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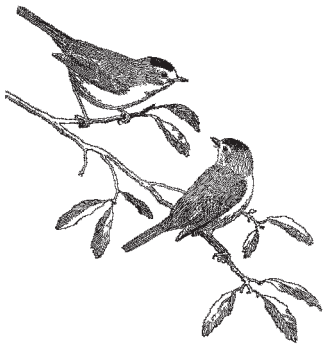

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THE NORTHERN BLACK SWIFT: MIGRATION PATH AND WINTERING AREA REVEALED

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ABSTRACT.—Winter ranges have been identified for most neotropical migrant bird species, those that spend the winter months in Central and South America and summer months in North America. Published accounts and specimen collections of the Northern Black Swift (*Cypseloides niger borealis*) during spring and fall migration are extremely limited and winter records are nonexistent. We placed light-level geolocators on four Black Swifts in August 2009, and retrieved three a year later. Data from the geolocators revealed initiation of fall migration (10 to 19 Sep 2009), arrival dates at wintering areas (28 Sep to 12 Oct 2009), departure dates from wintering areas (9 to 20 May 2010), and return dates to breeding sites (23 May to 18 Jun 2010) for Northern Black Swifts breeding in interior North America (Colorado, USA). Northern Black Swifts traveled 6,901 km from the Box Canyon breeding site and 7,025 km from Fulton Resurgence Cave to the center of the wintering area. The swifts traveled at an average speed of 341 km/day during the 2009 fall migration and an average speed of 393 km/day during the 2010 spring migration. This is the first evidence that western Brazil is the wintering area for a subset of the Northern Black Swift, extending the known winter distribution of this species to South America. *Received 30 August 2011. Accepted 11 November 2011.*

Knowledge of patterns and timing of migration of the Northern Black Swift (*Cypseloides niger borealis*) (Frontispiece) is virtually non-existent and the species' winter range is unknown. Published accounts and specimen collections for this subspecies during spring and fall migration south of the United States exist only for sites in south-central Mexico (Stiles and Negret 1994), off the Guatemalan coast (Davidson 1934), and off the southwest coast of Chiapas, Mexico (Buchanan and Fierstine 1964). Negret collected the first specimens of Northern Black Swift for South America in southwestern Colombia in October 1992 and 1993, suggesting a South American winter destination (Stiles and Negret 1994). Fall specimens originally reported to be *C. n. costaricensis* from south-central Mexico (Webster 1958) were subsequently identified as *C. n. borealis* (Stiles and Negret 1994). Flocks of Black Swifts thought to be migrating *C. n. borealis* in Costa Rica in spring had no specimens collected for confirmation (Stiles and Skutch 1990). Kiff (1975) tentatively assigned a female swift collected in Costa Rica to *C. n. borealis* based on

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wing and tail measurements that are within ranges for *C. n. costaricensis*, further highlighting the uncertainty of migration and winter distribution for this subspecies. Winter records for Northern Black Swift are non-existent.

Several factors contribute to the lack of knowledge about migration and winter distribution of this species, including difficulty in accurate field identification of individuals due to high and rapid flight, problems differentiating this species from similar-size members of *Cypseloides* that occupy Central and South America, and inability to verify observation records. No band recoveries exist outside of the United States from ~200 Northern Black Swifts banded from 1950 to present (Bird Banding Laboratory, pers. comm.).

Currently, satellite tracking devices which provide accurate tracking of individuals are not sufficiently small to place on a species the size of Black Swifts. However, light-level geolocators, devices that record ambient light levels at fixed intervals, are highly effective instruments for tracking long-distance migratory species and are sufficiently small to place on swifts. They are battery-powered instruments with a microprocessor, clock, and memory for data storage; geographical positions can be calculated from the data collected by the devices.

Geolocators must be retrieved to download data, and the Black Swift is particularly suited to recapture due to its high breeding colony fidelity and an individual propensity to reuse the same nest from year to year (Foerster 1987, Collins and Foerster 1995, Marín 1997, Hirschman et al. 2007). We placed geolocators on four Northern Black Swifts with the objective to gather information about the migratory path, timing, and winter destination of this species.

