

Migratory track from the United States breeding population of Cliff Swallows (*Petrochelidon pyrrhonota*) and effects of geolocators on annual survival

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ABSTRACT—In the last decade, geolocators have been implemented to track birds and have provided insights into the migration patterns of small birds not previously available. These devices have been assumed to have minimal impact on survival, although formal survival analyses are often not conducted when geolocators are used. We deployed geolocators on 29 Cliff Swallows and compared their survival rates over 2 subsequent seasons to 95 birds caught at the same time and site but that had standard aluminum bands only. We recovered 1 geolocator with usable data. The migratory track for this bird indicated stopover behavior, more rapid movement in spring than in fall, and significant over-water travel during spring migration. We found that birds with geolocators had an annual survival probability of 0.07, compared to 0.60 for birds without geolocators. Although this result should be interpreted with caution due to small sample sizes, it suggests that geolocators may affect survival of small aerial insectivore species. Geolocators provide invaluable information on migratory routes of birds, but the effects of geolocators on survival should be further studied. *Received 13 February 2024. Accepted 25 June 2024.*

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Until recently, logistics of studying birds outside of the breeding season have been difficult as researchers are limited in the amount of time that can be spent observing individuals and many animals travel to places inaccessible to researchers. Implementing tracking devices on animals can be expensive and, in some cases, impossible, as small birds cannot carry large tracking devices without inhibiting their flight. Geolocators offer a solution to these problems (Stutchbury et al. 2009, Bridge et al. 2013). These devices are lightweight and operate using a small battery, allowing them to be carried by small birds, and have been used to track birds such as buntings, swifts, swallows, flycatchers, and thrushes (Bridge et al. 2013). They operate by recording levels of sunlight at regular intervals. The amount of sunlight is used to determine where birds are traveling and how long they are staying in each location (Bridge et al. 2013).

There are several drawbacks to using geolocators. Tracked individuals must be recaptured to retrieve data, and recapture rates of birds vary depending on species. While the trackers are less than 5% of the bird's body weight (Fair et al. 2010), geolocators have the potential to inhibit

a bird's flight and thus impair annual survival (Bridge et al. 2013). Reviews of the effects of geolocators on apparent survival reveal inconsistent responses across different species, with some studies reporting no adverse effects and others evincing a negative effect on return rates of birds (Stutchbury et al. 2009, Barron et al. 2010, Bowlin et al. 2010, Bridge et al. 2013). Some work has shown that even when tracking devices have minimal apparent impact on the flight of birds, they can still affect nesting success and survival rates (Barron et al. 2010). In some studies, negative effects of geolocators appear to be more pronounced in smaller species (Bridge et al. 2013, Weiser et al. 2016) and aerial insectivores. In particular, swallows, including Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*), appear to be especially susceptible to the effects of tracking devices on apparent survival (Gómez et al. 2014, Scandolara et al. 2014).

Cliff Swallows (*Petrochelidon pyrrhonota*) were previously tracked with geolocators as part of a larger study on swallows migrating from northeastern Canada. Recapture rates for birds without geolocators were lower than for tagged birds, but total sample sizes for Cliff Swallows were small (Imley et al. 2018). Another study was conducted of a small and unusual Cliff Swallow population that had begun to breed in Argentina during the austral summer (Areta et al. 2021). There was no formal analysis of the effects of geolocators on these birds, although 6 of 18 birds with tracking devices were recaptured 1 year after tag deployment.

We deployed geolocators on Cliff Swallows in western Nebraska and attempted recapture for the next 2 years. We only recovered 1 functioning geocator from this effort, but it provides the first complete individual migratory track for the mid-continental North American breeding population of Cliff Swallows. In addition to retrieving descriptive data, we also performed a formal mark–recapture analysis to determine whether carrying a geocator had an effect on Cliff Swallow apparent annual survival.

