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BREEDING PHENOLOGY AND SUCCESS OF BLACK SWIFTS IN BOX CANYON, OURAY, COLORADO

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ABSTRACT.—This study presents 11 years of nesting success and phenology data for Black Swifts (*Cypseloides niger*) at Box Canyon in Ouray, Colorado. Nest data were recorded on a near-daily basis for 160 nest attempts. Nesting success was 72% and mean and extreme dates of nesting events, including arrival, egg-laying, onset of incubation, hatching, and fledging are reported. On average, Black Swifts arrived on 13 June, egg laying started on 28 June, incubation started on 1 July, hatching occurred on 26 July, and fledging occurred on 13 September. The average incubation period was 26 days and the nestling phase was 48 days. In seven instances, a second egg appeared after loss of the first egg and, in one case, a third egg appeared. It was not possible to ascertain whether second or third eggs represented a renesting attempt or nest usurpation. *Received 23 August 2006. Accepted 4 March 2007.*

Nesting phenology and nest success rate information of Black Swift (*Cypseloides niger*) is currently based on small sample sizes. Precise nest habitat requirements cause nesting colonies to be widely scattered across appropriate landscapes, often in disjunct and remote areas. Through the 1900s, investigators found that Black Swifts nested in western North America at cool, moist, dark sites, usually associated with waterfalls. Colonies often consist of only one or two nesting pairs, making observation of large numbers of nesting birds logistically challenging. The cryptic nature of the nests and their frequent placement in inaccessible niches makes detection difficult; the long breeding season requires a large investment of time to observe nesting phenology. Despite these challenges, investigators have long been intrigued by the unique nesting characteristics and phenology of the species. Previous studies have indicated that, unlike all other North American swifts, Black Swifts produce single-egg clutches and have long incubation and fledgling periods (Lowther and Collins 2002). Previously published reports (Bailey and Neidrach 1965; Foerster 1987; Marín 1997, 1999; Boyle 1998; Hirshman 1998) on nests of this species consisted of small sample sizes ranging from observations of 4 to 35 nests with little or no information about nesting phenology.

From 1949 to 1958, O. A. Knorr surveyed areas of Colorado with suitable Black Swift nesting habitat to ascertain the species' nesting distribution and cataloged 27 colonies. In 1950, he discovered a colony of approximately 10 nesting pairs in Box Canyon in Ouray, Colorado (Knorr 1961). This easily accessible colony became popular with birdwatchers and is currently the largest known Black Swift colony in Colorado.

SEH logged more than 7,000 hrs from 1996 through 2006 observing nesting Black Swifts at the Box Canyon colony. Each year, arrival, nest building, egg laying, incubation, hatching, rearing, and fledging of the swifts were monitored. Her notes, including 196 season-long individual nest records, comprise the most extensive body of observations for this species. Retrospective review and analysis conducted on these data provide new information on the breeding biology of Black Swifts and allow for nesting phenology comparisons with previous studies of other populations. The objectives of this paper are to present phenology and nest success at the largest known colony of Black Swifts in Colorado.

METHODS

Study Site.—Box Canyon is <2 km southwest of Ouray, Colorado (38° 01′ 06″ N, 107° 40′ 44″ W) at an elevation of 2,380 m. Canyon Creek has formed a deeply incised, 60-m waterfall in the dark green diabase (dolerite) and quartzite rock layer (Gregory 1984) resulting in a narrow, deep canyon with the cliff of the

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falls forming a "box." The amount of water in Canyon Creek varies throughout the year based on snowfall, spring runoff, flash floods, and drought. The precipitous canyon walls provide nesting ledges and niches for Black Swifts. Spray from the falls, nearly continuous shade, and luxuriant growth of moss combine to form a cool, moist microhabitat perfect for nesting. Flash floods carrying boulders and woody debris periodically reconfigure the falls, causing the water and mist to shift position at the head of the falls, possibly changing nest microhabitats. Installation of new stairs and walkways in 1998 changed tourist traffic and viewing patterns, and may have influenced aerial access to some nest sites for the swifts.

Data Collection.—Observations occurred yearly for a total of 1,082 days from 1996 through 2006, averaging ~6 hrs/day from when swifts arrived at the falls until the last chick fledged. Observations generally alternated between mornings, afternoons, and early evenings, but some visits encompassed the entire day. During 11 years of observation, only 31 days (3%) had no observations.

