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. hensiti. 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. brachyrhynchos (Sonsthagen et al. 2012), Picoides 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 (Drovettsk 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. albida, A. g. schwedowi, A. g. fujiyamae, A. g. marginatus, A. g. arrigoniti) 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 Volò 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] superspecies, 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; Padial 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. laiingi_ and _A. g. apache_, which were treated as a single OTU based on the results of Gerais 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 Komolgorov-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_ ≥ 0.1 as ‘very small’, _d_ ≥ 0.2 as ‘small’, _d_ ≥ 0.5 as ‘medium’, _d_ ≥ 0.8 as ‘large’, _d_ ≥ 1.2 as ‘very large’ and _d_ ≥ 2.0 as ‘huge’. All statistical analyses were performed with SPSS 28.0 (IBM Corp., Armonk, NY, USA), except Holm’s sequential Bonferroni test, which was carried out by hand using uncorrected significance data from SPSS 28.0.

### Table 1 Standardized canonical discriminant function coefficients examining trends in variance of six acoustic variables measured for calls of the _A. g. gentilis_-group, _A. g. atricapillus_-group and _A. henstii_.

| Variable                  | 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% |

* _d_ ≥ 1.2) or ‘huge’ (Cohen’s _d_ > 1.2) 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

### 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 Square$_{12}$ = 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 ± 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                  | gentilis-group (n=75) | atricapillus-group (n=37) | A. henstii (n=7) | gentilis-group vs. atricapillus-group Significance Cohen’s $d$ (interpretation) | gentilis-group vs. A. henstii Significance Cohen’s $d$ (interpretation) | atricapillus-group vs. A. henstii Significance Cohen’s $d$ (interpretation) |
|---------------------------|------------------------|---------------------------|------------------|--------------------------------------------------------------------------------|--------------------------------------------------------------------------------|--------------------------------------------------------------------------------|
| Call duration             | 4.320±1.710 (1.285–8.908) | 7.294±2.392 (2.219–15.567) | 8.101±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) $^f$ |
| Number of notes           | 22.9±9.4 (6.0–47.0)    | 28.9±10.6 (11.0–67.0)    | 15.6±3.3 (10.0–19.0)  | $P<0.01$ $^b$ 5.61 (very large) $^c$ | $P<0.05$ $^b$ 0.81 (large) $^c$ | $P<0.001$ 1.38 (very large) $^c$ |
| Note rate                 | 5.32±0.91 (3.59–8.03)  | 3.97±0.48 (2.78–4.96)    | 1.92±0.28 (1.52–2.32) | $P<0.001$ $^b$ 1.70 (very large) $^c$ | $P<0.001$ $^b$ 3.90 (huge) $^d$ | $P<0.001$ 4.61 (huge) $^d$ |
| Duration median note      | 0.046±0.009 (0.021–0.069) | 0.116±0.018 (0.092–0.158) | 0.238±0.043 (0.196–0.312) | $P<0.001$ $^b$ 5.49 (huge) $^d$ | $P<0.001$ $^b$ 13.33 (huge) $^d$ | $P<0.005$ 5.32 (huge) $^d$ |
| Max. freq median note     | 3060±317 (2581–4191)   | 2899±294 (2357–3520)     | 2281±487 (1763–3022) | $P<0.05$ $^b$ 0.52 (medium) $^c$ | $P<0.001$ $^b$ 2.37 (huge) $^d$ | $P<0.005$ 1.92 (very large) $^c$ |
| Min. freq. median note    | 1945±250 (1484–2748)   | 1960±221 (1355–2468)     | 1323±347 (837–1776)  | n.s. $^a$ 0.06 (negligible) | $P<0.001$ $^b$ 2.43 (huge) $^d$ | $P<0.001$ 2.60 (huge) $^d$ |
| Freq. range median note   | 1115±240 (579–1716)    | 939±281 (486–1603)       | 958±180 (709–1246)   | $P<0.001$ $^b$ 0.70 (medium) $^c$ | n.s. $^a$ 0.67 (medium) $^c$ | n.s. $^a$ 0.07 (negligible) |

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.
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 subject 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-
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

