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REVIEW

Status and trends of American Flamingos (*Phoenicopterus ruber*) in Florida, USA

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ABSTRACT

American Flamingos (*Phoenicopterus ruber*) are a cultural icon of Florida, USA, yet their status in Florida has been controversial for nearly a century. There is uncertainty regarding historical baselines and long-term trends in flamingo populations, whether flamingo nesting has occurred in Florida, and whether recent observations are wild birds or escapees from captive populations. We review historical and contemporary information to clarify the status and trends of flamingos in Florida and to lay a scientific foundation for their management. We compile historical information from early naturalists and museum records to describe historical abundance, distribution, and phenology. We show definitive evidence for 19th-century flamingo flocks numbering hundreds to thousands of individuals, with large flocks recorded through the year. Historical flocks were heavily hunted, and there is strong evidence that hunting led to extirpation of the historical population by ~1900. One plausible description of nesting and 4 egg specimens apparently collected in Florida in the 1880s suggest that flamingos probably nested in Florida, though the evidence is not irrefutable. Citizen science data from 1950 to 2015 reveal directional population increases over this period. Contemporary observations reveal dispersal from a breeding colony in Yucatan, Mexico, to Florida, but no conclusive evidence is available for escapes into wild populations. Recent population increases in Florida are best explained by immigration from expanding nesting populations in the Caribbean, rather than increased numbers of escaped individuals. Resolving the long-standing controversy over the status and origin of Florida's flamingos will help develop appropriate evidence-based management strategies for this species—a culturally significant component of Florida's avifauna.

Keywords: citizen science, endangered species, Everglades, extirpation, introduced species, plume trade, population biology, waterbirds

Estatus y tendencias de *Phoenicopterus ruber* en Florida

RESUMEN

La especie de flamenco *Phoenicopterus ruber* es un ícono cultural de Florida, pero aun así el estatus de los flamencos en Florida sigue siendo controversial después de casi un siglo. Existen dudas sobre las líneas de base históricas y las tendencias de largo plazo de las poblaciones de flamenco, sobre la ocurrencia de eventos de anidación de flamencos en Florida y sobre si las observaciones recientes son aves silvestres o escapadas de poblaciones cautivas. En este estudio, revisamos información histórica y contemporánea para clarificar el estatus y las tendencias de los flamencos en Florida y para establecer una base científica para su manejo. Compilamos información histórica proveniente de los primeros naturalistas y de registros históricos para describir la abundancia, la distribución y la fenología históricas. Brindamos evidencia definitiva para el siglo 19 de la existencia de bandadas de flamencos de cientos a miles de individuos, con grandes bandadas registradas a lo largo del año. Las bandadas históricas fueron sometidas a una fuerte presión de caza, y existe evidencia contundente de que la caza llevó a la extirpación de la población histórica hacia ~1900. Una posible descripción de anidación y cuatro muestras de huevos colectados aparentemente en Florida en la década de 1880 sugieren que los flamencos anidaron probablemente en Florida, aunque la evidencia no es irrefutable. Los datos de ciencia ciudadana desde 1950 a 2015 revelan aumentos de población direccionales a lo largo de este periodo. Las observaciones contemporáneas revelan dispersión desde una colonia reproductiva en Yucatán, México, hacia Florida, pero no contamos con evidencia conclusiva de escapes hacia poblaciones silvestres. Los aumentos poblacionales recientes en Florida son mejor explicados por inmigración a partir de poblaciones reproductivas en expansión en el Caribe, más que por un aumento en el número de individuos escapados. La resolución de esta

controversia de larga data sobre el estatus y el origen de los flamencos de Florida ayudará a desarrollar estrategias de manejo apropiadas basadas en evidencia científica para esta especie, que representa un componente cultural importante de la avifauna de Florida.

Palabras clave: aves acuáticas, biología poblacional, ciencia ciudadana, comercio de plumas, especies en peligro, especies introducidas

American Flamingos (*Phoenicopterus ruber*; hereafter "flamingos") are a cultural icon of Florida, USA (Price 2000, Irvine and Arluke 2017), yet their status in Florida has been controversial for nearly a century (Bailey 1925, Howell 1932, Allen 1956, Millsap et al. 1990, Stevenson and Anderson 1994, Hunter et al. 2006). Early naturalists reported large flocks of flamingos from southern Florida until around 1900 (Audubon 1839, Wurdemann 1860, Scott 1890, Ingraham 1893, Howe 1902), after which they were nearly absent for decades (Allen 1956, Stevenson and Anderson 1994). Rare observations for most of the 20th century were typically discounted as escapees from captive populations (Bailey 1932, Allen 1956, Stevenson and Anderson 1994). In recent decades, flamingo sightings appear to be on the rise, though there remains uncertainty about whether flamingo sightings today represent wild individuals dispersing from nearby populations in the Caribbean or escaped birds from captive colonies.

It is also unclear whether flamingos seen historically were nesting in Florida or were transients from other populations. Some early naturalists (Wurdemann 1860, Scott 1890) argued that those birds were year-round residents and nested in Florida, although they did not themselves observe nesting. Other naturalists suggested that flamingos were only seasonal visitors that foraged in Florida but nested in the Bahamas or Cuba (Howell 1932, Holt 1933). The limited available evidence for historical nesting has been evaluated repeatedly by ornithologists (Sprunt 1937a, Allen 1956, Stevenson and Anderson 1994) yet remains controversial and conjectural.

Appropriate management strategies cannot be developed until there is a consensus on the status of flamingos within Florida and the United States. For example, Florida's Fish and Wildlife Conservation Commission has considered the American Flamingo a nonnative species—thereby ineligible for protection by state wildlife laws (Millsap et al. 1990). In sharp contrast, an evaluation of waterbird conservation priorities for the southeastern United States by the U.S. Fish and Wildlife Service considered flamingos to be nearly extirpated and urged recovery attention (Hunter et al. 2006).

Fortunately, new tools are emerging that may help to clarify the history and status of flamingos in Florida. Museum specimen data are increasingly digitized and accessible online (Constable et al. 2010), and citizen science projects increasingly produce new distribution and population data (Dunn et al. 2005, Sullivan et al. 2017). Further, new research on the ecology of flamingos throughout their range (Baldassarre and Arengo 2000, Bildstein et al. 2000, Galvez et al. 2016) permits the application of evidence-based insights that would not have been available to earlier biologists.

Here, we seek to clarify the status of flamingos in Florida by (1) synthesizing historical evidence to produce a historical baseline, (2) examining all evidence for historical nesting, (3) compiling a time-series of flamingo observations in Florida from 1950 to 2015, and (4) evaluating escape from captive populations and dispersal from the Caribbean as origins for Florida flamingos. Our general aim is to provide a scientific synthesis for management decisions for this iconic species—Florida's lost wading bird.

Historical Presence, Abundance, and Distribution

Evidence from narrative accounts. Here, we review early accounts of flamingos in Florida, in chronological order. We include all firsthand reports of which we are aware but exclude secondhand material that is not attributable to a specific observer. Historical narrative accounts—though often limited in detail—can provide insights toward appropriate historical baselines for population size, distribution, and phenology.

McCall (1868) killed one adult flamingo and 3 juveniles in the Anclote Keys, north of Tampa, in 1827. Audubon (1839) saw a flock near Indian Key (Upper Florida Keys) on May 7, 1832, but did not estimate the number of individuals. Audubon also saw "a great number" of flamingos in the Florida Keys in 1832, stating that they occurred on salt flats on Key West and were hunted by locals but were rare and restricted to southern and western Florida.

