons 1980; Ferguson-Lees and Christie 2001).

Second, mitochondrial DNA sequences of the *gentilis*-group and the *atricapillus*-group form reciprocally

monophyletic groups and show evidence (albeit only moderately supported) of a non-sister relationship (Kunz et al. 2019). The authors noted that from an evolutionary viewpoint, classifying the Holarctic *A. gentilis* as a single species to the exclusion of the other three Old World species (*A. meyerianus*, *A. henstii*, and *A. melanoleucus*) seems untenable because the Palearctic *gentilis*-group is

more closely related to the other Old World taxa than to Nearctic *atricapillus*-group. Such a Holarctic *A. gentilis* species would be polyphyletic (Kunz et al. 2019).

Third, a comprehensive set of genomic SNP data show that North American and Eurasian *A. gentilis* represent two major groups and exhibit a pattern congruent with that found in mitochondrial DNA (Geraldès et al. 2019).

Strong and congruent differences in bioacoustic, morphological, mitochondrial DNA, and nuclear DNA data leave little doubt that the divergence between the *atricapillus*-group and the *gentilis*-group is real. Taken together, these four lines of evidence suggest that *A. gentilis* consists of two major groups which are best treated as two species:

***Accipiter gentilis* Eurasian goshawk**

Included taxa: *A. g. gentilis* (Linnaeus, 1758), *A. g. buteoides* (Menzbier, 1882), *A. g. albidus* (Menzbier, 1882), *A. g. schvedowi* (Menzbier, 1882), *A. g. fujiyamae* (Swann & Hartert, 1923), *A. g. marginatus* (Piller and Mitterpacher, 1783), and *A. g. arrigonii* (O. Kleinschmidt, 1903). Morphological variation within *A. gentilis* is clinal (Wattel 1973) and there is no evidence that these subspecies differ in other characters than morphology.

***Accipiter atricapillus* American goshawk**

Included taxa: *A. a. atricapillus* (A. Wilson, 1812), *A. a. laingi* (Taverner, 1940) and *A. a. apache* van Rossem, 1938. *A. a. laingi* occurs from coastal south east Alaska south to Haida Gwaii and Vancouver Island, British Columbia (Dickinson and Renssen 2013) It differs from the widespread *A. a. atricapillus* in plumage colour (Hellmayr and Conover 1949). Genomic data show that the population of *A. a. laingi* on Haida Gwaii is distinct from other populations of *A. a. laingi* and *A. a. atricapillus* indicating that variation in plumage and genomic data are not fully congruent (Geraldès et al. 2019). *A. a. apache* of the southwestern USA and Mexico differs from *A. a. atricapillus* and *A. a. laingi* by its larger size and darker plumage (Hellmayr and Conover 1949; Squires and Reynolds 1997) but does not form a monophyletic group in analyses of mitochondrial DNA (Bayard de Volo et al. 2013). Morphological variation within *A. atricapillus* is clinal (Squires and Reynolds 1997) and the taxon *A. a. apache* is not recognised by some authorities (e.g. AOU 1957; Palmer 1988).

Treatment of *A. atricapillus* as a species mirrors that of several other North American taxa that were recently separated from their Eurasian counterparts and upgraded to species rank, including *Larus brachyrhynchus* (Chesser et al. 2021), *Circus hudsonius* (Sangster et al. 2016; Chesser et al. 2017), *Picoides dorsalis* (Banks et al. 2003), *Pica hudsonia* (AOU 2000) and *Nannus pacificus* and *N. hie-malis* (Chesser et al. 2010). Several other Holarctic species may comprise multiple species but await comprehensive integrative taxonomic analysis (e.g. *Hirundo rustica*, *Eremophila alpestris*, *Pinicola enucleator*).

Vocalisations have long played an important role in diagnosing potentially reproductively isolated groups of birds (Lanyon 1961; Martens 1971) and new applications continue to be added (e.g. Sangster 2009). This is the first quantitative taxonomic study of vocalisations in Accipitridae. The consistent difference among three members of the *A. [gentilis]* superspecies observed in this study suggests that vocalisations may also be useful to illuminate taxonomic differences in other groups of Accipitridae. Potential candidates are the African *A. tachiro* and *A. francesiae* complexes, and the Asian *A. badius*-*A. brevipes*, *Pernis ptilorhynchus* and *Circus aeruginosus* complexes, which all have complicated taxonomic histories (Simmons 2000; Louette 2003, 2007; Breman et al. 2013).

A drawback of the present study is that recordings of only three of the seven Palearctic subspecies could be included. However, it is doubtful that this has biased the results of the study, based on two mitigating factors. First, there were no phylogeographic breaks among the Palearctic taxa in the mitochondrial study by Kunz et al. (2019). This means that there is no evidence that any Palearctic subspecies or group of subspecies has had a unique history separate from that of other Palearctic subspecies, allowing time to develop different vocalisations. Second, the recordings included in this study span the entire Palearctic from Britain (*A. g. gentilis*) to Japan (*A. g. fujiyamae*). Future studies should attempt to include recordings of the subspecies *A. g. buteoides*, *A. g. albidus*, *A. g. marginatus*, and *A. g. arrigonii*, and preferably also of the species *A. meyerianus* and *A. melanoleucus*, to obtain a more complete picture of vocal variation in the *A. [gentilis]* superspecies.

