California Partners in Flight Riparian Bird Conservation Plan

BANK SWALLOW (*Riparia riparia)*

Photo by James Gallagher, Sea and Sage Audubon

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RECOMMENDED CITATION

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SHORTCUTS:

range map

references

SUBSPECIES STATUS: *Riparia riparia riparia*

The Bank Swallow occurs as a breeding species in California in a hundred or so widely distributed nesting colonies in alluvial soils along rivers, streams, lakes, and ocean coasts. As its scientific name, *Riparia riparia*, implies, the Bank Swallow is largely found in riparian ecosystems, particularly rivers in the larger lowland valleys of northern California. Nesting colonies are located in vertical banks or bluffs in friable soils, and these colonies can support dozens to thousands of nesting birds. Nesting habitat is particularly prone to erosion, and habitat in some areas such as the Sacramento and Feather rivers is threatened with loss by flood control and bank protection projects. The Bank Swallow has one of the widest ranges of any bird in the world with a breeding distribution that is largely Holarctic and a wintering distribution that is largely confined to the Southern Hemisphere.

MANAGEMENT STATUS: **Threatened, California Department of Fish and Game**

DISTRIBUTION

HISTORICAL BREEDING DISTRIBUTION

The historical distribution of the Bank Swallow in California is based on a review of egg collections from major California natural history museums reported by Laymon et al. (1988) and the historical information reported by Grinnell and Miller (1944) (Figure 1). Most of the historical information indicates this species mostly occurred as a localized breeder along coastal areas and rivers in central and southern California (Grinnell and Miller 1944). Many historical colonies in southern California are from Santa Barbara County south to central San Diego County. These southern California populations are extinct, and a few central California populations are extant. The paucity of historical records from northern California and the fact that current population mostly occurs in northern California should not be considered a population shift. There is an apparent bias in historical records from egg collections because extensive collecting occurred in southern California, and few eggs records exist from northern California. There is no reason to suspect that habitat conditions have improved in northern California such that historical populations did not occur there. Undoubtedly, the localized nature of breeding colonies along rivers and streams made it difficult to collect eggs at colonies in northern California. The southern California populations have been extirpated due to habitat changes where rivers and streams have been channelized and coastal areas have been modified for human use. The veracity of some historical records is questionable due to the possible confusion with the Northern Rough-winged Swallow (*Stelgidopteryx serripennis*).

CURRENT BREEDING DISTRIBUTION

The Bank Swallow is a locally common to uncommon breeding season resident in northern and central California. Few colonies, if any, exist in southern California where colonies historically occurred. A single southern California colony has been recently reported from the Santa Clara River, Ventura County (S. Laymon pers. comm.). Because nesting only occurs in suitable habitat, breeding areas are widely dispersed throughout northern and central California in major lowland valleys and coastal areas where alluvial soils exist. The major breeding population is confined to the Sacramento and Feather rivers and their major tributaries north of their confluence where an estimated 75% of CaliforniaÕs breeding

population was found in 1987 (Laymon et al. 1988). The Sacramento River population represented approximately 50% of the state's population in 1987, and the population occurs between Redding, Shasta County, and the Yolo Bypass, Yolo County. The Feather River supported 25% of the state's population in 1987; this population occurs between Oroville, Butte County, and the confluence of the Sacramento and Feather rivers, Sutter County.

Other relatively large breeding populations of several colonies have been recently found in the following locations including: (1) Scott River, Siskiyou County; (2) Cache Creek, Yolo County; (3) Pit River, Shasta and Lassen counties; (4) American River, Sacramento County; (5) Cosumnes River, Sacramento County; (6) Salinas River, Monterey County; (7) Fall River, Shasta County; (8) Hat Creek and Lake Briton area, Shasta County; (9) Susan River and Baxter Creek, Lassen County; (10) Tule and Lower Klamath Lake area, Siskiyou and Modoc counties; (11) Clear Lake Reservoir, Modoc County; (12) Indian Creek, Plumas County; (13) Long Valley Creek, Lassen County; and (14) Bishop area, Inyo County (T. and J. Heindel pers. comm.). Single colonies are widely scattered at other locations including: (1) Smith River, Del Norte County; (2) Fort Funston/Lake Merced, San Francisco County; (3) Ano Nuevo, San Mateo County; (4) Pajaro River, Monterey and Santa Cruz counties; (5) Lake Crowley, Mono County; (6) Bridgeport, Mono County (T. and J. Heindel pers. comm.); (7) Topaz Lake, Mono County (T. and J. Heindel pers. comm.); (8) Lake Shastina, Siskiyou County; and (9) Santa Clara River, Ventura County (S. Laymon pers. comm.). Other nesting colonies may exist in areas of suitable habitat, but finding colonies is difficult due to the inaccessible nature of many smaller waterways. Nesting colonies are ephemeral which affects the distribution as sites become inactive as habitat conditions change.