Each nest was assigned a unique identification number in 1996, the first year of observation. New nests were assigned an alphanumeric label when found based on proximity to an existing nest (e.g., nest 6A is a new nest found near original nest 6). Nests were observed with 8 × 42 binoculars and a 20–40 × 60 tripod-mounted spotting scope. A handheld spotlight was used to illuminate nests and roosting sites during evening surveys.

We rated nests based on the observer's ability to view activity in the nest: (1) "excellent" indicates the nest, incubating adult, juvenile, and egg were visible under all conditions; (2) "good" indicates the nest, incubating adult, juvenile, and egg were detectable, but only under optimal natural lighting conditions; (3) "fair" denotes the nest, incubating adult, and older juvenile could be observed, but the egg and hatchling could not be seen and/or that the location was dark or misty; and (4) "poor" signifies that adults could be seen only flying to the site and/or only portions of the adult's body could be viewed during incubation, that juveniles could be seen only when they were large or were exercising wings prior to fledging, or that water, mist or darkness prevented good viewing. The designation for a nest changed in a few instances because nest edges were built-up so the observer could no longer see the nest contents or because construction of new walkways and stairs enabled the viewer to see the nest more clearly. Eight (31%) of 26 identified nests were "excellent", six nests (23%) were "good", three nests (12%) were "fair", and nine nests (34%) were rated as "poor" (Table 1).

Only events that were accurately viewed were included in our data analysis. Inferred, extrapolated or poorly observed events were not included. Only data from nests with "excellent" or "good" viewing designations (54% of nests) were used to ascertain dates of egg laying, onset of incubation, and hatching. Fledging dates used data from all successful nests, despite viewing designation, because these events were easily observed.

Arrival date was defined as the first observation of Black Swifts in the area. In late May and early June each year, SEH looked for Black Swifts by scanning the skies over Ouray and Box Canyon and, in some years, by visiting the colony site after dark for evidence of roosting birds.

Laying date was calculated as the average date the first egg was observed, and we included only nests in which the egg could be clearly seen. We also report laying date when nests with a second and third egg were included in the data analysis. We did not include laying dates for nests where the egg was first seen after incubation had begun.

Onset of incubation was defined as the date an adult was consistently incubating. Incubation period was the period starting with the day the adult was consistently on the nest until the day the chick was first observed. Hatching date was defined as the first day the chick was seen in the nest. Nestling stage was measured from the day the chick was first seen to the day the chick fledged. Fledging date was the date the nest was empty after having contained a near-fledging chick.

A nest attempt was defined as activity at a nest resulting in production of an egg (including second and third eggs) or as behavior indicating consistent incubation. Activity indicates interest in a nest without production of an egg, such as attendance at a nest by one or

TABLE 1. Nest presence and activity of Black Swifts at Box Canyon, Ouray, Colorado, 1996–2006.

Nest #	Year found	Years present	Status	Nest attempts	Years active	Years successful	Viewing designation
1	1996	7	Gone 2003	6	6	5	Excellent
1A	1997	4	Gone 2001	2	2	1	Poor in 1997, Good 1998–2000
1B	1998	3	Gone 1999; rebuilt 2004; gone 8 Jun 2006	3	3	3	Poor
2	1996	11	Present	9	9	6	Fair 1996–2004, Poor in 2005 and 2006
3	1996	7	Gone 2003	7	7	7	Good
4	1996	11	Present	12	11	10	Good
5	1996	11	Present	11	11	10	Poor
6	1996	11	Present	8	6	4	Excellent
6A	1998	9	Present	3	3	3	Poor
7	1996	11	Present	12	11	9	Excellent
7A	1996	11	Present	11	10	8	Excellent
8	1996	11	Present	10	10	7	Good
9	1996	10	Gone 6 May 2006	7	7	4	Good
9A	1998	9	Present	3	3	3	Poor
9B	1998	9	Present	9	9	7	Poor
10	1996	4	Gone 2000	4	2	1	Excellent
10A	1998	9	Present	10	9	5	Excellent
10AA	2006	1	Present	0	0	0	Excellent
10B	1998	9	Present	9	9	9	Good
10BB	2004	2	Present	2	2	2	Fair
10C	1999	7	Gone 13 Jun 2006	5	5	3	Fair
11	1996	2	Gone 1998	0	0	0	Excellent
12	1996	11	Present	7	7	4	Poor
12A	1997	2	Gone mid-1998	2	2	1	Poor
13	1998	7	Gone 2005	6	6	3	Poor
14	2003	3	Unsure if nest still present	1	1	1	Poor
Unknown[a]	1996	Unknown	Unknown	1	1	1	
Totals				160		117	

