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SPECIAL FEATURE: Species Limits and Taxonomy in Birds

Systematics and conservation of an endemic radiation of *Accipiter* hawks in the Caribbean islands

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ABSTRACT

More than one-third of the bird species found in the Caribbean are endemic to a set of neighboring islands or a single island. However, we have little knowledge of the evolutionary history of the Caribbean avifauna, and the lack of phylogenetic studies limits our understanding of the extent of endemism in the region. The Sharp-shinned Hawk (*Accipiter striatus*) occurs widely across the Americas and includes 3 endemic Caribbean taxa: *venator* on Puerto Rico, *striatus* on Hispaniola, and *fringilloides* on Cuba. These island populations have undergone extreme declines presumably due to ecosystem changes caused by anthropogenic factors, as well as due to severe hurricanes. Sharp-shinned Hawks, in general, and Caribbean Sharp-shinned Hawks, in particular, have not been placed in a modern phylogenetic context. However, the island taxa have historically been presumed to have some ongoing gene flow with mainland populations. Here we sequenced ultraconserved elements (UCEs) and their flanking regions from 38 samples, focusing on Caribbean taxa. Using a combination of UCEs, mitochondrial genome sequences, and single-nucleotide polymorphisms, we investigated the phylogenetic relationships among Caribbean lineages and their relationships to mainland taxa. We found that Caribbean Sharp-shinned Hawks are reciprocally monophyletic in all datasets with regard to mainland populations and among island taxa (with no shared mtDNA haplotypes) and that divergence in the NADH dehydrogenase 2 gene (ND2) between these mainland and island groups averaged 1.83%. Furthermore, sparse non-negative matrix factorization (sNMF) analysis indicated that Hispaniola, Puerto Rico, and mainland samples each form separate populations with limited admixture. We argue that our findings are consistent with the recognition of the 3 resident Caribbean populations as species-level taxa because nuclear and mitochondrial genetic data indicate reciprocal monophyly and have species-level divergences, there is no sharing of mitochondrial haplotypes among or between island taxa and those on the mainland; and they are diagnosable by plumage.

Keywords: Accipiter striatus, Cuba, Hispaniola, island radiation, morphometrics, Puerto Rico, Sharp-shinned Hawk, taxonomy, ultraconserved elements

LAY SUMMARY

- Using ultraconserved elements we reconstructed relationships among Sharp-shinned Hawk (*Accipiter striatus*) taxa in the Caribbean and mainland.
- Sharp-shinned Hawks in the Caribbean have undergone population declines and, in Puerto Rico, they are federally listed as endangered.
- Our analysis of both nuclear and mitochondrial genetic data supports the recognition of each Caribbean island population of Sharp-shinned Hawk as an endemic species.

Sistemática y conservación de una radiación endémica de los gavilanes Accipiter en las islas del Caribe

RESUMEN

Más de un tercio de las especies de aves que se encuentran en el Caribe son endémicas, ya sea a un grupo o a una sola isla. Sin embargo, nuestro conocimiento sobre la historia evolutiva de la avifauna del Caribe aún es básico y la falta de estudios filogenéticos recientes limita nuestro entendimiento de la magnitud del endemismo de la región. El Gavilán estriado (*Accipiter striatus*) se distribuye ampliamente a través de las Américas, incluyendo tres subespecies endémicas al Caribe: *venator* en Puerto Rico, *striatus* en la isla de la Española y *fringilloides* en Cuba. Las poblaciones del Caribe han sufrido disminuciones extremas, presuntamente por cambios en los ecosistemas debido a factores antropogénicos, así como consecuencia de huracanes severos. El Gavilán estriado en lo general y sus poblaciones del Caribe en lo particular no han sido estudiados desde un contexto filogenético moderno. Sin embargo, históricamente se ha asumido que los taxones insulares tienen un flujo genético con las poblaciones continentales. En el presente estudio secuenciamos elementos ultra-conservados (UCEs) y sus regiones flanqueantes de 38 muestras, enfocándonos principalmente en las poblaciones del Caribe. Usamos una combinación de datos generados por UCE, secuencias de genoma mitocondrial y polimorfismos de nucleótidos sencillos (SNPs) para investigar la relación filogenética entre los linajes del Caribe al igual que sus relaciones con las poblaciones continentales. Nuestros resultados sugieren que las poblaciones de Gavilán estriado del Caribe son recíprocamente monofiléticas entre sí y con respecto a las poblaciones continentales (no comparten haplotipos mtDNA) en todos nuestros conjuntos de datos y los niveles de divergencia en el gen 2 (ND2) de la deshidrogenasa NADH promedian 1.83% entre los grupos continentales e insulares. Adicionalmente, el análisis sNMF sugiere que las muestras de la Española, Puerto Rico y el continente forman cada una poblaciones separadas con una mezcla genética limitada. Por ello sugerimos que nuestros resultados son consistentes al reconocer a las tres poblaciones residentes del Caribe como especies diferentes, debido a que los ambos datos genéticos nucleares y mitocondriales indican reciprocidad monofilética, y divergencia a nivel de especie, no comparten haplotipos mitocondriales entre los taxones insulares o entre estos y los taxones continentales; y aparentemente son diagnosticables por plumaje.

Palabras clave: radiación insular, taxonomía, Gavilán estriado, *Accipiter striatus*, morfometría, Puerto Rico, Cuba, La Española, elementos ultraconservadores

INTRODUCTION

The origins of many Caribbean avian taxa can be traced to multiple and independent colonization events from the nearby continental landmasses (Bond 1978, Ricklefs and Bermingham 1997). The geological and evolutionary history of isolation has produced a diverse Caribbean avifauna (~700 species) that includes 7 endemic families (Hedges 2001, Woods and Sergile 2009, Kirwan et al. 2019). This diversity presents unique conservation challenges and holds great potential for evolutionary and ecological research (Ricklefs and Bermingham 1997).

The avifauna of the Caribbean remains poorly studied relative to continental faunas (Devenish-Nelson et al. 2019). The extent of species-level endemism in the region is often underappreciated and poorly understood. In recent decades, modern approaches to identify taxonomic limits have often resulted in the splitting of species complexes (e.g., Greater Antillean Oriole [*Icterus dominicensis*], Western Spindalis [*Spindalis zena*], and Adelaide's Warbler [*Setophaga adelaidae*]). Also, several endemic Caribbean populations are evidently distinct enough from widespread mainland species complexes to justify elevating them to species rank (e.g., Hispaniolan Crossbill [*Loxia megaplaga*] and Bahama Warbler [*Setophaga flavescens*]; Lovette and Bermingham 1999, Banks et al. 2000, 2003, Parchman et al. 2006, Price and Hayes 2009, Sturge et al. 2009, Chesser et al. 2010, 2011, McKay et al. 2010). However, species limits for most avian complexes in the region remain poorly explored.

The endemic avifauna of the Caribbean islands faces a combination of natural and anthropogenic threats. Hurricanes can have immediate and long-lasting impacts (e.g., changing the forest structure and the direction of forest succession) that influence the distribution and abundance of species and composition of biotic communities (Brokaw and Grear 1991, Brokaw and Walker 1991, Wiley and Wunderle 1993, Boose et al. 2004, Flynn et al. 2010, Wunderle and Arendt 2011). Hurricanes can trigger synergistic indirect effects (e.g., disease, parasitism, and predation) that negatively affect some species, especially those with low populations or more restricted habitat and dietary requirements (White et al. 2005, Beissinger et al. 2008, Wunderle and Arendt 2011, Gallardo and Vilella 2017). Although coastal species can show resilience to hurricanes (Field et al. 2019), species that depend on late-successional terrestrial habitats, such as mature forests, are particularly vulnerable. Recent hurricanes have been implicated in the likely extinctions of the Grand Bahama Brown-headed Nuthatch (*Sitta pusilla insularis*) and Cozumel Thrasher (*Toxostoma guttatum*), presumably by exacerbating pre-existing anthropogenic causes of decline, including invasive species and habitat fragmentation (Howell 2004). Given that many Caribbean bird populations are

threatened or endangered, it is important and necessary to test long-standing hypotheses about whether isolated island populations are divergent and/or diagnosable from closely related mainland populations. These data inform taxonomy and are necessary for ensuring that insular populations are given appropriate levels of legal protection and attention by conservationists.

The Sharp-shinned Hawk (*Accipiter striatus*, Vieillot 1807), the focus of this study, is a widespread species complex with 3 Caribbean taxa that were originally diagnosed from mainland forms on the basis of their smaller size and differences in plumage color (Wetmore 1914, Gallardo and Thorstrom 2019). Caribbean specimens are rare in museum collections and Wetmore was limited to examining a handful of specimens. However, living individuals from the Caribbean are distinct from mainland forms in both plumage and size (J. Gallardo and R. Thorstrom personal observation). It is believed that all endemic Caribbean taxa of Sharp-shinned Hawk are susceptible to population declines, as evidenced by naturally low population sizes and association with naturally fragmented montane habitats (Delannoy 1997, Gallardo and Thorstrom 2019). Populations have declined steeply during the last century and their current status remains unstable and uncertain. For example, the Puerto Rican taxon, *A.* [*s.*] *venator* Wetmore 1914 had a reported decline of 37.5% from 1985 (n = 240 individuals) to 1991–1992 (n = 150, and only 82 actually spotted) with a more severe decline in more isolated forest reserves (Delannoy 1997). As a result of this trend, this taxon (currently considered a subspecies) was listed as endangered by the United States Fish and Wildlife Service in September 1994 (Cruz and Delannoy 1983, Delannoy 1997). The ultimate cause of the decline is unclear, but it has been attributed to a suite of factors including changes in the forest composition and structure by hurricanes (Hugo in 1989 and Georges in 1998), high rates of ectoparasitism by *Philornis* spp. (Diptera, Muscidae), hunting pressure, and the increased prevalence of Pearly-eyed Thrasher (*Margarops fuscatus*), a predator of *A. striatus* eggs and nestlings (Wiley 1986, Delannoy and Cruz 1991, Arendt 2006). In 2017, Hurricane Maria caused widespread devastation on Puerto Rico, resulting in a reduction of 80–90% of the canopy cover in Toro Negro Forest (the last stronghold of the Puerto Rican taxon) and the surrounding areas (*fide* G. Hernández in Gallardo and Vilella 2017). This event devastated the remaining habitat and reduced the known population to 19 individuals (R. Thorstrom personal observation). During the following breeding season, The Peregrine Fund began hatching wild-laid eggs in captivity and hacking (a process by which young birds are provided food and shelter for a short period of time after release into the wild) the resultant fledglings to increase nesting success of the few remaining wild pairs, an expensive and labor-intensive process.

