Documentation of a Hybrid Bicknell's Thrush (Catharus bicknelli) × Veery (C. fuscescens) Using Vocalization and Genetic Data

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Documentation of a hybrid Bicknell's Thrush (*Catharus bicknelli*) × Veery (*C. fuscescens*) using vocalization and genetic data

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ABSTRACT—We combined data on morphology, behavior, and gene sequences to document the first known case of hybridization within the thrush genus *Catharus*. During June 2008 at a montane forest site in south-central Vermont, we observed a male bird that repeatedly exhibited song characteristics of both Bicknell's Thrush (*C. bicknelli*) and Veery (*C. fuscescens*). Handheld examination determined the bird to be a yearling male with plumage characteristics predominantly of Veery and morphometric traits within the ranges of both Bicknell's Thrush and Veery. While the hybrid vocalized only with Bicknell's Thrush calls, its songs were reminiscent of both Veery and a mixture of Bicknell's Thrush and Veery. Mitochondrial DNA (NADH dehydrogenase 2 and cytochrome *b* genes) revealed the bird's mother to be a Veery, and nuclear data (β-fibrinogen 7 and myoglobin 2 introns) revealed DNA of both Veery and Bicknell's Thrush, supporting Bicknell's Thrush as the father of the hybrid. This hybridization is notable given that Bicknell's Thrush and Veery generally breed in different habitat types at different elevations. This discovery is also important in light of the vulnerable conservation status of Bicknell's Thrush and recent declines in Veery populations across much of the species' breeding range. *Received 21 April 2016. Accepted 27 January 2017.*

Key words: *Catharus*, interspecific hybridization, thrush.

Documentación de un híbrido entre *Catharus bicknelli* × *C. fuscescens* utilizando datos genéticos y de vocalizaciones

RESUMEN (Spanish)—Para documentar el primer caso conocido de hibridación al interior del género *Catharus*, combinamos datos sobre morfología, comportamiento y secuencias de genes. Durante junio de 2008, en un sitio de bosque montano en el sur-centro de Vermont, observamos un macho que mostraba reiteradamente características de ambos, *Catharus bicknelli* y de *Catharus fuscescens*. Un examen en mano determinó que el ave era un macho del primer año con características preponderantemente de *C. fuscescens* y con caracteres morfométricos dentro de los rangos de ambas especies. Aunque el híbrido vocalizaba únicamente en respuesta a llamados de *C. bicknelli*, sus propios cantos se asemejan a ambos, el de *C. fuscescens*, y a una mezcla de *C. bicknelli* y *C. fuscescens*. El DNA mitocondrial (los genes NADH deshidrogenasa 2 y el citocromo b) revelan que la madre de este individuo era *C. fuscescens* y los datos nucleares (los intrones b-fibrinogen 7 y mioglobina 2) revelan DNA de ambas especies parentales, lo que apoya a *C. bicknelli* como el padre de este híbrido. Esta hibridación es notable, dado que *C. bicknelli* y *C. fuscescens* generalmente anidan en diferentes tipos de hábitats a diferentes elevaciones. Este descubrimiento es importante a la luz del estatus de conservación vulnerable de *C. bicknelli* y los declines recientes de *C. fuscescens* en gran parte de su rango reproductivo.

Palabras clave: *Catharus*, hibridización interespecífica, zorzal.

Hybridization between divergent forms is a widespread phenomenon and an important driver of speciation, especially in birds (Price 2008). Across the class Aves, the propensity for hybridization varies widely, with some families lacking any record of hybridization and others such as the wood warblers (family Parulidae) hybridizing more freely, including more than 50% of its species (Grant and Grant 1992, McCarthy 2006). Although the factors that promote natural hybridization between species are numerous, similarities in morphology, song type, geographical distribution, and genetics seem to be the most important determinants (Randler 2006). Reviews of hybridization studies indicate natural hybridization to be most common among closely related species, including sister taxa and species-rich groups that have undergone rapid adaptive radiations (Mallet 2007, Gholamhosseini et al. 2013). For such closely related species, reproductive isolating mechanisms and/or genetic incongruence may be insufficient to prevent introgression or to cause reduced hybrid vitality or fitness.

The thrush genus *Catharus* contains a dozen forest-dwelling New World species, including sedentary resident species distributed from Mexico to South America and migratory species that breed in North America and winter in the Neotropics (Clement 2000, Voelker et al. 2013). The Veery (*Catharus fuscescens*) and Bicknell's Thrush (*Catharus bicknelli*) are migratory species similar in morphology but distinguishable from one another based on vocal characteristics as well as non-overlapping breeding habitat and wintering ranges (Moskoff 1995, Rimmer et al. 2001, Bevier et al. 2005). Veery and Bicknell's Thrush are

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similar in size but differ primarily in the extent of spotting on the chest and coloration of upperparts (Fig. 1). These 2 long-distance migratory species are allopatric on their wintering grounds, with Bicknell's Thrush wintering in the Greater Antilles (Rimmer et al. 2001) and Veery wintering in northern and central South America (Remsen 2001, Bevier et al. 2005, Heckscher et al. 2011). The Bicknell's Thrush, classified as a globally Vulnerable species (BirdLife International 2016), occupies a limited and fragmented breeding range that includes portions of the Quebec and Maritime provinces of Canada and mountains in the northeastern United States. By contrast, the Veery, although declining across much of its range, has a much larger breeding area that encompasses most of southern Canada to regions of the northern, western, and eastern United States (Bevier et al. 2005, Townsend et al. 2015, BirdLife International 2016). While the 2 species overlap geographically during the breeding season, they generally occupy different habitat types, with Bicknell's Thrush breeding in high-elevation spruce–fir forest across the northeastern United States and at lower elevations in maritime fir forests in southeastern Canada (Rimmer et al. 2001) and Veery nesting in lower elevation hardwood forests or riparian areas, usually below 700 m (Noon 1981). Thus, niche partitioning by elevation and habitat seems to limit the degree of ecological overlap and opportunities for contact between the 2 species during their respective breeding seasons.