Wurdemann (1860) accompanied a local hunter on August 4, 1857, to a site northwest of Indian Key and saw a group of $\geq$500 flamingos. The hunter captured $>$100 flamingos and sold them for food in Key West. Apparently, capture by hand was possible because the birds were molting. Wurdemann also stated that flamingos were restricted to far southern Florida and that they were present year-round.

Ward (1914) said that "tens of thousands" of Roseate Spoonbills (*Platalea ajaja*) and flamingos fed at Pink Curlew Bar (south of Marco Island, Collier County) in 1880, though he did not directly estimate numbers of flamingos. He also reported 5 individuals from this site in 1886. Pierce (1962) accompanied a French naturalist

named LeChavelier on a plume-hunting expedition in the Florida Keys between March 11 and August 12, 1885 (Robertson 1962). Pierce saw one flamingo at Key Largo and 2 large flocks south of Pigeon Key (Upper Cross Bank, Florida Bay) sometime between April 1 and May 23, 1885. He provided no estimate of flock size and collected no flamingo specimens. Pierce reported that LeChevalier killed flamingos and sold their skins, but that they were rare, and noted that the price of a flamingo skin was $25, compared to $10 for Great White Herons (*Ardea herodias occidentalis*) and $0.50 for Brown Pelicans (*Pelecanus occidentalis*).

Ingraham (1893) saw 7 flamingos in "Caximas Bay" (likely Caxambas Bay south of Marco Island in Collier County) in the winter of 1884–1885 and collected at least one specimen there. He saw 31 flamingos several days later, a few miles east of Cape Sable (Monroe County). Shortly thereafter, he traveled to a shallow mud bay 15 miles wide (either Snake Bight, Garfield Bight, or Whitewater Bay), where he estimated >2,500 flamingos but was unable to obtain specimens. Ingraham returned to this site in the winter of 1885–1886, noted a flock of 1,000 flamingos over a period of 2 wk, and collected 6 specimens. In 1886–1887, he observed flamingos at the site over several weeks but made no estimate of numbers and collected no specimens. He stated that flamingos had been hunted for food in large numbers, both by Native Americans and by early settlers of Key West, and cautioned that hunting of such magnitude was likely to extirpate the population soon.

Scott (1890) saw ≥1,000 individuals, including 50 juveniles, at a site 18 miles east of Cape Sable (likely Snake Bight or Garfield Bight) in February 1890, collecting 3 specimens. A local man told Scott that this flock was present each year, from January through July, but dispersed around the keys in Barnes Sound and Biscayne Bay the rest of the year.

Howe (1902) reported a flock of 500–1,000 flamingos in a small bay to the east of Cape Sable (again, likely Whitewater Bay, Snake Bight, or Garfield Bight) on March 26, 1902. His observation was the last report of a flock of hundreds of flamingos from the 20th century; thereafter, observations were restricted to single birds, pairs, or small groups.

Ryman (1908) collected an individual in Lake Worth (Palm Beach County) in May 1905. Brodhead (1910) reported one individual killed by a hunter on March 7, 1906, near Upper Matecumbe Key. Holt (1924) wrote that 3 flamingos were seen in December 1923 on "Flamingo Bank" (likely the tidal flat just south of Flamingo Visitor Center in Everglades National Park). Stoddard (1928) saw a single flamingo in Wakulla County on the Florida Panhandle on September 24–25, 1927.

Howell (1932) reported 2 flamingos in March 1930 on Tamiami Trail near Miami, seen by Charles G. Wood, and one group of 14 flamingos in February 1931 just north of the Card Sound Bridge (Miami-Dade County). Holt (1933) reported one individual at Clive Key (Florida Bay) on May 11, 1932, and 4 individuals on October 1 and 11, 1932, near Buzzard Key (south of the mouth of the Chatham River, Everglades National Park). Howell (1937) reported one flamingo at Hobe Sound (near Jupiter) in August 1936. Sprunt (1937b) reported flamingos in the upper Florida Keys in May 1936 and 4 sightings of individual flamingos in the upper keys in September and October 1936. Sprunt (1939) reported individual flamingos seen near Tavernier and at Bottlepoint Key (now Bottle Key in Florida Bay) and 4 flamingos at Boca Chica Key (lower Florida Keys) in September and October 1938. Stimson (1939) reported 2 flamingos at West Lake (north of Florida Bay) on October 9 and 24 and December 19, 1938; one at West Lake on April 3, 14, and 15 and May 2 and 3, 1939; and reported that a hunter had recently shot a second individual. We are aware of no detailed written reports of specific observations between 1940 and 1950, although Sprunt (1954) and Allen (1956) indicated that flamingos were occasionally sighted around Miami, in Florida Bay, and in the Florida Keys.

Evidence from museum specimens. We searched the VertNet database of natural history collections (Constable et al. 2010) for all American Flamingo specimens collected within Florida, excluding specimens from captive colonies. When collection details (i.e. collector name, date, location) were unavailable, we asked curators or collection managers to provide these details.

VertNet yielded 16 wild flamingo specimens collected in Florida before 1904, and contact with museum staff yielded 6 additional specimens over this period (Table 1). Although at least 22 flamingo specimens were collected before 1904, only 7 flamingo specimens have been collected in Florida since 1904. No flamingo specimens were collected between 1904 and 1948, consistent with the period of fewest flamingo sightings in narrative accounts.

Historical baselines for population size and phenology. There is overwhelming evidence both from narrative accounts and from museum records that American Flamingos occurred naturally in large flocks in Florida and that the historical population was extirpated under strong hunting pressure by ~1900. While it is not possible to estimate a population size before collapse, estimates of flock sizes commonly ranged from 500 to 1,000 individuals (Wurdemann 1860, Scott 1890, Howe 1902) and included >2,500 individuals in one case (Ingraham 1893). Although flock size may serve as a minimum estimate for Florida population size, it is unclear whether one or more flocks existed in Florida before ~1900, and assumptions about the number of flocks would confound robust attempts to estimate population size. Further, all early naturalists mention hunting, and it is plausible that uncontrolled

TABLE 1. Adult American Flamingo specimens collected in Florida, USA, that are held in museums provide robust evidence for the historical presence of flamingos in Florida and confirm a timeline for their population decline. "ND" indicates no data. Asterisk indicates that the collection date is an estimate. Dagger indicates that a catalog entry or record of a specimen exists, but the specimen is lost or destroyed.

Specimen number	Collector	Date
ANSP 6116 [a]	ND	ND
USNM 8693†	Gustavus Wurdemann	August 6, 1857
USNM 8694†	Gustavus Wurdemann	August 6, 1857
USNM 8695†	Gustavus Wurdemann	August 6, 1857
USNM 8696†	Gustavus Wurdemann	August 6, 1857
USNM 8698	Gustavus Wurdemann	August 6, 1857
UMMZ 20587 [b]	Gustavus Wurdemann	August 6, 1857
MCZ 2746	J. E. Mills	March 6, 1858
MCZ 2747	J. E. Mills	March 6, 1858
MCZ 100685	Charles J. Maynard	May 1, 1870
USNM 202641	Pierre Louis Jouy	1874
USNM 84693	J. Scholl	Summer 1874
MCZ 229360	William E. D. Scott	February 25, 1890
MCZ 229361	William E. D. Scott	February 25, 1890
FMNH 47680	ND	Before 1893*
MCZ 301212	O. Tollin	March 1, 1898
MCZ 315289	"Howe-Shattuck Collection"	March 26, 1902
UF 19297	John Thomas	October 1904
ISM 600369	ND	Before 1918*
FSU 1505†	R. C. Hallman	June 22, 1948
FMNH 370865†	R. Lance	October 18, 1973
FMNH 375393	T. Dickel	April 12, 1974
FMNH 375394	T. Dickel	April 12, 1974
EVER 1834	Nancy Yawt	September 30, 2011
ISM 601147†	ND	ND
ISM 601148†	ND	ND
MCZ 76030	ND	ND [c]
UMMZ 27779	ND	ND
UMMZ 27780	D. P. Ingraham	ND [d]

[a] Donated to museum by Gustavus Wurdemann (who is a possible collector for this specimen). Possibly this specimen was formerly held as USNM 8693–8696.
[b] Formerly held as USNM 8697.
[c] No date is included with this specimen, but the catalog entry at MCZ reads "subs of 1851."
[d] Although no data are associated with this specimen at UMMZ, D. P. Ingraham reports collecting flamingos in Florida Bay between 1884 and 1886 (Ingraham 1893).

harvesting could have affected populations before the earliest count estimates in 1857.

