

*Riparia  
riparia*

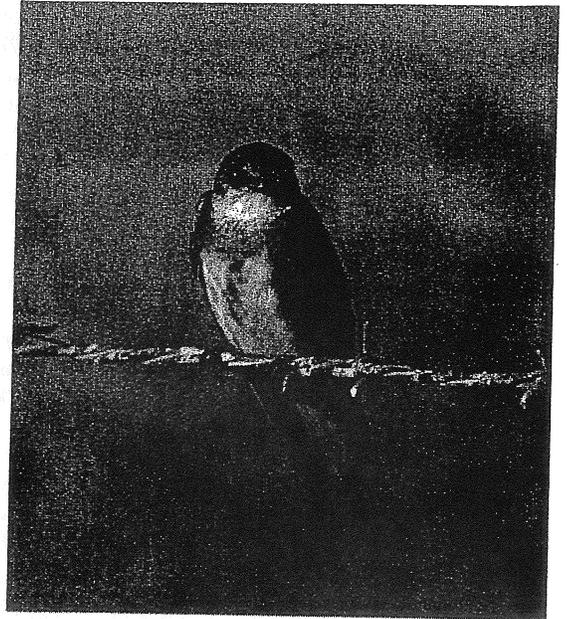
# Bank Swallow

FRENCH:  
*Hirondelle de rivage*  
SPANISH:  
*Golondrina ribereña,*  
*Golondrina Barranquera*

*Here at least is an unchangeable type, a visible link between Port Los Angeles and Florence on the Arno.*

*Communal life seems a pleasant thing to these Swallows, and there is usually a considerable stir of activity about the quarters.*

Dawson 1923: 534



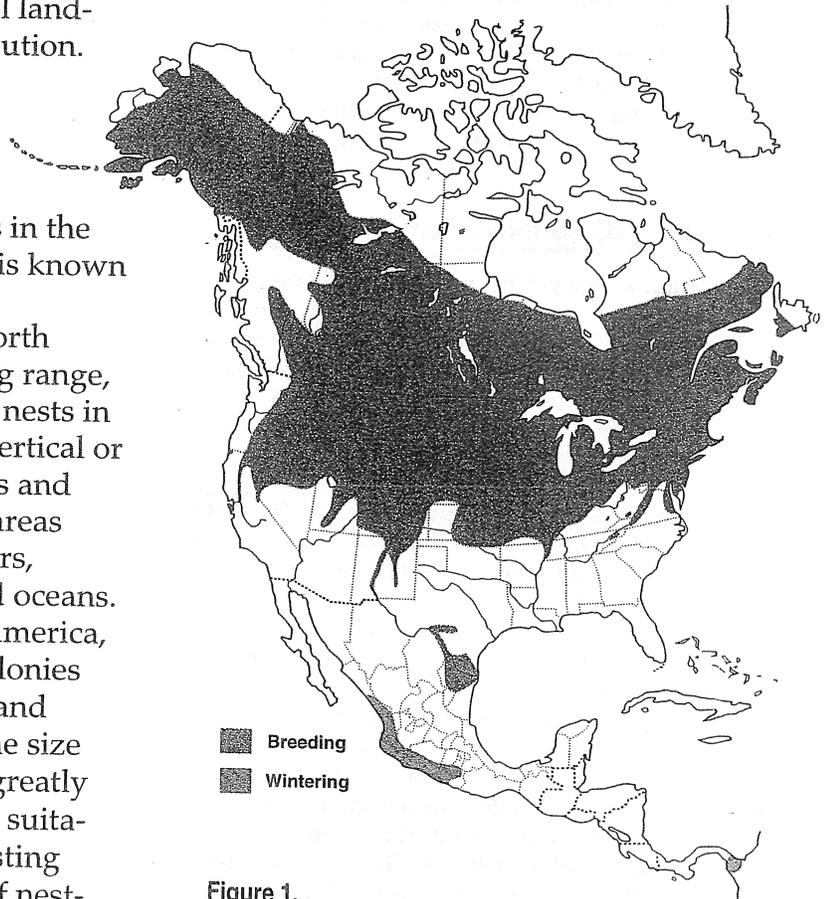
**T**he Bank Swallow's scientific name—*Riparia riparia*—aptly describes its affinity for nesting in the streamside (riparian) banks and bluffs of rivers and streams. This species is a highly social land-bird with a Holarctic breeding distribution. It nests in colonies ranging from 10 to almost 2,000 active nests. One of only a few passerines with an almost cosmopolitan distribution, it is one of the most widely distributed swallows in the world. In the Old World, this species is known as the Sand Martin.

Throughout much of its western North American breeding range, the Bank Swallow nests in erodible soils on vertical or near-vertical banks and bluffs in lowland areas dominated by rivers, streams, lakes, and oceans. In eastern North America, however, many colonies are found in sand and gravel quarries. The size

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Life Histories for the 21st Century

and longevity of colony sites depend greatly on erosion to maintain nesting-habitat suitability. The ephemeral nature of the nesting banks results in relatively low levels of nest-site fidelity, since there is little evolutionary benefit to maintaining long-term ties to specific colony sites.



**Figure 1.** Distribution of the Bank Swallow in North and Middle America. North American populations also winter in South America and the eastern Caribbean. Other populations breed throughout Europe, Asia, and North Africa.

Key studies of this species have come from North America and Europe. Hoogland and Sherman (1976) studied the advantages and disadvantages of Bank Swallow coloniality in Michigan; Emlen and DeMong (1975) studied breeding synchronization within colonies in New York; Persson (1987a, 1987b, 1987c) looked at age structure, sex ratios, and survival rates of populations in Sweden; Szep (1993, 1995a) explored how breeding populations in Hungary are affected by levels of rainfall on their African wintering grounds; Beecher et al. (1981a, 1981b) looked at parental recognition of nestling voices in colonies; Beecher and Beecher (1979) and Kuhnen (1985) studied how burrow-digging by nesting pairs helps establish and solidify the pair bond, although extra-pair breeding is common; and Jones (1986) researched how male Bank Swallows distinguish heavier, apparently receptive, females in flight and preferentially chase them for breeding.

Colonies at sand and gravel quarries are easily studied because of their accessibility, and countless banding studies have been conducted on this species, producing considerable information on the breeding-population dynamics and colony-site fidelity of Bank Swallows. Relatively little information exists, however, on postbreeding dispersal, migration, and wintering ecology.

## DISTINGUISHING CHARACTERISTICS

From Lethaby 1996 and Pyle 1997, except where noted. Small swallow: length 12 cm (Turner and Rose 1989), wing length 89–111 cm, mass 10.2–18.8 g (see Table 1). Sexes similar in appearance, and plumage similar throughout year. Adult has grayish brown mantle, rump, and wing-coverts, contrasting with darker brown remiges and rectrices; tertials entirely brown or brown with pale edgings; throat white, contrasting with distinct brown breast-band and grayish brown crown. Brown breast-band can extend to belly as sharp spike. Juveniles (hatch-year birds) are distinguished from adults by buff-edged or whitish upperparts, and buffy pink wash to throat. Slight notch in the medium-length tail is visible in the hand and while bird is perched. No sexual dimorphism; sexes are reliably distinguished by presence or absence of brood patch or cloacal protuberance.

Adults are distinguished from other North American swallows that are brown above and white below by combination of smaller size, grayish brown back that contrasts with darker (black) wings, clear white throat and underparts, distinct line along ear-coverts separating brown of crown and white of cheek, well-defined dark brown breast-

band that is broadest at center, completely brown rump, and mostly square tail. Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) has uniformly brown upperparts (back not contrasting noticeably with wings); diffuse brown wash over throat and breast (lacks distinct breast-band); and, in adults, entirely brown tertials (DeJong 1996). Juvenile Tree Swallows (*Tachycineta bicolor*) are larger and have evenly sooty brown upperparts; white throat with brown breast-band that is faintest in the center; diffuse line along cheek; white underbody that extends up sides of rump; and brown secondaries and tertials with obvious pale white tips. Juvenile Bank Swallows have narrow pale edges on tertials. In flight, Bank Swallows hold their wings more sharply angled at the carpal joint and have quicker, more flicking wing-beats than Tree and Northern Rough-winged swallows. Brown-chested Martin (*Progne tapera*) of South America has same plumage characteristics as Bank Swallow, but is much larger (16 cm in length, 117–137 cm in wing length, 30–40 g in mass; Turner and Rose 1989). Call of Bank Swallow is a grating *trrrt*, given in raspy chatter, while Tree Swallow gives soft 2-syllable *cher-wut* or *ter-reep*, and Northern Rough-winged Swallow a slightly buzzy or rolled *treep*, given singly. Bank Swallows have small tuft of feathers at base of hallux, a physical trait that is unique among North American swallows.

## DISTRIBUTION

### THE AMERICAS

**Breeding range.** Figure 1. Breeds locally throughout its range where suitable habitat exists, generally at lower elevations. Suitable conditions for breeding are often ephemeral; thus breeding locations may change frequently.

Breeds throughout central Alaska, Kodiak I., and Alaska Peninsula west to e. Aleutian Is., but absent from Brooks Range and north, and from coast of w. Alaska, and breeds only very locally in se. Alaska (Kessel and Gibson 1978). East of Alaska, breeding range extends north to n. Yukon, w. and s. Mackenzie, n. Manitoba, n. Ontario, central Quebec, throughout Maritime Provinces, and s. Newfoundland (Godfrey 1986, Cadman et al. 1987, Erskine 1992). Regular breeding extends south locally to n. California (Siskiyou, Shasta, and Lassen Cos., and along Sacramento River from Shasta Co. south to Yolo Co.; Small 1994), n. Nevada (Alcorn 1988), n. Utah (extending to s. Utah in central portion of state; Walters 1983), s. Colorado (Andrews and Righter 1992), n. New Mexico (extending south throughout Rio Grande Valley and occasionally south to lower Pecos River Valley; Hubbard

**Table 1.** Linear measurements (mm) and mass (g) of adult Bank Swallows (*R. r. riparia*) from North America. Data shown as mean  $\pm$  SD (range, *n*).

	Male	Female	Location	Source
Bill length <sup>1</sup>	6.4 (6.1–7.1)	6.1 (5.6–6.6)	E. North America	Oberholser 1974
	6.3 (5.9–6.9) <sup>2</sup>		Canada	Godfrey 1986
Wing length	99.1 (95.5–103.6)	99.1 (95.5–104.1)	E. North America	Oberholser 1974
	99.7 $\pm$ 2.71 ( <i>n</i> = 184)	100.7 $\pm$ 2.48 ( <i>n</i> = 154)	Virginia	Blem and Blem 1990
	99.9 (94–106, 74)	100.4 (96–105, 67)	New York	Freer 1977
	100.0 $\pm$ 2.40 (93–107, 914)	100.0 $\pm$ 2.59 (89–111, 1008)	Wisconsin	MacBriar 1995
	100.2 $\pm$ 2.59 (93–112, 565)	100.2 $\pm$ 2.43 (94–109, 851)	California	BAG
	101.4 (97.4–106.7)	101.3 (95.1–105.9)	Canada	Godfrey 1986
Tail length	48.0 (45.0–50.5)	48.3 (45.0–52.1)	E. North America	Oberholser 1974
	47.7 (45.0–50.5) <sup>2</sup>		Canada	Godfrey 1986
Tarsus length	10.9 (9.9–11.4)	10.9 (9.9–11.4)	E. North America	Oberholser 1974
	10.9 (10.5–11.0) <sup>2</sup>		Canada	Godfrey 1986
Mass	13.0 $\pm$ 1.05 (11.0–15.0, 61)	14.7 $\pm$ 1.48 (12.0–18.0, 61)	New York	P. Capainolo pers. comm.
	13.7 (11.8–16.1, 39)	14.8 (11.4–18.5, 82)	Wisconsin	Petersen 1955
	13.6 $\pm$ 1.36 ( <i>n</i> = 184)	15.0 $\pm$ 1.24 ( <i>n</i> = 154)	Virginia	Blem and Blem 1990
	12.7 $\pm$ 0.77 (10.6–14.7, 165)	13.4 $\pm$ 1.19 (10.2–17.0, 175)	New York	Freer 1977
	13.5 $\pm$ 0.93 (10.8–16.4, 942) <sup>3</sup>	14.4 $\pm$ 1.27 (10.6–18.7, 1,046) <sup>3</sup>	Wisconsin	MacBriar 1988
	13.0 $\pm$ 0.83 (10.9–16.4, 698)	13.9 $\pm$ 1.32 (11.1–18.8, 1,013)	California	BAG

<sup>1</sup>Exposed culmen.  
<sup>2</sup>Males and females combined.  
<sup>3</sup>Weights from birds >1 yr (after hatch year); weights from birds definitively aged  $\geq$  2 yr not included.

1978), s. Nebraska, eastern half of Kansas (west to Jewell and Stafford Cos.; Thompson and Ely 1992), ne. Oklahoma (including Alfalfa and Ottawa Cos.; Baumgartner and Baumgartner 1992), s. Missouri (Jacobs and Wilson 1997), and ne. Arkansas (Mississippi Co.; James and Neal 1986). East of Mississippi River, breeding extends south to w. Tennessee (areas bordering Mississippi River; Nicholson 1997), w. Kentucky (areas bordering Ohio River; Palmer-Ball 1996), throughout Ohio except the southeast (Peterjohn and Rice 1991), s. Pennsylvania (Brauning 1992), and s. New Jersey (Sibley 1993). Breeding extends south from this area to central Delmarva Peninsula (Robbins and Blom 1996, Virginia Breeding Bird Atlas [BBA] unpubl.), western shore of Virginia (Virginia BBA unpubl.), and easternmost West Virginia and adjacent portions of w. Virginia (Buckelew and Hall 1994, Virginia BBA unpubl.). Also breeds along north coast, central part of state, and in Mono Basin of California (Small 1994), in e.-central Kentucky (Palmer-Ball 1996), w. West Virginia (Buckelew and Hall 1994), easternmost Tennessee (Nicholson 1997), westernmost N. Carolina (Snively and Cul-

bertson 1978), s.-central Texas (south of 30°N; Texas BBA unpubl.), ne. Mexico (n. Veracruz, ne. San Luis Potosí, and extreme n. Coahuila; Howell and Webb 1995), and irregularly elsewhere south of main range. All breeding reports outside of main range should be carefully evaluated, however, because of potential confusion with the Northern Rough-winged Swallow (e.g., McNair and Post 1993). Largely absent as breeder west of Cascades from British Columbia south to Oregon and from large portion of n.-central British Columbia (Gilligan et al. 1994, Campbell et al. 1997).

**Winter range.** Winters primarily in South America, where range extends almost the entire length of the continent south to n. and central Chile and n. Argentina (Ridgely and Tudor 1989). Transient in Colombia, transient and wintering in Venezuela and Guyana, wintering in large numbers in Suriname, rare in French Guiana, transient and wintering in Ecuador, transient in Peru, transient and wintering in large numbers in Brazil, and transient and wintering in Bolivia, Argentina, Chile, Paraguay, and Uruguay (Paynter 1995). Uncommon migrant and winter visitor in Paraguay (Hayes et

al. 1990). Considered transient in Peru; lack of records there after mid-Feb may be attributed to small number of observers rather than to transitory status (Schulenberg 1987). Southernmost record for South America is from Brunswick Peninsula, Chile (Vuilleumier et al. 1993).

