Black Swift (*Cypseloides niger*): A Technical Conservation Assessment

Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project

January 26, 2004

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Peer Review Administered by
Society for Conservation Biology

Wiggins, D. (2004, January 26). Black Swift (*Cypseloides niger*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/blackswift.pdf [date of access].

ACKNOWLEDGEMENTS

Chris Schultz provided a wealth of information on black swift ecology and survey methods, as well as a thorough review of an early draft of this manuscript. Manuel Marín and Charles T. Collins provided copies of their published work. I also thank Sue Hirshman, Carolyn Gunn, Rich Levad, and Chris Schultz for allowing me to participate in their fieldwork on black swifts in southwestern Colorado, and Sue Hirshman, Rich Levad, and Chris Schultz for access to unpublished data. Charles Collins, Greg Hayward, Geoff Holroyd, and Chris Schultz read the entire manuscript and provided a number of suggestions that helped improve both the content and presentation.

AUTHOR'S BIOGRAPHY

David Wiggins developed an early interest in ornithology. During his high school years, he worked as a museum assistant under George Sutton and Gary Schnell at the University of Oklahoma. He later earned degrees from the University of Oklahoma (B.Sc. in Zoology), Brock University (M.Sc. - Parental care in Common Terns), and Simon Fraser University (Ph.D. – Selection on life history traits in Tree Swallows). This was followed by a National Science Foundation post-doctoral fellowship at Uppsala University in Sweden, where he studied life history evolution in Collared Flycatchers, and later a Fulbright Fellowship working on the reproductive ecology of tits (Paridae) in Namibia and Zimbabwe. He currently splits time between ecological consulting work in Sweden and North America.

COVER PHOTO CREDIT

Black swift (*Cypseloides niger*). Photograph by Chris Schultz. Used with his permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF BLACK SWIFT

Historically, black swifts (*Cypseloides niger*) have been one of the most poorly understood species of birds in North America. Although some information on the ecology and distribution of black swifts has recently become available, there remains considerable uncertainty regarding their distribution and life history traits (e.g., survival, dispersal). Swifts appear to be a relatively long-lived species with a fixed clutch size of one egg and an unusually prolonged and late breeding season. Nestling growth is slow, with the nestling typically leaving the nest 47 to 50 days after hatching.

Black swifts do not hold any special conservation status in Canada. In the United States, black swifts are considered a Species of Conservation Concern by the U.S. Fish and Wildlife Service, and a Sensitive Species by the U.S. Forest Service. Black swifts are also a National Audubon Society WatchList Species, and they are a Priority Species within many state and regional Partners in Flight conservation plans.

Although there is currently little direct information on the factors affecting black swift population viability, the main threats appear to be the lack of late summer water runoff, which affects the suitability of nest/colony sites, and decreased local food supplies. Although the hypothesis is speculative, forest management practices, such as logging, road building, and cattle grazing may reduce late summer water flows by reducing water retention. These practices, together with fire suppression, typically decrease local vegetative diversity and may therefore negatively affect food supplies (flying insects and arthropods). Although black swifts are apparently restricted to nesting in relatively rare, wet cliff faces, a lack of nesting sites does not appear to be controlling local population growth. While several Partners in Flight conservation plans list disturbance at the nest site as a potential threat to this species, there are only two reports of public visits to waterfalls that have led to negative impacts (i.e., loss of eggs). A lack of information also hinders any assessment of the possibility that pesticides or problems on the poorly delineated wintering grounds (i.e., habitat loss) may be having negative effects on black swifts

Recent census work in Colorado has identified over 100 occupied black swift colony sites across the central and western portions of the state. With the information currently available, it appears that black swift populations in Colorado have remained relatively stable over the past 50 years. To identify limiting factors for black swifts, a considerable amount of data is needed on the species breeding distribution (in Wyoming), reproductive success, survival and dispersal. Currently, we have an incomplete picture of the breeding distribution in Region 2 (the breeding range in Wyoming is unknown), little information on the factors affecting breeding success, and almost no information on survival of juveniles or adults or on dispersal. Until these data are collected and analyzed, it will remain difficult to assess the current conservation elements and management implications for the species.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). The black swift (*Cypseloides niger*) is the focus of an assessment because it is a sensitive species within Region 2 (see **Figure 1** for a map of Region 2) and it is a Management Indicator Species (MIS) on the White River National Forest. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance or in habitat capability that would reduce the species' distribution [FSM 2670.5 (19)]. A sensitive species may require special management, so knowledge of its biology and ecology is crucial. As a MIS, the black swift serves as a barometer for species viability at the forest level. MIS have a dual functionality: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a) (1)) and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a) (6)).

This assessment addresses the biology and conservation/management status of the black swift throughout its range, but with an emphasis on Region 2. Completing the assessment promptly required establishment of limits concerning the geographic scope of particular aspects of the assessment and further analysis of existing field data. This introduction defines

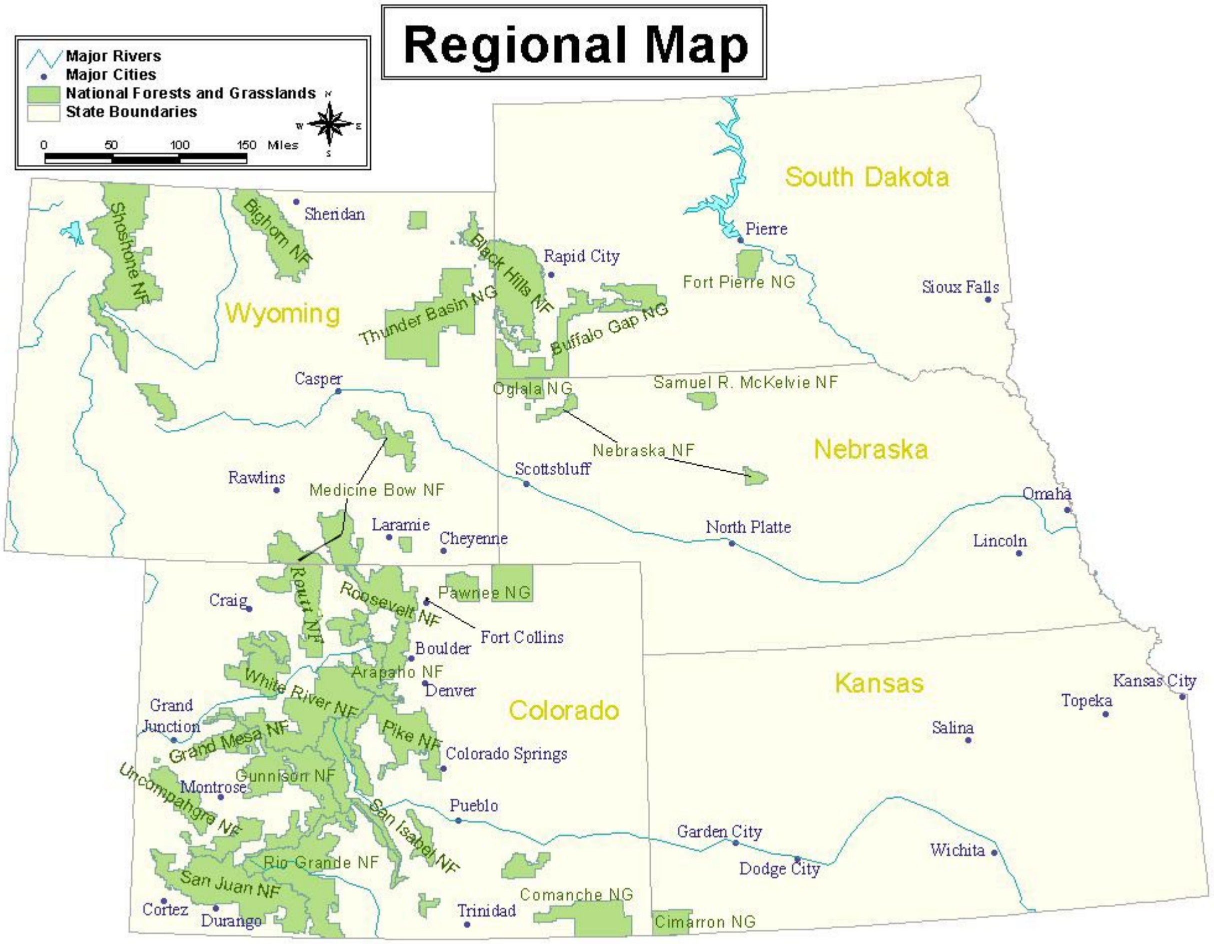

Figure 1. Map of national forests and national grasslands within USDA Forest Service Region 2.

the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal of Assessment

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species, based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations but provides the ecological background upon which management must be based. However, it does focus on the consequences of changes in the environment that result from management (i.e. management implications). Furthermore, it cites management recommendations proposed elsewhere and, when management recommendations have been implemented, the assessment examines the success of the implementation.

Scope and Limitations of Assessment

The black swift assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although a majority of the literature on the species may originate from field investigations outside the region, this document places that literature in the ecological and social context of the central Rockies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of black swifts in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on black swifts are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature, because this is the accepted standard in science. Non-refereed publications and reports were regarded with greater skepticism. I chose to use some non-refereed literature in the assessments, however, when information was otherwise unavailable.

Black swifts have always been rare and very local in distribution. Consequently, they have received relatively little attention from researchers. As a result, writing this Species Assessment required reliance on a relatively small set of publications and some unpublished information. Firm recommendations/conclusions were typically difficult to formulate.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, strong inference, as described by Platt, suggests that experiments will produce clean results (Hillborn and Mangel 1997), as may be observed in certain physical sciences. The geologist, T. C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (experiments, modeling, logical inference). Ecological science is, in some ways, more similar to geology than physical science because of the difficulty in conducting critical experiments and the reliance on observation, inference, and models to guide understanding of the world (Hillborn and Mangel 1997).

In this assessment, the strength of evidence for particular ideas is noted and, when appropriate, alternative explanations are described. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding features of biology.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates revision of the assessments, which will be accomplished based on guidelines established in Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessments.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

A number of regional and national conservation organizations have listed the black swift as a species of conservation concern. It is listed as a "Bird of Conservation Concern" by the U.S. Fish and Wildlife Service (USFWS), both nationally as well as within three USFWS regions (U.S. Fish and Wildlife Service 2002). The black swift is listed as "threatened and declining" on the Partners in Flight (PIF) "National Watch List" (http://www.abcbirds.org/pif/pif_watch_list.htm), and it is considered "yellow priority" on the Audubon Society's "Watch List" (http://audubon2.org/webapp/watchlist/viewWatchlist.jsp#swifts).

Within USFS Region 2, black swifts are listed as a Sensitive Species on a regional scale, and as a Management Indicator Species on the White River National Forest. In addition, the Forest Plan for Rio Grande National Forest recommends regular (every 3rd year) surveying of black swift nesting colony sites to monitor any changes in population status (see Table V-1 in Revised Land and Resource Management Plan, Rio Grande National Forest, 1996). Black swifts are not listed on the Colorado (2000) or Wyoming (2001) Bureau of Land Management State Director's Sensitive Species Lists.

A summary of the management status of black swifts within state and regional Partners in Flight plans is presented in **Table 1**. Black swifts are listed as a Priority Species in the Colorado plan (Beidleman 2000). They are not listed in the Wyoming plan, although they

Table 1. Management status of black swifts within Partners-in-Flight state and physiographic area Bird Conservation Plans.

State/PIF physiographic area	Status	Citation
Colorado[1]	Priority Species (cliff/rock habitat)	Beidleman 2000
Kansas[1]	State PIF plan not published	
Wyoming[1]	Not a Priority Species	Cervoski et al. 2001
Nebraska[1]	State PIF plan not published	
South Dakota[1]	State PIF plan not published	
Montana	Priority Species	Casey 2000
New Mexico	Highest Priority Species	Rustay 2001
Utah	Priority Species	Parrish et al. 2002
Idaho	High Priority Species (cliff/rock habitat)	Ritter 2000
Nevada	Not a Priority Species	Neel 1999
California	Focal Species (Sierra Nevada)	Siegel and DeSante 1999; CalPIF 2002
Arizona	Not listed as a Priority Species	Latta et al. 1999
Alaska	Priority Species (Southeast)	Andres 1999
Oregon/Washington	Focal Species in several physiographic areas	http://community.gorge.net/natres/pif/cons_page1_.html
Central Rocky Mountains	Priority Species	http://www.partnersinflight.org/
Southern Rocky Mountains	Priority Species	http://www.partnersinflight.org/
PIF Physiographic areas 93, 90, 89, 66, 64, 62, 94	Priority Species (see map in **Figure 3**)	http://www.partnersinflight.org/

[1] = Region 2 state.

are presumed to nest in Wyoming (Cerovski et al. 2002). State PIF plans for other states within Region 2 have not been published. Black swifts are also listed as a Priority or Highest Priority species within several other state and regional PIF plans (**Table 1** and **Figure 2**). Within Region 2 state Natural Heritage Programs, Colorado lists the black swift as a Sensitive Species (S3B), and a number of neighboring western states also list it as a Sensitive Species (**Table 2**).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Black swifts are protected under the Migratory Bird Treaty Act, but there are currently no published management plans or conservation strategies directed solely at black swifts. Several (PIF) state and regional plans have included management recommendations for black swifts. An overview of these recommendations is provided in **Table 3**. The primary management recommendation is that human activities at swift breeding sites (waterfalls) be minimized to avoid potential disturbance. However, it should be noted that there has been no study of the effects of human activity on black swifts. At Box Canyon Falls in southwestern Colorado, there is considerable human activity at the colony site every day during the breeding season, but there is little evidence to suggest any negative effects on breeding swifts (S. Hirshman personal communication 2002). Other waterfalls in Colorado (Cornet Falls, Cascade Falls, Treasure Falls, Ouzel Falls) also receive considerable human visitation during the summer, with little to no apparent effect on nesting swifts (C. Schultz personal communication 2003). Ice climbing activities have also been cited as a potential source of disturbance to nesting areas, but to date, there is no evidence that such activities negatively affect swift nesting sites. The other management recommendation (contained in Beidleman 2000) is to study contaminant levels in the food supply of swifts.

