

DISTRIBUTION, ABUNDANCE, AND NEST-SITE CHARACTERISTICS OF BLACK SWIFTS IN THE SOUTHERN ROCKY MOUNTAINS OF COLORADO AND NEW MEXICO

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ABSTRACT.—We surveyed 366 historical and potential nesting sites for Black Swifts (*Cypseloides niger*) from 1997 to 2005 in the Southern Rocky Mountains, evaluated their suitability for nesting, and searched for evidence of occupancy. Our surveys located 70 previously undocumented occupied sites, increasing the inventory of sites in the region from 33 to 103. Our results provide a preliminary estimate of Black Swift population size. Comparison of observed colony sizes with those reported in earlier studies suggests little or no change in population levels over the past 50 years. We rated each nest site on conformance to characteristics described in earlier studies. Analysis of 291 site evaluations support *a priori* assumptions that increasing stream flow, number of potential nest platforms, amount of available moss, shading of potential nest niches, topographic relief of surrounding terrain, and ease of aerial access to potential nest niches contributed to a higher probability the site would be occupied by Black Swifts. Received 14 March 2007. Accepted 11 September 2007.

Observers in the late 19th century believed Black Swifts (*Cypseloides niger*) nested in Colorado (Drew 1881, Bendire 1895), but the first breeding confirmation in the Southern Rocky Mountains did not occur until 1949 when O. A. Knorr found nests at two waterfalls near Silverton in San Juan County (Knorr 1950). Knorr searched the mountains of Colorado from 1949 through 1958 for Black Swift colonies and located ~80 nests at 25 sites in 10 counties (Knorr 1953, 1961). In the 38 years (1959–1997) following Knorr’s investigations, only seven additional colonies were located in Colorado, six at waterfalls (Bailey and Niedrach 1965; Boyle 1998; Hurtado 2002; Robert Righter, pers. comm.) and one in a limestone resurgence cave (Davis 1964). During this same time period, a single colony was located in the Southern Rocky

Mountain Region in northern New Mexico (Johnson 1990).

An ecological pattern emerged from Knorr’s investigations leading him to suggest that “five physical factors were found to be present to a greater or lesser degree in all the colonies” (Knorr 1961:167). These five factors included (1) the presence of water—“from a rushing torrent to a mere trickle,” (1961:168), (2) high relief—“a commanding position above the surrounding terrain,” (1961:168), (3) inaccessibility to terrestrial marauders, (4) darkness—Knorr “never found an occupied nest upon which the sun shone,” (1961:168), and (5) unobstructed aerial access—the birds “will not fly through a maze of trees to reach their nests” (1961:168). Later, after evaluating some apparently suitable but unoccupied sites, Knorr added a sixth physical factor of nest sites: the presence of niches in rock for nest placement (Knorr 1993). Subsequent studies have generally concurred with Knorr’s analysis of Black Swift nesting characteristics (Hunter and Baldwin 1962, Foerster 1987). The objectives of our paper are to: present (1) the results of extensive investigations of potential Black Swift nest sites in the Southern Rocky Mountains, and (2) a model for predicting Black Swift occupancy based on characteristics of known occupied sites.

METHODS

Field Methods.—The U.S. Forest Service (USFS) designated the Black Swift as a sensi-

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TABLE 1. Black Swift surveys in Colorado and northern New Mexico, 1997–2005. Prior to these investigations, 32 colony sites had been located in Colorado and one in New Mexico. Multiple evaluations were conducted at many sites.

State	Year	Sites in data base	New sites surveyed	Total sites surveyed	New colonies found
Colorado	1997	NA	2	4	2
Colorado	1998	NA	41	52	5
Colorado	1999	NA	37	56	5
Colorado	2000	NA	60	106	5
Colorado	2001	311	58	119	21
Colorado	2002	352	76	96	18
Colorado	2003	417	71	149	9
Colorado	2004	426	6	12	3
Colorado	2005	427	1	3	0
Subtotal		427	352	597	68
New Mexico	2003	16	9	9	1
New Mexico	2004	21	7	8	1
Subtotal		21	17	17	2
Totals		448	369	614	70

tive species in the Rocky Mountain Region in 1993 citing the need for more information about its distribution and abundance. The USFS subsequently, in cooperation with the Colorado Natural Heritage Program, canvassed museums and available literature and interviewed knowledgeable individuals to compile an inventory of historically active nest sites, currently active nest sites, potential nest sites, and incidental Black Swift observations. The list of potential nest sites included waterfalls from Conly's *Waterfalls of Colorado* (1993), Burns' *Colorado Ice Climber's Guide* (1997), 7.5-minute USGS topographic maps, and National Forest visitor maps. Surveyors discovered many more potential sites as they traveled to the waterfalls on the initial list.