Also fairly common winter resident along Pacific slope of s. Mexico from s. Sinaloa to ne. Guerrero (Howell and Webb 1995), rare and local winter resident in e. Panama Province, Panama (Ridgely and Gwynne 1989); rare regular winter resident on Puerto Rico and in Virgin Is. (Raffaele 1989); and uncommon winter visitor to major islands of Lesser Antilles (Evans 1990).

#### OUTSIDE THE AMERICAS

**Breeding range.** Widespread breeder throughout most of Europe and Asia from Hebrides, Orkneys, n. Scandinavia, n. Russia, and Siberia south to Mediterranean region, including Israel and Iraq, Nile River valley in Egypt, Algeria, Morocco, e. Iran, Afghanistan, n. India and Pakistan, nw. Africa, se. China, and Japan (Dement'ev and Gladkov 1968, Cramp et al. 1988, Turner and Rose 1989).

**Winter range.** Winters throughout much of Arabia and Africa, including Madagascar, extending south to approximately the Tropic of Capricorn to s. Mozambique, ne. South Africa, Zimbabwe, and Namibia. Other wintering grounds include Burma, Thailand, Indochina, the Philippines, central and s. India, and s. China (Dement'ev and Gladkov 1968, Am. Ornithol. Union 1998).

#### HISTORICAL CHANGES

In California, historical range in southern and central areas has been eliminated by loss of nesting habitat due to flood- and erosion-control projects (Garrison et al. 1987, Small 1994). In Arkansas, localized range changes are due to nesting-habitat losses from water-flow changes and bank-stabilization projects (James and Neal 1986). In Maryland, breeding populations have moved inland from coastal locations where habitats have been destroyed as result of shoreline development (Robbins and Blom 1996). Distribution of nesting colonies in New York has changed from coastlines and large lakes to sand and gravel quarries (Andrle and Carroll 1988). Distribution in Connecticut has been modified because of human use of sand deposits where colonies occur (Bevier 1994). Habitat gains from sand- and gravel-mining have not offset losses in Kentucky (Palmer-Ball 1996). In British Columbia, road-building has increased nest-site availability, and distribution has expanded accordingly, but some colonies in sand and gravel quarries are threatened by associated human activities (Campbell et al. 1997).

#### FOSSIL HISTORY

No information.

### SYSTEMATICS

#### GEOGRAPHIC VARIATION

Clinal variation in plumage coloration and size (wing length): Populations become paler and grayer dorsally and shorter-winged to the south throughout range. Slight variation within species attributed to wide dispersal of adults (Loske 1983). Color of upperparts said to be darker and more sooty brown (less rufescent) in North America compared with Eurasia. Fading and foxing (reddening of brown feathers) in specimens complicates assessment of this character. Breast-band is comparatively indistinct in central Asian populations (*R. r. diluta*). Wing length averages longer in w. North America compared with e. North America (Oberholser 1974); distinction, if any, is poorly quantified, however. On basis of small sample size, Phillips (1986) noted that populations breeding in ne. Mexico (e. Nuevo León) and locally along lower Rio Grande were small compared with other North American populations. No studies of genetic variation.

#### SUBSPECIES

Although 8 subspecies were listed by J. L. Peters (in Mayr and Greenway 1960), recent authorities might recognize only 3–4 subspecies (Phillips 1986, Cramp et al. 1988). One subspecies breeds in North America, and another is a vagrant here. Despite problems of discoloration of specimens and the slight and clinal differences in size, more rigorous study might reveal valid subspecific taxa. For example, a race described from migrants through Israel and a similar form, perhaps the same, described from Kazakhstan (Shirihai and Colston 1992; see comments in Shirihai 1996); populations in the Punjab, India, where birds are in breeding condition when more northern populations are in non-breeding condition (Abdulali 1975); and the smaller birds of ne. Mexico noted under Geographic variation, above (Phillips 1986). Only 3 subspecies are recognized here:

*R. r. riparia* (Linnaeus, 1758): Breeds throughout North America, Eurasia, Mediterranean region, and nw. Africa; winters in Central and South America and Africa (Am. Ornithol. Union 1957, Cramp et al. 1988). North American populations have been considered distinct under the name *R. r. maximiliani* (see Arny 1952, Oberholser 1974) on basis of supposed smaller size compared with Eurasian populations, but most authors find differences slight to negligible. Local breeding populations in ne. Mexico and extreme s. Texas that are somewhat isolated to

the south of main breeding population in North America were identified by Phillips (1986) as possibly distinct (smaller, lighter weight, slightly larger bill). Included here as a synonym is *R. r. ijimae* (ne. Asia, including "*taczanowskii*"). Birds ascribed to *ijimae* are reported to have occurred in Alaska, but identity is doubted (see Arny 1952, Phillips 1986, Gibson and Kessel 1997).

*R. r. diluta* (Sharpe and Wyatt, 1893): Breeds from s. Siberia and w. Mongolia south to e. Iran, Afghanistan, n. India, and se. China. Vagrant to arctic North America (Jenny Lind I., Northwest Territories, Canada) and Bermuda (Phillips 1986). Paler and grayer than nominate *riparia*, particularly on crown and back, with faded and indistinct breast-band. Chin and throat washed buff, even speckled brown (Cramp et al. 1988). Monroe and Sibley (1993) suggested that *diluta* might deserve recognition as separate species. Intermediates between *diluta* and nominate *riparia* exist where ranges meet. Other races sometimes recognized as distinct from *diluta* include *fokienensis* (central and s. China), *indica* (Afghanistan and n. India), and *tibetana* (central Asia).

*R. r. shelleyi* (Sharpe, 1885): Breeds in lower Egypt; chiefly migratory, with winter distribution in ne. Africa. Compared with nominate *riparia*, shorter and has narrower wings, more shallowly notched tail, and narrow, paler breast-band (Shirihai and Colston 1992). Short-winged individuals formerly ascribed to *shelleyi* have been described recently as *R. r. eilata* by Shirihai and Colston (1992) on basis of spring migrants noted to have buffish brown chin and brown spotting or mottling on throat, and upperparts darker brown than on *shelleyi*. Birds with these characters have an earlier peak migration through Elat, Israel, than either *diluta* or nominate *riparia* has. Taxonomic status uncertain because breeding and wintering grounds are unknown, characters are now known to be more variable, and relationship to form recently described from Kazakhstan is unresolved (Shirihai 1996).

#### RELATED SPECIES

Most closely related species in genus *Riparia* are Plain Martin (*R. paludicola*) and Congo Martin (*R. congica*). On basis of DNA-DNA hybridization studies and morphological considerations, Banded Martin (*R. cincta*) is highly diverged from *R. riparia* and perhaps deserves placement in separate genus, *Neophedina* (Sheldon and Winkler 1993). As a hole-excavating species, Bank Swallow is considered to be among more basally branching ("primitive") groups of swallows rather than those that build nests or adopt previously excavated cavities (Sheldon and Winkler 1993).

**Hybridization.** Single record of hybrid with Common House-Martin (*Delichon urbica*; Phillips 1986).

## MIGRATION

### NATURE OF MIGRATION IN THE SPECIES

Medium- to long-distance diurnal migrant. Typically migrates in mixed-species flocks with Cliff (*Hirundo pyrrhonota*), Tree, and Barn (*H. rustica*) swallows. Generally arrives on breeding grounds in North America during early spring and departs late summer-midfall. Migrates from breeding range to winter range widely through s. U.S., Mexico, Central America, West Indies, and n. South America (Am. Ornithol. Union 1998). Not known if intraseasonal movement occurs on winter range, although Bank Swallow probably is nomadic at that time, as is Sand Martin on its African wintering grounds (Cramp et al. 1988).

### TIMING AND ROUTES OF MIGRATION

Most migrants presumably follow Central America isthmus between North and South America, since the species is generally considered a rare to uncommon migrant on many Caribbean islands. Migration in both directions spans several months, and birds may be abundant during migration. Migrants observed primarily in coastal and lowland regions.

**Spring migration.** Begins leaving winter ranges in Feb; some individuals were present as late as 5 May in Colombia (Hilty and Brown 1986), 10 May in Chile (B. Swift pers. comm.), and 8 Jun in French Guiana (Paynter 1995). Rare spring migrant in Colombia, and uncommon from early Mar to early May in Panama (Hilty and Brown 1986). Fairly common spring transient throughout most of Mexico from mid-Mar to May (Howell and Webb 1995) and Puerto Rico (Raffaele 1989). Rare among the larger Virgin Is. (Raffaele 1989), uncommon migrant in e. Caribbean (Evans 1990), uncommon migrant from Apr to Jun in Bahamas (Brudenell-Bruce 1975), and scarce migrant from Apr to Jun in Bermuda (Amos 1991).

Spring migration through s. U.S. from early Mar and early Apr to mid- and late May: Early dates include 20 Feb in Texas (Oberholser 1974), 9 Mar in Florida (Stevenson and Anderson 1994), and 15 Mar in central California (BAG). Migration through states at middle latitudes from mid-Mar to late May: Early dates include 13 Mar in Indiana (Keller et al. 1986) and 19 Apr in W. Virginia (Hall 1983). Migration through states and Canadian provinces in northern latitudes from mid-Mar to mid-Jun: Early dates include second week of Mar in British

Columbia (Campbell et al. 1997), 2 Apr in New York (Bull 1985) and Wisconsin (Robbins 1991), and 12 Apr in Vermont (Laughlin and Kibbe 1985). Arrives earlier in coastal locations such as California and British Columbia (Campbell et al. 1997, BAG). Spring migration completed by mid- to late May to mid-Jun throughout much of range.

Spring-migration flocks appear to be smaller than fall-migration flocks. Flocks as large as 5,000 to 9,000 birds reported from New York (Bull 1985), but smaller maximum flocks (250 birds) reported from Illinois (Bohlen 1989).

**Fall migration.** Begins when nestlings fledge and as colony sites are vacated, so departure dates vary. Migration in U.S. and Canada peaks early Aug-late Sep, when hundreds to thousands may be seen moving south in mixed-species flocks (Dinsmore et al. 1984, Bohlen 1989, Paton and Fellows 1994). In states and Canadian provinces at northern latitudes, migration mid-Jul-late Oct; e.g., mid-Jul-late Sep in Michigan (Brewer et al. 1991), early Aug-early Sep in British Columbia (Campbell et al. 1997), and late Jul-early Sep in Connecticut (Zeranski and Baptist 1990). In central U.S., movement early Jul-early Oct; e.g., late Jul-early Sep in Iowa (Dinsmore et al. 1984), mid-Aug-mid-Sep in California (Small 1994), and early Jul-mid-Sep in Utah (Paton and Fellows 1994). In s. U.S., migration early Jul-early Nov; e.g., late Jul-early Nov in Florida (Stevenson and Anderson 1994), early Jul-early Nov in Louisiana (Lowery 1974), and mid-Aug-mid-Oct in Texas (Oberholser 1974). Representative late dates include 25 Oct in Illinois (Bohlen 1989), 7 Nov in Florida (Stevenson and Anderson 1994), and first week of Dec in Louisiana (Lowery 1974).

Fairly common to common fall transient in Mexico from Aug to Oct (Howell and Webb 1995), uncommon fall transient in Puerto Rico, rare transient in Virgin Is. (Raffaele 1989), uncommon migrant throughout e. Caribbean (Evans 1990), uncommon migrant from Aug to Oct in Bahamas (Brudenell-Bruce 1975), and scarce migrant from Aug to Nov in Bermuda (Amos 1991). Migrates through Costa Rica from late Aug to early Nov (Stiles and Skutch 1989) and early Sep to mid-Oct in Colombia, where it is sporadically common (Hilty and Brown 1986). Arrives as early as 10 Sep in Colombia, 16 Sep in French Guiana, 23 Sep in Bolivia, and 30 Oct in Argentina (Paynter 1995).

Major migration corridor exists in wetlands around Great Salt Lake, UT, where flocks as large as 10,000 birds occur (Paton and Fellows 1994). Concentrations of this size may represent communal roosting area as birds prepare to migrate over Great Salt Lake.

#### MIGRATORY BEHAVIOR

During spring and fall migrations, Bank Swallows occur in mixed-species flocks with Barn, Cliff, Northern Rough-winged, and Tree swallows and in loose conspecific flocks. In Great Britain, fall migration of adults begins shortly after young reach independence, since they move almost directly to communal roosts (Mead and Harrison 1979). Adult birds spend 10-14 d at communal roosts along coast preparing to cross water barrier presented by English Channel. Juvenile Sand Martins, however, wander extensively throughout large area, moving among several communal roosts over longer periods of time than adults. This wandering may serve to familiarize juveniles with natal areas and their landmarks for the subsequent spring return, as well as possibly to spatially segregate juveniles to different feeding sites to minimize competition with nesting adults (Mead and Harrison 1979). Juveniles begin fall migration earlier and continue later than adults. Spring-migration patterns are more rapid and direct than fall-migration patterns. First-year birds return to breeding colonies as much as 2-3 wk later than older adults (Freer 1977, 1979, Mead and Harrison 1979).

#### CONTROL AND PHYSIOLOGY

Little information. Fall migration across English Channel is triggered by calm weather (Mead and Harrison 1979).

#### HABITAT

##### BREEDING RANGE

Presently breeds primarily in lowland areas along ocean coasts, rivers, streams, lakes, reservoirs, and wetlands (Cramp et al. 1988, Turner and Rose 1989, Am. Ornithol. Union 1998). Vertical banks, cliffs, and bluffs in alluvial, friable soils characterize nesting-colony sites throughout North America. Nesting colonies also found in artificial sites such as sand and gravel quarries and road cuts. Historically, all colonies in North America were found in natural sites such as banks along rivers, streams, lakes, and coasts; today, many colonies are in human-made sites.

Most rivers and streams with nesting habitats are low-gradient, meandering waterways with eroding streamside banks. In coastal areas and lakeshores, waves caused by storms, tidal action, and wind erode banks, cliffs, and bluffs, creating vertical faces. Foraging habitats surrounding nesting colony include wetlands, open water, grasslands, riparian woodlands, agricultural areas, shrublands, and occasionally upland woodlands. A freshwater or saltwater source is often nearby,

but association is likely due to its role as source of soil deposition (freshwater) or erosive force. Bank Sparrows tend to avoid dense forests and woodlands, deserts, montane areas, and alpine areas because of paucity of suitable nesting habitat.

Altitudinal range extends from sea level to about 2,100 m in California (BAG), and from sea level to 900 m in British Columbia (Campbell et al. 1997). Most nesting colonies, however, are located in lowland alluvial valleys and coastal areas. No clear differences among subspecies in preferred breeding habitats. See also Breeding: nest site, below.

#### SPRING AND FALL MIGRATION

Seen in variety of open and water-associated habitats. Uses wetlands around Great Salt Lake, UT, in spring and fall (Paton and Fellows 1994); agricultural areas, marshes, and prairies in Florida (Stevenson and Anderson 1994); savannas and seashores in Trinidad and Tobago (French 1991); and bays, mangrove-sheltered lagoons, mudflats, and salt pans in Aruba, Curaçao, and Bonaire (Voous 1983). In Ecuador and Peru, found along Pacific Coast in lowland areas during fall migration (Paynter 1995).