[a] Fledgling from an unknown nest was seen 15 September 1996 and reported to SEH after she had left Ouray.

more adults for a short period of time. Hatching success indicates the percentage of eggs that hatched. Fledgling success is the percentage of eggs hatched that fledged young. Nesting success refers to the percentage of nesting attempts that fledged chicks.

We calculated nest success and daily survival rates using the Mayfield method (Mayfield 1961, 1975) rather than apparent nest success (proportion of observed nesting attempts that succeed) to compensate for the possibility that some nests may have failed before they were discovered. Although observations were missed in only 3% of the Box Canyon breeding seasons, and SEH is an experienced observer, search frequency and investigator skill can distort apparent nest success results.

RESULTS

Nests were present at 26 individual sites in at least 1 year during 11 years of observation. Fourteen nests were identified in the initial year and 12 were built during the ensuing 10 seasons (Table 1). Eight of the original 14 nests persisted throughout the 11-year period; one of these was not known to be active. All remaining 25 nests had activity in at least 1 year. Of the 196 season-long individual nest observations made over 11 years, SEH recorded activity such as examination, repair, or roosting by adults or non-breeding birds that

TABLE 2. Nesting phenology of Black Swifts, Box Canyon, Ouray, Colorado, 1996–2006.

Event	Average date or number of days	Range of dates or days	Sample size	SD (days)
Arrival	13 Jun	31 May–19 Jun	11	6.6
Interval between arrival and egg laying	9 days	1–22 days	11	6.8
Egg laying (does not include 2nd and 3rd eggs laid)	28 Jun	19 Jun–16 Jul	73	5.4
Egg laying (includes 2nd and 3rd eggs laid)	30 Jun	19 Jun–29 Jul	81	7.1
Incubation onset	1 Jul	16 Jun–16 Jul	83	5.9
Incubation length	26 days	22–32 days	56	2.4
Hatching	26 Jul	17 Jul–9 Aug	59	5.6
Nestling phase	48 days	40–58 days	56	3.6
Fledging	13 Sep	31 Aug–7 Oct	117	7.3

did not result in egg laying at 18 nests and no activity was recorded at 26 nests.

The Mayfield nest success rate for 160 nest attempts over the 11-year period with 9,718 nest exposure days was 72% with a hatch rate of 82% and fledging rate of 90%. The daily nest survival rate was 0.996 (SE = 0.001). Thirty-five nest attempts failed over the observation period. The adult incubated an egg in 18 nests from 1 to 59 days (average 28 days) before it abandoned the egg or the egg disappeared. The chick died or disappeared in 10 nests prior to fledging, living from 3 to 34 days. Three nests were either destroyed or abandoned after flash floods. Multiple eggs were laid in four unsuccessful nests: two had two successive eggs, one had one egg and one successive chick that died at ~3 days of age, and one had three successive eggs. In nests with two eggs, the first egg disappeared after 1, 6, and 8 days. In the nest with three eggs, each egg disappeared the day after it was laid.

In addition to the three unsuccessful nests in which a second egg was laid, a chick was fledged from a second egg in three instances. The average laying date of a second egg (regardless of success) was 13 July (range = 6–28 July). An average lapse of 18 days (range = 11–37 days) occurred between laying of first and second eggs (n = 7) and a lapse of 12 days occurred between second and third eggs (n = 1).

Black Swift nesting phenology at Box Canyon indicated average arrival on 13 June (31 May–19 Jun) with egg laying starting by 28 June (19 Jun–16 Jul) and incubation starting on 1 July (16 Jun–16 Jul). Hatching occurred on 26 July (17 Jul–9 Aug) with fledging occurring on 13 September (31 Aug–7 Oct). The incubation period was 26 days (22–32 days) and nestling phase was 48 days (40–58 days) (Table 2, Fig. 1).