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Appendix 1

Sound recordings analysed (n=119).

Taxon	Country	Recordist	Source
<i>A. g. gentilis</i>	Norway	E. A. Ryberg	XC405652
<i>A. g. gentilis</i>	Norway	S. Wahlstrom	Wahlstrom (1995)
<i>A. g. gentilis</i>	Sweden	P. Åberg	XC27024
<i>A. g. gentilis</i>	Sweden	P. Åberg	XC196982
<i>A. g. gentilis</i>	Sweden	T. Sirotkin	XC282488
<i>A. g. gentilis</i>	Sweden	P. Åberg	XC347575
<i>A. g. gentilis</i>	Sweden	L. Arvidsson	XC519963
<i>A. g. gentilis</i>	Sweden	L. Edenius	XC484611
<i>A. g. gentilis</i>	Sweden	L. Edenius	XC646584
<i>A. g. gentilis</i>	Sweden	L. Edenius	XC665202
<i>A. g. gentilis</i>	Sweden	T. Sirotkin	XC628989
<i>A. g. gentilis</i>	Finland	L. A. M. Benner	XC186183
<i>A. g. gentilis</i>	Finland	E. Paljakka	XC305744
<i>A. g. gentilis</i>	Finland	E. Paljakka	XC373099
<i>A. g. gentilis</i>	Finland	T. Linjama	XC341720
<i>A. g. gentilis</i>	Finland	H. Varkki	XC546384
<i>A. g. gentilis</i>	United Kingdom	G. Elton	XC617102
<i>A. g. gentilis</i>	United Kingdom	G. Elton	XC618956
<i>A. g. gentilis</i>	United Kingdom	P. Stronach	XC572464
<i>A. g. gentilis</i>	United Kingdom	P. Stronach	XC623478
<i>A. g. gentilis</i>	United Kingdom	S. Elliott	XC591235
<i>A. g. gentilis</i>	United Kingdom	T. Lowe	XC695135
<i>A. g. gentilis</i>	Netherlands	S. Bot	XC31651
<i>A. g. gentilis</i>	Netherlands	H. van der Meer	XC95713
<i>A. g. gentilis</i>	Netherlands	T. Fijen	XC126643
<i>A. g. gentilis</i>	Netherlands	B. Gras	XC199775
<i>A. g. gentilis</i>	Netherlands	J. van Bruggen	XC308130
<i>A. g. gentilis</i>	Netherlands	J. van Arneym	XC328061
<i>A. g. gentilis</i>	Netherlands	J. van Bruggen	XC361645
<i>A. g. gentilis</i>	Netherlands	F. Roos	XC416502
<i>A. g. gentilis</i>	Netherlands	R. de By	XC551452
<i>A. g. gentilis</i>	Belgium	F. Verbelen	XC98943
<i>A. g. gentilis</i>	Belgium	S. Cooleman	XC693275
<i>A. g. gentilis</i>	Belgium	D.F. Martinez	XC713496
<i>A. g. gentilis</i>	Germany	V. Arnold	XC72816
<i>A. g. gentilis</i>	Germany	V. Arnold	XC73002
<i>A. g. gentilis</i>	Germany	L. Lachmann	XC331689
<i>A. g. gentilis</i>	Germany	brickegickel	XC370973
<i>A. g. gentilis</i>	Germany	A. Ortiz Troncoso	XC401498
<i>A. g. gentilis</i>	Germany	B. Saadi-Varchmin	XC440310
<i>A. g. gentilis</i>	Germany	brickegickel	XC442629
<i>A. g. gentilis</i>	Germany	K-U Tielman	XC475347
<i>A. g. gentilis</i>	Germany	M. Waldeck	XC509242
<i>A. g. gentilis</i>	Germany	F. Holzapfel	XC544505
<i>A. g. gentilis</i>	Germany	S. Kransel	XC650705
<i>A. g. gentilis</i>	Germany	W. Agster	XC685091
<i>A. g. gentilis</i>	Germany	brickegickel	XC710926
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC102848
<i>A. g. gentilis</i>	Poland	K. Deoniziak	XC181140
<i>A. g. gentilis</i>	Poland	P. Szczypinski	XC181823
<i>A. g. gentilis</i>	Poland	T. Tumieli	XC215067
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC309591
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC309596
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC406834