#### WINTER RANGE

Little information. Grassland, savanna, open agricultural areas, and freshwater and brackish areas (Ridgely and Tudor 1989). In Paraguay, uses aquatic habitats more than fields, marshes, and beaches (Hayes et al. 1990). In Chilean desert, individuals observed feeding and roosting at a reservoir, the only large body of water in the area (Howell 1975). Flock of 60–80 observed feeding over coastal marsh at mouth of river in Chile (Schulenberg 1987).

### FOOD HABITS

#### FEEDING

*Main foods taken.* Takes flying or jumping insects almost exclusively on the wing. Occasionally eats terrestrial and aquatic insects or larvae. Rare consumption of vegetable matter appears to be accidental.

*Microhabitat for foraging.* Aerial feeder over lakes, ponds, rivers and streams, meadows, fields, pastures, and bogs; occasionally over forests and woodlands (Stoner 1936, Gross 1942, Turner and Rose 1989). When breeding, feeding sites usually are within 200 m of where young fed, but this distance may vary depending on availability of foraging areas (Mead 1979a, Turner 1980). Feeds at average height of 15 m over open ground in Great Britain (Waugh 1978), but may feed low over water

in bad weather (Turner and Rose 1989) or as high as 33 m (Bryant and Turner 1982).

*Food capture and consumption.* Aerial feeder from dawn to dusk. Occasionally takes items from surface of water and ground. Feeding on ground occurs sporadically; appears to be related to large, localized concentrations of suitable insect prey (Hobson and Sealy 1987). Feeds singly, in pairs, or in flocks, the latter more frequently when feeding on localized source of prey (Stoner 1936, Turner and Rose 1989).

Small colonies (5–55 nesting pairs) do not function as information centers for foraging birds; i.e., successful foragers do not transmit information about location of food centers to other individuals in the population (Hoogland and Sherman 1976, Stutchbury 1988). At a large (2,100 nesting pairs) Sand Martin colony in Hungary, however, group foraging synchrony was found to support the hypothesis of the colony as an information center (Szep 1991a). Therefore, colony size may influence social foraging behavior.

In Scotland, heavier insect boluses were brought to nestlings when foraging distances were greater, and bolus weight was significantly positively correlated with rainfall, flight speed, foraging distance and time, bolus collection time, and number of insects per bolus. Boluses weighed less when temperatures were low. Foraging-trip distance was significantly negatively correlated with prey mass and temperature but positively correlated with rainfall (Bryant and Turner 1982).

#### DIET

Stomach contents of 394 individuals were collected from Apr to Sep from various sites in U.S. and Canada (Beal 1918): Insects constituted 99.8% of diet; noninsects (spiders) and plant material represented the remainder. Insect composition included 33.5% ants, bees, and wasps (Hymenoptera), 26.6% flies (Diptera), 17.9% beetles (Coleoptera), 10.5% mayflies (Ephemeroptera), 8.0% bugs (Hemiptera), 2.1% dragonflies (Odonata), and 1.2% butterflies and moths (Lepidoptera). The diet of 21 adults from May to Jul in New York consisted of beetles (21.1% by frequency, 49.8% by weight); flies (20.0 and 27.6%); bugs (28.4 and 13.6%); ants, bees and wasps (16.8 and 3.3%); stone flies (Plecoptera; 1.1 and 4.5%); spiders (Araneida; 4.2 and 0.4%); other insects and vegetative material (8.4 and 0.8%) completed the diet (Stoner 1936). For 43 young from Jun to Jul in New York, diet consisted of flies (19.9% by frequency, 33.6% by weight); beetles (17.9 and 29.5%); bugs (34.3 and 29.0%); ants, bees and wasps (17.4 and 6.8%), and miscellaneous insect and vegetative material (10.5 and 1.1%; Stoner 1936). Soft-bodied flies constituted about

half the diet by weight of young during early part of nesting period (Jun) and about one-fifth during latter part of nesting period (Jul). Conversely, hard-bodied beetles constituted about one-fifth of the diet by weight in Jun and almost 40% in Jul.

Little information on diet during migration or on wintering grounds. Paton and Fellows (1994) found Bank Swallows feeding on the ground on adult brine flies (*Ephydra* spp.) during spring and fall migration periods at Great Salt Lake, UT.

#### FOOD SELECTION AND STORAGE

For food preferences, see Feeding, above. Not known to store or cache food.

#### NUTRITION AND ENERGETICS

See Turner 1982 for nutritional value of insect prey available to Sand Martins and for nutritional requirements of egg-laying females in Scotland. Female Sand Martins laying eggs may experience calcium deficits because of constraints in foraging time (Turner 1982). Incubating adults or those rearing nestlings can survive a day of normal activity without feeding only because potential energy reserves in body lipid and protein are small compared to the reserves needed for daily existence (Jones 1987a).

Daily energy budgets of Sand Martins during egg-laying and incubation periods in Scotland are estimated to be 24.8 and 17.5 kcal/d, respectively (Turner 1982). During incubation, daily energy expenditure of female Sand Martin averaged 81.70 kJ/d  $\pm$  0.41 SD ( $n = 3$ ); of flying female, 90.03 kJ/d  $\pm$  14.22 SD ( $n = 4$ ). During flight, daily energy expenditure of male Sand Martin averaged 93.66 kJ/d  $\pm$  12.17 SD ( $n = 6$ ; Westerterp and Bryant 1984). No energy studies exist for North America.

#### METABOLISM AND TEMPERATURE REGULATION

No data for North America. Average daily metabolic rate (ADMR) for incubating female Sand Martins in Scotland was 8.99 cm<sup>3</sup> CO<sub>2</sub>/g/h  $\pm$  0.28 SD ( $n = 3$ ), while ADMR for flying females was 10.88 cm<sup>3</sup> CO<sub>2</sub>/g/h  $\pm$  1.23 SD ( $n = 4$ ; Westerterp and Bryant 1984). ADMR for flying male Sand Martins was 11.55 cm<sup>3</sup> CO<sub>2</sub>/g/h  $\pm$  1.19 SD ( $n = 6$ ). Metabolic intensity of adult Sand Martins dropped as insect abundance increased and as weather conditions improved (Westerterp and Bryant 1984).

Metabolic rates of nestlings gradually increased from 4 to approximately 10 cal/(g•h) as body mass increased from 2.0 to 10.0 g (Marsh 1979). There is a rapid increase to a metabolic rate of >30 cal/(g•h) as body mass increases to 13.0 g. Nestlings become completely homoiothermic when they weigh >14 g at around 9 d, and active metabolic regulation

develops rapidly as nestlings increase in mass to >10 g (Marsh 1979).

#### DRINKING, PELLET-CASTING, AND DEFECATION

Drinks almost exclusively on the wing by skimming water surface and scooping up water with lower mandible. Drinks mostly in groups. Adults fly out of nest burrow several meters to defecate, and they remove fecal sacs of nestlings and drop them on the ground several meters from burrow entrance (BAG). No information on casting pellets.

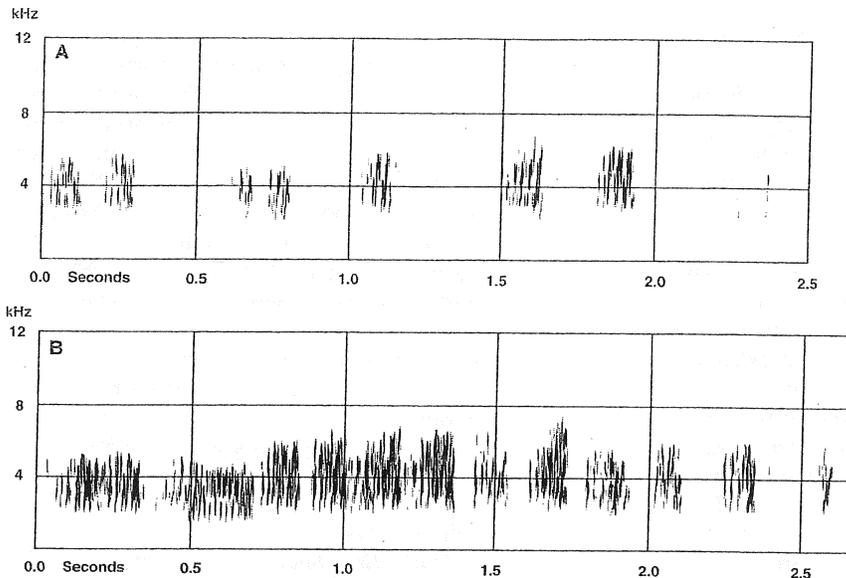
## SOUNDS

#### VOCALIZATIONS

**Development.** From Beecher et al. 1981a, 1981b, and Sieber 1985. Gives soft, low Food-Begging Calls from day of hatching. Food-Begging Calls are replaced by Signature Calls when chicks are 15–17 d old; Signature Calls are uniquely recognizable to adults. A few days before fledging, nestlings begin twittering and warbling while perched at burrow entrances; adults learn the calls of their nestlings in a few days. This development occurs during a period that coincides with intermingling of young from surrounding burrows, thus allowing adults to distinguish among young. No evidence for vocal learning, sensitive periods, or vocal mimicry.

**Vocal array.** The following discussion covers the species throughout its worldwide range. Signature Call is used by juveniles when soliciting food from adults; this call becomes louder with age (Beecher et al. 1981b, Sieber 1985, Cramp et al. 1988). Signature Call is given by juveniles in nest burrows and when assembled away from colony. Nestlings near fledging vocalize at burrow entrances. Feeding Call (see below) is given by adult entering burrow to feed nestlings.

**SONG.** Song is the most frequent and distinctive vocalization (Cramp et al. 1988), usually given by male for territorial advertisement, courtship, and mating. Adult males sing in flight, at nest hole, during mate-guarding chases, and when mounting female. Both sexes sing during pair formation and to threaten conspecifics. Song is harsh twittering, and little more than a sequence of Contact Call (see below; Cramp et al. 1988). Variations include harsh, bubbling, rapid (3–5/s) chatter—*chik-ik, chik-ik cheik cherk cherk cherk cherk* (Fig. 2A)—or continuous chattering—*ch-cher ch-cher cher chi-chi-chi-chi-chi-chi-chi-i-i-i-i-i* (Fig. 2B; Cramp et al. 1988). Song described as having 3 variants (Petersen 1955): soft twittering by both members of pair sitting together at nest entrance; louder, coarser, long irregular twittering when threatened; and harsh, almost



**Figure 2.** Sonogram of male Bank Swallow songs. Recorded 31 Jul 1956 at Cutler, ME. From Borror Laboratory of Bioacoustics (BLB) #2225. Sonograms produced by staff of BLB, Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with an effective frequency resolution of 75 Hz and a 200-point FFT transform size).

continuous bubbling chatter during mate-guarding chases.

**CONTACT CALL.** The most common call given by adults; a brief single rasp or 2-syllable *tschr* or *tschr* lasting 0.2–0.3 s (Sieber 1985, Cramp et al. 1988, D. Winkler pers. comm.); also described as strident *dsch* or *dsch-dsch* given by male before landing at nest site. In Contact Calls of males, first note is longer and overall call is shorter and of higher frequency than in Contact Calls of females (Sieber 1985).

**EXCITEMENT CALL.** Name from Cramp et al. 1988. Very similar to Contact Call; series of *dschad* sounds, given by females during nest-building in confrontations with intruding conspecifics (Kuhnen 1985).

**WARNING CALL.** Name from Sieber 1985. Unmodulated, pure-tone call of varying duration and repetition that sounds like *tsee-er* or *tsee-ip*. Given when ground or aerial predator approaches colony.

**ALARM CALL.** Lower-pitched than Warning Call; given singly by birds alerted by Warning Call. Nestlings retreat into burrows in response to Alarm Calls (Windsor and Emlen 1975). Birds give Warning and Alarm calls whenever they observe a predator, but most often while in flight (BAG), warning other members of colony. Alarm Call seems directed at predator; typically birds fly at predator, mobbing it, and emitting barrages of Alarm Calls. Other colony members respond by exiting burrows and joining mobbing group.

**FEEDING CALL.** Series of sweet, fine notes given by adults entering nest burrow to feed nestlings (Beyer 1938). Little geographic variation.

**Phenology.** Vocalizes freely throughout year. Sexual differences not known.

**Daily pattern.** Time of day has little influence on pattern of vocalizing; intensity is generally the same throughout the day.

**Places of vocalizing.** Vocalizations are common in both flying and perching birds, generally near nest site. Males are more likely to sing around nest site, while chasing mate, and when mounting female (Cramp et al. 1988). Some vocalization is given in burrow.

**Repertoire and delivery of vocalizations.** Food-Begging Call of nestling develops into Signature Call, which is individually distinctive enough that adults can recognize their own chicks (Beecher et al. 1981a, 1981b, Sieber 1985). Warning Call is elicited upon sudden appearance of anything alarming; Alarm Call is given in response to Warning Call. First bird detecting danger gives Warning Call. Adults and juveniles give Contact Calls when encountering mates or adults, respectively.

#### NONVOCAL-SOUNDS

Small nestlings give irregular “pop” sounds, which may be the result of bill-snapping (Cramp et al. 1988).

## BEHAVIOR

### LOCOMOTION

**Walking, hopping, climbing, etc.** Descends to ground away from nest burrow only when gathering nest materials or foraging (rarely). Ordinary gait is shuffling walk. Movement is jerky and rapid, seemingly nervous. Climbs along vertical banks at nesting colonies using feet and flapping wings.

Sidles along a wire, tree branch or root, or bank face using sideways walk.

**Flight.** From Blake 1948, except as noted. Fluttery, almost butterfly-like, with little gliding. Flight is fast, but involves more gliding and fewer twists and turns than flight of Barn Swallow; more fluttery than flight of Northern Rough-winged and Tree swallows (Lethaby 1996). Wing-beats are shallow and rapid (Turner and Rose 1989); glides are short (1–2 s) and unstable. Wings are sharply bent at carpal joint and held close to head, straight and transverse when gliding. Tail spread open with terminal margin appearing straight when gliding. Course changes are infrequent when bird is flying toward nesting colony, but relatively frequent and rapid during foraging. Averages 2.8 wingbeats/s  $\pm$  0.14 SD (range 2.6–3.1,  $n$  = 14) in coursing flight, 3.7 wingbeats/s  $\pm$  0.36 SD (range 3.1–4.5,  $n$  = 10) in climbing flight. Swoops low and approaches nest burrows on upward slant, spreading wings quickly to land on lip when perching. When feeding nestlings, darts directly into burrow without landing until inside; leaves burrow in straight, long glide, dropping sharply, wings held back, and generally without beating wings for >1 m.

**Swimming and diving.** Not known to swim or dive, but fighting adults, nestlings, and fledglings fall out of nests over water; young nestlings can drown; adults and fledglings can swim back to shore by propelling themselves with backward strokes of wings. Birds purposefully dive and hit water to gather nest materials, forage, bathe, and drink.

#### SELF-MAINTENANCE

**Preening, head-scratching, stretching, bathing, anting, dust-bathing, etc.** Preens singly or in large communal groups. Communal preening occurs primarily during migration (Cramp et al. 1988). Preening includes head-scratching over wing. Stretches by extending 1 wing at a time below feet, then extends both in "V" over back; sequence often immediately precedes flight. Dust-bathes on ground in areas of loose bare soil (Hobson and Sealy 1987) in large groups (up to 2,000–3,000 birds; Gross 1942). Bathes by wading into shallow water or hitting surface of water briefly while flying (Cramp et al. 1988). Not known to ant.