Two additional Sharp-shinned Hawk endemic subspecies, *A.* [*s.*] *fringilloides* Vigors, 1827 from Cuba and *A.* [*s.*] *striatus* from Hispaniola, face similar threats, but have not been listed as taxa of conservation concern, possibly in part due to a widespread perception that the Caribbean taxa are not distinct because of presumed ongoing gene flow with the (migratory) mainland form (Bildstein 2004, p. 94). Nevertheless, Gundlach's Hawk (*A. gundlachi*), an endemic Cuban raptor, is listed as endangered by the IUCN and the Cuban government, despite the fact that it is more common and widespread than the Cuban Sharp-shinned Hawk (Garrido 1985, González et al. 2012, BirdLife International 2017). Conservation listing is an expensive and arduous process that is made more complicated by disagreements among taxonomists over species concepts (Haig and D'Elia 2010). Often, allocation of conservation funding and protection efforts do not necessarily reflect conservation priorities. Public awareness and accurate or updated population trends have a great impact on the final expenditure pattern for conservation and recovery efforts (Restani and Marzluff 2002, Luther and Gentry 2019). Around 60% of species and subspecies listed in the Endangered Species Act are island endemics; however, they receive an order of magnitude less funding and have significantly more conservation actions recommended but not implemented when compared to mainland federally listed taxa (Luther and Gentry 2019). Furthermore, the delimitation methods used to distinguish and classify species-rank taxa have been shown to have repercussions on protection and conservation actions (Morrison et al. 2009).

Thus, given the lack of available information on taxonomic limits of the Caribbean Sharp-shinned Hawk taxa, and their dire conservation status, it is paramount to assess their phylogenetic and taxonomic status relative to the mainland forms. It is also critical to identify any potential population connectivity (i.e. gene flow) between forest fragments on individual islands and/or among islands. To accomplish this, we sequenced the flanking regions of ultraconserved elements (UCEs) from tissues, blood samples, and toepad samples of all 3 Caribbean taxa. We also assembled mitochondrial genomes from off-target reads, constructed haplotype networks of the mitochondrial NADH dehydrogenase 2 gene (ND2), and called single-nucleotide polymorphisms (SNPs) from the UCE contigs to assess population structure. Finally, we measured wing length (WL) in a sample of museum specimens to test for morphometric differences among and between Caribbean and mainland taxa. These data greatly expand our knowledge of phylogenetic relationships and species limits among these taxa and highlight the immediate need for targeted conservation action.

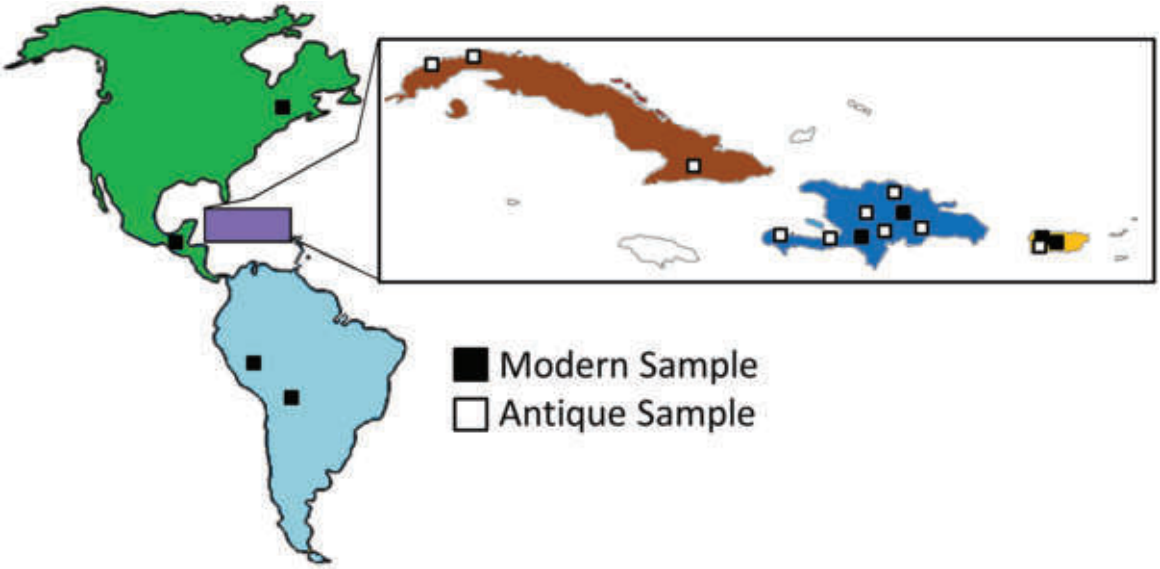

FIGURE 1. Collection localities of specimens for which UCEs were sequenced for this study. White squares denote toepad samples and black squares denote tissue or blood samples. Geographic regions are denoted with the following colors: Green = *A.* [*s.*] *velox* North America; Light blue = *A.* [*s.*] *ventralis and A.* [*s.*] *erythronemius* South America; Brown = *A.* [*s.*] *fringilloides* Cuba; Dark blue = *A.* [*s.*] *striatus* Hispaniola; Yellow = *A.* [*s.*] *venator* Puerto Rico. Note that this color scheme is used consistently throughout the figures in this article.

METHODS

DNA Extraction and Sequencing

We extracted DNA from muscle tissue (n = 1), blood (n = 23), and toepads (n = 11) collected from Caribbean Sharp-shinned Hawks (Figure 1 and Table 1). We also extracted DNA from 4 mainland hawks: *A.* [*s.*] *velox* (Wilson 1812) of North America; *A.* [*s.*] *chionogaster* (Kaup 1852) of Central America; *A.* [*s.*] *ventralis* (Sclater 1866) of northern South America; and *A.* [*s.*] *erythronemius* (Kaup 1850) of southern South America. For an outgroup, we extracted DNA from a sample of Eurasian Sparrowhawk (*A. nisus nisus*; Linnaeus 1758). All modern samples were acquired under applicable permits and institutional approval. For extracting DNA from tissue and blood samples, we followed the standard Qiagen Blood and Tissue Kit (Germantown, MD) protocol for muscle tissue or blood spots on FTA cards, respectively. DNA from study skin toepads was extracted either using a protocol developed specifically for degraded samples by Andres Cuervo (personal communication) and the QIAamp DNA Micro Kit (Germantown, MD) spin columns, or a Phenol–Chloroform extraction protocol followed by bead cleanup as described by Tsai et al. (2019). All toepad samples were extracted by individuals who had not handled modern tissue samples that day in a lab where no modern avian tissue or blood samples have been processed. Extracted DNA was quantified by either qPCR with PicoGreen (Blotta et al. 2005; Eugene, OR) or a Qubit (Eugene, OR). Samples were submitted to Rapid Genomics (Gainesville, FL) for library preparation and UCE sequencing. Libraries were enriched for UCEs using either the 2.5k tetrapod probe kit (2,386 UCEs) supplemented with ~100 avian exons or the standard 5k tetrapod probe kit (5,060 UCEs; Faircloth et al. 2012). Libraries were sequenced with either 100 base pairs (bp) (2.5k kit) or 150 bp (5k kit) paired-end reads on an Illumina HiSeq 3000/4000.

Read Processing, UCE Assembly, and Sequence Alignment

After sequencing, duplicate reads were discarded using the python script fastqSplitDups.py (https://github.com/McIntyre-Lab/mcscript). Adaptors and low-quality bases were eliminated using trimmomatic, as implemented in illumiprocessor (Lohse et al. 2012, Del Fabbro et al. 2013, Faircloth 2013, Bolger et al. 2014). At this point, each dataset (UCE, mitochondrial genomes, and ND2) was assembled separately as detailed below. Although there was substantial overlap between the datasets, some samples were not included in all datasets. For example, although blood samples result in high-quality UCE contigs, mitochondrial genomes from these extracts can be highly fragmentary because they have relatively low concentrations of mtDNA. Conversely, toepad samples often resulted in high-quality mitochondrial genomes, but lower quality UCEs. Mitochondrial data coverage across samples was also variable with some samples having a differing quality of full mitochondrial genomes vs. coverage for the ND2 dataset. Therefore, we included all possible samples in each of the datasets based on data quality

TABLE 1. List of tissue samples included in the study. Secondary Identifier refers either to a tissue sample number (when paired with an institutional code) or a USGS federal band number. Mitochondrial genomes with <5,000 bases were excluded from the mitochondrial phylogeny. Samples with <1,000 bp of ND2 data were not included in uncorrected *p*-distance calculations whereas those under 900 bp were not included in the haplotype network. DR = Dominican Republic; MFR = Maricao Forest Reserve; PR = Puerto Rico.

Taxon	Locality	Date	Sample type	Catalog number	Secondary identifier	Sample name	Total UCEs	Total UCE length (bp)	Average UCE length	Mitochondrial genome (bp)	ND2 length (bp)	SRA
A. n. nisus	England: Lytham	July 8, 2008	Tissue	ANSP 192586	ANSP 27864	Acc.nis.nisus.27864	2,037	1,305,214	641	13,964	N/A	SAMN17910809
A. [*s.*] *chionogaster*	Mexico: Chiapas: Teopisca, 4 km SW 16.51353°N, 92.47793°W; 1762 m	June 1, 2009	Tissue	UWBM10062		Acc.str. chionogaster. 10062	3,146	2,325,613	739	13,962	1,039	SAMN17910810
A. [*s.*] *erythronemius*	Bolivia: Santa Cruz: Cordillera: Izozog: Comunidad Karapari: Estancia San Julian, 1000 m W of Parapetí	November 9, 2011	Tissue	AMNH 833355	6098	Acc.str. erythronemius. 833355	3,139	2,512,772	801	13,959	1,039	SAMN17910811
A. [*s.*] *fringilloides*	Cuba: Pinar del Rio: Los Palacios	September 30, 1935	Toepad	FMNH 100835		Acc.str.fringilloides. 100835	3,134	682,399	218	13,962	1,039	SAMN17910812
A.[*s.*] *fringilloides*	Cuba: Santiago de Cuba: Pico Turquino	August 20, 1917	Toepad	AMNH 166358		Acc.str.fringilloides. 166358	3,100	390,092	126	13,963	1,039	SAMN17910813
A.[*s.*] *fringilloides*	Cuba: La Habana	?	Toepad	MCZ157618		Acc.str.fringilloides. 157618	2,573	279,060	108	<5,000	<900	SAMN17910814
A. [*s.*] *striatus*	DR: Arroyazo #1	June 24, 2017	Blood	DRAF1		Acc.str.striatus. DRAF1	3,140	2,037,314	649	<5,000	<900	SAMN17910815
A. [*s.*] *striatus*	DR: Arroyazo #1	June 24, 2017	Blood	DRNU1		Acc.str.striatus. DRNU1	3,148	2,315,059	735	10,150	1,018	SAMN17910816
A. [*s.*] *striatus*	DR: Arroyazo #2	June 18, 2017	Blood	DRAF2		Acc.str.striatus. DRNU2	3,149	2,246,850	714	10,068	<900	SAMN17910817
A. [*s.*] *striatus*	DR: Arroyazo #2	June 24, 2017	Blood	DRNU2		Acc.str.striatus. DRAF2	3,149	2,350,321	746	8,262	<900	SAMN17910818
A. [*s.*] *striatus*	DR: Azua Province: Azua, San Domingo	August 13, 1923	Toepad	AMNH 470540		Acc.str.striatus. 470540	3,136	582,022	186	13,962	1,039	SAMN17910819
A. [*s.*] *striatus*	DR: Independencia: Parque Nacional Sierra Baoruco, Pueblo Viejo	April 8, 2003	Tissue	KU 95077	KU 8119	Acc.str.striatus. 95077	3,132	1,949,073	622	13,962	1,039	SAMN17910820
A. [*s.*] *striatus*	DR: San Juan: Mt. Tina	January 15, 1917	Toepad	AMNH 165160		Acc.str.striatus. 165160	3,108	436,923	141	13,963	1,039	SAMN17910821
A. [*s.*] *striatus*	DR: Santiago: Hato Del Yague	March 25, 1932	Toepad	ANSP 111931		Acc.s.striatus. 111931	1,916	387,357	202	13,334	1,039	SAMN17910822
A. [*s.*] *striatus*	DR: Santiago: Mt. Rusilla	March 1, 1917	Toepad	AMNH 165158		Acc.str.striatus. 165158	N/A	N/A	N/A	9,933	<900	SAMN17910823