Evolutionarily, the relationship between Bicknell's Thrush and Veery has been examined and debated. By molecular phylogenetic analysis of mitochondrial genes, strong support existed for their status as sibling taxa, although Bicknell's Thrush was previously believed to be a sister taxon to Gray-cheeked Thrush (*Catharus minimus*) and was long considered a subspecies (Ouellet 1993, Marshall 2001, Rimmer et al. 2001, Outlaw et al. 2003, Winker and Pruett 2006). A recent study using 10 mitochondrial and nuclear genes provided the first fully resolved molecular phylogeny of *Catharus* with strong support for the sister taxa status of Bicknell's and Gray-cheeked Thrush, with Veery as the next closest relative (Voelker et al. 2013). This study placed the estimated divergence time between the Bicknell's/Gray-cheeked Thrush clade and Veery in the Pleistocene era ~0.8 million years before present (Voelker et al. 2013). The divergence of the migratory Bicknell's Thrush/Gray-cheeked Thrush/Veery (or *bicknelli*) clade from its presumed sedentary Central American–Mexican sister clade likely resulted from the reestablishment of migratory behavior in this clade of *Catharus* thrushes and subsequent colonization of North America (Voelker et al. 2013).

During 2008 field studies on the Vermont breeding grounds of Bicknell's Thrush, we encountered a male thrush singing the songs of both Bicknell's Thrush and Veery, although its plumage more closely resembled Veery. To investigate its ancestry, we captured the bird, took a blood sample, and examined distinct and independent molecular markers from the maternally inherited mitochondrial genome and the nuclear genome, which is biparentally inherited. If the individual was indeed a hybrid, we predicted it would be genetically intermediate between the parental species (Bicknell's Thrush and Veery) for the nuclear autosomal genes and identical to one of the parental species at the maternally inherited mitochondrial genes. We also report here on characteristics of plumage, morphometrics, and song and call type that lend support for the hybrid origin of this individual.

Methods

Field observations

During ongoing field work studying breeding songbirds on Stratton Mountain in southern Vermont (43°05′N, 72°55′W) at elevations from 1,000 to 1,200 m a.s.l. on 11 June 2008, we observed a thrush with an odd vocal repertoire. The individual was first detected and identified as a singing Veery, which is an unusual species at that elevation. A few minutes later, a Bicknell's Thrush was heard singing from the same location. Closer observations showed that the same individual was singing songs of both Bicknell's Thrush and Veery. It was captured in a mist net using a short playback of its own vocalizations obtained just moments prior to net deployment. As with all thrushes captured during this field study, we banded the bird with a US Fish and Wildlife Service aluminum leg band and a unique combination of colored leg bands. Approximately 50 μL of blood was obtained from the brachial vein and stored in a standard blood lysis buffer. We determined sex and age using plumage and morphological criteria