Narrative accounts also provide useful phenological information for the population. Before 1902, large flocks ($\geq$500 birds) were sighted in midwinter (Ingraham 1893), February (Scott 1890), March (Howe 1902), May (Audubon 1839), and August (Wurdemann 1860). However, we have no reports of flocks in June, in July, or between September and November. Specimens were collected in February, March, April, May, August, and October (Table 1). Plausibly, flamingos could have left Florida during June and July or from September to November or could have had erratic or nonseasonal movement patterns. However, flamingos could also have been undetectable to early naturalists if they shifted seasonally to sites where they were inaccessible—such as Lake Ingraham, the interior wetlands of Cape Sable, Whitewater Bay, or wetlands of the interior Everglades.

Evidence for Historical Nesting

Early naturalists speculated regularly about nesting activity in Florida on the basis of their field observations and anecdotal reports they received; however, they produced no firm evidence (Audubon 1839, Wurdemann 1860, Ingraham 1893). Howe (1902) stated that a French naturalist, likely LeChavalier (Robertson 1962), had collected a juvenile bird that appeared too young to have flown a long distance, but we are not aware of any such specimen. Scott (1890) stated that the ovaries of 3 female flamingos he collected near Cape Sable on February 25, 1890, indicated that laying would begin in 4 or 5 wk (Table 1).

Sprunt (1937a) reported that a resident of the Florida Keys (E. R. Lowe) witnessed 40–50 flamingos "standing straddle of what I took to be whitish stumps" on Sugarloaf Key in March or April 1901. Plausibly these whitish stumps could have been flamingos' volcano-shaped mud nests. Sprunt (1937a) appeared to be convinced by this report, but Allen (1956) was skeptical. We are aware of no other plausible narrative reports of nesting within Florida.

Four egg specimens, ostensibly from American Flamingos collected in Florida, are recorded in museum collections:

- **YPM 149176**, a set of 2 eggs (Figure 1) held at Yale's Peabody Museum of Natural History (YPM) with a stated locality of "Florida Keys" and a date of "June 15 1884." On each egg is written "585," the number for American Flamingos in Ridgway's (1880) checklist of American birds. The egg card states that the specimen was loaned from "E. Wilkinson" but does not specify a collector. The common name, species binomial, and locality are in the handwriting of Edward Wilkinson—a naturalist and curator at the Mansfield Memorial Museum in Ohio (Smith and Mittleman 1943). The egg card is typical of those used by Wilkinson between 1886 and 1892 (S. Schaut personal communication); however, the collection date is not in Wilkinson's handwriting and it is not clear who added it to the egg card. Wilkinson did not appear to collect any other specimens in Florida, but he did collect egg specimens and also advertised in *The Oologist* to buy and exchange specimens. It is not clear whether this specimen includes 2 eggs from a single nest or eggs from 2 nests. It is also

FIGURE 1. YPM 149176, an American Flamingo egg specimen currently held at Yale University's Peabody Museum of Natural History, and associated egg card.

unclear when this specimen left Wilkinson's custody, but most egg specimens at YPM are from the collections of Louis B. Bishop and Henry O. Havemeyer, and it is likely that YPM 149176 came from one of those collections.

- **WFVZ 114710**, an egg (Figure 2) held at the Western Foundation for Vertebrate Zoology (WFVZ). On the egg is written "585 1/1." The egg card indicates that the specimen was collected by J. W. Mann on April 19, 1886, with a location of "Florida Keys, So. Florida." The "1/1" indicates that a single egg was present in the nest. The egg card describes the nest as "dirt and roots scraped up by bird lightly hollowed on top on the ground." The egg card was printed by T. Vernon Wilson, a dealer in birds' eggs, and also bears a stamp indicating that the egg was subsequently owned by Letson Balliet of Des Moines, Iowa. The egg card is apparently a copy, but we are unaware of any record of the original egg card. We are aware of no field notes from J. W. Mann, nor of any other specimens he collected for any taxon, location, or time. The specimen was acquired by the WFVZ from the Natural History Museum of Los Angeles County in 1979.
- **MCZ 362616**, an egg (Figure 3) held at Harvard University's Museum of Comparative Zoology (MCZ). On the egg is written "182 Flamingo Florida Keys 1887." The number "182" corresponds to the American Ornithologists' Union number given to American Flamingos in the first 3 editions of the *Checklist of American Birds* (first published in 1886). There is no information on the collector or description of the nest. The egg card indicates ownership by William G. F. and Richard G. H. Harris and that the egg is "From the Manly Hardy Collection." William G. F. Harris was the Curator of Oology at the Aggasiz Museum (now the MCZ). Manly Hardy was a naturalist and collector who acquired an extensive collection of specimens from North America (Krohn 2005). Following Hardy's death, his egg collection was inherited by his grandson, Paul F. Eckstorm, who was a friend of Harris (Krohn 2005). By 1945, the egg had passed to Harris, and then subsequently to the MCZ.
- **AMNH 15153**, an egg (Figure 4) held at the American Museum of Natural History (AMNH). On the egg is written "Amr. Flimingo" [*sic*], "March, 20 1889," "35," "1/1," and "Tampa, Florida" in red ink. In black text is written "1/1," "No. Eggs 1," "4/1," and "1821" or "182/". The original card lists the collector as E. C. Greenwood, but this card was written by Clarence A. Smith according to notes on a subsequent egg slip written in the handwriting of Dean Amadon (former curator at AMNH). "E. C. Greenwood" is likely Emery C. Greenwood, a naturalist who collected extensively in Florida and was a partner in the natural history dealer "Field & Greenwood" of Brownsville, Texas (Field 1889). Clarence A. Smith was a naturalist who made several collection trips to northern and central Florida and donated specimens to the AMNH in 1889, 1895, and after his death in 1896 (Anonymous 1896)—presumably AMNH 15153 arrived at AMNH by 1896. While the date appears to be March 20, 1889, it is unclear what "4/1," "1821," and "35" indicate. We are aware of no notes from Greenwood or Smith that would provide further details regarding this specimen.