TABLE 1. Continued

Taxon	Locality	Date	Sample type	Catalog number	Secondary identifier	Sample name	Total UCEs	Total UCE length (bp)	Average UCE length	Mitochondrial genome (bp)	ND2 length (bp)	SRA
A. [s.] striatus	DR: Santo Domingo: Honduras	April 2, 1895	Toepad	FMNH 1842		Acc.str.striatus.1842	3,116	447,313	144	13,850	1,039	SAMN17910824
A. [s.] striatus	Haiti: Ouest: Petionville, Le Coup	March 3, 1881	Toepad	FMNH 93200		Acc.str.striatus.93200	N/A	N/A	N/A	13,865	1,039	SAMN17910825
A. [s.] striatus	Haiti: Sud: La Hotte Mts.	July 3, 1917	Toepad	AMNH 166361		Acc.str.striatus.166361	3,124	430,188	138	13,962	1,039	SAMN17910826
A. [s.] velox	United States: New Hampshire: Deerfield	August 5, 2007	Tissue	ANSP 193578	ANSP 28134	Acc.s.velox.28134	2,046	1,247,030	609	13,962	1,039	SAMN17910827
A. [s.] venator	PR: 8.5 mi. N Sabana Grande	April 30, 1961	Toepad	LSU 141445		Acc.str.venator.141445	2,966	332,106	112	5,069	<900	SAMN17910828
A. [s.] venator	PR: Adjuntas	February 13, 2018	Blood	Blue 3/S	1093-62334	Acc.str.venator.62334	3,147	2,289,835	728	<5,000	<900	SAMN17910829
A. [s.] venator	PR: Guularte/La Olimpia: Adjuntas 3	June 20, 2018	Blood	Black5/B left		Acc.str.venator.B5BL	3,148	2,331,082	740	10,787	<900	SAMN17910830
A. [s.] venator	PR: Guularte/La Olimpia: Adjuntas 3	June 20, 2018	Blood	Green7/A left		Acc.str.venator.G7AL	3,149	2,305,458	732	12,046	1,018	SAMN17910831
A. [s.] venator	PR: MFR: Campground #1	May 26, 2016	Blood	Blue/Orange #302	1573-57702	Acc.str.venator.57702	3,135	1,778,759	567	<5,000	<900	SAMN17910832
A. [s.] venator	PR: MFR: Campground #1	May 26, 2016	Blood	Orange/Pink #201	1093-62311	Acc.str.venator.62311	3,147	2,166,286	688	<5,000	<900	SAMN17910833
A. [s.] venator	PR: MFR: Campground #1	May 26, 2016	Blood	Red/Blue #301	1573-57701	Acc.str.venator.57701	3,141	1,782,706	568	<5,000	<900	SAMN17910834
A. [s.] venator	PR: MFR: Campground #1	May 1, 2017	Blood	PRNU1		Acc.str.venator.PRNU1	3,147	2,147,068	682	12,887	958	SAMN17910835
A. [s.] venator	PR: MFR: Campground #2	July 8, 1905	Blood	Black/Black #004	822-74379	Acc.str.venator.74378b	3,149	2,190,791	696	<5,000	<900	SAMN17910836
A. [s.] venator	PR: MFR: Campground #2	July 8, 1905	Blood	Blue/Black #003	822-74378	Acc.str.venator.74378a	3,147	2,159,569	686	<5,000	<900	SAMN17910837
A. [s.] venator	PR: MFR: Campground #2	July 8, 1905	Blood	Orange/Blue #306	1093-62315	Acc.str.venator.62315	3,145	1,942,895	618	<5,000	<900	SAMN17910838
A. [s.] venator	PR: MFR: Campground #2	February 12, 2018	Blood	Blue 3R	1093-62316	Acc.str.venator.62316	3,148	2,353,188	748	<5,000	<900	SAMN17910839
A. [s.] venator	PR: Maricao: Cabin	June 21, 2018	Blood	Red5/3 right		Acc.str.venator.R53R	3,148	2,270,408	721	8,778	<900	SAMN17910840
A. [s.] venator	PR: Maricao: Cabin	June 21, 2018	Blood	Red5/4 right		Acc.str.venator.R54R	3,149	2,046,443	650	10,313	<900	SAMN17910841
A. [s.] venator	PR: Maricao: DRNA office	June 03, 2018	Blood	Black5/A right		Acc.str.venator.B5AR	3,149	2,263,140	719	9,801	<900	SAMN17910842
A. [s.] venator	PR: Maricao: DRNA office	June 03, 2018	Blood	Blue2/Z left		Acc.str.venator.B2ZL	3,148	2,340,010	743	10,072	988	SAMN17910843

TABLE 1. Continued

Taxon	Locality	Date	Sample type	Catalog number	Secondary identifier	Sample name	Total UCEs	Total UCE length (bp)	Average UCE length	Mitochondrial genome (bp)	ND2 length (bp)	SRA
A. [s.] venator	PR: Toro Negro: 143-#1	May 27, 2016	Blood	Blue/Orange #303	1093-62312	Acc.str.venator.62312	3,149	2,055,837	653	<5,000	<900	SAMN17910844
A. [s.] venator	PR: Toro Negro: Bruma 1	June 21, 2018	Blood	Black5/C right		Acc.str.venator.B5CR	3,136	2,111,455	673	8,896	<900	SAMN17910845
A. [s.] venator	PR: Toro Negro: Bruma 1	June 21, 2018	Blood	Green8/M left		Acc.str.venator.G8ML	3,147	2,167,128	689	12,838	1,033	SAMN17910846
A. [s.] venator	PR: Toro Negro: Cristo Viene	June 11, 2016	Blood	Red/Blue #305	1093-62314	Acc.str.venator.62314D	3,149	2,051,919	652	<5,000	<900	SAMN17910847
A. [s.] ventralis	Peru: Junín: along Rio Satipo	September 19, 2008	Tissue	KU113717	KU 17336	Acc.str. ventralis.113717	3,138	2,447,438	780	13,962	1,039	SAMN17910848

and excluded samples only when data were of low quality, resulting in each dataset being composed of slightly different sample sets (Table 1; Supplementary Material Table 1). This approach allowed us to include the maximum number of samples in each dataset without compromising data quality.

For UCE samples we then assembled the trimmed reads using ABySS 2.1.5 (Jackman et al. 2017) as implemented in Phyluce (Faircloth et al. 2012, Faircloth 2016) following the standard Phyluce pipeline for UCEs. Phyluce then matched the assemblies to UCE probes and produced concatenated files for alignment. However, rather than aligning these files, we used a series of custom scripts to create a single FASTA file containing the longest contig from each UCE (https://github.com/juliema/phylogenomics_scripts). We used this file as a new set of target sequences to match reads using aTRAM v. 2.3.0 (Allen et al. 2018), a pipeline that iteratively assembles reads to form contigs by matching them first to a provided target sequence and then to the results from the previous iteration for subsequent iterations of targeted assembly. We performed 5 iterations using ABySS (Jackman et al. 2017) as the assembler. We selected the longest contig for each assembled UCE, then grouped all taxa by UCE and aligned each UCE using MAFFT (Katoh 2013). We selected the longest contig rather than the results from the last iteration because most variation in UCEs occurs in the flanking regions rather than the central probe area. By keeping the longest contig we kept the maximum number of informative sites. However, this necessitated additional quality control steps as described below.

Each alignment was verified by eye using Geneious 8.0.4 (https://www.geneious.com). Because assemblies from DNA generated from degraded DNA extracted from toepad tissues can possess a higher frequency of errors (Axelsson et al. 2008, Molak and Ho 2011, McCormack et al. 2016), we manually performed 2 types of quality control to remove erroneous sites from these samples. First, any unalignable portions of a contig were removed. We then looked for individual mismatches within each alignment. Sequencing errors are more likely located toward the ends of reads (Schubert et al. 2012) and read coverage tended to decrease at the ends of contigs in all samples. In the case of tissue or blood samples, if mismatches occurred toward the center of a sequence (outside of the 15 bases on either end), these mismatches were kept. However, for toepad samples, we re-coded mismatches as "N" regardless of where in the sequence the mismatch occurred because coverage was lower across the entire sequence, whereas tissue and blood samples had low coverage typically only at the ends. When a mismatch was identical to any other sequence, regardless of whether the sequence it matched was extracted from frozen tissue, blood, or a toepad, we retained the base call.

Second, we deleted entire UCE alignments if multiple samples had identical, but divergent, sequences as compared to other samples in the UCE probe portion of the alignment. The UCE probes bind to regions that are highly conserved across all tetrapods and thus these regions are unlikely to exhibit large amounts of sequence variation, particularly among samples of closely related taxa (Faircloth et al. 2012). These 2 additional data processing steps were necessary for sequences from toepads because libraries prepared from toepad samples provided lower coverage and poorer quality reads than libraries prepared from higher quality tissues or blood spots. These 2 factors may result in sequencing errors, which are then misinterpreted by the assemblers as actual sequence data, leading to erroneous conclusions about toepad data that appear to be more divergent than a modern sample from the same population. Because we had high-quality tissue and blood samples from multiple populations across the islands, we were able to examine the mismatches in sequence data to identify sites that were also variable in the toepad samples. This provided data from additional individuals from the same island, but different collecting locations. We feel these quality control steps greatly improved the signal-to-noise ratio of our toepad data (by removing variation most likely caused by sequencing errors and low-quality DNA) while at the same time maintaining impartiality by retaining mismatches occurring at sites where other samples also exhibit polymorphism regardless of where these samples were from. After these quality control steps, contigs were then realigned using MAFFT and lightly trimmed using trimAL 1.2 (Capella-Gutierrez et al. 2009) to remove all columns with 3 or fewer samples (thus preserving as many informative sites as possible) while removing portions of the alignment with missing data from a majority of samples.