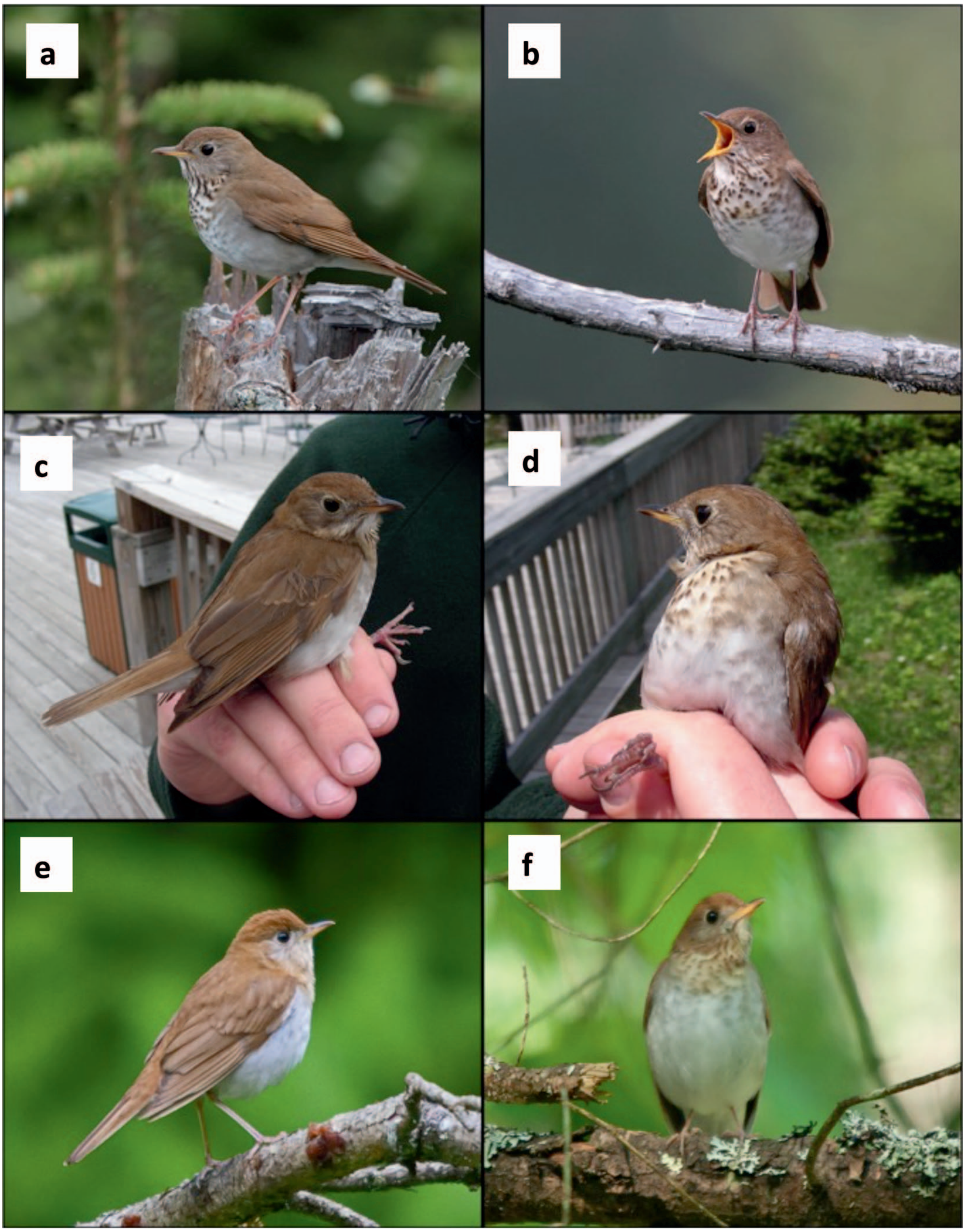

Figure 1. Photographs comparing the (a, b) side and front of *Catharus bicknelli* (8 Jun 2010, Whiteface Mt, Wilmington, NY; Jeff Nadler), (c, d) *C. bicknelli* × *C. fuscescens* (11 Jun 2008, Stratton Mountain, VT; K.P. McFarland), and (e, f) *C. fuscescens* (23 May 2012, Menden, VT, and 24 May 2010, Rutland, VT; Marvin Elliott).

(Pyle 1997) and collected standard morphometric data, including wing chord, primary formulae, and weight.

On 19 June (1:15 min) and 25 June (5:42 min), we recorded vocalizations of the individual using a Sony Hi-MD MZ-RH910 digital recorder with a Sennheiser ME66 shotgun microphone. Using the same equipment, we recorded calls and songs of Bicknell's Thrush on Mount Mansfield on 10 June and on Stratton Mountain on 25 July 2008, and of Veery in Woodstock, Vermont, on 27 June 2008. Spectrograms of the calls and songs of the putative hybrid and parental species were visualized using Raven Pro 1.5 and aligned on the same time and frequency axes (Bioacoustics Research Program 2014). Recordings were archived at the Cornell Lab of Ornithology Macaulay Library (ML204463, ML204464, ML204465, ML174416, ML174417, ML174418, and ML174419; http://macaulaylibrary.org).

DNA extraction and sequencing

Genomic DNA was isolated from the putative hybrid individual as well as from 2 individuals from each putative parent species (Bicknell's Thrush and Veery) using the Biosprint 96 System following manufacturer's guidelines (Qiagen); samples were stored at –20 °C until polymerase chain reaction (PCR) and sequencing. The remaining blood sample and DNA extract are archived at the Vermont Center for Ecostudies. We chose molecular markers that demonstrate fixed differences between Bicknell's Thrush and Veery for determination of the maternal and paternal origin of the putative hybrid individual. We amplified mitochondrial DNA from the NADH dehydrogenase 2 (ND2) gene using primers L5216 and H6313 (Sorenson et al. 1999) and for the cytochrome *b* (cyt*b*) gene using the primers Cytb1 and Cytb2 (Dumbacher et al. 2003). Nuclear DNA from the β-fibrinogen intron 7 (FIB7) was amplified using the primers FIB-B17U (Prychitko and Moore 1997) and FIBCathL1 (Winker and Pruett 2006) and for the myoglobin intron 2 (MB) using a nested PCR with primers MYO2 and MYO3F followed by primers MYOintF and MYOintR (Kimball et al. 2009, Voelker et al. 2013). Mitochondrial PCR products were amplified using a thermocycler regime of 95 °C for 7 min followed by 30 cycles of 95 °C for 30 s, 52 °C for 30 s, 72 °C for 30 s, and a final extension period of 72 °C for 7 min. The nuclear introns were amplified using a touch down PCR regime with an initial denaturation period of 95 °C for 7 min followed by 10 cycles of 95 °C for 30 s, 54 °C for 30 s, 72 °C for 30 s, 10 cycles of 95 °C for 30 s, 52 °C for 30 s, 72 °C for 30 s, 15 cycles of 95 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s, and a final extension period of 72 °C for 7 min. All PCR products were visualized by gel electrophoresis before purification using ExoSAP-IT (Affymetrix). PCR products were then cycle-sequenced using BigDye Terminator 3.1 (Applied Biosystems), the sequencing products cleaned with Sephadex G-50 columns, and then sequenced on an ABI 3130xl Sequencer at the Smithsonian Conservation Biology Institute's Center for Conservation Genomics. All sequences were manually edited in Sequencher 5.0 (Gene Codes Corporation).

Sequences from the putative hybrid individual were then compared to Bicknell's Thrush and Veery sequences obtained from our own lab work (for mitochondrial genes) and the Genbank database for all 4 genes (Table 1); these were aligned and visualized using Geneious. To ensure we did not accidentally amplify nuclear copies of the mitochondrial genes, we carefully inspected the mtDNA sequences for co-amplified peaks and translated them into amino acids to ensure open reading frames. We also compared our sequences to those from Gray-cheeked Thrush (*Catharus minimus*) from Genbank (Table 1) to ensure that this closely related species was not a parent of the hybrid.

