

ACOUSTIC DIFFERENCES BETWEEN THE SCOTERS *MELANITTA NIGRA NIGRA* AND *M. N. AMERICANA*

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ABSTRACT.—Scoter vocalizations may have a role in pair formation and pair bonding. I compared the courtship calls of male Black Scoters (*Melanitta nigra nigra* and *M. n. americana*) using published and archived recordings. Courtship calls of the two subspecies differed diagnosably in duration. In contrast, recordings from different localities within the ranges of each taxon showed no diagnosable differentiation. This finding represents the first indication these taxa differ in characters other than bill morphology and supports recent proposals to treat *M. n. americana* as a distinct species (*M. americana*). Vocal displays, in contrast to courtship displays, of anatids have not been used for assessment of species limits in Anatidae. My results indicate vocalizations are a potentially useful additional character in species-level taxonomy of anatids. Received 7 September 2004. Accepted 10 May 2009.

Courtship displays of anatids have attracted substantial attention from behavioral scientists (e.g., Heinroth 1911, Lorenz 1951–1953, Johnsgard 1965), and interspecific variation has been analysed and interpreted in an evolutionary context (Johnsgard 1960, Johnson 2000). Vocal displays, in contrast, have received far less attention (e.g., Abraham 1974) and their possible use in anatid taxonomy has been neglected. Some closely related species are known to have different vocalizations (Livezey and Humphrey 1992), but vocalizations have not been used to support proposals to revise species limits.

The Black Scoter (*Melanitta nigra*) is currently recognized as polytypic with two subspecies: the western Palearctic *M. n. nigra* (hereafter *nigra*) and the eastern Palearctic and Nearctic *M. n. americana* (hereafter *americana*). These forms were recognized as separate species in the 19th and early 20th centuries (Baird et al. 1884, AOU 1931, Kortright 1952) but were considered a single species after introduction of the polytypic species concept to ornithology (Hartert 1915, Witherby 1924). This treatment subsequently gained broad acceptance in North America (AOU 1957) and Eurasia (Voous 1960, Vaurie 1965). Some authors in recent years have treated *americana* as a full species (Stepanyan 1990, Livezey 1995, Sangster et al. 1999, Collinson et al. 2006) based on morphological differences (Johnsgard 1978, Dean and BBRC 1989). Most authors continue to treat *americana* as a subspecies of *M. nigra* because (1) there has been no

evidence of differentiation in other characters, and (2) evidence for reproductive isolation has been lacking.

The vocal repertoire of Black Scoters appears to be small (Cramp and Simmons 1977, Bordage and Savard 1995). The most commonly heard vocalization is the courtship call given by males in courtship parties of several (5–8) unpaired males and 1–2 females (Gunn 1927, McKinney 1959, Bengtson 1966). It is also given by paired males during courtship (Humphrey 1957). Within courtship groups, male calls are directed towards females, which form the nucleus of groups. Pair formation in Black Scoter begins in winter flocks and continues into late spring on the breeding grounds (Bengtson 1966, Cramp and Simmons 1977). Most females are already paired when they arrive on the breeding grounds, although unpaired females can be seen as late as mid-June (Bengtson 1966). Because of its likely importance in pair formation, the courtship call was selected for taxonomic comparison. Although several descriptions and spectrograms of the courtship call have been published (e.g., Phillips 1926, Gunn 1927, Humphrey 1957, McKinney 1959, Cramp and Simmons 1977, Bergmann and Helb 1982, Bordage and Savard 1995), there have been no comparisons of the calls of *nigra* and *americana*. My objective is to compare the vocalizations of two allopatric duck taxa of uncertain taxonomic rank.

METHODS

Recordings (Table 1) of the courtship call of *nigra* ($n = 10$) and *americana* ($n = 18$) were obtained from sound libraries, individual recordists, and published commercial recordings (Simms 1970, Palmer and Boswall 1972, Ferdinand et al.

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TABLE 1. Recording localities and recordists of scoter sounds reviewed.