Mitochondrial Genome Assembly and Alignment

Mitochondrial DNA fragments are also included with the nuclear DNA when preparing UCE libraries for sequencing, and it is possible to assemble complete (or nearly complete) mitochondrial genomes from sequences of UCE enriched libraries (Amaral et al. 2015). Using the map to reference function in *Geneious* 8.0.4, we mapped our libraries to an existing complete mitochondrial genome of Eurasian Sparrowhawk (KJ680300) with no trimming, using the medium sensitivity/fast setting with up to 5 iterations. These assemblies were checked by eye. We then extracted and aligned individual rRNAs and genes and combined these individual alignments into a single concatenated alignment for analysis. We also created a second alignment of ND2 sequences including Sharp-shinned Hawk samples previously deposited in GenBank (Fuchs et al. 2015, Cheek et al. 2018) and unpublished ND2 sequences from Neotropical Sharp-shinned Hawks (Supplementary Material Table 1).

Phylogenetic Analysis

UCE data. We used 2 methods for phylogenetic analysis: maximum likelihood (ML) as implemented in RAxML 8.2 (Stamatakis 2014) and SVDquartets (Chifman and Kubatko 2014) as implemented in PAUP* 3.99.166.0 (Swofford 2003). We used Partitionfinder 2.1.1 (Lanfear et al. 2017) to select the best partitioning scheme and substitution models (limited to GTR, GTR + G, and GTR + I + G) with AIC_c as the selection criterion and the rclusters heuristic search (Lanfear et al. 2014), treating each UCE as a unique partition and setting the reduce rcluster-max to 100. Using the selected partitioning scheme and a GTR model for each partition (since RAxML only allows one model to be selected), we ran an ML tree with 500 bootstraps in RAxML 8.2.12. We chose SVDquartets over gene tree/species tree methods (i.e. ASTRAL-III; Zhang et al. 2018), which have been shown to perform poorly in instances where individual genes have low levels of genetic variation, as occurs for UCE data, particularly in studies of closely related taxa such as ours, where entire UCE alignments are identical or nearly so (McCormack et al. 2013, Xi et al. 2015). Conversely, SVDquartets does not rely on the inference of individual gene trees and instead uses a supertree approach to combine individual quartets generated from single positions within an alignment and is thus able to handle this type of data and produce robust trees. Although this method was originally developed for SNP data, later work by Chifman and Kubatko (2015) showed it was accurate when a traditional multilocus alignment is used (rather than unlinked SNPs), despite the violation of the assumption of independence. For our SVDquartet analysis, we used the same dataset as in our UCE RAxML analysis. We exhaustively evaluated all quartets with parameters set as default and performed a bootstrap analysis with 1,000 pseudoreplicates to assess nodal support. Finally, to identify any impacts resulting from the inclusion of nonrandom missing data (e.g., from the 3 samples sequenced using the 2.5k probe set) we reconstructed an unpartitioned ML tree in RAxML with a dataset restricted to UCEs in which the outgroup was included.

Mitochondrial data. We used Partitionfinder 2.1.1 (Lanfear et al. 2014, 2017) to select the optimal partitioning scheme and substitution models (limited to GTR, GTR + G, and GTR + I + G) with AIC_c as the selection criterion and a greedy search scheme. For mtDNA, the optimal partitioning scheme treated each codon position separately and selected a GTR + G model for all partitions. We used the Windows executable version of RAxML 8.2.10 (as compiled by I. Michalak; Stamatakis 2014) to infer a mitochondrial phylogeny and perform bootstrap analysis with

the parameters set to those selected by PartitionFinder 2.1.1 and with Eurasian Sparrowhawk assigned as the outgroup. We allowed the bootstrap analysis to autocomplete using the autoMR function.

Calculation of Uncorrected *p*-Distances and Construction of ND2 Haplotype Networks

We used PAUP*4 3.99.166.0 (Swofford 2003) to calculate pairwise uncorrected *p*-distances from ND2 sequences from all samples for which at least 1,000 bases (out of 1,039 bases) were sequenced. These pairwise *p*-distances were then used to calculate average uncorrected *p*-distances both between and among taxa. We also constructed an ND2 haplotype network with the R package *Pegas* (Paradis 2010), including sequences for which at least 900 bases of ND2 were sequenced. *Pegas* builds haplotype networks using an infinite site model and pairwise deletion of missing data. After building the haplotype network, we manually checked samples to confirm that those with missing data did not result in an incorrect network being calculated.

SNP Identification and Analysis

To produce a dataset of unlinked SNPs, we used Phyluce (Faircloth et al. 2012, 2016, Andermann et al. 2019) to extract a SNP at random from each UCE alignment. To minimize missing data, we only included SNPs from tissue and blood samples (eliminating all samples from *A.* [*s.*] *fringilloides*, which were from toepads) and only from UCEs that were also sequenced from the outgroup sample (*A. nisus*). Although this resulted in fewer SNPs than if we had used all UCEs, this approach minimized the influence of nonrandom missing data that might have resulted from some samples being sequenced with only the 2.5k probe set. We performed *phyluce_align_explode_alignments* to split untrimmed UCE alignments (because the pipeline does not always work properly with trimmed data) and then re-concatenated them by sample (rather than by UCE). Next, we used the *phyluce_snp_bwa_multiple_align* command to map the reads cleaned by illumiprocessor to individual contigs. The resulting sets of reads were then phased using *phyluce_snp_phase_uces* and aligned using MAFFT (phyluce_align_seqcap_align). Alignments were translated into FASTA files, and a SNP from each alignment was picked using the command *phyluce_snp_get_from_uce_alignments*, with missing data allowed (— missing). If multiple SNPs were present in an alignment, then one was selected at random. This process only selects SNPs that are usable in SNAPP (only 2 nucleotide states, resulting in a coding of 0 (homozygous for original state), 1 (heterozygous), or 2 (homozygous for derived state).

We then used SNAPP as implemented on CIPRES (Miller et al. 2010) to analyze the resulting SNP alignment and generate a species tree. We tried 2 different population assignments in the species tab. The first was assigned based on taxonomy. The second subdivided each island based on a forest reserve. Our data only contained polymorphic sites and we used default parameters, with the exception of lambda, for which we used a gamma distribution. We then performed 2 identical runs of 2 million Markov chain Monte Carlo (MCMC) generations with a burn-in of 10%. The log and tree files from these 2 runs were combined using LogCombiner 2.6.1. We calculated posterior probabilities using TreeAnnotator 2.6.0 and visualized the combined log files and tree files using Tracer 1.5 and Densitree 2.2.7, respectively.

We used the same process to create a second SNP dataset, wherein *A. nisus* was excluded, and used sparse non-negative matrix factorization (sNMF) (Frichot et al. 2014) as implemented in the R package *LEA* 2.2.0 (Frichot and François 2015) to calculate admixture coefficients and select the number of populations that best represent that data based on the lowest cross-entropy score. We tested K between 1 and 9, based on the number of unique localities, and ran 1,000 repetitions of sNMF. We tested 3 values of alpha (10, 25, and 50) then selected 25 based on cross-entropy score.

Morphometric Data Collection

Wing morphology is positively correlated with dispersal ability at broad taxonomic scales, and differences between migratory and non-migratory taxa are evident (Claramunt et al. 2012, Sheard et al. 2020). Therefore, information about geographic variation in wing morphology in the *A. striatus* complex may be useful for making inferences about the probabilities of dispersal within and between Caribbean islands and the mainland. To investigate differences among Caribbean, North American, and South American taxa, one author (T.A.C.) took the following measurements from study skins in the collections at the Academy of Natural Sciences of Drexel University (ANSP), Field Museum of Natural History (FMNH), University of Kansas Biodiversity Institute (KU), and American Museum of Natural History (AMNH): (1) length of the right wing (WL), measured to the nearest 1 mm with a ruler by lightly pressing on the wing while recording the distance from the carpal joint to the tip of the longest primary remex; if the right wing was molting or damaged then the left wing was used; (2) length of the longest secondary remex (SL), measured to the nearest 1 mm with a ruler from the carpal joint. Although SL is a standard measurement, when taken from study skins it may be influenced by shrinkage, a side effect of the common practice of stripping secondaries from the ulna during specimen preparation (T. A. Catanach and M. R. Halley, personal observation). Along with measurements, we took scaled photographs of

each specimen and compared specimen data in collections databases to verbatim label data. Finally, as Sharp-shinned Hawks exhibit extreme reverse sexual dimorphism, which could distort morphological analyses, we determined sex using a combination of label data and a comparison to measurements in the published literature (Wetmore 1914, Mueller et al. 1979, 1981, Henny et al. 1985). In most cases, the sex noted on the label matched the sex indicated by the measurements. However, in a few instances (16 females apparently misidentified as males and 8 males misidentified as females), morphological data suggested label data were incorrect. We assumed in these cases that the sex of the bird was incorrectly determined by the preparator; paired ovaries, which are found in hawks, but are unusual in other birds, may be mistaken for testes. In these cases, we assigned the sex that matched the measurements. When sex was not noted on the label (n = 42), we assigned sex according to measurement data, unless the specimen was from the narrow range of overlap between males and females (n = 4), in which case the data were not used in the analysis.

Morphological Data Analysis

We performed statistical analyses in R as implemented in R-Studio (R Core Team 2014). All means are reported with ± 1 standard deviation (SD). We analyzed data separately for the 2 sexes, and independent analyses were performed to test for differences among 3 geographic regions (i.e. Caribbean, North America, and South America). We calculated Spearman's rank correlation coefficients (ρ) to test for covariance between the 2 wing variables. Because of significant covariance, we combined the variables by calculating hand-wing index (HWI), equal to 100 × ((WL – SL)/WL), a metric used widely in comparative studies as a proxy for dispersal ability (Claramunt et al. 2012, Sheard et al. 2020). Within each sex, we tested HWI for normality (Anderson–Darling test, α = 0.05) and equal variances (Levene's test, α = 0.05) relative to the independent variable, to determine whether the data were suitable for parametric analysis. HWI in females was not normally distributed, so we proceeded with non-parametric Kruskal–Wallis tests, and pairwise Wilcoxon signed-rank tests with Bonferroni corrections for multiple comparisons, to determine whether the HWI data from the 3 geographic areas originated from the same distribution (i.e. whether the ranked medians differed) and which group pairs were significantly different (α = 0.05).

RESULTS

Phylogenetic Analysis of UCE and Mitochondrial Genome Data

Out of 5,060 UCEs from the 5k probe set on average, we assembled 4,780 UCEs per tissue or blood sample (n = 27) and 4,523 UCEs for toepads (n = 8). Out of a potential 2,386 UCEs from the 2.5K probe set, we assembled 2,330 UCEs per tissue sample (n = 2) and 2,137 UCEs from the single toepad sample. We restricted our final alignment to only include UCEs for which at least 90% of sequences were represented in the alignment. This resulted in a total of 3,149 UCEs (average of 3,145 UCEs for 5k tissue/blood; 3,032 UCEs for 5k toepads; 2,042 UCEs for 2.5k tissues; 1,916 UCEs for the 2.5k toepad sample). Although the number of UCEs recovered was similar between tissues/blood samples and toepads enriched with the same probe kit UCEs assembled from toepad samples were often shorter than those assembled from tissue or blood samples (153 bp SD = 37 bp vs. 666 bp SD = 128 bp). UCE length between tissue and blood samples was similar (699 bp vs. 658 bp, respectively).