**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* Flatanger, Norway, Markus Varesvuori/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.
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 Remsen 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 brachyrhynchos (Chesser et al. 2021), Circus hudsonius (Sangster et al. 2016; Chesser et al. 2017), Picoïdes 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           |
|---------------|------------|----------------------------|------------------|
| *A. g. gentilis* | Norway     | E. A. Ryberg               | XC405652         |
| *A. g. gentilis* | Norway     | S. Wahlstrom               | Wahlstrom (1995) |
| *A. g. gentilis* | Sweden     | P. Åberg                   | XC27024          |
| *A. g. gentilis* | Sweden     | P. Åberg                   | XC196982         |
| *A. g. gentilis* | Sweden     | T. Sirotkin                | XC282488         |
| *A. g. gentilis* | Sweden     | L. Arvidsson               | XC519963         |
| *A. g. gentilis* | Sweden     | L. Edenius                 | XC484611         |
| *A. g. gentilis* | Sweden     | L. Edenius                 | XC646584         |
| *A. g. gentilis* | Sweden     | T. Sirotkin                | XC628989         |
| *A. g. gentilis* | Finland    | L. A. M. Benner            | XC186183         |
| *A. g. gentilis* | Finland    | E. Paljakka                | XC305744         |
| *A. g. gentilis* | Finland    | E. Paljakka                | XC373099         |
| *A. g. gentilis* | Finland    | T. Linjama                 | XC341720         |
| *A. g. gentilis* | Finland    | H. Varkki                  | XC546384         |
| *A. g. gentilis* | United Kingdom | G. Elton               | XC617102         |
| *A. g. gentilis* | United Kingdom | G. Elton              | XC618956         |
| *A. g. gentilis* | United Kingdom | P. Stronach         | XC572464         |
| *A. g. gentilis* | United Kingdom | S. Elliott            | XC591235         |
| *A. g. gentilis* | United Kingdom | T. Lowe               | XC695135         |
| *A. g. gentilis* | Netherlands | S. Bot                     | XC31651          |
| *A. g. gentilis* | Netherlands | H. van der Meer           | XC395713         |
| *A. g. gentilis* | Netherlands | T. Fijen                   | XC126643         |
| *A. g. gentilis* | Netherlands | B. Gras                    | XC199775         |
| *A. g. gentilis* | Netherlands | J. van Bruggen             | XC308130         |
| *A. g. gentilis* | Netherlands | J. van Arneym              | XC328061         |
| *A. g. gentilis* | Netherlands | J. van Bruggen             | XC361645         |
| *A. g. gentilis* | Netherlands | F. Roos                    | XC416502         |
| *A. g. gentilis* | Netherlands | R. de By                   | XC351452         |
| *A. g. gentilis* | Belgium     | F. Verbelen                | XC398943         |
| *A. g. gentilis* | Belgium     | S. Cooleman                | XC693275         |
| *A. g. gentilis* | Belgium     | D. F. Martinez             | XC713496         |
| *A. g. gentilis* | Germany     | V. Arnold                   | XC72816          |
| *A. g. gentilis* | Germany     | V. Arnold                   | XC75302          |
| *A. g. gentilis* | Germany     | L. Lachmann                | XC331689         |
| *A. g. gentilis* | Germany     | brickegickel               | XC370973         |
| *A. g. gentilis* | Germany     | A. Ortiz Troncoso          | XC401498         |
| *A. g. gentilis* | Germany     | B. Saadi-Varchmin          | XC440310         |
| *A. g. gentilis* | Germany     | brickegickel               | XC442629         |
| *A. g. gentilis* | Germany     | K-U Tielman                | XC475347         |
| *A. g. gentilis* | Germany     | M. Waldeck                 | XC509242         |
| *A. g. gentilis* | Germany     | F. Holzapfel               | XC544505         |
| *A. g. gentilis* | Germany     | S. Kransel                 | XC650705         |
| *A. g. gentilis* | Germany     | W. Agster                  | XC685091         |
| *A. g. gentilis* | Poland      | J. Matusiak                | XC102848         |
| *A. g. gentilis* | Poland      | K. Deonizak                | XC181140         |
| *A. g. gentilis* | Poland      | P. Szczypinski             | XC181823         |
| *A. g. gentilis* | Poland      | T. Tumiel                  | XC215067         |
| *A. g. gentilis* | Poland      | J. Matusiak                | XC309591         |
| *A. g. gentilis* | Poland      | J. Matusiak                | XC309596         |
| *A. g. gentilis* | Poland      | J. Matusiak                | XC406834         |
| Taxon          | Country           | Recordist     | Source          |
|---------------|-------------------|---------------|-----------------|