Egg specimens provide the best evidence to date that flamingos historically nested within Florida. Still, museum records can be labeled erroneously (Chilton and Sorenson 2007, Boessenkool et al. 2010) or can be fraudulent (Rasmussen and Collar 1999). None of these egg specimens is accompanied by field notes, and the collection location of AMNH 15153 (Tampa) is questionable (Stevenson and Anderson 1994). Although 3 other egg specimens at AMNH that were collected by Greenwood are from southern Florida in 1889, and Greenwood made

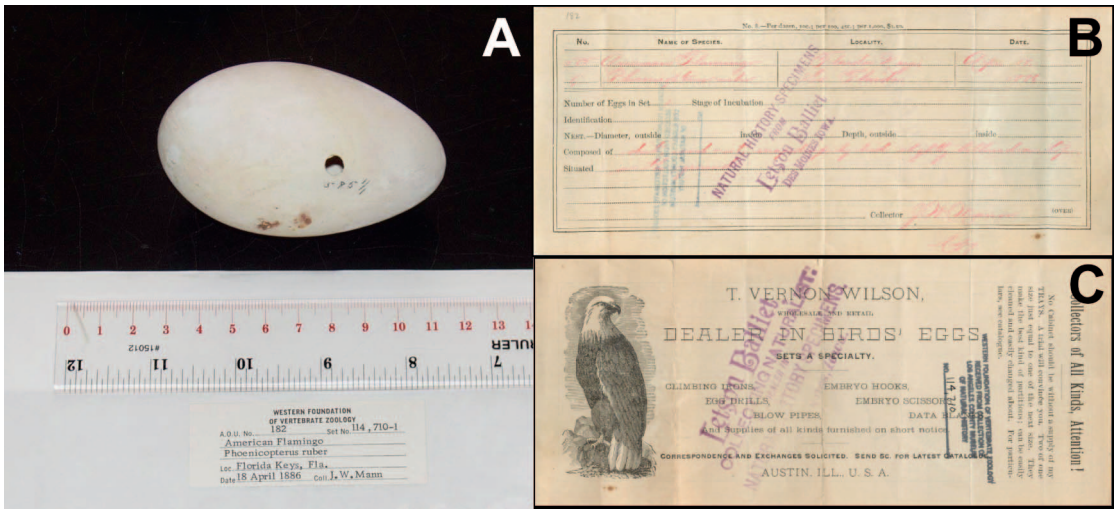

FIGURE 2. WFVZ 114710, an American Flamingo egg specimen currently held at the Western Foundation for Vertebrate Zoology (WFVZ). The locality reads "Florida Keys, Fla." and the date reads "18 April 1886." (**A**) Egg and WFVZ egg card. (**B**) The front of an egg card that arrived at WFVZ with the egg specimen and (**C**) the reverse of that egg card.

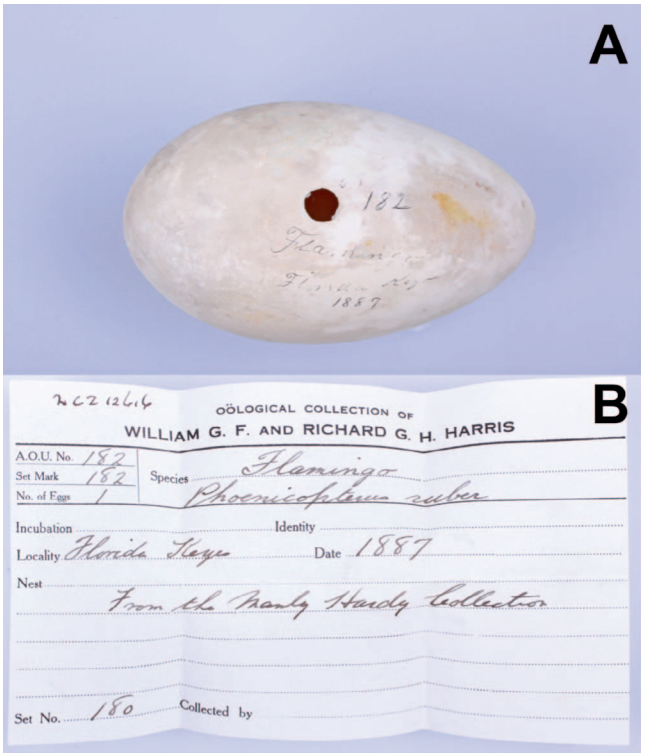

FIGURE 3. MCZ 362616, an American Flamingo egg specimen held at Harvard University's Museum of Comparative Zoology (MCZ). The locality is listed as "Florida Keys" and the date reads "1887." (**A**) The egg specimen and (**B**) the egg card associated with it.

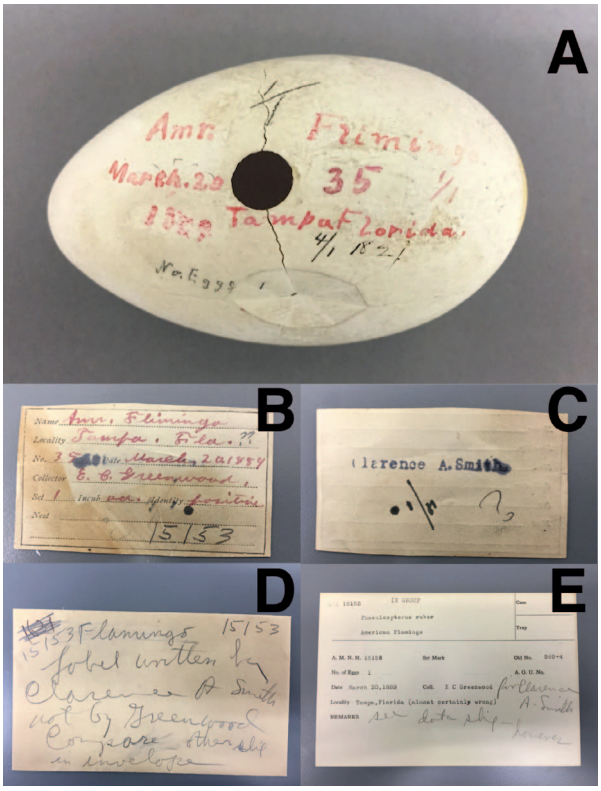

FIGURE 4. AMNH 15153, an American Flamingo egg specimen held at the American Museum of Natural History (AMNH). (**A**) The egg specimen. (**B**) Front of a data slip accompanying the specimen and (**C**) back of that data slip. (**D**) Envelope associated with the specimen. (**E**) Index card at AMNH with notes from Dean Amadon, former curator at AMNH.

repeated collecting trips to Florida, VertNet lists other specimens he collected in March 1889 in Texas—supporting Stevenson and Anderson's (1994) indication that many of Greenwood's specimens have erroneous collection information.

Each of the egg specimens is from a separate year in the 1880s, and when collection dates are available these dates are consistent with known nesting seasons for flamingos in the Bahamas and Cuba (April–June; Childress et al. 2009). The timing of Scott's (1890) gravid females would be consistent with collection dates for AMNH 15153 and WFVZ 114710. Finally, the possible report of nesting on Sugarloaf Key in 1901 was from March or April (Sprunt 1937a).

A limited collection of egg specimens for species nesting in far southern Florida is not unusual, given that low human population, lack of roads, and shallow passage through Florida Bay made collection expeditions difficult. For example, VertNet lists only 3 Reddish Egret (*Egretta rufescens*) specimens from Monroe and Miami-Dade counties between 1800 and 1900, none of which are eggs. Only 4 eggs or egg sets from Roseate Spoonbills were collected in Monroe and Miami-Dade counties between 1800 and 1900. Between 1800 and 1900, there is a single specimen (an adult) for the White-crowned Pigeon (*Patagioenas leucocephala*), a species restricted to far southern Florida. Limited collections of egg specimens are not strong evidence against nesting, given the limited sampling in the area.

