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Freshwater parasites as potential barriers to seabird dispersal: Evidence from vagrant booby specimens in western North America

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ABSTRACT—Inland vagrancy and overland dispersal by seabirds are rare phenomena for which the causes and consequences are poorly understood. Studying inland occurrences of seabirds is important because continental land masses form barriers to dispersal of genes and parasites; thus, the permeability of land barriers influences the extent to which seabird populations evolve on separate trajectories and co-evolve with distinct parasite faunas. The boobies (*Sula* spp.) are a clade of saltwater-obligate species occurring in tropical and subtropical oceans. Booby species tend to exhibit population genetic structure among oceanic regions. Although they rarely wander inland, the Brown Booby (*Sula leucogaster*) has occurred numerous times as a vagrant in interior North America. Previous inland records from far western North America originated from Pacific populations (subspecies *brewsteri*), whereas those from eastern and midwestern North America originated from Caribbean populations (subspecies *leucogaster*). In this paper, we describe 2 new specimens of *S. leucogaster*, first state records for New Mexico and Colorado, salvaged from localities nearly equidistant from Pacific and Caribbean source populations. We used mitochondrial DNA sequences to conclusively demonstrate that both specimens originated in the Caribbean. We next examined the helminth parasite fauna of the 2 *S. leucogaster* specimens and an inland-vagrant Blue-footed Booby (*S. nebouxii*) from New Mexico. The guts of these boobies contained a suite of helminths, including multiple freshwater-obligate taxa. Based on our findings, we suggest that susceptibility to freshwater parasites may cause overland dispersal to fail for boobies, or other seabirds. Thus, freshwater parasites may contribute to explaining the relative rarity of transcontinental dispersal, maintenance of strong inter-ocean population genetic structure, phylogenetic conservatism of specialization on salt-water habitats, and the strictly pelagic distributions of ocean-dwelling species from several avian families. *Received 16 September 2022. Accepted 11 August 2023.*

Key words: freshwater, helminth, parasite, specimen, *Sula*, vagrancy.

Parásitos de agua dulce como barreras potenciales de dispersión de aves marinas: Evidencia de especímenes de alcatraces errantes del oeste de Norte América

RESUMEN (Spanish)—La errancia y dispersión en tierra adentro de las aves marinas son fenómenos raros cuyas causas y consecuencias se entienden poco. Estudiar registros en tierra adentro de aves marinas es importante ya que las masas continentales forman barreras a la dispersión de genes y parásitos; por lo tanto, la permeabilidad de las barreras terrestres influye en qué tanto las poblaciones de aves evolucionan en trayectorias distintas y co-evolucionan con faunas parásitas distintas. Los alcatraces (*Sula* spp.) constituyen un clado de especies obligadas de agua salada que se encuentran en oceános tropicales y subtropicales. Las especies de alcatraces tienden a exhibir estructura genética poblacional entre regiones oceánicas. Aunque raramente deambula en tierra firme, el alcatraz pardo (*Sula leucogaster*) se ha reportado muchas veces como errante en tierra adentro de Norteamérica. Previos reportes de tierra adentro en el lejano oeste Norteamericano se originaron de poblaciones del Pacífico (subespecies *brewsteri*), mientras que los del este y el medioeste de Norteamérica se originan de poblaciones del Caribe (subespecie *leucogaster*). En este artículo, describimos 2 especímenes nuevos de *S. leucogaster*, primeros registros estatales para Nuevo México y Colorado, procedentes de localidades casi equidistantes de poblaciones fuente de Pacífico y el Caribe. Utilizamos secuencias de ADN mitocondrial para mostrar conclusivamente que ambos especímenes se originaron en el Caribe. Luego, examinamos la fauna de helmintos parásitos de ambos especímenes de *S. leucogaster* y de un alcatraz de patas azules (*S. nebouxii*) que vagaba tierra adentro en Nuevo México. Los intestinos de estos alcatraces contenían una serie de helmintos, incluyendo varios taxa obligadas de agua dulce. Con base en nuestros hallazgos, sugerimos que la susceptibilidad a los parásitos de agua dulce puede ocasionar que la dispersión en tierra adentro no sea exitosa para los alcatraces u otras aves marinas. Por lo tanto, los parásitos de agua dulce pueden contribuir a explicar la relativa rareza de la dispersión transcontinental, el mantenimiento de la fuerte estructura genética inter-oceánica, la conservación filogenética de la especialización en hábitats de agua salada y la distribución estrictamente pelágica de especies oceánicas pertenecientes a varias familias de aves.

Palabras clave: agua dulce, errancia, espécimen, helmintos, parásito, *Sula*.

At least 254 bird species from 11 families are restricted to saltwater habitats (Howell and Zufelt 2019). The volant seabird species are strong fliers, characterized by high aspect-ratio wings. It is therefore paradoxical that most widespread seabird species exhibit inter-oceanic population structure, suggesting that their dispersal is limited by continental land barriers. High natal site fidelity at the level of specific islands or archipelagoes is an evolved trait in seabirds that may contribute to population genetic structure and speciation (Bried and Jouventin 2001, Friesen et al. 2007, Taylor et al. 2018). Breeding populations of

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widespread oceanic species can be separated by thousands of kilometers of island-less ocean, or by land barriers, either of which can limit dispersal and reinforce population structure (Wooller et al. 1992, Avise et al 2000, Steeves et al. 2003, Morris-Pocock et al. 2010). For example, the island-less Eastern Pacific Basin is an effective barrier to maternally mediated gene flow in Brown Boobies (*Sula leucogaster*; Steeves et al. 2003, Morris-Pocock et al. 2010), and the Isthmus of Panama maintains genetic structure between Pacific and Atlantic Ocean populations of several tropical seabird species, including *S. leucogaster* (Steeves et al. 2003). An outstanding question is why highly volant seabirds exhibit such strong philopatry, strict preference for saltwater habitats, and aversion to overland dispersal.

Host organism distribution, evolution, and ecology can be illuminated by study of parasite species assemblages (Hoberg 1996, Marcogliese and Cone 1997, Marcogliese 2004, Nakama 2018), which provide a plethora of information about community food webs, host–parasite ecology, migration, population dynamics, coevolution, and habitat use (Williams et al. 1992; Balbuena and Raga 1994; Hoberg 1996; Marcogliese and Cone 1997; Brooks et al. 2006; Violante-González et al. 2011; Wagner et al. 2012; Locke et al. 2013; Galen and Witt 2014; Malcicka et al. 2015; Sheehan et al. 2016, 2017; Clark et al. 2018; Williamson et al. 2019; Lockley et al. 2020; Hoberg and Soudachanh 2021; McNew et al. 2021). Many parasites, particularly helminths (parasitic worms), can additionally elucidate trophic dynamics in ecosystems due to their complex life cycles, including dependency on multiple hosts at different trophic levels (Marcogliese and Cone 1997, Lafferty et al. 2008). Inland vagrant seabirds—or any host found outside of its expected range—provide an opportunity to ask whether parasite communities, such as helminths, change during vagrancy. Thus, analyzing parasite communities can reveal where a vagrant host has foraged, as well as possible negative impacts of parasite infections that are novel to the host (e.g., Ditmer et al. 2020).