Field verification began on a small scale in 1997 and, in 1998, the Rocky Mountain Bird Observatory (RMBO) joined USFS and greatly expanded the survey effort (Table 1). From 1998 through 2005, USFS and RMBO personnel and trained volunteers surveyed and evaluated potential Black Swift sites in Colorado. In 2003 and 2004, RMBO, under contract with the New Mexico Department of Game and Fish, conducted surveys in New Mexico. We included sites in northern New Mexico that are within the Southern Rocky Mountain Physiographic Region. We did not conduct any surveys in the small portion of

this physiographic region that extends into southern Wyoming.

Surveyors field-tested a Black Swift survey and monitoring protocol during 1998 and 1999 to evaluate it as a status and population trend-monitoring tool. This field protocol, with minor revisions through the course of investigations (Schultz and Levad 2001, 2003), guided our surveys. Surveyors evaluated each site for suitability for Black Swift occupancy using a rating scale based upon, but not identical to, the characteristics described by Knorr (1953, 1961, 1993). Six habitat parameters at each site were individually assigned a numeric rating ranging from 1 to 5 based on increasing abundance or extent (Table 2). The six habitat parameters were: FLOW (the amount of flowing surface water during late summer), RELIEF (the extent of relief or prominence over surrounding terrain from the top of the site), ACCESS (the extent of aerial access to or from the nest niches), SHADING (the extent of shading of nest niches), NICHES (the number of suitable nest niches inaccessible to ground predators), and MOSS (the amount of moss available at the nest site). We conducted an intensive training session for surveyors each year to standardize interpretation of the subjective descriptors of nest site characteristics.

Surveyors searched each potential site for nests and other evidence of Black Swift occupancy, such as the presence of urates. They recorded the maximum number of adult swifts seen simultaneously flying about or roosting at the site to develop an estimate of minimum colony size. Observers remained at the site until dark when feasible to detect and/or count adults arriving to roost.

Sites were rated as occupied if any of three conditions were met: (1) a nest containing an incubating Black Swift adult, egg, or chick was observed; (2) a used Black Swift nest was observed; or (3) Black Swifts were observed coming to roost at a suitable nest location. We cautiously applied the second criteria because Cordilleran Flycatcher (*Empidonax occidentalis*) and Townsend's Solitaire (*Myadestes townsendi*) nests can be confused with those of Black Swifts. Nests of these three species were distinguished by structure, placement, and materials. The third criterion does not meet the standard for confirmation of nesting for most species, but we designated these sites

TABLE 2. Rating scale for Black Swift colony site characteristics.

	1	2	3	4	5
FLOW RELIEF	None Falls at bottom of terrain	Weak Little view from top of falls	Moderate little spray Moderate view from top of falls	Moderate much spray Good view from top of falls	Heavy Commanding view from top of falls
ACCESS	No clear access	Access clear to 1/4 of niches	Access clear to 1/2 of niches	Access clear to 3/4 of niches	Access clear to all niches
SHADING NICHES	Nest niches sunlit all day No suitable niches present	Sunlit >3 hrs/day Few niches and/or all niches accessible	Sunlit 1-3 hrs/day Some niches and most niches accessible	Sunlit <1 hr/day Some niches and most niches inaccessible	Shaded all day Many niches and most niches inaccessible
MOSS	No moss	Trace of moss	Scattered moss	Frequent moss	Abundant moss

as occupied because there is no confirmed record of Black Swifts roosting during the breeding season at a site where nests were not present (Lowther and Collins 2002; O. A. Knorr, pers. comm.). “Occupied” thus does not absolutely indicate that nests are present; but that Black Swifts use the site and the probability of nests being present is extremely high. We designated as occupied all sites that had been found to meet any of these criteria, whether that finding was made in the current study or by earlier observations.