Regardless of historical evidence for nesting, the extensive coastal mudflats, salt flats, and inland lakes of Florida Bay, the Florida Keys, and extreme southwest Florida today are geomorphologically similar to nesting sites used by flamingos elsewhere in the Caribbean. Despite dramatic hydrological alterations to the Greater Everglades ecosystem and Florida Bay resulting from Everglades flow interruptions (Davis and Ogden 1994), repeated hurricanes (Smith et al. 2009), and sea-level rise (Fourqurean and Robblee 1999, Smith et al. 2009), it is clear from naturalists' descriptions that suitable environments existed in the late 1800s and early 1900s.

The evidence for nesting presented here is considerably more extensive than the evidence evaluated by earlier ornithologists. Allen (1956), apparently unaware of egg specimens from Florida, discounted nesting. Stevenson and Anderson (1994) acknowledged 2 eggs: AMNH 15153 (documented only from a card at that time) and WFVZ 114710. With the evidence we present here, it is logical to conclude that flamingos did historically nest within Florida, although the cumulative evidence is not irrefutable.

Recent Population Trends (1950–2015)

We constructed a dataset to evaluate recent abundance and geographic distribution and to identify any directional trends in flamingo occurrence within Florida. We compiled quantitative data spanning 7 decades from (1) rare bird reports from *Audubon Field Notes* (and subsequent titles from 1947 to 2007; Bowman 1978, Loftin et al. 1991); (2) field observation reports from *Florida Field Naturalist* (1989–2014); (3) Audubon's Christmas Bird Count (Dunn et al. 2005); (4) eBird (Sullivan et al. 2017); (5) EDDMapS (an online reporting system for invasive species); and (6) the Frezza dataset—P.F. began documenting Florida flamingo sightings starting in the early 2000s—including personal observations and reports from coworkers, collaborative scientists, and fishing guides.

Time-series compilation and analysis. We used the dates, numbers, and locations of observations for our analyses. Where exact ("eight flamingos were sighted") or approximate (i.e. "approximately eleven flamingos were seen") quantitative estimates were provided, we used them. In some cases, quantitative ranges were provided (i.e. "18–22 flamingos were sighted") and we took an average of high and low estimates. When minimum ("at least 20 flamingos") or maximum ("up to 11 flamingos were seen") quantitative estimates were provided, we used the numerical estimate provided and did not infer greater or lower numbers. Usually, exact dates were provided, though in some cases, observations spanned a multi-month observation season (i.e. December 1–February 28). In such cases, we used the median month as an approximate date. Occasionally, reports described observations spanning more than a single month (i.e. "13 flamingos at Snake Bight between late November and early January") and we divided these into multiple instances (13 flamingos in November, and a separate entry for January). We removed observations that were repeated in multiple forums but did not exclude observations that are likely repeat counts of the same individual(s) by multiple observers.

To analyze directional trends in observations from 1950 to 2015, we analyzed our data using 3 metrics: (1) number of observations (total number of observations from all data sources, not considering number of flamingos per observation); (2) total number of individuals observed (sum of all flamingos from all observations in a given year, including number of observations and number of flamingos per observation); and (3) maximum group size (greatest number of flamingos per group seen in a given year). To analyze trends in number of observations and maximum group size, we used a generalized linear model with year as a continuous predictor variable, specified number of flamingo observations or maximum group size as response variables, and specified Poisson error distributions and a log link for each analysis (as is typical for analysis of count data; Zuur et al. 2009). To analyze trends in total number of flamingos, we used a general linear model with year as a predictor variable and total number of individuals observed as a response variable.

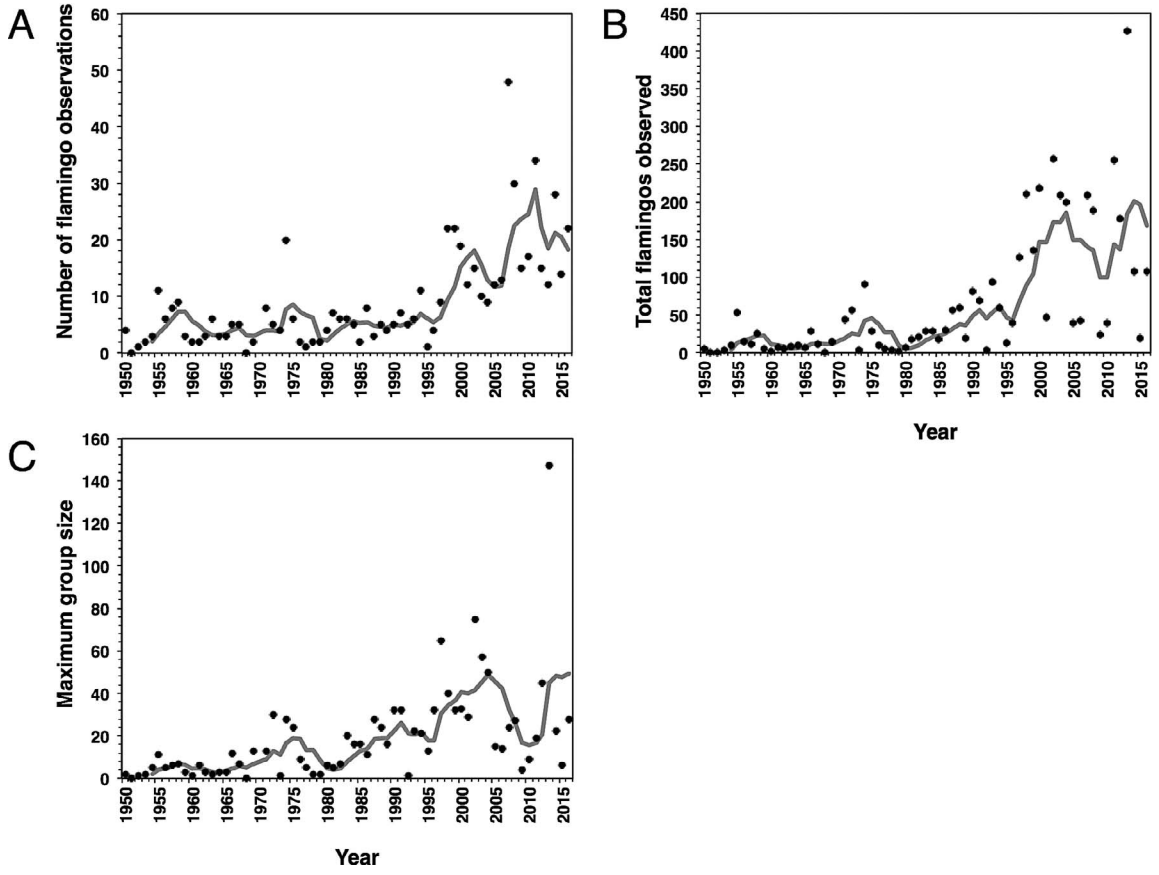

FIGURE 5. Quantitative trends in American Flamingo observations in Florida, USA (1950–2016): (**A**) total number of observations, (**B**) total number of flamingos observed (all observations pooled), and (**C**) largest group size in a given year. Gray line indicates a 5 yr moving average.

We were also interested in spatiotemporal patterns in flamingo observations. We sorted observations into 6 regions. "Florida Bay/Florida Keys" included all of Florida Bay, the Florida Keys, and inland lakes on the northern coast of Florida Bay (Bear Lake, West Lake, etc.). "Northern Everglades" included observations south of Lake Okeechobee but north of Everglades National Park. "Biscayne Bay" included Biscayne Bay and its coasts. "Gulf Coast" included sightings between Everglades City and Cedar Key. "East Coast" spanned the East Coast north of Lake Okeechobee to Jacksonville. "Panhandle" included observations from Cedar Key west to the Alabama border. For the 3 regions with the greatest number of observations, we examined seasonal patterns in distributions. We calculated each of 3 metrics (number of observations, total number, and maximum group size) by region and month and conducted chi-square tests of independence to evaluate different patterns among regions.