Methods

Cliff Swallows are aerial insectivores. They nest throughout North America in colonies primarily on concrete bridges and culverts (Brown and Brown 1996, Brown et al. 2020). In North America, Cliff Swallows breed from February to August. Migration begins typically in late July and early August with birds nearly gone from the United States by late September (Brown et al. 2020). It is suspected that the majority of Cliff Swallows travel south by land through Mexico and Central America and stay east of the Andes as they migrate south. Although relatively little is known about the species on its wintering range, it appears to occur primarily throughout Argentina and Brazil (Brown et al. 2020).

Geolocators were deployed and all recapture attempts made at a single Cliff Swallow colony (41°15'5.43"N, 101°37'6.52"W) in Keith County, western Nebraska. The colony was under a railroad culvert that was built in 1995. Cliff Swallows began building nests on the structure in 1997 and have nested there continually since then. The colony has been monitored as part of ongoing studies on Cliff Swallows and is partially fumigated to control ectoparasites (Brown et al. 2021). The colony contained approximately 1,975, 1,650, and 1,450 active Cliff Swallow nests in 2021–2023, respectively.

Birds were caught for geocator deployment on 21 June 2021. Cliff Swallows were captured with mist nets placed inside the concrete culvert, with the nets parallel to a wall. This net placement made it more likely that we caught colony residents exiting their nests, rather than transient birds more likely to be captured at culvert entrances (Roche et al. 2013). We captured and banded a total of 124 Cliff Swallows with standard U.S. Fish and Wildlife Service aluminum

leg bands and recorded body mass and sex. Geolocators were attached to 29 of these individuals before release. Each geocator was custom built by ESB, weighed 0.6 g, and was secured using a backpack harness (Rappole and Tipton 1991, Jirinec et al. 2021). Weight of captured birds ranged from 19.0 to 33.5 g, so all geolocators made up less than 4% of the birds' body mass. We returned to the same location on 18–19 May 2022, 16–18 June 2022, and 19–24 June 2023 to recapture birds.

The geolocators logged light level values at 5 min intervals. Light levels were represented by values ranging from 0 to 127 and were scaled logarithmically to maximize sensitivity at low light levels typical of twilight events. The raw light data were cleaned to remove obvious errors (e.g., light at night), and we removed data associated with nesting activity (which was marked by frequent periods of darkness during daylight hours). We also adjusted time values to compensate for clock drift during the data collection period. The usable series of light-level readings went from 30 July 2021 to 7 May 2022. We established a calibration period of 30 July–14 August 2021, for which we assumed the bird remained in the general vicinity of the breeding location, based on visual confirmation of constancy in the light data.

We analyzed the light level data using the R programming environment along with functions in the *TwGeos* package (Lisovski et al. 2016) and the *SGAT* package (Sumner et al. 2009, Lisovski and Hahn 2012). We established an initial track using the *thresholdPath()* function in *SGAT*. This path was derived from twilights established with the *findTwilights()* and *twilightEdit()* functions in *TwGeos* with a threshold of 15.5, which corresponded to light levels when the sun was, on average, 2.2 degrees below the horizon during the calibration period. We then used this initial track as the prior for an MCMC analysis from the *SGAT* package that combined light-thresholding with a land mask and a simple animal movement model. The land mask reduced the likelihood of locations at sea, and the movement model was implemented as a gamma distribution with mean 0.7 and standard deviation 0.6. We established a final model that used the “ModifiedLogNormal” distribution to describe variation in twilight times. We did 3 successive burn-in runs with 2,000 iterations each and then used the burn-in parameters to initiate a final MCMC run of 5,000 iterations. We used a customized function called *migSchedule()* (M. Hallworth, pers. comm.) to derive daily median locations and to identify clusters of points that likely represent stopover locations. The cleaned light level data, R analysis code, and a set of coordinate data are archived on MoveBank under the project ID 2611337538.

We calculated survival estimates in Program MARK (White 2017). MARK estimates the probability of survival and recapture for individuals subject to at least 2 recapture occasions, allowing separate estimation of the likelihood of survival and recapture. Group models can provide estimates for individuals associated with different categorical variables, and time-dependent models provide estimates for each year of the study (Lebreton et al. 1992).