Biology and Ecology

Systematics

The American Ornithologists' Union (1957) recognizes three subspecies for *Cypseloides niger*, largely based upon the isolation of breeding populations in: 1) the West Indies, 2) Mexico and Central America, and 3) the United States and Canada. There is little geographic variation in plumage characteristics, but

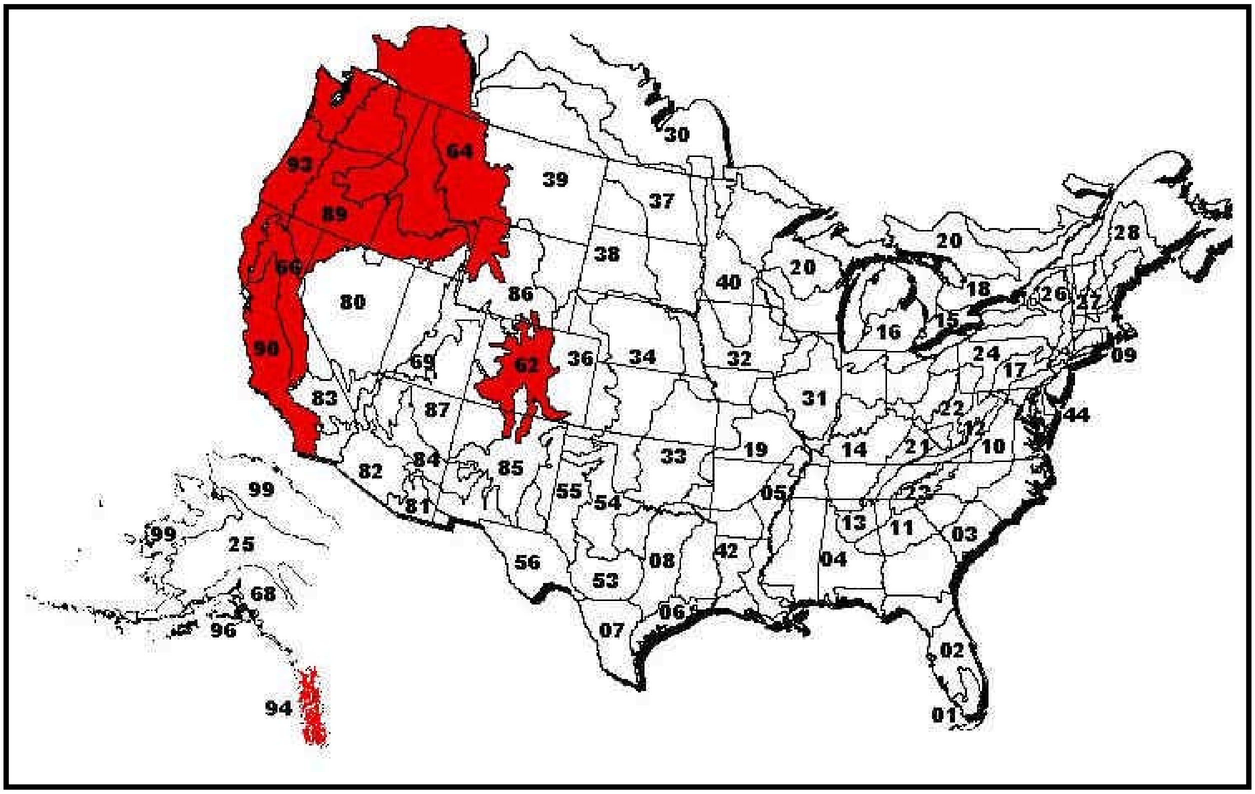

Figure 2. Map of Partners In Flight physiographic regions showing (in red) regions containing management recommendations for black swifts.

Table 2. State-based management status of black swifts within Region 2 states (*) and surrounding states.

State	State Rank	Date accessed or publication date	Reference
Wyoming*	Not listed	30 August 2002	Fertig and Beauvais 1999
South Dakota*	Not listed	30 August 2002	http://www.state.sd.us/gfp/divisionwildlife/Diversity/rareanimal.htm
Colorado*	S3B[1]	3 September 2002	ftp://ftp.cnhp.colostate.edu/pub/99Handbook.pdf
Nebraska*	Not listed	5 May 2002	http://www.natureserve.org/nhp/us/ne/birds.html
Kansas*	Not listed	5 May 2002	http://www.kbs.ukans.edu/
Oklahoma	Not listed	30 August 2002	ftp://www.biosurvey.ou.edu/pub/verteb0503.pdf
Montana	S3[2]	August 2001	http://nhp.nris.state.mt.us/
Idaho	S1B[3]	1996	http://www2.state.id.us/fishgame/info/cdc/animals/birds.htm
Utah	SP/SD[4]	January 1998	http://dwrcdc.nr.utah.gov/ucdc/ViewReports/sslist.htm
Arizona	SN[5]	30 August 2002	http://www.gf.state.az.us/w_c/edits/hdms_species_lists.html
New Mexico	Sensitive	7 July 2002	http://www.gmfsh.state.nm.us/

[1] S3B = Either very rare and local throughout its range, or found locally in a restricted range, or vulnerable to extinction throughout its range because of other factors: breeders.

[2] S3 = Either very rare and local throughout its range, or found locally in a restricted range, or vulnerable to extinction throughout its range because of other factors.

[3] S1B = Critically imperiled because of extreme rarity; breeder.

[4] SP/SD = Sensitive species with declining population and limited distribution.

[5] SN = Sensitive species not known to regularly breed in the state.

Table 3. A selection of management recommendations for black swifts in Partners In Flight state plans.

State/Recommendations	Specifics	Presumed benefits
Colorado		
Protect known or potential nest sites (waterfalls)	Minimize disturbance, re-route hiking trails away from waterfalls, enforce seasonal buffer zones near base and top of nesting cliffs	Minimize disturbance at nesting sites
Study effects of ice climbing on cliff habitat	Determine if ice climbing has negative effects on plants or niches	Maintain fragile nesting substrates
Study contaminant levels in food supply	Assess levels of herbicides and pesticides in flying ants	Determine if chemical contaminants are affecting food supply and/or swifts
Montana		
Discourage recreational use of waterfall colony sites		Minimize disturbance at nesting sites
Utah		
Protect/restore water flow to waterfalls	Identify current and historical waterfalls and assess any problems with water flow; protect surrounding habitats so as to maintain water flow	Maintain/increase potential nest sites
Avoid pesticide applications in swift nesting areas	Decrease the accumulation of pesticides in the food supply	Improve swift survival and increase local food supply
Avoid human disturbance at nest sites	Minimize disturbance from 1 June 15 September	Increase reproductive success
Create additional nesting sites	Create nesting pockets/niches on existing waterfalls	Increase the number of colonies

wing length and body mass are greater among birds breeding north of Mexico (Marín 1999a).

Distribution and abundance

The historical distribution of black swifts is difficult to estimate, given their habit of nesting in inaccessible sites at widely spaced localities. Their preference for damp cliffs (e.g., near waterfalls) in montane areas (inland populations) and for damp coastal caves (coastal populations) as nesting sites has led to a patchy breeding distribution within North America. The general picture from historical data is that the distribution of black swifts was very poorly known, and only with recent dedicated survey work has their distribution been more fully documented. For example, in Colorado, the species had been observed sporadically during the summer months for over 70 years before the first nests were confirmed in 1950 (Knorr and Bailey 1950). Despite widespread breeding season observations in British Columbia, only two nests are documented there (Campbell et al. 1990). This lack of historical reference data on distribution and abundance leads to considerable uncertainty regarding population trends.

The historical breeding distribution (**Figure 3**) includes: southeastern Alaska (no definite nesting records, but swifts have seen during summer months in the Stikine River Valley, Boca de Quadra, Revillagigedo Island, and other river valleys in southeastern Alaska; Gabrielson and Lincoln 1959, Andres 1999), northwestern, central, and southern British Columbia (where swifts are sometimes abundant during the summer months, but where only two definite nesting locations have been verified; Campbell et al. 1990), southwestern Alberta (Banff and Jasper National Parks; Holroyd and Van Tighem 1983, Semenchuk 1992), northwestern Montana (Hunter and Baldwin 1962, Weydemeyer 1975), northern Idaho (Dumroese et al. 2001), northern and south-central Washington (the entire Cascade range, though with only a single breeding site identified) south to extreme northeastern Lewis County (Smith et al. 1997), western Oregon (Cascades, though only one definite breeding site identified) and probably northeastern Oregon (Wallowa Mountains; Gilligan et al. 1994), isolated mountains in northern and central Utah (Knorr 1962, Hayward et al. 1976), the montane, western half of Colorado (C. Schultz personal communication 2003), north central New Mexico (Jemez Falls; Johnson 1990), extreme southeastern Arizona (Knorr and Knorr 1989), California (Sierra Nevada range, Michael 1927; mountains in southern California, Foerster and Collins 1990, Marín 1997a; and at coastal sites near Monterey, Roberson and Tenney 1993). The distribution and breeding status in Wyoming is poorly known (R. Levad and C. Schultz personal communication 2003). The breeding and wintering distributions in Mexico, Central America, and South America are poorly known, but centered around high elevation mountain ranges (Stiles and Negret 1994, Howell and Webb 1995). Black swifts are widespread, but uncommon breeders in the West Indies (Raffaele et al. 1998).

Although quantitative data are scarce, most historical works suggest that black swifts were relatively common within their restricted range. For example, Cooke (1897) listed black swifts as “abundant, locally” in southwestern Colorado, but with no direct evidence of nesting. Taverner (1926) noted them as common in British Columbia and southwestern Alberta, but also noted that their nesting habits remained “a mystery”. In the past few decades, increasing knowledge of the species’ natural history has led to the discovery of new breeding sites and, consequently, an increase in the estimated North American population size and breeding distribution. This expansion of the recognized breeding distribution likely points more to an earlier lack of knowledge, rather than an increase in distribution and abundance *per se*.

Migratory pathways are generally unknown, although occasional flocks of black swifts are sometimes seen at low elevations during poor weather. In Alaska, most presumed migratory flocks have been seen along coastal river valleys. Pacific coast populations appear to follow coastlines, but southbound flocks have been observed well off the Pacific coast of Chiapas and Guatemala (American Ornithologists’ Union 1998). There is no information on the migratory pathways of interior populations. Scattered reports from the plains of eastern New Mexico and western Texas (e.g., Seyffert 2001) are in need of confirmation. As mentioned above, observations of black swift flocks in early June in the Rocky Mountains are typically made at relatively low elevations during cloudy, cool weather, and thus they may not accurately reflect the species’ typical migratory behavior.