| A. g. gentilis | Poland            | I. Oleksik    | XC600687        |
| A. g. gentilis | Poland            | J. Matusiak   | XC626012        |
| A. g. gentilis | Poland            | J. Matusiak   | XC627173        |
| A. g. gentilis | Poland            | I. Oleksik    | XC627730        |
| A. g. gentilis | Poland            | J. Matusiak   | XC631750        |
| A. g. gentilis | France            | J. Berteau    | XC388950        |
| A. g. gentilis | France            | J. Hervé      | XC425339        |
| A. g. gentilis | France            | B. Van Hecke  | XC425936        |
| A. g. gentilis | France            | V. Palomares  | XC545490        |
| A. g. gentilis | France            | S. Wroza      | XC619727        |
| A. g. gentilis | France            | S. Wroza      | XC627256        |
| A. g. gentilis | Switzerland       | P. Christie   | XC302363        |
| A. g. gentilis | France            | J. G. Sáez    | XC709596        |
| A. g. gentilis | Spain             | Sergi         | XC700706        |
| A. g. gentilis | Urzhumka, Russia  | A. Lastukhin   | XC109711        |
| A. g. gentilis | Mari El Republic, Russia | A. Lastukhin   | XC167479        |
| A. g. gentilis | Chuvashia, Russia | A. Lastukhin   | XC306147        |
| A. g. schwedowi | Khinganskiy Zapovednik, Russia | A. Thomas | XC378250        |
| A. g. fusiyamae | Japan             | A. Torinni    | XC320249        |
| A. g. atricapillus | Quebec, Canada, | F. Cloutier   | ML342036571     |
| A. g. atricapillus | Quebec, Canada, | M. Vachon     | ML352729551     |
| A. g. atricapillus | Maine, USA       | A. Spencer    | XC49345         |
| A. g. atricapillus | Maine, USA       | T. Brooks     | XC59174         |
| A. g. atricapillus | Maine, USA       | C. Duncan     | ML82371         |
| A. g. atricapillus | New Hampshire, USA | L. Burford   | XC567216        |
| A. g. atricapillus | Vermont, USA     | L. Holmes     | ML240620231     |
| A. g. atricapillus | Massachusetts, USA | T. Spahr  | XC183577        |
| A. g. atricapillus | New York, USA    | L. Elliott    | Elliott (1997)  |
| A. g. atricapillus | New York, USA    | M. Epstein    | ML360314421     |
| A. g. atricapillus | New York, USA    | P.P. Kellogg  | ML4150          |
| A. g. atricapillus | Ontario, Canada  | M. Brigham    | Brigham (1992)  |
| A. g. atricapillus | Ontario, Canada  | F. Pinilla    | ML416445881     |
| A. g. atricapillus | Ontario, Canada  | S. Craig      | ML344414941     |
| A. g. atricapillus | Michigan, USA    | A. Simon      | ML357433541     |
| A. g. atricapillus | Michigan, USA    | D. Haan       | ML240023181     |
| A. g. atricapillus | Michigan, USA    | K. Vande Vusse| ML105522131     |
| A. g. atricapillus | Alaska, USA      | A. Spencer    | XC1885619       |
| A. g. atricapillus | Alaska, USA      | J. Saunders   | ML280504581     |
| A. g. atricapillus | Alaska, USA      | M. Andersen   | ML132244        |
| A. g. atricapillus | Washington, USA  | B. Lagerquist | XC586893        |
| A. g. atricapillus | Oregon, USA      | G.A. Keller   | Keller (2003)   |
| A. g. atricapillus | Oregon, USA      | D. Herr       | ML63118         |
| A. g. atricapillus | Idaho, USA       | Naomi         | XC711109        |
| A. g. atricapillus | Nevada, USA      | B. Wilcox     | XC369692        |
| A. g. atricapillus | Nevada, USA      | R. E. Webster | XC270158        |
| A. g. atricapillus | Utah, USA        | K. Colver     | Colver (1999)   |
| A. g. atricapillus | Colorado, USA    | D. Tennessen  | MIL75106421     |
| A. g. atricapillus | Colorado, USA    | G. Goodrich   | ML255141781     |
| A. g. atricapillus | Colorado, USA    | K.M. Dunning  | ML144074751     |
| A. g. atricapillus | locality unknown | T. Sander     | Sander (1996)   |
| A. g. apache   | Arizona, USA      | K. Blankenship| XC330757        |
| A. g. apache   | Arizona, USA      | G.A. Keller   | Peyton (1999)   |
| A. g. apache   | Arizona, USA      | J. C. Arvin   | FLMNH12059      |
| A. g. apache   | New Mexico, USA   | J. Swackhamer | XC319149        |
| A. g. apache   | New Mexico, USA   | J. McCullham  | ML258120351     |
| A. g. laingi   | Haida Gwaii, Canada | G. Morigeau | XC126082        |
| Taxon   | Country     | Recordist | Source        |
|---------|-------------|-----------|---------------|
| *A. henstii* | Madagascar | D. Lane   | XC026465      |
| *A. henstii* | Madagascar | H. Matheve | XC155062      |
| *A. henstii* | Madagascar | T. Mark   | XC156686      |
| *A. henstii* | Madagascar | P. Gregory | XC158244      |
| *A. henstii* | Madagascar | M. Nelson | XC162904      |
| *A. henstii* | Madagascar | R. Gallardy | XC419026     |
| *A. henstii* | Madagascar | P. Huguet | Huguet & Chappuis (2003) |