Identifying the connectivity of a migrating species between breeding sites and wintering areas is crucial to understanding the species' ecology and in guiding conservation efforts. Time spent in widely separated and ecologically disparate locations by migrating species and the strength of this link can have great biological consequences for individuals and populations, including reproductive success, population dynamics, behavioral ecology, evolution, and response to changing selective pressures (Webster et al. 2002). Advances in geolocator technology can provide this information by tracking individuals at high resolution. We conducted this study because information on migration and wintering areas of Northern Black Swifts was virtually nonexistent (Lowther and Collins 2002, Wiggins 2004). The small sample does not tell us how weak or strong the migratory connectivity is for this subspecies, but forms a foundation for additional knowledge of this species' ecology and can guide future studies.

METHODS

Study Sites.—Northern Black Swifts nest at or near waterfalls typically inaccessible due to steep and vertical configuration (Knorr 1961, Levad et al. 2008). More than 100 breeding sites of this species have been documented in North America (Lowther and Collins 2002, Levad et al. 2008) with only a few records of alternate types of sites such as sea caves in California (Legg 1956), small cave-like boulder configurations in streams (Foerster and Collins 1990, Johnson 1990, Hurtado 2002), and caves (Davis 1964, Northern British Columbia Caving Club 2003).

We chose Fulton Resurgence Cave (39° 49′ N, 107° 24′ W) and Ouray Box Canyon Falls (38° 1′ N, 107° 40′ W) in Colorado because of accessibility and the probability of capturing and recapturing Black Swifts using hand-held or mist nets. These breeding colonies are two of the largest in Colorado (Levad et al. 2008) with an average of eight nesting pairs (range 7–9, n = 6 yrs) at Fulton Resurgence Cave (KMP, pers. obs.) and an average of 11 nesting pairs (range 7–15, n = 10 yrs) at Box Canyon Falls (Hirshman et al. 2007, Levad et al. 2008). Fulton Resurgence Cave is a limestone cave with a small stream issuing from it, forming a microhabitat conducive for a Black Swift breeding colony (Knorr 1961). Mist nets placed near the mouth of the cave, the only ingress/egress for swifts, have resulted in a recapture rate of 41% since banding of adults began in 2006 (KMP, pers. obs.). Box Canyon Falls is a popular tourist site and walkways provide views of the falls. The walkways allow access to several nest sites and, with the aid of ladders, several nests can be reached with hand-held nets.

Data Collection.—We used four Mk10S model geolocators, manufactured by the British Antarctic Survey (BAS), programmed to continuously measure light levels every minute and archive the maximum measurement for each 10-min period. The devices weighed 1.2 g, measured 18 × 9 × 6 mm, and have a light sensor mounted at the tip of a 10-mm stalk angled at 15° to prevent it from being covered by feathers. The instruments are

encapsulated in a water-resistant housing with two external terminals for commands and data transfers.

We designed a backpack harness system modified from Buehler et al. (1995) because Black Swift legs are too attenuated for the leg-loop harness often used for geolocators on passerines (Rappole and Tipton 1991). The harness material, 5 mm tubular Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA), was attached at four points to the geolocator and crossed under the keel. We secured the free ends of the ribbon with size 69 bonded right twist Kevlar thread (The Thread Exchange Inc., Weaverville, NC, USA) and stitched the ribbon where it crossed the keel to avoid shifting. We applied cyanoacrylate glue on all stitches and cut ends to prevent fraying.

We attached geolocators to four adult Black Swifts in August 2009, three at Fulton Resurgence Cave (2 females, 1 male) and one at Box Canyon Falls (male); the birds weighed 49.5–51.5 g. Each geolocator, including harness materials, weighed 1.5 g, representing 2.9–3% of body weight, well within guidelines suggested by Caccamise and Hedin (1985).

Data Analysis.—We conducted pre-deployment calibration for ~9 days and post-deployment calibration for ~7 days by placing them at a known location with a clear view of the sky. We retrieved three of the four geolocators in July and August 2010.

We used software programs (BASTrak) developed by BAS to download, process, and interpret data archived by the loggers, each of which had collected data throughout their entire deployment. We rejected latitude data gathered ~30 days before and after the equinoxes since day lengths at the equinoxes are equal at all latitudes, resulting in poor location fixes. Internal clocks maintained accuracy during deployment and there was no need to correct for clock drift.