S. leucogaster is a pantropical seabird that exhibits geographically structured populations and 4 subspecies that are subtly phenotypically distinguishable: *S. l. plotus* is found throughout the central and southwestern Pacific and Indian Oceans; *S. l. brewsteri* breeds in the eastern Pacific Ocean (i.e., Gulf of California region); *S. l. etesiaca* also breeds in eastern Pacific Ocean, generally farther south than *brewsteri* on offshore islands of Central and South America; and the nominate subspecies, *S. l. leucogaster*, is found in the Caribbean Sea, Gulf of Mexico, and east to the Cape Verde Islands (Nelson 1978, Schreiber and Norton 2020). MtDNA population structure in the species follows a similar though not identical pattern to the subspecies taxonomy: 4 major clades are found in the (1) Caribbean Sea, (2) central Atlantic, (3) central and southwest Pacific Ocean and Indian Ocean, and (4) eastern Pacific, respectively (Morris-Pocock et al. 2010, 2011). In the far southwestern United States, *brewsteri* is the expected inland vagrant and has been definitively documented in Arizona, California, and Nevada (Monson 1946, McMurry 1948, Phillips 1964, Lawson 1973). Over the last 2 decades, observations of *S. l. brewsteri* off the west coast of the United States have significantly increased, with records as far northward as Alaska (Morgan et al. 2009, Sullivan et al. 2009, Gibson and Withrow 2015). Over the same time period, in the eastern and central United States, inland vagrant records of the Caribbean form, *S. l. leucogaster*, have dramatically increased (Sullivan et al. 2009, Roy 2014, Skevington et al. 2015). To date, no *S. leucogaster* is known to have crossed the continent.

Here, we took advantage of a rare opportunity to characterize the helminth parasite assemblages and phylogeographic affinities in 3 vagrant seabirds, each of which had likely been foraging in freshwater habitats prior to its demise in far-interior North America. We examined 2 specimens of *S. leucogaster* that represented first state records of the species for New Mexico and Colorado, respectively, and 1 Blue-footed Booby (*Sula nebouxii*) specimen from New Mexico. We used mitochondrial DNA to determine geographic provenance of the *S. leucogaster* specimens, a method that has been shown effective when haplotype differences are fixed among source populations (e.g., Baumann et al. 2011, 2013; Johnson et al. 2011). Our results have potential implications for dispersal, vagrancy, and genetic population structure of bird species restricted to saltwater habitats.

Methods

Collection and preparation of specimens

The New Mexico *S. leucogaster* specimen (MSB:Bird:48800) was received by Desert Willow Wildlife Rehabilitation Center on 18 May 2018 after it was found perched on equipment near evaporation ponds by mining staff approximately 23 km southeast of Carlsbad. It was severely emaciated but responded well to initial care until it died on 1 June 2018. The specimen was transferred to the Museum of Southwestern Biology (MSB) at the University of New Mexico (UNM), where it was preserved as a dried study skin and partial skeleton, with frozen heart, muscle, liver, and brain tissues.

The Colorado *S. leucogaster* specimen (DMNS: Bird:45970) was first spotted in Lefthand Canyon west of Boulder on 22 June 2016. The bird was struck by a vehicle near Nederland, Colorado, a few days later, and was brought to the Birds of Prey Foundation in Broomfield, Colorado, for rehabilitation. Entry records indicated the bird suffered head trauma, was dehydrated, and emaciated. After treatment, the bird survived for several months in captivity and perished on 5 September 2016. The specimen was taken to the Denver Museum of Nature and Science where it was preserved as a dried study skin with a spread wing and partial skeleton and frozen heart, muscle, kidney, and liver tissues.

The New Mexico *S. nebouxii* specimen (MSB: Bird:40479) was found on 11 August 2013 at Chaparral Park in Lovington. Its health gradually declined during its stay at the park until it was eventually taken to Desert Willow Wildlife Rehabilitation Center on 13 August 2013. It died on 16 August 2013. The specimen was transferred to the MSB, where it was preserved as a dried study skin and partial skeleton, with frozen heart, muscle, and liver tissues.

Examination and identification of parasites

We examined the body cavities, hearts, livers, kidneys, and gastrointestinal tracts of the New Mexico *S. leucogaster* and *S. nebouxii* specimens for helminths, both by eye and with a dissecting microscope. Hearts, liver, kidneys, and intestinal veins were additionally screened by dissecting microscope for blood flukes (family Schistosomatidae). The small intestine, large intestine, and cecal contents were pooled and decanted. Helminths were separated by taxon and gross morphological similarity and saved in 80% ethanol. When multiple specimens of the same putative species were identified, several were saved in 95% ethanol and frozen for genetic work. A few trematodes and cestodes were mounted on slides and stained in alum potassium carmine, dehydrated in a series of ethanol concentrations, cleared in clove oil, and mounted in Canada balsam. The Colorado specimen of *S. leucogaster* was tested for West Nile virus and examined for gastrointestinal helminths.

We attempted to sequence a nuclear *28S* DNA barcode for the digenetic trematodes and a mitochondrial *nad1* for the Echinostomatidae trematodes. DNA was extracted from each putative trematode species using the QIAamp DNA Micro Kit (Qiagen, Valencia, CA, US). We followed manufacturer protocols but eluted samples with 30 mL buffer to increase DNA concentration. Extracted DNA was amplified by PCR (TaKara Ex Taq kit, Takara Biomedicals, Otsu, Japan) and sequenced with previously published primers *28S* nDNA region (U178, L1642 Lockyer et al. 2003), *nad1* mtDNA partial region forward NDJ11 (Morgan and Blair 1998), and reverse NDJ2a (Kostadinova et al. 2003) using the Applied Biosystems BigDye direct sequencing kit, version 3.1 (Applied Biosystems, Foster City, California, USA). Samples with both forward and reverse primers were sequenced on ABI 3130 sequencer at the UNM Molecular Biology Core Facility. Chromatograms were edited in Sequencher 5.0 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The length of usable sequence of *28S* varied from 500 to 1,200 bp and *nad1* from 390 to 450 bp. GenBank Accession numbers were assigned for *28S* (OQ211110–OQ2111130) and *nad1* (OQ249636 OQ249635).