**Sleeping, roosting, sunbathing.** Sunbathes by spreading open both wings slightly away from body, ruffling feathers, gaping, rolling over to one side, and slightly raising uppermost wing (Barlow et al. 1963); may sunbathe in mixed-species flocks with Cliff Swallows.

Roosting described by Petersen (1955), Sieber (1980), and Cramp et al. (1988), except as noted. From start of nest-building through beginning of

egg-laying, both members of pair usually roost in nest burrow; roosts in other burrows and on trees and shrubs near colony when nestlings are  $\geq$ 12 d old. Female roosts mostly in nest burrow while incubating eggs and brooding young nestlings at night, while male roosts nearby, although male is known to brood nestlings at night. Young roost in nest burrow for approximately 1 wk after fledging. After fledging and before fall migration, juveniles and adults roost together in trees, on exposed roots on banks, in shrubs, and on logs on sandbars and gravel bars. In adverse weather, several adults may cluster together in small groups of birds in burrows (Cramp et al. 1988). During migration, roosts communally in large groups (as large as 50,000–2 million birds; Great Britain); migration roosts include vegetation at wetlands and marshes (Paton and Fellows 1994).

**Daily time budget.** No quantitative data from North America. Upon arrival on breeding grounds in spring, birds generally spend much of day foraging, gradually spending more time at colony site as season advances. Spends much time in courtship activities and nest-building early in breeding period, before egg-laying. Once eggs are laid and nestlings hatch, adults spend considerable time incubating or brooding and foraging. After young fledge, birds gradually spend more time foraging away from colony sites each day until migrating. In Scotland, Sand Martins feeding nestlings aged  $\geq$ 7 d had daily time budgets of 33% roosting, 12% resting, and 55% flying (Turner 1983). Female and male Sand Martins, respectively, spent 70 and 63% of the day on nest during incubation, and 51 and 55% of the day flying while feeding nestlings (Westerterp and Bryant 1984).

#### AGONISTIC BEHAVIOR

**Physical interactions.** Birds fight by grappling and falling to ground, and physical contact is common among birds fighting for nests, mates, and nest materials. In fights around nest sites, individuals push intruder forcefully with bill, or hover, grasp nape, and pull intruder away; this behavior often leads to fights in which both birds peck, and fall locked together by feet to ground, where they struggle for several seconds. Fighting generally ends once young have hatched (Petersen 1955, Hoogland and Sherman 1976, Cramp et al. 1988).

**Communicative interactions.** From Kuhnen 1985 from nw. Germany, except as noted. Because of colonial habits, most interactions occur at colonies during nesting period. When nest tunnel is dug, one member of pair sits in entrance facing outward, and male sings through excavation period. Vocal threats and pushes are more effectively directed at intruders below or to either side of the burrow, so

burrows at higher positions become dominant. Male performs Advertising Display if another bird approaches: Sings Excitement Call, ruffles head- and throat-plumage, and vibrates closed wings (Petersen 1955). Preferred burrows are visited by several competing females, and paired females drive off intruders by spreading neck-feathers and aggressively displaying. After expelling intruding females, paired female displays bill-gaping postures, bristled head-feathers, and vibrating wings to paired male until she recognizes him (Kuhnen 1985).

#### SPACING

**Territoriality.** Actively defends only nest burrow and immediate vicinity. Defends area around occupied burrow early in nesting period, but after eggs hatch defends only burrow. Males vacate burrows that do not attract mates and establish new territories within colony, thereby causing surplus of burrows (Kuhnen 1985). Nest owners attack other birds that try to build a nest within 8–12 cm of their nest. Some nest tunnels, however, join other tunnels, leading to abandonment, presumably, of later tunneling attempt. Distances between nest burrows reported as 17.8–43.2 cm in Pennsylvania ( $n = 20$  colonies; Spencer 1962), 18.5 cm (range 10.2–43.2,  $n = 72$  burrows) in Wisconsin (Petersen 1955), and  $13.2 \text{ cm} \pm 1.1 \text{ SD}$  (range 1–59,  $n = 32$  colonies) in California (Humphrey and Garrison 1987).

**Individual distance.** Extremely social at all times, seeking out other individuals whenever away from nest. Preening birds on wires and vegetation are often spaced as closely as 3–4 cm, or with shoulders touching (BAG). Bank Swallows sometimes huddle with their bodies pressed together with those of conspecifics and Tree Swallows during periods of cold weather (Meservey and Kraus 1976).

#### SEXUAL BEHAVIOR

**Mating system and sex ratio.** Socially monogamous; only 1 male and 1 female tend nest; neither sex is known to establish ownership of >1 nest. No information from DNA studies.

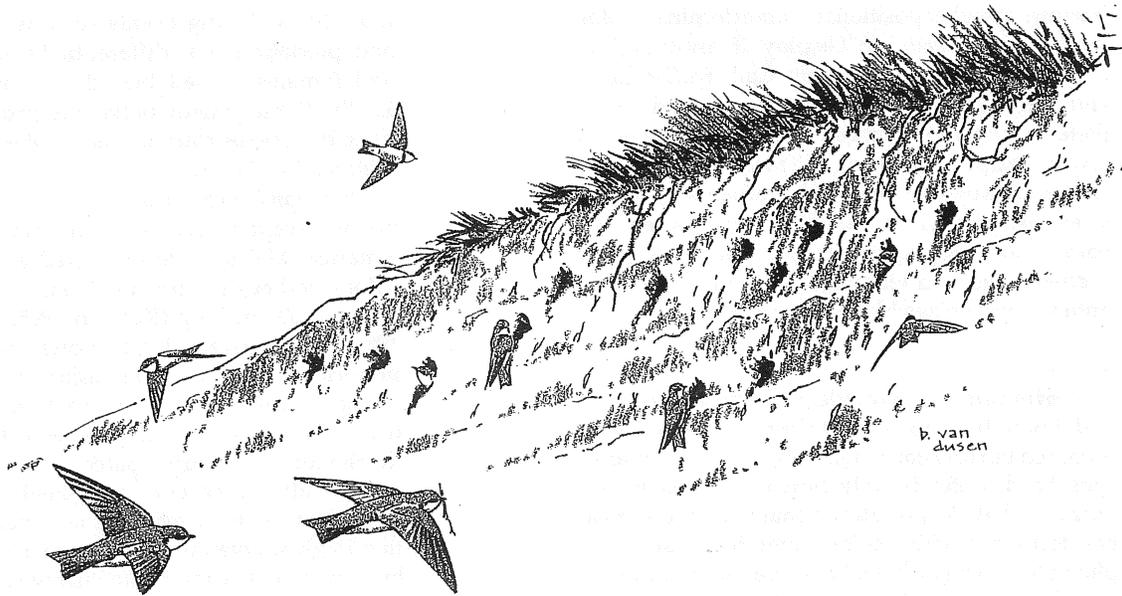
Adult sex ratio information from some banding studies indicates sex ratios slightly biased toward females, but bias likely exists with banding because birds are trapped at nest burrows, where females do most of incubating and brooding, and because identification of sexes can be difficult early in breeding period. Adult male:female sex ratios from North American banding efforts include 1:1.16 ( $n = 1,969$ ; Freer 1977) or 1:1 ( $n = 122$ ; P. Capainolo pers. comm.) in New York; 1:1.09 in Wisconsin ( $n = 2,156$ ; MacBriar 1988); and 1:1.24 in California ( $n = 1,676$ ; BAG). In Sweden, however, male:female sex ratios in captured Sand Martins were highly variable, ranging from 1.95:1 to 1:1.30 over 4-yr period;

mortality-inducing events such as bank collapse and predation that differentially affected males and females caused biased sex ratios (Persson 1987b). Some genetic polygamy probably occurs, since both sexes routinely attempt extra-pair copulations (see below).

**Pair bond.** From Kuhnen 1985 from nw. Germany, except where noted; no data from North America. Males settle into fixed area of nesting colony and begin attracting females when burrow is about 30 cm long (Kuhnen 1985, Cramp et al. 1988). While excavating burrows, unpaired male performs Territory Circle-Flights: Flies and sings in small circles around burrow entrance advertising to unpaired females; male perches on burrow ledge displaying white throat-patch if female lands near burrow after Territory Circle-Flight (see Fig. 3). When burrow is excavated, males perform Invitation Flights: Overtake flying females and land at burrows to entice them into burrows. During nest-building, males perform Guarding Flights, accompanying flying females with nest materials to burrow. Mate-Pursuit Flights (sexual chases), in which paired males drive away intruding males, occur 3–5 d before egg-laying. Unpaired males perform Advertising Displays (see Agonistic behavior, above) where they face out from burrow. As pair bond forms, both sexes sing twittering songs while perched side by side or facing each other at burrow entrance.

Pair bonds have been formed when (1) female regularly visits a particular burrow, where she engages in sporadic excavations while male does most excavation; (2) both birds spend long periods of time together (including the night) in burrow; and (3) male performs Invitation and Guarding flights. Copulations occur mostly in burrows and are rarely observed, but they also occur on the ground, wires, and bank face, and in the air (Turner and Rose 1989). In copulation, male sings while approaching female, sometimes quivering his wings; mounts and copulates with wings raised.

**Extra-pair copulations.** Mate-Pursuit Flights (see above) by males for extra-pair copulations are common (Petersen 1955, Beecher and Beecher 1979, Kuhnen 1985). Males apparently attempt extra-pair copulations with females only during their fertile period (Hoogland and Sherman 1976, Jones 1986). Competing females visit burrows of breeding pairs, and paired females drive off intruders (Kuhnen 1985). Males perform Guarding and Mate-Pursuit flights during egg-laying, in which they protect mates from insemination by other males and search for opportunities for promiscuous copulations, respectively (Beecher and Beecher 1979). Mate-Pursuit Flights typically involve the female, her mate, and 1–5 other males. All males



follow the intricate maneuvers of the female, and paired males try to steer the female back to nest burrow (Beecher and Beecher 1979, Kuhnen 1985). Because of success of mate-guarding, promiscuous copulations are not as common as frequency of Mate-Pursuit Flights (Beecher and Beecher 1979). Males selectively chase heavier female Bank Swallows for extra-pair copulations because females are heaviest during laying and prelaying periods (Beecher and Beecher 1979, Jones 1986).

#### SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** Strongly colonial, typically nesting in colonies of up to 1,500 nesting pairs; rarely nests solitarily (Hoogland and Sherman 1976, Cramp et al. 1988, Turner and Rose 1989). Many complex social behaviors have evolved as a result of this highly colonial nature, including coordinated foraging activities, territoriality, courtship, parent-offspring recognition, and predator avoidance (Emlen and Demong 1975, Windsor and Emlen 1975, Hoogland and Sherman 1976, Beecher et al. 1981a, Turner and Rose 1989).

**Nonpredatory interspecific interactions.** Other birds routinely nest in Bank Swallow colonies in other burrows or nests, including Barn Owl (*Tyto alba*), Belted Kingfisher (*Megaceryle alcyon*), Northern Rough-winged Swallow, and Cliff Swallow (Lunk 1962, BAG).

Bank Swallows routinely flock with other swallow species during migration, but there is no evidence of any cooperative or commensal foraging.

#### PREDATION

**Kinds of predators.** Mammals, birds, and snakes prey on Bank Swallow. In California, American

**Figure 3.** A Bank Swallow colony with birds doing many courtship and pair-bond behaviors including Guarding Flight, Advertising Display, and Territory Circle-Flight. Drawing by Barry Van Dusen.

Kestrels (*Falco sparverius*) take birds primarily on the wing; gopher snakes (*Pituophis melanoleucus*) are the predominant predator of nestlings in burrows at colonies (BAG). In other areas, important predators include American Kestrels in New York (Freer 1973, Windsor and Emlen 1975), Michigan (Hoogland and Sherman 1976), and Alaska (Hickman 1979); and black rat snakes (*Elaphe obsoleta*) in Virginia (Blem 1979).

No information on predators during migration and on winter range.

**Manner of predation.** Snakes climb into burrows from bottom or top of nesting banks (BAG). Snakes can spend several days in a colony, feeding on an entire brood, coiling inside a nest, digesting food, shedding skin, then moving to another burrow. Snakes appear to be the most important predators because the close proximity of burrows and clustering of successful nests enhances a snake's access and foraging success. American Kestrels take individuals in the air by flying into mobbing flocks or chasing birds singled out from aerial groups; kestrels also take nestlings from burrow entrances or reach into burrow with one foot (Windsor and Emlen 1975). Most aerial predation by American Kestrels and other raptors takes place during fledging period, when young are vulnerable (Windsor and Emlen 1975, Szep and Barta 1992).

Number of attacks and number of Sand Martins caught by Hobbies (*Falco subbuteo*) at colonies in Hungary increased with colony size (Szep and Barta 1992).

**Response to predators.** Typical response of Bank Swallows to aerial predators is high-pitched Warning Call (see Sounds: vocalizations, above) given in triplets. This initial Warning Call causes other adults

to form loose flock, and they begin to utter Alarm Calls. As first Alarm Calls are given, nestlings perched at burrow entrances begin tail-first retreat into their tunnels (Windsor and Emlen 1975). Predators largely ignore mobbing individuals (Windsor and Emlen 1975), although mobbing behavior of Bank Swallows was occasionally effective at deterring predation of nestlings by Blue Jay (*Cyanocitta cristata*; Hoogland and Sherman 1976). Larger colonies detect and mob potential predators more rapidly than do smaller colonies (Hoogland and Sherman 1976). Colony sites have been deserted as habitat suitability decreased and predation by black rat snakes increased (Blem 1979).

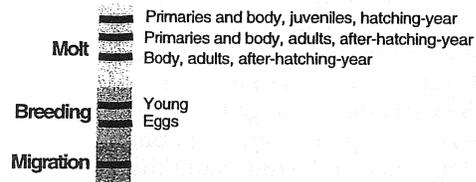
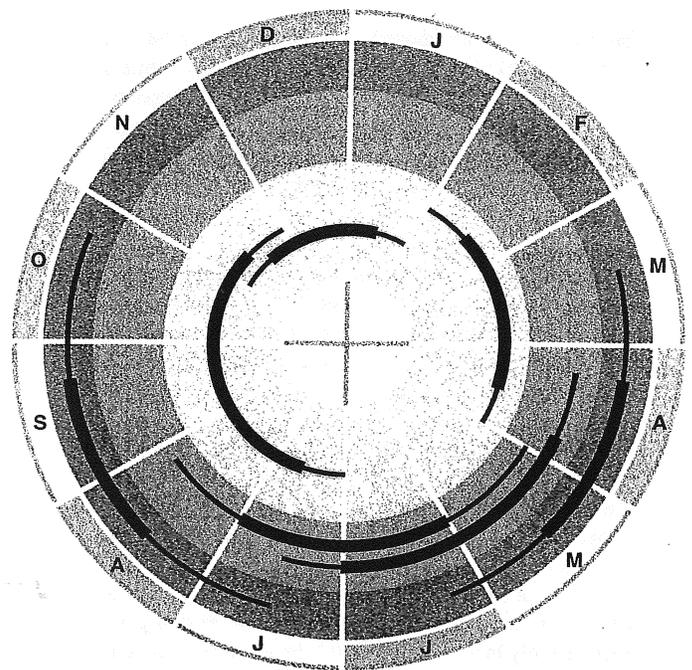
Warning and Alarm calls and mobbing are elicited only by flying American Kestrels; perched individuals are largely ignored (Windsor and Emlen 1975). In California, however, Bank Swallows have not been observed to mob Belted Kingfishers, which nest in same banks as Bank Swallows, and Bank Swallows seem to ignore gopher snakes exposed on bank face (BAG).