Some populations in the West Indies (Jamaica, Cuba, Hispaniola) are apparently resident (Raffaele et al. 1998), although more information on their winter occurrence is needed. The winter distribution of continental populations of black swifts is poorly known, but it is presumed to be montane areas of South America (Stiles and Negret 1994, Lowther and Collins 2002). The difficulty in clearly defining the species’ winter distribution has been attributed to identification problems relative to other Cypseloidine swifts in South

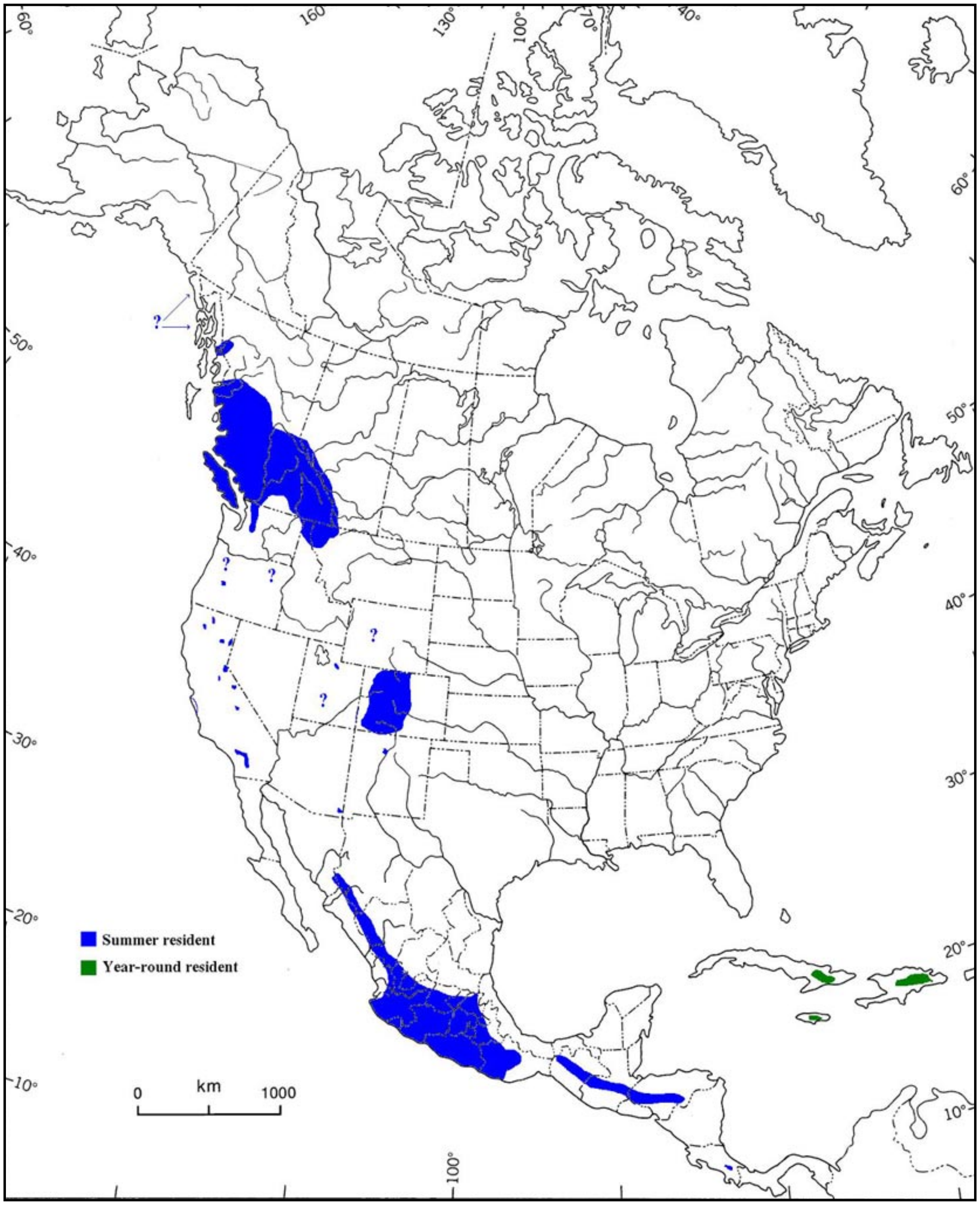

Figure 3. Map of the breeding range of black swifts in North America. The figure was modified from data provided in Lowther and Collins (2002).

America, as well as a lack of specimen records (Stiles and Negret 1994).

Regional distribution and abundance

Within Region 2, black swifts have been recorded from Colorado, only sporadically in Wyoming (e.g., not listed by Knight 1902), and not at all in South Dakota, Nebraska, or Kansas. Their current status is as follows:

South Dakota. There are no historical (South Dakota Ornithologists' Union 1991, Peterson 1995) or recent (Tallman et al. 2002) records of black swifts in the state.

Nebraska. Black swifts have not been officially recorded in the state (Sharpe et al. 2001).

Wyoming. Black swifts are seen regularly during the summer months in Wyoming, but there are no known breeding sites in the state (Scott 1993). Black swifts were not listed on the recent Wyoming vertebrate atlas (Luce et al. 1999).

Colorado. The Colorado Breeding Bird Atlas (Kingery 1998) recorded potential breeding at scattered locations in central and western Colorado, with the largest concentration of presumed nesting colonies in the San Juan Mountains, and smaller numbers in the Sangre de Cristo, Flat Tops, Gore and Front ranges. The total number of breeding pairs in the state was estimated at a few hundred (Boyle 1998). Current surveying work by the USFS and the Rocky Mountain Bird Observatory has inventoried over 375 waterfalls in Colorado, with over 100 sites occupied by breeding black swifts (Levad and Schultz personal communication 2003). This work has shown that black swifts are more widely distributed in Colorado than was suggested by the Colorado Breeding Bird Atlas work, with centers of concentration in the San Juan Mountains in the southwest, and in Rocky Mountain National Park in the central part of the state.

Kansas. Black swifts have not been recorded in Kansas (Thompson and Ely 1989, www.ksbirds.org).

Regional discontinuities in distribution and abundance

Given their strict nesting requirements, it is not surprising that black swifts are patchily distributed throughout their North American range. Within Region 2, the current known distribution of nesting colonies is patchy, relative to most other species of birds, and largely limited by the availability of tall cliffs with waterfalls or otherwise wet conditions. Colony sizes tend to be small (mean = 2.3 pairs/occupied site; Levad and Schultz personal communication 2003) and the areas with the highest abundance of swifts appear to be the San Juan Mountains (southwest Colorado) and Rocky Mountain National Park (central Colorado). The distribution in Colorado is now known to be much more widespread in the central and western portions of the state (Levad and Schultz personal communication 2003), and thus populations may be more tightly linked than previously thought. In Colorado, approximately 70 percent of all permanent waterfalls occur on National Forest System land, and 76 percent of all black swift colony sites are also on National Forest System land (Levad and Schultz, unpubl. data). Thus, USFS land management practices will play a pivotal role in determining the long-term sustainability of black swift populations in Region 2.

Population trend

Data from the North American Breeding Bird Survey (BBS; Sauer et al. 2003) are summarized in **Table 4**. Black swifts are poorly censused with BBS methodology, so the data are consequently difficult to interpret. The general pattern is that numbers have increased or remained steady in California and the central Rocky Mountains, but they have decreased in Washington and British Columbia. Analyses suggest only weak support for any of the observed trends; this subsequently suggests a lack of any geographic pattern based on BBS results. The downward patterns in the Pacific Northwest and the upward trends in California and the central Rocky Mountains have the greatest (statistical) support. Overall, however, the BBS data provide little insight into overall population trends.

As mentioned elsewhere in this report, given the paucity of known breeding sites, analysis of long-term population trends for this species is difficult. Nonetheless, a recent comparison of 27 known nesting

Table 4. Black swift trend results from North American Breeding Bird Surveys from 1966 to 2002, from Sauer et al. (2003). Trend indicates the percentage change/year, while N indicates the number of survey routes used.

	1966-1979			1980-2002			1966-2002		
Region	***N***	**Trend**	***P***	***N***	**Trend**	***P***	***N***	**Trend**	***P***
British Columbia	11	15.0	0.71	25	- 8.7	0.06	26	- 8.8	0.08
Washington	5	- 7.7	0.70	12	3.8	0.17	15	- 2.2	0.61
Central Rockies	4	223.6	0.30	13	- 1.0	0.84	14	2.6	0.40
Cascade Mountains	4	- 8.1	0.69	8	6.1	0.12	9	- 1.1	0.78
North Pacific Rainforests	8	- 9.1	0.79	13	- 14.1	0.02	14	- 12.3	0.06
United States	7	- 0.2	0.99	16	3.3	0.24	21	6.2	0.40
Canada	12	14.8	0.71	25	- 8.8	0.06	27	- 8.8	0.08
Survey-wide	19	5.4	0.83	41	- 6.8	0.07	48	- 7.1	0.11

sites in Colorado suggests no long term (50 year) decline in the population, as 25 located sites still contained breeding swifts (Schultz personal communication 2003). Although sample sizes were much lower, comparisons of colony size at these historic sites revealed a strong correlation between numbers seen by Knorr and numbers seen at the same sites more recently. For example, Hirshman (1998) noted that the size of the swift colony at Box Canyon, near Ouray, Colorado had not changed appreciably between Knorr's visit there in 1950 (when 10 nests were found) and more recent surveys in 1997-1998; the number of breeding birds at Box Canyon has fluctuated between 9 and 18 pairs since 1997 (Hirshman personal communication 2002). Taken together, the above data suggest that black swift colony sites and population sizes have remained relatively stable in Colorado for over 50 years. In Alberta, the number of nests in Johnston Canyon, Banff National Park, varied from 7 to 12 during annual surveys between 1975 and the early 1990's, but then dropped to three pairs and has remained at the number in recent years (Holroyd and Holroyd 1987, Holroyd personal communication 2003).

Activity pattern and movements

Black swifts migrate from western North American and Caribbean breeding grounds to unknown wintering areas in South America (Stiles and Negret 1994). Populations on Jamaica, Hispaniola, and Cuba appear to be resident (Raffaele et al. 1998). Major migratory paths for Pacific coast birds are along coastal western Mexico, with records at sea off the coast of Chiapas and Guatemala (Lowther and Collins 2002). Although migratory routes of interior montane populations (e.g., those in Region 2) are unknown, scattered records in montane areas of New Mexico and Colorado during late spring and fall suggest that swifts follow mountain ranges during spring and fall migrations. Populations in the northern Rockies may use routes followed by other aerial insectivores (e.g., tree swallows (*Tachycineta bicolor*) and violet-green swallows (*T. thalassina*). That is, in spring, migration is typically along the Pacific coast and then inland along major river valleys, with the reverse pattern used in fall migration. In western North American populations, breeding occurs during late summer (typically July-September; see Breeding Biology section), and spring and fall migrations are therefore relatively late (**Table 5**). At Box Canyon in southwestern Colorado, the first swifts typically arrive at the colony in mid June, and the last birds leave in mid to late September (**Table 5**; Hirshman 1998).

As with other aspects of their biology, little is known of black swift movement patterns away from their nest sites. During the breeding season, black swifts are thought to forage at high elevations where they feed on aerial insects (see Food habits section), except when weather conditions (e.g., low pressure, precipitation) drive them to lower elevations (Udvardy 1954). Although individual birds have not been followed on foraging trips, the occurrence of birds during summer at sites far from known nesting areas has led to the conclusion that adults may travel long distances each day in search of food (Udvardy 1954, Knorr 1961, Lowther and Collins 2002). There are no data on sex- or age-related differences in migration or dispersal patterns.

The degree to which black swift populations in the southern Rockies (Colorado, Wyoming, New Mexico) are linked is unclear. Nest and colony sites in western Colorado have been used over long periods (Schultz personal communication 2003), suggesting that black swifts show extremely high site fidelity (see also Marín 1997a). Therefore, they may be susceptible to local extinction through lack of population connectivity. High site fidelity appears to be the norm for black swifts, with long-term site occupancy noted also in California

Table 5. Timing of the average arrival and departure dates for western North American breeding populations of black swifts.

Area	Average spring arrival date	Average fall departure date	Citation
California (southern)	early May to mid June	late August to mid September	Marín 1997a
California (Monterey Co.)	May	August to early September	Bailey 1993
Oregon	mid May to early June	late August to September	Gilligan et al. 1994
Washington	May	mid September	Jewett et al. 1953
Colorado (Box Canyon)	18-19 June (first birds)	15-24 September (last birds)	Hirshman 1998
Alberta	mid June	mid September	Semenchuk 1992
British Columbia	mostly mid to late May	late August to early October	Campbell et al. 1990
Costa Rica	April early May	September to early October	Stiles and Skutch 1989

(Collins and Foerster 1995, Marín 1997a) and in Alberta (Kondla 1973, Holroyd and Holroyd 1987). As very few birds have been banded, there is little information on adult or juvenile dispersal. However, Collins and Foerster (1995) cite records of seven banded adults that were recaptured in later years at the original banding sites. Again, these data, although scant, suggest little movement by adults between colony sites.

Habitat

Nesting habitat

In western North America, breeding black swifts are restricted to two main habitat features – sea caves and cliffs along the Pacific coast, and adjacent to or near wet cliff sites in montane canyons (e.g. Smith 1928). Data from ongoing survey work in Colorado suggest that nests are typically placed on recesses/ledges near waterfalls or dripping water on cliffs. Most nests within interior North America have been on shaded cliff walls near areas of dripping water (usually active waterfalls), with a few near the entrances of wet caves. Nest sites are typically small pockets or recesses on rock cliff faces, often in moist areas very near spray, and are usually difficult to access from the ground. **Table 6** summarizes black swift nest site characteristics.

Knorr (1961, 1993) listed six features that are strongly associated with black swift nest sites: 1) falling or dripping water, 2) high relief, 3) inaccessibility to ground predators, 4) unobstructed flyways in the immediate nest vicinity, 5) shade during a major portion of the day, and 6) the presence of suitable nest niches. Marín and Stiles (1992) and Marín (1997a) suggested that high relief, inaccessibility to ground predators, and unobstructed flyways were all secondary consequences of selecting nests behind or near waterfalls. These authors also suggested that nesting close to falling water served two main purposes: 1) to maintain a more constant temperature in the immediate vicinity of the nest, and 2) to facilitate attachment of nest material (usually mud and moss) to the nest substrate. However, as black swifts lay only a single egg and have a relatively long nesting period (and thus little chance to renest after failure), it is likely that inaccessibility to ground predators is a very important component of nest site selection. Knorr's (1993) idea that the presence of suitable nest niches is critical to black swift colony establishment has been reinforced by recent survey work in Colorado, where many otherwise suitable nesting sites were not used, apparently due to a lack of suitable nest niches/pockets (Levad and Schultz personal communication 2003).