Country	Location	Date	Recordist	Recordings	Source ^a
<i>Melanitta nigra nigra</i>					
France	Cotentin Peninsula	Oct 1991	C. Chappuis	1	Chappuis (2000)
Northern Ireland	Co. Fermanagh	May 1967	E. Simms	1	Simms (1970)
Iceland	Lake Myvatn	May 1991	P. A. D. Hollom	1	BLSA 10632
	Lake Myvatn	Jun 1967	S. Palmer	1	Palmer and Boswall (1972)
Norway	Lake Myvatn	Jun 1967	P. Sellar	1	BLSA 4735
	Hofði	Jun 1983	A.G. Knox	1	BLSA 70435
	Norwick	May 1980	R. Goodwin	1	BLSA 12510
Sweden	Tröndelag	Jun 2004	M. Schubert	1	Bergmann et al. (2008)
	Locality unknown	Jun 1961	L. Ferdinand	1	Ferdinand et al. (1991)
Russia (western)	South Yamal Peninsula, Yadakhodayakha R.	1976	V. K. Ryabitsev	1	VPAV 203143
<i>Melanitta nigra americana</i>					
Canada (British Columbia)	Comox, Vancouver Island	Jan 1999	J. Neville	1	Neville (1999)
Japan	Aomori Prefecture	Mar 1995	H. Ueda	1	Ueda (1998) and unpublished
	Hokkaido	Dec 1974	T. Kabaya	1	Kabaya and Matsuda (2001)
	Hokkaido	Feb 2002	M. Matsuda	1	Unpublished
	Hokkaido	Mar 1993	H. Ueda	1	Unpublished
Russia (eastern)	Hokkaido	Mar 2000	H. Ueda	1	Unpublished
	Magadan Region, Chukcha River	Jun 1996	E. A. Krechmar	2	VPAV SP01_04; SP01_05
	Chukotka, Krasnoye Lake	Jun 2006	V.Yu. Arkhipov	1	XC 30210
USA (Alaska)	Nome	Jun 1998	K. Colver	1	Unpublished
	Kodiak Island	Mar 1998	K. Colver	6	Colver (1999) and unpublished
USA (New Jersey)	Cape May Pointe	Feb 2004	D. Jones	1	XC 1138
	Barnegat Light	Feb 2006	G. Vyn	1	MLNS 130900

^a BLSA = British Library Sound Archive (London); MLNS = Macaulay Library of Natural Sounds (Ithaca); VPAV = Veprintsev Phonoteca of Animal Voices (Moscow); XC = www.Xeno-Canto.org.

1991, Ueda 1998, Colver 1999, Neville 1999, Chappuis 2000, Kabaya and Matsuda 2001, Bergmann et al. 2008). Analog recordings were downloaded onto a computer using a Sound Blaster Audigy 2 sound card and transformed into wave files with CoolEdit 2000 (Johnston 2000). Digital audio recordings were transformed into wave files using Cdex (Faber 2003). All files were stored on hard disk as mono wave files at 8 kHz with 16-bit precision.

Spectrograms of recordings were examined and measured using CoolEdit 2000. Syrinx (Burt 2006) was used to make the spectrograms used into illustrations. One temporal character (call duration) and one frequency character (frequency at midpoint of the call duration) were examined. Most recordings were of calls given in flocks comprising several males, and it was not possible to separate individual birds. Thus, to obtain a

sufficient sample of intrapopulation variability, 25 calls were measured for each recording where possible. Character states, following Isler et al. (1998), were considered to differ diagnosably if two criteria were met: ranges of measurements did not overlap, and the means (\bar{x}) and standard deviations (SD) of the populations with the smaller (a) and larger metrics (b) met the following requirement:

$$\bar{x}_a + t_a \text{SD}_a \leq \bar{x}_b - t_b \text{SD}_b,$$

where t_i is the value of Student's t at the 97.5 percentile for $n - 1$ degrees of freedom. Assumptions of normal distribution and/or homogeneity of variances were violated, and the Mann-Whitney U -test with a sequential Bonferroni correction (Rice 1989) was used to examine whether call duration and midpoint frequency

differed among groups. SPSS (SPSS Institute 2008) was used to calculate descriptive statistics and perform statistical tests. All statistical tests used $\alpha = 0.05$.

RESULTS

The courtship calls of *nigra* and *americana* are clearly different to the human ear and from examination of spectrograms (Fig. 1). The call of *nigra* is a single repeated note (Fig. 1A–C) that on average lasts slightly over 0.1 sec. It starts at a frequency of ~1,400–1,520 Hz and decreases in pitch to ~1,350–1,460 Hz near the end of the call. It is best transcribed as a short, abrupt-ending *pju* or *pjut*. The call of *americana* also comprises a single note (Fig. 1D–F) but is much longer, averaging almost 0.7 sec in duration. Most start at a frequency of 1,480–1,770 Hz, rise slightly in pitch to ~1,510–1,850 Hz and then taper off to a frequency of 1,500–1,670 Hz (some show a clear rise in frequency toward the end; Fig. 1F). They can be transcribed as a mournful *whuuuuuw*, *huuuuw* or *huuwuw*.