We considered sites vacant when one or more surveys were completed and no birds or swift nests were detected. We considered a survey completed when all potential nest niches were examined or when an evening watch was conducted. Sites were rated as occupancy unknown when it was not possible to examine all potential nest niches and when an evening watch was not conducted.

Data Analysis.—The variables FLOW, RELIEF, ACCESS, SHADING, NICHES, and MOSS were used to develop a model to predict Black Swift occupancy at 291 sites using “all-subsets selection” binary logistic regression analysis and the Akaike information-theoretic approach (Burnham and Anderson 2002). These authors have stressed that an informed selection of independent variables is critical to meaningful model inferences. We based our model on the variables outlined by Knorr (1953, 1961, 1993) and followed by Hunter and Baldwin (1962) and Foerster (1987). We combined two of Knorr’s criteria—presence of niches and their accessibility by ground predators—because we were evaluating potential as well as actual nest sites. We added moss availability as a characteristic for evaluation because all nests in the Southern Rockies up to this time have been constructed of moss (Lowther and Collins 2002). The six variables we used in our model were weakly correlated with each other (*r* values < 0.55). Wald Chi-square was used to test the significance of each predicting variable (Kleinbaum 1994). Logistic regression calculations were performed using SAS Enterprise Guide software (SAS Institute 2001).

RESULTS

We compiled a catalog of 427 potential Black Swift nesting sites in Colorado and an

additional 21 sites in northern New Mexico by the end of the 2005 field season. We completed 597 visits at 352 sites in Colorado and an additional 21 visits at 17 sites in northern New Mexico (Fig. 1). Some sites in both Colorado and New Mexico were visited more than once, and each visit generated an evaluation form.

We confirmed occupancy by Black Swifts in at least 1 year at 96 sites in Colorado and three sites in New Mexico. We located 68 new nest sites in Colorado and two new sites in New Mexico during the course of this study. We located active nests at 58 of the new sites and observed adults coming to roost at the remaining 12.

Binary logistic regressions for the dependent variable OCCUPIED were calculated for 63 combinations of the predicting variables FLOW, RELIEF, ACCESS, SHADING, NICHES, and MOSS, plus the intercept-only (null) model, and evaluated for best fit using Akaike's Information Criterion (AIC). Variance inflation factors for the six-predictor variables ranged from 1.15 to 1.98. Multicollinearity was not a concern with the models. Only two candidate models had $\Delta\text{AIC} < 10$ of the best model (Table 3). Generalized R^2 for the three top candidate models ranged from 0.596 to 0.610, in order of decreasing AIC value. The global model was the best model and accounted for 93% of the Akaike weights in the all-subset evaluation of the six variables. Given the 291 sample sites, the best model was approximately 10^{56} times more likely to be the correct model than the intercept-only model. The importance values were 1.0 for RELIEF, ACCESS, SHADING, and NICHES, and 0.98 and 0.95 for FLOW and MOSS, respectively. The equation for the best model was:

$$P_i = 1/(1 + e^{-z_i}),$$

where P_i = the probability of Black Swifts not being detected at site i and

$$\begin{aligned} z_i = & 30.664 - (0.760 \times \text{FLOW}_i) \\ & - (1.225 \times \text{RELIEF}_i) \\ & - (2.123 \times \text{ACCESS}_i) \\ & - (1.534 \times \text{SHADING}_i) \\ & - (1.596 \times \text{NICHES}_i) \\ & - (0.947 \times \text{MOSS}_i). \end{aligned}$$

Each predicting variable was significantly

different from zero ($P < 0.01$). The best model correctly predicted occupancy for 95% of the original sites ($n = 291$) that were used to build the model (Table 3).