The final alignment of 38 samples was 2,727,137 bp long with all samples ranging from 229,225 to 2,512,772 bp with 3,821 parsimony informative sites. Twenty-nine mitochondrial genomes were assembled (*A.* [*s.*] *chionogaster*: n = 1, A. [*s.*] *erythronemius*: n = 1, *A.* [*s.*] *fringilloides*: n = 2, *A.* [*s.*] *striatus*: n = 11, *A.* [*s.*] *venator*: n = 10, *A.* [*s.*] *velox*: n = 1, *A.* [*s.*] *ventralis*: n = 1, *A. n. nisus*: n = 1, *A. n. nisosimilis* KM360148: n = 1) with blood samples performing poorly compared to tissue or toepad samples, which is expected given that avian blood is rich in nuclear DNA and poor in mtDNA. Once the control regions and tRNAs were removed, the final mtDNA alignment was 13,979 bases long with 931 parsimony informative sites. We excluded mitochondrial genomes with fewer than 5,000 bp.

The resulting phylogenetic reconstructions, including an ML analysis of UCE data (Figure 2), an ML analysis of mitochondrial genomes (Figure 3), and an SVDquartet approach using UCE data (Supplementary Material Figure 1), broadly matched in topology. All 3 analyses inferred a monophyletic Sharp-shinned Hawk clade (mitochondrial BS = 100%). Within this clade *A.* [*s.*] *erythronemius* was sister to all other Sharp-shinned hawks. The rest of the clade was divided into 2 distinct, well-supported lineages, a mainland lineage containing the samples from North America, Central America, and northern South America (UCE BS = 100% and mitochondrial BS = 99%), and a second clade containing all Caribbean Sharp-shinned Hawks (UCE BS = 100% and mitochondrial BS = 100%). Within the Caribbean clade, Sharp-shinned Hawk samples from each island formed well-supported (UCE and mitochondrial BS = 100% for all 3 clades) reciprocally monophyletic clades with respect to those from the other islands. Relationships between samples collected from a given island were unresolved and differed between the 3 phylogenies, although the ML trees were less influenced by data quality, compared to SVDquartets tree, in which all *A.* [*s.*] *striatus* samples from toepads formed a single clade

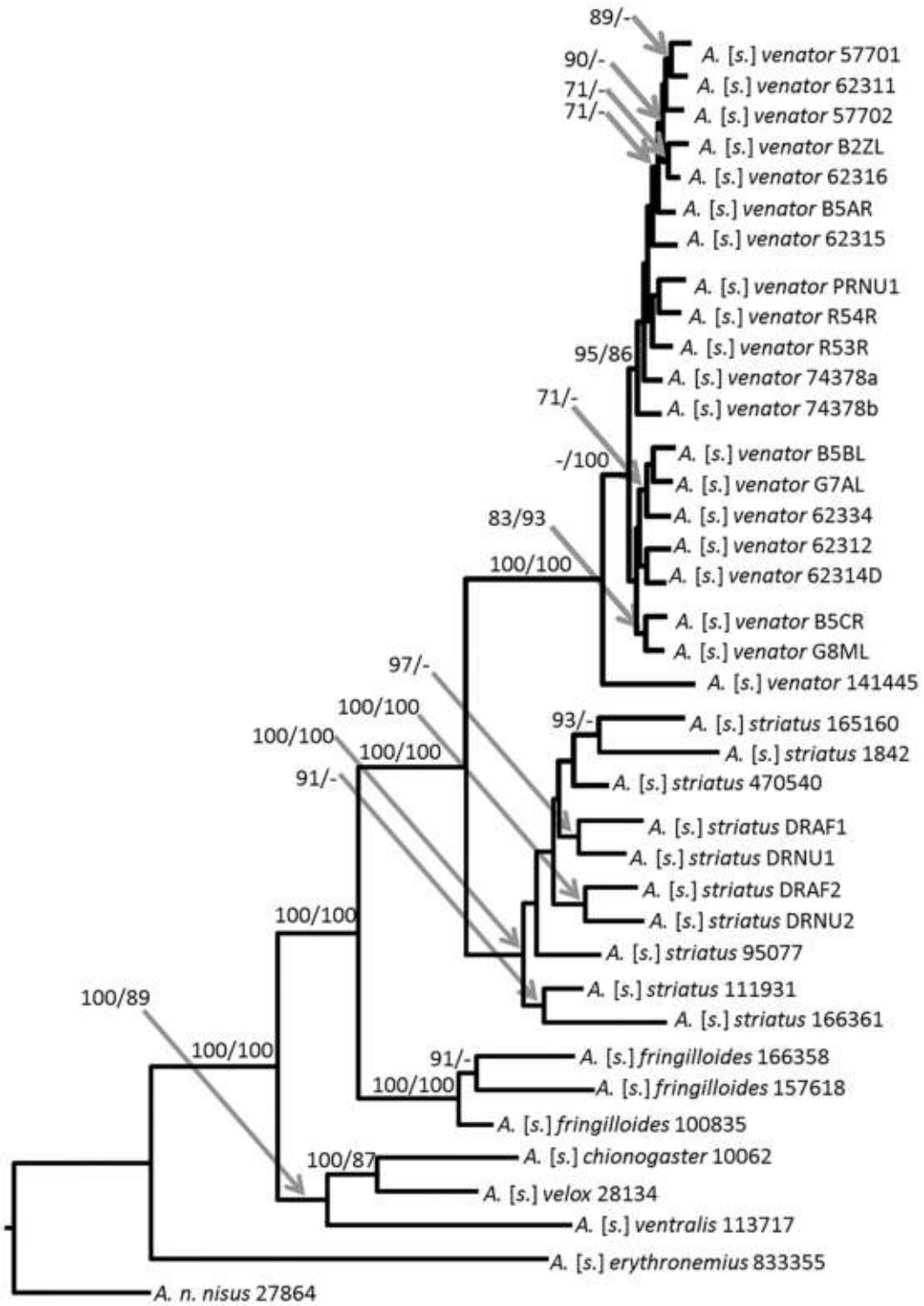

FIGURE 2. Maximum likelihood phylogeny based on UCE data. Values above branches are ML bootstrap values followed by SVDquartet bootstrap values corresponding to nodes directly to the lower right. Only values above 70 are shown.

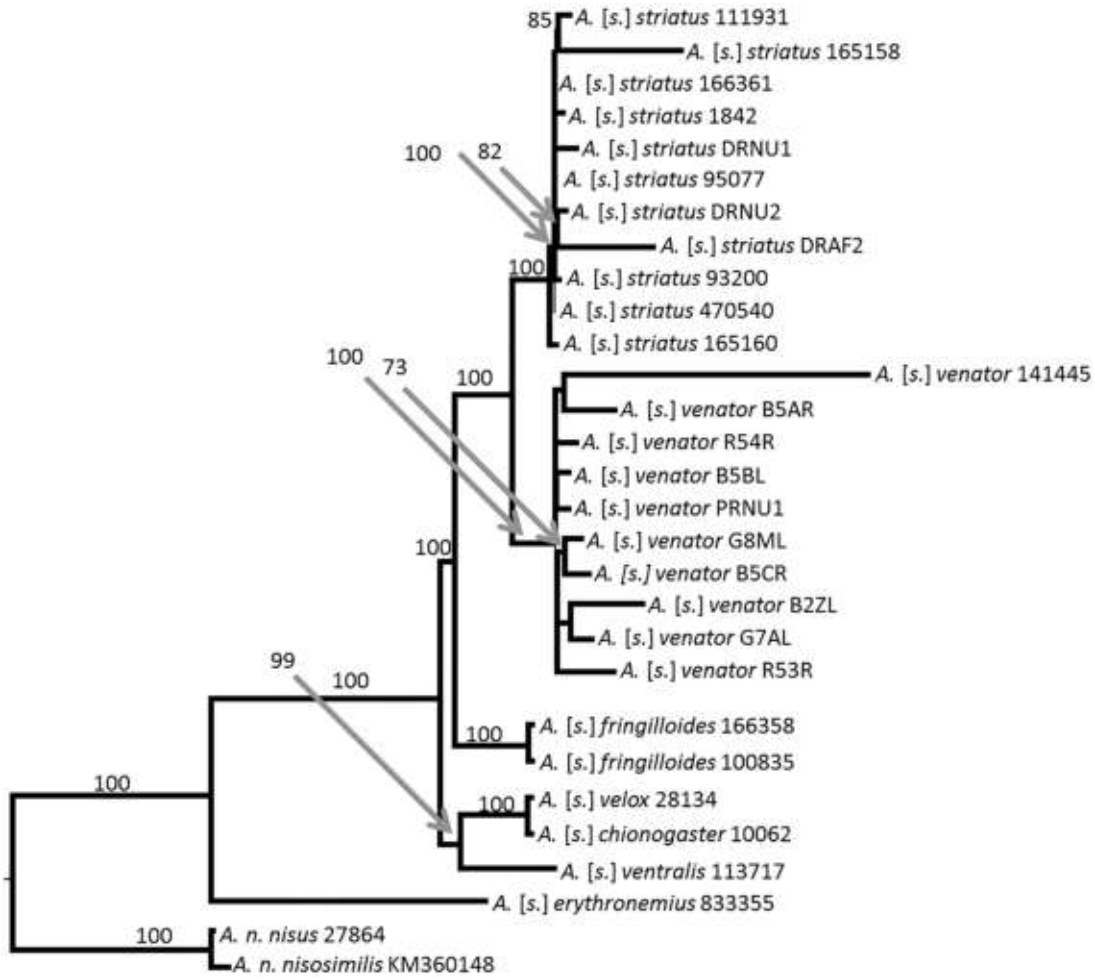

FIGURE 3. Maximum likelihood mitochondrial phylogenetic reconstruction. Numbers above branches denote ML bootstrap values of nodes directly to the lower right.

embedded within the *A.* [*s.*] *striatus* clade, whereas the ML analysis reconstructed a phylogeny where toepad samples were intermixed with tissue samples.

Uncorrected *p*-Distances and ND2 Haplotype Networks

The ND2 uncorrected *p*-distance between North American and Caribbean samples averaged 1.83% (range: 0.88–2.11%; Figure 4A). Cuban samples were more similar to the North American samples than were Hispaniolan and Puerto Rican samples. The South American samples were distinct from both North American (2.10%) and Caribbean (2.66%) samples. Within a given geographic region, uncorrected *p*-distances were low (ranging from 0.05% among North American samples to 0.20% among Puerto Rican samples) with the exception of South America where uncorrected *p*-distances averaged 1.90. We recovered 2 mtDNA haplotypes in Cuba, 3 in Puerto Rico, and 5 in Hispaniola (Figure 4B). We recovered 8 haplotypes among the North American samples (with 21 individuals sharing a single haplotype and the remaining 7 haplotypes separated from the most common haplotype by at most 4 base differences). South American samples were substantially different (at least 15 bases) from the most common North American haplotype. Although most South American samples clustered together, 1 sample was highly divergent (with 40 bases different) and was linked to the Cuban sample rather than other mainland samples. Finally, in the haplotype network, Cuban haplotypes were placed as intermediate between North American and Caribbean haplotypes from Hispaniola and Puerto Rico.