Results

Plumage and morphology

When the bird was first observed and captured, its plumage appeared similar to that of a Veery. Handheld examination determined it to be a yearling (second-year) by buff-tipped greater coverts and rectrix shape (Pyle 1997; Fig. 1) and a male by cloacal protuberance (Pyle 1997). Its wing chord of 95.5 mm was intermediate for males of both species breeding in south-central Vermont: higher than the mean wing chord of male Bicknell's Thrush (91.0 mm, standard deviation [SD] 2.75 mm; range = 85.5–97.0, *n* = 60; Townsend et al. 2015) and lower than that of male Veery breeding in Vermont (96.5 mm [SD

Table 1. Genbank accession numbers for the hybrid individual from this study and sequences for the putative parental species (Bicknell's Thrush, Veery, and Gray-cheeked Thrush) used for maternal and parental identification. Genetic data were sourced from the mitochondrial cytochrome *b* (cyt*b*) and NADH dehydrogenase 2 (ND2) genes and nuclear β-finbrinogen 7 (FIB7) and myoglobin 2 (MB) genes. Genbank sequences for the putative parental species were initially reported in Outlaw et al. (2003), Winker and Pruett (2006), and Voelker et al. (2013).

Taxon	Cyt*b*	ND2	FIB7	MB
Putative hybrid	KY451621	KY451622	KY451623	KY451624
Bicknell's Thrush	AY049490, AF529137	AY049520	AY049475	KC693105
Veery	AY049495, AY049496	AY049519	AY049474	KC693109
Gray-cheeked Thrush	AY049502	AY049526	AY049481	KC693113

3.17 mm]; range = 89–102, *n* = 54; CCR, KPM, and S. Faccio, unpubl. data). The bird's weight of 31.4 g was higher than the mean mass of males of both species breeding in south-central Vermont. Male Bicknell's Thrush had a mean weight of 27.5 g (SD 1.95 g; range = 21.0–32.4, *n* = 62; Townsend et al. 2015), whereas male Veery breeding in Vermont had mean weights of 30.2 g (SD 1.37 g; range = 27.0–32.2, *n* = 62; CCR, KPM, and S. Faacio, unpubl. data). Following Pyle's (1997) terminology, primary formulae were: P8–P6 = 6.38, P8–P5 = 13.43, and P6 was slightly emarginated; these also fall within the range for males of both species (Pyle et al. 1997, Frey et al. 2008). Overall, the bird's plumage resembled that of Veery far more than that of Bicknell's Thrush (Fig. 1). We released the bird after collecting blood samples.

The bird was subsequently observed and heard on multiple dates through 25 June, and we recaptured it in a mist net on 19 June. During the 2-week period we observed the bird, it moved and vocalized widely over our ~25 ha study site at elevations ranging from 1,100 to 1,200 m in montane fir forest, the typical breeding habitat of Bicknell's Thrush (Rimmer et al. 2001). We obtained no evidence that the bird was associated with an active nest, and its apparent departure in late June led us to conclude it likely did not breed.

Vocalizations

The song and calls of Bicknell's Thrush and Veery are distinct from one another. Vocalizations of the hybrid individual were first recognized as a mixed Bicknell's Thrush and Veery song on 11 June. During subsequent observations and recordings, the bird was found to sing either a complete Veery song or a mixed song (Fig. 2). The hybrid sang 51 times during 6:57 minutes of recording on 19 and 25 June, with only 27% identified as the mixed song. It never repeated the mixed song in sequence, but often delivered the Veery song in rapid succession. Only Bicknell's Thrush calls were given (*n* = 30, 6:57 min.), including one *growl* call type (Fig. 3). Bicknell's Thrush calls have a distinctive *peer* verses the *veer* call of Veery and normally range from 3.2 to 5.8 KHz (Ouellet 1993), whereas Veery calls are of lower frequency, ranging from 4 KHz down to ~1.5 KHz (Bevier et al. 2005).

Genetic analyses

From the putative hybrid individual we successfully amplified and aligned to sequences of Bicknell's Thrush and Veery ~280 base pairs (bp) of the cyt*b* gene, 700 bp of the ND2 gene, 880 bp of the FIB7 intron, and 340 bp of the MB intron. For both mitochondrial genes (cyt*b* and ND2), which are inherited maternally, sequences from the putative hybrid individual identified 100% to sequences of Veery for all nucleotide positions that displayed fixed differences between individuals of the 2 parental species (*n* = 14), indicating that the female parent of this individual was a Veery (Table 2). In contrast to mitochondrial DNA, nuclear DNA is inherited biparentally and holds the potential to resolve both male and female parentage of an individual. Because general nuclear DNA evolves at a slower rate than mitochondrial DNA, however, it offers a decreased degree of divergence between species compared to mitochondrial DNA and thus fewer fixed nucleo-