The current breeding distribution of the Bank Swallow in California was determined from a variety of sources and methods including a statewide survey conducted in 1987 by the California Department of Fish and Game (Laymon et al. 1988), county breeding bird atlas projects, Breeding Bird Surveys coordinated by the National Biological Service, and colony occurrences in the California Department of Fish and Game's Natural Diversity Data Base (Figure 1). Most of the nesting colonies were found through targeted surveys of rivers, streams, lakes, and coastal and wetland areas where appropriate nesting habitat exists. Point counts away from preferred nesting habitats, as are many of the Breeding Bird Surveys, are mostly inadequate for determining distribution and population trend. Because of this scattered distribution, focused surveys of suitable habitat in areas dominated by alluvial river systems is the most appropriate method for determining breeding distribution.

ECOLOGY

There appears to be no bioregional differences in the ecology of the Bank Swallow. In fact, the ecology of this species is remarkably similar throughout its extensive mostly Holarctic breeding range.

AVERAGE TERRITORY SIZE

This highly colonial species actively defends only the immediate area around the nesting burrow. The area around the occupied burrow is defended early in nesting period, while the burrow is defended after eggs hatch. Males vacate burrows that do not attract mates and establish new territories within the colony, thereby causing a 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, do join other tunnels leading to abandonment of the later nesting attempt. Distances between nesting burrows have been reported as 12.7-17.8 cm (Freer 1977), 17.8-43.2 cm in Pennsylvania (n = 20 colonies) (Spencer 1962), 18.5 cm (range 10.0-43.2, n = 72) in Wisconsin (Petersen 1955), and 13.2 cm (SD = 1.1, range 1-59, n = 32 colonies) (Humphrey and Garrison 1987). Bank Swallows are extremely social at all times, seeking out other individuals whenever away from their nests. Preening birds on wires and roots are often spaced as closely as 3-4 cm or with shoulders touching.

TIME OF OCCURRENCE AND SEASONAL MOVEMENTS

Bank Swallows arrive on their breeding grounds in California beginning in late March and early April, and the bulk of breeding birds arrive in late April and early May. Birds vacate their breeding grounds as soon as juveniles begin dispersing from the colonies around late June and early July. Limited band recovery records during the later part of the breeding season indicates that post-breeding dispersal occurs in the general vicinity of breeding populations. Breeding areas are essentially devoid of Bank Swallows by mid-July to early August. The spring migration period begins in early March and extends through early May as birds arrive at their nesting areas in a protracted period. The fall migration period moves south through the state from early August to mid-September, with some stragglers recorded in southern California in early November (Small 1994). The Bank Swallow is essentially absent from the state during the winter period as Small (1994) reports that the species is an exceedingly rare winter visitor in central and southern California.

MIGRATION STOPOVER CHARACTERISTICS

Little information exists on migration stopovers in North America. The Bank Swallow tends to use freshwater and estuarine wetlands during migration, and large communal roosts of migrating birds at large wetland areas are known from Europe (Cramp 1988) and the Great Salt Lake in Utah (Paton et al. 1994). However, this phenomenon has not been observed in California. Bank Swallows tend to use these stopover areas for several days before moving on (Cramp 1988). During migration, birds roost communally in groups as large as 50,000-2 million birds reported from England (Cramp 1988). Migration roosts include vegetation at wetlands and marshes (Cramp 1988, Paton et al. 1994). Birds remain at migration stopovers for periods ranging from 10-14 days (Cramp 1988, Turner and Rose 1989). In Europe, juveniles dominate the communal roosts with adults representing 7-17% (Cramp 1988). Weights of birds from spring and autumn migrations are similar to birds at breeding colonies (Cramp 1988).