DISCUSSION

There is scant information published on nesting phenology of Black Swifts. Initial observations of Black Swifts in Box Canyon in 1996–1997 have previously been reported (Hirshman 1998). Boyle (1998) reviewed egg and hatching dates based on two published reports and only four data points collected during surveys for the Colorado Breeding Bird Atlas. Bailey and Niedrach (1965) reviewed all known nesting information, which at that time represented 35 individual nest reports in Colorado, only 13 of which had phenological events observed and recorded. Outside of Colorado, the most thorough Black Swift nesting studies were in southern California. Marín (1997, 1999) reported 20 direct field observations and reviewed 67 egg data cards, and Foerster (1987) observed breeding of 13–14 pairs over a 2-year period. Other studies presented extrapolated or estimated phenological events (Murphy 1951, Hunter and Baldwin 1962).

The inability to consistently view all nests in our study may have introduced some minor error in the data set. Many factors, including location and height of the nest, darkness, mist, and water affected how well nests could be observed. Eggs and small chicks could be difficult to view, whereas older, larger and more active chicks could be seen even in cases where earlier events at the nest could not be accurately observed. Length of brooding could not be precisely established due to viewing limitations.

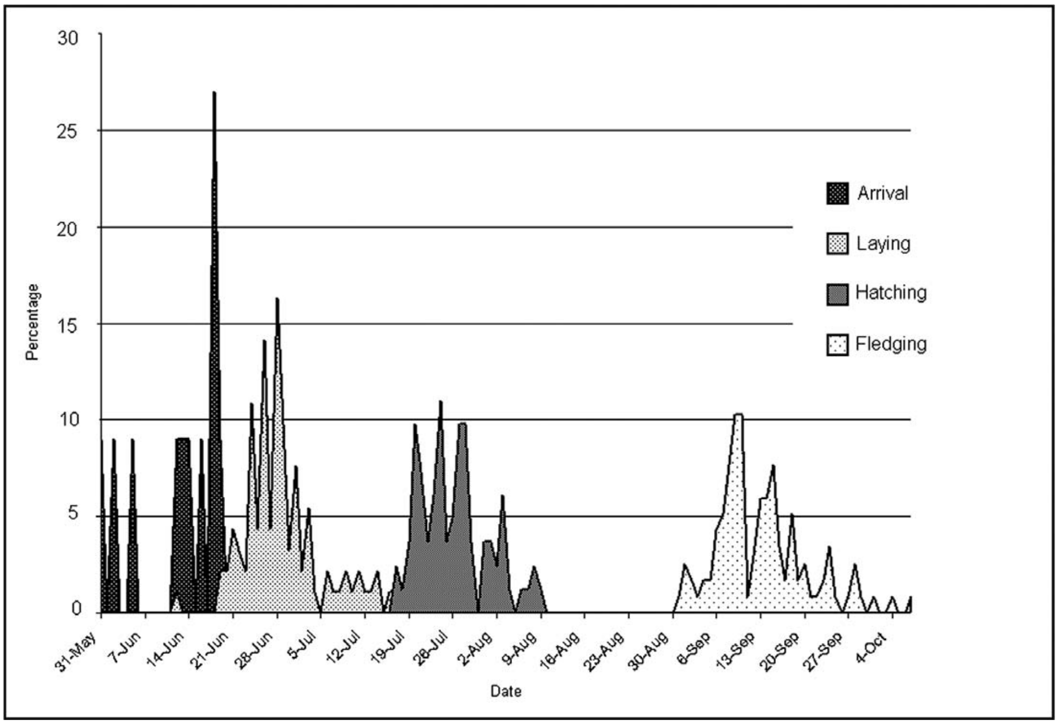

FIG. 1. Nesting phenology of Black Swifts, Box Canyon, Ouray, Colorado, 1996–2006.

The Mayfield nest success rate (72%) was similar to the apparent nest success rate of 73% (95% CL: 65–79%). The Mayfield method also produced a hatch rate and a fledging rate <1% different from the apparent rates (81.8 vs. 81.3% and 89.8 vs. 90.0%, respectively). These similarities suggest that few, if any, nesting events were not detected near the time of occurrence.

The Mayfield method nest success reported here (72%) is slightly lower than that reported by Foerster (1987) who measured an apparent rate of 80% (n = 20) over a 2-year period. Fledgling success at Box Canyon (90%) was lower than the 95% apparent rate reported by Foerster (1987). In the Hunter and Baldwin study (1962), two of the five nests failed during the early nestling period. Fledgling success rate at Box Canyon in 2002, during the worst drought in recorded history, was 52%. Excluding 2002, the fledgling success rate at Box Canyon over the remaining 10 years was 93%. Hatching success at Box Canyon (82%) was similar to the 81% (n = 16) reported from southern California (Marín 1997).