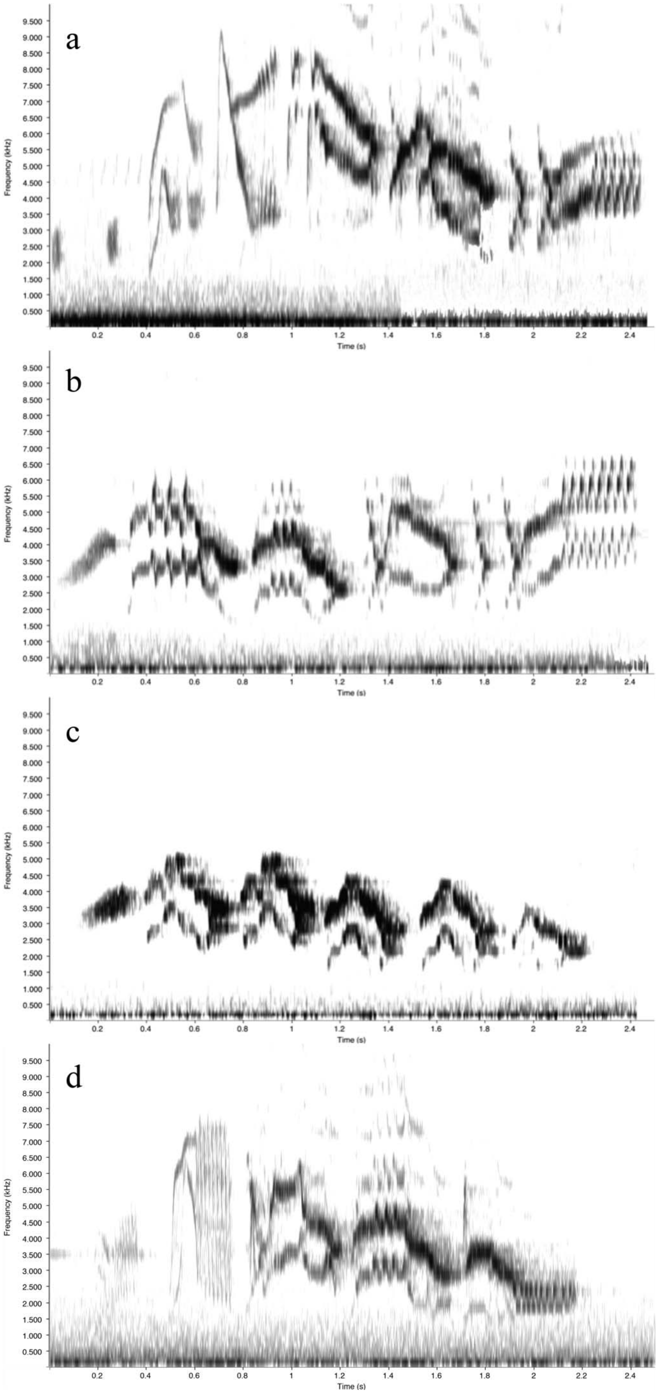

Figure 2. Sonograms (frequency vs. time) of songs of (a) *Catharus bicknelli*, (b) *C. bicknelli* × *fuscescens* mixed type, (c) *C. fuscescens*, and (d) *C. bicknelli* × *fuscescens* Veery song type. Songs of *C. bicknelli* were recorded on Mt. Mansfield, VT, on 12 June 2008, *C. bicknelli* × *fuscescens* on Stratton Mountain on 25 June 2008, and *C. fuscescens* in Woodstock, VT, on 27 June 2008. All recordings were made using a Sony Hi-MD MZ-RH910 with a Sennheiser ME66 shotgun microphone. Recordings were archived at the Cornell Lab of Ornithology Macaulay Library (ML174416, ML174417, and ML174419; http://macaulaylibrary.org).