Two values are required for analyzing and plotting the geolocator data: the dusk/dawn light transition threshold and the corresponding sun elevation angle at this threshold. We chose a sensitive light transition threshold value of two to reduce variation in day length due to the effects of shading which influences the resulting distribution of location fixes. We used static pre-deployment calibration to calculate the corresponding sun elevation angles (-6.4°, -6.5°, and -6.6°). We calculated times of sunrise and sunset using TransEdit2; positions were calculated with BirdTracker which derives longitude from absolute time of local midday/midnight and calculates latitude by comparing day/night length, a technique which provides two geographical positions/day. We used only midnight fixes to produce maps based on the assumption that swifts were roosting at night and migrated during the day. We identified days with irregular shading events, resulting in shorter day lengths or anomalous transition times, by visually inspecting sunrise and sunset times and excluded them from the analysis. An average of 145 fixes for each bird remained to map wintering range and an average of 26 fixes remained to map the spring migration path. Mapping of fall migration was not possible due to overlap with the fall equinox.

We calculated kernel density surfaces using the wintering area data from each geolocator with the Spatial Analyst Kernel Density function (ESRI 2009). This function calculates density of fixes in a search radius around those fixes. These densities fit a smoothly curved surface over each location. The surface value was highest at the location of the point and diminished with increasing distance from the point. We used a fixed kernel with a search radius of 185 km to compensate for the approximate average error in latitude and longitude known to occur in geolocator data (Phillips et al. 2004). The kernel function is based on the quadratic kernel function described in Silverman (1986). We calculated the density surfaces at 1-km resolution as this is adequate to capture density at a small scale over a large geographic area. We calculated 90%, 75%, and 50% density polygons from the kernel density surfaces to enhance graphic displays of higher use density areas. We used the average nearest-neighbor distance function in ArcInfo Spatial Statistics (ESRI 2009) to characterize the spatial point pattern of winter locations. This function quantifies and characterizes the spatial pattern of each geolocator and indicates if the pattern is evenly dispersed, random, or clustered compared to a spatial random distribution. We estimated approximate migration duration, arrival, and departure events from plotting longitude and date. We used the 50% kernel density polygons for all three swifts to describe land cover use and overlaid those with a global land cover layer using 2009 satellite imagery at a 300-m resolution produced by the European Space Agency GlobCover 2009 Project (Bontemps et al. 2010).

TABLE 1. Phenology of migration stages of three Northern Black Swifts[a].

Departure from Colorado	14 Sep (10–19 Sep)
Arrival at wintering area	5 Oct (28 Sep–12 Oct)
Time spent at wintering area	220 days (209 to 227 days)
Departure from wintering area	13 May (9–20 May)
Arrival in Colorado	1 Jun (23 May–18 Jun)
Duration of southbound migration	21 days (18 to 23 days)
Duration of northbound migration	20 days (14 to 29 days)

[a] Arrival and departure dates are presented as means with range in parenthesis.

RESULTS

Geolocators recovered from two females at Fulton Resurgence Cave and one male at Box Canyon Falls represent a 75% recovery rate. The Black Swifts initiated fall migration from Colorado beginning on 10 September and continued through 19 September 2009. We used longitudinal information around the time of the autumnal equinox and documented the swifts arrived at their wintering location in South America between 28 September and 12 October 2009. Approximate dates of migration initiation north from wintering areas began on 9 May and continued through 20 May 2010. Dates of arrival at breeding sites began 23 May and continued through 18 June 2010 (Table 1, Fig. 1).

Kernel density estimates indicate all three birds over-wintered primarily in the lowland rainforest of western Brazil with some kernels extending into Bolivia, Colombia, Peru, and Venezuela (Fig. 2). Average nearest-neighbor distance analysis for all geolocators exhibited clustering with nearest-neighbor ratios = 0.89 ($P = 0.02$), 0.74 ($P < 0.001$), and 0.77 ($P < 0.001$) for geolocator #553, #554, and #556, respectively. The distance between the Ouray Box Canyon Falls breeding site and the center of the wintering range in Brazil (#554) is 6,901 km and the average distance between the Fulton Resurgence Cave breeding site and the center of the wintering range in Brazil (#553 and #556) is 7,025 km. The swifts traveled at an average speed of 341 km/day during the 2009 fall migration and an average speed of 393 km/day during the 2010 spring migration. The inaccuracy of geolocators precludes precise calculation of an average daily distance covered by each bird.