SNAPP Analysis

SNAPP analysis based on taxonomic groupings revealed relatively low levels of topological conflict among genes except in the placement of *erythronemius* relative to *A. nisus* (Figure 5). The sister relationship of the 2 island taxa was supported and island populations were distinct from all continental Sharp-shinned Hawks. A second clade contained *A.*

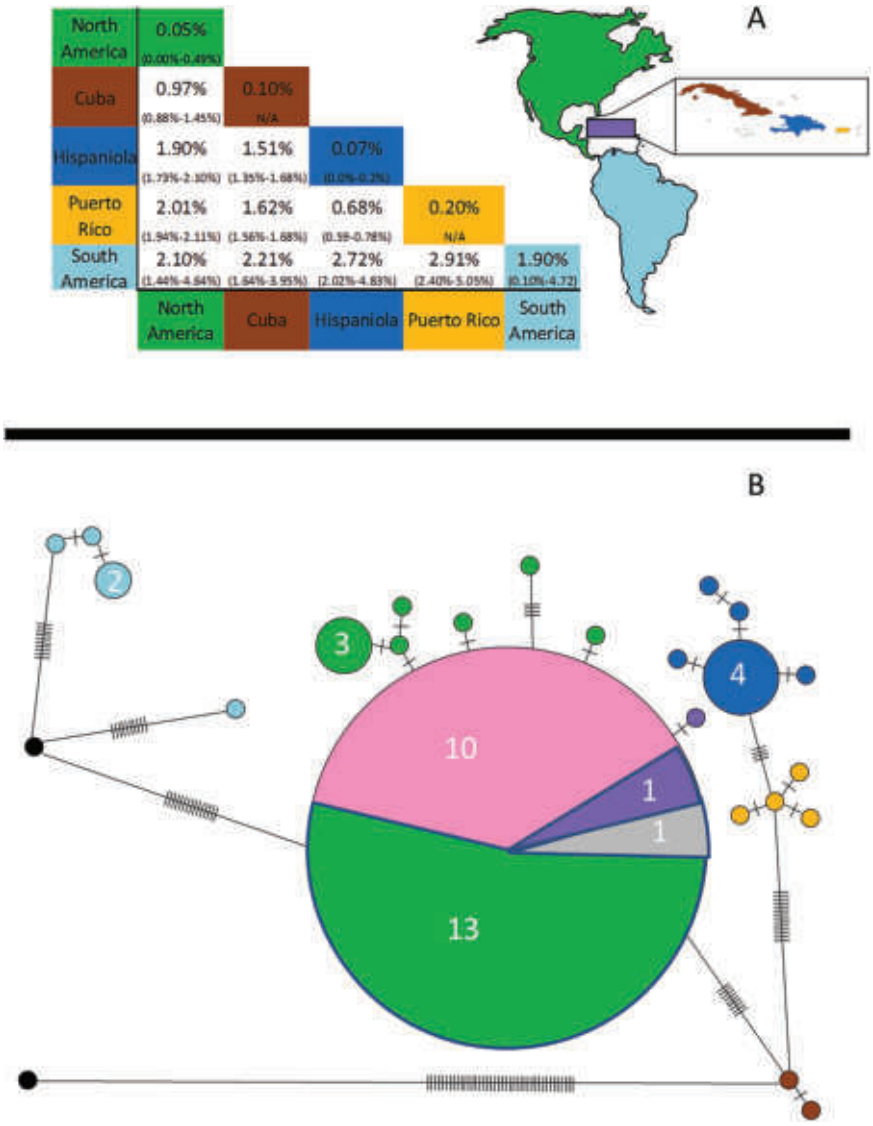

FIGURE 4. (A) Table of mean pairwise uncorrected *p*-distances (upper number) and ranges (lower numbers) by sampling region. Sequences were only included in *p*-distance calculations if they were at least 1,000 base pairs in length, resulting in the following sample sizes: Cuba (n = 2), Hispaniola (n = 8), Puerto Rico (n = 2), North America (n = 27), and South America (n = 1). (B) Haplotype network of ND2 sequences from Sharp-shinned Hawk samples used in this study. Sequences were only included in the haplotype network analysis if they were at least 900 base pairs in length, resulting in the following sample sizes: Cuba (n = 2), Hispaniola (n = 8), Puerto Rico (n = 4), North America (n = 30), and South America (n = 7).

[*s.*] *velox*, *A.* [*s.*] *chionogaster*, and *A.* [*s.*] *ventralis*. However, when (intra-island) populations from each potentially isolated forest reserve were coded as separate populations, SNAPP analysis revealed conflict in the placement of Puerto Rican samples with alternative topologies suggesting different relationships between the forest fragments. A similar arrangement was found within the 2 locations *A.* [*s.*] *striatus* samples were obtained from. Due to the large amounts of missing data from toepad samples, we were unable to include any Cuban samples and some Hispaniolan and Puerto Rican samples in this analysis.

sNMF Analysis

The lowest cross-entropy score calculated (K = 3) corroborated 3 geographically structured populations. Puerto Rico and Hispaniola each were distinct populations whereas mainland samples (including representatives from both North and South America) comprised a single population (Figure 6). The second most favored scenario (K = 4) indicates that mainland samples are further subdivided, with the distinct southern South America *erythronemius* separated from the other mainland samples (northern South

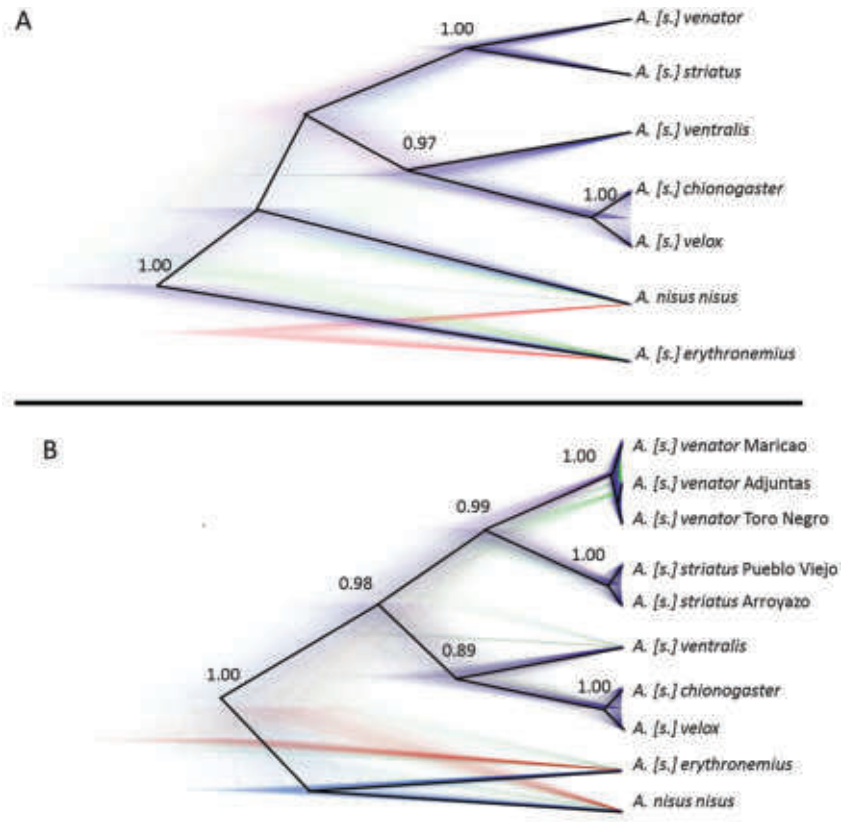

FIGURE 5. Results from the SNAPP analysis of (A) taxa and (B) forest patches. Blue lines represent the trees congruent with the maximum clade credibility tree, whereas trees with alternative topologies are in red and green. The summary tree is shown in black, with posterior probabilities (>0.80) labeling nodes.

America—*ventralis*; North America—*velox*; and Central America—*chionogaster*), each of which is a separate population. Furthermore, this analysis indicates low admixture levels between island populations (Puerto Rico and Hispaniola) and also between these 2 island populations and the mainland.

Morphometric Analysis

We analyzed the wing morphology of 231 individuals (Figure 7, Table 2; female: $n = 133$, male: $n = 98$). WL and longest secondary length (SL) were positively correlated in both sexes (Spearman rank test; female: $\rho = 0.407$, male: $\rho = 0.449$). Among females, there were significant differences in HWI among 3 geographic groups (Caribbean, North America, and South America; Kruskal–Wallis test, $H = 40.97$, df = 2, $P < 0.001$). Pairwise tests with Bonferroni corrections showed that Caribbean females (*A.* [*s.*] *striatus* and *A.* [*s.*] *fringilloides*) had lower HWI than North American females (*A.* [*s.*] *velox* and *A.* [*s.*] *suttoni*; Wilcoxon test, $P < 0.001$); and South American females (*A.* [*s.*] *erythronemius* and *A.* [*s.*] *ventralis*) had lower HWI than North American females (Wilcoxon test, $P < 0.001$). There was no difference between Caribbean and South American females. Among males, there were significant differences in HWI among 3 geographic groups (Kruskal–Wallis test, $H = 37.10$, df = 2, $P < 0.001$). Pairwise tests with Bonferroni corrections showed that Caribbean males had lower HWI than North American males (Wilcoxon test, $P < 0.001$), and South American males had lower HWI than North American males (Wilcoxon test, $P < 0.001$). There was no difference between Caribbean and South American males.

DISCUSSION

This is the first study to reconstruct a phylogenetic hypothesis of the Caribbean taxa in the *A. striatus* complex with phylogenomic data. We found that each of the Caribbean taxa is genetically diagnosable from each other and together form a monophyletic clade with respect to the mainland taxa. These findings are reflected in phylogenetic analyses of mitochondrial and nuclear DNA sequences (via UCEs and SNPs), which corroborate patterns of plumage color characters (Wetmore 1914). In all molecular analyses (UCEs, mitochondrial genomes, ND2 haplotype networks, and SNP data), samples from the Caribbean taxa formed a monophyletic clade to the exclusion of mainland taxa. This contrasts with Bildstein's

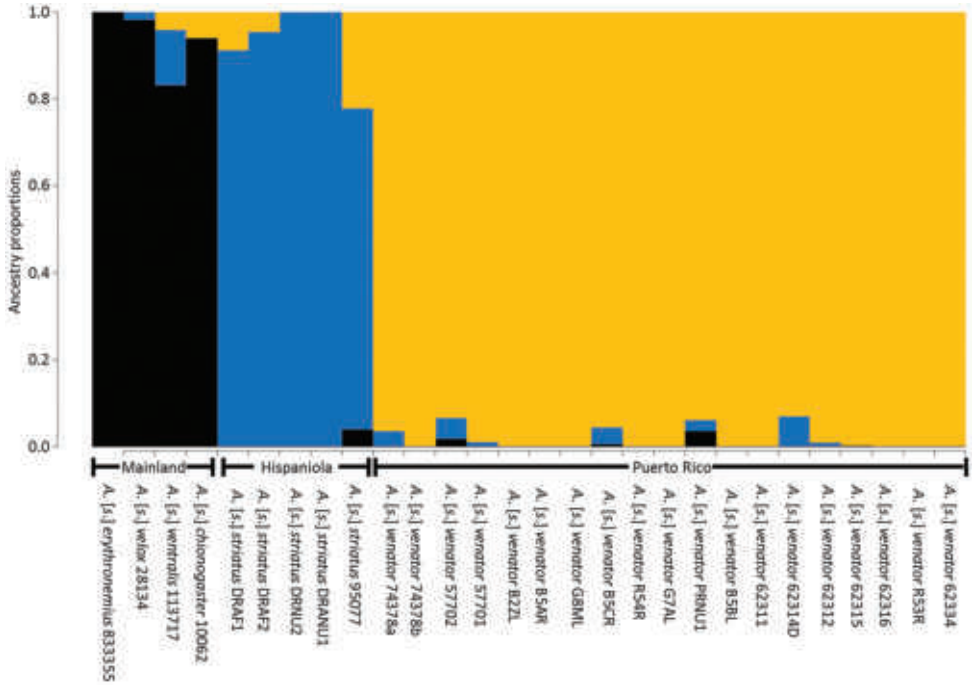

FIGURE 6. Results from sNMF analysis with a cross-entropy score ($K = 3$) corroborating the presence of 3 geographically structured populations. Each bar represents a sampled individual and coloration indicates the relative proportion of ancestry from the 3 different populations with black bars indicating the proportion of ancestral alleles from the mainland population (*chionogaster*, *ventralis*, *velox*, *erythronemius*), blue bars indicating the proportion of ancestral alleles from Hispaniola (*striatus*), and yellow bars indicating the proportion of ancestral alleles from Puerto Rico (*venator*).