**BREEDING**

**PHENOLOGY**

**Pair formation.** Pairs form as soon as birds begin visiting colony sites; pair formation coincides with establishment of nest ownership or beginning of nest-building. For representative arrival dates, see Migration: timing and routes of migration, above, and Figure 4. Birds arrive at colony sites in flocks of usually unpaired males and females, and first flocks consist of approximately balanced sex ratios of older, experienced birds visiting traditional nesting-colony sites (Kuhnen 1985). First birds to arrive in California spend first 2-3 wk mostly foraging, and probably do not begin pair formation immediately; later-arriving birds visit colonies and start forming pairs immediately upon arrival (BAG). Those arriving during next 1-2 wk are mainly first-year birds (Mead and Harrison 1979, Kuhnen 1985). Flocks arrive separately in different areas with suitable habitat, and pair-formation activities are synchronized within these areas, thus forming subcolonies (Petersen 1955, Kuhnen 1985).

**Nest-building.** Shortly follows completion of pair formation and digging of burrow; males begin excavating burrow before securing mate. Burrow excavation takes 4-5 d (maximum 14) to complete, depending on weather conditions and soil (Sieber 1980, Turner and Rose 1989). Nest-building begins immediately after burrow is completed and takes additional 1-3 d (Asbirk 1976, Sieber 1980). Nest-building recorded as early as 12 Apr in California



**Figure 4.** Annual cycle of breeding, migration, and molt of Bank Swallow. Thick lines show peak activity; thin lines, off-peak.

(BAG), 29 Apr in Illinois (Graber et al. 1972), and 19 May in Michigan (Brewer et al. 1991).

**First/only brood per season.** Probably single-brooded throughout North American range, although replacement clutches are produced if nest fails during early or middle part of breeding season. Egg-laying recorded as early as 11 Apr in California (BAG), 27 Apr in British Columbia (Campbell et al. 1997), and 4 May in Ontario (Peck and James 1987). Most clutches are initiated after these dates. Peak periods of egg-laying include 20 Apr-10 May in California (BAG), 2-15 Jun in Ontario (Peck and James 1987), and 15-28 Jun in British Columbia (Campbell et al. 1997). Egg-laying recorded as late as 19 Jul in British Columbia (Campbell et al. 1997), 13 Jul in New York (reported as second brood; Bull 1985), and 17 Jul in Ontario (Peck and James 1987). Young have fledged from most populations by mid-Jul, but slightly earlier in mid-latitude states.

Initiation of egg-laying in Swedish Lapland is related to emergence dates and abundance of flying insects, which are in turn affected by amount of snow-free ground and by temperatures in May and Jun (Svensson 1986).

**Second/later brood(s) per season.** Second broods not fully documented in North America (Petersen 1955, Peck and James 1987), but see Bull 1985 and

Hjertaas 1984 for possible exceptions. Incidents with second clutches laid in burrow that previously fledged young may represent nesting attempts by different adults (Peck and James 1987). Second broods are known from Sand Martins in most of their w. Palearctic range (Cramp et al. 1988).

#### NEST SITE

**Selection process.** Individuals choose colony site first, then burrow site. Birds range over several kilometers within larger population area while assessing colony sites before selecting one. Colony-site selection probably is based on colony size and breeding success of the previous year as larger colonies with successful breeding tend to be re-colonized (Freer 1979). The ephemeral nature of colony sites results in relatively low levels of tenacity to previous colony sites (Freer 1979, Hjertaas 1984, Jones 1987b).

As adaptations for burrow-digging, Bank Swallows have smaller, more conical bills, and a proportionately larger cucullaris-lateral rectus muscle complex than other swallows (Gaunt 1965). Burrows are dug with the bill, feet, and wings (Stoner 1936) as birds cling to a slight projection on the bank face, and dig using their bill in a rapid, slashing motion and feet in a scratching motion. Dislodged material from inside the burrow is ejected with vigorous kicks and wriggling body and wing shuffling movements. Burrows are excavated by groups of individuals, and excavation tends to be clustered in colony so that breeding is synchronized within sections (Hoogland and Sherman 1976, Freer 1977, Sieber 1980). See Behavior: sexual behavior, above.

Males settle on fixed area in colony to begin excavating burrow; attract females when burrow tunnel is at least 30 cm deep (Kuhnen 1985). On arrival at colony site, >90% of first landings are at old burrows (Sieber 1980), mostly by males (Cramp et al. 1988). Unpaired males dig only a shallow hole during early stages of selection phase (Petersen 1955). Females hover in front of burrows looking for prospective mates (Kuhnen 1985). To inspect sites, prospective pairs land at burrow entrance, run into burrow, and excavate. Males dig most of burrow and nest chamber; females build most of nest (Kuhnen 1985). Birds >1 yr old arrive at colony sites 2–3 wk before first-year birds (Mead and Harrison 1979, Jones 1987b); thus older birds have greater choices of nest sites within colony, and they settle in best area of colony (Jones 1987b). High-quality locations are higher up on bank face in areas of firmer soils to reduce risk of predation and collapse (Sieber 1980, Jones 1987b). Reproductive success is greater for higher burrows (Hoogland and Sherman 1976, Cramp et al. 1988). Selection of burrow sites is affected by presence of conspecifics;

individuals are more likely to visit areas of high burrow density than areas of low density, but number of competitive interactions increases with increasing burrow density (Sieber 1980).

**Microhabitat.** Generally digs burrow parallel to ground surface and perpendicular to bank face. Depth of nest burrow averages 58.8 cm  $\pm$  11.1 SD (range 25–102,  $n$  = 25 colonies, 2,384 burrows) in Pennsylvania and Vermont (Spencer 1962), 61.5 cm  $\pm$  1.7 SD (range 10–105,  $n$  = 32 colonies) in California (Humphrey and Garrison 1987), 63.6 cm  $\pm$  19.3 SD (range 15–145,  $n$  = 545 nests) in Saskatchewan (Hjertaas 1984), 64.4 cm  $\pm$  19.7 SD (range 28–137,  $n$  = 512 nests) in Alaska (Hickman 1979), 71 cm (range 38–119,  $n$  = 89 nests) in New York (Stoner 1936), and 90 cm (range 42–180,  $n$  = 39 nests) in British Columbia (Campbell et al. 1997). Burrows in gravelly soils are often shallower than those in sandy, silty, loamy soils (Petersen 1955, Hickman 1979), but see Hjertaas 1984. In Switzerland, burrows in loose sand were deeper than those in compact sand, and deep burrows had greater breeding success than shallow burrows (Sieber 1980). Burrows started later in breeding period are shorter than those started earlier (Hickman 1979). Height and width of burrow entrances averaged 3.8  $\times$  6.4 cm in Alaska (Hickman 1979), 5.5 cm  $\pm$  0.6 SD  $\times$  7.2 cm  $\pm$  1.1 SD in California (range 3–11 height, 5–14 width;  $n$  = 32 colonies; Humphrey and Garrison 1987), and 6  $\times$  7 cm in British Columbia (range 4–10 cm height, 6–10 cm width,  $n$  = 28 burrows; Campbell et al. 1997).

Burrows are excavated at various rates throughout Bank Swallow's range, depending on soil friability (Petersen 1955, Spencer 1962, Hickman 1979). Average daily excavation rates reported for Alaska include 2.7 cm  $\pm$  1.4 SD ( $n$  = 24) in gravel; 10.0 cm  $\pm$  8.9 SD ( $n$  = 76) in coarse, compact soil; 8.3 cm  $\pm$  5.5 SD ( $n$  = 74) in fine, compact soil; 12.8 cm  $\pm$  10.7 SD ( $n$  = 19) in coarse soil with gravel; and 9.4 cm  $\pm$  8.2 SD ( $n$  = 12) in fine soil (Hickman 1979). Nest cavity is located at terminal end of burrow and enlarged upward and to both sides, and nest-cavity floor is level with burrow floor (Hickman 1979).

**Site characteristics.** See above; also Habitat, above. Nesting colonies are generally located along rivers, streams, lakes, and ocean coasts, or in sand and gravel pits. Often near open water, probably because of alluvial nature of soils and role of water as erosive force. Often located along larger rivers, streams, and lakes because birds require relatively large open areas for vertical flying space around nest burrows (Hjertaas 1984).

In Pennsylvania and Vermont, 13 (52%) of 25 colonies were in gravel and sand pits, 5 (20%) in road-cut banks, 5 (20%) in building-site excavations, 1 (4%) in coal pile, and 1 (4%) in riverbank (Spencer

1962). In Ontario, 430 (60%) of 713 individual nest records were from natural banks, 266 (37%) from sand and gravel pits, 9 (1%) from sand dunes, 5 (1%) from human-made piles of sand, gravel, and sawdust, and 3 (<1%) from plastic tubes in banks (Peck and James 1987). In British Columbia, 220 (27%) of 815 colonies were in road-cut banks, 139 (17%) colonies were in banks and cliffs of lakeshores, 65 (8%) colonies were in gravel pits, 57 (7%) were in riverbanks, and the other 334 (41%) were not documented (Campbell et al. 1997). In contrast, 105 (95%) of 111 colonies in California were in banks along rivers, lakes, streams, and coastlines, with remaining 6 (5%) colonies in an earthen berm, quarry, road-cut, or ground-potato mounds (Laymon et al. 1988).

Colonies are located in vertical faces of banks and bluffs in friable soils that are mostly sandy, silty, loamy soils, all characterized by small particle sizes. In Pennsylvania and Vermont, 2 (8%) of 25 colonies were in gravel soils, 5 (20%) in sand soils, 12 (48%) in loamy sand soils, and 6 (24%) in sandy loam soils (Spencer 1962). In California, 14 (64%) of 22 colonies were in sandy loam soils, 4 (18%) in loam sand soils, 3 (14%) colonies in loam soils, and 1 (5%) in sand soils (BAG). Specific soil composition around nests was 7–10% silt and 87–90% sand in Ottawa ( $n = 26$ ; John 1991); 2–48% silt, 2–12% clay, and 48–95% sand and gravel in Pennsylvania ( $n = 25$  colonies; Spencer 1962); and 3–61% silt, 2–30% clay, and 22–93% sand in California ( $n = 71$ ; BAG). Bank Swallows strongly selected ( $p < 0.001$ ) for soils with relatively large amounts of fine gravel and sand (particle size 0.425–12.5 mm) and against silts (particle size <0.15 mm; Hjertaas 1984).

Heights of vertical banks at nesting colonies averaged 1.8 m (range 0.5–6.6,  $n = 60$ ) in Saskatchewan (Hjertaas 1984, Hjertaas et al. 1988), 3.2 m  $\pm$  1.9 SD (range 0.9–7.6,  $n = 25$ ) in Pennsylvania and Vermont (Spencer 1962), and 3.3 m  $\pm$  1.7 SD (range 1.3–7.3,  $n = 32$ ) in California (Humphrey and Garrison 1987). In Saskatchewan, average height of vertical banks with nesting colonies (1.8 m,  $n = 60$ ) was significantly ( $p < 0.002$ ) greater than that of unused banks (1.4 m,  $n = 349$ ; Hjertaas 1984). Lengths of banks at nesting colonies averaged 30.9 m (range 4.2–221.0,  $n = 60$ ) in Saskatchewan (Hjertaas 1984, Hjertaas et al. 1988), 57.1 m  $\pm$  58.6 SD (range 9.1–304.8,  $n = 25$ ) in Pennsylvania and Vermont (Spencer 1962), and 455 m  $\pm$  441 SD (range 13–1,900,  $n = 32$ ) in California (Humphrey and Garrison 1987). Longer banks are found along rivers and streams. In Saskatchewan, average length of nesting banks (30.9 m,  $n = 60$ ) was significantly longer ( $p < 0.044$ ) than that of unused banks (21.9 m,  $n = 349$ ), and there was no particular preference in compass orientation of colonies (Hjertaas 1984).

Burrows are mostly in upper third of bank (Spencer 1962, Humphrey and Garrison 1987, Hjertaas et al. 1988), where they are less susceptible to many ground predators (Sieber 1980). Burrow density decreases from top to bottom of bank (Sieber 1980). Burrows in Saskatchewan averaged 111.2 cm  $\pm$  49.1 SD (range 25–340,  $n = 545$ ) from base of bank and 64.5 cm  $\pm$  45.5 SD (range 10–320,  $n = 545$ ) from top of bank (Hjertaas et al. 1988), while burrows in Pennsylvania and Vermont averaged 85.1 cm  $\pm$  80.4 SD (range 17.7–320.2,  $n = 25$ ) from top of bank (Spencer 1962). Top burrows averaged 70 cm  $\pm$  57 SD (range 5–140,  $n = 32$  colonies) from top of bank in California (Humphrey and Garrison 1987).

Nesting colonies are ephemeral, particularly those on banks and bluffs along waterways where primarily erosion determines habitat suitability. Larger colonies are located on longer banks, and these larger colonies tend to persist longer than smaller colonies (Freer 1977, BAG).

#### NEST

**Construction process.** Construction begins shortly after burrows are completely excavated (Beyer 1938, Petersen 1955, Sieber 1980, Cramp et al. 1988). Birds gather materials from the ground, and tear roots and rootlets from exposed roots on vertical banks (Petersen 1955). Male begins building nest; nest-building is continued by both sexes, then by female (Kuhnen 1985). Nest-building, including burrow excavation, takes up to 14 d (average 4.4,  $n = 96$ ; Sieber 1980).

**Structure and composition matter.** Composition of nests varies and is indicative of materials available in area. Nests in British Columbia are flat platforms composed of grasses, feathers (42% of 12 nests), twigs (17% of 12 nests), straw, rootlets, plant stalks, or leaves (Campbell et al. 1997); Ontario nests are flat platforms usually composed of grass stalks and straw, and less often twigs, plant stalks, leaves, and rootlets (Peck and James 1987).

**Dimensions.** Nest mat is about 2.5 cm thick in middle and thinner toward edges, conforming to saucer form of burrow-chamber floor (Petersen 1955). In Alaska, nest cavities in burrows averaged 16.9 cm  $\pm$  2.2 SD long, 11.5 cm  $\pm$  1.5 SD wide, and 8.7 cm  $\pm$  1.1 SD high ( $n = 40$ ; Hickman 1979). In Ontario, outside diameter of 1 nest was 12.5 cm (Peck and James 1987).

**Microclimate.** Temperatures more constant within nest cavities than outside the burrows. Nest-cavity temperatures in Montana averaged 20.3°C  $\pm$  2.2 SD (range 15.0–24.9,  $n = 1,471$ ), while temperatures on bank face outside ranged from 2.4 to 46.7°C ( $n = 1,471$ ; Ellis 1982). CO<sub>2</sub> concentrations increased while O<sub>2</sub> concentrations decreased in burrows as nestlings aged and increased in size

(Wickler and Marsh 1981) and as number of adults and nestlings in burrow increased (Birchard et al. 1984). CO<sub>2</sub> concentrations in burrow's air can cause high CO<sub>2</sub> levels in nestling's blood, causing chronic acidosis and increased respiratory rates (Wickler and Marsh 1981), although Bank Swallows are physiologically adapted to high CO<sub>2</sub> levels in blood (Kilgore and Birchard 1980). There is lowered convective ventilation in deeper burrows; hence CO<sub>2</sub> levels are greater in deeper burrows (Birchard et al. 1984).