All helminths recovered from *S. leucogaster* and *S. nebouxii* specimens, as well as host voucher specimens and frozen tissues, were deposited in the MSB to facilitate future research. Vouchered specimen records are searchable in the Arctos database (www.arctosdb.org) online (Table 1).

Test of host provenance using mtDNA

DNA was extracted from muscle tissue sampled from the New Mexico and Colorado *S. leucogaster* specimens using the Qiagen DNeasy Blood & Tissue Kit, following manufacturer protocol. The mtDNA gene CR2 was amplified via PCR using 1.25 μL AmpliTaq Gold DNA Polymerase (Applied Biosystems), 1X PCR Buffer II, 2.5 mM $MgCl_2$, 0.2 mM dNTP, 0.5 μM primer, and 1.25 ng template DNA for a total reaction volume of 25 μL. We used primers SdMCR-H750 (5′-GGGAACCAAAAGAGGAAAACC-3′) and SlMCR-L160A (5′-ATCCACATTGCACATTTAAA-3′) for the New Mexico booby specimen, and primers SdMCR-H750 and SlMCR-L162A (5'-CATTGCACATTTAAATYCC-3') for the Colorado booby specimen, as described in Morris-Pocock et al. (2010) and Steeves et al. (2005). The reaction annealing temperature was 61.5°C. Each sample was sequenced in both directions using dye terminator cycle sequencing on an ABI 3130 sequencer at the UNM Molecular Biology Core Facility.

Sequences were trimmed to match the gene fragment analyzed by Morris-Pocock et al. (2010). A total of 118 *S. leucogaster* CR2 sequences from Morris-Pocock et al. (2010) and 1 *S. leucogaster* CR2 sequence from Skevington et al. (2015) were downloaded from GenBank. All sequences (121 total) were aligned using the Geneious Prime default alignment. We estimated phylogenetic relationships using maximum likelihood in RAxML 8.2.10 (Stamatakis 2014). We used the GTR+GAMMA model of nucleotide substitution and conducted a rapid bootstrap analysis with 1,000 replicates, after which we searched for the best ML-scoring tree. We did not specify an outgroup during the analysis.

Previous records of vagrancy and helminths from *Sula* spp.

Inland records of *S. leucogaster* from the western United States were compiled from the literature (i.e., Roy 2014, Skevington et al. 2015), including eBird records (Sullivan et al. 2009) and published state bird records committee reports through the year 2020. We considered "inland" to include any record >65 km from a coastline. We also compiled an annotated list of previously published helminth taxa and localities from *Sula* species to put our findings into context.

Results

Specimen characteristics and data

The New Mexico *S. leucogaster* specimen, a female, weighed 713.7 g upon intake and 950 g at the time of preparation. Its ovary measured 18 × 7 mm, ova were 1.5 mm in diameter, and the oviduct was straight and 2.5 mm wide. It had a bursa of Fabricius measuring 11 × 1.5 mm. The bird had trace fat, was molting the sixth rectrix on each side of its tail, and had trace body, neck, and head molt. Wing chord measured 412 mm and tail length was 189 mm.

The Colorado *S. leucogaster* specimen weighed 940 g at the time of preparation (i.e., after a period in captivity). Wing chord and total body length were measured at 389 and 660 mm, respectively. The preparator was unable to find gonads; thus sex determination as female is based on plumage. The specimen had light fat and no molt.

The New Mexico *S. nebouxii* specimen was a male that weighed 721.5 g at preparation. Its left testis measured 10 × 2 mm and its right 8 × 2 mm. It had a bursa of Fabricius measuring 20 × 8 mm. It had no fat and no molt. The wing chord measured 382 mm and tail length was 157 mm.

Parasite findings and identifications

We tentatively recovered at least 14 species, but as many as 19 species, of helminth from the New Mexico *S. leucogaster* specimen (Fig. 1), and at least 9 species, but as many as 12 species, of helminth from the *S. nebouxii* specimen. Helminths were found only in the liver and intestine. More detailed examinations and summary of helminth species can be made later from our deposited

Table 1. List of helminth taxa recovered from host species of *Sula* and *Morus*, from the Caribbean Sea and Gulf of Mexico including tentative identifications from this study (host in bold). Life cycles are listed as marine or freshwater as is known. This table does not list all the hosts from which any one of the listed helminth species has been found, nor is it exhaustive. The number of helminths (*n*) found is listed only for this study.

Helminth	Host	*n*	Life cycle	Locality	Reference	MSB catalog number
TREMATODA						
Digenea sp.	***Sula nebouxii***	1	unknown	New Mexico, USA	This study	MSB:Para:28948
Echinostomatidae						
Drepanocephalus spathans	***Sula leucogaster***	7	freshwater	New Mexico, USA	This study	MSB:Para:27859
	Sula nebouxii	1	freshwater	New Mexico, USA	This study	MSB:Para:35966
	Sula leucogaster		freshwater	Caribbean waters of Colombia	Rietschel and Werding 1978	
Echinoparyphium-like sp.	***Sula nebouxii***	8	unknown	New Mexico, USA	This study	MSB:Para:18947
Echinoparyphium-like sp.	***Sula leucogaster***	2	unknown	New Mexico, USA	This study	MSB:Para:29146
Paryphostomum parvicephalus	***Sula leucogaster***		unknown	Caribbean waters of Colombia	Rietschel and Werding 1978	
Stephanoprora denticulata	*Morus bassanus*		Freshwater/brackish/ marine	Florida, USA	Nakama 2018	
Psilostomatidae						
Ribeiroia ondatrae	***Sula leucogaster***		freshwater	Caribbean waters of Colombia	Rietschel and Werding 1978	
	Morus bassanus		freshwater	Florida, USA	Nakama 2018	
Cyathocotylidae						
Mesostephanus microbursa	***Sula nebouxii***	20	marine	New Mexico, USA	This study	MSB:Para:18946
	Sula nebouxii		marine	Mexico	Rubio-Godoy et al. 2011; Hernandez-Cruz et al. 2017	
Mesostephanus sp.	***Sula leucogaster***	14	likely marine	New Mexico, USA	This study	MSB:Para:27860
Mesostephanus fajardensis	***Sula leucogaster***		marine	Puerto Rico, Brazil	Price 1934, Cable 1960	
	Sula dactylatra		marine	Colombia	Velez 1980	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
Mesostephanus appendiculatoides	***Sula leucogaster***		marine	Puerto Rico	Cable 1960	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
Diplostomatidae						
Hysteromorpha triloba	***Sula leucogaster***	7	freshwater	New Mexico, USA	This study	MSB:Para:27861
Posthodiplostomum sp. 1	***Sula leucogaster***	50	freshwater	New Mexico, USA	This study	MSB:Para:27863
Posthodiplostomum sp. 2	***Sula leucogaster***	15	freshwater	New Mexico, USA	This study	MSB:Para:29139
Posthodiplostomum pricei	*Morus bassanus*		freshwater	Florida, USA	Nakama 2018	

Table 1. Continued.