(2004) assertion that continual gene flow from the migratory North American taxon (*A.* [*s.*] *velox*) has prevented the differentiation of Caribbean and mainland taxa. Rather, we found that each island supports its own endemic, monophyletic clade. Samples from Puerto Rico and Hispaniola were more similar to each other than either was to those from Cuba. The traditional treatment of the Caribbean taxa, as subspecies in a polytypic *A. striatus* complex, is predicated on the (now unsupported) assumption of gene flow from the migratory taxa into Caribbean populations (Bildstein 2004). Despite opportunities for gene flow (Garrido 1985, Wallace et al. 1996), our results do not support a recent history of genetic admixture among the mainland and Caribbean taxa, nor among the allopatrically distributed Caribbean taxa.

We reconstructed the same general pattern of relationships with 3 different molecular datasets (UCE data, mitochondrial genomes, SNP data). In both the UCE and mitochondrial genome topologies, *A.* [*s.*] *erythronemius* was the sister group to all other Sharp-shinned Hawk taxa. Conversely, SNP data conflicted with this arrangement and placed *erythronemius* as sister to *A. nisus nisus* or alternatively as sister to all other Sharp-shinned Hawks + *A. n. nisus*. None of these arrangements was well supported, except for the topology in the mitochondrial tree, which had an ML bootstrap value of 100. Additional sampling in South America, and the inclusion of more outgroups from the *A. nisus* complex, is needed to determine the position of *A.* [*s.*] *erythronemius*. Nevertheless, this determination is not critical to the assessment of the Caribbean taxa. Every analysis produced a clade that included all Caribbean taxa reconstructed as sister to a clade including most mainland samples: *A.* [*s.*] *velox*, *A.* [*s.*] *chionogaster*, and *A.* [*s.*] *ventralis*. This contrasts with Bond's (1978) speculation that Caribbean populations are more closely related to North American taxa than South American taxa. Alternatively, Storer (1952) argued that the Caribbean taxa were more closely related to the South American taxa on account of their barred underparts. Additional sampling, particularly across the continental Neotropics, is required before the biogeographic history of the *A. striatus* complex can be effectively modeled in a phylogenetic context to more rigorously test these hypotheses.

In the ND2 haplotype network (Figure 4B), Cuban samples were placed between all mainland taxa and the taxa from the more distant islands of Hispaniola and Puerto Rico. Furthermore, a single sample of *A.* [*s.*] *erythronemius* is connected to a sample from Cuba, although they differ by 40 bp; in comparison, Cuba and the most common North American haplotype differ by only 9 bp. This *A.* [*s.*] *erythronemius* sample is divergent from all other Sharp-shinned Hawk specimens sequenced, so

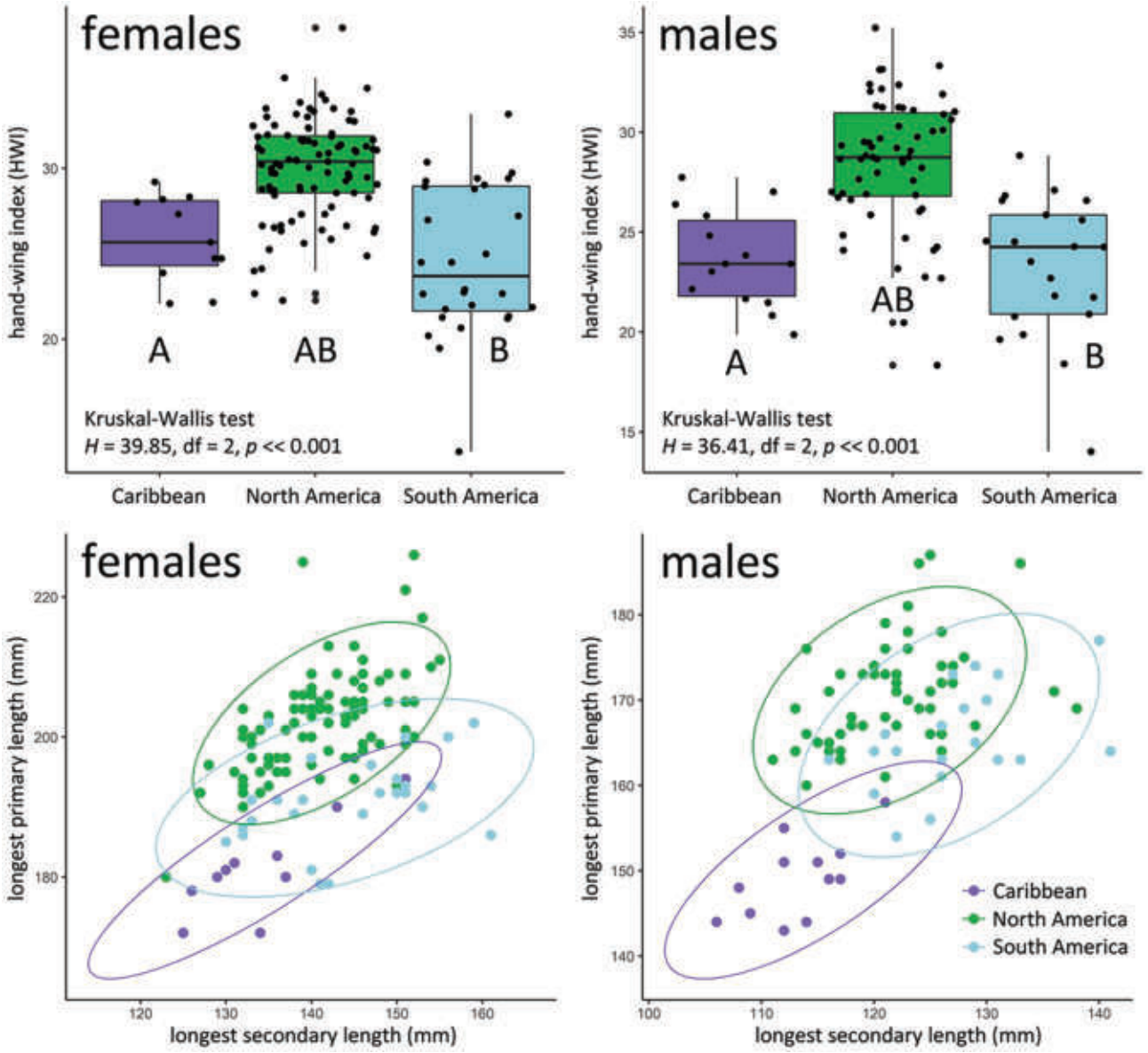

FIGURE 7. Variation in wing morphology by sex, among Caribbean (female: $n = 11$; male: $n = 14$), North American (female: $n = 94$; male: $n = 63$), and South American specimens (female: $n = 28$; male: $n = 21$) in the *Accipiter striatus* complex. Boxplots that do not share a letter (A, B) have significantly different means. Plots and "normal [95%] confidence ellipses" were drawn with *ggplot* implemented in R (R Core Team 2014).

additional samples are required before any conclusions can be drawn about the placement of this taxon. Focusing on the other taxa, which include multiple ND2 samples, the network suggests that mainland birds first colonized Cuba and then expanded their range south along the Greater Antilles. However, the Cuban haplotypes are more similar to Puerto Rican haplotypes than they are to the geographically closer Hispaniolan haplotypes (Figure 4B). For this reason, we cannot rule out an evolutionary history that includes multiple independent colonizations from Cuba to the other Caribbean islands. However, our data do support a single origin of the Caribbean clade. This may have resulted from migratory individuals becoming permanent residents in the island wintering grounds of their ancestors, with one or more transitions from migratory to sedentary behavior as suggested by Bildstein (2004) and inferred for harriers (Oatley et al. 2015) and falcons (Fuchs et al. 2015). This hypothesis is supported by the fact that the migratory taxon *A.* [*s.*] *velox* winters in small numbers in Cuba, albeit in lowland regions instead of montane forests where the endemic taxon resides (Garrido 1985, Wallace et al. 1996), and is also rare during

TABLE 2. Summary statistics for wing length (WL), longest secondary length (SL), and hand-wing index (HWI) by geographic region. All means (±SD) are reported in millimeters (mm).

Character	Sex	Group	*N*	Mean	SD	Min	Max
WL	F	Caribbean	11	182.00	7.06	172.00	194.00
		North America	94	202.12	7.55	179.00	226.00
		South America	28	191.14	6.35	179.00	202.00
	M	Caribbean	14	150.21	5.16	143.00	158.00
		North America	63	170.59	6.08	156.00	187.00
		South America	21	165.76	6.14	154.00	177.00
SL	F	Caribbean	11	135.00	8.05	125.00	151.00
		North America	94	141.34	6.67	123.00	155.00
		South America	28	143.96	9.14	130.00	161.00
	M	Caribbean	14	114.64	5.36	106.00	125.00
		North America	63	121.97	5.79	111.00	138.00
		South America	21	127.14	6.18	116.00	141.00
HWI	F	Caribbean	11	25.85	2.53	22.09	29.21
		North America	94	30.05	2.98	21.23	38.22
		South America	28	24.66	4.41	13.44	33.17
	M	Caribbean	14	23.68	2.41	19.87	27.74
		North America	63	28.46	3.50	18.34	35.23
		South America	21	23.26	3.43	14.02	28.83

winter in Hispaniola and Puerto Rico (Keith et al. 2003, Latta et al. 2006). The low level of admixture detected in our sNMF analysis suggests that although mainland birds may sometimes winter in the Caribbean, there is no genetic signature of interbreeding with the resident populations. Furthermore, migrants favor lower elevation areas than resident birds, which suggests that these divergent populations do not come into contact during the non-breeding season (i.e. seasonally sympatric but not syntopic).