The land cover overlay maps for 50% kernel density areas for all three birds indicate a dominant land cover (>86%) of closed to open broadleaved evergreen or semi-deciduous forest and a small percentage (2–10%) of the kernel density areas are classified as closed to open

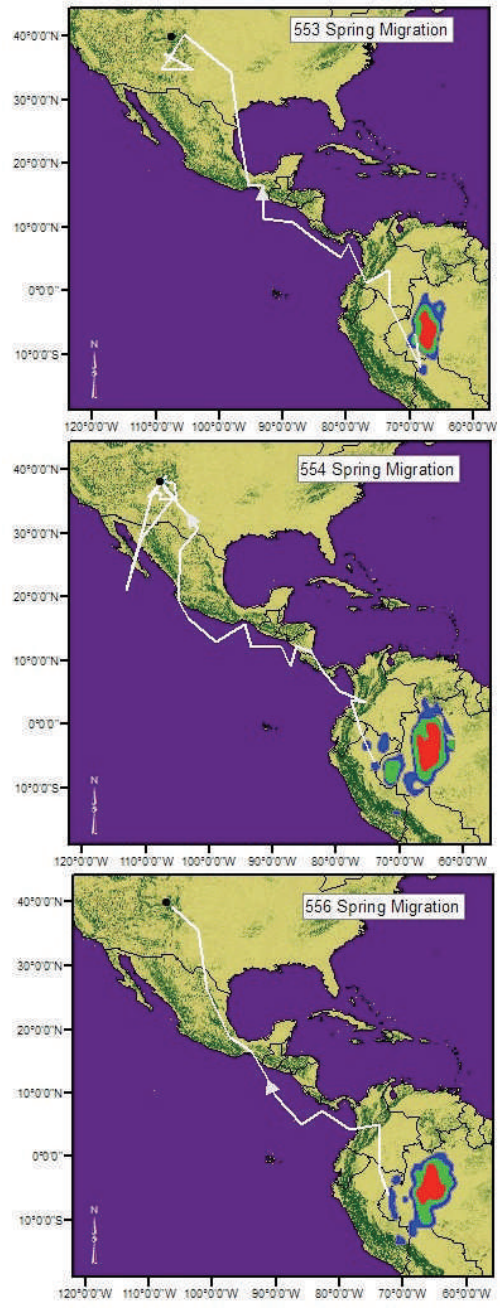

FIG. 1. Spring migration routes for three (#'s 553, 554, 556) individual Northern Black Swifts marked in Colorado.