The relatively high concentration of nest sites in southwestern and central Colorado (e.g., San Juan Mountains and Rocky Mountain National Park) is likely correlated with the high relief in those mountains and the consequent abundance of waterfalls in the area.

Table 6. Characteristics of black swift nest sites in western North America.

Region	N	Nest site characteristics	Site elevation	Height	Citation
California (Santa Cruz Mountains)	3	2 located behind falling water, 1 to the side	—	not reported	Smith 1928
Southern California	13	On cliffs or cave walls near waterfalls	550 - 1620 m	4 - 10 m	Foerster and Collins 1990
Montana (Mission Mountains)	5	4 nests behind falling water, 1 to the side	4700'	not reported	Hunter and Baldwin 1962
Idaho	5	4 nests behind falling water, 1 to the side	3300'	2 to 6.5 m	Dumroese et al. 2001
Colorado	> 100	typically to the side of falls, but within mist/spray zone	7000' - 11000'	often 8 to 10' but maybe > 100'	C. Schultz, personal communication 2003
British Columbia	2	close to waterfall	—	3 to 4.5 m	Campbell et al. 1990

There is little indication of the factors responsible for the species' occurrence at coastal sites, although damp sea caves and waterfalls near the coast appear to be favored habitat (Lowther and Collins 2002).

Wintering habitat

On large islands in the West Indies, black swifts winter in the same general areas that they nest (Raffaele et al. 1998). In South America, black swifts were collected during the presumed migration period (late September to mid October) at 1800 m elevation in the foothills of the Andes Mountains (Stiles and Negret 1994). However, it should be noted that these records likely involved migrating birds. Thus, while they may occupy such sites further south on the presumed wintering grounds, there is no information available on the wintering habitat of black swifts in South America.

Foraging habitat

Black swift foraging habitat is poorly known, as there have been no studies of foraging behavior. All published information on foraging habitat is anecdotal. During warm, clear weather, foraging is presumed to occur at high altitudes, where blooms of aerial insects are available (Lowther and Collins 2002). Bailey and Niedrach (1965) cite observations made near Silverton, Colorado, where black swifts fed "at a height of from 1000 to 2000 feet" above ground during the day, but moved to within 100 feet of the ground during the late afternoon. Chapman (1954) suggests that flying ants, one of the primary prey of breeding black swifts (see the Food habits section), typically swarm on mountain and ridge tops. Several of the breeding season observations listed by Bailey and Niedrach (1965) are of birds flying at high altitudes at or near mountain summits and peaks, up to 13,980 feet. During inclement weather and during migration, swifts appear to forage at lower elevations, often over lakes or other bodies of water (Bailey and Niedrach 1965, Lowther and Collins 2002).

Food habits

During the breeding season, black swifts feed primarily on winged ants and termites, as well as flying insects. Marín (1999b) found that 91 percent of 1179 food items in boluses (n = 10) delivered to nestlings in southern California were comprised of flying ants (Formicidae), with an average length of 7.4 mm. Marín (1999b) concluded that there was little evidence for prey size selection by black swifts, as prey items fed to nestlings did not appear to change with nestling age. However, it is possible that the lack of variability in prey size in Marín's study may have resulted from a lack of variation in the local food supply, rather than a lack of prey selection by the parents. In addition, all of Marín's data were collected at a single site, and thus it may not be appropriate to generalize results from that area to other colony sites. In an earlier study at the same colony site, Foerster (1987) found that two food boluses contained 98 percent winged ants. Food boluses from two adults (feeding nestlings) in Mexico contained 72 percent winged ants, averaging 8.6 mm in length (Collins and Landy 1968). When weather conditions are poor (low clouds, precipitation) however, black swifts appear to take a much more variable diet of flying insects. Stomach analyses of adults collected in Washington State contained ants, bees, wasps, a variety of flies, beetles, and leafhoppers (summarized in Lowther and Collins 2002). In many of these cases, individual birds consumed primarily a single prey type. There are no data available on the food habits of black swifts in Region 2.

The apparent dependence of black swifts on ephemeral, swarming prey is likely responsible for several unusual aspects of their breeding biology. Long periods away from the nest (up to 12 hours in southern California; Marín 1997a), a single egg, and extended incubation and nestling growth (Marín 1999b) are all typical of bird species that rely on unpredictable and/or ephemeral food resources during breeding (Lack 1968).

Winged ants are high in fat content, which varies from 23.8 to 59.5 percent of dry mass in female ants and 3.3 to 9.6 percent in males (Redford and Dorea 1984, Marín 1999b). The use of this high fat food source is likely the primary factor that allows nestling black swifts to achieve large body masses (up to 146 percent of adult mass) at fledging.

Breeding biology

Courtship and pair formation

There is little information available on courtship and pair formation in black swifts. Marín (1997b) attributed two forms of chasing behavior to pair formation and pair bonding. Group chases, where several birds chase a lead bird (presumably a female) while emitting high-pitched sounds, were assumed to be a form of pair formation. Pair chases, where two birds engage in high-speed dives and erratic maneuvers, occurred during the early and middle portions of the breeding season and were thought to function in pair bond formation and/or maintenance.

Nest-site selection

Black swifts place their nests on small ledges on the walls of cliffs, caves, or other vertical surfaces. Nests are almost always located close to water (Knorr 1961); nests along the Pacific coast are often in sea caves (Lowther and Collins 2002), while inland nests are usually located near dripping water sources, waterfalls, or turbulent water sprays. Nests are also typically located in dim areas, away from sunlight. Although nesting in shaded areas could be interpreted simply as an indirect consequence of nesting on cliff faces, several authors have suggested that black swifts show a preference for nesting within shaded areas and avoiding sites that receive direct sunlight (Knorr 1961, Bailey and Niedrach 1965, Levad and Schultz personal communication 2003). Nesting materials vary according to geographic location. At seaside nests, there is typically little nesting material other than mud and occasionally seaweed (Lowther and Collins 2002). At most inland nests, mosses are the typical nest material (Marín 1997a). There is no indication of whether the nest is built only by the female, or whether the male contributes to nest construction. Nest site characteristics are summarized in **Table 6**.

Several observers have commented on the reuse of old nesting sites by black swifts (Foerster 1987, Marín 1997a, Hirshman 1998). Old nest structures (moss) are typically re-used if present, with a new layer of fresh moss added to the top layer (Hirshman 1998). Marín (1997a) found that the same nest pockets were used each year during a three-year study in southern California, and that often the same individual birds were using those sites. Collins and Foerster (1995) documented two cases of black swifts being captured on the exact same nest pocket in different years. In one case, a brooding female black swift was caught at the same nest pocket in successive years. In the other case, an adult was caught at the same nest pocket (details of the nest contents were not provided) in 1985 and again in 1988. This site tenacity may be due to the scarcity of nesting sites; Knorr (1993) noted that on repeated visits to nesting colonies throughout southwestern United States (primarily southwestern Colorado), there had been no colony abandonment over a 40-year period.

Clutch and brood size

Black swifts lay a single egg, with no geographical or seasonal variation (Marín 1997a). There is a single case of a nest that "appeared to have two eggs" at Box Canyon in Colorado (Hirshman 1998), but this may have been a case of a female laying a replacement clutch after the first egg failed to hatch (Hirshman personal communication 2003).

Parental care and offspring behavior

Incubation is by both sexes (Marín 1997), but there is no quantitative information on how the sexes share incubation duties. Incubation bouts typically last more than four hours (Marín 1997a). Incubation lasted a mean of 24 days (range 23 to 26) in California (Marín 1997a), 29 days in Costa Rica (Marín 1999a), and 26 to 27 days in Colorado (Hirshman 1998).

Brooding behavior by the adults has not been closely studied, but the young are apparently brooded for a large portion of the day until they develop the ability to thermoregulate at about 13 days of age (Marín 1997a). At night, both parents typically roost at the nest site, with one brooding the nestling, until the young reaches about 20 days old. From that point on, one adult will remain on the nest at night while the other will typically roost nearby. In California, the nestling was typically fed in two pulses, once in the morning (0830 – 1230) and again in the evening (after 1830, often during the twilight period; Lowther and Collins 2002). In Colorado, young swifts are more typically fed only in the evening, although mid-day visits occur there also (Boyle 1998, Hirshman personal communication 2002). Young are fed from a large bolus-like mass of food collected during the foraging bouts, and such feeding may continue after the parent has settled on the nest for the night (Collins and Peterson 1998).

Nestling growth

Foerster (1987) and Marín (1999a) studied nestling growth in black swifts in southern California, while Marín (1999a) also made a comparative study of the growth of nestlings from Costa Rica. Nestling growth is relatively slow, with chicks in California taking an average of 49 days from hatching to fledging. This is an unusually long period for such a small-bodied, temperate-zone bird. In Colorado, Hirshman (1998) studied the length of the nestling period during two years and reported mean nestling periods of 50 (n = 5 nestlings) and 47 (n = 11 nestlings) days. Growth is slightly slower at lower latitudes, where adult body size is smaller. The growth of nestling black swifts is also unusual in that nestlings put on considerable fat before leaving the nest, reaching about 146 percent of adult mass at the time of fledging.

Timing of breeding and breeding success

Table 7 provides a summary of the timing of major reproductive events. Given the large latitudinal range of black swifts, there is surprisingly little latitudinal variation in the timing of breeding. For example, swifts breeding in southern Mexico appear to have a similar breeding schedule as those breeding in southern Alberta. However, swifts breeding at low altitudes appear to initiate breeding earlier than those at higher altitudes (**Table 7**). It is not yet known whether the unusually late breeding by black swifts is related to nest site conditions (e.g., low water flow), to food abundance, or to a combination of the two factors. Quantifying black swift reproductive success is difficult due to the long nestling period and the difficulty in accessing nest sites. Reproductive success has not been well studied in black swifts. At a breeding site in southern California, hatching success (percent of eggs laid that hatched) was 81 percent (Marín 1997a) in one year, while fledging success was 90 percent during another year at the same site (**Table 8**; Foerster 1987). In Region 2, Hirshman (1998) recorded fledging success rates of 78 percent (n = 9) and 100 percent (n = 13) in two years at Box Canyon Falls, Colorado.

Demography

Genetic characteristics and concerns

Black swifts occupy a patchy distribution within their North American breeding range. In addition, breeding site fidelity appears to be extremely high among adult swifts, which would suggest a high degree of genetic isolation among populations. However, there are no data available on the dispersal patterns of juvenile swifts, and thus the degree to which neighboring populations may be genetically linked remains unknown. There have been no studies of the geographical pattern of genetic variation in black swifts and no observations that are suggestive of negative consequences (e.g., hatching failure) due to inbreeding.

Life history characteristics

Black swifts lay a single egg and are single brooded. If nesting failure occurs very early in the season, a replacement clutch may be laid (Hirshman personal communication 2003). Although longitudinal studies of marked individuals are lacking, swifts are thought to breed first when one year old (Lowther and Collins 2002). However, there are observations of extra-pair birds feeding young at nests in Box Canyon, southwestern Colorado (Hirshman personal communication 2003). In addition, observations of "floaters", or non-breeding birds at a site in southern California (Marín 1997a) suggest that, occasionally at least, either young, non-breeding birds, or non-breeding floaters exist in some populations. In a long-lived species with a prolonged breeding season and low reproductive output (e.g., in many species of pelagic seabirds), deferred age of first breeding is typical. This is an aspect of black swift reproductive ecology that needs further study.

T**able 7.** Approximate timing of breeding in black swifts in North America. Adapted from information in **Appendix B** and from cited accounts.

Study area	**Latitude**	**Elevation**	**Egg laying date**	**Hatch date**	**Fledge date**	**Citation**
Mexico (Oaxaca)	17	6000'	early July	late July-early August	early-mid September	Binford 1989
Mexico (Veracruz)	20	9100'	17 June	14 July	27 August	Collins and Landy 1968
California	37	sea level	primarily in June	July-August	2 August	Foerster 1987, Marín 1999b
California	34	4900'	22 June	19 July	1 September	Marín 1997a
Colorado	37	10100'	8 July	4 August	17 September	Appendix B
Colorado	38	7800'	3 July	30 July	14 September	Hirshman 1998
Montana	47	4700'	18-20 June	15-17 July	30 August -2 September	Hunter and Baldwin 1962
Alberta	51	?	early July	late July-early August	early-mid September	G. Holroyd, personal communication 2003
British Columbia	51	?	mid-June to early July	mid-late July	late August to September	Campbell et al. 1990

Table 8. Breeding success in black swifts.