We created a time-dependent, group model where each individual bird from 2021 was assigned to 1 of 2 groups indicating whether it had a geocator. Two birds that lost their geolocators before recapture were removed from the dataset as it is possible that they lost them shortly after deployment. We compared group models with time-dependent effects for survival and recapture to constant models, using a ΔAICc of 2 to indicate which model was a better fit to the data. Top models within 2 AIC were averaged to generate parameter estimates. We report only apparent survival probabilities, as we could not estimate survival beyond our study area.

Results

In 2021, we captured and banded 124 Cliff Swallows and deployed geolocators on 29 of these.

Several geolocators were secured to birds that had been banded previously ($n = 5$), indicating that some individuals at this site were philopatric.

In 2022 we recaptured 30 individuals banded the previous year that did not have geolocators, and 2 individuals had geolocators. Data from 1 of the geolocators was corrupted, but the other was viable.

In 2023, we recaptured 10 individuals from the 2021 cohort. No geolocators were retrieved. However, the same 2 birds from which we had retrieved geolocators in 2022 returned in 2023, and 2 birds that initially had geolocators in 2021 also returned but had lost their geolocators at some time in the previous 2 years.

Our analysis of the 1 functioning geocator we retrieved yielded a posterior distribution of 5,000 locations for each half day over a period of 280 d. The estimated locations based on the median location each day (Fig. 1) suggest an initial northward movement from Nebraska into South Dakota in mid-August; however, these locations are likely inaccurate and may be due to subtle changes in the bird's behavior or microhabitat that influenced its exposure during twilight periods following the calibration period. The first clear southward movement occurred on 2 September 2021, in which the bird traversed Kansas to arrive near the border of Oklahoma and the Texas panhandle. The fall migration then appeared to follow the Gulf and Caribbean coasts through Mexico and Central America before the bird crossed the Amazon to reach its wintering area near the border of Brazil and Uruguay on or around 20 November 2021. There were evident stopovers during fall migration near the Isthmus of Tehuantepec in Mexico (16–21 Sep 2021) and in the state of Minas Gerais in southeastern Brazil (5–11 Nov 2021).

Spring migration began in mid-March 2022 with gradual northward movement that became more pronounced around 20 March. Although the path of the spring migration was similar to that of the fall migration, it was notably faster: 49 d versus 79 d in the fall. There were no apparent stopovers during spring migration, and several successive location estimates from 18 to 22 April suggest a period of over-water flight from Columbia to Mexico's Yucatan Peninsula as part of the spring migration. There also may have been a shorter over-water flight across the Gulf of Mexico a few days later. Spring migration appeared to end on 7 May 2022, when the light-level data indicated frequent shading events consistent with nesting (or nest prospecting) activity (Areta et al. 2021) and with arrival times of Cliff Swallows in our study area.

The top 2 models (models 1 and 2; Table 1) both included group effects on survival and differed only in model 1 also having a group effect for recapture parameters. With model averaging for the top 2 models, the estimated probability of annual survival for 2021–2022 ($\pm$ SE) was 0.07 ($\pm$ 0.05) for birds with geolocators and 0.60 ($\pm$ 0.32) for those without geolocators. Estimated probability of recapture was 0.83 ($\pm$ 0.26) for birds with geolocators and 0.38 ($\pm$ 0.20) for birds without geolocators. Survival and recapture probabilities for 2022–2023 were not separately estimable.

Discussion

The data retrieved from our geocator reveals previously unknown information about Cliff Swallows. Our results suggest wintering grounds farther to the east than often assumed (Brown et al. 2020, Areta et al. 2021), although overwintering sites likely vary for different populations (Hobson et al. 2015). Previous studies have found evidence of some individual Cliff Swallows overwintering in multiple locations (Imlay et al. 2018). We did not observe this in our tracked individual. We also found fall stopover locations in Brazil and Central America. Swallows were previously assumed to migrate mostly continuously without stopping as they can feed in the air

(Brown et al. 2020), but our study joins others suggesting that this is not the case (Laughlin et al. 2013, Imlay et al. 2020, Areta et al. 2021). The dominant landcover type in the vicinity of the apparent stopover location in Mexico is high rainforest, but there are also other forest types in the area that could have been used by the bird. The Yucatan Peninsula is an important stopover location for dozens of species, and Cliff Swallows have been documented at the site (Deppe and Rotenberry 2005).