**Maintenance or reuse of nests, alternate nests.** From Petersen 1955 and Hickman 1979. Digs new burrows each year, especially if bank or cliff face used for nesting the previous year collapsed from erosion or human activities and no old burrows remain. If old burrows remain, some may be reused, enlarged and deepened with excavation activities that are part of pair-bond formation. Old nests are often removed from reused burrows and new nests constructed. Generally avoids reusing old nests because of increased likelihood of infestation by fleas (*Ceratophyllus* spp.; Haas et al. 1980). Males producing second broods in Germany reused first-brood burrows more often than females did (Sieber 1980).

**Nonbreeding nests.** None.

#### EGGS

**Shape.** Subelliptical (Harrison 1984: 212).

**Size.** Mean length and breadth: Eggs from Michigan and Indiana averaged 18.1 x 12.9 mm (range 16.7–19.6 x 12.2–13.9,  $n = 11$  clutches, 48 eggs; J. Hinshaw unpubl.). From many locations in North America, egg length and breadth averaged 17.2 x 12.4 mm (range 15.2–18.9 x 11.3–13.3,  $n = 21$  clutches, 98 eggs; Western Foundation of Vertebrate Zoology [WVZ]). For Eurasian measurements, see Dement'ev and Gladkov 1968 and Cramp et al. 1988. No information on effects of female age or size, of clutch size, or of laying date on egg size.

**Mass.** Average wet-shell egg weight: 1.43 g (Turner and Rose 1989). One egg is about 10% of female mass.

**Color.** White (Harrison 1984: 212).

**Surface texture.** Smooth and slightly to moderately glossy (Harrison 1984: 212).

**Eggshell thickness.** Mean empty shell weight: Eggs from Michigan and Indiana weighed 0.073 g (range 0.056–0.086,  $n = 11$  clutches, 48 eggs; J. Hinshaw unpubl.). From many locations in North America, empty shells weighed 0.067 g (range 0.051–0.084,  $n = 21$  clutches, 98 eggs; WVZ).

**Clutch size.** In Alaska, mean 4.09 eggs/clutch  $\pm 0.78$  SD (range 2–6,  $n = 242$ ; Hickman 1979); in Ontario, 4.44 (range 1–9,  $n = 261$ ; Peck and James 1987); in Saskatchewan, 4.87  $\pm 0.92$  SD (range 2–7,  $n = 218$ ; Hjertaas 1984); in British Columbia, 3.51  $\pm 1.53$  SD (range 1–7,  $n = 67$ ; Campbell et al. 1997); in

Michigan, 4.98  $\pm 0.74$  SD (range 3–8,  $n = 217$ ; Hoogland and Sherman 1976); in New York, 4.38  $\pm 1.04$  SD (range 2–7,  $n = 170$ ; Freer 1977). In Wisconsin, clutches laid before 15 Jun averaged 5.03 eggs  $\pm 0.69$  SD (range 3–6,  $n = 104$ ), while clutches laid after 15 Jun averaged 4.00 eggs  $\pm 0.84$  SD (range 2–5,  $n = 21$ ). Entire Wisconsin sample averaged 4.86 eggs  $\pm 0.81$  SD (range 2–6,  $n = 125$ ; Petersen 1955). In Swedish Lapland, average clutch size varied annually during 15-yr study (3.85–5.00 eggs), largely because of changes in median egg-laying dates (Svensson 1986).

**Egg-laying.** Determinate layer, normally lays 1 egg/d during night and early morning (Petersen 1955, Hoogland and Sherman 1976). Deviations from pattern of 1 egg/d might be due to parental responses to unfavorable weather, or slight delays in timing of egg deposition or variations in timing of nest examinations, while consistency in pattern of 1 egg/d suggests little intracolony brood parasitism (Hoogland and Sherman 1976). Egg-laying in Sand Martins from Scotland is influenced by availability of small and medium-sized insects in spring, and sharing of incubation duties by both adults allows Sand Martins to nest earlier than other swallows despite greater risk of inclement weather (Turner 1982).

#### INCUBATION

**Onset of broodiness and incubation in relation to laying.** Sustained incubation initiated by female begins 1–2 d before clutch is complete (Petersen 1955, Turner and Rose 1989).

**Incubation patch.** Single medial abdominal patch develops in female during egg-laying; male lacks patch (Pyle 1997).

**Incubation period.** Little variation within and among populations. In Wisconsin, 13–15 d ( $n = 11$ ; Petersen 1955); in New York, 14–16 d (Stoner 1936); in Alaska, 14–15 d (Hickman 1979); and in Ontario, 13–16 d ( $n = 12$ ; Peck and James 1987).

**Parental behavior.** Female does majority of incubation; male incubates when female leaves nest. At night, female generally incubates; e.g., in Wisconsin, females incubated alone at 21 (66%) of 32 nests, males alone at 2 nests (6%), and both sexes in burrow at 9 nests (28%) with one bird incubating (Petersen 1955). In Montana, eggs were incubated an average of 75.9%  $\pm 8.7$  SD (range 40–100,  $n = 4$  nests) of the time, with individuals spending an average of 30.8 min  $\pm 26.2$  SD (range 5–180,  $n = 4$  nests) per incubation bout; incubation effort increased with decreased nest-cavity temperature (Ellis 1982).

**Hardiness of eggs against temperature stress; effect of egg neglect.** From Ellis 1982. Eggs can tolerate relatively cold temperatures and interruptions in incubation; burrows help ameliorate weather effects. Temperatures of incubated eggs at individual nests in Montana ranged from 29.4 to 34.4°C during day and

from 30.0 to 34.8°C at night; lowest egg temperature when eggs were unincubated was 21.1°C.

#### HATCHING

*Preliminary events and vocalizations.* No information.

*Shell-breaking and emergence.* Hatching of entire brood takes 2–3 d (Petersen 1955). In New York, high degree of within-colony hatching-date synchronization; 67% of all clutches hatched within 6 d ( $n = 400$ ; Emlen and Demong 1975).

*Parental assistance and disposal of eggshells.* Parents are not known to assist. Adults remove eggshells from nest upon hatching (Petersen 1955, Hickman 1979). Dropped eggshell fragments accumulate on ground below nests. The paucity of observations of birds removing eggshells suggests that eggshells are eaten (Hickman 1979).

#### YOUNG BIRDS

*Condition at hatching.* Young are naked and bright reddish pink, and weigh approximately 1.6 g (Beyer 1938, Petersen 1955, Marsh 1979). Nape, back, and base of wings have scanty covering of pale gray or gray-brown down. Eyes are large and black through closed lids. Inside of mouth and bill flanges are lemon yellow, bill is yellowish gray, and feet are pinkish gray (Beyer 1938).

*Growth and development.* Mass increases most rapidly between 2 and 10 d of age; peaks at 12–14 d, then gradually decreases until fledging at 18–22 d (Petersen 1955, Marsh 1979). For fledging weights, see Fledgling stage, below. Beginning of outer primary (P9) is evident by day 7 (Petersen 1955, Marsh 1979, Turner and Bryant 1979), and feather-tips break sheaths on days 9–10. Length of primaries increases linearly with age, at rate of approximately 0.062 cm/day (Turner and Bryant 1979). Nestling Sand Martins 11 d old can be aged using regression equation where length of P9 is the  $x$  variable:  $y = 4.72x - 51.18$ ,  $r = 0.98$  ( $p < 0.001$ ; Turner and Bryant 1979). By 10 d of age, nestling appears spiny because of growth of closed feather-sheaths with almost full coat of dense, short, gray-brown down between sheaths (Cramp et al. 1988).

Tarsus length is approximately 6 mm at 2 d old, reaching approximately 12 mm at fledging. Tarsi grow rapidly for first 6–8 d, by which time tarsi reach 77% of adult length; growth slows considerably thereafter (Turner and Bryant 1979). Early tarsus growth facilitates upright posture during begging, and allows nestlings to move toward parents to be fed. Bill grows most rapidly during first 7–8 d, with gape width reaching maximum at about middle of nestling period, then decreasing rapidly (Turner and Bryant 1979). Fat is added rapidly during first 2–8 d, coinciding with period of most rapid weight gain.

When peak weight is reached at 12–14 d, large but variable proportion of nestling's weight is fat (Marsh 1979, Turner and Bryant 1979).

For first few hours after hatching, head is normally forward and resting close to breast; chick sprawls for several days. At 5–7 d, can crouch temporarily with head erect. By 8–10 d, can sit erect and use shuffling walk to move out of nest (Hickman 1979), and at 9 d old, nestlings rush adults in burrow to be fed (Petersen 1955). Begging is confined to movements of head and neck until 13–15 d of age, when young begin to quiver wings during begging. Young move to burrow entrances at 15–17 d, but Petersen (1955) reported that nestlings at 12 d wait 15 cm from burrow entrance to be fed by adults. Fear response well developed by day 15. Young exercise by stretching and flapping wings before fledging. Young can fly when leaving nest the first time.

#### PARENTAL CARE

*Brooding.* From Petersen 1955, except as noted. Begins at hatching. Largely continuous for first 2–3 d of nestling life, then gradually begins to diminish until ceasing completely by about days 7–10 (Beyer 1938). Amount of brooding decreases by shortening duration of brooding period. On hatching day at 1 nest, brooding periods averaged 12.3 min  $\pm$  7.9 SD (range 7–28,  $n = 6$ ); 2 d later, brooding occurred with same frequency but duration was 3–5 min shorter, with longer periods of absence from nest. Nestlings are brooded at night by adults until day 10, and females do most brooding at night; both sexes together and males alone brood less prevalently.

*Feeding.* Begins at hatching and continues until 3–5 d after fledging. Both sexes feed nestlings, but males make more feeding visits than females (Petersen 1955, Hickman 1979, Westerterp and Bryant 1984). Parent compresses multiple insects into bolus before giving to young. Places bolus directly into nestling's mouth with quick jab of bill. Feeding rates in North America range from average of 24.7 visits/h in Wisconsin ( $n = 33$  h; Petersen 1955) to 22.1–28.2 visits/h in Alaska ( $n = 29$  h; Hickman 1979). Parents spend 10–15 s within burrow feeding nestlings, then fly away, often with fecal sac. Intervals between feedings range from 15 s to 25 min, with most absences lasting 1–5 min (Moreau and Moreau 1939, Hickman 1979).

Feeding rates increase with increasing brood sizes. Average feeding rates include 24.1 and 25.7 visits/h ( $n = 21$  and 12 h, respectively) for 3- and 4-nestling broods, respectively, in Wisconsin (Petersen 1955), and 32.4 and 34.7 visits/h ( $n = 14$  and 10 h, respectively) for 3- and 4-nestling broods, respectively, in Great Britain (Moreau and Moreau 1939). Despite slight increases in feeding rates per nest with increasing brood sizes, feeding visits per nestling generally decrease with increasing brood size (Moreau and

Moreau 1939, Petersen 1955). Feeding rates seem relatively consistent throughout daylight hours and across ages of nestlings (Stoner and Stoner 1941, Petersen 1955). Adults feed juveniles only irregularly after fledging (Emlen and Demong 1975); adults stop feeding young 1 wk after fledging (Petersen 1955, Cramp et al. 1988).

Adults bring typical brood about 7,000 insects (total dry weight approximately 7 g)/d (Cramp et al. 1988), averaging 60 prey items/visit (Turner 1980).

**Nest sanitation.** From Petersen 1955 and Hickman 1979, except as noted. Young back up from nest and defecate at edge of nest at 4–14 d old, and parents remove fecal sacs from burrow. In Alaska, fecal sacs were removed every 13.1 visits to burrow ( $n = 29$  h). Adults may swallow sacs of 5- to 6-d-old nestlings (Beyer 1938). Adults deposit sacs on ground near burrow. At 14 d old, young begin to appear at burrow entrance and defecate outside of burrow.

**Carrying of young.** Not reported in this species.

#### COOPERATIVE BREEDING

Not known to occur.

#### BROOD PARASITISM

Intraspecific brood parasitism not known to occur (Hoogland and Sherman 1976). Single record of parasitism by Brown-headed Cowbird (*Molothrus ater*; Friedmann 1963) when nest was exposed because bank face fell away. No records of cowbird parasitism from 261 nests in Ontario (Peck and James 1987) and 313 nests in British Columbia (Campbell et al. 1997).

#### FLEDGLING STAGE

**Departure from nest.** On average, young depart nest at age  $22.3 \text{ d} \pm 2.1 \text{ SD}$  ( $n = 30$ ) in Scotland (Turner and Bryant 1979);  $18.7 \text{ d} \pm 1.0 \text{ SD}$  ( $n = 50$ ) in Massachusetts, Michigan, and Washington (Beecher et al. 1981a); 20 d in Wisconsin (Petersen 1955); and 18–21 d in Pennsylvania (Beyer 1938). Nestlings are capable of weak, labored flight a few days before fledging (BAG). Adults reduce feeding rates and use vocalizations (perhaps Contact and/or Feeding calls; see Sounds: vocalizations, above) to motivate nestlings to fledge (Petersen 1955). Fledglings return to burrow for 4–5 d after first flight, and land in neighboring burrows or perch on roots, twigs, and branches around nesting banks (Turner and Bryant 1979). Juveniles as old as 28 d roost in their own burrows (Petersen 1955); most juveniles are independent of parents at 30 d old (Cramp et al. 1988); join other juveniles and adults in flocks that remain in colony area for about 1 wk after fledging (Freer 1977).

**Growth.** At fledging, mean mass  $13.0 \text{ g} \pm 1.02 \text{ SD}$  (range 10.0–16.2,  $n = 363$ ) for unknown sex hatch-year birds (presumably fledglings) in Wisconsin (MacBriar 1988);  $13.0 \text{ g} \pm 1.54 \text{ SD}$  (range 9.3–19.4,  $n = 309$ ) in California (BAG). Wing-chords averaged 91.6 mm

$\pm 6.1 \text{ SD}$  (range 74–102,  $n = 282$ ; BAG) in California, and 96.6 mm (Turner and Bryant 1979) and 97.8 mm  $\pm 4.5 \text{ SD}$  ( $n = 6$ ; Jones 1987a) in Scotland. Length of P9 is  $>60 \text{ mm}$  at fledging for birds in Wisconsin (Petersen 1955) and reaches lengths of about 50 mm in fledglings from Scotland (Turner and Bryant 1979). Fledglings are structurally smaller than adults but have more subcutaneous lipids than adults have (Jones 1987a).

**Association with parents or other young.** For parental feeding, see Parental care, above. Fledglings rest and roost with other young in burrows, and independent birds may be from different broods. Fledglings may use burrows other than burrow from which they fledged (Hickman 1979). Soon after fledging, young gather together with similar-aged birds in large groups. These groups perch together on trees, shrubs, logs, roots, wires, and sides of cliffs. Birds in these groups likely come from several nearby colonies. As breeding season winds down, adults without dependent young join these groups before migration. Parents recognize their fledglings by their unique vocalizations (see Sounds: vocalizations, above).

