

*Hirundo
pyrrhonota*

FRENCH:
Hirondelle à front blanc
SPANISH:
Golondrina castaña,
Golondrina risquera

Cliff Swallow

Doubtless the Lord—to paraphrase Lincoln’s aphorism—must love the Cliff Swallows, else he would not have made so many of them.

William C. Dawson (1923)

The Cliff Swallow is one of the most social landbirds of North America. These birds typically nest in large colonies, and a single site may contain up to 3,500 active nests. Cliff Swallows originally were birds of the western mountains, where they still nest commonly underneath horizontal rock ledges on the sides of steep canyons in the foothills and lower elevations of the Sierra Nevada and Rocky and Cascade mountains. In the past 100 to 150 years, these birds have expanded their range across the Great Plains and into eastern North America, a range expansion coincident with the widespread construction of highway culverts, bridges, and buildings that provide abundant alternative nesting sites.

New colonies continue to appear each year in areas where Cliff Swallows were previously unrecorded as breeders.

The Cliff Swallow was one of the first North American birds to be described. Although its discovery in Colorado is usually

credited to Thomas Say on Stephen Long’s expedition to the Rocky Mountains in 1820 (James 1823), the bird and its colonial breeding habits were first mentioned by the Spaniard Silvestre Velez de Escalante in September 1776



Figure 1.
Distribution of the Cliff Swallow in North America.
See text for details on wintering range.

**The
Birds of
North
America**
Life Histories for
the 21st Century

when he encountered large numbers in the Wasatch Range of Utah (Coues 1899). Formerly placed in the genus *Petrochelidon*, the Cliff Swallow bears some ecological similarity to the more familiar and now congeneric Barn Swallow (*Hirundo rustica*). Both species build mud nests on vertical substrates, but Cliff Swallows are distinguished by their enclosed, gourd-shaped nests and much larger colonies. Their highly colonial life style has led to the evolution of some complex behavioral traits. For instance, Cliff Swallows brood-parasitize neighboring nests both by laying parasitic eggs and by moving eggs from their own nest into others; have a sophisticated vocal system for distinguishing their own young from the offspring of many other individuals within a colony; and observe each other's foraging success and learn from other colony residents the locations of food. The Cliff Swallow's social behavior during the breeding season has been studied extensively, and this species has figured prominently in our understanding of the evolution of coloniality in birds (Brown and Brown in press). However, we know little about its migration, and surprisingly, no one has studied this bird on its poorly known wintering range.

DISTINGUISHING CHARACTERISTICS

Separated in all plumages and ages from all other North American swallows except Cave Swallow (*H. fulva*) by square tail and orange rump. In all populations, exhibits a chestnut-colored throat, and most subspecies show a cream- or white-colored, triangular-shaped forehead patch, characters that separate the species from Cave Swallow. Head and neck are noticeably thicker than in other North American swallows. No sexual dimorphism; sexes can be reliably distinguished only by the presence or absence of a brood patch or cloacal protuberance, although males generally have a larger patch of dark blue at the base of throat. Juveniles (hatching-year birds) show extreme variability in color and degree of white speckling on throat and forehead; this individual variation is among the greatest seen in Juvenal plumage of any North American bird.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Extends from w. and central Alaska, n. Yukon, n. Mackenzie, central Keewatin, n. Manitoba, n. Ontario, s. Quebec (including Anticosti I.), New Brunswick, Prince

Edward I., and Nova Scotia south to s. Alaska, n. Baja California (Am. Ornithol. Union 1983, Godfrey 1986, Phillips 1986), the Pacific slope of Mexico south to Sinaloa and along the Mexican plateau south to central Oaxaca (Howell and Webb 1995), s. Texas, Arkansas (James and Neal 1986), Tennessee (Robinson 1990), w. Virginia (Kain 1987), se. Pennsylvania (Brauning 1992), w. Connecticut (Bevier 1994), and ne. Massachusetts (Veit and Petersen 1993). Northern limit of range imprecisely known; assumed not to go beyond treeline, but colonies have been found north of treeline in Alaska (Sage 1973). Rare and local breeder in Gulf states, e.-central and ne. U.S., and in parts of Ohio Valley, but increasing in most of these areas, especially Gulf states, the Carolinas, and Tennessee.

Winter range. Extends apparently from s. Brazil (São Paulo province) and possibly se. Paraguay south to s.-central Argentina. Distribution within this region is poorly known, although it appears that most birds winter in lowlands along the Rio Paraná and Rio Uruguay north and northwest of Buenos Aires (Buenos Aires, Entre Rios, and Corrientes provinces of Argentina, and w. Uruguay; Olrog 1967, P. Burke pers. comm., A. Jaramillo pers. comm.). Wintering birds have also been recorded west to Tucumán province, Argentina. South of Buenos Aires, birds occasionally occur in large numbers but are more irregular than farther north (A. Jaramillo pers. comm.). Recorded several times as far south as Tierra del Fuego and occasionally in the Falkland I. Rare in Chile and the high Andes. The subspecies *H. p. pyrrhonota* winters in ne. Argentina, *H. p. melanogaster* in nw. Argentina; the wintering ranges for *H. p. ganieri*, *H. p. tachina*, and *H. p. hypopolia* are unknown (Fjeldså and Krabbe 1990). Small numbers are reported to winter occasionally with flocks of Barn Swallows in the Pacific slope lowlands of Panama (Ridgely 1976). Casual in Barbados in winter (Bond 1971). Stragglers are reported in Dec in the Imperial Valley of California (Grinnell and Miller 1944), along the Lower Colorado River in Arizona (Phillips et al. 1964), and on the Pacific Coast (north to Vancouver) and Gulf Coast on Christmas Bird Counts. Report of Cliff Swallows being "common" in the Salton Sea region in winter (van Rossem 1911) is likely erroneous.

OUTSIDE THE AMERICAS

Accidental on Wrangel I., Siberia, and s. Greenland (Am. Ornithol. Union 1983). Two Oct records—both juveniles—for the British Isles (Crosby 1988, Little 1990).

HISTORICAL CHANGES

This species' breeding range has been influenced heavily during the last 100–150 yr by widespread construction of bridges, buildings, and culverts, which provide nesting sites in areas formerly uninhabited, and by the introduction of House Sparrows (*Passer domesticus*) which usurp nests. In the ne. U.S., where Cliff Swallows were probably never common, this swallow began to increase in the early to mid-1800s as land was cleared and more buildings constructed (Bent 1942). With the introduction of the House Sparrow in the late 1800s, and its usurpation of swallow nests, Cliff Swallow numbers began to decline in the ne. U.S. and remain low today (Forbush 1929, Silver 1993).

In the se. U.S., the breeding range has expanded south and east during the last 25–50 yr with new colonies found each year. A major eastward range expansion has occurred in Tennessee since the 1930s (Alsop 1981). Breeding began in Georgia in 1965 (Dopson and Peake 1967), Florida in 1975 (Sykes 1979), the Carolina piedmont in 1965 (McConnell 1981), and Louisiana in 1980 (Viers 1991). Breeders reached the Mississippi coast by 1986 (Spence and Toups 1986).

The breeding range has also expanded elsewhere east of the Great Plains but has been less thoroughly documented. Breeders have increased since the mid-1970s in the coastal plain of Maryland (Patterson 1981), since the early 1980s in W. Virginia (Igo 1986), and since the late 1980s in s. Illinois (Robinson 1989). The species is probably breeding in larger numbers in the eastern Great Plains (Nebraska, S. Dakota) than 25 yr ago. Only in the ne. U.S. does nest usurpation by House Sparrows appear to be limiting breeding-range expansion.

FOSSIL HISTORY

The only information is from excavations of caves where this species presumably bred, although distinguishing fossil Cliff from Cave Swallows may be problematic. Reported in Nuevo León, Mexico, during the late Pleistocene from 11,000 to 27,000 years before present (ybp; Steadman et al. 1994); in British Columbia 10,500 ybp (Driver and Hobson 1992); in Nevada 4,570 ybp (Nelson 1972); also reported from the late Pleistocene (Rancholabrean North American Land Mammal Age [NALMA], <400,000 ybp) of California (Miller and DeMay 1942), Virginia (Wetmore 1962, Guilday et al. 1977), and Tennessee (Guilday et al. 1978).

SYSTEMATICS

GEOGRAPHIC VARIATION

Species exhibits clinal variation in body size, with birds in the north (Alaska and w. Canada) larger than those in the south (s. Arizona and Mexico). Most of the variation is in wing and tail length, with little difference in bill size or tarsus length among populations (Behle 1976). Southern birds show darker forehead patches; extreme is *H. p. melanogaster* of s. Arizona and Mexico with a dark chestnut forehead patch and no white. Other subspecies (*H. p. ganieri*, *H. p. tachina*, *H. p. pyrrhonota*) show buffy to cream-colored forehead patches, with the most northerly (*H. p. hypopolia*) being the whitest. Rump patches and underparts tend to be lighter among birds to the north; more southerly birds often show tinges of rust or rufous on the flanks (Behle 1976).

SUBSPECIES; RELATED SPECIES

Nominate race *H. p. pyrrhonota* (Vieillot) is the most widespread, breeding in e. North America (exclusive of the range of *ganieri*) west to Rocky Mtns., Manitoba, and sw. British Columbia south through Washington, Oregon, and California west of the Cascade Mtns. and Sierra Nevadas to nw. Baja California. Forehead varies from white to pale brown but usually cream-colored (lighter than *tachina* but not as white as *hypopolia*); body size between *hypopolia* and *melanogaster*; rump and flanks darker than *hypopolia* but lighter than *tachina* and *melanogaster*. Recently, *H. p. ganieri* was recognized by Phillips (1986) and Browning (1990). Distinguished from *pyrrhonota* primarily by less chestnut washing on the underparts and darker chestnut undertail coverts, *ganieri* breeds west of the Appalachians from w.-central Tennessee west to central Texas and south to s. Texas.

Most northerly race, *H. p. hypopolia* Oberholser, breeds from central Alaska, Yukon, Mackenzie (NWT), Alberta, and Saskatchewan south through central and se. British Columbia, e. Washington, e. Oregon to e.-central California, central Nevada, n. Utah, Montana, and nw. Wyoming. This is the largest of the subspecies, with the whitest and largest forehead patch, lightest (least rusty) breast, grayest flanks, and palest rump. *H. p. aprophata* Oberholser is regarded as indistinct from *H. p. hypopolia* (Behle 1976). Despite some apparent differences between *pyrrhonota* and *hypopolia* (Behle 1976, Phillips 1986; see Table 1), there is little basis for recognizing *hypopolia* as distinct from nominate *pyrrhonota* (Browning 1992).

Table 1. Representative measurements (in mm) of four subspecies of Cliff Swallows. For geographic ranges of these subspecies, see Systematics. Data shown as mean (SD, range).

	<i>H. p. hypopolia</i> ¹	<i>H. p. melanogaster</i> ²	<i>H. p. pyrrhonota</i> ³	<i>H. p. tachina</i> ⁴
Bill length	7.4 (-, 6.1–8.1)	6.9 (-, 6.1–7.1)	5.78 (0.41, 5.05–6.70)	7.6 (-, 7.1–8.4)
Wing length	111.23 (2.74, 106.8–116.5)	103.10 (-, 100.1–108.0)	108.80 (2.7, 103.0–114.0)	104.32 (2.57, 100.5–110.2)
Tail length	48.68 (2.20, 44.2–52.0)	46.50 (-, 43.9–50.0)	48.75 (2.05, 44.45–52.65)	46.61 (1.68, 42.7–49.5)
Tarsus length	12.2 (-, 10.9–13.0)	11.9 (-, 10.9–13.0)	12.10 (1.0, 10.6–14.0)	12.7 (-, 11.9–13.2)

¹Bill and tarsus from Oberholser (1974), wing and tail from British Columbia population in Behle (1976).

²From Oberholser (1974; sample size not available).

³Unpublished (CRB, MBB) from Nebraska population. Oberholser's bill measurements for other subspecies probably taken in different (undetermined) way and may not be comparable to that for *H. p. pyrrhonota*.

⁴Bill and tarsus from Oberholser (1974), wing and tail from Utah population in Behle (1976).

H. p. tachina breeds from extreme sw. Utah south through the Lower Colorado River valley to extreme ne. Baja California, central Arizona, and central New Mexico to sw. Texas. It is similar to nominate race but smaller and forehead usually light cinnamon or fawn color. *H. p. melanogaster* breeds from extreme se. Arizona and sw. New Mexico south over the Mexican plateau to Oaxaca and the Pacific plains to Nayarit. It is similar in size to *H. p. tachina* but has a deep cinnamon-rufous or chestnut-colored forehead patch (same color as the sides of the head and throat) and a deep cinnamon-colored rump. The ranges of *tachina* and *melanogaster* overlap in parts of se. Arizona, and both were found in the same colony near Fairbank, AZ (Jeter 1959). *H. p. minima* van Rossem and Hachisuka is considered synonymous with *H. p. melanogaster* (Phillips et al. 1964, Behle 1976). Phillips (1986) uses *swainsoni* instead of more widely used *melanogaster*.

Cave Swallow is the North American swallow most closely related to Cliff Swallow. Formerly little breeding sympatry, but these species have come into contact in s. Texas as bridges and highway culverts have been constructed. Although there are no known cases of Cliff x Cave hybridization, an extralimital Cave Swallow paired and attended a nest with a Cliff Swallow in Tucson, AZ, in 1984 (Huels 1985); it is unknown whether the offspring produced were hybrids. There are 3 records of hybrid Cliff x Barn swallows: from Pennsylvania (Trotter 1878), sw. Texas (Mearns 1902), and e. Washington (P. Stoddard pers. comm.). There is 1 specimen of a hybrid Cliff x Tree (*Tachycineta bicolor*) swallow (Chapman 1902) from Massachusetts. Repeated

hybridization between Cave and Barn swallows in s. Texas (Martin 1980) was the basis for merging *Petrochelidon* into *Hirundo* (Am. Ornithol. Union 1983). However, *Petrochelidon*, a more phylogenetically derived genus than *Hirundo* (Sheldon and Winkler 1993), represents a distinct grouping of red-rumped, retort-nesting, colonial species distributed worldwide and should probably be retained for the 7 species of true cliff swallows (*pyrrhonota*, *fulva*, *preussi*, *rufigula*, *spilodera*, *fluvicola*, and *ariel*).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Migrates from breeding range to wintering range via Mexico, the Central American isthmus, and n. South America, staying east of the Andes. Apparent migrants are also recorded rarely in Bahama I., Cuba, and Virgin I. (Am. Ornithol. Union 1983). It is not known whether any intraseasonal movement occurs on the wintering range, although the species probably is nomadic at that time.

TIMING AND ROUTES OF MIGRATION

Most migrants presumably follow the Central American isthmus between North and South America. Migration in both directions seems leisurely and spans several months; there are fewer observations of spring than of fall migrants.