Helminth	Host	*n*	Life cycle	Locality	Reference	MSB catalog number
Bursatintinnabus bassanus	*Morus bassanus*		unknown	Texas, Gulf of Mexico, USA	Tehrany et al. 1999	
Bursacetabulus morus	*Morus bassanus*		unknown	Texas, Gulf of Mexico, USA	Tehrany et al. 1999	
Diplostomatidae 2–4 spp.	***Sula leucogaster***		unknown	New Mexico, USA	This study	MSB:Para:27867
	Sula nebouxii	30	unknown	New Mexico, USA	This study	MSB:Para:28949 MSB:Para:29138 MSB:Para:29139 MSB:Para:27867
Strigeidae						
Strigeidae at least 2 spp.	***Sula nebouxii***		unknown	New Mexico, USA	This study	MSB:Para:25661
Strigeidae sp.	***Sula leucogaster***	1	unknown	New Mexico, USA	This study	MSB:Para:27866
Ichthyocotylurus erraticus	*Morus bassanus*		Freshwater/brackish/ marine	Florida, USA	Nakama 2018	
Immature Strigeidae	*Morus bassanus*		unknown	Florida, USA	Nakama 2018	
Opisthorchiidae						
Amphimerus-like sp. (liver)	***Sula leucogaster***	38	freshwater	New Mexico, USA	This study	MSB:Para:27856
Clinostomidae						
Clinostomum sp.	***Sula nebouxii***	2	freshwater	New Mexico, USA	This study	MSB:Para:18945
Heterophyidae						
Heterophyidae 1–3 spp.	***Sula nebouxii***	9	unknown	New Mexico, USA	This study	MSB:Para:28950
Heterophyidae 1–3 spp.	***Sula leucogaster***	6	unknown	New Mexico, USA	This study	MSB:Para:27862
Ascocotyle longa	***Sula leucogaster***	5	marine	New Mexico, USA	This study	MSB:Para:32435
	Sula leucogaster		marine	Caribbean waters of Colombia	Rietschel and Werding, 1978	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
Galactosomum puffini	***Sula nebouxii***		marine	Mexico	Rubio-Godoy et. al. 2011	
	Sula leucogaster		marine	Puerto Rico	Cable 1960	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
Galactosomum cochlear	***Sula leucogaster***		marine	Brazil	Travassos 1928	
Galactosomum conchleariforme	*Sula dactylatra*		marine	Colombia	Velez 1980	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
Galactosomum johnsoni	***Sula leucogaster***		marine	Puerto Rico	Price 1934, Cable 1960	
	Sula dactylatra			Colombia	Velez 1980	
Galactosomum spinetum	*Morus bassanus*		marine	Florida, USA	Nakama 2018	

Table 1. Continued.

Helminth	Host	*n*	Life cycle	Locality	Reference	MSB catalog number
Galactosomum darbyi	*Morus bassanus*		marine	Florida, USA	Nakama 2018	
Galactosomum sp.	***Sula leucogaster***		marine	New Mexico, USA	This study	MSB:Para:27862
Galactosomum sp.	***Sula nebouxii***		marine	New Mexico, USA	This study	MSB:Para:28950
Opisthometra planicollis	***Sula nebouxii***		marine	Mexico	Rubio-Godoy et. al. 2011	
	Sula leucogaster		marine	Brazil	Travassos et. al. 1969, Thatcher 1993	
	Sula leucogaster		marine	Colombia	Velez 1980	
	Sula leucogaster		marine	Puerto Rico	Cable 1960	
	Sula leucogaster	1	marine	New Mexico, USA	This study	MSB:Para:32436
	Sula dactylatra		marine	Colombia	Velez 1980	
Scaphanocephalus expansus	*Morus bassanus*		marine	Florida, USA	Nakama 2018	
CESTODA						
Dilepididae	***Sula leucogaster***	22	likely marine	New Mexico, USA	This study	MSB:Para:27858 MSB:Para:27857
Dilepididae	***Sula nebouxii***	1	likely marine	New Mexico, USA	This study	MSB:Para:25662
Tetrabothriidae						
Tetrabothrius bassanus	*Morus bassanus*		marine	Caribbean waters	Burt 1978	
Tetrabothrius sp.	***Sula nebouxii***		marine	Mexico	Rubio-Godoy et al. 2011	
	Morus bassanus		marine	Florida, USA	Nakama 2018	
ACANTHOCEPHALA						
Polymorphidae						
Polymorphidae sp.	***Sula leucogaster***	1	unknown	New Mexico, USA	This study	MSB:Para:27865
Andracantha mergi	*Morus bassanus*		marine	Florida, USA	Nakama 2018	
NEMATODA						
Nematode sp.	***Sula leucogaster***	1	unknown	New Mexico, USA	This study	MSB:Para:27864
Contracaecum pelagicum	***Sula leucogaster***		likely marine	Brazil	Silva et al. 2005	
	Morus bassanus		likely marine	Florida, USA	Nakama 2018	
Porrocaecum sp.	***Sula nebouxii***		unknown	Mexico	Rubio-Godoy et al. 2011	
Tetrameres sp.	***Sula nebouxii***		unknown	Mexico	Rubio-Godoy et al. 2011	
Contracaecum sp.	***Sula nebouxii***		unknown	Mexico	Rubio-Godoy et al. 2011	