Study area	Number of nests	Hatching success	Fledging success	Citation
California	16	81%	not studied	Marín 1997a
California	?	—	90%	Foerster 1987
Montana	5	not studied	maximum 60%	Hunter and Baldwin 1962
Colorado	22	95%	91%	Hirshman 1998

There are no available data on post-fledging survival or age-related variation in reproductive success. There are limited data suggesting relatively high adult survival in black swifts, with a maximum known age of 16 years and one month (Lowther and Collins 2002). Collins and Foerster (1995) recaptured several banded adults at the same nest colonies in southern California over periods of up to nine years apart, again suggesting relatively high adult survival. Adult survival in Eurasian swifts (*Apus apus*) is high, averaging 84 to 85 percent in a well-studied population in England (Cramp 1985). Eurasian swifts are similar in body size to black swifts, but lay larger clutches (2 to 3 eggs), and it is therefore likely that adult survival in black swifts is higher than in Eurasian swifts. A reasonable estimate of annual survival rate in black swifts is 88 to 92 percent.

Analysis of life-cycle diagrams and their associated demographic matrices is problematical given the lack of key life history data for black swifts. However, the analysis in **Appendix A** uses limited data from studies in Colorado (Hirshman 1998) and southern California (summarized in Lowther and Collins 2002), together with survival data inferred from detailed studies of the European swift (Cramp 1985). At the simplest level, the modeling suggests that black swift population growth is more sensitive to variation in survival rates than to variation in reproductive rates. More detailed analyses suggest that the survival of adults (relative to first-year swifts) is the primary factor affecting black swift population dynamics. Although reproductive success and the survival of first-year birds are also important factors, the survival of adults appears to be the critical demographic trait buffering populations against environmental uncertainty. It is important to note here that adult survival, the most important factor in regulating black swift population growth and thus a critical data point when considering black swift conservation, is also one of the most difficult traits to measure. Estimating adult survival rates is clearly a primary information need for black swifts in Region 2 (see the Information Needs section).

Summary of major conclusions from matrix projection models (see **Appendix A** for details):

- Survival accounts for 79 percent of the total "possible" sensitivity, with adult survival as the most important (56 percent of total) distantly followed by first-year survival (23 percent of total). Any absolute changes in survival rates will have major impacts on population dynamics.

- Adult survival (e_{22} = 80.8%) and, to a much lesser extent, first-year survival and adult reproduction (e_{21} = e_{12} = 9.3%) account for the great majority of the total elasticity. Proportional changes in adult survival rates will have a major impact on population dynamics.

- The reproductive value of older females is high. Thus adult females appear to be the key reservoir of population dynamics, and a buffer against environmental stochasticity, under the model formulated here. The reproductive value of adult females is almost four times that of young of the year. The higher reproductive value of adults makes them possible buffers against the detrimental effects of variable conditions. However, because the model was 'female focused', this result should not be taken to suggest that male survival is not important. The monogamous nature of swift breeding suggests that 'adult' survival is the important element.

- Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival rates to population dynamics. Black swifts appear fairly vulnerable to environmental stochasticity that would affect adult survival.

Social patterns and spacing

There is no indication of any territorial behavior in black swifts. The species breeds singly or in "colonies", and although there are observations of swifts engaging in aerial chases, such behavior is usually viewed as a form of pair bond formation or maintenance (Marín 1997b). Marín (1997b) also suggested that several forms of in-flight contact between birds may be aggressive behavior. Such behavior included "pair contact" whereby two birds in flight briefly touched feet, and "touch and grasp", which involves two birds clasping feet and then tumbling through the air for several meters.

Factors limiting population growth

Given the lack of information on reproductive success and survival, it is difficult to assess which factors are the keys in limiting population growth in black swifts. As waterfalls (or other wet, cliff areas) are relatively rare, stable, and patchily distributed within the species' range, it seems likely that breeding site availability may play an important role in limiting population growth. However, at most colony sites, only a subset of the available (apparently suitable) nesting ledges are typically used (Levad and Schultz personal communication 2003), suggesting that, at least within established sites, nest sites are not limited. Thus, although black swift population growth may be affected by colony site availability at the Regional scale, there is no indication of nest site limitation at the local scale. This argument assumes, however, that black swift nest site choice is currently well understood. Given that many apparently suitable nest pockets are not used, it may be that when choosing nest sites, swifts are cuing in on one or more factors that are not readily apparent to human observers.

Given that black swifts appear to be a long-lived species with a low reproductive rate, food availability is likely playing a significant role in regulating population growth. An experiment carried out by Marín (1997a) suggested that adult black swifts are able to successfully fledge more than one offspring, although raising two young caused an 11-day delay in fledging in the smaller nestling. It is important to note that Marín's experiment was carried out in only a single nest, and that a much larger sample size would more adequately answer the question of whether black swifts are constrained by food availability during the breeding season. In addition, Marín's study did not address the possibility that energetic constraints on parents may act at other times of the breeding cycle (e.g., during egg formation or during incubation).

Community ecology

Interactions between black swifts and their competitors and environment are summarized in **Figure 4**. The factors thought to be most important for black swift reproductive success are colony and nest site availability and the abundance and dispersion of food. The factors affecting the abundance of the primary food resource, flying ants and other swarming insects, are not well understood, but the temporal and spatial patterns of local water flow are likely correlated with the pattern of insect abundance. Water availability is also known to be an important factor affecting late summer flow rates at waterfalls, and thus may also directly influence nest site quality for black swifts. A factor that appears to be important during periods of inclement weather is the availability of (relatively) low elevation wet habitats such as lakes, bays, and wet meadows (Udvardy 1954). Such sites are typically only used during cool, wet periods, when the normal food supply at higher altitudes is apparently unavailable (Lowther and Collins 2002).

As mentioned earlier, the extent to which colony and nest sites are limiting is still unknown. Surveys in Colorado (Schultz and Levad personal communication 2003) have documented many waterfalls with seemingly suitable nesting habitat for black swifts, but with no active swift colonies. Nonetheless, it is clear that to some extent, the distribution of black swifts is limited by the availability of suitable, wet, cliff sites. As a consequence, hydrological processes likely play an important role in determining the number and quality of nest sites. In montane areas, years with poor snowfall and little summer rain not only reduce the number of available waterfalls, but also reduce the flow at existing falls, which may lead to declines in the number of nesting swifts (Hirshman personal communication 2002). In addition, the timing of water flows appears to be important, as black swifts are relatively late nesters and thus rely on continued water flow during the mid and late summer periods.

Vegetative diversity may be an important factor affecting the diversity of local insect prey, given that there is typically a positive correlation between the two. That is, areas with a relatively high diversity of landscape patterns, forest types, and plant species diversity support a greater diversity of insects, and such diversity may be particularly important to black swifts. Different forest management practices likely have varying effects on swift prey species. For example, clear-cut logging and subsequent reforestation efforts may negatively affect insect diversity by lowering the local diversity of plant species, by decreasing the variation in forest stand age structure, and by altering the temporal and spatial characteristics of local wetland habitats. Management techniques that tend to reduce plant species diversity, that tend to homogenize the age

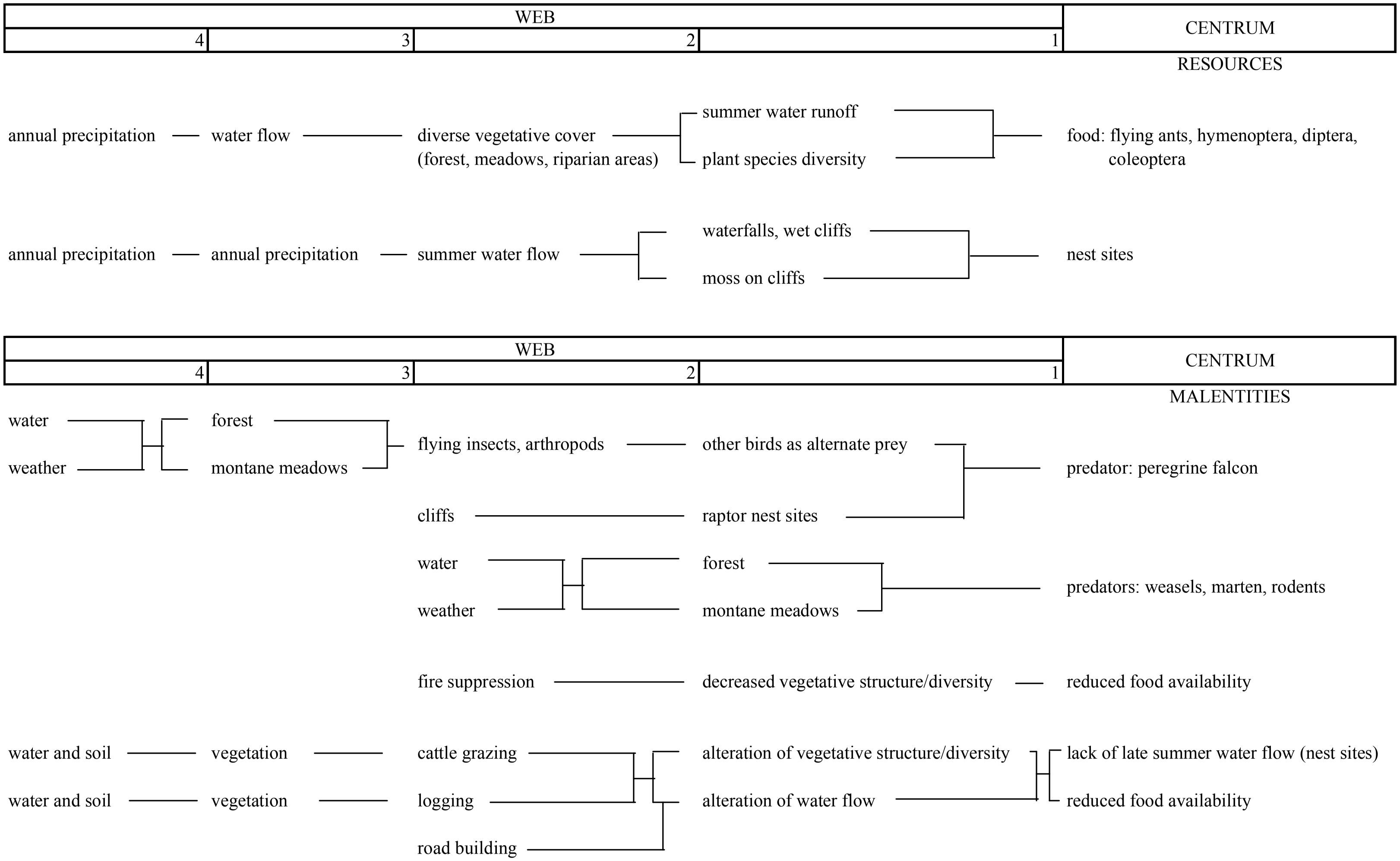

Figure 4. Envirogram representing the web of linkages between black swifts and the ecosystem in which they occur.

structure of the dominant tree species in forests, and that change the flow of water through local wetland habitats will likely act to decrease the local diversity of insect prey, and thus have negative effects on black swifts.

Predators and relationship to habitat use

Predation on adult black swifts has rarely been recorded. Marín (1997a) found the remains of an adult under a nest site in southern California and presumed it was taken by a terrestrial predator. Their only known predator is the peregrine falcon (*Falco peregrinus*; Hunter and Hazard 1998), which nests in habitats similar to those preferred by black swifts (e.g., montane and coastal cliffs). It appears that several features of black swift breeding ecology have evolved to reduce the likelihood of predation at nests. Black swifts have a relatively long breeding cycle, thus exposing the egg/nestling to potential predation over a period of about 11 weeks. Clearly, selecting a nest site that will remain secure from predators during this long nestling stage is critical. The unusual dark gray dorsal skin color and the blackish down of nestlings may also contribute to reducing predation by helping to reduce the visibility of the nestling during periods when the parents are off the nest.

Competitors

Because of their unique nest site preferences, black swifts have few known competitors for nest sites. In Region 2, the primary species that may compete for nest sites is the cordilleran flycatcher (*Empidonax occidentalis*), which sometimes also nests on niches on cliffs. However, the extent to which any competition for nest sites occurs is unknown. Other species that may nest in similar situations are Townsend's solitaire (*Myadestes townsendi*), white-throated swift (*Aeronautes saxatalis*), and violet-green swallow. Although black swifts may roost on the wintering grounds with other swifts (Stiles and Negret 1994) and occasionally migrate with other swifts and swallows (Lowther and Collins 2002), there is no evidence of interspecific competition for food.

Parasites and disease

The few studies of black swift parasites were reviewed in Lowther and Collins (2002). Parasites of feathers include two species of feather mites (Peterson et al. 1980) and two species of feather lice (Emerson and Pratt 1956). Adults have been found with a species of Hippoboscid fly (Parsons and Collins 1975), and an 11 day old nestling in Costa Rica was host to five botfly (*Philornis*) larvae.

CONSERVATION

Threats

It is difficult to assess the extent to which current management activities are affecting black swifts in Region 2. Part of this uncertainty relates to the lack of knowledge concerning swift nesting success, distribution, and dispersal. In addition, there have been no studies of the effects of forest management practices on any aspect of black swift ecology. As a consequence, the discussion in this section is largely speculative and largely concerned with probable indirect effects of management activities on black swifts. One of the potential problems faced by swifts is a lack of sufficient water flow in late summer, a time during which most montane waterfalls reach their lowest flow rate of the year (Conly 1993); this problem will be taken up at several points below. In general, the potential for indirect effects of forest management activities on black swifts include effects on swift nest site suitability and on prey availability.