Spectrogram analysis revealed the calls of the two taxa differ in duration, frequency, structure, and variability. The duration of courtship calls differed diagnosably, i.e., character distributions did not overlap (Table 2) and the distributions met the statistical test described by Isler et al. (1998). Within-taxon differences were not diagnosable. The parameters for *nigra* from France, Northern Ireland, Iceland, Norway, Sweden, and western Russia overlapped widely, as did those of *americana* from Japan, eastern Russia, Alaska, British Columbia, and New Jersey (Table 2), although in *americana* most samples differed significantly (Table 3).

The midpoint frequency of *americana* was significantly higher than that of *nigra* (1,701 Hz in *americana* vs. 1,507 Hz in *nigra*; Mann-Whitney *U*-test; $P < 0.001$). The difference, however, was not diagnosable due to the wide overlap of measurements (Table 2). Within-taxon differences were not diagnosable, although some samples of *nigra* differed significantly (Table 3).

The structure of the calls of *nigra* and *americana* differs as follows: the calls of *nigra* appear in spectrograms as a horizontal or slightly downward element ending in a sharp downward twist. The calls of *americana* are more protracted and often involve a rise in pitch (either at the start of the call, in the middle of the note, or towards the end) which is not observed in *nigra*.

The calls of *nigra* and *americana* also differ in variability. The call of *nigra* is stereotypical in shape, with little individual variation. The calls of *americana* are more variable in shape (Fig. 1D–F). Variation in call duration, expressed as the CV (standard deviation divided by the sample mean), was higher in *americana* (0.242) than in *nigra* (0.113). The difference in the CV of *nigra* and *americana* is not diagnosable, however, due to the relatively variable sample from Norway that stems from a single outlying point. Variation in midpoint frequency was similar in both taxa (0.056 in *americana* vs. 0.059 in *nigra*; Mann-Whitney *U*-test; $P > 0.05$).

DISCUSSION

The character states should be homologous across taxa and differences among taxa should be diagnosable for a character to be useful in species-level taxonomy. I consider the vocalizations used in this study as homologous because: (1) they are consistent with published descriptions of courtship calls of *nigra* (Gunn 1927, Bengtson 1966) and *americana* (Phillips 1926, Humphrey 1957, McKinney 1959), and (2) detailed field studies indicate these calls are given in the same behavioral context (*nigra*: Gunn 1927, Bengtson 1966; *americana*: Phillips 1926, Humphrey 1957, McKinney 1959).

The courtship calls of *nigra* and *americana* are diagnosably different in duration, but do not differ diagnosably among populations within either taxon. They further differ non-diagnosably in midpoint frequency. The structure (shape) of the calls is visually different (Fig. 1), although this difference could not be quantified. My study demonstrates the existence of acoustic differences between *nigra* and *americana* and is the first to show these taxa differ in characters other than bill morphology. The geographic pattern of variation in vocalizations matches the geographic distribution of *nigra* and *americana* based on morphological variation. The congruence of acoustic and morphological variation suggests that *nigra* and *americana* have had a prolonged period of separate evolutionary history.

The diagnostic difference in courtship calls is relevant to the taxonomic status of *americana*. Populations, according to the Phylogenetic Species Concept (PSC) (Cracraft 1983, 1997), are treated as species if they are diagnosable by a unique character state or a unique combination of character states. The diagnostic differences in