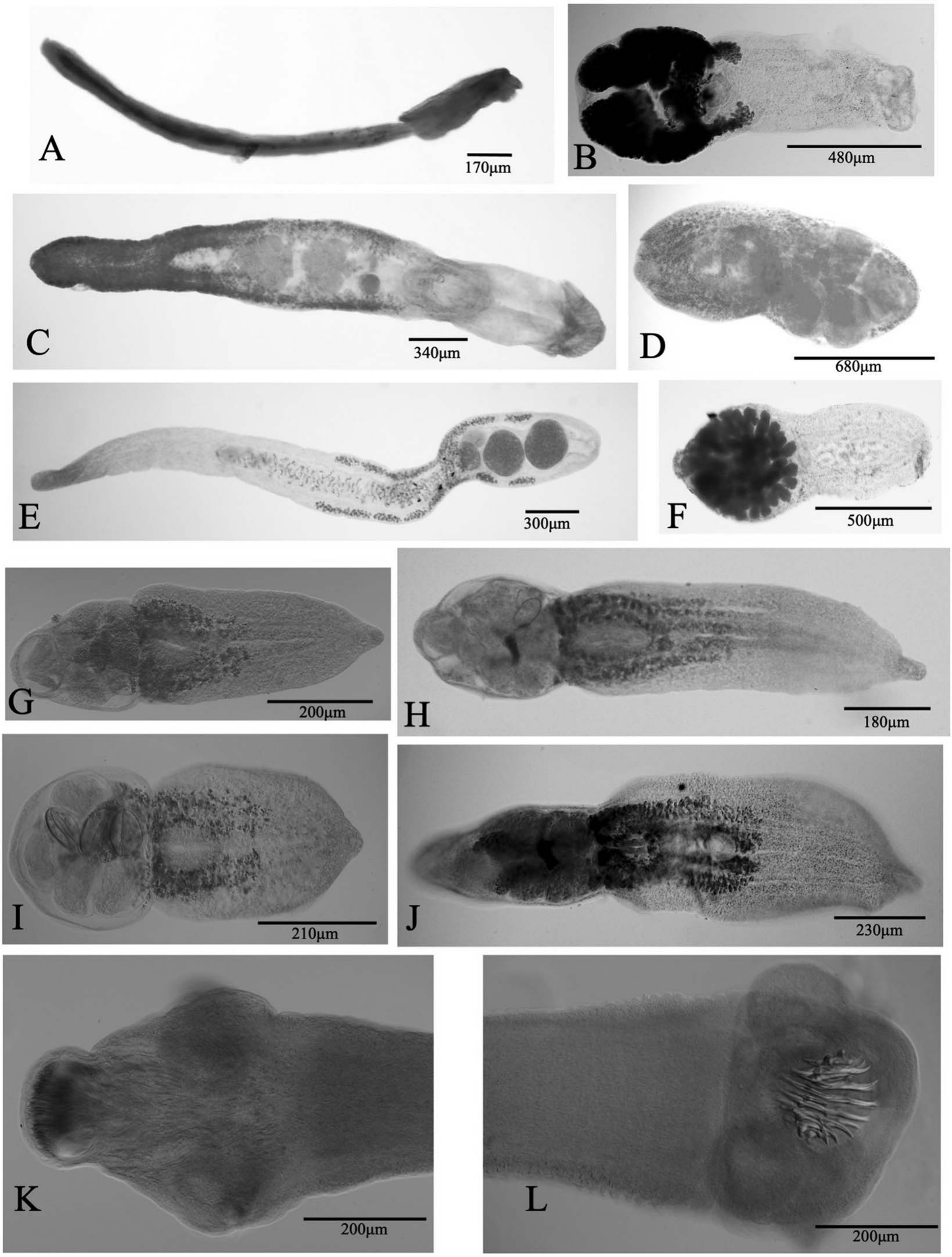

Figure 1. Selected images of flatworms found in the *Sula leucogaster* specimen from New Mexico. (A) Strigeidae (MSB: Para:25661), (B) Heterophyidae (MSB:Para:27862), (C) Drepanocephalus (Echinostomatidae; MSB:Para:27859), (D) Hysteromorpha (Diplostomidae; MSB:Para:27861), (E) Amphimerus-like (Opisthorchiidae, MSB:Para:27856), (F) Mesostephanus (Cyathocotylidae, MSB:Para:18946), (G) Posthodiplostomum (Diplostomidae; MSB:Para:27867), (H) Posthodiplostomum (Diplostomidae; MSB:Para:27863), (I) Posthodiplostomum (Diplostomidae; MSB:Para:35967), (J) Posthodiplostomum (Diplostomidae; MSB:Para:29139), (K–L) Dilepididae (Cestoda; MSB:Para:27857; MSB:Para:27858).

museum vouchers (Table 1). The cestodes and digenetic (having 2 or more hosts in the life cycle) trematodes were all mature. The maturity of the *Echinoparyphium*-like worm, nematode, and acanthocephalan was not determined. The helminth taxa identified from both New Mexico *Sula* specimens included species previously reported from the Family Sulidae (Table 1). Although we attempted to get a *28S* partial sequence for most trematodes and *nad1* for the Echinostomatidae, primers only worked for a few taxa (Table 1). A total of 6 trematode identifications were corroborated by *28S* and *nad1* partial gene sequence barcodes, out of the tentative 20 putative trematode species from both birds.

We recovered at least 6 putative species of freshwater digenetic trematodes from both of the New Mexico *Sula* specimens. *Hysteromorpha* sp. and an opisthorichiid *Amphimerus*-like trematode were recovered from *S. leucogaster,* and *Clinostomum* sp. was recovered from *S. nebouxii*. At least 2 species of *Posthodiplostomum* and a *Drepanocephalus* sp. were recovered from both individuals.

Nematodes are common in marine birds; however, no nematodes were found in *S. nebouxii* and we found only 1 very small, thin nematode from the small intestine of *S. leucogaster* (Table 1). Similarly, we did not find acanthocephalans from *S. nebouxii* and found only a single individual from the small intestine of *S. leucogaster* (Table 1). Without species-level identifications of the nematode and acanthocephalan species, it was not possible to know whether their life cycles occur in freshwater or saltwater.

We found no endo- or ectoparasites from the Colorado *S. leucogaster* specimen, which was not unexpected due to the bird's extended stay in rehabilitation. However, the bird tested positive for West Nile virus.

Origin of vagrants and previous inland Brown Booby records from North America

Our maximum-likelihood phylogeny placed both the New Mexico and Colorado *S. leucogaster* specimens within the Isla Monito haplotype of the Caribbean clade of *S. l. leucogaster* (Fig. 2). In total, 9 states in the western United States have records of inland *S. leucogaster* (Fig. 3, Supplemental Table S1). All records involved single individuals except for Lake Mead, Nevada (1971; 2 birds), Benbrook Lake, Texas (2016; 2 birds), and Salton Sea, California. In the Salton Sea, an inland lake with salinity approximately 2-fold higher than that of seawater, *S. leucogaster* is a rare but regularly occurring post-breeding disperser in summer and fall, with high counts of 8 individuals in 1970 and 1990, respectively (Patten et al. 2003).