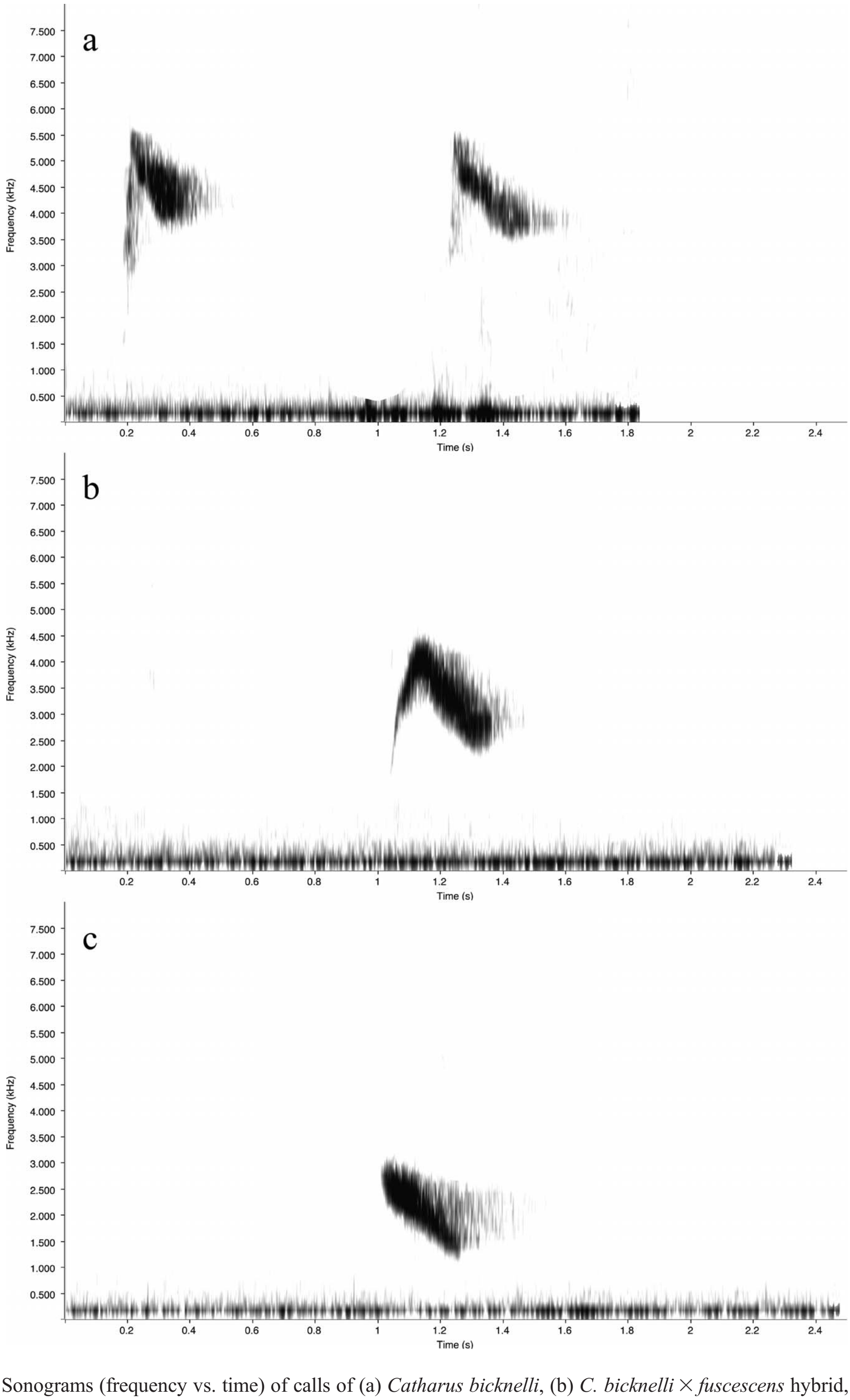

Figure 3. Sonograms (frequency vs. time) of calls of (a) *Catharus bicknelli*, (b) *C. bicknelli* × *fuscescens* hybrid, and (c) *C. fuscescens*. Call of *C. bicknelli* and *C. bicknelli* × *fuscescens* were recorded on Stratton Mountain, VT, on 25 July 2008 and 25 June 2008, respectively; and *C. fuscescens* in Woodstock, VT, on 27 June 2008. All recordings were made using a Sony Hi-MD MZ-RH910 with a Sennheiser ME66 shotgun microphone. Recordings were archived at the Cornell Lab of Ornithology Macaulay Library (ML174416, ML174417, and ML174418; http://macaulaylibrary.org).

Table 2. Variable nucleotide sites ($n = 19$) between sequences from the 2 putative parent species (Bicknell's Thrush and Veery) for the mitochondrial NADH dehydrogenase 2 (ND2) and cytochrome *b* (cyt*b*) genes and nuclear β-fibrinogen intron 7 (FIB7) and myoglobin intron 2 (MB) and nucleotides at these sites for the putative hybrid individual in this study. Site numbers relative to the start of each gene are also provided.

	ND2													Cyt*b*	FIB			MB	
	28	36	108	288	294	316	321	393	398	450	495	550	627	312	816	858	869	697	700
Bicknell's Thrush	G	C	T	A	A	T	A	C	C	T	A	A	T	T	A	T	A	C	G
Veery	A	T	C	G	G	C	G	T	T	C	G	G	A	C	T	C	G	T	C
Putative Hybrid	A	T	C	G	G	C	G	T	T	C	G	G	A	C	A/T	T/C	A/G	C/T	G/C

tide differences, especially for species as recently diverged as Bicknell's Thrush and Veery (Brown et al. 1979, Voelker et al. 2013). For the nucleotide positions that displayed fixed differences between Bicknell's Thrush and Veery for the nuclear intron FIB7 ($n = 3$) and the nuclear intron MB ($n = 2$), the putative hybrid's sequence displayed 2 bases on the chromatogram at each of these sites, with a nucleotide identifying to both Bicknell's Thrush and Veery (Table 2). This sequence did not present 2 bases at any additional nucleotide positions. Because a Bicknell's Thrush and Veery parental origin for this individual cannot be ruled out, the nuclear data suggest Bicknell's Thrush as the father parent. These data also suggest that the bird is likely a first generation (or F1) hybrid. Together the mitochondrial and nuclear DNA support the origin of this hybrid individual from an interspecific mating involving a male Bicknell's Thrush and a female Veery.

Discussion

Using morphological, behavioral, and genetic data, we provide evidence for a hybridization event between Bicknell's Thrush and Veery. This is the first known incidence of hybridization within the genus *Catharus*, despite numerous independent studies of *Catharus* species over many decades (Dilger 1956, Rimmer et al. 2001, Bevier et al. 2005). Genetic mixing has been documented to occur rarely between divergent populations within *Catharus* species, including Swainson's Thrush (*Catharus swainsoni*) and Hermit Thrush (*Catharus guttatus*), with divergent populations within these species likely arising during the Pleistocene and exhibiting different migratory routes (Ruegg et al. 2006, Alvarado et al. 2014, Delmore and Irwin 2014). Among species of the thrush family, which is diverse and distributed worldwide, hybridization has been documented in nature between species within the genera *Luscinia*, *Monticola*, *Myadestes*, *Myiophonus*, *Oenanthe*, *Phoenicurus*, *Saxicola*, *Sialia*, *Tarsiger*, *Turdus*, and *Zoothera* (McCarthy 2006). Therefore, it is not entirely unexpected to find hybridization between species within the genus *Catharus*.

The evolutionary history and close phylogenetic affinity of Bicknell's Thrush and Veery may explain why they have not fully developed mechanisms for species recognition and reproductive isolation. Divergences in the *bicknelli* clade, which includes Bicknell's Thrush, Gray-cheeked Thrush, and Veery, date back to 0.41 and 0.8 million years ago and support a Pleistocene divergence between these migratory *Catharus* species resulting from isolation in breeding refugia or in areas south of the edge of ice sheets (Voelker et al. 2013). Gradually, these 3 species evolved allopatric wintering ranges, although they retained some degree of overlap in their breeding ranges. Aggressive behavior among *Catharus* thrush species, as well as breeding habitat differences and other factors, may have then led to the further differentiation of these species upon secondary contact after the Pleistocene, despite their partial breeding range overlap (Dilger 1956). The breeding habitats of Bicknell's Thrush and Veery differ markedly and consistently across their respective ranges; primary differences include elevation, tree species composition, understory density, and moisture regime (Bevier et al. 2005, Townsend et al. 2015). Veery prefer wet-mesic, deciduous, or mixed forest, especially in late shrub or early successional stages, at low- and mid-elevations, often in riparian areas (Bevier et al. 2005). Bicknell's Thrush is more narrowly specialized on montane and maritime forests dominated by balsam fir (*Abies balsamea*), with lesser amounts of red spruce (*Picea rubens*), black spruce (*P. mariana*), white birch (*Betula papyrifera* var. *cordifolia*), mountain ash (*Sorbus* sp.), and other hardwood species (Townsend et al. 2015). Bicknell's Thrush often inhabits recently disturbed areas undergoing vigorous succession, characterized by standing dead conifers and dense regrowth of balsam fir. Despite these elevational and ecological differences in breeding habitats, genetic and morphological similarities among *Catharus* thrushes owing to their relatively recent speciation may facilitate interbreeding.