Spring migration. Birds begin leaving wintering range in early Feb, although some individuals are still present in Apr (Hudson 1920). Thousands were observed migrating through Panama on 24 Feb 1994, passing continuously for at least 1 h in

a narrow front about 0.4 km wide at a rate of about 150 birds/min (E. Morton pers. comm.). Some birds pass through Colombia and Panama as late as early May (Ridgely 1976, Hilty and Brown 1986). Migrants are seen in Sinaloa, Mexico, as early as 14 Feb and commonly in Oaxaca by mid-Mar, with migration in Mexico lasting until at least 30 May (Phillips 1986).

Birds first arrive in s. California in early Feb (rarely in late Jun; Small 1994), Arizona usually in early Mar (rarely as early as 9 Feb; Phillips 1986), Texas in early Mar (rarely 24 Feb; Oberholser 1974), Arkansas in early Apr (rarely late Mar; James and Neal 1986), Nebraska in mid-Apr (usually 16–18 Apr; CRB, MBB), Illinois in early Apr (rarely 29 Mar; Graber et al. 1972), Minnesota in late Apr (rarely 13 Apr; Roberts 1936), Idaho in early Apr (Burleigh 1972), Massachusetts in mid-Apr (rarely 9 Mar; Veit and Petersen 1993), and Alaska in mid-May (rarely 7 May; Gabrielson and Lincoln 1959). For other first arrival dates, see Bent 1942. Northerly populations generally arrive later than more southerly ones; however, *H. p. melanogaster* typically arrives on its se. Arizona breeding range 6–8 wk later than *H. p. tachina* and nominate *H. p. pyrrhonota* in n. Arizona (Phillips et al. 1964). The first birds to arrive in a breeding area usually do so in groups (Shaw 1991, CRB, MBB).

Fall migration. Begins when nestlings fledge and as colony sites are vacated, so departure can be staggered within a locale and quite variable between years. In sw. Nebraska, birds begin departing in early Jul in some years; most are gone by early Aug, although some late nesters may not leave until early Sep (CRB, MBB). Peak of migration in U.S. apparently is in Aug and early Sep when flocks of thousands may be seen moving south (e.g., Bent 1942). Migrants recorded in Mexico from 24 Jul (Veracruz) to 5 Nov (also Veracruz); in Costa Rica from 29 Jul to 30 Nov (Phillips 1986); in Panama from 29 Jul to late Oct (Ridgely 1976); in Colombia from early Sep to mid-Oct, with the largest number recorded on 13 Sep (Hilty and Brown 1986); in Venezuela from early Aug to Oct (Meyer de Schauensee and Phelps 1978); in Bolivia from early Oct to early Dec, with the bulk of birds 23 Nov to 5 Dec (Parker and Rowlett 1984); and in nw. Paraguay (Chaco region) 5 Dec (J. Unger pers. comm.). Some birds are in Argentina, presumably on wintering range, by Oct (Pereyra 1938) and continue to arrive through Dec. Migration dates divided by subspecies are given in Phillips 1986.

MIGRATORY BEHAVIOR

Little information. Usually seen in groups of

up to several hundred, occasionally several thousand, birds. Probably exclusively diurnal migrants, foraging as they move. Cool and rainy weather forces spring migrants in Nebraska to concentrate over lakes, ponds, and rivers where they may spend several days foraging low over the water surface. These concentrations can sometimes exceed 5,000 birds in a 1- to 2-km stretch of lake or river (CRB, MBB). Often seen in flocks with other swallows. Sleep in marsh vegetation during migration (Kirby 1978).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Historically inhabited open canyons, foothills, escarpments, and river valleys that offered a vertical cliff face with a horizontal overhang for nest attachment. With the present use of artificial nesting structures such as bridges and buildings, the species is now found in a wide variety of habitats: grasslands, towns, broken forest, riparian edge. Avoids heavy forest, desert, and alpine areas. Most colony sites are located near open fields or pastures where the birds forage, and a water source is often nearby. Proximity to mud source (for nest-building) is often cited as a breeding-habitat requirement (Emlen 1941, 1952), although some colonies are located several kilometers from the nearest mud supply (Coffey 1980, CRB, MBB). The species probably has more specific habitat requirements that are presently unknown, as Cliff Swallows are strangely absent from certain localities within their breeding range that would seem to offer appropriate nesting sites (Phillips et al. 1964, CRB, MBB).

Altitudinal range extends from Lower Sonoran through Transition zones, from sea level to about 2,770 m. Colonies rarely to 3,000 m; highest known to us is one of 50–100 nests at 3,200 m on Rendezvous Mtn., Teton Range, WY (CRB, MBB). There are no clear differences among subspecies in preferred breeding habitat.

SPRING AND FALL MIGRATION

Little information. Often seen in savannahs and near bodies of water, but probably migrates through (over) a wide variety of habitats. Commonly seen in coastal lowlands in Panama (Ridgely 1976). Probably migrates mostly at elevations below 1,000 m, but transients recorded to 3,800 m in South America (Meyer de Schauensee and Phelps 1978, Ridgely and Tudor 1989).

Migrants concentrate over water surfaces and marshes when poor weather reduces abundance of flying insects (see Migration: migratory behavior).

WINTER RANGE

Little information. Apparently occurs in grasslands, agricultural areas, near towns, and in marshes. A roost of up to 50,000 birds was found in wetlands along the Rio Paraná in Argentina, about 50 km north of Buenos Aires (P. Burke pers. comm.). Birds were sleeping in marsh vegetation, fanning out to forage over surrounding areas during the day, perhaps up to 20 km distant from roost site. Smaller roosts have been seen in marshes in Entre Rios province, Argentina (A. Jaramillo pers. comm.).

FOOD HABITS

FEEDING

Main foods taken. Flying insects at all times of the year. Occasional pieces of seeds are found in stomachs (Beal 1918), but these represent either accidental ingestion or use as grit. Birds sometimes pick up small bits of gravel, probably to aid digestion of insect exoskeletons. A report of 2 birds with stomachs full of juniper (*Juniperus*) berries (Beal 1918) was likely based on misidentifications of Tree Swallows.

Microhabitat for foraging. Feeds above the ground at altitudes of 50 m or more. Seems to prefer to feed over grassy pastures, plowed fields, and other open areas, but also feeds over floodplain forest, above canyons, and near towns. Forages over water (lakes, ponds, rivers) primarily when cool or rainy weather reduces insect availability and prevents formation of thermals that concentrate insects (Brown 1988, Brown and Brown in press). Birds in e. Washington have been seen walking on ground and picking ants off bare dirt (P. Stoddard pers. comm.).

Food capture and consumption. Exclusively a diurnal forager, usually feeding in groups on swarming insects. In Nebraska, foraging groups during the breeding season vary from 2 to >1,000 birds. Birds often rely on local enhancement to discover insect swarms, watching nearby foragers and converging on a spot where the prey-capture behavior of other birds indicates a food source (Brown 1988, Brown and Brown in press). While foraging, Nebraska birds use the Squeak Call (see Sounds: vocal array) to signal when a food patch has been discovered. This call attracts other foragers and may serve to ensure that the insect

swarm will be effectively tracked and that the discoverer can remain knowledgeable of its whereabouts (Brown et al. 1991). However, this call is used only in bad weather (poor foraging conditions) and relatively early in the season, and thus contexts promoting calling are not well understood. The Squeak Call is used exclusively by birds on foraging grounds and not at colonies (Brown et al. 1991).

Foraging groups often feed on the lee side of bluffs or road cuts where insects concentrate (Brown 1988). Birds cue on thermals that passively transport insects aloft and on insect mating swarms and other types of aggregations (Brown and Brown in press). Thermals and convection currents lead to a patchy distribution of insects, with the birds' prey abundantly but unpredictably concentrated in several spots near a colony. When the air temperature is not warm enough for convection, birds feed lower over grass tops or water surfaces and in a more dispersed fashion (smaller groups). In cold weather, birds in Nebraska forage a few centimeters above water and pick aquatic insects off the surface. Before nest-building starts, birds feed throughout the day in long bursts and may spend the entire afternoon away from colony sites. After egg-laying begins, birds feed in more frequent and shorter bursts and are not absent from the colony for prolonged periods at any time of day. After nestlings fledge, birds resort to longer foraging periods, like those early in season.

While parents are feeding nestlings, Cliff Swallow colonies serve as information centers (Brown 1986). When a bird unsuccessful at finding food returns to its nest, it may watch its close neighbors; after a neighbor returns with food, the unsuccessful bird may follow that neighbor to a current food source when the neighbor next leaves the colony. Information transfer is unintentional; birds simply observe each other, with no evidence of active signaling at the colony to alert others that food has been found. However, Stoddard (1988) reported a *tseer* call used in rare circumstances by birds at colonies in Washington; the call seemed to signal that food was available. There is no evidence that birds try to disguise their foraging success to prevent others from following them (Brown 1986, Brown and Brown in press). All birds alternate being followers and leaders, although how they discover insect swarms initially is unclear. Birds in small colonies (with few neighbors) do not wait at nests to monitor neighbors and instead spend that time searching for prey themselves. In huge colonies ($\geq 1,000$ nests), birds are less likely to monitor specific neighbors and often join large groups

which continually stream between the colony and food patches (Brown and Brown in press).

Foraging in groups and using others to find food results in higher mean food intake rates for Cliff Swallows in groups than for birds feeding solitarily. Variance in prey-encounter rates is lowest for birds foraging in large groups (Brown 1988, Brown and Brown in press). Consequently, birds nesting in larger colonies feed more efficiently and deliver more food to their offspring than do birds in small colonies. See Brown and Brown in press for a full discussion of how foraging efficiency is affected by colony size.

Nothing is known about feeding behavior in the wintering range, but the large numbers of birds typically seen together (Hudson 1920, P. Burke pers. comm.) suggest that social foraging continues in winter and during migration.

DIET

Major food items. Insects taken reflect local availability and may vary considerably among colonies located only a few kilometers apart (Brown and Brown in press). The only generalization possible is that the birds prefer swarming taxa; 10 of the 15 most common families taken in Nebraska were ones known to swarm or otherwise aggregate (Brown and Brown in press). A total of 84 insect families were represented in the diet of Nebraska birds, including homopterans, dipterans, hymenopterans, coleopterans, neuropterans, ephemeropterans, hemipterans, lepidopterans, orthopterans, and odonates. Grasshoppers are commonly taken during mid-to-late summer when hot temperatures apparently reduce populations or activity levels of other taxa (Brown and Brown in press). Insects not normally considered aerial are sometimes taken when they are transported aloft by thermals and convection currents.

Quantitative analysis. In Nebraska, the most common family taken was Cicadellidae, followed in order by Dolichopodidae, Simuliidae, Formicidae, Empididae, Chironomidae, Muscidae, Culicidae, and Argidae (Brown and Brown in press). In California (Beal 1907), families were not given, but the most common order was Hymenoptera (39% of total food), followed by Hemiptera (including Homoptera; 27%), Coleoptera (19%), and Diptera (12%). In a larger study of birds from unspecified parts of North America (Beal 1918), Hymenoptera again was the most frequent (28.7%), followed by Coleoptera (26.8%), Hemiptera-Homoptera (26.3%), and Diptera (13.9%).

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

Food-harvest rates of adults in California are estimated to be at least 3.40, 3.80, and 3.50 kcal/h during nest-building, incubation, and nestling periods, respectively (Withers 1977). Birds extend legs in flight to dissipate heat when ambient air temperature reaches 21–28°C (Butler 1982a) and gape and pant when hot.

DRINKING, PELLET-CASTING, AND DEFECATION

Birds drink exclusively on the wing by skimming water surface and lapping up water with lower mandible. Drinking is often done in groups, with many individuals suddenly starting and stopping simultaneously. Adults fly out from nest several meters to defecate.

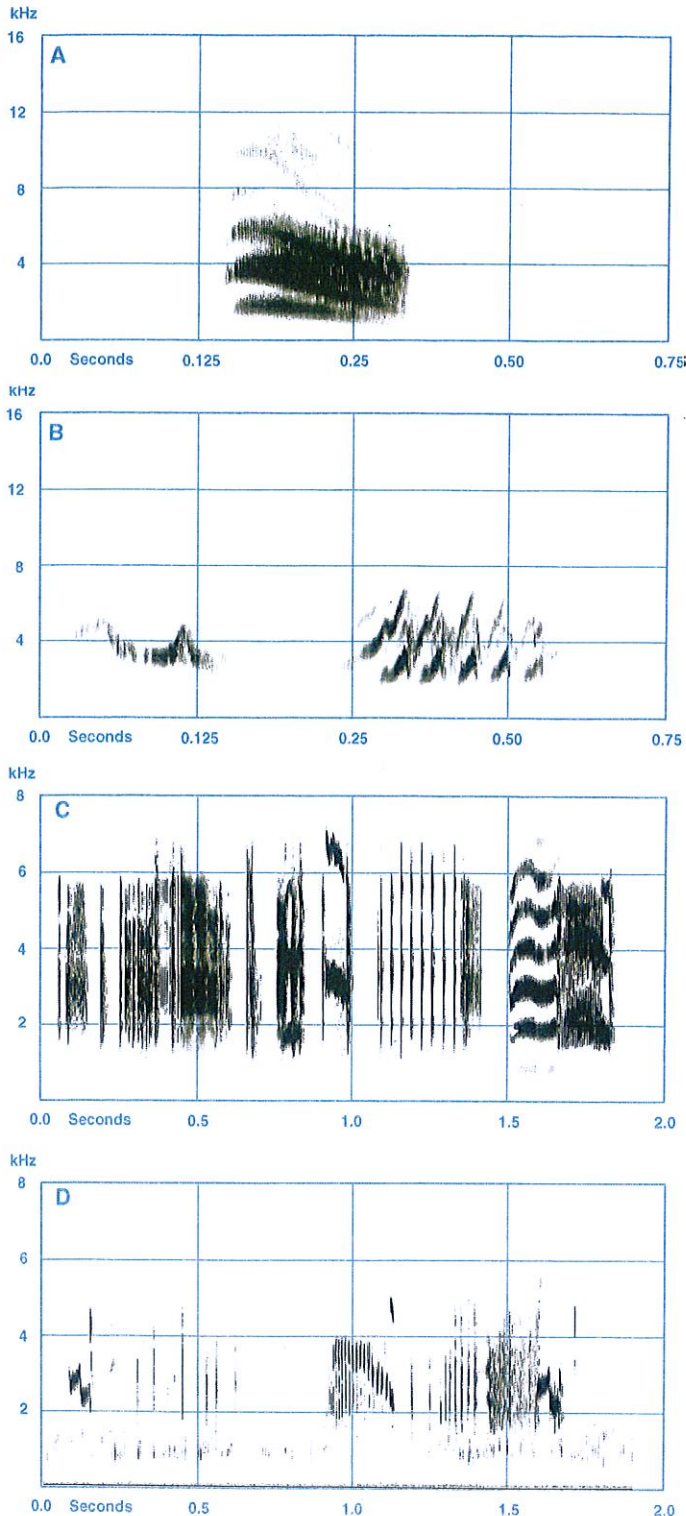
SOUNDS

VOCALIZATIONS

Development. Young begin vocalizing at least by 5–6 d of age. Call of each chick becomes uniquely recognizable by day 15 and is pure and consistent in structure by day 18–21 (Stoddard and Beecher 1983). Calls of siblings are structurally similar. Sib-sib similarity is genetically based, rather than reflecting vocal imitation among nest mates (Medvin et al. 1992). There is no evidence for vocal learning, sensitive periods, or vocal mimicry. The juvenile's Begging Call (see below) develops into the Chur Call of adult. Call resembling Purr Call (alarm) was given by juveniles that were about 6 wk old (CRB, MBB).