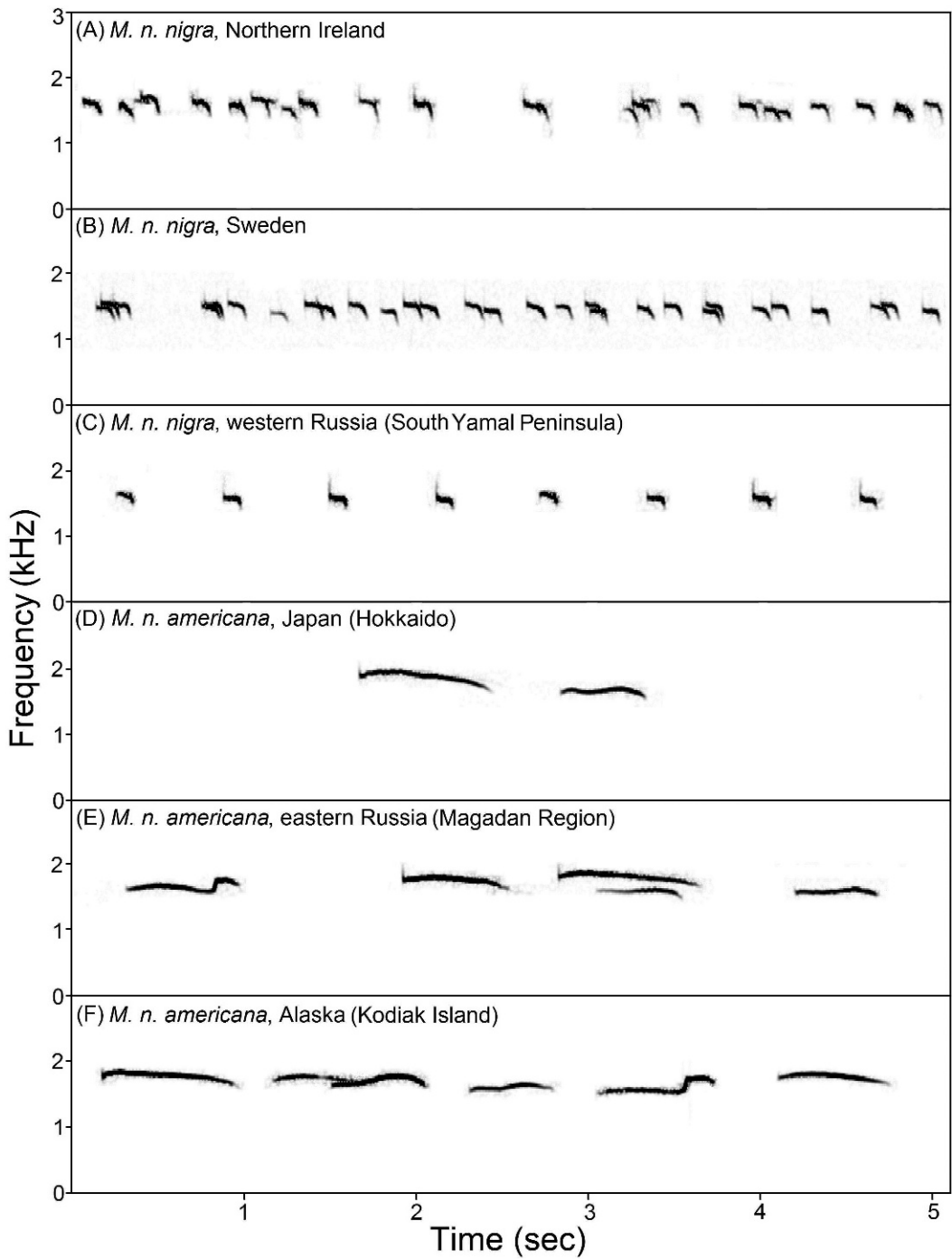


FIG. 1. Spectrograms of courtship calls of *Melanitta nigra nigra* (A–C) and *M. n. americana* (D–F).

TABLE 2. Duration and midpoint frequency of *Melanitta nigra nigra* and *M. n. americana* calls from 11 localities.

Location	n	Call duration			Midpoint frequency		
		Mean ± SD (msec)	CV	Range (msec)	Mean ± SD (msec)	CV	Range (msec)
<i>Melanitta nigra nigra</i>							
France	19	109 ± 12	0.110	83–126	1496 ± 90	0.060	1361–1621
Northern Ireland	25	107 ± 8	0.075	91–120	1544 ± 47	0.030	1464–1629
Iceland	81	106 ± 10	0.094	75–122	1510 ± 116	0.077	1331–1764
Norway	34	102 ± 19	0.186	75–180	1494 ± 54	0.036	1411–1644
Sweden	25	112 ± 7	0.063	93–131	1450 ± 40	0.028	1363–1510
Western Russia	18	104 ± 4	0.038	99–115	1563 ± 22	0.014	1528–1590
All samples	202	106 ± 12	0.113	75–180	1507 ± 89	0.059	1331–1764
<i>Melanitta nigra americana</i>							
Japan	77	840 ± 151	0.180	440–1089	1705 ± 111	0.065	1341–1879
Eastern Russia	46	674 ± 142	0.211	406–910	1687 ± 107	0.063	1526–1878
Alaska	119	618 ± 124	0.201	341–994	1710 ± 86	0.050	1529–1953
British Columbia	19	569 ± 105	0.185	309–741	1701 ± 56	0.033	1613–1816
New Jersey	29	732 ± 169	0.231	470–946	1673 ± 89	0.053	1518–1820
All samples	290	694 ± 168	0.242	309–1089	1701 ± 96	0.056	1341–1953

structure and color pattern of the bill justify the treatment of *americana* as a species under the PSC. Most authors who have treated *americana* as a full species either implicitly (Stepanyan 1990) or explicitly (Livezey 1995, Sangster et al. 1999) applied the diagnosability criterion of the PSC.