Other behavioral and ecological variables may have also been at play in promoting hybridization between a female Veery and male Bicknell's Thrush. Long-term studies of breeding Bicknell's Thrush have revealed a pronounced and unusual adult sex bias of 2.5:1 male:female ($n = 1{,}231$, 1993–2007; Townsend et al. 2009). Both male Bicknell's Thrush and Veery tend to mate with multiple females during the breeding season (Rimmer et al. 2001, Goetz et al. 2003, Halley et al. 2016) and thus may be prone to explore extra pair copulation opportunities. Male Bicknell's Thrush regularly venture downslope early in the breeding season, probably to escape bad weather and poor feeding conditions at higher elevations (Rimmer et al. 2001), so the possibility of encounter between a male Bicknell's Thrush and female Veery is not unlikely. Presumably, a female Veery in late May or early June may be receptive to mating because they arrive back a week or 2 earlier and initiate breeding earlier than most Bicknell's Thrush females (Kibbe 2013). The opposite scenario may also have occurred on Stratton Mountain, with the female Veery venturing upslope into Bicknell's Thrush habitat; Veery occur (albeit rarely) at elevations up to 1,000 m during the breeding season, although breeding has not been confirmed (KPM and CCR, pers. obs.). Limited favorable breeding habitat has been shown to constrain mate choice and potentially lead to hybridization events in birds (Price 2008). Thus, if a female Veery occurred at higher elevations in the absence of male conspecifics but in the presence of male Bicknell's Thrush, her standards for mate selection might become compromised. Additional investigation of hybridization between these 2 *Catharus* species is needed to better understand its frequency and causes.

Global climate change has been suggested to drive hybridization between closely related species (Garroway et al. 2010) and has been identified as an imminent threat to the coniferous montane forests in which Bicknell's Thrush breed (Rodenhouse et al. 2008, Freeman and Montgomery 2016). As the breeding habitat and current breeding range of Bicknell's Thrush contract via predicted upslope migration of the balsam fir climatic envelope (Rodenhouse et al. 2008), and as northern hardwoods forests move upslope (Beckage et al. 2008), contacts between Bicknell's Thrush and Veery would be predicted to increase. Results of multi-year surveys of breeding songbirds across an elevational gradient in the White Mountains of New Hampshire conform to this prediction. The upper elevational boundary of 9 of 16 low-elevation species shifted upslope by an average of 99 m (DeLuca and King 2016); however, 9 of 11 high-elevation species shifted downslope an average of 19 m, including 17.4 m for Bicknell's Thrush. For North American wood warblers, Willis et al. (2014) found that the propensity for hybridization decreased with range size and increased with the degree of breeding sympatry, the degree of co-occurrence of heterospecifics during the breeding season, and the phylogenetic closeness of species. By this assessment, the likelihood of hybridization between Bicknell's Thrush and Veery will increase over time, given that the current breeding range of Bicknell's Thrush is restricted and contracting, phylogenetic distance between the 2 species is relatively small, and their breeding ranges are sympatric.

The discovery of hybridization between Bicknell's Thrush and Veery raises many questions, including how frequently the 2 species hybridize. Although hybridization has not previously been documented between *Catharus* species, it may be that hybridizations within this genus have gone largely undetected because of similarities in plumage and morphology (Bevier et al. 2005). Hybridization may be more cryptic and difficult to detect for bird species that have similar plumage and morphology (Willis et al. 2014, Ralston et al. 2015). In this study, we were only alerted to an individual's possible hybrid origin by our field observations of its mixed-species song type. Further, hybridization between Bicknell's Thrush and Veery, species that occupy different elevations across most of their respective breeding ranges, indicates the potential role of climate-induced shifts and contractions in breeding habitat, as well as existing biases in breeding adult male:female ratios, in increasing the propensity for hybridization. Finally, in light of Bicknell's Thrush's classification as a globally Vulnerable species (BirdLife International 2016) and documented declines of Veery populations across much of its breeding range, our results emphasize the importance of more closely investigating hybridization between these and other *Catharus* species.

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Literature cited

Alvarado AH, Fuller TL, Smith TB. 2014. Integrative tracking methods elucidate the evolutionary dynamics of a migratory divide. Ecology and Evolution. 4:3456–3469.

Beckage B, Osborne B, Galvin DG, Pucko C, Siccama T, Perkins T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences USA. 105:4197–4202.

Bevier LR, Poole AF, Moskoff W. 2005. Veery (*Catharus fuscescens*). In: Poole A, editor. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology. https://birdsna.org/Species-Account/bna/species/veery/

BirdLife International. 2016. *Catharus bicknelli*. The IUCN Red List of threatened species 2016: e.T22728467A94987334. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22728467A94987334.en

Brown WM, George M Jr, Wilson AC. 1979. Rapid evolution of animal mitochondrial DNA. Proceedings of the National Academy of Sciences USA. 76:1967–1971.

Clement P. 2000. Thrushes. Princeton (NJ): Princeton University Press.

Delmore KE, Irwin DE. Hybrid songbirds employ intermediate routes in a migratory divide. Ecology Letters. 17:1211–1218.

Dilger WC. 1956. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. Auk 73:313–353.

Dumbacher JP, Pratt TK, Fleischer RC. 2003. Phylogeny of the owlet nightjars (Aves: Aegothelidae) based on mitochondrial DNA sequence. Molecular Phylogenetics and Evolution. 29:540–549.