Vocal array. Limited vocal repertoire. Five vocalizations: Begging Call (Stoddard and Beecher 1983), used by juveniles when soliciting food from adults; Purr Call (see Fig. 2A), used as alarm call when predators approach; Chur Call (see Fig. 2B), commonly used in many contexts (Brown 1985); Twitter-squeak Song (see Fig. 2C), up to 6 s in typical duration, composed of many guttural gratings, and used primarily during courtship and nest establishment; and Squeak Call (see Fig. 2D), used as a food-finding signal (Brown et al. 1991; see Food Habits: feeding). Squeak Call is structurally similar to much longer Twitter-squeak Song and may be derived from song. Both sexes give Begging Call, Purr Call, Chur Call, and Squeak Call; presumably only males give the Twitter-squeak Song, but no study of singing with marked birds has been done. Apparently there is little geographic variation. Descriptions of vocalizations were similar for

Figure 2. Sonograms of Cliff Swallow vocalizations. A: Purr Call, recorded 7 June 1992, Pumas Co., CA (Borror Laboratory of Bioacoustics [BLB] #18734). B: Chur Call, recorded 15 June 1977, Ward Co., ND (BLB #14592). C: Twitter-squeak Song, recorded 3 July 1989, Lincoln Co., ME (BLB #17534). D: Squeak Call, recorded 15 June 1993, Matanuska, AK (BLB #18607).



birds from W. Virginia and Nebraska (Samuel 1971a, Brown 1985), although the rarely used *tseer* call of birds in the Pacific Northwest does not apparently occur in the Great Plains.

Phenology. Begging Call is used only until juveniles become independent of parents in midsummer, then changes to Chur Call. Purr and Chur calls are used at all times of the breeding season; birds seem rarely to vocalize in winter (A. Jaramillo pers. comm.). Twitter-squeak Song is used primarily in spring while birds are establishing pairs, declines in usage when parents are feeding nestlings, and then is used again during a brief period in late summer while postbreeding birds are defending nests and assessing colony sites (Brown and Brown in press). Songs presumably are not used on migration or during winter. Squeak Call is used from time of birds' arrival on breeding grounds until midsummer; it is unknown if this call is used at other times of the year (Brown et al. 1991).

Daily pattern of vocalizing. Time of day has little influence on pattern of vocalizing. Begging Call, Chur Call, and Twitter-squeak Song are given by birds at night (2200–0400 h; MDT) while inside their nests (CRB, MBB).

Places of vocalizing. Begging Call is given by juveniles inside nests and when assembled away from colony in creches. Purr Call is usually given in flight, although occasionally a bird in a nest uses Purr Call upon approach of a terrestrial predator. Chur Call is used at nests and in flight. Twitter-squeak Song is given by birds at nests and occasionally in flight as 1 or more birds (males?) chase another (female?). Squeak Call is given only in flight.

Repertoire and delivery of songs. No information for Twitter-squeak Song. Begging Call of juvenile is individually distinctive enough to represent a "signature" that parents use to identify their own chicks (Stoddard and Beecher 1983, Medvin et al. 1993). Chur Call of adult may also be distinctive enough to allow juveniles to recognize their own parent (Beecher et al. 1985).

Social context and presumed functions of vocalizations. Begging Call probably reflects food needs of chicks, as hungrier nestlings call more loudly and more readily when adults pass by. Primary function of Begging Call may be to allow parents to recognize their offspring. Parents learn their chicks' calls as they develop, so that parental recognition of offspring is well developed by the time nestlings fledge (Stoddard and Beecher 1983, Medvin et al. 1993). Parents in small colonies in Washington discriminate among chicks of similar age and evict intruding ones from their nest (P. Stoddard pers. comm.); eviction

of intruders has not been observed in Nebraska colonies which tend to be larger (Brown and Brown in press). Parents locate their own offspring in a creche (see Breeding: fledgling stage) by the juveniles' Begging Calls, although the parents' efficiency at discriminating their own chicks' voices from others declines in large groups (Medvin et al. 1993, Brown and Brown in press).

Purr Call is the Cliff Swallow's alarm call, used whenever an aerial or terrestrial predator approaches a colony. The call often seems directed at the predator, with birds typically swirling directly above a predator and emitting barrages of Purr Calls. Other colony members respond by exiting their nests. Purr Call is occasionally given when no apparent predator is present, causing some birds to flush from their nests, whereupon others in the colony use the opportunity to intrude into neighboring nests (Brown and Brown in press). Such circumstances might represent a deceptive use of alarm calling (Brown and Brown 1989). Chur Call is a multipurpose vocalization used widely, most often when birds are undisturbed, and may be used for individual recognition between members of a pair, parents and offspring (Beecher et al. 1985), and perhaps neighboring residents within a colony. Twitter-squeak Song may serve to attract a female to a male's partially or completely constructed nest and allow her to assess male quality. Squeak Call and *tseer* call (Brown et al. 1991, Stoddard 1988) are used by foragers to signal the location of a food patch (see Food Habits: feeding).

NONVOCAL SOUNDS

None known.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing. When on ground, walks exclusively. Goes to ground only to collect mud or grass, to attempt forced copulations, to pick up bits of gravel, to sunbathe, or occasionally to eat ants. Sidles along a wire, tree branch, or cliff face using a sideways walk, usually to fight with another Cliff Swallow for unknown reasons.

Flight. Flies at various heights, from just above ground to 60 m or more. Typical flight speed is estimated at 8.7 m/s (Withers 1977), although some birds commuting from mud holes to colony sites were clocked at 15.5 m/s (CRB, MBB). Changes altitude more frequently than other swallows (Blake 1948). Glides are short and frequent, usually from 2–3 s in length but sometimes up to 10 s. This is the only North

American swallow that customarily slants its wings downward when gliding (Blake 1948). Flapping rates range from 2.9 to 4.5 flaps/s, with a mean of 3.9. Faster flapping rates are employed for climbing and turning, averaging 4.6 flaps/s (Blake 1948). When turning, tail is overspread, showing a convex terminal margin. When pursuing insect prey, the birds make sudden turns to either side or upward, accelerate, and then flare the tail as the insect is caught, whereupon there is a return to close to the original altitude (Brown 1988).

Swimming and diving. Not known to swim or dive, but fighting birds sometimes fall out of nests over water (Brown and Brown in press); some become waterlogged and "swim" to shore by propelling themselves with backward strokes of wings.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Assembles in groups to preen, often on wires or a rock face near the colony site. Birds spend more time preening (and less time watching for predators) in larger flocks, and birds on the edge of a group preen less than those closer to the center (Brown and Brown 1987, in press). Preening occurs most often in mid- to late summer after the young fledge, when adults and independent juveniles gather in huge premigratory flocks. During the breeding season, preening occurs mostly in early to mid-morning and for an hour or so before sunset. Head-scratches over the wing. Stretches by extending 1 wing at a time below feet, then extends both in a "V" over back. This stretching sequence often immediately precedes taking flight. Yawns sometimes accompany stretches. Bathes by skimming water surface and "hitting" surface briefly in a violent collision, sometimes several times in succession. Bathing is communal, and many birds often simultaneously start and stop bathing. Anting is not known to occur. Did not respond when solicited by a Brown-headed Cowbird (*Molothrus ater*) in a preening-invitation display (CRB, MBB).

Sleeping, roosting, sunbathing. Sleeps in nest once ownership is established and nest becomes 50–75% complete. Before nest is large enough to sit in or before a colony site is selected, sleeps in trees. Early in the breeding season, one radio-tagged female returned to the same tree on 4 consecutive nights to sleep (Brown and Brown in press). Once the young fledge and become independent, some birds (including independent juveniles) continue sleeping in nests, but others start using trees. Presumably sleeps in trees and marshes (Kirby 1978, P. Burke pers. comm.)



during migration and in winter. Sunbathes by rolling over to one side, ruffling feathers, drooping wings, fanning tail upward, opening bill, and pointing 1 eye toward the sun (Barlow et al. 1963). Sunbathing often occurs in preening flocks, especially among birds gathered on cliff faces or bare ground exposed to hot afternoon sunlight.

Daily time budget. During nest construction, birds in California spent 9.5 h each day foraging, 3.0 h building nest, and 11.5 h in nest (including sleeping; Withers 1977). During incubation, 6.8 h foraging, 0.4 h refurbishing nest, and 16.8 h in nest. During nestling period, 7.5 h foraging, 0.2 h refurbishing nest, and 16.3 h in nest. Time spent nest-building and foraging varies with colony size in Nebraska (Brown and Brown in press). Generally, birds upon arrival in spring spend much of day foraging, gradually spending more time at the colony site each day as the season advances. After the young fledge, birds begin gradually to spend more time foraging away from the colony site each day until migrating.

AGONISTIC BEHAVIOR

Physical interactions. Birds fight for nest sites by grappling and falling out of a partially built nest or off the substrate wall. Physical contact is common among birds fighting for nests. In fights, they peck with their beaks and strike with their wings, and they often pull out feathers. Some birds fight repeatedly with each other for 15 min or more. When fighting birds separate after falling out of a nest, one often chases the other for several meters. Birds have been known to fall into water below nests while fighting and drown (Brown and Brown in press). Once nests are built, owners defend the nest by sitting in the tubular entrance and lunging at intruders. Intruders usually retreat without a fight, but sometimes an

Figure 3.

Portion of Cliff Swallow colony, illustrating typical nest placement and different stages of nest construction. Photo by the authors.

intruder forces its way into a nest, leading to a fight in the nest. The owner ousts the intruder from the nest by using its bill to hold the intruder's back and shove it out the entrance. Later in summer, conspecific intruders enter unattended nests with young and peck nestlings on the head, visibly wounding and occasionally killing them for unknown reasons (CRB, MBB). In preening flocks on wires, a bird often approaches another from the back and tries to knock it off the wire for unknown reasons; others sidle toward the bird next to it and try to peck it and force it to fly. In early spring, several birds sometimes chase another in flight; this may be a form of courtship, as this behavior is often accompanied by Twitter-squeak Songs. When attempting extra-pair copulations at mud holes, males sometimes seem to mistake other males for females, and a copulation attempt turns into a fight in the mud (Brown and Brown in press).

Communicative interactions. No threat or appeasement displays are known. When defending the nest, both sexes often slightly raise feathers of head and neck, making them look larger ("puffed up"). White forehead patch, which shows easily in darkness of nest entrance, probably serves as a signal to potential intruders that a nest owner is home, as birds constantly face out of entrance when present at nest.

SPACING

Territoriality. The only defended area is the nest or (early in breeding season) a region on vertical wall where a nest is to be built. Space defended is interior of nest and that area within a bird's reach when sitting in partial nest or clinging to substrate. Once a nest is complete, outside of nest is not defended; other birds may sit atop a nest while an owner is inside peering out. Nest owners attack other birds that try to build a nest within 8–12 cm directly below a nest's entrance; this usually prevents later-nesting birds from blocking the entrance of existing nests (Brown and Brown in press), leading to a honeycombed pattern of nest placement in most colonies (Fig. 3).

Individual distance. Cliff Swallows are extremely social at all times, seeking out other individuals whenever away from their nests. Preening birds on wires are often spaced as closely as 10 cm (Emlen 1952), and sometimes to 3–4 cm or with shoulders touching (CRB, MBB; see Social and Interspecific Behavior, below).

SEXUAL BEHAVIOR

Mating system and sex ratio. Socially monogamous; only 1 male and 1 female tend a

nest; neither sex is known to establish ownership of >1 nest. Genetically polygamous, as both sexes routinely mate with multiple members of the other sex (see below). Sex ratio in Nebraska is male-biased at about 1.32 males:1 female (Brown and Brown in press).

Pair bond. Pair bond is more accurately a form of "mutual tolerance" of the other sex at the nest (Emlen 1954); sexes do not associate together away from the nest. Male sings to female while nest ownership is being decided, but there is little formal courtship, and singing declines once egg-laying and incubation begin. There is no mate-guarding (Brown and Brown in press).

Copulation between nest owners occurs within nest after nest has been built to at least a shallow cup (Emlen 1954). Some copulations are preceded by the male leaving his mate at the nest entrance, retiring to the back of nest, and uttering a soft Chur Call. Female follows male to the back of nest and crouches, whereupon he mounts her. Copulating birds often tumble out of the nest if it is still incomplete (Emlen 1954), but in a complete nest, copulation ends with both birds returning to the nest entrance. The male often repeats copulatory invitations by going to the back of nest several times in succession; female may ignore him and remain at the entrance. The male also frequently attacks his mate just after her return from a mud hole and copulates in a forced way. This may reflect sperm competition; a male's probable defense against extra-pair copulations experienced by his mate at mud holes is frequent intrapair copulation (Brown and Brown in press). Copulation begins 4–6 d before the first egg is laid and continues frequently until the afternoon preceding the laying of the last egg (Emlen 1954). The pair bond dissolves after the young fledge, and any re-pairing in a subsequent year is merely coincidental when both birds return to the same part of a colony (Mayhew 1958, Brown and Brown in press). Mutual tolerance by 2 birds at the same nest in late summer during postbreeding colony visitation may reflect former nest owners reuniting briefly, but no studies of marked birds have been done to confirm this.