The apparent stopover location in Brazil is close to the boundary between the Atlantic Forest and Cerrado. This area is also a destination for many migratory birds that may be used for stopovers or nonbreeding residency. Further studies should examine what habitats Cliff Swallows use as stopover sites. We also found that this bird may have migrated offshore in the spring; it was previously thought that Cliff Swallows primarily migrated over the Central American isthmus (Brown et al. 2020). This bird exhibited similar routes in spring and fall while in Mexico and the United States (Fig. 1), but only crossed over the Gulf in the spring. This pattern is distinctive from other swallows tracked with geolocators (Stutchbury et al. 2009, Bradley et al. 2014, Areta et al. 2021). Our results also show a faster spring than fall transit between wintering and breeding grounds, which agrees with reports for other swallows (Stutchbury et al. 2009, Neufeld et al. 2021). We caution, however, that our inferences are made from only 1 bird.

Our results suggest that geolocators have an effect on Cliff Swallows' survival, with survival estimates for birds with geolocators lower than for birds without geolocators. The results should be interpreted cautiously. Sample sizes were relatively small, and our estimates resulted in relatively large standard errors, particularly for birds without geolocators. Moreover, return rates for Cliff Swallows equipped with geolocators in Argentina and Canada were notably higher, with recapture rates of 33% and 21%, respectively, compared to 7% in our study (Imlay et al. 2018, Areta et al. 2021). The other studies on Cliff Swallows involved much smaller populations than ours and/or potentially fewer colony sites where the birds might have settled, and thus recapturing the same birds a year later may have been more likely than in our study, where colonies can consist of thousands of nests (Brown et al. 2013).

Birds with geolocators deployed may have been more likely to disperse to other sites or have been less likely to breed, perhaps due to the trauma associated with capture and attachment or the costs of carrying it over the long term. A study on Tree Swallows found no effect on short-term reproduction but still found potential for geolocators to result in low recapture rates and higher emigration rates (Gómez et al. 2014). A study on Barn Swallows found that birds with geolocators had lower nesting success and later start dates along with estimated survival rates (Scandolara et al. 2014). If this were the case for our Cliff Swallows, even if birds are attempting to breed, they may be using nests for shorter periods of time, limiting our chances of recapture.

Finally, our finding 2 birds that had lost their geolocators may indicate that our attachment method had flaws. Nevertheless, the total sample size of birds in this study ($n = 124$) and the statistical results from MARK suggest some degree of negative effect of geolocators on Cliff Swallows. Studies using geolocators should report corresponding survival analyses, so that the impact on birds can be better understood. Further studies should be done on what features of geolocators can minimize impacts on survival and return rates.

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Table 1. Candidate models examining the influence of geolocators on Cliff Swallow survival. Model describes the predictor variables incorporated in models. S denotes survival parameters. P denotes recapture parameters. Geo = Geolocator, Time = Time dependent parameters, . = Null model. LL is the log likelihood. K is the number of estimated parameters for each model. ΔAICc is the difference between AICc scores of the top-ranked model and the listed model.