DISCUSSION

Knorr's decade of work extended the known geographical distribution of Black Swifts breeding in Colorado from the San Juan Mountains in the southwestern part of the state north to the White River Plateau and Rocky Mountain National Park, and east to the eastern flank of the Sangre de Cristo Mountains (Knorr 1953, 1961). Our study only slightly changed the overall distribution from what Knorr described. The discovery of a colony site on the West Fork of the Elk River in Routt County, Colorado, made the greatest expansion, extending the known range in the Southern Rocky Mountains ~65 km northward.

Occupied swift sites are not uniformly distributed across the region (Fig. 1) because locations of waterfalls are not uniform. Three geographic areas contained a high percentage of the occupied sites visited during our study: the San Juan Mountains in southwestern Colorado, Rocky Mountain National Park in northern Colorado, and the White River Plateau in central Colorado. We found that occupied sites often occur in relatively close proximity, forming groups of 4–10 sites that are likely well within the daily foraging distance of adults (Lowther and Collins 2002). This apparent clustering suggests swifts from neighboring sites may interact and groups of occupied sites may form core areas that could contribute to swift population dynamics and broad-scale population persistence. Research into the meta-population dynamics and extent of relatedness in these groups would be informative.

Our study slightly extended the elevation range for Black Swift colonies in the Southern Rocky Mountains. Prior to this study, the elevation of known colonies ranged from 2,195 to 3,505 m. We found sites that ranged in elevation from 2,024 to 3,560 m, with only two sites lower and one higher than the range of earlier sites. The mean elevation of all currently known Southern Rocky Mountain Black Swift colonies is 3,035 m.