Quantitative patterns and trends. Our dataset yielded 495 observations of a cumulative 3,119 flamingos observed in Florida between 1950 and 2015. Of these, 157 were from *Audubon Field Notes*, 123 from eBird, 69 from *Florida Field Naturalist*, 51 from Christmas Bird Count, 37 from EDDMapS, and 58 from the Frezza dataset. The number of observations increased strongly between 1950 and 2016 ($Dev_1 = 246.3$, Resid $Def_{65} = 239.6$, $P < 0.0001$; Figure 5A). Our data also indicate an increase in total number of flamingos observed between 1950 and 2015 ($F_{1,65} = 41.74$, $MS = 181{,}037$, $P < 0.0001$; Figure 5B). Finally, maximum group size increased strongly between 1950 and 2016 ($Dev_1 = 562.21$, Resid $Def_{65} = 770.87$, $P < 0.0001$; Figure 5C). Between 1950 and 1972, only individuals or pairs were reported in most years. Since 1972, flamingos appeared most years in groups of >2 individuals. Maximum group size increased most dramatically between 1990 and 2015, with a maximum group of 147 individuals in 2014.

Observations were unevenly distributed among regions. Florida Bay and the Florida Keys had the greatest number of sightings since 1950 (total of 2,204 flamingos sighted among 297 observations, with the largest group being 65 individuals reported on November 1, 2003). The Northern Everglades totaled 572 flamingos across 36 observations, with a maximum group size of 147 (this flock was in Stormwater Treatment Area 2 between April 29 and May

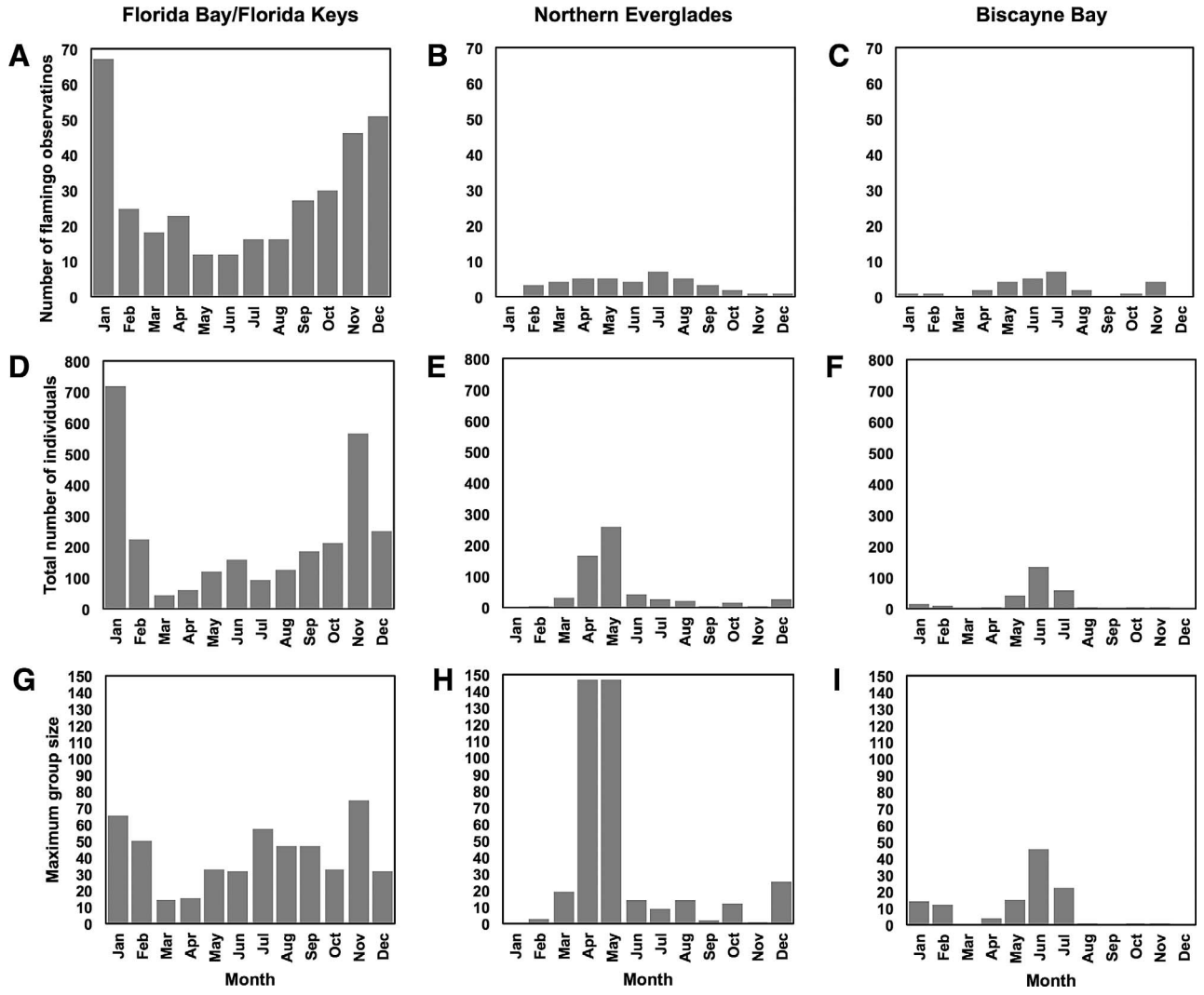

FIGURE 6. Spatiotemporal patterns in the occurrence of American Flamingos in Florida, USA, using 3 metrics: number of flamingo observations (**A**, **B**, **C**), total number of flamingos observed (**D**, **E**, **F**), and maximum group size (**G**, **H**, **I**). A, D, and G indicate data from Florida Bay and the Florida Keys. B, E, and H indicate data from the Northern Everglades. C, F, and I indicate data from Biscayne Bay.

1, 2014). Biscayne Bay included 18 observations of 183 birds, with a maximum group size of 45 seen in Matheson Hammock Park and Matheson Hammock Channel between June 11 and 22, 2013. The Gulf Coast included a total of 85 flamingos across 74 observations and a maximum group size of 17 at Naples Beach on February 24, 1975, although in almost all cases observations were of individuals or pairs. East Coast included a total of 48 flamingos across 42 observations, with a maximum group size of 3 individuals seen at Sebastian Inlet between July 26 and August 4, 1966; all other observations from this region were of individuals or pairs, and most observations in this region were centered on Brevard County. The Panhandle included 19 observations of 18 birds—all individual birds, though one observation did not explicitly specify the number of flamingos.

There were also apparent seasonal patterns in observations, which differed among geographic regions for total number observed ($\chi^2 = 2{,}407.2$, df = 22, $P < 0.0001$; Figure 6A–6C), number of observations ($\chi^2 = 81.2$, df = 22, $P < 0.0001$; Figure 6D–6F), and maximum group size ($\chi^2 = 689.1$, df = 22, $P < 0.0001$; Figure 6G–6I). For Florida Bay–Florida Keys, flamingos have been observed in every month, and numbers of observations and of individuals peak from November through January. By contrast, for Biscayne Bay and the Northern Everglades, the number of observations and total number of individuals are lowest in December–January and peak from April through July.