The results of this study support the treatment of *americana* as a species under the PSC by documenting a diagnostic difference in a second character.

Assessment of the taxonomic status of *americana* under the Biological Species Concept (BSC)

TABLE 3. Differences in call duration (above diagonal) and midpoint frequency (below diagonal) among samples of *Melanitta nigra nigra* and *M. n. americana*. Combinations of samples marked X are diagnosably different^a. Pairs marked S are significantly different^b (Mann-Whitney *U*-test, with Bonferroni-correction) but not diagnosably different.

	New Jersey (<i>americana</i>)	Alaska (<i>americana</i>)	Eastern Russia (<i>americana</i>)	Japan (<i>americana</i>)	British Columbia (<i>americana</i>)	Western Russia (<i>nigra</i>)	Sweden (<i>nigra</i>)	Norway (<i>nigra</i>)	Iceland (<i>nigra</i>)	Northern Ireland (<i>nigra</i>)	France (<i>nigra</i>)
France (<i>nigra</i>)	X	X	X	X	X	ns ^c	ns	ns	ns	ns	—
Northern Ireland (<i>nigra</i>)	X	X	X	X	X	ns	ns	ns	ns	—	ns
Iceland (<i>nigra</i>)	X	X	X	X	X	ns	ns	ns	—	ns	ns
Norway (<i>nigra</i>)	X	X	X	X	X	ns	ns	—	ns	ns	ns
Sweden (<i>nigra</i>)	X	X	X	X	X	ns	—	ns	ns	S	ns
Western Russia (<i>nigra</i>)	X	X	X	X	X	—	S	S	ns	ns	ns
British Columbia (<i>americana</i>)	ns	ns	ns	S	—	S	X	S	S	S	S
Japan (<i>americana</i>)	ns	S	S	—	ns	S	S	S	S	S	S
Eastern Russia (<i>americana</i>)	ns	ns	—	ns	ns	S	S	S	S	S	S
Alaska (<i>americana</i>)	ns	—	ns	ns	ns	S	X	S	S	S	S
New Jersey (<i>americana</i>)	—	ns	ns	ns	ns	S	S	S	S	S	S

^a Criteria for diagnosability given in Methods.

^b A value of $P < 9.09 \times 10^{-4}$ was considered significant (Bonferroni correction for 55 comparisons).

^c ns = not significant.

(Mayr 1940, 1982) is more problematic because the taxonomic criterion of the BSC—reproductive isolation—cannot be directly applied to taxa that do not co-exist during pair-formation. Indirect evidence is sought in such situations in the form of differentiation in characters that affect species recognition, pair formation, or mate choice. Courtship calls in the scoters are given in parties composed of one female and several unpaired males (Gunn 1927, McKinney 1959, Bengtson 1966). It is likely that pair formation occurs within courtship parties and that vocalizations may have a role in mate choice. Courtship calls are also given by the male of an established pair (Humphrey 1957), and the call additionally appears to serve in the maintenance of pair bonds. The precise role of vocalizations in pair formation in *Melanitta* is still unclear, but it seems possible the difference between *nigra* and *americana* in courtship calls affects mate choice of female *nigra* and *americana*.

The results of this study suggest that anatic calls can be useful in species-level taxonomy. The Velvet Scoter (*M. fusca*) complex would be an obvious candidate for vocal analysis. The three taxa in this complex are recognized on the basis of morphological differences, but their taxonomic status is controversial with up to three species being proposed (Stepanyan 1990, Livezey 1995, Sangster et al. 1999, Garner et al. 2004, Collinson et al. 2006). Some taxa in the *M. fusca* complex differ in tracheal anatomy (Miller 1926), which suggests there might be vocal differences in this taxonomic group as well (Johnsgard 1961, 1971).

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Veprintsev Phonoteca of Animal Voices or the Xeno-Canto data base, which enabled me to conduct this study.

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