FOOD HABITS

FORAGING STRATEGY

The Bank Swallow forages predominantly on flying or jumping insects that it captures almost exclusively on the wing. Terrestrial and aquatic insects or larvae are occasionally eaten. Vegetable matter is rarely eaten and appears to be accidental. Foraging habitats include aerial areas over lakes, ponds, rivers and streams, meadows, fields, pastures, bogs, and occasionally over forests and woodlands (Stoner 1936, Gross 1942, Turner and Rose 1989). During breeding, feeding sites are usually within 200 m of the colony when young are being fed, however, this distance may vary depending on the availability of good foraging areas (Turner 1980). Mead (1979a) felt that 8-10 km was the normal maximum feeding range from the colony. Along the Sacramento River, adult birds are commonly observed foraging within 50-200 m of the colony site when feeding nestlings. Bank Swallows feed at an average height of 15 m over open ground (Waugh 1979). However, they may feed low over water in bad weather (Turner and Rose 1989) or as high as 33 m (Bryant and Turner 1982).

Foraging occurs from dawn to dusk, and aerial feeding is the primary foraging method. Bank Swallows occasionally take items from the surface of water and ground. Ground feeding occurs sporadically, and it appears to be related to large, localized concentrations of suitable insect prey on the ground (Clegg 1977, Hobson and Sealy 1987). This bird feeds singly, in pairs or in flocks, the latter occurring more frequently when feeding on a localized source of prey (Stoner 1936, Turner and Rose 1989). Turner (1980) found that parents bring back on average of 60 prey items per visit to the nest.

Stutchberry (1988) found that three colonies in Iowa with 26-52 nesting pairs did not function as information centers for foraging birds where successful foragers transmit information about the location of food centers to other individuals in the population. Most birds foraged alone, and there was no difference in the proportion of successful and unsuccessful foragers being followed away from the colony. Yet, Emlen and Demong (1975) and Hoogland and Sherman (1976) hypothesized that Bank Swallow coloniality enhances foraging opportunities by sharing information about locations of food sources. Data from Hoogland and Sherman (1976) did not support a social foraging benefit, but the data were from a

small colony of 5 nesting pairs. Yet, at a 2100 nesting pair Sand Martin colony in Hungry, group foraging synchrony occurred that supported an information center hypothesis (Szep 1991a). Therefore, colony size may influence social foraging behavior.

DIET

The diverse dietary habits of the Bank Swallow do not appear to influence its occurrence or viability. Bank Swallows tend to forage in areas that support large amounts of insect biomass, and reproductive success does not appear to be food limited because colonies are generally located in areas with sufficient insect resources. Wintering populations, however, appear to be affected by food resources when drought conditions occur (Cowley 1979, Szep 1995a and 1995b).

Stomach contents of 394 individuals collected from various sites in the U.S. and Canada (Beal 1918) found that insects comprised 99.7% of the diet, while non-insects (spiders) and plant material represented the remainder. Insect composition included 33.4% Hymenoptera (13.4% ants [Formicidae]), 26.6% Diptera, 17.9% Coleoptera, 8.0% Hemiptera, 2.1% Odonata, 1.2% Lepidoptera, and 10.5% other insects (mostly mayflies [Ephemeroptera]). Twenty-five Bank Swallows collected in Texas contained 68 boll weevils (Coleoptera) (Gross 1942). Using 14 samples from feces and gizzards during the egg-laying period, Turner (1982) found that the Sand Martin's diet in southern England consisted of 26.7% Coleoptera, 16.2% Schizophora, 14.9% Bibionidae, 12.2% Brachycera, 10.1% Aphidoidea, and 19.9% other items. Turner (1982) also found that birds fed upon insects that were most available early in the breeding season, including Coleoptera, Bibionidae, and Schizophora. Stoner (1936) quantified food habits from stomach samples of nesting adult and young Bank Swallows in New York. The diet of 21 adults was comprised of Coleoptera (21.1% by frequency, 49.8% by weight), Diptera (20.0%, 27.6%), Hemiptera (28.4%, 13.6%), Hymenoptera (16.8%, 3.3%), Plectoptera (1.1%, 4.5%), Araneida (4.2%, 0.4%) and other insects and vegetative material (8.4%, 0.8%) completed the diet.