#	Model	AICc	ΔAICc	K	LL
1	S(geo*time) P(geo*time)	167.24	0	4	1
2	S(geo*time) P(time)	168.58	1.34	3	0.51
3	S(time) P(time)	176.96	9.72	2	0.0078
4	S(.) P(.)	176.99	9.75	2	0.0076
5	S(geo) P(geo)	178.21	10.97	4	0.0041

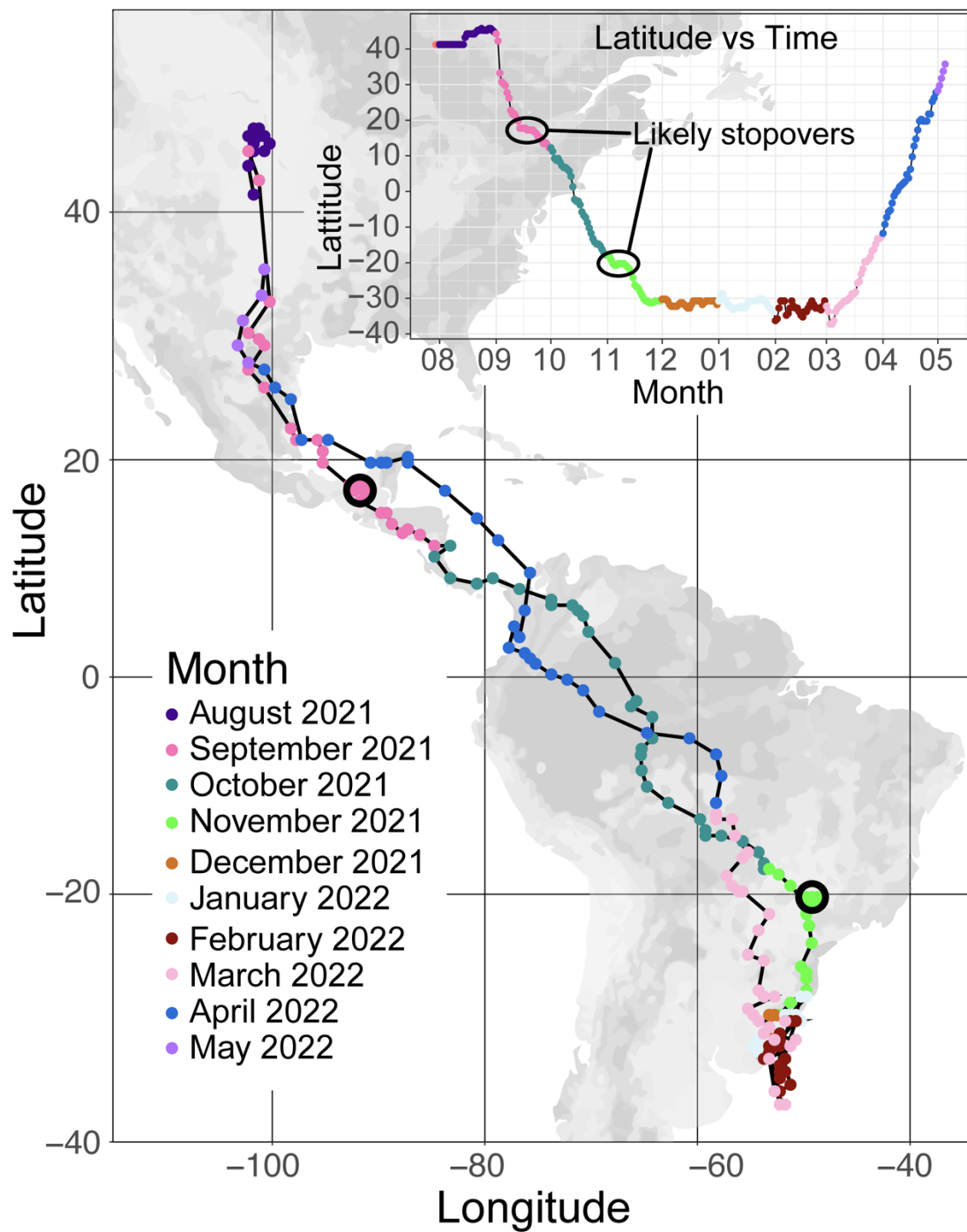


Figure 1. Cliff Swallow migration track with points representing median daily locations designated by color for each month of the migration period. Black circles indicate likely stopover locations during the fall migration.