Most (93%) of the occupied nest sites vis-

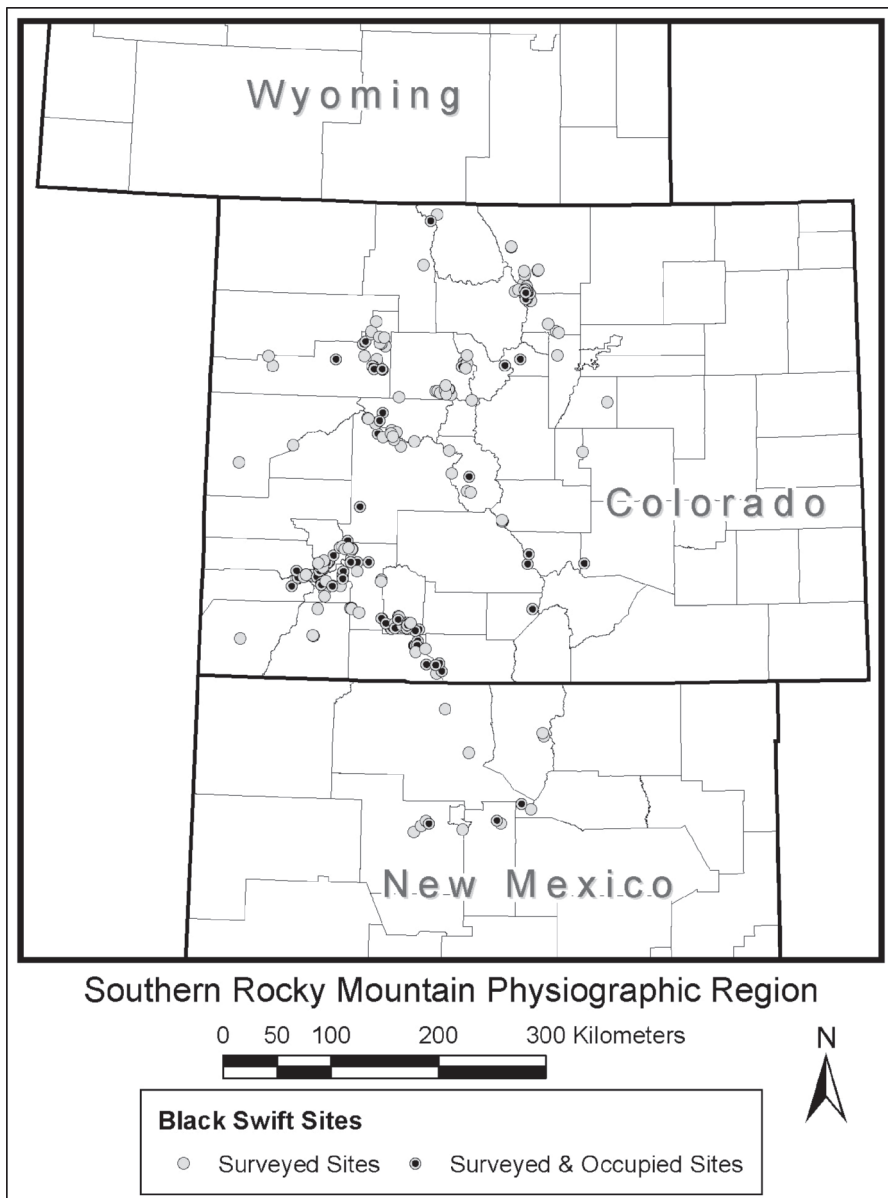


FIG 1. Sites surveyed and occupied by Black Swifts in the Southern Rocky Mountains, 1997–2005.

ited were at waterfalls with drops ranging from 5 to more than 100 m. Five sites were unusual in that colonies occupied shallow caves or drippy alcoves. Of these five sites, four are within 200–400 m of occupied waterfalls and each supports only one or two pairs of swifts. The most unusual site is a large colony nesting in a resurgence cave

where up to nine pairs of swifts nest as much as 23 m from the cave entrance.

Black Swifts are known to have strong fidelity to their nesting sites (Collins and Foerster 1995, Lowther and Collins 2002), a characteristic that was further corroborated by our study. We believe we located 24 of the 25 sites Knorr found in Colorado in the 1950s

TABLE 3. Binary logistic regression models for detecting Black Swifts at waterfall sites in Colorado and northern New Mexico evaluated with Akaike's Information Criterion (AIC). Shown are the intercept-only (null) model and all candidate models with ΔAIC^a values < 10 .

Model terms ^c	ΔAIC	w^d	Correct predictions, % ^b	
			Unoccupied sites ($n = 191$)	Occupied sites ($n = 100$)
FLOW, RELIEF, ACCESS, SHADING, NICHES, MOSS	0	0.928	96.3 (87.4)	91.0 (77.0)
RELIEF, ACCESS, SHADING, NICHES, MOSS	5.74	0.053	95.8 (85.9)	91.0 (72.0)
FLOW, RELIEF, ACCESS, SHADING, NICHES	7.814	0.019	94.8 (85.3)	90.0 (70.0)
Null (intercept only)	261.785	10^{-57}		

^a Difference in AIC values compared to the best model.

^b A correct prediction is a site that is correctly identified as occupied or unoccupied with a probability > 0.50 . In parentheses is the percent of correct predictions with $P > 0.80$.

^c Model terms are in text.

^d Akaike weight (Burnham and Anderson 2002). The ratio of w_a/w_b shows the odds that Model a is better than Model b , given the independent variables and data set selected for testing.

although there is some uncertainty concerning the location of a few of those sites due to lack of documentation. We confirmed continued occupancy at 23 of these 24 sites nearly 50 years after their discovery. We surveyed all of the Southern Rocky Mountain sites discovered by others between 1950 and 1996 and confirmed continued occupancy at five of the seven sites in Colorado as well as at the lone site in New Mexico. We were unable to conduct evening watches at any of the three historical sites where we failed to detect swift occupancy and cannot conclude these sites are vacant.

The historically documented size of Black Swift colonies in the Southern Rocky Mountains ranges from a single pair to 18 pairs. The largest known colony, averaging 11 active nests, is in Box Canyon Falls in Ouray County, Colorado, a site that was discovered by Knorr in 1950. Some small colonies of one or two nests appear to be intermittently occupied, but larger colonies seem to be occupied annually and to remain relatively stable in size.