Black Swift arrival dates had a wider variation than might be expected. Some variation may be attributed to regional weather and food availability. Finding swifts by inspecting the sky is also somewhat dependent on luck. Swifts fly quickly and their presence in the skies can be easily overlooked. Inspecting roost sites in 2004, 2005, and 2006 at Box Canyon after dark revealed the birds' presence 10–16 days earlier than had been observed in previous years, suggesting that direct inspection of known roost/nest sites is probably a more accurate method to ascertain arrival date.

Overall, the interval between arrival of swifts and onset of egg laying averaged 9 days. However, in the first 8 years of the study, arrival of swifts was recorded by seeing the adults flying over the colony site during the day, resulting in an interval of 6.5 days. We believe this method is not as accurate as inspecting the colony nesting site at night. During the last 3 years of observation, using the latter technique produced an interval of 16 days, indicating that swifts may have a longer interval between arrival and laying than previously calculated. The delay is probably attributable to formation or reaffirmation of pair bonds, courtship displays, mating, inspection and selection of nest sites, and refurbishing or rebuilding of nests. Energetics, food availability, and environmental influences such as temperature and precipitation may affect length of this interval.

SEH observed repair of existing nests or complete rebuilding of nests at sites where previous nests had disappeared in four instances. Nest-building activities took 13–15 days. SEH did not observe building of a new nest and most nest-building activity apparently occurred early or late in the day, outside of observation periods. Marín (1997) observed nest building only once, but no time period was given. However, he refers to an egg data card indicating a nest was built in 4 days. Lowther and Collins (2002) provide no information for nest building.

On average, incubation began 3 days after laying. In a few cases, incubation started the day of laying, while in others it was delayed up to 7 days. Incubation periods reported by Marín (1997) averaged 24 days (range = 23–26, n = 6). Legg (1956) reported a 27-day incubation period (n = 1), and Murphy (1951) estimated incubation to be 24 days (n = 1). These dates generally agree with the average 26-day incubation period found in this study (n = 56).

The variation in length (40–58 days) of the nestling stage is difficult to explain. The duration of nestling stage may be a phenotypic plastic life history trait in Black Swifts. Eggs and nestlings of swifts in the Family Apodidae are resistant to cooling, and nestlings can go into torpor to conserve energy (Camfield 2004), especially when adults are away on feeding forays. During torpor, which is also influenced in intensity by the nest's microclimate, metabolism decreases and possibly influences the chick's growth, contributing to the wide variation in the nestling stage. Nestling growth is also affected by weather, since adult foraging success and subsequent feeding frequencies of the chick depend on insect swarms (Camfield 2004). Foerster (1987) reported a nestling period averaging 48 days (n = 14), with a range of 45 to 51 days. Marín (1997) reported an average nestling period of 48 days (n = 9) in his 3-year study, and Legg (1956) reported a nestling period of 45 days for one chick. A second source of variation in nestling stage could be caused by difficulties in viewing the hatching event. Despite using only nests with "excellent" or "good" viewing designations, identification of the exact day of hatching can be difficult.

Black Swift nests were relatively persistent within the colony, some lasting 11 years, although most received repairs each year (Table 1). A nest's longevity depends on its location, how sheltered it is from weather and runoff from the falls, whether it receives any repair, and the durability of construction and materials. Of 196 season-long nest observations at 25 nest sites over 11 years, 178 (91%) recorded either nest attempts (n = 160) or activities that did not result in egg laying (n = 18). Thus, most nests receive some attention by pairs in most years. This activity may indicate that available nest and roost sites in Box Canyon are or nearly are saturated.

Causes of nest failure are difficult to accurately identify. Most avian species abandon their eggs during incubation when foraging becomes difficult or when their energy reserves dwindle to critical levels (Gill 1994). Other causes of nest failure include loss of one of the adults, infertile or otherwise defective eggs, environmental causes such as flash floods, disturbance due to human activity, parasites and disease, displacement of nestlings from the nest, and improper microhabitat at the nest. No predation was observed at Box Canyon, but terrestrial and aerial predators could be a cause of nest failure in other colonies. American Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), and Steller's Jays (*Cyanocitta stelleri*) occasionally were seen to approach the mouth of the canyon, but none has been observed entering or approaching the swift nests.