**Ability to get around, feed, and care for self.** Young depend on parents for food an average of  $4.7 \text{ d} \pm 1.2 \text{ SD}$  ( $n = 3$  nests; Turner and Bryant 1979) after last nestling has fledged. Frequency and duration of juvenile's flight increases daily. Juvenile's flight pattern, speed, endurance, and maneuverability are indistinguishable to unaided eye from adult's when juvenile is 5–6 wk old (BAG).

#### IMMATURE STAGE

From Petersen 1955, except as noted. Once independent, juveniles spend much time foraging, usually in conspecific flocks of juveniles and adults in general area around natal colony. When not foraging, juveniles spend their time preening, roosting, and loafing in large groups. Independent young are excluded from daytime loafing in their natal nest site by their parents, but they may use other burrows (Asbirk 1976). Postbreeding flocks of juveniles and adults regularly land on ground to sunbathe, dust-bathe, and preen (Barlow et al. 1963, Cramp et al. 1988). Juveniles also engage in attempted copulations, incipient excavation, nest-building, and brooding. Little is known about activities during and after migration.

## DEMOGRAPHY AND POPULATIONS

#### MEASURES OF BREEDING ACTIVITY

**Age at first breeding; intervals between breeding.** Females and males can breed in first year after fledging (Cramp et al. 1988). Annual breeding thereafter.

**Clutch.** See Breeding: eggs, above.

**Annual and lifetime reproductive success.** No information on lifetime reproductive success.

Breeding success is greater in early nesters than in late nesters, and higher degree of brood synchronization results in greater breeding success because food resources are used more efficiently through group foraging (Emlen and Demong 1975, Sieber 1980). Nesting success is greatest at nests in central area of colony; peripheral nests are subjected to greater levels of predation (Emlen 1971, Freer 1977). Overall hatching success (% eggs in clutch that hatch) reported as 69% ( $n = 187$  eggs) in Denmark (Asbirk 1976), and 90.5% ( $n = 241$  eggs) in Saskatchewan (Hjertaas et al. 1988). Fledging success (% young from brood that fledge) is correlated with burrow length: Burrows dug by Sand Martins <70 cm long had 50.9% fledging success, those >70 cm long 73.2% (Sieber 1980). Hjertaas et al. (1988) calculated that a Bank Swallow starting egg-laying had a 44.4% chance of fledging young in 1980 and 64.2% chance in 1981 in Saskatchewan. On average in Saskatchewan, 4.4 young fledged/nest  $\pm 0.99$  SD (range 2–6,  $n = 91$ ; Hjertaas et al. 1988). In California, average number of young near fledging age was  $4.11 \pm 0.34$  SD (range 3.4–4.3,  $n = 7$  colonies, 177 nests; BAG). In British Columbia, average brood size of various-aged young was 2.65 (range 1–6,  $n = 246$ ; Campbell et al. 1997).

*Number of broods normally reared per season.* See Breeding: phenology, above.

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

*Colony occupancy.* Because males leave burrows that do not attract females (Kuhnen 1985), or are blocked with large rocks or thick plant roots (BAG), not all burrows in colony are used for nesting. Levels of burrow occupancy by nesting pairs are  $42.6\% \pm 14.6$  SD (range 14.6–85.7,  $n = 17$ ) in Alaska (Hickman 1979);  $55.9\% \pm 2.7$  SE ( $n = 26$ ) in California (Garrison et al. 1987);  $59.6\% \pm 11.2$  SD (range 46–81,  $n = 15$ ) in Swedish Lapland (Svensson 1986); and  $76.5\% \pm 13.3$  SD (range 57.1–88.2,  $n = 5$ ) in New York (Freer 1977). Persson (1987a) found that larger colonies have greater occupancy levels than smaller ones, and that colonies in rocky soils had smaller occupancy levels than colonies in sandy soils.

#### LIFE SPAN AND SURVIVORSHIP

The following mortality and survivorship estimates must be cautiously interpreted because none accounted for inability to control for dispersal or differential mortality probabilities, many did not consider annual variation in survival, and few used life-table analysis. On basis of live recoveries of banded birds in Sweden, average mortality of birds banded as juveniles and adults was estimated to be 59.7% ( $n = 458$  recoveries) and 57.3% ( $n = 1,471$  recoveries), respectively (Persson 1987b). These estimates were corroborated with life-table analyses in which average

annual mortality rate for juveniles was 67.0% and for adults 59.7% (Persson 1987b). Using live recaptures of Sand Martins in Great Britain, Harwood and Harrison (1977) and Cowley (1979) estimated average first-year mortality of 80 and 77% and annual adult mortality of 60 and 58%, respectively. On basis of live recaptures and life-table analyses, average survival of all age classes was 34.9% in Wisconsin (MacBriar and Stevenson 1976) and 53% in New York (Freer 1977). Annual survival rates in Hungary varied among years, and low rainfall amounts on wintering grounds lowered annual survival rates (Szep 1993).

There are 2 records of Bank Swallows living at least 9 yr (Petersen and Mueller 1979, Szep 1992).

#### DISEASE AND BODY PARASITES

*Diseases.* Little information, but Dement'ev and Gladkov (1968) reported an unnamed epizootic disease killing all but a few members of 2 colonies in n. Kazakhstan.

*Body parasites.* In North America, fleas, including *Ceratophyllus styx riparius* in Alaska (Haas et al. 1980) and New York (Beyer 1938); *Celsus celsus celsus* in Alaska (Haas et al. 1980); and *Ceratophyllus riparius* in Michigan (Hoogland and Sherman 1976) and Pennsylvania (Beyer 1938). In Scotland, parasitism by *C. styx* lowered body mass of nestlings by 5% compared to unparasitized nestlings (Alves 1997). Larval blowflies (Diptera: Calliphoridae) were found in New York (*Protocalliphora splendida*; Stoner 1936); in Ontario (*P. braueri*); in Ontario, Yukon Territory, Montana, and New York (*P. hirundo*); in e. North America (*P. metallica*); and throughout North America (*P. sialia*; Sabrosky et al. 1989).

*P. chrysorrhoea* has a Holarctic distribution that it is restricted almost entirely to nests of Bank Swallow (Sabrosky et al. 1989). In Utah, 81% of Bank Swallow nests were infested by *P. chrysorrhoea*, and 44 of the infested nests had 1–25 fly larvae (Whitworth and Bennett 1992). Parasitism by *P. chrysorrhoea* significantly reduced hematocrit and hemoglobin levels in Bank Swallow nestlings, but did not increase nestling mortality (Whitworth and Bennett 1992).

Mites (*Liponyssus sylviarum* and *Atricholaelaps glasgowi*) found in Pennsylvania (Peters 1936), and lice (*Myrsidea dissimilis*) in New York (Stoner 1936). Feather lice (Mallophaga) found in North America north of Mexico include *Brueelia tenuis* and *Myrsidea latifrons* (Emerson 1972).

*Internal parasites.* The nematode *Acuaria atteruata* has been found between tunics of gizzard of Bank Swallows (Gross 1942).

#### CAUSES OF MORTALITY

*Exposure.* Sensitive to cold weather that reduces availability of insects for food; individuals become weakened and succumb in many ways. During an unseasonably cold spell during late spring migration

in Saskatchewan, 39 Bank Swallows died, along with some Tree, Cliff, and Barn swallows; dead birds were found in groups, suggesting that Bank Swallows form clusters with conspecifics and suffocate despite potential heat-exchange benefit (Sealy 1966).

Nestlings often die when burrows collapse or erode because of high water from late-spring and early-summer rainstorms or high water flow from regulated rivers (California; BAG). Nest sites also collapse as result of digging by predators, such as European badger (*Meles meles*; Persson 1987b). Colonies in quarries also collapse and cause nestling mortality (Mead 1979b).

**Predation/parasitism.** See Behavior: predation, above.

**Competition with other species.** Little information. European Starlings (*Sturnus vulgaris*; BAG) and House Sparrows (*Passer domesticus*) are known to appropriate Bank Swallow nest burrows, and nestling House Sparrows have been found in these burrows (Gross 1942). Effect of starling competition on nesting success of Bank Swallow is unknown. Bank Swallows nest together with Northern Rough-winged Swallows and sometimes interact with them physically (Lunk 1962), but competition for nest sites is not known.

**Other.** From Mead 1979b in Great Britain. Collisions with moving vehicles, mostly automobiles, were primary causes (45.2%) of known deaths for 336 banded Sand Martins; human causes (outside of Great Britain, mostly shooting) accounted for 15.5% of deaths; other sources of mortality included predation (11.9%), miscellaneous sources (e.g., tangling in fishing line, being exposed to inclement weather, and hitting windows, buildings, and structures; 11.3%), hitting wires (8.0%), and collapse of nesting colonies (8.0%). Juveniles and first-year birds were more likely than adults to be killed in collisions with moving vehicles, and juveniles were more likely than older birds to be killed by wires. Mortality from all sources for all age classes was greatest in May and declined throughout breeding season.

#### RANGE

**Initial dispersal from natal site.** Percentage of individuals banded as nestlings or juveniles and recaptured the next year at natal colonies include 50% ( $n = 10$ ) in Wisconsin (MacBriar and Stevenson 1976), and 46% ( $n = 15$ ) in New York (Freer 1979). In United Kingdom, 70, 17, 7, and 6% of juveniles were recaptured 10–49, 50–99, 100–199, and >199 km, respectively, from their natal colonies ( $n = 352$ ; Mead 1979a). In Hungary, 59% of banded juveniles recaptured in a subsequent year were at their natal banks, and 55, 31, and 14% ( $n = 120$ ) were recaptured 0–10, 10–25, and >25 km, respectively, from their natal colonies (Szep 1990).

In New York State, males showed greater level of natal-site fidelity than females; females may be less

likely to breed as yearlings (Freer 1979). In Great Britain, return rates for first-year males were >3 times greater than those for first-year females (Holmes et al. 1987).

**Fidelity to breeding site and winter home range.** On basis of live recaptures, colony-site fidelity of adults encountered in subsequent breeding seasons is 55.6% ( $n = 20$ ) in Illinois (Petersen and Mueller 1979); 67.9% ( $n = 235$ ) in New York (Freer 1979); 70.2% in Wisconsin ( $n = 203$ ; MacBriar and Stevenson 1976); 77.3% in New York (Stoner 1941); and 92% ( $n = 195$ ) in e. Hungary (Szep 1990). Individuals show high fidelity to same section of colony where originally captured (Bergstrom 1951). All these fidelity figures, however, may underestimate colony fidelity because they are based on number of recaptured birds that returned to original colony, and it is unknown whether birds that do not return are dead, dispersed, or returned to colony but were not caught. In New York State, site fidelity in adults was approximately equal for males and females (Freer 1979), but see Holmes et al. 1987 and Mead 1979a for Great Britain, where males showed greater fidelity than females.

Individuals rarely change colony sites in same breeding season (MacBriar and Stevenson 1976); 6 of >1,500 adults caught at colony in Great Britain moved from nearby colony in same breeding season (Holmes et al. 1987). Fidelity to areas larger than colony site is particularly high. In a 1,075-km<sup>2</sup> study area with 2 subareas in Sweden containing 120 colonies, 99.9% of recaptured Sand Martins were found in subsequent breeding seasons in same sub-area where initially captured; 0.1% were recaptured in the other subarea (Persson 1987a).

Maximum distances of live recaptures that changed colony sites in subsequent years were 15 km in Illinois (Petersen and Mueller 1979), 403 km in Wisconsin and Michigan (MacBriar and Stevenson 1976), 114 km in Wisconsin and Michigan (Bergstrom 1951), and >199 km in Great Britain (Mead 1979a). Sand Martins in Great Britain change colonies at great distances, even across English Channel and North Sea (Mead 1979a).

Site fidelity increases with age; return rates for adults were >2.5 greater than those for juveniles (Freer 1979). Birds are more likely to return to breeding colony of the previous year if they successfully fledged young at that site in the previous year and the colony site has relatively high degree of habitat stability (Freer 1979).

No information on fidelity to winter home range, although birds seem to be nomadic in winter.

**Dispersal from breeding site or colony.** See above. Little information on long-distance dispersal. In Hungary, Sand Martin adults had shorter dispersal distances (mean 2.1 km  $\pm$  5.4 SD,  $n = 1,604$ ) between consecutive years than did juveniles (mean 4.4 km  $\pm$  8.2 SD,  $n = 480$ ), while juvenile males had shorter dispersal distances (mean 3.5 km  $\pm$  7.3 SD,  $n = 295$ )

than did juvenile females (mean 5.3 km  $\pm$  9.1 SD,  $n = 176$ ). Dispersal distances were similar for adult males (mean 2.0 km  $\pm$  5.1 SD,  $n = 759$ ) and adult females (mean 2.2 km  $\pm$  5.7 SD,  $n = 838$ ; Szep 1995b). Considerable differences exist in mean dispersal distances for juvenile males and juvenile females between any 2 given years (Szep 1995b).

**Home range and homing.** Little information. In Scotland, foraging flights averaged 0.19 km  $\pm$  0.16 SD ( $n = 91$ ) in straight-line distance (Bryant and Turner 1982); in New York, most foraging flights were within 0.8 km of a colony (Stoner and Stoner 1941). Within-season homing is well developed over moderately long distances. Four (30.8%) of 13 adult Bank Swallows experimentally displaced 81 km from their colony site in Minnesota returned within 5 d of release (Mayhew 1963). Adult birds were released 260 times in Wisconsin 1.6–282 km from their nest sites, and individuals returned 120 (46.2%) times to their nest sites within 24 h. None of 16 juveniles returned when released 80–161 km from natal colony (Sargent 1962). Return rates were higher at shorter distances, and birds released 2–3 times returned at higher rates than those released once. Individuals incubating or rearing young had higher return rates than preincubating birds. Bank Swallows use landmarks, such as hills, bodies of water, and buildings, to orient toward colonies when released during studies, and use of landmarks is more pronounced at distances closer to colonies (Sargent 1962, Downhower and Windsor 1971).

#### POPULATION STATUS

**Numbers.** Little information on population size in North America. Better estimates for Sand Martin populations in Europe (Cramp et al. 1988). Breeding populations are difficult to census accurately, since birds are concentrated locally at colony sites, which vary erratically in suitability and occupancy on an annual basis. Population estimates based on burrow counts must be cautiously interpreted because approximately 50% of burrows lack nests (see Measures of breeding activity, above).

Breeding population in 1987 in California estimated at 111 colonies, with about 25,180 pairs (Laymon et al. 1988). A population on a 48-km reach of Sacramento River, CA, averaged 2,082 pairs  $\pm$  1,064 SD (range 1,044–4,326,  $n = 12$ ) and 14.8 colonies  $\pm$  5.3 SD (range 10–28,  $n = 12$ ) between 1986 and 1997 (BAG).

Colony sizes are extremely variable, ranging from <10 nesting pairs to several thousand (Cramp et al. 1988, Turner and Rose 1989). Most colonies are small, with usually fewer than several hundred pairs. North American colonies have the following average sizes: in Saskatchewan, 7.7 nests  $\pm$  7.9 SD (median 5, range 1–48,  $n = 79$  colonies; Hjertaas 1984); in Ontario, 45 nests (range 1–1,500 pairs,  $n = 99$  colonies; Peck and James 1987); in Michigan, 58.6 nests (range 1–451,  $n = 54$  colonies; Hoogland and Sherman 1976); in Alaska,

64.5 burrows  $\pm$  57.9 SD (median 46, range 7–177,  $n = 17$  colonies; Hickman 1979); in Pennsylvania and Vermont, 95.4 burrows  $\pm$  86.0 SD (median 64, range 13–300,  $n = 25$  colonies; Spencer 1962); in California, 367.8 burrows  $\pm$  444.6 SD (median 240, range 10–3,440,  $n = 406$  colonies; BAG); and in British Columbia, 3–3,035 burrows ( $n = 491$  colonies; Campbell et al. 1997). Similar patterns in size classes of colonies are known from European populations (Cramp et al. 1988, Szep 1991b).