Water diversion

Local water diversion projects (e.g., irrigation) may affect swifts by altering stream flows, and consequently altering the temporal and spatial patterns of insect abundance. In addition, water diversion schemes at relatively high altitudes may lead to decreased flows at waterfalls, and thus reduce the number of potential colony sites for black swifts. However, it is not currently clear whether water diversion practices are negatively affecting black swifts within Region 2.

Effects of recreation

There have been no studies of the effects of human recreational activities on black swifts. Incidental observations at a swift nesting colony in a cave in southern California (Marín 1997a) and at Box Canyon Falls in Colorado (Hirshman 1998) suggest that humans occasionally disturb black swift nesting attempts. However, both of these situations were somewhat unusual in that the nests were readily accessible to human visitors. Although there has been concern expressed over the effects of ice climbing on swift nesting cliffs (e.g., Beidleman 2000), recent colony visits in Colorado have not documented any apparent problems related to ice climbing (Schultz personal communication 2003).

Timber management

Logging may affect local water retention and runoff by altering the pattern of snow accumulation and runoff, and by decreasing the retention of water within watersheds. In a similar way, the presence of roads within forests may also alter the natural water flow regime, typically by expediting the flow of water through the system. Therefore, road building and various other forms of forest manipulation may indirectly degrade the nesting habitat (waterfalls) of swifts by decreasing water flow regimes later in the summer. The same factors may affect the timing and abundance of local flying insect blooms, again by altering the pattern of local water retention and runoff.

Livestock grazing

Livestock grazing is a common feature in many areas within Region 2. Livestock grazing may degrade forest understories, riparian woodlands, and open habitats such as meadows. Kovalchik and Elmore (1992) have identified a number of negative effects of livestock grazing on stream flow patterns:

- Decreased water storage in soils; lowered water table
- Increased runoff
- Decreased summer and late-season stream flows
- Loss of ephemeral streams
- Conversion of perennial streams to ephemeral streams

All of these effects may have indirect impacts on black swifts by significantly decreasing late summer stream flows. The number of black swifts breeding at Box Canyon Falls in southwestern Colorado is known to correlate positively with the extent of late season stream flow (S. Hirshman personal communication 2002). Extensive cattle grazing in western forests may be altering local hydrological patterns, and thus may be having negative effects on black swifts, primarily during drought years. Heavy livestock grazing may also reduce local floral and faunal diversity in western riparian areas (Kauffman et al. 1983, Rinne 1985, Kovalchik and Elmore 1992, Green and Kauffman 1995) and may thus indirectly affect swifts by decreasing their food supply. It is important to note, however, that current management approaches to livestock grazing and logging do not appear to have led to a decline in the regional population of black swifts.

Natural disturbances

The primary natural disturbance that may have negative impacts on black swifts is drought. For example, ongoing surveys for nesting black swifts in Colorado have revealed that some waterfalls have, at least temporarily, disappeared due to lack of runoff during drought conditions and that at other waterfalls, flow has decreased significantly. This may have reduced the amount of suitable nesting habitat in the surrounding rock faces. Drought conditions may also negatively affect the supply of flying insects, thereby reducing swift foraging and nesting success. Breeding success at Box Canyon Falls in southwestern Colorado has been measured annually since 1996, and success was lowest in the most severe drought year (Hirshman personal communication 2002).

Fire likely has significant short-term effects on swifts, both by altering local water flow, and by affecting (either positively or negatively) the availability of flying insects. The intensity and distribution of fires likely affects the extent to which black swift reproductive success is impacted.

There is no indication of any interaction with exotic species in Region 2, and there is no known harvest of black swifts by humans.

Conservation Status of Black Swifts in Region 2

Our knowledge of the distribution and abundance of black swifts in Region 2 is increasing as dedicated surveys at potential nest sites are carried out each year. However, until the overall range and abundance are understood in Region 2 (e.g., there is currently little known of the species' breeding range or abundance in Wyoming), assessments of conservation status for the entire Region will be hampered. Breeding bird surveys currently being conducted by the Rocky Mountain Bird Observatory within many of the national forests in Wyoming may soon provide further information on the local range of the species, but dedicated surveys for swifts at suitable cliff sites are clearly needed. The limited evidence available from Colorado suggests that black swift populations are and have been relatively stable in that state for a long period (over 50 years), and that the species' habitat is generally secure.

Habitats within Region 2 vary considerably in their ability to support breeding populations of black swifts. However, rather than being a function of local land use or habitat management, this variation appears to be largely due to inherent geology and physical relief, with relatively tall mountain ranges (e.g., San Juan Mountains) containing more waterfalls and other wet runoffs that are the preferred nesting habitat of the species. The degree to which variation in habitat or vegetation features affects the preferred food supply is not known. Although swarms of flying ants are thought to be concentrated near elevated ridges and mountaintops (Chapman 1954), black swifts may take a wider array of prey items that may be found over a range of habitats and elevations. To date, there have been no studies of black swift food habits in the Rocky Mountains, and the relationship between habitat features and food supplies is thereby speculative.

The apparent dependence of black swifts on waterfalls (at least within Region 2) as nesting sites means that they are restricted to very few potential breeding sites within their geographic range. Further, drought conditions as well as local forest management practices (e.g., road-building) may have negative impacts on black swift nest site suitability. In this sense, black swifts should be considered vulnerable to habitat/environmental change. The degree to which the species is able to recover from short- (drought) and long-term (e.g., road-building effects on water retention and local hydrology) perturbations in the environment are not currently known, but it is likely dependent on adult survival rates. There is currently a lack of information on whether inactive colony sites are later recolonized.

Although black swifts are habitat specialists and may be vulnerable due to their unusual life history (single egg, long breeding season), there is no direct evidence that habitat is declining or that current management techniques are affecting the species. The available data give no indication that populations within Region 2 are currently at risk. However, given the incomplete state of knowledge of black swift distribution and abundance in the Region, the species' current population trend (and even distribution) cannot be accurately assessed. Data on the species' distribution in Wyoming, adult survival, and reproductive success would help to more accurately assess the population status of black swifts in Region 2.

Management of Black Swifts in Region 2

Implications and potential conservation elements

Environmental impacts on the abundance and distribution of black swifts in Region 2 are currently difficult to detect. This largely stems from the lack of information on the breeding distribution, abundance, reproductive success, and survival of swifts in the region. Unlike most other Neotropical migrants, black swifts are difficult to survey, as only dedicated nest site searches by trained observers are likely to identify breeding sites. Although such surveys are being carried out in Colorado, no such surveys have been done in Wyoming, where the species' distribution and abundance remain almost unknown. Given this background, it is difficult to derive any conclusions regarding the result of forest and landscape management activities on black swifts. However, given the long-term site occupancy at known Colorado nesting sites, it appears that colony site selection has not been affected strongly by either local or broad scale changes in habitat, and only slightly by annual variation in weather conditions.

As mentioned previously, the two factors that are critical to breeding populations of black swifts are waterfalls or wet cliff sites for nesting and swarms of flying ants and insects for food for nestlings. At present it is unclear how management practices may be affecting these two resources, but it is likely that recreation activities at nest sites could influence nesting swifts and that road building and water diversion schemes may negatively affect both stream flows and insect abundance. In addition, environmental stochasticity (e.g., periods of drought) likely has negative impacts (via water flow rates and insect abundance) on the reproductive success of swifts. However, much more information on the factors affecting breeding success, site tenacity, adult survival, and other aspects of black swift life history are needed before the effects of management practices can be accurately measured. Under current management approaches, and with the limited information available, the consequences of logging and livestock grazing do not appear to be important factors in managing swift populations.

Tools and practices

There is currently a black swift inventory project underway in Colorado, organized by the Rocky Mountain

Bird Observatory (Rich Levad) and the USFS (Chris Shultz, Durango office). This project is attempting to survey most waterfalls in Colorado for signs of nesting activity by black swifts. These surveys typically consist of mid-day visits to each waterfall where the adjoining cliff faces are scanned with binoculars for evidence of moss nest structures. In addition, early evening visits serve to detect whether adults are flying into the area to roost. Detailed survey methodology is presented in **Appendix B** and **Appendix C**.

The current method used to identify potential black swift nesting sites is to consult publications (e.g., "Waterfalls of Colorado", Conly 1993) and various maps (USGS, USFS, BLM) that can be used to identify waterfalls and other potential wet cliff habitats, and then to visit those sites to conduct surveys.

Long-term breeding site monitoring is currently carried out only at Box Canyon Falls in southwestern Colorado, where Sue Hirshman has been monitoring the swift colony since 1996. At this site, almost daily records are kept of nest contents and the presence of adults. **Appendix B** provides an outline of a proposed population monitoring scheme. It contains suggestions on how to carry out local population surveys, but it does not suggest methodology for a regionwide plan. At the regional scale, different sampling regimes will entail different costs and benefits. For example, sampling a range of geographic areas for colony inventories would entail moderate costs (but may be reasonably accomplished using volunteers to collect the data). On the other hand, sampling every three years would be more cost-effective, but would have the limitation of not being able to accurately measure nest and colony site use, or the effects of stochastic (e.g., weather) events on colony status. A region-wide monitoring scheme, covering 30 to 50 sites throughout Colorado and Wyoming (once breeding sites in the latter state are identified), would likely provide a wealth of information. Ideally, sites chosen for visitation each year should be randomly chosen from known and potential nesting sites.

There have been no population or habitat management approaches adopted for black swifts. However, ongoing survey work in Colorado is beginning to provide the necessary baseline data on population size and geographic distribution that will be needed to establish a population management plan.

Information Needs

The primary information needed for effective conservation of black swifts in Region 2 is a clearer picture of the species' breeding distribution. An expansion of the existing breeding site surveys to Wyoming would fill this gap in knowledge. There are no accepted records of black swifts in South Dakota, Nebraska, or Kansas, but there are summer records for Wyoming, where the species likely breeds at scattered sites in the Rocky Mountains.

There is currently little direct evidence of how black swifts respond to fine and broad scale changes in habitat. Rather, the links between habitat management and swift population status are hypothetical and based upon known or presumed effects of habitat management on water flow and insect abundance. Gathering data on the indirect effects of management practices and natural disturbances on black swifts can best be carried out by continued monitoring of known and potential nest sites, by assessing reproductive success at a sub-sample of sites, and by relating these results to local habitat management activities (e.g., recreation, stream flows). At some subset of colony sites data should be collected on the flow rate patterns of surrounding streams. These data should then be analyzed with respect to any local changes in habitat management. To date, there is little indication of a reduction in the number of occupied breeding sites in Colorado, where most historical nests sites continue to be occupied (Levad and Schultz personal communication 2003). This finding, together with little indication of a reduction in population size at known colony sites (Hirshman 1998, Schultz personal communication 2003), suggests that there has been little effect of habitat management activities on black swift population status in Colorado over the past 50 years.

For black swifts breeding in Region 2, there is little information on migration routes, wintering areas, or even daily foraging movements. Although adults remain away from the nest for long periods, the habitats they visit during these trips are mostly unknown. In addition, there is little direct information on how flying ants and other volant insects respond to small or large scale changes in habitat. If these insects are typically found at high altitudes, as many observations suggest, it will remain a difficult problem to study.

Black swift demography is poorly known and should be studied within Region 2 to help better understand population viability. It appears that adults are long-lived, that site fidelity is relatively high, and that colonies are used consistently over long time periods. However, the degree to which adults and juveniles move among colony sites is not known. In addition, there are no data on juvenile (first-year) survival or on age-related patterns of reproduction. These data could be gathered by banding adults and young at nearby colony sites and subsequently monitoring intra-colony movements and patterns of reproduction.

Current surveying methodology (see **Appendix B** and **Appendix C**) developed by Chris Schultz and Rich Levad could be used to monitor population trends. This would ideally be accomplished in several ways. First, annual or semi-annual checks for the total number of active nests at a subset of the known nesting sites should be made to provide a long-term picture of colony attendance. A number of potential colony sites should also be monitored every 3 to 5 years to assess whether swifts are colonizing new sites.

Detailed studies of reproductive success should also be made at a subset of nesting sites. These data would include the timing of egg-laying, as well as hatching and fledging success. Assessing reproductive success would require a much greater time investment, with repeated visits at the beginning of the egg-laying period, and again near hatching and fledging. A good possibility here is to use volunteer observers to collect much of the reproductive success data. The best data set on long-term reproductive trends in black swifts comes from Sue Hirshman, a volunteer observer at Box Canyon Falls in southwestern Colorado. Similar observations at 10 to 15 other nesting sites would likely provide a good indication of any local changes in reproductive success. Given our lack of knowledge on the factors that affect survival, reproductive success, prey populations, and other key factors, it will be exceedingly difficult to plan any restoration program if black swift populations decline.

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APPENDIX A

Matrix Model Assessment of the Black Swift

Life cycle graph and model development

Analyses of life cycle diagrams and associated demographic matrices (McDonald and Caswell 1993, Caswell 2001) can provide valuable insights into which life-history stages may be most critical to population growth. However, constructing models based on incomplete and/or poor quality data may have little relevance (Reed et al. 2002). The following analysis has been constructed using the best available data for black swifts – while there is some uncertainty surrounding some of the input parameters (especially juvenile survival), the results should provide a reasonable estimate of which parameters are critical in determining population growth in black swifts.