Caveats and potential biases in reconstructed time-series. The dataset we synthesize here is the best available approximation of the recent population history of American Flamingos in Florida, yet it is limited and has several

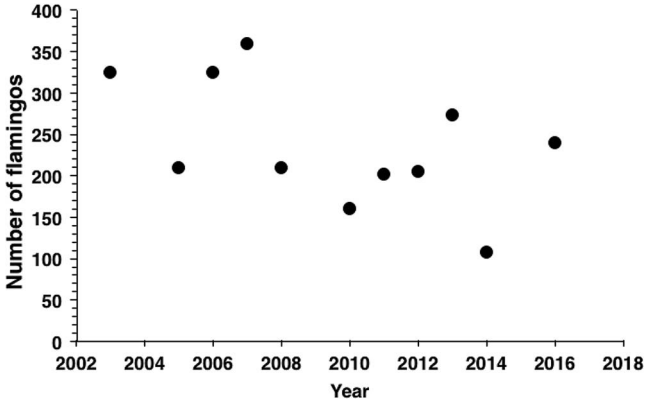

FIGURE 7. Recent counts of feral American Flamingos at Hialeah Park, Florida, USA, from Christmas Bird Counts.

potential biases. First, citizen science sources are likely to count the same individuals by multiple observers, leading to an overestimation of our metric "total number observed" in relation to the actual number of individuals. Maximum group size should be free from this bias, and long-term patterns for this metric mirror the others. Second, an increase in total number of flamingos and number of observations may be expected given the growing human population, growing interest in recreational birding, and growth of citizen science projects between 1950 and 2016; it is currently not possible for us to differentiate between increase in number of flamingos and increase in number of citizen scientists. Finally, detection probability likely varies with spatial and seasonal variation in the number of citizen scientists, which may complicate our efforts to understand spatiotemporal patterns.

Despite these biases and limitations, the most reasonable interpretation of these trends is a directional increase in the number of wild flamingos in Florida between 1950 and 2016. However, a plausible alternative hypothesis is that the number of flamingos within Florida has not showed directional change since 1950, and that the detection probability for these flamingos has increased instead. Ultimately, standardized surveys for flamingos, or mark–recapture techniques to empirically evaluate detection probability, would be required to produce more detailed population trends than those that we produce here. In any case, we can conclude with high confidence that the Florida flamingo population between 1950 and 2016 never approximated the historical population size repeatedly reported by early naturalists, and we can conclude with reasonable confidence that the number of flamingos present in Florida shows an increase over the past ~65 yr.

Origins of Recent Flamingos

Captive colonies and escapes. Captive flamingo colonies are a plausible source for flamingo observations after ~1925. The earliest captive flamingo colony in Florida, to our knowledge, was the Mountain Lake Sanctuary at Bok Tower, in Lake Wales, Florida. Reports from Bok Tower indicate that between 1925 and 1940, at least 40 flamingos (including American Flamingos, Chilean Flamingos [*Phoenicopterus chilensis*], and Greater Flamingos [*P. roseus*]) were imported and released at the site (J. Fogel personal communication). At least one individual escaped from the site, on December 11, 1927, which suggests that the birds were not pinioned or regularly wing-clipped. There is no evidence that this population ever nested, and the population experienced high mortality from cold weather and predation. Notes from Bok Tower indicate that the last flamingo died in December 1944.

Bailey (1928) was the first to present escape as an origin for Florida flamingos when he suggested that an individual observed in Wakulla County (Stoddard 1928) was an escapee from Bok Tower, ~370 km southeast. However, Bailey (1928) also reasoned that a flamingo in September would travel south, though he appears to have assumed erroneously that Bok Tower was north of Wakulla County.

In January 1931, Joseph Widener (owner of the Hialeah Park Race Track in Miami) introduced 20–30 flamingos from Cuba in an artificial pond at Hialeah Park (Allen 1956). These flamingos apparently left the site the next day, as they were neither pinioned nor wing clipped. Additional flamingos were then imported and pinioned, nested successfully beginning in 1937 (Allen 1956), and this population persists and nests at Hialeah Park in 2017. Allen (1956) stated that between 1942 and the early 1950s, ~65 young were reared each year and were pinioned at 2 mo of age. However, starting in 1952, some chicks were not pinioned, and by 1956 Allen estimates that of 750 flamingos in the Hialeah Park flock, 150 were flighted (Allen 1956). At some point, pinioning was abandoned entirely, and as of 2016 all Hialeah Park flamingos appear to be flighted. Recent counts (2003–2016) of the Hialeah Park flock have been conducted during Audubon's Christmas Bird Count and indicate a population size between 108 and 360 individuals (Figure 7). We cannot account for interannual fluctuations in population size, which could result from either variation in count methods or population processes (births, deaths, immigration, or emigration).

The Hialeah Park flock is the only known large, breeding population of flighted flamingos within Florida, yet several other Florida animal-based attractions held flamingos beginning in the early 20th century. Between 1938 and 1961, the Miami Rare Bird Farm in Kendall (Miami-Dade County) held a number of flamingos (likely <20), but there is no evidence for breeding there, and the fate of the flamingos is not clear after the farm closed in 1961. Five flamingo specimens at the Florida Natural History Museum (UF 23155, UF 23156, UF 23157, UF 23160, and UF 23170) originated at the Miami Rare Bird Farm,

and these specimens were not pinioned (T. Webber personal communication). The Florida Natural History Museum holds 2 flamingo specimens (UF 23165 and UF 23166) that originated at the Ross Allen Reptile Institute in Silver Spring (Marion County), indicating that this site also held flamingos, and one of these specimens is pinioned (T. Webber personal communication). Several other animal-based attractions likely held flamingos in Florida during the second half of the 1900s (Crandon Park Zoo, Miami MetroZoo, and Parrot Jungle in Miami-Dade County; Lion Country Safari and the Avian Breeding and Research Center in Palm Beach County; Brevard Zoo in Brevard County; Busch Gardens Tampa Bay in Hillsborough County; Homosassa Springs Wildlife State Park in Citrus County; and Sarasota Jungle Gardens in Sarasota County). Most flamingos held by zoos are pinioned or have identification bands—usually both—which would prevent escape and greatly facilitate identifying an origin, though pinioning and banding may not have been conducted regularly until the late 1900s. In general, the spatial distributions of flamingo sightings do not correspond to the locations of these institutions.

Allen (1956) attributed flamingo sightings since the 1930s to escapes from captive colonies. Specifically, he attributed several observations in the early 1930s to the escape of the initial flamingos from Hialeah Park—including 14 seen on the Card Sound Bridge in February 1931 (Howell 1932) and a number of sightings in Florida Bay in 1932 (Holt 1933). Allen (1956) argued that most sightings in Florida Bay in the 1930s were derived from the Hialeah Park flock. However, the only observations from our database of flamingos reported within Miami were a pair of individuals seen repeatedly from 2005 through 2017 in Aventura, ~18 km from Hialeah Park. One recent museum specimen (FMNH 370865) was collected near Hialeah Park in 1973. Ultimately, it may not currently be possible to determine whether sightings through the 20th century represent escapes or dispersers from around the Caribbean, yet there remains no direct evidence for escape as an origin for individuals in Florida Bay and the Florida Keys, Biscayne Bay, or the Northern Everglades.

Natural dispersal and linkages to Caribbean populations. There is direct and indirect evidence for natural movement of flamingos into Florida from the Caribbean. McNair and Gore (1998) evaluated 8 records of flamingos in northern Florida and determined that 4 were associated with tropical cyclones, suggesting that cyclones disperse flamingos from the Caribbean. Three flamingos were observed on May 22, 2013, at Fort Jefferson at Dry Tortugas National Park, >100 km west of Key West, likely indicating dispersal of flamingos to or from Florida (Hockenbury 2013).