Throughout North America, larger colonies are found along larger river systems, and smaller colonies along small rivers and streams (Hjertaas 1984, BAG). Some of the largest colonies reported include 1,500 pairs in Ontario (Peck and James 1987); 2,000 nests in Illinois (Bohlen 1989); 2,000 pairs in New York (Bull 1985); 3,440 burrows in California (BAG); 4,228 burrows and 2,500 pairs at a Sand Martin colony in Hungary (Szep 1991b); and 6,000 burrows in Illinois (Fawks 1938).

**Trends.** For Bank Swallow, because the bird's colonial nesting habits and the ephemeral nature of colony sites make it difficult to consistently detect at many points, Breeding Bird Surveys (BBS) are not the best long-term population-monitoring techniques. Atlasing is a better technique because colony sites can be sought out and documented more readily. On basis of BBS data, however, breeding populations were stable between 1966 and 1991 for North America. Populations increased significantly between 1966 and 1991 in the Upper Coastal Plain and Great Lakes Plain physiographic strata, and decreased significantly in the Driftless Area, Adirondack Mtns., Closed Boreal Forest, and Till Plains strata. Statistically significant trends in BBS data must be interpreted cautiously, since abandonment or recent colonization of nest sites along survey routes may greatly bias relative estimates of abundance. Nesting populations were reported to be declining in California (Humphrey and Garrison 1987) and Kentucky (Palmer-Ball 1996). Bank Swallow nesting populations appear stable in Connecticut (Zeranski and Baptist 1990), Michigan (Brewer et al. 1991), and Ontario (Cadman et al. 1987).

Population size can vary greatly over relatively short time periods because of ephemeral nature of nesting habitat and weather-influenced mortality on wintering grounds (Szep 1993, 1995a; see Population regulation, below).

#### POPULATION REGULATION

Little quantitative information from North America. Drought conditions in North African wintering grounds may have contributed to decreases in Sand Martin breeding populations in Great Britain (Cowley 1979), Scotland (Jones 1987c), and Hungary (Szep 1993), but see Svensson (1986). Reduced body size in Sand Martins in Great Britain coincided with reduced breeding populations after African drought in 1983–

1984, suggesting that weather in winter range affects breeding populations by selecting for smaller birds that are better able to survive periods of reduced populations of insect prey (Jones 1987c, Bryant and Jones 1995).

In e. Hungary, survival rates of adult Sand Martins for both sexes were not related to rainfall amounts from winter range, but populations did decline (Szep 1995a, 1995b). Declining populations were stabilized by immigration of breeding birds from other areas and recruitment of first-time breeders, while localized declines coincided with emigration.

In sw. Sweden, proportion of females increased to buffer populations against catastrophic winter mortality and/or reproductive failure. An 11-yr population cycle resulted from such population regulation, and mortality caused by wintering-area drought and a sunspot cycle created the regulatory mechanism (Persson 1987c).

Availability of nesting habitat is major factor affecting size and distribution of breeding populations throughout Bank Swallow's Holarctic distribution (Cramp et al. 1988, Turner and Rose 1989). Breeding colonies typically do not occupy all available nesting habitat (BAG). Number of colonies and number of nest burrows per colony in Hungary were significantly correlated with total area of suitable nesting habitat (Szep 1991b).

## CONSERVATION AND MANAGEMENT

### EFFECTS OF HUMAN ACTIVITY

**Shooting and trapping.** See Demography and populations: causes of mortality, above. Historically, nestlings were removed from nest burrows and used as fishing bait (Dawson 1923).

**Pesticides and other contaminants/toxics.** Little information. No detectable levels of pesticides or other contaminants found in 3 eggs collected in 1986 from a colony in California (BAG).

**Collisions with stationary/moving structures or objects.** See Demography and populations: causes of mortality, above.

**Degradation of habitat.** In California, much of Bank Swallow's nesting habitat in southern and central areas has been eliminated by flood- and erosion-control projects (Garrison et al. 1987, Small 1994). These projects destroy or alter nesting habitat when banks are sloped to 45° and large rocks (riprap) are placed on slope. In Arkansas, nesting habitat was lost as result of water-flow changes and bank-stabilization projects (James and Neal 1986); in Connecticut, breeding populations have declined since mid-1990s as gravel-mining operations have declined (Zeranski and Baptist 1990). Colony sites are destroyed by road-building (Petersen and Mueller 1979) and by the increasing regulation of water flow from reservoirs

that exacerbates erosion (BAG). Closure of sand and gravel pits has caused localized population declines in Virginia (Blem and Blem 1990).

**Disturbance at nest and roost sites.** Generally Bank Swallow is quite tolerant of human disturbance in general vicinity of colonies, as evidenced by propensity of this bird to nest in active sand and gravel quarries. See Management, below.

**Direct human/research impacts.** Little information, but suspected to be minimal, especially given the extensive amount of research conducted on this species at nesting colonies. Sections of nesting banks occasionally collapse as researchers climb banks (BAG).

### MANAGEMENT

**Conservation status.** Listed as Threatened in California (Schlorff 1992), Species of Special Concern in Kentucky (Palmer-Ball 1996), and Sensitive Species in Oregon (Csuti et al. 1997). No special status in other states. Protected migratory bird in Canada and the U.S.

**Measures proposed and taken.** Human activities creating sand and gravel quarries, road cuts, and other vertical banks in friable soils have directly benefited the Bank Swallow by increasing its distribution in Canada. Several active sand and gravel quarries avoid extraction activities around active nesting colonies to minimize disturbance to nesting birds (Erskine 1979).

Recovery plan has been written for Bank Swallow in California (Schlorff 1992); artificial banks and enhanced natural banks were built along Sacramento River to mitigate loss of colony sites from flood-control projects (Garrison 1991). In 1986, 100 nest burrows were dug with hand auger on Sacramento River, CA (BAG).

**Effectiveness of measures.** Listing of this species as Threatened in California has protected some nest sites from proposed flood- and erosion-control projects, but a few sites have been destroyed by emergency projects (BAG). In general, population dynamics of this species make success difficult to achieve for any management action other than conservation of suitable nest sites. Integrating protection of Bank Swallow habitat with larger-scale riparian-ecosystem conservation efforts appears promising, as is occurring along Sacramento River, CA, in cooperative efforts between state and federal agencies and private landowners (BAG).

Between 1989 and 1991, Bank Swallows occupied 1 of 2 artificial sites and 5 of 6 enhanced sites for 1–2 yr following construction. At the artificial and enhanced colonies, nestlings were produced at levels equivalent to natural sites. Sites were abandoned, however, within 3 yr, since no maintenance was conducted on the sites, thereby rendering them unsuitable (Garrison 1991). This short-term response indicates that habitat enhancements can be undertaken, but construction and maintenance costs and the small amount of area

affected makes this management not very cost-effective. The 100 artificial burrows dug in California (see above) were not used (BAG).

## APPEARANCE

Following description is based on nominate race found in North America, *R. r. riparia*, and is largely from Oberholser 1974, Cramp et al. 1988, and Pyle 1997.

### MOLTS AND PLUMAGES

**Hatchlings.** At hatching, down is long, consisting of sparse pale gray or gray-white tufts on crown and back. By day 10, appears spiny because of growth of closed feather-sheaths with almost full coat of dense, short gray-brown down.

**Juvenal plumage.** Acquired by complete Prejuvenal (postnatal) molt. No information on sequence of Prejuvenal molt, but molt occurs in burrow before fledging during nestling period. Plumage is similar to Definitive Basic (adult) plumage, but feathers of tertials, wing-coverts, rump, and uppertail-coverts are broadly tipped with light cinnamon buff, pale wood brown, or dull white. Upperwing-coverts are more narrowly margined with same color; tail entirely lacks narrow, obscure, darker bars; chin, throat, and side of neck often are slightly washed with pink or buff and sometimes with faint, grayish brown spotting. Some individual variation in extent and color of pale fringes and rufous wash. In worn plumage, very similar to adult, but traces of off-white fringes remain longer along upperwing-coverts, tertials, rump, secondaries, and inner primaries. Sexes similar.

**Definitive Basic plumage.** Definitive Prebasic molt complete in both adult and hatch-year birds. Molt begins on breeding grounds about time young have completed fledging (Jul) and is suspended during fall migration, then completed on wintering grounds by Nov. In European populations (Sand Martin), complete molt takes 120–150 d, so some molts begin before fall migration (Mead 1970). Molt of mantle, scapulars, tail-coverts, tail, and occasionally tertials occurs mainly Jul–Sep in North American populations. Juveniles do not initiate molt of flight-feathers until migration is completed, and molt is initiated later in juveniles than in adults, with considerably more variation in timing.

Following description of primary molt is based on Mead 1970 and Pyle 1997, except as noted. Some body-feathers and a few inner primaries are replaced in small number of birds before fall migration (Mead 1970, Freer and Belanger 1981, Cramp et al. 1988). In European populations, about 2% of 3,465 adults trapped at fall communal roosts in Great Britain had new 1–5 primaries and some secondaries, and a few adults may continue their wing molt during fall migration (Mead 1970). This primary molt started with innermost primaries and progressed outward,

and tertials and rectrices are rarely molted this early. North American birds in their first Basic plumage are indistinguishable from older birds, except some third-year or older birds may show 2–4 very worn inner primaries and unworn outer primaries, indicating suspended molt during previous fall migration (Freer and Belanger 1981). Limited Prealternate molt may occur in Apr–May. See Cramp et al. 1988 for molting patterns of other subspecies.

Upperparts, remiges, and rectrices dark brown, with gray tone when fresh. In fresh plumage, feather-tips faintly edged pale gray. In European populations, pale edges are widest on feather of forehead, rump, uppertail-coverts, and median and greater upperwing-coverts (Cramp et al. 1988). Sandy wash on forehead, rump, wing-coverts, and tertials when worn. Dark brown of upperparts extends over cheeks and into broad, complete band across upper breast, with brown smudges on flanks. Breast-band is widest at center of breast. Remiges, rectrices, and greater upper primary-coverts black-brown, with slight olive tinge. Remiges and secondaries faintly edged white along outer webs and tips when fresh; outermost primaries and tips of other flight-feathers blacker, less tinged olive. Shafts of primaries white below and dark horn-brown above. Upper wing-coverts darker and less grayish than remaining upperparts. Under wing-coverts and axillaries dusky gray-brown, with pale gray fringe to lesser undersecondary-coverts. Lores and feathering near gape pale gray-brown or pale gray, often slightly tinged buff when fresh. Dull black spot in front of eye, and upper cheeks and ear-coverts, earth brown or gray-brown. Rest of body, including throat, lower breast, and sides, white. Chin and throat silky white, usually with faint, pale buff tinge around chin when fresh. Plumage remarkably cryptic against many backgrounds. Other races, including *shelleyi* and *diluta*, have paler brown coloration and breast-band (see Systematics, above). Sexes similar.

Appreciable difference between fresh Basic plumage and appearance during breeding season caused by feather wear. Pale edges of tertials, secondaries, and greater wing-coverts are worn away during breeding season.

### BARE PARTS

**Bill and gape.** Bill black or brown-black, except in nestlings, when bill and gape flanges are pale lemon yellow. Juveniles have horn-brown bill and pale yellow bill flanges in first months after fledging. Mouth-lining yellow and unspotted, with pale yellow bill flanges in nestling.

**Iris.** Dark brown in adult; lighter brown in juvenile.

**Legs and feet.** Legs and feet black-brown or dark brown in adults; flesh-brown or horn-brown at fledging. Claws of juveniles dull yellow. Tuft of pale brown feathers at upper base of hind toe at joint with base of tarsus.

## MEASUREMENTS

### LINEAR

See Table 1 for measurements of *R. r. riparia* in North America. See Dement'ev and Gladkov 1968 and Cramp et al. 1988: 247 for other linear measurements, including those of different races and geographic localities.

**Wing length.** Male and female wing lengths are equivalent (Petersen 1955, MacBriar 1995). Wing lengths of 1-yr-old male birds are shorter ( $p < 0.001$ ) than those of males from age classes  $\geq 2$  yr, while wing lengths were equal among all age classes of females  $\geq 2$  yr old (Freer 1977). Wing disc-loading for Sand Martins in Scotland was  $44.0 \text{ cm}^2/\text{g}$  (Westerterp and Bryant 1984).

**Tail length.** Compared to Barn Swallow and Common House-Martin, with their longer and/or heavier tail-feathers, the shorter, straighter, lighter tail-feathers of Bank Swallow result in shorter tail muscles (Moreno and Moller 1996).

### MASS

See Table 1 for adult male and female Bank Swallows from North America. Mass of Sand Martin from Eurasia is similar (Westerterp and Bryant 1984, Cramp et al. 1988). Males and females have similar body mass except during egg-laying period when females are heavier (Petersen 1955, MacBriar 1988). Body mass varies throughout breeding season, with greater variation in females (Petersen 1955). For males, mass decreased slightly during nest-building, egg-laying, and brooding, and increased during incubation (Petersen 1955). Female mass increased during late nest-building stages, paralleling development of ovary and oviduct, and during first half of incubation; and decreased toward end of during egg-laying, beginning of incubation, and raising nestlings (Petersen 1955).

Weight of male testes averaged 87.6 mg (range 46.2–163.7,  $n = 32$ ) during entire breeding season, peaking during egg-laying and incubation periods (Petersen 1955). Female ovary weight averaged  $261.8 \text{ mg} \pm 231.7 \text{ SD}$  (range 22.0–778.3,  $n = 18$ ) during nest-building and egg-laying periods, 31.3 mg (range 16.2–52.1,  $n = 28$ ) during incubation period, and 22.4 mg (range 6.6–44.1,  $n = 31$ ) during brooding period (Petersen 1955). See Dement'ev and Gladkov 1968 and Cramp et al. 1988: 247 for other body weights, including different races and geographic localities.

## SKULL PNEUMATIZATION

Occurs in hatching year from Oct through Dec. Some second-year birds (about 20%) retain windows of unpneumatized skull through spring, and these pinhole-sized ( $\leq 2$  mm diameter) windows can be

retained in some after-second-year birds (Freer and Belanger 1981).

## PRIORITIES FOR FUTURE RESEARCH

The Bank Swallow has been one of the mostly intensively studied swallows in the world, and much is known about its life history during the breeding period in North America and Europe, particularly of the nominate race, *R. r. riparia*. Yet little is known about this species' habitat usage, distribution, and behavior during migration and winter in the Americas. Comparatively little information, particularly about population dynamics and breeding habitat, exists for other subspecies. The question of whether North American birds can produce 2 broods a year needs to be investigated more fully and lifetime reproductive success needs study. The effect of ectoparasites on reproductive success and nestling survivorship needs study, particularly given the influence of ectoparasites on the reproductive ecology of the Cliff Swallow, another highly colonial swallow (Brown and Brown 1995).

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