Extra-pair copulations. Common at mud holes where birds collect mud for nest-building (Emlen 1952, Butler 1982b, Brown and Brown in press). Also occurs when birds go to the ground to gather grass for nest lining. Both males resident at a colony and nonresident males engage in extra-pair copulations (EPCs; Brown and Brown in press). Females sometimes resist, other times accept EPCs. The number of EPCs/female increases with the size of the mud-gathering group and in larger colonies (Brown and Brown

in press). When gathering mud, both sexes flutter wings above back to prevent being attacked by males seeking EPCs (Butler 1982b, Brown and Brown in press; see Agonistic Behavior). Other EPCs occur at the colony when a male intrudes into a neighboring nest and forcibly copulates with the female nest-owner. The success of EPCs in leading to fertilizations is unknown, but allozyme exclusion analyses (Brown and Brown 1988a) suggest that collectively up to 43% of nests in Nebraska contain 1 or more nestlings not related to either father (EPC) or mother or both (intraspecific brood parasitism; see Breeding: brood parasitism).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. The Cliff Swallow shows the highest degree of coloniality of any swallow in the world. Colonies often number 200–400 nests and routinely range up to 1,000 nests, with a maximum of 3,700 in Nebraska (Brown and Brown in press). Solitary nesting does occur, however, sometimes only a few kilometers from the largest colonies. Colonies are smallest in e. North America, especially in areas where the species has been breeding only a short time, and in parts of the sw. U.S. There is great diversity in colony size within a population, although the basis for colony size variation is still poorly understood (Brown and Brown in press). In Nebraska, colonies on bridges and highway culverts average larger than those on cliffs, but in the Rocky Mtns. and other parts of w. North America, substrate type probably has no effect on colony size. Some colony sites are used perennially, others more erratically. Often 1 yr (and occasionally up to 5 yr) may elapse between use of a given site in California (Grinnell et al. 1930), Texas (Sikes and Arnold 1984), Oklahoma (Loye and Carroll 1991), Arizona (S. Speich pers. comm.), and Nebraska, but the reason(s) for alternate-year usage patterns are not clear. Coloniality probably evolved initially to facilitate efficient social foraging during the breeding season, and birds may have subsequently clustered their nests in high densities to exploit secondary benefits of group living (see Brown and Brown in press for details). Species remains in large groups during nonbreeding season; flocks of thousands are often seen together in Argentine wintering range (Hudson 1920, P. Burke pers. comm.). Birds may be nomadic during winter, traveling over large areas in search of insect emergences (A. Jaramillo pers. comm.).

Play. In Nebraska appears to occur when groups of adults (and, later in summer, independent juveniles) all try to crowd onto the same

space of ≤ 1 m along a wire. Birds on a wire pack themselves together tightly (bodies touching) and try to maintain their position as dozens of others hover behind them and try to knock them off and usurp their places. Incumbents often hang off a wire upside down in an attempt to keep their places. Sometimes 75–100 birds engage in these jousting events; that there is always ample perching space and that birds cease this activity after 10–15 min and resume normal spacing on nearby parts of wire suggest that it is a form of play (CRB, MBB).

Nonpredatory interspecific interactions. Usurps inactive and active Barn Swallow nests, expelling owners. Domes over Barn Swallow nest, turning it into a typically shaped Cliff Swallow nest. Usurped a Say's Phoebe (*Sayornis saya*) nest that had been constructed in an old Cliff Swallow nest fragment; invading swallows killed the nestling phoebes and threw them out of the nest (Brown and Brown in press). Sometimes nests in Bank Swallow (*Riparia riparia*) colonies (Carpenter 1918, Monroe and Mengel 1942, Emlen 1954, CRB, MBB), although it is unknown if active Bank Swallow burrows are usurped. Probably comes into frequent contact with Cave Swallows in mixed-species culvert colonies in s.-central Texas (Thayer 1915, Martin 1980), but behavioral interactions between Cliff and Cave swallows have not been studied.

Cliff Swallow nests have been used for breeding by Say's Phoebes, Chestnut-backed Chickadees (*Parus rufescens*), Plain Titmice (*P. inornatus*), House Wrens (*Troglodytes aedon*), Eastern Bluebirds (*Sialia sialis*), House Sparrows, and House Finches (*Carpodacus mexicanus*) (Mayhew 1958, CRB, MBB); all but the phoebe may usurp active nests (see Predation, below, for discussion of House Sparrows). White-throated Swifts (*Aeronautes saxatalis*) occasionally nest and forage among Cliff Swallows (Mayhew 1958). A House Sparrow repeatedly fed nestling Cliff Swallows in an Alberta colony (Hofman 1980). Cliff Swallows routinely flock with other swallow species during migration, but there is no evidence of any cooperative or commensal foraging with these species. In mixed-species perching flocks, Cliff Swallows attack Bank and Barn swallows and drive them off wires. In Nebraska, both Eastern (*Tyrannus tyrannus*) and Western (*T. verticalis*) kingbirds often chase Cliff Swallows for no apparent reason, sometimes driving a swallow to the ground (CRB, MBB). Bats roost in abandoned Cliff Swallow nests, and during the winter Canyon Wrens (*Catherpes mexicanus*) and Rosy Finches (*Leucosticte arctoa*) use Cliff Swallows nests as dormitories (Sooter et al. 1954).

PREDATION

Kinds of predators. Primarily birds and snakes. In Nebraska, Sharp-shinned Hawks (*Accipiter striatus*), American Kestrels (*Falco sparverius*), Barn Owls (*Tyto alba*), Great Horned Owls (*Bubo virginianus*), Black-billed Magpies (*Pica pica*), Loggerhead Shrikes (*Lanius ludovicianus*), Common Grackles (*Quiscalus quiscula*), and bull snakes (*Pituophis catenifer*) attack colonies (Brown and Brown in press). In other areas, predators include American Kestrels, Acorn Woodpeckers (*Melanerpes formicivorus*), Loggerhead Shrikes, and unspecified ants in California (Bent 1942, Wilkinson and English-Loeb 1982, Fajer et al. 1987); Peregrine (*F. peregrinus*) and Prairie (*F. mexicanus*) falcons and Mississippi Kites (*Ictinia mississippiensis*) in Oklahoma (Byard et al. 1979, C. Hopla and J. Loye pers. comm.); Red-headed Woodpeckers (*Melanerpes erythrocephalus*) in Ohio (Jones 1883); bull snakes in Washington (Thompson and Turner 1980) and Oklahoma (C. Hopla pers. comm.); rat snakes (*Elaphe obsoleta*) in Oklahoma (Oliver 1970), Texas (W. Pulich pers. comm.), and Tennessee (Bullard 1963); coachwhip snakes (*Masticophis flagellum*) in Oklahoma (C. Hopla pers. comm.); rattlesnakes (*Crotalus* sp.) in Montana (Bent 1942); minks (*Mustela vison*) in Washington (P. Stoddard pers. comm.); and fire ants (*Solenopsis invicta*) in Texas (Sikes and Arnold 1986). Domestic cats prey on mud-gathering birds in Massachusetts (M. Silver pers. comm.). House Sparrows and deer mice (*Peromyscus maniculatus*) usurp nests and in the process destroy large numbers of eggs and nestlings; mice in Nebraska eat eggs and chew on nestlings' feathers (CRB, MBB). No information on predators during migration and on wintering range.

Manner of predation. Sharp-shinned Hawks attack colonies at dusk by catching adults in flight as they come into roost. American Kestrels and other falcons hunt adults and fledged juveniles primarily by diving from above colonies and striking birds flying below them. Occasionally American Kestrels fly up to nest and try to pull nestlings out of the entrance hole. Owls fly through colonies at dusk and presumably try to catch birds sitting on the outside of nests. Magpies perch on top of cliff or bridge containing nests and fly out toward incoming adults, trying to collide with them, and also scavenge birds of all ages found on the ground. Loggerhead Shrikes fly into large colonies and try to collide with incoming or outgoing birds. Grackles attack mud-gathering and grass-gathering adults by walking toward them and pouncing on a bird from the side or above. Grackles also cling to nest exteriors and try to pull nestlings out, attack birds perching

on wires, chase down and catch recently fledged juveniles near colonies, and scavenge nestlings that fall out of nests. In Nebraska certain grackles learn to specialize on Cliff Swallows; one grackle killed 70 birds (mostly yearlings) over a 12-d period, often eating only the brains (Brown and Brown in press). Woodpeckers alight at nest entrances and pull eggs and nestlings out; Red-headed Woodpeckers have been seen to drill holes in the mud nest to reach inside (Jones 1883). Avian predators recruit to larger Cliff Swallow colonies, and per-capita risk of predation increases for birds breeding in large colonies (Brown and Brown in press).

Snakes climb to nests and can reach colonies located on cliffs, buildings, concrete culverts, and metal bridges. Bull snakes may spend up to 3 d in a colony, coiling inside a nest, out of sight, and grabbing nest owner when it enters nest. One bull snake in Nebraska consumed about 150 eggs in a single colony over a 3-d period (Brown and Brown in press). Snakes, probably the most important predators, are also attracted to larger colonies. Stacking of nests close together in large colonies enhances snakes' access and may represent a cost of coloniality (Brown and Brown in press). Fire ants crawl up substrate to reach nests and feed on eggs and nestlings (Sikes and Arnold 1986).

House Sparrows destroy eggs in attempts to usurp nests; a single House Sparrow may clean out 12–15 adjacent nests before selecting one as its own. Cliff Swallows seem completely intimidated by House Sparrows and do not attempt nest defense against them. In W. Virginia, 48% of Cliff Swallow nests were lost to House Sparrows in 1 yr (Samuel 1969a), and in Nebraska House Sparrows destroyed contents of all nests in a 100-nest colony (Brown and Brown in press). Deer mice scale vertical walls on which colonies are located and chew through walls of adjacent nests. In addition to destroying eggs and small nestlings, mice chew on wing and tail feathers of older nestlings, often impairing flight when these birds fledge (CRB, MBB). An unknown predator (fish or turtle) captured a bathing Cliff Swallow by grabbing it and pulling it below the water surface (Brown and Brown in press). Snapping turtles (*Chelydra serpentina*) scavenge doomed nestlings that fall out of nests.

Response to predators. Typical response to most predators consists of colony residents milling above predator and alarm-calling (Purr Call) heavily. When a falcon or hawk approaches, colony residents exit colony, fly in a very coordinated, tight flock to altitude of predator, then spread out above predator in loose group

and follow it as it moves, alarm-calling continuously. This seems to signal to the predator that it has been detected (Brown and Brown in press). Birds mill above predators that approach from ground level (snakes, woodpeckers, grackles) and give barrages of alarm calls. They typically do not dive at predators (Brown and Hoogland 1986). Less pronounced responses are given to predators such as shrikes, grackles, and snakes, with some colony residents not exiting colony during alarm. Alarm calls are not given to House Sparrows.

The distance at which an approaching predator is detected increases with colony size, and thus large colonies may confer a benefit by enabling mates and nearly fledged juveniles to escape predation more often (Brown and Brown 1987, in press). Vigilance is enhanced in preening flocks away from colonies, in creches, and in mud-gathering groups; an important advantage of flocking in both breeding and nonbreeding seasons is that per-capita time spent in vigilance can be reduced (Brown and Brown 1987, in press). Birds on edges of preening flocks (closest to a predator's approach) are more vigilant than birds closer to center.

BREEDING

PHENOLOGY

Pair formation. Occurs as soon as birds begin visiting colony sites and coincides with establishment of nest ownership or beginning of nest-building. For representative arrival dates, see Migration: timing and routes of migration, and Figure 4. First birds to arrive in Nebraska spend first 2–3 wk mostly foraging and probably do not begin pair formation immediately, but later arriving birds visit colonies and start forming pairs immediately upon arrival (CRB, MBB).

Nest-building. Shortly follows pair formation; some males begin nest-building before securing a mate. Delay between arrival and commencement of nest-building in Nebraska is several weeks for first arrivals; earliest arrival date recorded is 18 Apr, and earliest date nest-building has been observed is 3 May (CRB, MBB). In same area, birds arriving in mid- to late May may begin nest-building only a few days after arrival.

First/only brood per season. Single-brooded throughout range, although replacement clutches are produced if nest fails in early part of breeding season. Egg-laying recorded as early as 1 Apr in Texas, 5 Apr in California, 3 May in Nebraska, 7 May in Idaho, 20 May in Illinois, 21 May in Massachusetts, 31 May in Pennsylvania, and 3

Jun in se. Arizona (Bent 1942, Mayhew 1958, Burleigh 1972, Graber et al. 1972, Oberholser 1974, M. Silver pers. comm., CRB, MBB). Most clutches are initiated after these dates. Egg-laying probably occurs mostly in Jun at higher elevations of Rocky Mtns. and Sierra Nevada, and in Jul in se. Arizona (*H. p. melanogaster*) where breeding is synchronized with onset of summer monsoon (S. Speich pers. comm., CRB). Peak of egg-laying is 20 May–5 Jun in Nebraska, with little yearly variation in timing of peak; latest clutch initiation date known is 28 Jul (CRB, MBB). Young have fledged in most populations by end of Jul, slightly later in montane areas and se. Arizona.

Second brood per season. Reports (Sharpe and Wyatt 1885–1894, Bent 1942) of second broods being routine are likely erroneous and probably are based on birds renesting after nest failure (Mayhew 1958, CRB, MBB). Bona fide double broods occur rarely in Nebraska; in documented cases, egg-laying of second clutch began on about 25 Jun with young fledging in early Aug (CRB, MBB). There are no confirmed cases of double-broodedness from other parts of range; reports of double broods from W. Virginia and Virginia (Samuel 1971b, Grant and Quay 1977) are unsubstantiated and apparently did not involve marked birds.

NEST SITE

Selection process. Birds choose colony site first, then establish ownership of existing nest or space on substrate to build nest (Brown and Brown in press). Nebraska birds range over 23 km along the North Platte River valley while assessing colony sites early in year, and they visit several sites before selecting one. Colony selection probably is based on colony size (number of other birds present). After making provisional colony choice, birds continue to visit other colonies for 1–3 d, probably to gain information on alternative sites in case nest fails at chosen site (Brown and Brown in press). Females spend more time than males assessing colony sites before settling. Nest site within colony often is not chosen until 3–5 d after colony site is selected; one female did not choose nest site until 12 d after settling in colony (Brown and Brown in press). Unmated males often take over existing nest or begin nest construction and later attract female. Cues for nest-site selection within colony are not fully known. Early in season, birds hover in front of old nests, often not entering. They probably assess ectoparasites clustered at nest entrance and avoid old nests still infested from the previous summer (Brown and Brown 1986, in press). When constructing new nests, birds first cling to substrate

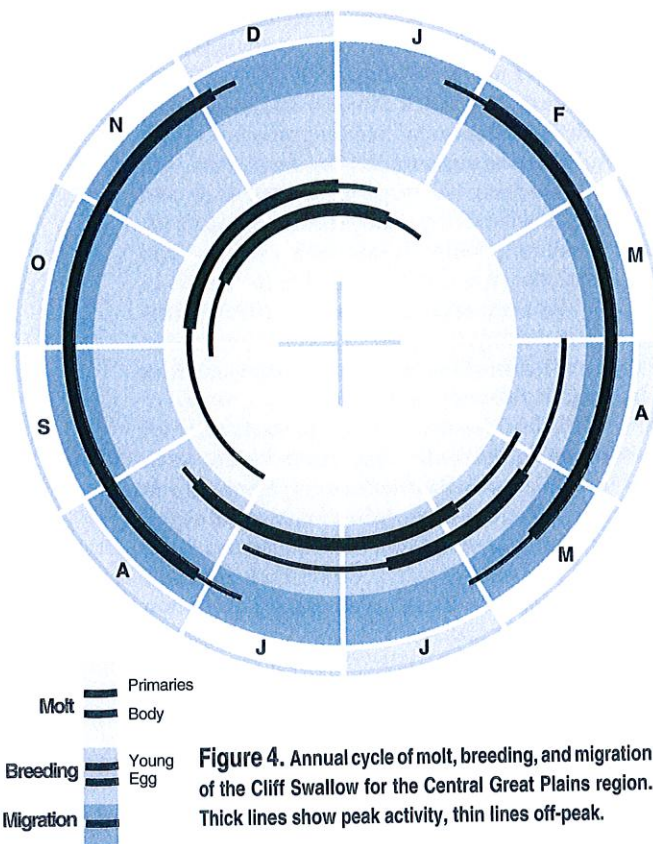


Figure 4. Annual cycle of molt, breeding, and migration of the Cliff Swallow for the Central Great Plains region. Thick lines show peak activity, thin lines off-peak.

in several places, gradually confining their activity to 1 spot where nest is to be built (Emlen 1954, CRB, MBB).