Two flamingos banded as chicks in Yucatan, Mexico, have been sighted in Everglades National Park—direct evidence of natural dispersal. On October 20, 2002, a flamingo banded "DFJV" was sighted at Flamingo Point, Everglades National Park. On December 27, 2002, DFJV was resighted at Gator Lake, Everglades National Park, with at least 6 other flamingos. This individual was banded as a chick in Peten Hu in the Yucatan of Mexico on August 12, 2000 (Galvez et al. 2016), and was resighted in the Yucatan in 2003, 2006, and 2007 (X. Galvez personal communication). On September 6, 2012, a flamingo banded "HRTJ" was sighted at Flamingo Point in Everglades National Park. This individual was seen over a period of 5 wk with a group of up to 3 additional flamingos. HRTJ was banded at Charcas Salinera La Esperanza in the Yucatan on September 4, 2010 (Galvez et al. 2016). To our knowledge, HRTJ has not been resighted at any location. These 2 observations provide incontrovertible evidence that natural dispersal occurs, and the case of DFJV indicates dispersal and return between the Yucatan and Everglades National Park.

While evidence for dispersal into Florida from the Caribbean is limited to 2 observations, results of other studies suggest that long-distance movements are common. Galvez (2016) showed that flamingos banded in the Yucatan have been resighted in the Cayman Islands, Cuba, Texas, and Florida. There are records of a flamingo banded in the Yucatan that was sighted on the Louisiana coast intermittently between 2007 and 2011 (Louisiana Bird Records Committee 2017). Johnson (1989) showed that for the closely related Greater Flamingo, chicks banded in the Camargue of France have been resighted in Spain, Iran, and Russia. Also in Greater Flamingos, Baker et al. (2006) showed that 3 individuals each moved >500 km across Kenya and Tanzania over a 24 mo period. By comparison, nesting sites in the Yucatan are ~750 km from Everglades National Park, Cuba is ~220 km away, and Inagua in the Bahamas is ~800 km away. Movement studies of Greater Flamingos have also shown that movements are not specifically migratory, but erratic (Johnson 1989, Baker et al. 2006).

Drivers of Population Trends: Hunting and Pan-Caribbean Recovery

Population trends that we reconstructed indicate dramatic population decline in the late 1800s and the first few years of the 1900s, followed by an apparent increase in numbers since 1950—though never reaching historical population size. The decline until ~1900 is most easily interpreted as near total extirpation under pressure of hunting for meat and plumes. Nearly all early accounts describe hunting of flamingos by locals, and Wurdemann's (1860) report of 100 flamingos killed in a day would clearly represent severe hunting pressure on a population of a few thousand individuals. Pierce (1962) indicated a high price for flamingo skins compared to the skins of other birds

hunted by plume traders, and others provide specific accounts of hunting for meat (Wurdemann 1860, Brodhead 1910, Stimson 1939). The late 1800s were the peak of the plume trade, and plume hunters exerted severe pressure on many species of southern Florida wading birds (Frohring et al. 1988, Powell et al. 1989). Flamingo extirpation in Florida is also consistent with pan-Caribbean trends; of ~30 Caribbean nesting sites before 1900, only 4 nesting sites remained by the 1950s (Allen 1956).

Population recovery beginning mid-century is also consistent with pan-Caribbean trends (Allen 1956, Wiley and Wiley 1979). Legal protections for birds and active conservation programs have led to population increases in several Caribbean regions. Populations in the Yucatan increased from 6,057 individuals in 1954 to 27,000 in 1998 (Baldassarre and Arengo 2000). Populations in Cuba and Inagua also appear to be increasing in recent decades (Johnson 2000). In Venezuela, populations doubled from ~18,000 in the 1970s to ~37,000 in 1996 (Espinoza et al. 2000), and flamingos resumed nesting in mainland Venezuela in 1987 after a 35 yr gap (Casler et al. 1994). Populations declined dramatically in Hispaniola in the early 20th century (Allen 1956), yet in 2008 flamingos nested in the Dominican Republic for the first time since 1977 (Garrido et al. 2010). Flamingos were extirpated from Anegada in the British Virgin Islands, though reintroduction has successfully reestablished a small population there (Lazell 2001).

Future Directions

Advance basic information on biology of flamingos in Florida. There is a clear need to understand basic biology of flamingos within Florida, including numbers, habitat use and habitat suitability, residency times within Florida, and linkages to populations outside the United States. Although our citizen science data show basic trends, comprehensive censuses or mark–recapture methods that can account for detection probability would greatly improve our understanding of total population size and population trends. Habitat use could be evaluated by characterizing environmental factors used by flamingos within Florida today (including foraging and nesting site suitability), or by empirical comparison with known foraging and nesting habitats throughout the Caribbean.

Validate or refute existing information on historical nesting. Although the evidence we present in support of nesting is considerable, and more extensive than has been examined previously, it remains plausible that egg specimens from Florida are mislabeled or fraudulent. Comprehensive evaluations of the oological collections of Hardy, Wilson, Wilkinson, and Greenwood may indicate whether their collections are generally reliable. Analytical approaches to validate species identity and geographic origin (i.e. Chilton and Sorenson 2007) may provide new empirical evidence. Finally, discovery of additional egg specimens or narratives from Florida could add new information.

Determine relative contributions of dispersal and escape to Florida's flamingo population. Although there is support for natural dispersal (at least from the Yucatan to Florida), it remains unclear what proportion of flamingos seen in Florida are dispersers or escapees, and which breeding colonies through the Caribbean are the primary origins for Florida's flamingos. Several approaches may help resolve this controversy. Satellite telemetry may provide definitive evidence for specific linkages between Florida and the Caribbean and could also reveal habitat use and residency times within Florida. Population genetics may help identify geographic linkages for both current and historical populations and relation to known captive colonies. Stable isotope analysis is commonly used to track animal geographic origins (Kelly et al. 2002, Wunder et al. 2005) and also may distinguish among wild and captive animals (Kays and Feranec 2011, van Schingen et al. 2016). While plumage color intensity in wild flamingos is highly variable, the low-carotenoid diet of Hialeah Park's population produces generally pale plumage, bills, and legs in relation to wild flamingo populations. Perhaps evaluation of plumage, bill, and leg coloration could be used to estimate the contribution of escapes from Hialeah Park to wild Florida flocks. Banding flighted captive populations would clearly help readily identify escapees. Each of these approaches would provide new empirical evidence and help resolve decades of controversy and speculation.

Evaluate management plans and/or species protections. The population history for American Flamingos described here is consistent with those of other avian species that are protected by state or federal endangered species laws. Despite a relatively recent call for population recovery for flamingos (Hunter et al. 2006), to our knowledge there has been no consideration of flamingos as a threatened species by state or federal wildlife agencies, and no management attention directed toward the species. However, several aspects of the life history of flamingos (aggregation at very few breeding sites, low reproductive potential, and high specialization in nesting sites) are variables that contribute toward Florida's quantitative ranking system for species protection (Millsap et al. 1990). Furthermore, the current low population size, population history of anthropogenic decline, reduction in extent of range, and historical and current limited distribution within Florida are also factors that would urge protection under Florida's species protection criteria (Millsap et al. 1990). We anticipate that the synthesis of history and status of flamingos we have produced here will be useful in evaluating management plans and protection needs for American Flamingos—a lost Florida icon.

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