Discussion

Recent work suggests that parasites of seabirds and other waterbirds are important as indicators of environmental quality, biogeography, coevolutionary history, ecology, and trophic dynamics (Hoberg 1996; Marcogliese and Cone 1997; Sures et al. 1999; Marcogliese 2004; Hoberg 2005; Locke et al. 2013, 2014; Mendes et al. 2013; Nakama 2018; Hoberg and Soudachanh 2021). Helminth assemblages of seabirds are known to vary due to host phylogeny, geography, foraging habitat, prey species composition, diet breadth, trophic position, ontogenetic or seasonal shifts in diet, or host–host interactions (Hoberg 1996, Marcogliese 2004, Sukhdeo and Hernandez 2005, Locke et al. 2013, Nakama 2018). Here we collected novel data on helminth assemblages of wild collected seabirds that perished after wandering to freshwater habitats, allowing us to test whether inland vagrant seabirds are potentially susceptible to freshwater helminth parasites. Because the parasite communities of freshwater and saltwater tend to be distinct, it is possible that saltwater-obligate avian hosts could be susceptible to novel parasites when they wander to freshwater habitats. Susceptibility to novel parasites is an evolutionary force that would be expected to favor philopatry and habitat specialization (Ricklefs 2010). On longer time scales, it is plausible that this mechanism could help to explain the known tendency for evolutionary conserved habitat preferences across the phylogeny of birds (Hackett et al. 2008, Feng et al. 2020).

Few previous studies have included helminth examinations of sulids from the Pacific or Atlantic oceans. We identified several notable genera of digenetic trematodes (*Drepanocephalus*, *Posthodiplostomum*, *Hysteromorpha*, *Amphimerus*, *Ascocotyle*,

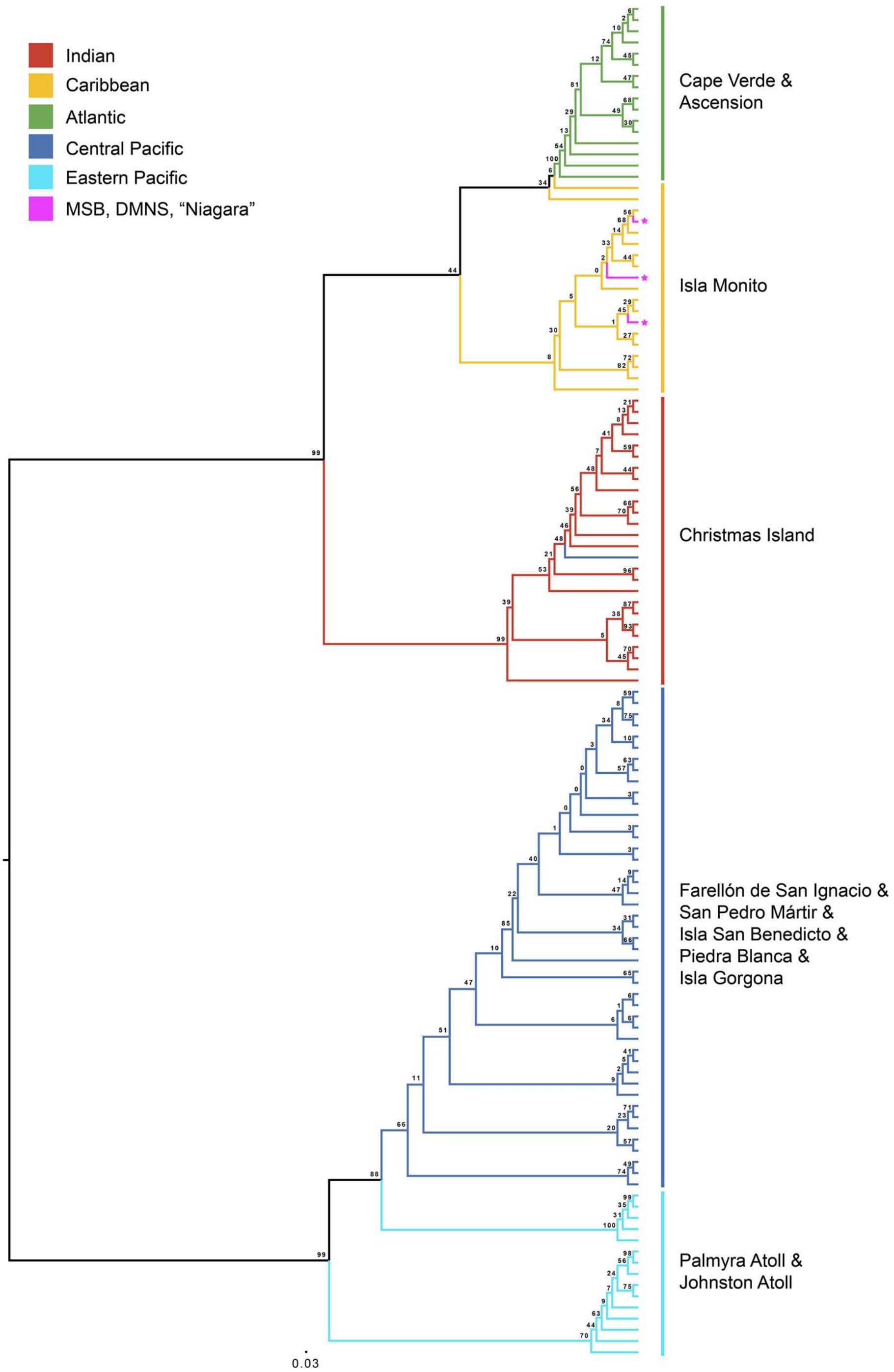

Figure 2. Phylogenetic relationships among *Sula leucogaster* haplotypes. Museum of Southwestern Biology (MSB), Denver Museum of Nature and Science (DMNS), and the "Niagara" bird recorded by Skevington et. al. (2015) were placed to the Isla Monito haplotype in the Caribbean clade (indicated by pink stars and branches). The tree is midpoint rooted, with bootstrap percentages indicating strength of support for each node.

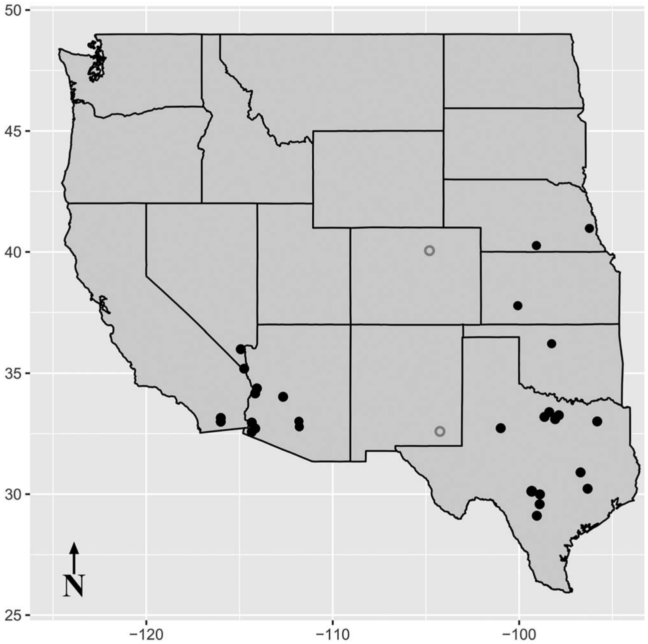

Figure 3. Inland *Sula leucogaster* records from the western United States from any time in the past through 2020. Open circles represent the new specimen records of *S. l. leucogaster* sampled from New Mexico (MSB:Bird:48800) and Colorado (DMNS:Bird:45970). Specimens east of the new records are presumed to be *S. l. leucogaster* of Caribbean (Atlantic) origin; those to the west are presumed to be *S. l. brewsteri* of Pacific origin.