Disappearance of eggs during incubation and early abandonment of the nest by adults have been noted by others (Hunter and Baldwin 1962, Foerster 1987, Marin 1997). All nests at Box Canyon are out of reach of site visitors, and no terrestrial or aerial predation has been observed. Foerster (1987) reported a rock being thrown at a nest as cause for egg breakage, and this cannot be dismissed as a possibility at Box Canyon. Visitation at this site from 1997 to 2004 averaged 57,781 people annually (Box Canyon Falls Park 2005). It is also possible an egg could be pushed from the nest by the adult swifts, either intentionally or accidentally, or removed from the nest by an antagonistic conspecific.

Possible causes for chick loss include disease, ectoparasites, lack of proper brooding, starvation, desertion, improper nest microhabitat (too wet, too dry, too cold or too hot), and displacement from the nest prior to fledging. Hunter and Baldwin (1962) reviewed the existing accounts of nesting and noted a large proportion of nesting failures involved mysterious disappearance of the young, young found dead in the nest, or young falling from the nest. Knorr (1961) observed a chick falling from a nest and being swept away in a stream. In three instances, SEH or others found chicks on the ground near the nest site. In 2005, a chick fell from its nest and was returned to the nest with the aid of a 3-m metal pole wrapped with cloth to which the chick could cling; the chick successfully fledged 13 days later. In 2004, a chick spent 2 days on the canyon floor and was attended by an adult. SEH placed this chick in a crack on the canyon wall from which it fledged a few days later. In 2003, a new nest site was discovered only after the chick from that nest was found on the canyon floor, probably the result of an unsuccessful fledging attempt. The chick was placed near the newly discovered nest and it fledged the following day. These observations suggest that young falling from nests may significantly contribute to nesting attempt failure in Black Swifts.

Of the 35 instances in which a nest attempt failed, egg replacement occurred seven times (20%), and a third egg was laid once (2%). The latest date of appearance of a second egg from which a chick was successfully raised was 28 July; the chick fledged on 7 October. Marín twice observed loss of eggs without replacement eggs being laid and stated, "The Black Swift lays a single egg, and if this egg is lost, there is no attempt to replace it" (Marín 1997:302). Using banded birds during the breeding seasons of 1999 and 2000, Marín observed four nests in which a second egg was laid and in all cases the replacement egg was laid not by the original female, but by other females from the colony or a different colony, usually younger females (M. Marín, unpubl. data). Foerster (1987) reported clutch size to be one egg in all cases and did not observe replacement eggs. It is not known why a second egg is laid in some instances of loss or failure of the first egg and not in others. Ability to renest depends upon food supplies, accumulated reserves and nutritional status of the female, mating opportunities, nest availability and microclimate, and continued help by mates. The amount of energy invested in a first nesting attempt and lateness of the season (effects of photoperiod) can further influence renesting (Gill 1994).

Our observations generally agree with those of other investigators that once young fledge, both young and adults leave the colony. However, during a bout of inclement weather, one chick that fledged in the early morning and was gone all day returned to roost at its nest one more night. It is believed that young of many swift species fledge in the morning before 0800 hrs (Lack 1973, Marín 1997). The majority of the swifts in our study fledged between 1600 hrs on one day and 0800 hrs the following morning. However, seven chicks were observed to fledge between 0900 and 1840 hrs.

Relationships between nesting success and weather elements such as temperature and precipitation are often obscure. The study period included the most severe drought experienced in the area in more than a century (Western Regional Climate Center 2005). The 11-year observation period was too short and provided a sample size too small to develop statistically significant results correlating weather and nesting success. Although the poor nest success rate of 2002 (50%) coincided with the worst year of drought, the rate was 44% in 2006, a year of near-normal precipitation. Most nests (5 of 7) failed in the nestling phase during the 2002 drought year, and all nest failures (6) in 2006 occurred during the incubation stage. These differences suggest the cause of nest failures differed between years.

The Black Swift colony at Box Canyon has apparently remained stable or perhaps even increased over 57 years. Nest site fidelity is one attribute, along with adult longevity, believed to be responsible for long-term traditional nest site use noted for this species (Collins and Foerster 1995).

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