Taxon	Country	Recordist	Source
<i>A. g. gentilis</i>	Poland	I. Oleksik	XC600687
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC626012
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC627173
<i>A. g. gentilis</i>	Poland	I. Oleksik	XC627730
<i>A. g. gentilis</i>	Poland	J. Matusiak	XC631750
<i>A. g. gentilis</i>	France	J. Berteau	XC388950
<i>A. g. gentilis</i>	France	J. Hervé	XC425339
<i>A. g. gentilis</i>	France	J. Hervé	XC425936
<i>A. g. gentilis</i>	France	J. Hervé	XC428837
<i>A. g. gentilis</i>	France	B. Van Hecke	XC543700
<i>A. g. gentilis</i>	France	V. Palomares	XC545490
<i>A. g. gentilis</i>	France	S. Wroza	XC619727
<i>A. g. gentilis</i>	France	S. Wroza	XC627256
<i>A. g. gentilis</i>	Switzerland	P. Christe	XC302363
<i>A. g. gentilis</i>	Spain	J. G. Sáez	XC709596
<i>A. g. gentilis</i>	Spain	Sergi	XC700706
<i>A. g. gentilis</i>	Urzhumka, Russia	A. Lastukhin	XC109711
<i>A. g. gentilis</i>	Mari El Republic, Russia	A. Lastukhin	XC167479
<i>A. g. gentilis</i>	Chuvashia, Russia	A. Lastukhin	XC306147
<i>A. g. schvedowi</i>	Khinganskiy Zapovednik, Russia	A. Thomas	XC378250
<i>A. g. fujiyamae</i>	Japan	A. Torimi	XC320249
<i>A. g. atricapillus</i>	Quebec, Canada,	F. Cloutier	ML342036571
<i>A. g. atricapillus</i>	Quebec, Canada,	M. Vachon	ML352729551
<i>A. g. atricapillus</i>	Maine, USA	A. Spencer	XC49345
<i>A. g. atricapillus</i>	Maine, USA	T. Brooks	XC59174
<i>A. g. atricapillus</i>	Maine, USA,	C. Duncan	ML82371
<i>A. g. atricapillus</i>	New Hampshire, USA	L. Burford	XC567216
<i>A. g. atricapillus</i>	Vermont, USA,	L. Holmes	ML240620231
<i>A. g. atricapillus</i>	Massachusetts, USA	T. Spahr	XC183577
<i>A. g. atricapillus</i>	New York, USA	L. Elliott	Elliott (1997)
<i>A. g. atricapillus</i>	New York, USA,	M. Epstein	ML360314421
<i>A. g. atricapillus</i>	New York, USA,	P.P. Kellogg	ML4150
<i>A. g. atricapillus</i>	Ontario, Canada	M. Brigham	Brigham (1992)
<i>A. g. atricapillus</i>	Ontario, Canada,	F. Pinilla	ML416445881
<i>A. g. atricapillus</i>	Ontario, Canada,	S. Craig	ML344414941
<i>A. g. atricapillus</i>	Michigan, USA,	A. Simon	ML357433541
<i>A. g. atricapillus</i>	Michigan, USA,	D. Haan	ML240023181
<i>A. g. atricapillus</i>	Michigan, USA,	K. Vande Vusse	ML105522131
<i>A. g. atricapillus</i>	Alaska, USA	A. Spencer	XC185619
<i>A. g. atricapillus</i>	Alaska, USA	J. Saunders	ML280504581
<i>A. g. atricapillus</i>	Alaska, USA	M. Andersen	ML132244
<i>A. g. atricapillus</i>	Washington, USA	B. Lagerquist	XC586893
<i>A. g. atricapillus</i>	Oregon, USA	G.A. Keller	Keller (2003)
<i>A. g. atricapillus</i>	Oregon, USA	D. Herr	ML63118
<i>A. g. atricapillus</i>	Idaho, USA	Naomi	XC711109
<i>A. g. atricapillus</i>	Nevada, USA	B. Wilcox	XC369692
<i>A. g. atricapillus</i>	Nevada, USA	R. E. Webster	XC270158
<i>A. g. atricapillus</i>	Utah, USA	K. Colver	Colver (1999)
<i>A. g. atricapillus</i>	Colorado, USA	D. Tønnessen	ML175106421
<i>A. g. atricapillus</i>	Colorado, USA	G. Goodrich	ML255141781
<i>A. g. atricapillus</i>	Colorado, USA	K.M. Dunning	ML144074751
<i>A. g. atricapillus</i>	locality unknown	T. Sander	Sander (1996)
<i>A. g. apache</i>	Arizona, USA	K. Blankenship	XC330757
<i>A. g. apache</i>	Arizona, USA	G.A. Keller	Peyton (1999)
<i>A. g. apache</i>	Arizona, USA	J. C. Arvin	FLMNH12059
<i>A. g. apache</i>	New Mexico, USA	J. Swackhamer	XC319149
<i>A. g. apache</i>	New Mexico, USA	J. McCullough	ML258120351
<i>A. g. laingi</i>	Haida Gwaii, Canada	G. Morigeau	XC126082

Taxon	Country	Recordist	Source
<i>A. henstii</i>	Madagascar	D. Lane	XC026465
<i>A. henstii</i>	Madagascar	H. Matheve	XC155062
<i>A. henstii</i>	Madagascar	T. Mark	XC156686
<i>A. henstii</i>	Madagascar	P. Gregory	XC158244
<i>A. henstii</i>	Madagascar	M. Nelson	XC162904
<i>A. henstii</i>	Madagascar	R. Gallardy	XC419026
<i>A. henstii</i>	Madagascar	P. Huguet	Huguet & Chappuis (2003)