Microhabitat. Nest is placed at a 90° juncture of vertical wall and horizontal overhang. On cliff sites, distribution of overhangs usually dictates where nests can be placed and accounts for irregular distribution of nests within colony. Successive arrivals often build nests directly below first tier of nests, offsetting nests slightly in honeycombed pattern. Up to 8 horizontal tiers of nests may be built in larger colonies, and occasionally nests may be stacked in deeper layers on cliff sites (CRB, MBB). Substrate texture seems to affect nest attachment in ways not fully understood. Birds in Nebraska tend to avoid wooden bridges and strongly prefer concrete ones where mud attaches better (CRB, MBB). Where wooden barns are used, birds are said to prefer unpainted ones of rougher texture (Townsend 1917, Forbush 1929). The absence of colonies from some cliffs may reflect substrate composition; birds apparently avoid nesting on unstable sandstone which crumbles frequently.

Site characteristics. Nests are placed on vertical cliff faces, entrances to caves, under branches of large tree limbs (rarely), under eaves

of buildings, under bridges, in highway culverts, and under overhangs on dams. Cliff sites vary substantially in height; nests may be placed from 1.5 m to ≥ 10 m above ground or water surface. There is no apparent preference for direction of nest exposure on any type of nesting site, although west-facing nests receive more direct afternoon sunlight and may be much warmer than nests facing in other directions. Surfaces of west-facing cliffs in Oklahoma can be as much as 17°C warmer than the ambient temperature in summer (C. Hopla pers. comm.). Cliff sites are always open and free of vegetation, allowing birds an unobstructed flight path to and from nests. Caves used are primarily of the limestone sinkhole type favored by Cave Swallows; nests are placed near ceiling just inside entrance. Cave sites are not commonly used; reported mostly in Bosque and Hill counties, central Texas (Pulich 1988, CRB), but there are fossil records from caves throughout the species' range (see Distribution: fossil history).

Birds use buildings of all types, including sheds and barns, residences, and office buildings. It is unclear in most cases why birds choose a particular building for nesting, often perennially, while they never use apparently identical structures nearby. Nests are placed on bridges of all types, including ones over busily traveled roads. In Nebraska, birds seem to prefer bridges (and perhaps cliffs) over water; on a new bridge, the first nests are usually built on the sections over water (CRB, MBB), but sites over land are used, sometimes commonly. Highway culverts used are box-shaped ones with a 90° angle between wall and ceiling; those with a slanted juncture between wall and ceiling are used less often, presumably because nest attachment is more difficult. Culverts must be open and free of vegetation on each end. Cliff Swallows prefer taller culverts than those used by Barn Swallows; the shortest culvert used by Cliff Swallows in Nebraska had a ceiling 1.5 m above ground; most were taller (CRB, MBB). Often uses culverts with multiple tunnels, and birds frequently alternate in using different tunnels each year; they seem to prefer tunnels over water. On dams, they place nests under overhang or parapet on either side. Occasionally build nests under large limbs of trees in California (photo in Dawson 1923); circumstances leading to this type of nesting are not known. Occasionally appropriate Bank Swallow burrows, natural crevices in cliff, or holes in human-made structures; build mud front with characteristic entrance tunnel across face of opening (Dawson 1923, Emlen 1954, CRB, MBB). Cliff Swallows take over Barn Swallow nests in mixed colonies (see Behavior: social and

interspecific behavior).

The primary geographic difference in site usage is a stronger preference for buildings in California, the Pacific Northwest, and parts of the ne. U.S. Buildings are not commonly used in the Midwest or Southeast. In Nebraska from 1982–1994, only 8.1% of 172 colony sites were on buildings; 34.9% were on bridges, 34.3% in culverts, and 22.6% on cliffs (CRB, MBB). There is no evidence that colony sites are limited in supply or that nest sites are limited within colonies; coloniality thus is not likely a result of breeding-site shortages (Brown and Brown in press).

NEST

Construction process. Both sexes build the nest, although the male may initiate construction before he attracts a mate. Birds gather mud in their bills along the bank of a stream, lake, or temporary puddle (e.g., ruts in road), usually at a site within 0.5 km of the colony but sometimes several kilometers distant. Birds in larger Nebraska colonies travel farther to get mud than do birds in smaller colonies (Brown and Brown in press). Birds bring mud pellet back to colony and mold it into nest with a shaking motion of bill. A newly built nest begins as a narrow mud ledge affixed to wall, positioned between 10 and 12 cm below the overhang or lowest tier of existing nests (see Fig. 3). Birds add to the ledge until it is a crescent shape projecting 2–6 cm outward. They then extend lateral and ventral walls upward to form a broad half-cup projecting 5–10 cm outward (Emlen 1954). They eventually extend walls to connect with the overhang or base of nest above, extend the floor rim forward, and narrow the opening. A roof is added by doming over the sides, creating a complete retort projecting 15–20 cm outward with an entrance tunnel pointing downward by a turning down of the ventral lip (Emlen 1954). The birds continue to lengthen the walls of the entrance tunnel as the season progresses; in some nests the entrance becomes a long tube. Birds steal wet mud from unattended neighboring nests (Brown and Brown in press). They refurbish nests throughout the season, and if the entrance or roof cracks or falls off, they quickly repair the damage even if they are feeding young. They are less likely to patch holes in the floor or lower sides, and eggs and nestlings sometimes fall through holes in the bottom of the nest when mud crumbles (CRB, MBB). Birds add dry grass stems to nest as lining, beginning when nest is about 75% complete. There is substantial variation among nests in the amount of grass added. Grass is collected from a creek bank, haystack, pasture, or similar area near the colony,

and neighbors steal grass from each other when nests are left unattended (Brown and Brown in press). In California, the total energetic cost of nest-building was estimated at 122 kJ, with a total of about 24 h invested in actual construction (Withers 1977).

Birds gather mud in large synchronized groups. Those in larger groups collect mud more efficiently (spend less time looking around) because of vigilance advantages (Brown and Brown 1987, in press). Early in season, birds gather mud in intermittent bursts, mostly in morning, periodically ceasing and leaving to forage. As the season advances, mud collection becomes more continual and gradually expands to early and mid-afternoon. Nest-building is described in detail by Emlen (1954).

The time it takes to build a nest varies, principally in response to weather. Cool, rainy, or very windy weather prevents mud collection. Mud pellets are added at a rate of 0.2–2.0/min, depending on the distance of the mud source from the colony (Emlen 1954). A pair can bring as many as 44 mud pellets in a 30-min period, adding more than 1.5 cm to the nest rim during that time. If birds build too quickly, hunks of wet mud fall off before drying, which happens often (CRB, MBB). Completely new nests took about 7 d to build in Wyoming (Emlen 1954), between 3 and 27 d (mean 10.0) in Nebraska (CRB, MBB), and between 8 and 18 d in Quebec (Gauthier and Thomas 1993a). Time taken to build nest (and energetic cost) is influenced by how many walls are shared with adjacent nests (Gauthier and Thomas 1993a, Brown and Brown in press). Birds prefer nests that share walls with neighbors. Nests with no abutting neighbors require more energetic expenditure to construct and weigh more, but they probably adhere to the substrate better and thus are structurally safer than nests attached to others within a cluster (Gauthier and Thomas 1993a). With more abutting nests in larger colonies, the average time taken to construct a nest decreases with colony size (Brown and Brown in press).

Structure and composition matter. Birds apparently assess mud composition. In Montana, nests were composed of 61.4% sand particles, 25.7% silt particles, and 12.7% clay (Kilgore and Knudsen 1977). There is little organic material in mud; grass is not mixed into mud, unlike in Barn Swallow nests. In Quebec, Cliff Swallows were presented with mud of differing adhesive properties (densities of clay and silt particles); birds chose the mud that adhered best (Robidoux and Cyr 1989). Dry grass stems used for lining typically are 5–15 cm long. Feathers are not used

but may sometimes remain in an old nest formerly occupied by House Sparrows or Barn Swallows.

Dimensions. Average nest contains 900–1,200 individual mud pellets (Emlen 1954). Sample of 15 nests from Wyoming measured (all means) 19.6 cm in overall length and 16 cm in basal width. Entrance 4.3 cm in height and 5 cm wide. Height of nest at the back (outside) 10–11.4 cm. Thickness of floor and side walls varied from 0.6 cm in depressions between pellets to 1.7 cm at the center of large pellets (mean 1.1 cm). Walls were slightly thinner toward the roof and entrance. Two average-sized nests weighed 578 and 816 g when dry (Emlen 1954). Entrances of 2 adjacent nests can be as close as 5 cm; 77.5% of nests in Nebraska ($n = 4,853$) were <20 cm apart, entrance to entrance (CRB, MBB).

Microclimate. Nest retains heat and is warmer than outside temperature at night and in early morning. In one California nest, the air and nest temperature were both 23°C at 2130 h; 3.5 h later, the air temperature was 18.5°C and the nest was still 23°C (Mayhew 1958). Also in California, temperature gradient between the inside and outside of nest ranged up to 7°C warmer inside; even interiors of unoccupied nests were up to 4°C warmer than the ambient temperature during the day (Withers 1977). The interior of nests on west-facing cliffs in Oklahoma can exceed 62°C on summer afternoons (C. Hopla pers. comm.). Humidity is generally greater inside than outside nest. Carbon dioxide concentrations inside nests are greater than for many species because of enclosed nest; highest concentration (0.32%) is during nestling period, but it is not high enough to stress birds or affect hatchability of eggs (Withers 1977). Nests offer greatest advantage in preventing radiative heat loss at night, and protect well against wind chill and rain.

Maintenance or reuse of nests, alternate nests. Cliff Swallows commonly reuse old nests from previous years. They repair nests if necessary; sometimes occupy partial nests which are later built into complete nests. Birds avoid old nests that are infested with ectoparasites or filled with House Sparrow or deer mouse nesting material. Birds are more likely to reuse old nests in small colonies than in large colonies, perhaps because there are fewer ectoparasites in small colonies from the previous year (Brown and Brown 1986, in press; see Demography and Populations: disease and body parasites). Upon arrival at breeding colonies, birds fight for existing suitable nests from previous year (see Behavior: agonistic behavior). Fighting is more intense for nests in the center of the colony than nearer the edges, probably because predators are more likely to

attack edge nests. Fighting is more intense for incomplete nests, probably because complete nests are easier to defend and the odds of take-over are lower (Brown and Brown in press). In Nebraska, overall reproductive success for birds in new versus old nests did not differ (Brown and Brown in press).

Nonbreeding nests. None known.

EGGS

Shape. Ovate to elliptical-ovate or rarely to elongate-ovate (Bent 1942).

Size. From Western Foundation of Vertebrate Zoology (means and extremes based on clutch averages). *H. p. pyrrhonota*, $n = 20$ clutches (81 eggs): length 20.42 mm (18.12–21.61), breadth 14.25 mm (13.71–15.10), empty shell weight 0.130 g (0.107–0.154). *H. p. hypopolia*, $n = 20$ clutches (83 eggs): length 20.58 mm (19.19–21.68), breadth 14.24 mm (13.28–14.98), empty shell weight 0.125 g (0.106–0.143). *H. p. tachina*, $n = 20$ clutches (93 eggs): length 20.37 mm (18.32–23.67), breadth 14.00 mm (13.14–14.58), empty shell weight 0.125 g (0.105–0.132). *H. p. melanogaster*, $n = 10$ clutches (40 eggs): length 20.05 mm (18.89–21.33), breadth 13.80 mm (13.28–14.54), empty shell weight 0.109 g (0.093–0.124).

Mass. Mean 1.97 g (range = 1.4–2.4 g), $n = 15$ clutches (52 eggs; Stoner 1945). About 8% of female weight.

Color. Ground color white, creamy white, or pinkish white. Speckling of various shades of light and dark browns ("brownish drab") or small blotches in the paler shades of "Quaker drab" (Bent 1942). Variability in amount of marking; some eggs are finely marked with small spots, others thickly marked with densely concentrated blotches, often around larger end. Although within-clutch variability in spot patterns is less than between-clutch variability, eggs are probably not individually distinctive enough to enable birds to discriminate safely their own eggs from those of intraspecific brood parasites (Brown and Sherman 1989).

Surface texture. No information.

Eggshell thickness. No pre- and post-DDT comparisons available. Empty shell weight (see above) is presented for future reference.

Clutch size. For first clutches, mean (\pm SD, n) 3.31 (\pm 0.30, 35) in W. Virginia (Samuel 1971b), 3.32 (\pm 0.72, 60) in Virginia (Grant and Quay 1977), and approximately 4.0 ($n = 73$) in British Columbia (calculated from Myres 1957), 3.74 ($n = 71$) in New Brunswick (Erskine and Teeple 1970). Replacement clutches in W. Virginia 2.89 (\pm 0.15, 9) and in Virginia 3.00 (\pm 0.85, 12). Overall mean for all clutches in Nebraska, 1982–1991, 3.48



Figure 5. A Cliff Swallow about to transfer an egg to a neighboring nest—a behavior rarely seen in any other species. Physical transfer of eggs represents a form of intraspecific brood parasitism. Drawing by Julie Zickefoose.

(\pm 0.95, 8,094); clutch size declines by about 1.0 egg across laying season (Brown and Brown in press). Range in clutch size typically is 1–6 eggs. Clutches of >6 eggs probably represent cases of intraspecific brood parasitism (Brown and Brown 1989), and clutches of 1 may reflect undetected egg destruction by neighbors (see below).

Egg-laying. Often begins before nest is finished, occasionally in nests only half completed. Nonparasitic laying occurs in early morning before 0800 h (Brown 1984). One egg is laid/24 h. When ≥ 2 eggs appear/d, it represents intraspecific brood parasitism; 1- to 2-d gaps in laying probably mean that the nest owner laid parasitic egg elsewhere those days (Brown 1984, Brown and Brown 1989; see Brood Parasitism). Pairs guard nest continually during laying period, male and female trading places so that 1 owner is nearly always at nest. There is no mate-guarding away from nest. Nest owners continue attempts to intrude into other nests within colony and will destroy single eggs in unattended neighboring nests (Fig. 5; Brown and Brown 1988b). They usually throw out only 1 egg at a time and seldom destroy neighbor's entire clutch. Egg destruction is not related to attempts to usurp nests but may be a prelude to later brood parasitism of a neighbor's nest via physical egg transfer (see Brood Parasitism). The Cliff Swallow may be a partially indeterminate layer, because the addition of parasitic eggs to the clutch during the first 1–2 d of laying seems to cause early cessation of laying; a normal-sized clutch is produced if eggs are added midway or at the end of the

laying period (Brown 1984, Brown and Brown 1989).