Galactosomum, and *Mesostephanus*) from inland-vagrant booby specimens that have previously been identified from fish-eating waterbirds, the pelicans and cormorants, which use both freshwater and saltwater habitats (e.g., Travassos 1928, Price 1934, Alegret 1941, Cable 1960, Hutton and Sogandares-Bernal 1960, Pense and Childs 1972, Velez 1980, Threlfall 1982, Thatcher 1993, Dyer et al. 2002, Monteiro et. al. 2011, Rubio-Godoy et. al. 2011, O'Hear et al. 2014, Hernandez-Cruz et. al. 2017). The most recent studies of helminths of *S. leucogaster* off the Caribbean coast of Colombia (Rietschel and Werding 1978, Velez 1980) found the same genera (i.e., *Drepanocephalus*, *Galactosomum*, *Mesostephanus*, *Ascocotyl*, *Opisthometra*). A recent study of *S. nebouxii* off the western coast of Mexico (Rubio-Godoy et al. 2011) also identified 2 of the same parasite taxa, *Galactosomum* and *Mesostephanus*. A survey of Northern Gannets (*Morus bassanus*; a sister species to *Sula*) off the coast of Florida (Nakama 2018) had in common with our study species of *Posthodiplostomum*, *Galactosomum*, *Mesostephanus*, *Ascocotyl*, and Strigeidae (Table 1). Species of *Tetrabothrius* (the larvae of which are thought to occur in planktonic cephalopods or teleost fish intermediate hosts) are commonly reported in fish-eating seabirds, particularly in species of *Sula*, but they were not found in our specimens (e.g., Hoberg 1984, 1996).

Our discovery of 6 genera of putative freshwater helminths in a strictly marine host species raises the possibility that these sulids were exposed to novel parasites after foraging on freshwater fish in inland waters. We define freshwater helminths as those that have freshwater gastropods as their first intermediate host, and typically have freshwater fish as their second intermediate host (Sereno-Uribe et al. 2019, Romero-Alvarez et al. 2020). The freshwater helminth genera identified from the New Mexico *S. leucogaster* and *S. nebouxii* specimens (*Hysteromorpha*, *Posthodiplostomum*, *Amphimerus*-like, and *Clinostomum*) were previously unknown from *Sula*, a strictly marine seabird genus. It is possible that *Posthodiplostomum* is not a strictly freshwater helminth taxon, as a single record of *P. pricei* was recovered from another strictly marine sulid, *Morus* *bassanus*, from Florida (Nakama 2018). *Drepanocephalus*, a primarily freshwater helminth taxon found in both New Mexico *Sula* spp. specimens, was previously reported from *S. leucogaster* (Rietschel and Werding 1978). *Drepanocephalus* is considered a freshwater-obligate parasite (Hernandez-Cruz et al. 2017), but future genetic characterization and life cycle studies could uncover a marine connection by second intermediate host fishes (e.g., Beaver 1941, Gonchar and Galaktionov 2020) such as siluriforms (e.g., Alberson et al. 2022).

From the few large-scale studies of obligate saltwater-foraging seabirds, the family Alcidae has been found to harbor helminth taxa thought to be freshwater restricted, such as Strigeidae, Diplostomidae, and Echinosomatidae (Hoberg 1984, 1996; Muzaffar and Jones 2004). Previous work has shown that helminths from Caribbean *Sula* are similar to those from cormorants (Phalacrocoracidae); in particular, the 2 hosts tend to share *Drepanocephalus* sp. (Flowers et al. 2004, Monteiro et al. 2011, Sheehan et al. 2016, Hernandez-Cruz et al. 2017, Sereno-Uribe et al. 2019). Overlap in parasite taxa between these 2 bird families may be due to similar prey, similar body sizes (Hoberg and Soudachanh 2021), and phylogenetic relatedness (Hoberg 1996, Nakama 2018, Barrow et al. 2019). In sum, our evidence suggests that the New Mexico *S. leucogaster* and *S. nebouxii* specimens were exposed to and infected by freshwater helminths during vagrancy; however, scarce data on parasite systematics and life history makes this conclusion tentative for some helminth genera.

Inland vagrant infection from exposure to freshwater helminths would result if birds consumed infected prey and our findings suggest that the *Sula* specimens became infected after foraging in fresh water. For example, the life cycle of *Hysteromorpha* uses Planorbidae snails (*Gyraulus*, *Biomphalaria*) as a first intermediate host, several families of freshwater fish (e.g., Cyprinidae or Ameriuridae) as a second intermediate host, and waterbird species occurring in both freshwater and saltwater habitats (such as cormorants, pelicans, egrets, and herons) as the definitive host (Hugghins 1954, Lopez-Hernandez et al. 2019, Sereno-Uribe et al. 2019). In experimental work with *H. triloba* by Hugghins (1954), it took 14–15 d for cercariae to emerge from the snail host, 12 weeks for metacercariae to develop to maturity in fish, and 2.5 d for mature gravid adults to appear in cormorants after ingesting the metacercariae. The specimens of *H. triloba* identified from our study were mature, thus it is likely that the 2 boobies must have been foraging on freshwater fish for at least 2.5 d after dispersing inland. The greater the time spent in freshwater, the higher the probability to encounter an infected fish. Fish can remain infected with metacercaria over weeks, months, and years. The experimental life cycle of *Drepanocephalus spathans* similarly found eggs in the feces 3–8 d post exposure to metacercariae from fish (Alberson et al. 2022). The short time required for ingested metacercariae to mature are consistent with infection having occurred after wandering inland, but before being captured for rehabilitation; however, it is possible that the New Mexico *S. leucogaster* was exposed to novel helminths during its stay in rehabilitation, where it was briefly fed a combination of frozen and live minnows from a local bait shop. The New Mexico *S. nebouxii* did not survive long enough in rehabilitation to be fed whole food and was only given fluids and electrolytes; the freshwater taxa (e.g., *Posthodiplostomum* and *Clinostomum*) among its high diversity of mature helminths indicate that it foraged on infected fish during its time as an inland vagrant. More helminth survey data are needed to test whether *Hysteromorpha* and other putative freshwater helminths undergo their full life cycles in New Mexico, or whether these taxa could infect sulids not foraging in freshwater. It is plausible that obligate marine seabirds could be infected with putatively freshwater species of helminths if 1 or more of the intermediate hosts can move between freshwater and marine habitats. For example, some species in the family Diplostomidae or Strigeidae use as second intermediate hosts fishes that are anadromous or cataromous and have been found in freshwater and brackish water (e.g., Swennen et al. 1979, Marcogliese and Locke 2021, Pérez-Ponce de León et al. 2021) and may also cycle through gastropods (such as Hydrobiidae) that can tolerate a wide range of salinity (e.g., Skirnisson et al. 2004).