A life cycle graph (Caswell 2001) was formulated that comprised two stages (censused at the fledgling stage and as "adults"). Given that clutch size is a single egg, a change in fertility (number of fledged female offspring) with age, from 0.25 in the first year, to 0.425 for older birds, was assumed. As estimates of annual survival for this species, 0.255 was used for first-year birds and 0.9 for adult survival (see Life history characteristics section above). From the resulting life cycle graph (**Figure A1**), a matrix population analysis was produced, with a post-breeding census, for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001).

The model had two kinds of input terms: P_i describing survival rates, and m_i describing the number of female fledglings per female (**Table A1**). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values.

The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. Note also that the fertility terms (F_i) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just after the breeding season) to the next birth pulse almost a year later. The population growth rate, λ, was 1.004, based on the estimated vital rates used for the matrix. Although this suggests a growing population, the value derives from approximations for the vital rates, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

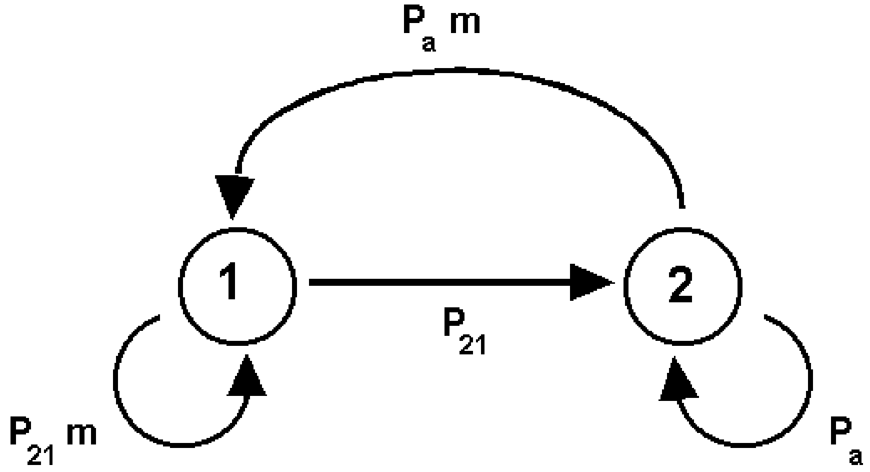

Figure A1. Life cycle graph for the black swift. The numbered circles ("nodes") represent the two stages (first-year birds and adults). The arrows ("arcs") connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ji}) or fertility (the arcs pointing back toward the first node).

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for black swift.

Parameter	Numeric value	Interpretation
m_1	0.25	Number of female fledglings produced by a first-year female
m_a	0.425	Number of female fledglings produced by an adult female
P_{21}	0.255	First-year survival
P_a	0.9	Survival rate of adults

$$\begin{array}{c|cc|} & 1 & 2 \\ \hline 1 & P_{21}m & P_a m \\ 2 & P_{21} & P_a \\ \hline \end{array}$$

Figure A2a. Symbolic values for the projection matrix of vital rates, **A** (with cells a_{ij}) corresponding to the black swift life cycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1.**

$$\begin{array}{c|cc|} & 1 & 2 \\ \hline 1 & 0.064 & 0.383 \\ 2 & 0.255 & 0.9 \\ \hline \end{array}$$

Figure A2b. Numeric values for the matrix of **Figure A1** and **Figure A2a.**

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, A [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to population growth rate (λ), which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. Sensitivities can be used to assess the relative importance of survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of threatened species or the "weak links" in the life cycle of a pest.

Figure A3 shows the sensitivity matrix for black swifts. The summed sensitivity of λ to changes in survival (79% of total sensitivity accounted for by survival transitions) is higher than that for fertility (21%). Adult survival was the most important transition (**Figure A3**). The major conclusion from the sensitivity analysis is that survival rates, especially adult survival, are most important to population viability – given the proviso that the changes in the vital rates are absolute (as opposed to proportional, as discussed below in the section on elasticity analysis).

$$\begin{array}{c|cc|} & 1 & 2 \\ \hline 1 & 0.099 & 0.244 \\ 2 & 0.366 & 0.901 \\ \hline \end{array}$$

Figure A3. Sensitivity matrix, **S**. The λ of black swifts is most sensitive to changes in adult survival (Cell $s_{22} = 0.9$), followed by first-year survival (Cell $s_{12} = 0.37$).

Elasticity analysis

Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, one might reasonably equate changes in survival rates or fertilities of 1%). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original vital rates (the a_{ij} arc coefficients on the graph or cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for black swift are shown in **Figure A4**. λ was most elastic to changes in adult survival (e_{22} = 80.1%, where e_{22} is the percentage of total elasticity on arc P_{22}, the self-loop from the second node back to the second node in **Figure A1**). Next most elastic were first-year survival and adult reproduction ($e_{12} = e_{21}$ = 9.3%). Least important was reproduction by first-year birds (0.6% of total elasticity). The sensitivities and elasticities for Black Swift were generally consistent in emphasizing survival transitions, with the elasticities strongly emphasizing adult survival, whereas the sensitivity analysis gave a slight edge to first-year survival. Thus, survival rates, particularly adult survival rates, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable stage distribution (SSD; **Table A2**) describes the proportion of each age-class or stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. At the time of the post-breeding annual census (just after the breeding season), young of the year represent 28.9 percent of the black swift population, while adults represent 71.1 percent of the population. Reproductive values (**Table A3**) can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (in this case, young of the year) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by convention, always 1.0. An adult female individual in Stage 2 is "worth" 3.7 young of the year. The adult females are therefore important stages in the life cycle. The cohort generation time for this species was 10.4 years (SD = 9.5 years).

$$\begin{array}{c|cc|} & 1 & 2 \\ \hline 1 & 0.006 & 0.093 \\ 2 & 0.093 & 0.808 \\ \hline \end{array}$$

Figure A4. Sensitivity matrix, **E**. The λ of black swifts is most elastic to changes in adult survival ($e_{22} = 0.81$), followed by adult fertility and first-year survival ($e_{12} = e_{21} = 0.09$).

Table A2. Stable age distribution (right eigenvector). At the census, 28.9 % of the individuals in the population should be young of the year. The rest will be older "adult" females (yearlings or older).

State	Description	Proportion	Mean age (± SD)
1	First-year females	0.289	0 ± 0
2	"Adult" females	0.711	9.7 ± 9.2

Table A3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, young of the year) age-class or stage. The reproductive value of the first age class is always 1.0.

Age class	Description	Reproductive value
1	First-year females	1.0
2	"Adult" females	3.7

Stochastic model

To mimic the potential perturbations that may be faced by natural populations, a stochastic matrix analysis was conducted for black swifts. Stochasticity was incorporated in several ways (**Table A4**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. The amount of fluctuation was varied by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation, a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis) was used. Under Case 1, the fertility arcs (F_{11} and F_{12}) were subjected to high levels of stochastic fluctuations (SD one quarter of the mean). Under Case 2, the adult survival arc (P_{22}) was varied with high levels of stochasticity (SD one quarter of mean). Under Case 3, adult survival (P_{22}) was varied with low levels of stochastic fluctuation (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) of the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). The stochastic growth rate, log λ_s, was calculated according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

Table A4. Summary of four variants of stochastic projections for black swift with N_0 = 10,000 individuals (the initial population size).

	Case 1	Case 2	Case 3
Input factors:			
Affected cells	F_{11} and F_{12}	P_{22}	P_{22}
S.D. of random normal distribution	1/4	1/4	1/8
Output values:			
Deterministic λ	1.004	1.004	1.004
# Extinctions/100 trials	0	98	21
Mean extinction time	n.a.	491	1,367
# Declines/# survived pop	0/100	2/2	52/79
Mean ending population size	1.5×10^7	8.7	1.6×10^6
Standard deviation	1.7×10^7	2.5	9.7×10^6
Median ending population size	1.3×10^7	8.7	1,849
Log λ_s	0.0034	-0.0299	-0.0021
λ_s	1.0035	0.9774	0.998
% reduction in λ	0.03	2.6	0.59

The stochastic model (**Table A4**) produced two major results. First, stochastic fluctuations in survival transitions had appreciably greater detrimental effects than did varying fertility transitions. Even low-level stochastic fluctuations in survival (Case 3, SD of one eighth) resulted in more extinctions (21 vs. 0) and more declines (73 vs. 0) than did varying the fertility rates under high levels of stochastic fluctuation (Case 1). High levels of stochastic fluctuation in survival (Case 2) led to substantial extinction losses (98/100). Second, the level of the stochastic fluctuations greatly affected the strength of the detrimental effects (Case 2 vs. Case 3; 98 vs. 21 extinctions). The difference in the effects of which vital rate was most important is predictable largely from the elasticities as well as the variance-stabilized sensitivities of Link and Doherty (2002) shown in **Figure A5**, which again put strong emphasis on survival rates and remove the dependence of the variance on the mean. λ was most elastic to changes in adult survival. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell, 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. The extinctions and declines simulated should not be interpreted as estimates of extinction risk — instead they should be viewed as a way to compare the detrimental effects of stochasticity within the bounds of the models. That is, Case 2 (**Table A4**) does not indicate a 98 percent chance of extinction, but does suggest that fluctuations in adult survival rates will have much stronger effects on population dynamics than will fluctuations in fertility rates. These results indicate that populations of black swift are vulnerable to stochastic fluctuations in adult survival, especially when the magnitude of fluctuations is high. Nevertheless, the importance of adult survival to the life cycle of black swift ($e_{22} = 0.808$ in **Figure A5**) may, to some extent, help buffer them against environmental stochasticity. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Thus, on an evolutionary timescale, black swift life histories may have been shaped to reduce factors that contribute to variability in adult survival.

Potential refinements of the models

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in any demographic analysis. The most important "missing data elements" in the life history for Black Swift are for first-year survival, which emerges as a vital rate to which λ is fairly sensitive as well as elastic. Better data on adult survival rates and their variability would also be useful. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on the "uncorrelated" assumption, by incorporating forces that were not considered. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

$$\begin{array}{c|cc|}
 & 1 & 2 \\
\hline
1 & 0.02 & 0.12 \\
2 & 0.16 & 0.27 \\
\hline
\end{array}$$

Figure A5. Rescaled, variance-stabilized (square root arcsine transform) matrix of sensitivities, V (Link and Doherty, 2002), which provides a prospective view of the impact of environmental stochasticity. Using this rescaled sensitivity, the λ of black swifts is most strongly affected by changes in adult survival ($v_{22} = 0.27$), followed by first-year survival ($v_{21} = 0.16$).

APPENDIX B

Black Swift Survey Protocol

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General species information

The black swift (*Cypseloides niger*) is a long-distance neotropical migratory bird that breeds in western North America in close association with mountain waterfalls or sea-side cliffs (Knorr 1961, Foerster 1987, Dobkin 1994). Known breeding populations are disjunct and are associated with highly specialized habitat characteristics. Black swifts are presumed to winter in South America, but the exact range is poorly known (Collins personal communication ???date, include in Appendix references). The most obvious threats to breeding success are development of sea-side nesting cliffs and alteration of intermountain stream flows resulting in reduced nesting success (Colorado Natural Heritage Program 1997). The North American Breeding Bird Survey does not adequately sample the species due, in part, to its limited breeding distribution and very restricted habitat requirements, and in part to the inaccessability of its preferred breeding habitat. Partners in Flight ranks the black swift as a species of high priority for conservation concern (Carter et al. 1996) and, within the western United States, as a priority species for virtually every state within its documented breeding range (Rich and Beardmore 1997). The USDA Forest Service has designated the species as sensitive in every agency Region in which it breeds. Colorado is estimated to host between 10 and 20 percent of the world's breeding population, yet less than 30 active nesting sites are known, most on National Forest System lands. Therefore, there is a clear need for a standardized survey protocol and monitoring program that could provide data for evaluation of long-term population status and trends. This document proposes a standardized survey protocol for black swift nesting colonies and a conceptual method for evaluating species' status and trend.

Survey protocol

Sampling parameters

We suggest the most appropriate sampling parameter for black swifts might be a simple count of the maximum number of individuals seen simultaneously flying about or roosting on the nesting cliff. At sites where more than one annual visit can be consistently achieved, the logical parameter to track among years is the mean of the maximum daily counts. There are several benefits to conducting multiple site visits. The first benefit is the potential to place statistical parameters on estimates of colony size. The second benefit is reducing the possibility that stochastic weather events might significantly affect results of a single site visit and thus bias annual colony size estimates.

Another logical sampling parameter, counting the number of nests in a colony, may be difficult to achieve consistently among years, due to the cryptic nature of swift nests (Knorr 1961, Farrand 1990) and the distance from the nest cliff at which many observations must be conducted. In addition, counts of nests are precluded at some locations, such as many sea-side cliffs, where the only accessible viewing site is on the rim. However, at those sites where access and viewing from below can be done consistently, we believe counts of occupied nests, vacant nests, number of adults on nests, and number of nestlings on nests can provide valuable data on reproductive success and productivity at individual sites. Therefore, where possible, we recommend recording the number of visible nests, adults on nests and nestlings observed.