Laying within a colony is highly synchronous (Emlen 1952, Myres 1957, Brown and Brown 1987, in press). In Nebraska colonies, typically a few birds lay eggs first, followed very closely by large numbers of colony residents, tapering off more gradually after the peak (Brown and Brown in press). Approximately 75% of clutches in small colonies are initiated during periods of 6 d or less, versus 20–21 d in larger colonies. Synchronized laying may reflect each individual in colony laying as early as it possibly can to minimize effects of ectoparasites, which increase during the summer. There is no evidence that synchrony is an antipredator benefit or direct response to resource availability (Brown and Brown in press), except perhaps in se. Arizona where *H. p. melanogaster* times breeding to coincide with the start of summer rains (see Breeding: Phenology).

Replacement clutches are produced if nests fail during the first part of the breeding season (CRB, MBB). In Nebraska, birds whose nests fail usually switch to another nest and often to another colony for their second breeding attempt. Waves of late nesters that sometimes join the larger colonies or start new colonies may represent individuals whose nests failed elsewhere (Brown and Brown in press).

For a full discussion of intraspecific egg dumping, see Brood Parasitism, below.

INCUBATION

Onset of broodiness and incubation in relation to laying. Intermittent incubation begins after 2–3 eggs are laid and becomes continuous the day before the last egg is laid (Mayhew 1958, Samuel 1971b).

Incubation patch. Single medial abdominal patch in females. Some males exhibit thinly feathered to bare spots on lower belly that, though not true incubation patches, may help to warm eggs.

Incubation period. Varies considerably within and between populations. In W. Virginia, 15 d for 7 nests (Samuel 1971b); in Virginia, 13.5 d (range 11–16 d, $n = 20$; Grant and Quay 1977); and in Nebraska, 13.6 d (range usually 10–19 d, $n = 3,371$; CRB, MBB). Variation may reflect in part microclimate of different nesting structures and insulative properties of different mud compositions. Incubation periods of ≤ 11 d probably represent physical transfer into nests of eggs incubated elsewhere (Brown and Brown 1988; see Brood Parasitism).

Parental behavior. Both sexes incubate about equally (Samuel 1971b, CRB, MBB). Incubating bird retreats to the back of nest and sits on eggs;

does not look out entrance when on eggs. Alarm calls cause incubating birds to get off eggs and peer out entrance. There is little ceremony or display when one sex relieves the other; departing bird may give Chur Call. When not incubating, other sex usually is away from colony, presumably foraging.

Hardiness of eggs against temperature stress; effect of egg neglect. Eggs can tolerate relatively cold weather and interruptions in incubation. Snaps of cold weather in Nebraska during late spring reduce flying insect abundance, occasionally forcing birds to spend all day foraging and leading to long periods (several hours) of egg neglect. There is no evidence that this affects hatchability (CRB, MBB). In one 4-d spell of unusually cold weather that caused some adult mortality, all nestlings died, but eggs that had not hatched to that point were unaffected (Brown and Brown in press). Insulative property of enclosed nest (Withers 1977) allows moderate egg and chick neglect without serious consequence (see Mayhew 1958).

HATCHING

Preliminary events and vocalizations. No information.

Shell-breaking and emergence. Hatching occurs at all times of day and during night (CRB, MBB). No information on time taken to hatch. All eggs within clutch typically hatch within a 24-h period. Occasionally a single egg, probably one added to the nest by an intraspecific brood parasite after incubation began, hatches 3–4 d after the rest of clutch.

Parental assistance and disposal of eggshells. Parents are not known to assist. Parents pick up eggshells and drop them out of nest entrance; shells accumulate on ground below nests. Parents do not fly away with eggshells and have not been seen eating eggshells.

YOUNG BIRDS

Condition at hatching. Young are naked, bright reddish pink, and weigh 1.6–2.2 g (Stoner 1945). They begin to gape for food immediately upon hatching. Mean tarsal length is 3.0 mm, mean ulnar length 5.1 mm, mean humeral length 4.5 mm, mean body temperature 35.3°C (range 31.1–37.8°C) (Stoner 1945).

Growth and development. Mass increase is most rapid between 4 and 10 d of age; average increase during this time is 2.36 g/d (Stoner 1945). At 10 d, Nebraska birds averaged 22.1 g (SD ± 3.0 , $n = 1,035$ broods; CRB, MBB). Maximum weight is attained on about day 12, then gradually diminishes until time of fledging. New York birds

averaged 21.5 g at time of fledging (Stoner 1945). Tarsus grows fastest during first 6 d and reaches maximum length on day 12–13 (11.0 mm in New York birds). Rate of increase in length of ulna and humerus is greatest during first 10 d, averaging about 1.76 mm/d for ulna and 1.03 mm/d for humerus, but both continue to grow at a slower rate throughout nestling period (Stoner 1945).

Beginning of outer primary is evident by day 4 and averages 0.13 mm on day 5. Outer primary increases to an average of 9.08 mm at day 10; 37.29 mm at day 15; 51.07 mm at day 18; 60.63 mm at day 20; 73.06 mm at day 23; and 78.16 mm at day 26 (Stoner 1945). Vane of outer primary breaks sheath on about day 9; average length of vane beyond sheath is 2.71 mm at day 10; 18.47 mm at day 15; 30.60 mm at day 17; and 45.13 mm at day 20. Inner primary grows at about the same rate as outer until about day 15. Between 15 and 20 d, average growth rate of inner primary is 2.6 mm/d, versus 4.26 mm/d for outer primary (Stoner 1945). Upper coverts of outer and inner primaries appear externally on about day 8. Between 8 and 28 d, inner primary covert increases at an average of 1.60 mm/d, versus 1.02 mm/d for outer covert (Stoner 1945). Tail feathers appear on day 2–3. Average length of outer tail feather is 1.05 mm at day 7; 7.57 mm at day 10; 21.20 mm at day 15; 36.30 mm at day 20; and 45.66 mm at day 26. Average length of middle tail feather is 6.14 mm at day 10; 20.97 mm at day 15; 35.27 mm at day 20; and 44.16 mm at day 26 (Stoner 1945). Juvenal plumage is attained by time of fledging. Body temperature is 39.1°C at day 5; 41.2°C at day 10; 42.1°C at day 20; and 43.0°C for adults (Stoner 1945).

Young sit facing entrance by day 6–7 and routinely stick heads out of entrance by day 12. They gape and give Begging Call (see Sounds: vocal array) whenever parents arrive or other birds pass near. Gaping birds sometimes grasp bills of nest mates in apparent competition over food (CRB, MBB). Young begin to preen by day 9, especially when ectoparasites are numerous. Fear response begins to appear by day 10 and is well developed by day 12–13, with young ceasing calling and going toward the back of nest when adults alarm-call. Young exercise by stretching and flapping wings before fledging.

PARENTAL CARE

Brooding. Begins at hatching. Largely continuous for first 2–3 d of nestling life, then gradually begins to diminish until ceasing completely by about day 11–12. Both sexes brood.

Feeding. Begins at hatching and continues until 3–5 (occasionally more) d after fledging. Both

sexes feed about equally. Parent compresses multiple insects into tight bolus before giving to young. Bolus is placed directly into nestlings' mouths with quick jab of adult's bill; large single insects (e.g., grasshoppers) are not easily compressed into a bolus and sometimes escape during transfer. After fledging, parents feed young in flight, by flying together for direct transfer between bills or by parent dropping insect and young catching it (CRB, MBB). Prior to about day 6–7, young are fed small, soft-bodied insects (often dipterans and homopterans); after that time food is same as adults' (see Food Habits: diet). Feeding rate varies widely among broods of similar age (e.g., from mean of 3.4 to 18.4 food deliveries by both parents/h), affected by brood size, colony size, and local food availability (Brown and Brown in press). Feeding rate increases to about day 10, remains stable until about day 17, then declines slightly until fledging. Feeding rates in Nebraska seem to peak in colonies with about 100 nests, perhaps reflecting a lack of social foraging opportunities in smaller colonies and competition for food in larger colonies (Brown and Brown in press). Amount of food delivered to young parallels mass gain. Amount delivered/foraging trip increases with colony size; for young 10- to 17-d old, average bolus mass ranged from 0.27 g in a 10-nest colony to 0.88 g in a 2,000-nest colony (Brown and Brown in press). Parents usually feed 1 nestling/visit and so far as known do not apportion food among brood.

Nest sanitation. Young back up to nest entrance and defecate through opening, beginning at about 7–8 d of age. Parents remove feces before that time, usually dropping them out of entrance. Young sometimes lose their balance while defecating and fall out of nest. Piles of feces accumulate below nest; nestlings can be entombed by their own excrement when feces pile up on top of lower nest and block parents' access (Stoddard 1983, Brown and Brown in press).

Parental carrying of young. Birds occasionally transfer young between nests by carrying them in bill (CRB, MBB). This may represent a form of intraspecific brood parasitism. It apparently occurs at low frequency, but behavior has not been studied.

COOPERATIVE BREEDING

Does not occur. Reports of 3 birds tending a single nest (Bent 1942) are likely erroneous.

BROOD PARASITISM

Identity of the parasitic species. Rare interspecific parasitism by House Sparrows and

House Finches. In New York a House Sparrow egg was laid in a Cliff Swallow nest, the egg hatched, and the young House Sparrow was raised by the parental swallows; the swallows' own young hatched several days after the House Sparrow and did not survive (Stoner 1939). House Sparrow eggs are occasionally found in Cliff Swallow nests in Nebraska, but the eggs are not known to hatch (CRB, MBB). They may represent cases of House Sparrows losing their own nest during laying. A Cliff Swallow nest in California was found with 3 swallow and 2 House Finch eggs; swallow owners incubated eggs, but apparently nest failed (Shepardson 1915). Report of Brown-headed Cowbird parasitism (Bent 1942) is likely erroneous.

Major form of brood parasitism is intraspecific. In Nebraska, residents within a colony frequently lay eggs in, or physically transfer (with bill) eggs laid in their own nest to, neighboring nests (Brown 1984, Brown and Brown 1988c, 1989). The parasites own nests and raise broods themselves, but they supplement their reproduction by parasitizing others. There are no known cases of nonresidents parasitizing nests within a colony.

Frequency of occurrence, seasonal or geographic variation. In Nebraska up to 22% and perhaps as many as 43% of nests contain at least 1 parasitic egg laid by a conspecific; parasitism increases with colony size (Brown and Brown 1989). Intraspecific parasitism is most common among nests initiated early in the season and during the peak of nesting, and declines in late nests. Parasitism is usually directed at nests located 1–5 nests from the parasite's own nest (Brown and Brown 1989). In Sierra Nevada of California, the incidence of intraspecific parasitism is unexplainably much lower—only about 3.7% of nests (Smyth et al. 1993).

Timing of laying in relation to host's laying. Intraspecific parasitism via laying usually occurs 1–4 d before host begins laying or during first 1–2 d of host's laying period (Brown and Brown 1989). Parasitism via physical transfer may occur at any time during host's laying or incubation period; parasites that transfer eggs are usually closely synchronized with host, enabling transferred eggs to hatch with host's even when transfer occurs well into incubation (Brown and Brown 1988c). The typical placement of parasitic eggs into host nests that are at appropriate temporal stages enhances survival of parasitic young (see below). Parasites lay eggs in other nests before, while, and after laying eggs in their own nest (Brown and Brown 1989).

Response to parasitic mother, eggs, or nestlings. Birds defend nest vigorously against

all other Cliff Swallows. There are no increased responses to known intraspecific parasites; parasitism occurs only when a nest happens to be left unattended momentarily (Brown and Brown 1989). Any egg added to a nest ≤ 4 d before owner begins laying is accepted; there is no ability to discriminate or reject parasitic eggs. There are no differences in the way host cares for parasitic young and own young. Host parents presumably learn Begging Call of parasitic young in same way they learn their own young's calls (see Sounds: vocal array).

Effects of parasitism on host. Intraspecific parasitism is deleterious to the host in causing reduction in host egg output when a parasitic egg is added early in the laying period (Brown 1984, Brown and Brown 1989). Parasites occasionally destroy 1 of the host's eggs at the time of laying the parasitic egg. Nests with eggs destroyed by conspecifics (Brown and Brown 1988b; see Breeding: eggs) are more than 3 times more likely than other nests to have a parasitic egg added later by physical transfer, suggesting that parasites or their mates "prepare" a nest for parasitism by removing one of the host's eggs in advance. There is no evidence that the parasitic young outcompete the host's young or that the presence of parasitic young otherwise affects the host's reproductive success.

Success of parasites. Intraspecific parasites assess nests within a colony and preferentially parasitize nests that are more likely to fledge young (Brown and Brown 1991). This is done in part by the parasites predicting patterns of ectoparasite infestation among nests early in the season and selecting those nests that will later be relatively uninfested. In Nebraska, 73.8% of parasitized nests later fledged ≥ 1 young, compared to 76.6% of nests in general. Counting young raised in their own nest plus those raised parasitically, parasitic individuals have greater annual reproductive success than hosts or birds not known to be either parasites or hosts (Brown and Brown 1989). However, parasites themselves are frequently parasitized because they more often leave their nests unattended in search of host nests; without genetic analyses of parentage, it may be impossible to know the actual reproductive success of parasites or other classes of birds. Intraspecific parasitism increases in Nebraska colonies where reproduction is less certain, suggesting that another benefit of parasitism is to spread eggs among nests and reduce the likelihood of total reproductive failure in risky environments (Brown and Brown 1989, in press).

FLEDGLING STAGE

Departure from the nest. Young are reported to fledge at day 20–21 in New York (Stoner 1945), day 23 in California (Mayhew 1958), day 23.6 (mean) in W. Virginia (Samuel 1971b), and day 22 in Virginia (Grant and Quay 1977). Birds in Nebraska usually fledge at day 23–26, although they are capable of labored flight by about day 20 (CRB, MBB). Juveniles often remain in nests for several days after becoming able to fly or may return to the nest after a brief initial flight, making it difficult to determine the exact time of fledging. Birds are likely to fledge at younger ages when their nest is heavily infested with ectoparasites (CRB, MBB). At time of fledging, young generally fly well and can sustain flight for relatively long periods (5–10 min) without perching. Fledging appears to occur at all times of day, usually when a parent has just departed from the nest after delivering food or is flying nearby. Parents and young call frequently during and after fledging. Parents often lead young back to the nest on the day of fledging. Young follows closely behind parent, who guides it to the correct nest. Young bird sometimes misses nest and flies away, whereupon parent escorts it back again, or juvenile enters a nearby nest (see Immature Stage).