Freeman BG, Montgomery G. 2016. Interspecific aggression by the Swainson's Thrush (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush (*Catharus bicknelli*) in the Adirondack Mountains. Condor: Ornithological Applications. 118:169–178.

Frey SJK, Rimmer CC, McFarland KP, Menu S. 2008. Identification and sex determination of Bicknell's Thrushes using morphometric data. Journal of Field Ornithology. 79:408–420.

Garroway CJ, Bowman J, Cascaden TJ, Holloway GL, Mahan CG, et al. 2010. Climate change induced hybridization in flying squirrels. Global Change Biology. 16:113–121.

Gholamhosseini A, Vardakis M, Allabadian M, Nijman V, Vonk R. 2013. Hybridization between sister taxa versus non-sister taxa: a case study in birds. Bird Study. 60:195–201.

Goetz JE, McFarland KP, Rimmer CC. 2003. Multiple paternity and multiple male feeders in Bicknell's Thrush (*Catharus bicknelli*). Auk. 120:1044–1053.

Grant PR, Grant RB. 1992. Hybridization of bird species. Science. 256:193–197.

Halley MR, Heckscher CM, Kalavacharla V. 2016. Multi-generational kinship, multiple mating, and flexible modes of parental care in a breeding population of the Veery (*Catharus fuscescens*), a trans-hemispheric migratory songbird. PLOS ONE. doi:10.1371/journal.pone.0157051

Heckscher CM, Taylor SM, Fox JW, Afanasyev V. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. Auk. 128:531–542.

Kibbe DP. 2013. Veery (*Catharus fuscescens*). In: Renfrew RB, editor. The second atlas of breeding birds of Vermont. Lebanon (NH): University Press of New England. p. 324–325.

Kimball RT, Braun EL, Barker FK, Bowie RCK, Braun MJ, et al. 2009. A well-tested set of primers to amplify regions spread across the avian genome. Molecular Phylogenetics and Evolution. 50:654–660.

Mallet J. 2007. Hybrid speciation. Nature. 446:279–283.

Marshall JT. 2001. The Gray-cheeked Thrush, *Catharus minimus*, and its New England subspecies, Bicknell's Thrush, *Catharus minimus bicknelli*. Cambridge (MA): Nuttall Ornithological Club.

McCarthy E. 2006. Handbook of avian hybrids of the world. New York: Oxford University Press.

Moskoff W. 1995. Veery (*Catharus fuscescens*). In: Poole A, editor. Birds of North America. Ithaca (NY): Cornell

Lab of Ornithology. https://birdsna.org/Species-Account/bna/species/veery/

Noon BR. 1981. The distribution of an avian guild along a temperate gradient: the importance and expression of competition. Ecological Monographs. 51:105–124.

Ouellet H. 1993. Bicknell's Thrush: taxonomic status and distribution. Wilson Bulletin. 105:545–572.

Outlaw DC, Voelker G, Mila B, Girman DJ. 2003. Evolution of long-distance migration in and historical biogeography of *Catharus* thrushes: a molecular phylogenetic approach. Auk. 120:299–310.

Price T. 2008. Speciation in birds. Greenwood Village (CO): Roberts and Co.

Prychitko TM, Moore WS. 1997. The utility of DNA sequences of an intron from the β-fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution. 8:193–204.

Pyle P. 1997. Identification guide to North American Birds. Bolinas (CA): Slate Creek Press.

Ralston J, Ermacor DA, Kirchman JJ. 2015. A new wood warbler hybrid (*Oreothlypis celata* × *O. ruficapilla*) from the Adirondack mountains, New York. Wilson Journal of Ornithology. 127:21–28.

Randler C. 2006. Behavioural and ecological correlates of natural hybridization in birds. Ibis. 148:459–467.

Remsen JV. 2001. True winter range of the Veery (*Catharus fuscescens*): lessons for determining winter ranges of species that winter in the tropics. Auk. 118:838–848.

Rimmer CC, McFarland KP, Ellison WG, Goetz JE. 2001. Bicknell's Thrush (*Catharus bicknelli*). In: Poole A, editor. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology. https://birdsna.org/Species-Account/bna/species/bicthr/

Rodenhouse N, Matthews SN, McFarland KP, Lambert JD, Iverson LR, et al. 2008. Potential effects of climate change on birds of the Northeast. Mitigation and Adaptation Strategies for Global Change. 13:517–540.

Rounds RC, Munro HL. 1982. A review of hybridization between *Sialia sialis* and *Sialia currucoides*. Wilson Bulletin. 94:219–223.

Ruegg KC, Hijmans RJ, Moritz C. 2006. Climate change and the origin of migratory pathways in the Swainson's Thrush, *Catharus ustulatus*. Journal of Biogeography. 33:1172–1182.

Sorenson MD, Ast JC, Dimcheff DE, Yuri T, Mindell DP. 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Molecular Phylogenetics and Evolution. 12:105–114.

Townsend JM, McFarland KP, Rimmer CC, Ellison WG, Goetz JE. 2015. Bicknell's Thrush (*Catharus bicknelli*). In: Poole A, editor. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology. https://birdsna.org/Species-Account/bna/species/bicthr/

Townsend JM, Rimmer CC, McFarland KP. 2009. Investigating the limiting factors of a rare, vulnerable species: Bicknell's Thrush. Proceedings of the fourth International Partners in Flight Conference: tundra to tropics; p. 91–95.

Voelker G, Bowie RCK, Klicka J. 2013. Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. Molecular Ecology. 22:3333–3344.

Willis PM, Symula RE, Lovette IJ. 2014. Ecology, song similarity and phylogeny predict natural hybridization in an avian family. Evolutionary Ecology. 28:299–322.

Winker K, Pruett CL. 2006. Seasonal migration, speciation, and morphological convergence in the genus *Catharus* (Turdidae). Auk. 123:1052–1068.