The lack of rampant or even modest gene flow (based on low levels of admixture shown in the sNMF analysis), and the lack of any shared mtDNA haplotypes, between continental and island populations, and among the islands, is surprising because Cuba is separated from the Florida Keys by only 150 km and the distances between Cuba and Hispaniola (90 km), and Hispaniola and Puerto Rico (115 km), are even smaller. Although *A.* [*s.*] *velox* is known to cross water barriers during migration, Sharp-shinned Hawks are rarely reported from any other Caribbean islands, suggesting that *A.* [*s.*] *velox* is not a common visitor to the region. Furthermore, Kerlinger (1984, 1985) observed that *A.* [*s.*] *velox* crossed water only when the land was visible on the opposite shore, and even then, ~30% of birds refused to cross Lake Superior's Whitefish Bay, an overwater stretch of ~18 km. Instead, they stopped or turned back part way before flying along the coastline, adding hundreds of kilometers to their total migratory distance. Conversely, Anders (1991) observed many immature Sharp-shinned Hawks (101/136 raptors detected) migrating over the Dry Tortugas, FL, most of which continued west when they reached the end of the island. Deployment of tracking devices may shed more light on how often these overwater migration attempts are successful. Our finding that the Caribbean taxa have divergent wing morphology, with lower HWI values than the North American *A.* [*s.*] *velox*, is further evidence that the probability of inter-island dispersal is low in the Caribbean taxa.

The mean uncorrected *p*-distance for ND2 sequences was 1.83% between the Caribbean clade and the clade containing all Sharp-shinned Hawks except *A.* [*s.*] *erythronemius*. Among haplotypes from individual islands, the least divergent pair was Puerto Rico and Hispaniola (mean uncorrected *p*-distance = 0.68%) and haplotypes from both of these islands were 1.53% divergent from Cuban haplotypes. SNAPP analysis showed low levels of conflict among gene trees indicating that the birds from a given island form reciprocally monophyletic groups, suggesting there has been no recent gene flow. The sNMF analysis, which found $K = 3$ populations, also provided little evidence of admixture between the Puerto Rican and Hispaniolan taxa and between these 2 island taxa and those on the mainland. The second-best scenario, $K = 4$, retained the Caribbean samples as 2 distinct populations, but further subdivided the mainland samples. However, because we were only able to include a single tissue sample from each of the included mainland subspecies, and no samples from Cuba, further sampling is needed to clarify species limits within the mainland taxa. The sNMF analysis did not support further subdividing individual island populations, to reflect potential differences between isolated forest fragments, which suggests that birds are moving between forest fragments within each island (but not between islands). When forest fragments were treated as populations, there was a low resolution

FIGURE 8. Ventral, lateral, and dorsal views of included Sharp-shinned Hawks taxa: (A) *A.* [*s.*] *venator* male LSU 141445, (B) *A.* [*s.*] *striatus* male AMNH 7337, (C) *A.* [*s.*] *fringilloides* immature female ANSP 111889, (D) *A.* [*s.*] *velox* male ANSP 182137, (E) *A.* [*s.*] *chionogaster* immature male ANSP 90555, (F) *A.* [*s.*] *erythronemius* male ANSP 145505, and (G) *A.* [*s.*] *ventralis* male 145506. Photos of (A) (*venator*) provided by Donna L. Dittmann and scaled to match other taxa, photos of (B) (*striatus*) taken by T.A.C. and scaled to match other taxa; photos of other taxa (C–G) taken by M.R.H.

for separating forests within Puerto Rico, suggesting that there is either ongoing gene flow or insufficient time for sorting of SNPs among sampled locations within Puerto Rico. This finding is corroborated by 2 recent sight records of banded first-year females moving 25 and 27 km, one of which courted with a territorial male, but several weeks later returned to her natal area. This was evidently the first time *A.* [*s.*] *venator* has been documented moving between forest fragments in Puerto Rico (H. Weaver personal communication).

In addition to genetic differences, the plumages of these populations have also been considered to be diagnosable (Figure 8). Plumage-based diagnoses were given by Wetmore (1914), who compared the color of adult male specimens (although limited to one individual per taxon due to the scarcity of specimens in collections) of the Caribbean taxa to standardized colors in Ridgway (1912). We have included digital photographs of one representative of each taxon to demonstrate variation between each taxon (Figure 8). The Cuban taxon, *A.* [*s.*] *fringilloide*s Vigors, 1827, has the (1) "forehead distinctly tinged with hazel," unlike *A.* [*s.*] *striatus* and *A.* [*s.*] *venator* in which the forehead has "no hazel"; (2) "white" thighs that are "faintly barred with mouse gray," unlike the white thighs barred with "pecan brown intermixed with distinct dark purplish gray" for *A. striatus* and "hazel [thighs] barred with white" for *A.* [*s.*] *venator*; (3) no concealed white spot on inner tertials of *A.* [*s.*] *fringilloides*, vs. a "large concealed white spot on three inner tertials on each side" for *A.* [*s.*] *striatus* and *A.* [*s.*] *venator*; (4) "sides of the upper breast rood's brown" for *A.* [*s.*] *fringilloides* vs. "hazel" for *A.* [*s.*] *striatus* and *A.* [*s.*] *venator*. The barring on the upper side of the tail also differs between *A. striatus* ("dark bars indistinct") and *A.* [*s.*] *venator* ("sharply defined black bars") and the "black shaft marks of feathers on [the] underside" are "strongly defined" for *A.* [*s.*] *striatus*, vs. "less distinct" for *A.* [*s.*] *venator* (Wetmore 1914, p. 120). All Caribbean forms can be separated from migratory North American birds by their small size and the presence of a hazel cheek, whereas migratory North American birds have light brown cheeks (some with a light hazel wash).

With respect to species delimitation, there is no standard threshold for species-level divergence and yardstick approaches are fraught with subjectivity, sampling bias, and assumptions about the rate and direction of divergence (Halley et al. 2017). In this case, multiple lines of evidence (nuclear DNA, mitochondrial genomes, ND2 haplotypes, morphometric divergence, and apparent plumage color divergence) support the conclusion that the Caribbean taxa are on independent evolutionary trajectories and have unique evolutionary histories. There is no evidence of recent gene flow among the islands or between the island taxa and mainland populations. The taxa are divergent, diagnosable, and, despite their allopatric distributions, meet the criteria for species rank under both the Phylogenetic Species Concept and the Morphological Species Concept. We contend that species rank should even be applied under the Biological Species Concept (BSC), because the lack of shared mitochondrial haplotypes among the islands indicates that there is genetic isolation among females, and SNP data indicate that there is no recent history of even modest nuclear gene flow among males or females from different islands. Therefore, we recognize these genetically and phenotypically diagnosable taxa as an island radiation of endemic species.

Other recent studies of endemic island radiations have advocated for taxonomic revisions after finding similar patterns of genetic and phenotypic variation among allopatric populations. For example, the Greater Antillean Oriole complex provides a similar case. After analysis of ND2 and cytochrome *b* sequences indicated that it was polyphyletic (Sturge et al. 2009) and diagnosable via plumage coloration (Price and Hayes 2009), the complex was split by the North American Checklist Committee into 4 allopatric species (Chesser et al. 2010). Our study is in line with the taxonomic revision above and our conclusions are based on multiple lines of evidence with robust data to support the taxonomic split of the *A. striatus* complex in the Caribbean.

Taxonomic Implications

Vieillot (1807, p. 43, pl. 14) based his description of "*Accipiter striatus*" on a single specimen in his personal collection and mentioned that the only place he encountered the species was in western Hispaniola: "Je n'ai rencontré cette espèce qu'à Saint-Domingue" (= modern day Haiti). His comment "le devant de cou, la poitrine et les tempes, d'un roux clair" ("the front of neck, chest and temples, a light reddish color") confirms that his specimen was of the Hispaniolan resident population and not a North American migrant. The next author to describe a taxon in the Sharp-shinned Hawk complex was Wilson (1812, p. 116, pl. 45), who based his "Sharp-shinned Hawk/*Falco velox*" on a specimen collected "on the banks of the Schuylkill, near Mr. Bartram's" (= Philadelphia, PA, USA). To reconcile nomenclature with our updated understanding of Sharp-shinned Hawk phylogeography, in conjunction with our morphometric analysis and diagnostic plumage characters in the published literature (Wetmore 1914), we consider that the name *A. striatus* Vieillot 1807 should be limited to the resident population on the island of Hispaniola, and that it and the Cuban and Puerto Rican taxa should be elevated to species rank, the latter 2 as *A. fringilloides* Vigors, 1827 and *A. venator* Wetmore, 1914, respectively.

When *A. striatus* is treated as endemic to Hispaniola, the oldest available name for the continental complex

is *A. velox* (Wilson 1812), type locality Philadelphia, Pennsylvania, which applies to populations that occur during the breeding and migratory periods in continental North America from "Alaska and Canada, north almost to treeline … south locally to central California, Texas, and the northern parts of the Gulf states" (Peters 1979, 1, p. 343). The results of our haplotype network analysis suggest that further refinement of species limits within mainland taxa is required, but the taxonomic rankings of resident populations in Haida Gwaii, Central America, and South America are beyond the scope of this study. Therefore, we propose retaining their current classification as subspecies of *A. velox* (Wilson 1812) until additional data are analyzed.

Conclusion and Conservation Implications

The Sharp-shinned Hawk has historically been considered a polytypic species with a broad distribution in the western hemisphere, but our results demonstrate that island taxa from Cuba, Hispaniola, and Puerto Rico (1) form a genetically and morphologically divergent clade that is diagnosable from mainland populations, (2) are genetically diagnosable and divergent from each other, and (3) are more appropriately treated at species rank. The endemic *Accipiter* hawks of the Caribbean islands should be considered as high conservation priorities because of recent population declines resulting from habitat loss, invasive parasitic flies, expansion of nest predators, and hurricanes (Delannoy and Cruz 1991, Gallardo and Vilella 2017). Historically, federally listed Caribbean taxa have been the beneficiary of conservation actions and funding at rates disproportionately lower than mainland taxa (Restani and Marzluff 2002, Luther and Gentry 2019). Based on multiple lines of molecular and morphological evidence, we advocate that the *Accipiter* hawks of the Caribbean islands be appropriately recognized as an underappreciated, endemic island radiation of species that require immediate conservation funding and protective action, before these small, declining populations succumb to extinction.

SUPPLEMENTAL MATERIAL

Supplementary material is available at *Ornithology* online.

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Author contributions: T.A.C., J.A.J., R.T., J.C.G., and J.D.W. designed the study; T.A.C., M.R.H., C.P.T., and S.P. collected data; T.A.C., M.R.H., and J.M.A. analyzed data; T.A.C. and M.R.H. wrote the paper with edits from all authors.

Data availability: Raw Sequencing Reads are deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (PRJNA701772). Scripts are available on github (https://github.com/juliema) or as noted in the Methods section. Data is available from Catanach et al. (2021).

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