Association with parents or other young. Young are dependent on parents for food for 3–5 d after fledging and may be fed occasionally for several days after that. Parents often lead young back to nest to sleep each evening while young are still dependent, and they may also escort young back to nest for brief periods during the day if a thunderstorm develops or for other unknown reasons (CRB, MBB). Fewer parents lead young back to the nest if the colony is infested with ectoparasites; parents and young sleep in trees if not in nest. Presumably parents gradually stop feeding young and the family breaks apart, but there is no information on how young learn to catch insects for themselves.

Soon after fledging, young gather with chicks of similar age in large groups, or creches. Creches assemble on wires, in trees, and on sides of cliffs. Nebraska creches may comprise up to 1,000 birds. Parents do not sit with young for very long but usually forage nearby. Parents find their own chicks within a creche and feed them there. Speed at locating one's own chick declines as creche size increases, representing a cost of creching (Brown and Brown in press). Parents locate young by their Begging Calls and perhaps use distinctive forehead and throat markings (Stoddard and Beecher 1983; see Appearance: molts and plumages). Juveniles may respond more loudly when their own parent approaches based on

recognition of parent's Chur Call (Beecher et al. 1985), but chicks beg from all passing adults. It is unknown how often parents make mistakes and feed unrelated chicks, but it probably occurs relatively often in larger creches (Brown and Brown in press). Juveniles seem to stay in creche primarily while dependent on parents, but independent juveniles join creches for brief periods. Juveniles often preen while waiting for parents to arrive.

Juveniles travel up to 2–3 km from their natal colony to a creche site as soon as they fledge (CRB, MBB). Birds from different colonies may mix in the same creche, with membership changing daily as more young fledge and others become independent and leave. Birds often creche at the same physical location throughout a season or until all young from the local colonies have fledged. Creching probably confers antipredator benefits through improved vigilance (Brown and Brown in press). When a predator approaches, it is quickly detected by one of the adults foraging nearby. Alarm calls flush all creche members, which remain airborne until the predator departs, then creche members return to perching sites.

Some juveniles still dependent on parents kleptoparasitize food brought to smaller young in nests at colony (see Immature Stage).

Ability to get around, feed, and care for self. A juvenile's ability to fly improves each day after fledging. Undertakes more flights from creche, and flights last longer with each passing day. Juvenile's flight pattern, speed, endurance, and maneuverability are indistinguishable from adult's by the time a juvenile is 6 wk old (CRB, MBB). For time to independence, see above.

IMMATURE STAGE

Once independent, juveniles spend much time foraging, usually in flocks. They often travel in small squads of 10–20 birds, comprised mostly of other juveniles of similar age (CRB, MBB). Independent juveniles commonly return to colonies and enter active nests containing smaller chicks and steal (kleptoparasitize) food brought by parents of the smaller young (Brown and Brown in press). In Nebraska, kleptoparasites are rarely evicted from nests and are readily fed by adults (CRB, MBB), although parents in smaller colonies in Washington apparently more often recognize the intruders and evict them (P. Stoddard pers. comm.). Kleptoparasites enter nests containing chicks as young as 7 d; parents tolerate kleptoparasites presumably in part because they have not yet learned their own chicks' signature calls. The incidence of kleptoparasitism increases with colony size and among later nests; independent juveniles recruit to larger

colonies where the chances of finding a nest to kleptoparasitize are greater (Brown and Brown in press). Kleptoparasites are found in nonnatal nests between 1 and 14 d after fledging, indicating that some are still not capable of finding food themselves, but most are >3 d postfledging and thus independent of parents (Brown and Brown in press). Some kleptoparasites move up to 60 km from their natal site during the first 3 d after fledging (Brown and Brown in press). Kleptoparasitism has been studied only among Nebraska birds but apparently also occurs in California (Robertson 1926). It is unknown how much total food kleptoparasites receive in nests or how costly the loss of food may be to younger chicks.

Independent juveniles also travel among colonies in late summer and inspect nests, as do adults at the same time of year (Brown and Brown in press). Juveniles enter empty nests—ones both active and inactive earlier that year—and may briefly defend nests against other birds. Occasionally they gather mud but do not seem to know what to do with it once collected; they have not been seen to put it on nests (CRB, MBB). Some juveniles cling to outsides of nests or perch on substrate and appear to be assessing nest or colony sites. They usually travel in large groups (which include many adults) when assessing sites. Colony visitation typically occurs mostly in morning and again in evening. Some independent juveniles sleep in nests (often a different nest or colony each night) for 1–2 wk before leaving area. Juveniles probably are familiar with most colony sites near their natal site and may use this information when selecting breeding locations the next summer (Brown and Brown in press). When not visiting colonies, juveniles spend their time either foraging or preening and sunbathing in large groups.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Both first-year males and females typically breed. There is no evidence of age bias among nonbreeders or among surplus males (see Behavior: sexual behavior) (CRB, MBB).

Clutch. In Nebraska, clutch size is slightly lower for first-year females: mean 3.3 eggs versus 3.7 for 2- and 3-year-olds (Brown and Brown in press). There is no information on age-related patterns from other parts of range (see also Breeding: eggs).

Annual and lifetime reproductive success. Both measures vary extensively within a population, affected especially by colony size, date of nest initiation, age of parent, spatial position in colony,

and extent of ectoparasitism (Brown and Brown in press). Overall mean number of young fledged/nest: 2.24 in Texas (Hamilton and Martin 1985), 1.96 in Nebraska (CRB, MBB), 0.92 in Colorado (Stuart 1973), 2.38 in Virginia (Grant and Quay 1977), and 1.56 in Quebec (Gauthier and Thomas 1993b). These figures represent approximate annual reproductive success, since only 1 brood is usually reared/season (see Breeding: phenology). Mean lifetime reproductive success for breeders, obtained by multiplying average number of young fledged/nest/year times average breeding life span, was estimated to vary between 3.0 and 7.0 young/breeder depending on colony size, although these estimates are preliminary and do not account for instances in which some young are unrelated to parent(s) through extra-pair fertilizations and/or intraspecific brood parasitism (Brown and Brown in press). In Nebraska, the highest number of young fledged from a single nest under natural conditions ($n = 2,420$) was 6; when ectoparasites were removed by nest fumigation ($n = 5,509$), the highest number was 7 (CRB, MBB).

Proportion of total females that rear at least one brood to nest-leaving or independence. No information, because the fraction of the population that does not breed in a given year is unknown.

LIFE SPAN AND SURVIVORSHIP

Maximum recorded life span is 11 yr (2 birds) from Nebraska (CRB, MBB). Probability of annual survival, based on mark-recapture (methods of Lebreton et al. 1992), is estimated at 0.17 during first year and averages 0.57 for all older age classes, although first-year survivorship is likely an underestimate owing to undetected permanent emigration (Brown and Brown in press). There are no differences in survivorship between males and females. Yearly variation in adult survivorship is 0.47 to 0.64; highest survival is associated with warm summers. Survival probability of adults increases with size of breeding colony occupied (Brown and Brown in press). First-year survivorship peaks at intermediate-sized colonies of 100–249 nests and declines as extent of natal ectoparasitism increases and for birds fledging later in summer. For details see Brown and Brown (in press). Estimates of survival probabilities from California and Texas (Mayhew 1958, Sikes and Arnold 1984) were not based on appropriate statistical methodology and hence are unreliable.

DISEASE AND BODY PARASITES

Diseases. Little information. Wild birds are infected with Fort Morgan virus (Togaviridae,

Alphavirus) of equine encephalitis-related complex (Hayes et al. 1977, Scott et al. 1984). In Colorado colonies, about 7% of nestlings were viremic, but encephalitic infection appeared to have no effect on fledging success. A related virus occurs among birds in Oklahoma (Hopla et al. 1993); its effects are unknown. Captive Cliff Swallows have been known to be infected with avian pox virus (*Avipoxvirus*; Shaw 1992).

Body parasites. Include cimicid bugs, ticks, fleas, dipterans, dermestid beetles, lice, mites, nematodes, cestodes, trematodes, acanthocephalans, and protozoans. The ectoparasitic swallow bug *Oeciacus vicarius* (Hemiptera: Cimicidae) is common throughout the Cliff Swallow's breeding range, although less numerous to absent from parts of N. Dakota, Minnesota, interior Canada, and the e. U.S. (Usinger 1966, J. Faaborg pers. comm.). Swallow bugs overwinter in nests, travel on the birds relatively rarely, and feed on the blood of both adults and nestlings. Bug populations are reduced when a colony site is unoccupied for ≥ 1 yr, but some bugs can survive in the absence of swallow hosts for up to 3 yr (CRB, MBB). Parasitism by these bugs increases with Cliff Swallow colony size and nest density (up to 2,500 bugs/nest in some colonies) and harms nestlings by reducing body mass, growth rates, and pre-fledging survivorship (Brown and Brown 1986, in press, Chapman and George 1991).

Ectoparasitic ticks include *Ixodes baergi* (Acari: Ixodidae) from colonies in Arkansas, Illinois, Oklahoma, Texas, and Colorado; *I. howelli* from Montana and Colorado; *Argas cooleyi* (Argasidae) from Washington and Montana south to California and Texas; *Ornithodoros concanensis* (Argasidae) from Texas and Oklahoma north to Montana but rarely as far east as w. Nebraska or as far west as California; and *O. turicata* from Texas (Kohls and Ryckman 1962, Howell and Chapman 1976, Hopla and Loye 1983, CRB, MBB). Ticks are also confined to swallow nests or crevices in substrate, feeding on the blood of adults and nestlings; they rarely travel on birds. Tick reproduction is closely synchronized with that of swallows within a colony (Hopla and Loye 1983, Larimore 1987), and deleterious effects on birds can be substantial.

Ectoparasitic fleas include at least 7 species of *Ceratophyllus* (Siphonaptera: Ceratophyllidae). The most common is *C. celsus*, occurring widely throughout most of the Cliff Swallow's range from Texas to Canada. Also relatively common is *C. petrochelidoni*, with a poorly known distribution extending from California and New Mexico north to British Columbia and Ontario but not as far north as Alaska. More rarely reported species on

Cliff Swallows are *C. arcuegens* from nw. Canada and Alaska, *C. calderwoodi* from New Brunswick and Ontario, *C. coahuilensis* from Texas, *C. idius* from Ontario, and *C. scopulorum* from Alaska, nw. Canada, and New Brunswick (Eads 1956, Hopla 1965, Foster and Olkowski 1968, Wheeler et al. 1970, Galloway 1987, Wheeler and Threlfall 1989). In 1977, neotropical *Hectopsylla psittaci* (Siphonaptera: Pulicidae) were discovered in Cliff Swallow colonies in California (Schwan et al. 1983). Fleas feed on the blood of adult and nestling birds and, though overwintering in nests, travel on adults during the breeding season more than do swallow bugs or ticks. Infestations of *C. celsus* in Nebraska increase with colony size but do not seem to have serious effects on nestlings or adults (Brown and Brown 1986, in press).

Other Cliff Swallow parasites have been studied less systematically; for the following, there are few data on geographical distribution, prevalence, or effects on the birds. At least 4 species of blowflies (Diptera: Calliphoridae) have been reported from Cliff Swallows, including *Protocalliphora hirundo* from Alaska south to California and east to Iowa and New Mexico, *P. asiovora* from Oregon, *P. braueri* from British Columbia and New Mexico, and *P. sialia* (= *splendida*) from various locations across North America (Sabrosky et al. 1989). Dermestid beetles (Coleoptera: Dermestidae) have been found in Cliff Swallow nests in California, Oklahoma, and Nebraska (Linsley 1944, J. Loye pers. comm., CRB, MBB). Feather lice (Mallophaga) include *Machaerilaemus malleus* (Amblycera: Menoponiidae) and *Brueelia longa* (Ischnocera: Philopteridae) from Nebraska and California, *Phlopterus excisus* from California, and *Myrsidea dissimilis* from New Hampshire and Arkansas (Peters 1936, Baerg 1944, Emerson 1972, Brown and Brown in press). Mites include *Dermanyssus gallinae* (Acari: Dermanyssidae) from British Columbia and Quebec, *D. hirundinis* from British Columbia (Wheeler and Threlfall 1989), and from Texas *D. hirundinis*, *D. triscutatus*, *Cheyletus* sp. and *Ornithocheylea* sp. (Cheyletidae), *Hirstiosoma* sp. (Smarididae), *Eutrombicula alfredugesia* (Trombiculidae), *Dermatophagoides evansi* (Pyroglyphidae), *Proctophyllodes* sp. (Proctophyllodidae), and the nasal mite *Ptilonyssus echinatus* (Rhinyonyssidae) (Howell and Chapman 1976).

Nematodes include *Hadjelia pyrrhonota* (Nematoda: Spiruridae), *Acuaria* sp. (Acuariidae), *Microtetrameres inermis* (Tropisuridae), *Splendidofilaria* sp. (Dipetalonematidae), and *Diplotriana* sp. (Filariidae), all from Colorado (Kayton and Schmidt 1975), and *Splendidofilaria caperata* from Alberta (Wong et al. 1990). Cestodes include

Angularella audubonensis (Cestoda: Dilepididae), *A. beema*, *Anonchotaenia globata*, *Vitta magniuncinata*, *V. parvirostris*, *V. riparia*, and *Mayhewia ababili* (Hymenolepididae), all from Colorado (Stamper and Schmidt 1984). Trematodes include *Collyriclum faba* (Trematoda: Troglotremitidae) from California (Speich 1971) and *Concinnum minor* (Dicrocoeliidae), *Brachylecithum marinholutzi*, *Plagiorchis maculosus* (Plagiorchiidae), and *Stomylotrema gratiosus* (Stomylotrematidae) from Colorado (Kayton and Schmidt 1975). Acanthocephalans include *Mediorhynchus grandis* (Acanthocephala: Gigantorhynchidae) and *M. papillosus* from Colorado (Kayton and Schmidt 1975). Blood parasites (Hematozoa) were found in 30.6% of birds ($n = 291$) from California and included *Hepatozoon*, *Trypanosoma*, *Haemoproteus*, *Leucocytozoon*, and microfilariae (Clark and Swinehart 1966). The protozoan *Isoospora petrochelidon* (Protozoa: Eimeriidae) was described from Cliff Swallows in Colorado (Stabler and Kitzmiller 1972).

CAUSES OF MORTALITY

Exposure. Cliff Swallows are sensitive to cold weather that reduces availability of flying insects (Kimball 1889, Krapu 1986, Littrell 1992). When late spring cold snaps (daily highs $\leq 10^{\circ}\text{C}$) last ≥ 4 d, mortality of adults due to starvation can be substantial. Hundreds of birds perished throughout the n. and central Great Plains after a cold spell 25–28 May 1992 (Brown and Brown in press, A. Jaramillo pers. comm.). Weather-related starvation is likely the most important cause of adult mortality during the breeding season and may also affect nestlings if cold weather occurs later in summer.