First site visit

At sites that have not been previously surveyed, we recommend an initial daytime reconnaisance visit to the area. At this time, the waterfall can be evaluated for potential for black swift occupancy based on the criteria described by Knorr (1961, 1993). At this time, selection of the best observation site should also be done, and that location should be marked on a USGS topographic map. Recommended trails or access routes should also be mapped for future reference. If the first site visit must occur on the day of the first survey, observers must arrive in the area with enough time to thoroughly explore all possible observation sites and area departure routes before observations are begun.

Season

We recommend targeting colony visits to start about two weeks after eggs have hatched to avoid potentially biasing samples with the inclusion of late migrants or nonresident floating individuals (hatch date varies by site latitude and elevation, see **Table B1**). This problem was noted by Foerster and Collins (1990) in their analysis of swift observation data from California. Also, prior to hatch and until the young reach about 12 days of age, it is likely that one adult remains on the nest most of the time. Therefore, after about two weeks post-hatch, there is a much better chance of both adults being in sight over the colony at the same time, and thus better chance of obtaining a full colony count. Because black swifts are known to be a late nesting species at high elevations and northern latitudes (Knorr 1961, Hunter and Baldwin 1962), post-hatch survey visits may also provide better colony access at mountain sites due to reduced stream flows and drier trail conditions in late summer, and thus provide more consistent survey effort.

Due to the protracted nature of the black swift nestling period (45 days; Foerster 1987, Marín 1997), we suggest that annual survey effort should consist of three colony visits, beginning approximately two weeks after mean hatch date for that latitude, and spaced approximately two weeks apart. If only one site visit can be consistently achieved, this visit should occur approximately four to six weeks after mean hatch date. For reference in planning site visits, **Table B1** provides approximate timing of black swift breeding events at a variety of latitudes and elevations (data is from Knorr (1961), Hunter and Baldwin (1962), Collins and Landy (1968), Collins and Foerster (1995), Marín (1997), Hirshman (1998), and personal observations.)

Time of day and weather

Published literature (Foerster and Collins 1990) and personal experience suggest that the most productive survey time for conducting counts of flying adults is the final two hours of daylight when chick provisioning rates may increase and adults are returning to the colony to roost. Targeting surveys for the last hours of daylight should also maximize the probability of counting local residents and might limit the potential influence on the data of non-resident foraging individuals. An important side benefit of targeting observations during the hours of hypothesized maximum swift activity is the potential for simultaneously gathering site-specific data on nest location and numbers, roost site selection, micro-habitat features, or other site-specific information which might be important to land management decisions.

However, the previous statements should not be interpreted as implying that site visits conducted during mid-day are not worthwhile, and mid-day visits can provide valuable swift monitoring data. In our experience, counts of nests and determination of occupancy status of individual nests is best accomplished during mid-day when lighting inside dark nest niches is likely to be brightest and viewing conditions are best. Therefore, we recommend that if the purpose of a site visit is to count nests or document occupancy of status of nests, the visit should be conducted during mid-day.

All surveys should occur under relatively similar, and favorable, weather conditions. Favorable weather conditions are light winds, little to no overcast, no precipitation and seasonally moderate temperatures. Gusty onshore winds are usually present at coastal sea cliffs, and upslope winds are often found at mountain falls until just before dark and cannot be avoided.

Table B1. Approximate timing of black swift breeding events by nest location.

Location	Latitude	Begin Incubation	Hatch	Fledge
Mexico (9,100')	20° N	17 June	14 July	27 August
California (4,900')	34° N	22 June	19 July	1 September
California (sea level)	37° N	23 May	19 June	2 August
Colorado (10,100')	37° N	8 July	4 August	17 September
Colorado (7,800')	38° N	3 July	30 July	14 September
Montana (4,700')	47° N	15 June	12 July	25 August

Reproductive parameters:

Average clutch and brood size: 1.

Incubation period: 24-27 days with both sexes sharing duties.

Nestling period: 45 days with both sexes feeding young.

However, observations should be scheduled to avoid the passage of frontal systems or afternoon thunderstorms.

Observation location

An observation location should be chosen that maximizes the view of the nesting cliff and aerial access routes. This location should then be used consistently for all subsequent surveys. At mountain falls, this will often be a location near the base of the nest cliff or falls where a clear view of the sky allows maximum ability to spot birds flying into the colony, especially in dim light conditions just before dark. At colonies where the only accessible observation sites are on the rim, choosing an observation site with the brightest possible backdrop will maximize observers' ability to spot flying swifts during and after dusk.

Observers and safety

If at all possible, there should be two observers present at each colony visit. With two observers present, counts of flying swifts will likely be more accurate and observations of nests or roosting adults will be more complete. For consistency of sampling effort, we recommend that no more than two observers be used at known occupied sites. Further, we recommend that both observers watch from the same location and not attempt to cover two viewing stations simultaneously. However, in the case of surveying previously unvisited areas or large waterfall and cliff systems for new colonies, any number of additional observers will significantly increase the likelihood that swifts will be detected if they are present, and consistency of observation effort is not critical.

A second, but no less important, reason for having two observers present at each colony visit is for observer safety. Working around wet, moss-covered cliffs is inherently dangerous, especially after dark, and the presence of a second observer provides a margin of safety beyond that of a lone observer. For safely reasons, we strongly recommend scouting departure routes during daylight hours to ensure safely exiting the area after dark, and carrying a working backup flashlight in case the primary light fails. A final safety consideration when working on cliff rims or bases is potential exposure to lightning and falling rock. Observers should always be aware of approaching thunderstorms, and take cover immediately if necessary.

Data considerations

This proposed survey protocol provides, at best, an estimate of the maximum number of adult black swifts present in suitable breeding habitat during the breeding season. It may, at some individual sites, provide annual measures of colony size and reproductive success. A weakness of this survey protocol is that it likely underestimates colony size and at more inaccessible sites direct measures of nesting success or productivity are unlikely to be obtained. However, at those nesting colonies that are readily accessible and survey efforts are most consistent, it is logical to expect that data on nesting success and productivity will be obtained. An additional benefit to adopting this, or any other, consistent rangewide survey protocol is the legitimate expectation of obtaining at least qualitative information about black swift colony persistence and metapopulation dynamics.

Acknowledgements

We thank Bob Altman and Dr. Charles Collins for very helpful and timely reviews of earlier drafts of this protocol.

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APPENDIX C

Black Swift Field Survey Form

Developed by Chris Schultz, San Juan National Forest

Observer Name:____________________ Date:________ Begin Time:______ End Time:______.
Your mailing and e-mail address:____.

Black Swifts Seen? (✓) ☐ Yes ☐ No. If Yes, Estimate Minimum Colony Size (# of adults):________.
Number of Nests:___ . Number of Nestlings:____ . Nest Niche (✓): ☐ Ledge ☐ Pocket ☐ Other
American Dippers Seen? (✓) ☐ Yes ☐ No. If Yes, Number of Dippers:___ . Number of Dipper Nests:__ .

Site or Waterfall Name:________________. Stream Name:_________________ . County:__________.
Aspect (direction falls face):_______° Elevation (top of falls):__________ft
Ownership (✓): ☐ Public ☐ Private Management Area:_________________________________.

Location: USGS Quad Map:________________ . UTM - Zone:____S E:_________ . N:__________.

Directions to Falls and Best Observation Point:____.
____.

Waterfall Type and Height:
Total Height of Falls___ft Plunge:____ft Horsetail:____ft Fan:____ft Cascade:____ft
Segmented? (✓) ☐ Yes ☐ No. Tiered? (✓) ☐ Yes ☐ No.

Flowing Surface Water during late summer (✓): Points:___.
☐ No flowing water (1) ☐ Flows weak (2) ☐ Flows moderate, little spray (3)
☐ Flows moderate, some spray (4) ☐ Flows heavy, much spray (5)

Relief (commanding view) from Top of Falls over Surrounding Terrain (✓): Points:___.
☐ Falls at bottom of terrain (1) ☐ Little view from falls (2) ☐ Moderate view from falls (3)
☐ Good view from falls (4) ☐ Commanding view from falls over terrain (5)

Number of Suitable Nest Niches (pockets or ledges) and Accessability to Ground Predators (✓): Points:___.
☐ No suitable niches present (1) ☐ Few niches and/or all niches accessable (2)
☐ Some niches and/or most niches accessable (3) ☐ Some niches and/or most niches inaccessable (4)
☐ Many suitable niches and/or all niches inaccessable (5)

Unobstructed Aerial Access to or from Nest Niches (✓): Points:___.
☐ No clear access (1) ☐ Clear to ¼ of niches (2) ☐ Clear to ½ of niches (3)
☐ Clear to ¾ of niches (4) ☐ Clear to all of niches (5)

Shading of Nest Niches (✓): Points:___.
☐ Nest niches sunlit all day (1) ☐ Sunlit >3hr/day (2) ☐ Sunlit 1-3hr/day (3) ☐ Sunlit <1hr/day (4)
☐ Shaded all day (5)

Moss Availability (✓): Points:___.
☐ No moss present (1) ☐ Trace of moss (2) ☐ Scattered moss (3) ☐ Frequent Moss (4)
☐ Abundant moss (5)

Total Points:____.

Weather, observations, comments, nests (location, height, distance from falls, presence of whitewash) etc.:
____.
____.
____.
____.
____.

(Over)

07/27/00

Completed Forms: Send **original with topo map** to area wildlife manager. Send **copy of form and map** to Chris Schultz, San Juan National Forest, 15 Burnett Court, Durango, CO 81301; cschultz@fs.fed.us.

Survey Methods:

The probability of detecting a new Black Swift colony is highest when they are feeding young, which, in the Rocky Mountains, is **mid July to early Sept**. The most productive time to count flying birds is the **final two hours of daylight** when adult swifts return to the colony to roost and feed young. Estimate the **minimum number of adults** flying about or roosting on the nest cliff. Therefore, select an observation location that maximizes the view of the potential nest cliff and aerial access routes. At falls, this will usually be near the base where there is a clear view of the sky, especially in the dim light conditions just before dark. Please describe locations birds are seen roosting so they can by checked for nests in daylight.

Choose **weather conditions** with light winds, little or no overcast, light precipitation and seasonally mild temperatures. For safety reasons, there should be two observers present at all visits, with both observers watching from the same location. Always carry a primary and backup flashlight with spare batteries in case one dies while walking out after dark. Be aware of lightening, and remember, working around wet, moss-covered cliffs is inherently dangerous, especially after dark. BE CAREFUL.

Waterfall Type: Descriptions are from Marc Conly's 1993 book, Waterfalls of Colorado, Pruett Publishing Co.

Plunge: water is free-falling for most of its height without coming into contact with the underlying rock.

Horsetail: water maintains some contact with underlying rock for much of its height.

Fan: like a horsetail, but the stream of falling water gets wider as it descends.

Cascade: water flowing over a broad face with too many small leaps or segments to count.

Segmented: water is divided into two or more streams falling parallel to each other.

Tiered: the length of the water's drop is broken into distinct falls that are separated by short runs.

Black Swift Habitat Characteristics:

Flowing Surface Water: The most documented nesting habitat requirement is close proximity to falling water. No Black Swift nests have been found along intermittent streams, thus year-round flows appear to be required. The nest structures are usually in small cavities within the spray zone or directly behind the sheets of falling water, and are described as wet and dark. Occasionally, nests are located away from the spray zone but these are usually on ledges that are moist from other water sources.

Commanding View (relief): The second most commonly noted nesting habitat attribute is a commanding view from the nest colony over the surrounding terrain. The ability of a swift to fly straight out from the nest colony and very quickly be hundreds of feet above the valley floor appears to be very important for site occupancy. Swifts are known to nest in the bottom of deep canyons and in caves but in these cases there is usually a broad view from the nest cliff down the canyon or from the mouth of the cave.

Number of Nest Niches and Accessibility to Ground Predators: Black Swift nests are almost always built in a small pocket or ledge on a sheer face. Occupied nest niches are always inaccessible to mammalian ground predators. The placement of nests out of reach of ground predators may be an evolutionary response to low reproductive rates. All reports of Black Swift clutch sizes are of one egg only. Therefore, failure of the nest structure itself is the leading cause of reproductive failure.

Unobstructed Aerial Access: A third habitat attribute that is related to commanding views is that aerial access to the nest niche is usually free of obstructions to flight. Black Swifts appear reluctant to fly near or through tree crowns and branches to access nest niches. Therefore, screening of potential nest cliffs by trees or other debris appears to significantly reduce the likelihood that otherwise suitable nest cliffs will be occupied by swifts.

Shaded Nest Sites: Black Swift nest ledges are rarely sunlit, and then only late in the day as ambient air temperatures decline. The nest structures are invariably placed in microsites that are in deep shade the majority of the day. However, nestlings do not appear bothered by sunlight and often become more active while in direct sunlight.

Moss Availability: The nest niche often has water flowing around or in front of the opening but the nest cup itself is usually dry. Because of their dampness and darkness, the nest niches are often covered with moss and other hydrophytic plants, and due to their ready availability, swift nests are constructed almost exclusively of mosses, lichens and other fine plant material.