Our surveys produced an estimate of 2.5 pairs per occupied site based on counts of adults and nests. If those counts are accurate, the total Black Swift breeding population at documented occupied sites in the Southern Rocky Mountains ($n = 103$) is ~ 500 breeding adults. If the rate of occupancy at presently identified potential sites that have not yet been surveyed ($n = 58$) is similar to those that have already been surveyed, those sites may support an additional 75 breeding adults. If our model is accurate in predicting occupancy at sites where surveys were inconclusive ($n =$

76), those sites could support another 300 breeding adults. Although our catalog of potential nest sites contains all published and mapped waterfalls in the region, our field experience indicates there are a number of potential sites that appear neither in publications nor on maps. A review of topographical maps in the region, focusing on permanent streams flowing through steep gradients, produced estimates ranging from 105 to 420 additional potential sites that remain to be catalogued. These sites may support another 200–750 birds. These calculations produce an upper population estimate of $\sim 1,000$ – $1,600$ breeding birds, which is quite similar to the estimate of 1,400–1,600 breeding birds in Colorado provided by Boyle (1998).

Our analysis of the six habitat characteristics at Black Swift nesting sites supports Knorr's conclusions about their relationship to swift occupancy. Some of these characteristics may be by-products of nest site selection rather than nesting requirements (Marín and Stiles 1992, Marín 1997). Our most parsimonious model supported the *a priori* assumptions that volume of stream flow, number of potential nest platforms, amount of moss cover, extent of shading of potential nest platforms, extent of topographic relief, and ease of aerial access to the potential nest sites each significantly contributed to a higher probability the site would be occupied by Black Swifts. Discussion of nest requirements by Marín (1997) suggests a simpler model using only FLOW and NICHES. This model correctly predicted occupancy for 84.2% of the sites in our study. The Akaike weights suggest the global model

was about 10^{21} times more likely to be the correct model than this two-variable model based on our data set.

The best model predicted that three occupied sites had <20% chance of being used. These are small sites, each hosting a single nest. Occupancy at one site appears to be intermittent and the other two were the only occupied sites that received a rating of "2" (of a maximum possible score of "5") for NICHES. All three sites have other, larger colonies nearby and may represent sub-optimal habitat sites occupied only when all available nest niches at the primary sites are in use. It is possible that some similar sites we counted as unoccupied are actually used intermittently and we failed to detect empty nest structures.

Black Swift nest site selection provides several advantages. The inaccessibility of nest niches makes nests and eggs nearly invulnerable to terrestrial predation. This low predation rate enables relatively high nest success (72%; Hirshman et al. 2007) and maintenance of population stability (Hunter and Baldwin 1962, Foerster 1987, Lowther and Collins 2002, Hirshman et al, 2007) despite a relatively low reproductive rate (1 egg/clutch and 1 clutch/year). Temperature parameters have not been measured at the nest, but the shaded, damp sites are cool and likely have minimal temperature fluctuation. These factors may slow the metabolism of nestlings and permit adults to leave them unattended for long periods during their wide-ranging foraging flights (Lowther and Collins 2002). The high relief above surrounding terrain typical of most nest sites enables adults to reach high altitudes at which they forage quickly and with little effort.

CONSERVATION IMPLICATIONS

A common but largely untested hypothesis in avian ecology is that animals tend to select habitats that increase fitness, survival, and reproductive success. Our best model predicted that <2% of the 191 waterfalls where we failed to detect Black Swifts had a greater than 80% probability of occupancy. If the sites sampled in our study are representative of all potential sites in the region, our model results suggest that most of the highest quality swift nesting habitat is already occupied, and population size of Black Swifts may be limited

by suitable nesting habitat. Locating and protecting the limited number of suitable nesting sites that are currently available, and identifying their occupancy status, should remain a high priority for conservation of this species.

In Colorado, low population numbers have resulted in the Black Swift being designated a sensitive species on National Forest lands and listed as a vulnerable breeder by the Colorado Natural Heritage Program. The U.S. Forest Service clearly carries the greatest conservation responsibility for this species in the Southern Rocky Mountains. Within Colorado, 73% of all occupied Black Swift sites are on National Forest lands. Colorado's San Juan National Forest hosts 26% of the state's known occupied sites while the White River National Forest and Uncompahgre National Forest each host 18%. Two of the three confirmed sites in New Mexico are on National Forest lands. Our model should be helpful for identifying which sites are most likely to provide nesting habitat and for prioritizing survey efforts among sites where occupancy has not been ascertained. Our field survey protocol appears to be effective and the model predicts the probability of site occupancy with confidence.

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