Nestlings often die when nests are destroyed in storms. Strong wind can drive rain underneath the overhangs that normally protect nests, soaking the nests and causing them to crumble and fall. About 1,400 nests on cliffs along a Nebraska lakeshore were destroyed in a single thunderstorm in which wind drove waves unusually high (Brown and Brown 1989). Nestling mortality also occurs when floors of nests crumble, usually in hot weather that desiccates mud of nest. Young can be lost to heat when temperatures inside nests exceed 40°C (C. Hopla pers. comm.).

Predation/parasitism. Predation on adults during the breeding season is relatively rare and probably not an important cause of mortality; there is no information for the nonbreeding season (see Behavior: predation). Bull snake predation on eggs and nestlings can be significant if a snake remains in a colony for several days, but relatively few colonies are attacked (Brown and Brown in press).

The greatest cause of nestling mortality is

ectoparasitism by swallow bugs (see Disease and Body Parasites). In larger colonies where bug infestations can be substantial, many nestlings are killed by the bugs that feed on them (Brown and Brown 1986, in press). Bug parasitism increases as summer progresses, and later nests within a colony or entire late-starting colonies may have 100% nestling mortality because of bugs. Birds abandon nests that still contain eggs or newly hatched young, and entire colonies may desert a site en masse, when bug parasitism is high (Foster 1968, Loye and Carroll 1991, Brown and Brown in press).

Competition with other species. Eggs are often lost to House Sparrows that compete for Cliff Swallow nests (see Behavior: predation). Nestlings are sometimes killed or wounded by House Sparrows that search for nests later in summer; House Sparrow-caused mortality is greatest at colonies near towns and ranches where House Sparrows are most numerous. House Sparrows may be a significant cause of the total egg and nestling loss in e. North America where Cliff Swallows are less common (Bent 1942, Samuel 1969b, Silver 1993); in w. North America, House Sparrows probably have primarily a local impact at certain sites (Krapu 1986, Brown and Brown in press).

RANGE

Initial dispersal from natal site. Cliff Swallows show greater natal philopatry than other swallows. Of birds banded as nestlings or juveniles in California, 19% were recaptured in a subsequent year at or in the vicinity of their natal colony (Mayhew 1958); in Nebraska, about 22% (Brown and Brown in press). It is impossible to separate dispersal from mortality, but clearly not all surviving first-year birds return to the vicinity of natal site. One yearling born in sw. Nebraska was found near Edmonton, Alberta, about 1,700 km northwest of its birthplace. Males are slightly more likely than females to return to the vicinity of natal site, although the difference is not great (Mayhew 1958, Brown and Brown in press).

Among birds banded as nestlings or juveniles and recaptured the next year, about 59% in California, 48% in Texas, and 74% in Nebraska returned to their natal colony site (Mayhew 1958, Sikes and Arnold 1984, Brown and Brown in press). Remaining birds settled mostly within 3.5 km of natal site, although this pattern was likely a result of difficulty in detecting marked birds as the distance from study area increased. Some yearlings are detected as far from their natal site as 56 km in Nebraska (Brown and Brown in press) and 77 km in California (Mayhew 1958). Yearlings prefer colonies similar in size to their natal colony, even when dispersing to a nonnatal site; whether birds disperse to a nonnatal

site is largely determined by the extent of swallow bug and flea parasitism they experienced as nestlings at their natal colony (Brown and Brown 1992). Dispersal decisions are possibly influenced in part by information gained during colony explorations the summer of fledging (see Breeding: immature stage).

Fidelity to breeding site and winter home range. Between 30 and 50% of adults are typically recaptured in a later year at or in the vicinity of the breeding colony where they were banded (Mayhew 1958, Brown and Brown in press). However, this is not a useful measure of breeding fidelity because it is unknown whether birds that do not return are dead or have dispersed. Among banded adults encountered the next breeding season, 82% in California, 45% in Texas, and 59% in Nebraska returned to the same breeding-colony site the second year (Mayhew 1958, Sikes and Arnold 1984, Brown and Brown in press). Remaining settled mostly within 3.5 km of previous year's site, as for first-year birds, but pattern likely was an observational artifact (see above). Birds were detected breeding at sites as far as 64–66 km from their previous year's breeding colony in Nebraska and California (Mayhew 1958, Brown and Brown in press). Birds are more likely to return to the previous year's breeding colony if they were successful in fledging young at that site in previous year, and breeders prefer colonies similar in size to those used the previous year (Brown and Brown in press). In Nebraska, as birds get older, some switch to smaller colonies in successive years. Size preferences probably reflect different payoffs of colony size to individuals of different "quality" and result in phenotypic sorting of birds among colonies (Brown and Brown in press). About 9% of breeders in California and about 5% in Nebraska switch to a second breeding colony during the same nesting season (Mayhew 1958, Brown and Brown in press). Some of these birds are ones whose nests failed at their first colony. Some birds move relatively long distances between colonies within a season: up to 40 km in California and 64 km in Nebraska. Adults, like juveniles, spend up to a week or more in mid- to late summer visiting multiple colony sites near their breeding colony of that year. Birds probably use this time to assess suitability of sites (e.g., parasite load, food availability) and use that information in part to choose colonies the next spring (Brown and Brown in press).

There is no information on fidelity to winter home range, although birds seem to be nomadic in winter, implying little or no site fidelity.

Dispersal from breeding site or colony. See

above (also Brown and Brown in press). There is little information on long-distance dispersal.

Home range. While selecting colonies in early spring, males and females generally ranged linear distances of 2–15 and 9–14 km, respectively, along a Nebraska river valley where colony sites were located (Brown and Brown in press). Once a bird selects a colony, most foraging is confined to areas within about a 1.5-km radius of the colony site (Brown et al. 1992), although birds occasionally forage up to 6 km from their colony (Emlen 1952). Late in season, after young fledge, birds of all ages and sexes travel widely and visit colonies up to 60 km (and probably farther) from their natal or breeding colonies (CRB, MBB). Two radio-tagged postbreeding males confined their activities to a linear region of 15 and 19.5 km along a river valley for at least 6–8 d (Brown and Brown in press). Within-season homing is well developed over moderately long distances: adults in California were released at distances of 58, 68, 112, 136, and 184 km from their nesting sites, and birds from each distance returned to their colonies (Mayhew 1963). Overall, 45% of birds displaced homed back to the original capture site.

POPULATION STATUS

No information on population size. Breeding population is difficult to census accurately by transect methods since birds are locally concentrated at colony sites, many of which are erratically occupied from year to year (Brown and Brown in press). Breeding Bird Survey (BBS) data suggest no overall change in total population size across North America from 1966 to 1991. Significant increases appear to have occurred in the central Great Plains from Colorado east to Illinois and Michigan, especially in Nebraska since 1982, and in the Appalachian Mtns. Significant decreases have been primarily in New Hampshire since 1966 and in s. California since 1982. Even statistically significant trends in BBS data for this species must be interpreted cautiously, as abandonment or recent colonization of certain nesting sites along survey routes may greatly bias relative estimates of abundance.

POPULATION REGULATION

Little quantitative information. See Causes of Mortality, above.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

There is little evidence of any appreciable harm caused by humans. Winter habitat apparently

comprises largely grassland and agricultural areas which are less sensitive to degradation by human activity. Breeding habitat has been enhanced by widespread construction of bridges, culverts, and buildings which provide alternative nesting sites. Some natural cliff nesting sites probably have been destroyed by development in certain areas, but the net effect of humans on this species has been positive. Cliff Swallows are extremely tolerant of disturbance by humans and rarely abandon nests unless their access is blocked (e.g., by construction), the nests get wet and fall, or birds are caught inside their nests at night for banding before eggs are laid (CRB, MBB).

MANAGEMENT

Conservation status. Attempts have been made to restore populations in parts of ne. U.S.; listed as Threatened for Pennsylvania and New Jersey (Kitson and McNaught 1991). Most conservation efforts, however, have been limited and localized (e.g., Krapu 1986, Silver 1993).

Measures proposed and taken. House Sparrow control seems to be the most effective means of increasing Cliff Swallow numbers locally and probably regionally (Samuel 1969b, Krapu 1986, Silver 1993). Trapping and shooting House Sparrows at colony sites vary in effectiveness but eventually eliminate most individuals. Knocking down all old Cliff Swallow nests after the breeding season also controls House Sparrows, by removing places for them to roost during the winter and preventing them from becoming established in the existing nests at a colony site before the Cliff Swallows return in the spring. A colony in Wisconsin grew from 1 to > 2,000 nests over a 38-yr period, primarily through House Sparrow control and removal of old nests over the winter (Buss 1942). Nest removal also reduces buildups of ectoparasites from year to year. Fumigation of nests with the insecticide Dibrom is effective in eliminating parasites (Brown and Brown 1986, in press) but has not been used for management to date.

An increase in painted barns in the twentieth century is believed to have reduced the population in parts of the ne. U.S. because nests are thought to adhere less well to painted surfaces (Townsend 1917, Forbush 1929). However, nests were equally likely to fall from painted and unpainted rafters at a Massachusetts colony (Silver 1993). Attaching wooden strips along a wall may enhance the structural stability of nests on buildings by providing a more secure base for nests to be built on (Buss 1942). Artificial nests and half-nests made out of plaster have been installed to provide safer nesting sites that are

less likely to fall (Kitson and McNaught 1991, Silver 1993); plaster nests have also been used for research purposes (Mayhew 1958, CRB, MBB). Birds in Pennsylvania, New Jersey, and California readily occupied plaster nests, but in Nebraska plaster nests were often ignored for several years before being occupied if at all. Installation of artificial nests is unlikely to be an effective management strategy unless accompanied by House Sparrow control, because House Sparrows quickly become established in plaster nests. House Sparrows are less likely to occupy plaster half-nests (M. Silver pers. comm.).

Recommendations for rehabilitating birds in captivity are given by Shaw (1992).

Effectiveness of measures: the species' response. With House Sparrow control, local colony size can increase substantially; annual increases at one N. Dakota site averaged 97% when House Sparrows were trapped (Krapu 1986). See Buss 1942 for details on a major increase in colony size at a managed colony in Wisconsin. Removal of ectoparasites via nest fumigation can also result in colony size increases at some sites (CRB, MBB). However, whether any of the proposed conservation measures actually increase total population size over time, instead of causing mostly redistribution of birds among sites, is unknown.

APPEARANCE

The following is based on the nominate race, *H. p. pyrrhonota*, and is largely from Dwight (1900) and Oberholser (1974).

MOLTS AND PLUMAGES

Hatchlings. See Breeding: young birds.

Juvenal plumage. Acquired by a complete Prejuvenal molt. Similar to Definitive Basic (breeding adult) plumage but much duller without any distinctly metallic coloration. Upperparts fuscous black; hindneck pale dull fuscous; forehead dull russet to gray, often mixed with white, and pattern of forehead quite variable among individuals (see Stoddard and Beecher 1983). Feathers of back and scapulars are edged narrowly with buffy white or dull buff; upper tail-coverts and tertials are tipped broadly with same colors. Rump is light cinnamon. Below, dull white, strongly washed on the throat, sides, and undertail coverts with vinaceous cinnamon, hair brown, or buff. Chin and forepart of throat are mixed with white, dull black, gray, dull russet, or cinnamon, with extensive variation among individuals. This plumage is retained until sometime after the birds depart from North

America in the fall; specimens from Central America on 20 Oct were still in Juvenal plumage (Dwight 1900).

Definitive Basic plumage. Results from complete Definitive Prebasic molt after species has departed from North America, although some molt may begin in late summer and during migration. Prebasic molt is probably complete by late Jan. Birds in Argentina on 24 Jan were in fresh breeding plumage, although some were still replacing primaries (A. Jaramillo pers. comm.). Birds in their first Basic plumage apparently indistinguishable from older birds.

Similar to appearance of plumage during breeding season (after pale feather tips have worn away; see below), but feathers of back and scapulars with narrow brownish gray edgings; dulling color of upper surface; upper tail-coverts broadly tipped with buff, brownish white, or buffy white; all upper wing-coverts narrowly tipped with brownish white or light brownish gray; tertials and inner secondaries rather conspicuously tipped with white or brownish white.

By breeding season pale feather tips have worn away producing the following plumage. Forehead cream (most populations), pale wood brown, buffy, or chestnut to cinnamon rufous (depending on subspecies; see Systematics: geographic variation). Crown and back metallic bluish black or greenish slate black, back with a few narrow vertical streaks of dull white formed by edges of feathers; neck dull hair brown, anteriorly tinged with chestnut, sometimes forming an almost complete narrow collar; rump tawny to pinkish buff; upper tail-coverts dull hair brown, margined at tips with grayish white; wings and tail chaetura drab on exposed surfaces with slight metallic greenish sheen; lesser upper-wing coverts slightly more metallic, chaetura drab, or fuscous and lighter on inner webs; tertials and inner secondaries very narrowly tipped with brownish white; chin, throat, and sides of neck chestnut; center and base of throat metallic greenish or bluish slate black; chest and breast dull light drab, washed with buff or ochraceous; rest of lowerparts dull white; central portions of longer, under tail-coverts hair brown; under wing-coverts dull drab, occasionally washed with chestnut. Males and females identical in all plumages, except males average larger bluish spot on lower throat (CRB, MBB).

BARE PARTS

Bill and gape. Bill and lores dull black, except as nestling when bill is clove brown with basal portion of mandible pale yellow. Gape dull pink in adult, orange-yellow in nestling.

Iris. Dark claret brown or vandyke brown.

Legs and feet. In adults, dusky brown, fuscous, or sepia; in juveniles, vinaceous pink changing to true cinnamon to burnt sienna as bird ages (CRB, MBB).

MEASUREMENTS

LINEAR

See Table 1.

MASS

See Brown and Brown in press. In Nebraska, across a 9-yr period, masses (g) of males and females during nest-building and egg-laying averaged 23.90 ($n = 6,797$) and 24.15 ($n = 3,566$), respectively; during incubation, 23.15 ($n = 7,011$) and 23.76 ($n = 5,864$); and during feeding of young, 22.25 ($n = 10,387$) and 22.22 ($n = 8,170$). There were no consistent mass differences between yearlings and older age classes (CRB, MBB). Mass generally declines over the summer while birds are breeding, as birds exhaust fat reserves. Renesting birds in Quebec had 60.3% lower fat reserves than birds breeding earlier in the season (Gauthier and Thomas 1990).

PRIORITIES FOR FUTURE RESEARCH

Almost all research to date has been on the nominate race, *H. p. pyrrhonota*. Southwestern and Mexican birds in particular (*H. p. tachina* and *H. p. melanogaster*) have been virtually unstudied. Their darker forehead patches suggest fundamental differences in their social behavior as compared to *H. p. pyrrhonota*. The late summer synchronization between breeding by *H. p. melanogaster* and the start of the monsoon in Arizona is unlike anything seen in other races. Geographic differences in ectoparasite load, incidence of intraspecific brood parasitism, type of food calls, and mean colony size (smaller colonies in the sw., se., and ne. U.S.) all suggest substantial variation among populations in social behavior and life history. Range and behavior during winter are poorly known and should be investigated, especially given that Cliff Swallows remain highly social in winter and perhaps maintain year-round the same associations of birds that earlier bred together.

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