An outstanding question is whether freshwater helminths could be detrimental to the health of sulids or other seabirds; none of the helminths that we found were present in exceptionally high intensity, nor did we observe gross pathologies in the intestines or liver. However, the *Sula* specimens in this study provided unique insight into the helminth infracommunities of inland-vagrant seabirds: they contained obligate marine trematode taxa, part of the parasite infracommunity preceding vagrancy, as well as putative freshwater-obligate trematode taxa that appear to have been acquired after wandering inland. Because the freshwater helminths were not from taxa to which the seabird species were normally exposed and infected during their evolutionary history, they could plausibly threaten the survival of seabirds using freshwater habitats (Ricklefs 2010, Roy and St-Louis 2017).

It has become possible in recent years to examine the origins of migrating, dispersing, and vagrant birds using diverse approaches that include genetics, parasites and prey identification, stable isotope ratios, and microbiome characterization (Rubenstein and Hobson 2004, Engel et al. 2011, Locke et al. 2012, Levin et al. 2016). These varied techniques have also provided novel information about breeding or wintering locations and differential movements of populations of the same species (Paxton et al. 2013). Both the New Mexico and Colorado *S. leucogaster* specimens were unequivocally found to originate from the *S. l. leucogaster* population in the Caribbean Sea, based on mtDNA haplotypes (Fig. 2). Skevington et al. (2015) used mtDNA from feces to demonstrate that an individual *S. leucogaster* on Lake Erie had also originated from the Caribbean Sea. It is likely that all of the other inland records of *S. leucogaster* from the eastern half of North America (east of the New Mexico and Colorado specimens) were also of Caribbean origin, and that the records west of the New Mexico and Colorado specimens represent the eastern Pacific *brewsteri* population. As genetic resources and occurrence data for helminth parasites improve, we may be able to use DNA sequences of the museum-archived helminth specimens in this study to pinpoint their geographic origins, as well.

Both of the *S. leucogaster* specimens represented first state records, adding to the growing number of sightings of this species in the interior United States. Most inland records of *S. leucogaster* have occurred during the warmer months of the year during approximately May–September (Sullivan et al. 2009). New Mexico and Colorado in the western United States are each approximately equidistant from the Pacific and Atlantic Oceans. There are previous records of pelagic seabirds from New Mexico and Colorado originating from the Pacific Ocean, including Long-billed Murrelet (*Brachyramphus perdix*, MSB:Bird:29200; Sullivan et al. 2009, Witt et al. 2010), Ancient Murrelet (*Synthliboramphus antiquus,* MSB:Bird:9287, MSB:Bird:50983, DMNS:Bird:33827, DMNS:Bird:41653, DMNS:Bird:41654, DMNS:Bird:42662, UCM:Bird:6282; Sullivan et al. 2009), Blue-footed Booby (MSB:Bird:40479), Least Storm-Petrel (*Oceanodroma microsoma*, MSB:Bird:9087; Zimmerman 1992), and Elegant Tern (*Thalasseus elegans*; Sullivan et al. 2009). Seabirds originating from the Atlantic Ocean have also occurred in New Mexico and Colorado, including Sooty Tern (*Onychoprion fuscatus*; Percival 2009, Johnson et al. 2011) and Sandwich Tern (*Thalasseus sandvicensis*; Sullivan et al. 2009).

Storms have been implicated in inland vagrancy of seabirds; however, the strong winds of a storm may not be necessary for vagrancy to occur, nor for vagrants to perish. Favorable environmental conditions, such as seasonal shifts in prevailing wind direction, were found to have direct correlation with inland procellariid vagrancy, rather than tropical storms or El Niño Southern Oscillation events (Patten and Minnich 1997). The *S. leucogaster* and *S. nebouxii* specimens from New Mexico and Colorado seemingly were not driven inland by storms. Tropical Storm Danielle formed in the Bay of Campeche, Mexico, and made landfall in the state of Veracruz on 20 June 2016; 2 d later, the Colorado *S. leucogaster* was found in Boulder, Colorado, over 2,200 km away. Dispersal due to this tropical storm is plausible but seems unlikely given the distance and paltry strength of the storm. The New Mexico *S. leucogaster* was brought into rehabilitation on 18 May 2018, several days before the formation of Tropical Storm Alberto, the only named storm in the Gulf of Mexico that month. Prior to the *S. nebouxii* arriving in New Mexico on 11 August 2013, 2 named hurricanes (Gil and Henriette) were active in the

Eastern Pacific around the same time; however, both formed ∼2,000 km offshore southwest of the Baja Peninsula and continued westward before dissipating over open ocean, never making landfall. Dispersal related to these hurricanes is unlikely due to the distance and direction both moved after formation. Continued, thorough documentation of vagrant seabirds, especially the archiving of physical specimen materials, when possible, will provide useful information about drivers of dispersal patterns as well as causes of demise for dispersing individuals.

This study was made possible by careful salvaging, preparation, and curation of bird and parasite specimens for museum collections. Well-prepared scientific specimens can be used for genetic sequencing, parasite infracommunity characterization, isotope-ratio signatures, biochemical and trace element accrual, and 3-dimensional scanning, among a growing set of technology-driven uses (Schmitt et al. 2019). Salvaged specimens, in particular, provide unique opportunities for research because they are often the only material available for relatively rare species, such as inland-vagrant seabirds. Modern, "holistic" specimens offer the opportunity to integrate across different types of preserved materials that contain complementary information, such as we have done here by leveraging linked parasites, frozen tissues, and bird specimens. Salvaged bird specimens will continue to provide a valuable long-term resource for study of migration, dispersal, vagrancy, genomics, and the broader principles that underlie generation and maintenance of biodiversity. Accordingly, all of the samples preserved during this study are available to confirm or extend the present work (see Table 1 for searchable catalog numbers).

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