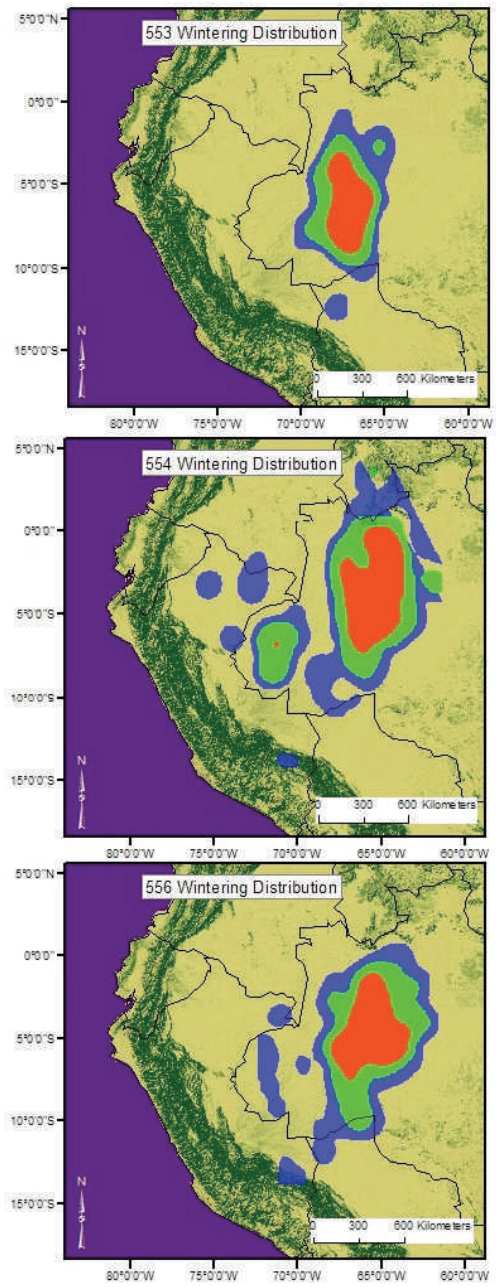

FIG. 2. Northern Black Swifts marked in Colorado wintering distribution kernel density contours (red = 50%, green = 75%, blue = 90%) from 28 September–12 October 2009 to 9–20 May 2010.

broadleaved forest regularly flooded. Areas of mosaic cropland/vegetation, mosaic forest shrubland/grassland, closed to open shrubland or grassland, bare areas, and water bodies represented <2% use.

DISCUSSION

We documented the timing of fall and spring migration, wintering area, and spring migration paths for three Northern Black Swifts using geolocators. The return dates to breeding sites after spring migration and dates of the initiation of fall migration correlate with data collected in other research (Hirschman et al. 2007). Wintering area locations were previously unknown, and only sporadic reports existed which did not fully delineate migratory paths.

The highest kernel density estimates indicate the three birds wintered almost entirely within the State of Amazonas, Brazil. The clustering of the three individuals exhibited by nearest-neighbor analysis might be expected based on the birds seeking a physiologically optimal climate, preferred habitat, abundant prey, or other factors within a certain geographic area. Amazonas is composed almost entirely (~98%) of lowland rainforest at elevations between 34 and 116 m. The area is sparsely populated with a density of 2.05 inhabitants/km^2 with 78% of the population in cities (IBGE 2011). Amazonas has an equatorial tropical rainforest climate with annual rainfall of 1.50–2.50 m and all months have a mean precipitation of at least 60 mm (IBGE 2011). The average temperature per day per year is 26.7 °C (23.3–31.4 °C) with high humidity (Brasil Travel Guide 2011).

The three birds tracked in this study represent only a small geographical subset of the Northern Black Swift population and further studies are needed to delineate more completely the full extent of the wintering distribution of this subspecies. The three birds wintered in the same general area, suggesting a high level of connectivity between breeding and wintering populations. Stutchbury et al. (2009) found a similar connectivity for Wood Thrush (*Hylocichla mustelina*), not previously documented for migratory songbirds. The large wintering areas may reflect a temporal movement noted for each bird. The data indicate a trend for each bird to be in the eastern portion of the kernels in October with gradual movement west in April and May. The most likely explanation for this replicated non-random change

in position is that the birds moved, perhaps following their food source. This net westward directional movement is less likely to be an artifact due to shading or weather-related variation because it was consistent among the three birds tracked.

Northern Black Swift roost sites and roosting behavior in South American wintering areas are unknown. Waterfalls, caves, and dripping rock faces serve as roosting and breeding sites in breeding areas. There is only one documented observation of a roost site for Northern Black Swifts in South America, discovered during fall 1992 and 1993, on the walls of a steep gorge along the Río Cauca in the foothills of Colombia. Black Swifts roosted consecutively at dusk for a week in a compact group, mainly with White-collared Swifts (*Streptoprocne zonaris*), clinging to the volcanic rock of a 40-m cliff overlooking the river, indicating that rocky river banks are used as roosting sites during migration (Stiles and Negret 1994). Similar sites may be used in wintering areas if available, but this information is completely lacking. Non-breeding Common Swifts (*Apus apus*) are known to 'roost' aerially in breeding areas and it is believed they spend ~9 months of the year continuously on the wing. Non-breeding birds may fly continuously for several years (Bäckman and Alerstam 2001, Tarburton and Kaiser 2001). Common Swifts are also known to occasionally roost at night by hanging on the foliage of trees (Holmgren 2004). Any of these scenarios is possible for Northern Black Swifts in wintering areas. Foraging activities of the Northern Black Swift in wintering areas are unknown but kernel densities indicate the swifts range over a large area in winter, suggesting the birds spend a lot of time on the wing.

The capability of geolocators for tracking small birds is still being explored and the potential is great. However, the devices are not without limitations. A major obstacle for success is that once the devices are deployed, the bird must be recaptured after a complete migration cycle has occurred to obtain data. Our study indicates the suitability of the Northern Black Swift for geolocator deployment and recapture, primarily due to this species' strong nesting colony fidelity and ability to carry small devices for long periods of time.

Calculation of latitude is unreliable around each equinox and near the equator because length of day and night is equal. The accuracy of calculated day length is especially affected for terrestrial species by shading factors that alter recorded light levels such as cloudy weather, foliage, and topographic shading of roost sites, resulting in latitude uncertainties. Fudickar et al. (2011) found the devices had an error of 201 ± 43 km for latitude and 12 ± 3 km for longitude (±95% CI) for stationary geolocators (n = 30) in forested habitat. The apparent retreat of bird #554 from Colorado to the Pacific Ocean south of Baja California (Fig. 1) during spring migration is the result of one data point and the accuracy of this fix is questionable. It may or may not represent an actual movement by the bird and is possibly the result of an extended period of shading. We did not eliminate this position fix since the total day length did not drastically differ from the other day lengths of that time period.

Accurate longitudinal information can be ascertained as this is not affected by equinox and we successfully used longitude near the autumnal equinox to indicate when the birds arrived at their wintering location. Black Swift breeding requirements, such as nesting behind waterfalls in deeply shaded niches in steep and narrow canyons, or in caves where the performance of geolocators is often compromised by darkness, resulted in some unusable data during the breeding season. Documented Black Swift nocturnal roosting behavior during migration is limited and indicates this could be a factor influencing the effectiveness of geolocators for tracking this species. If winter nocturnal roost sites are similar to those documented in migration and at breeding sites, this will also influence the accuracy of the data collected by geolocators. Despite these limitations, geolocators far surpass band recovery information or dependence on sporadic sightings to identify migratory paths and winter distribution of the Northern Black Swift.

Understanding the theory behind geolocation is extremely important for interpreting and using the data collected to produce maps showing animal movements (Hill 1994). Once the theory is understood, knowledge of the behavior of the animal being studied and of weather patterns in the area where the animal was tracked can be used to provide insight into movement patterns. The mapped winter range of Black Swifts is an area that typically experiences high cloud cover. Thus, a significant number of the location fixes are most likely shifted to the north artificially because of cloud cover in the winter range as compared to the

Colorado calibration location. Therefore, the southern portion of the mapped winter range is most likely the area where the swifts spent the winter. The technical limitations of geolocators and lack of knowledge of Black Swift behavior in wintering areas, such as daily foraging flight distance, and roosting locations and timing further confound data interpretation.

The Black Swift is protected under the Migratory Bird Treaty Act in the United States and the Convention for the Protection of Migratory Birds and Game Mammals in Mexico. This study documents Northern Black Swifts spending ~220 days in Brazil during winter 2009–2010, the first records of the species in this country. This study identifies an annual non-breeding geographic area of the Northern Black Swift and is a significant step toward conservation of this species.

Future studies could include use of geolocators on subsets of Northern Black Swifts from other areas of North America which would help delineate the strength of migration connectivity for this subspecies. Development of satellite transmitters small enough for use on Black Swifts will provide greater accuracy than geolocators and can possibly answer questions about roosting and foraging behavior.

CONSERVATION IMPLICATIONS

Knowledge of migratory pathways and winter distribution of a species enables evaluation of those geographical areas, including ecologic analysis and research, identification of potential habitat threats, and development of conservation strategies. The homogeneity of the wintering areas for Northern Black Swifts evidenced in this study suggests limited winter resource use by this subspecies, which could have long-term conservation impacts. The current rate of deforestation in Brazil could directly threaten this subspecies. One of the most refined computer models for simulating deforestation, SimAmazonia I, indicates the rate of deforestation in the State of Amazonas will increase rapidly in the coming decades which could result in a loss of up to 30% of the forest cover by 2050 (Soares-Filho et al. 2006). Climate change and global warming predictions also pose threats to habitat and prey availability for this subspecies. Roberson and Collins (2008) identified declines in some Northern Black Swift populations but it is unknown if declines are due to environmental problems in breeding areas, during migration, in wintering areas, or some combination of these possibilities.

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