Using insect wings from fecal samples from colonies in Scotland, Waugh (1979) reported the nesting period diet to consist of Diptera (69.3%), Hemiptera (12.5%), Coleoptera (10.7%), Hymenoptera (4.9%), and other insects (2.6%). Aquatic insects, such as mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera), did not contribute as much to the diet as did terrestrial insects. In Scotland, nestling Sand Martins were fed mostly Diptera, Homoptera, Coleoptera, and Hymenoptera (Waugh 1979).

The diet of nestling Bank Swallows consists of proportionately greater amounts of soft-bodied insects than adults. For 43 young Bank Swallows, Stoner (1936) found their diets to consist of Diptera (19.9% by frequency, 33.6% by weight), Coleoptera (17.9%, 29.5%), Hemiptera (34.3%, 29.0%), Hymenoptera (17.4%, 6.8%), and miscellaneous insect and vegetative material (10.5%, 1.1%). Soft-bodied Diptera comprised approximately half the diet by weight of the young during the early part of the nesting period (June) and approximately one-fifth during the later part of the nesting period (July). Conversely, the hard-bodied Coleoptera comprised approximately one-fifth of the diet by weight in June and almost 40% in July (Stoner 1936). Beyer (1938), Gross (1942), and Turner (1980) also reported the prevalence of soft-bodied insects, such as mayflies (Ephemeroptera) and Diptera, in the diet of young. Turner (1982) found that insect prey weighed averaged 1.15 mg (SD = 0.94, n = 288, dry weight) and winglength averaged 4.90 mm (SD = 1.73, n = 288).

Turner (1980) found that Sand Martin nestlings in Scotland were fed mostly Plecoptera, Diptera, and plant bugs. Bottomley (1993) observed a Sand Martin in Britain catching a small fish, but the bird flew away before it could be determined whether the bird ate the fish or not. The typical brood is brought around 7000 insects (total dry weight approximately 7 g) per day (Cramp 1988) with adults bringing an average of 60 prey items per visit (Turner 1980). Bryant and Turner (1982) found that Sand Martin insect prey weight averaged 1.26 mg (SD = 1.28, n = 8080, dry weight), while Waugh (1979) found dry prey weight to average 1.90 mg. Sand Martins in Scotland brought heavier insect boluses to nestlings when foraging distances were greater, and bolus weight increased with rainfall, flight speed, foraging distance, bolus collection time, insects per bolus, and foraging time. Bolus weight declined as maximum temperature increased. Foraging trip distance decreased as prey size and temperature increased, while trip distance increased as rainfall increased (Bryant and Turner 1982).

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

DRINKING

Bank Swallows drink water, and they also get moisture from the insects they eat.

BREEDING HABITAT

Breeding habitat in California is extremely consistent with regard to the microsite. Nesting colonies only occur in vertical banks or bluffs of friable soils suitable for burrowing by these small birds. Banks or bluffs must be at least 1 m tall to have some predator deterrence values, and some source of continual erosion is almost always present. Breeding habitat vegetation is extremely varied because breeding sites are mostly selected for the suitability of the nesting bank.

NEST SITE

Nests occur in colonies of 5->3000 pairs, and occurrences of single nests are rare. A colony with over 6000 burrows (approximately 3000 pairs) has been reported by Fawks (1938). Nesting colonies are generally located in tall, vertical banks in friable soils along rivers, streams, lakes, and ocean coasts. Sand and gravel quarries are less prevalent as colony sites in California than in other parts of the species range. In California, 14 of 22 (64%) colonies were in sandy loam soils, 4 (18%) were in loamy sand soils, 3 (14%) were in loam soils, and 1 (5%) was in a sand soil (B. Garrison unpubl. data). Colonies are often near water, but this proximity is largely an artifact of the alluvial soils and the role of water as an erosive force. Colonies tend to be located along larger rivers, streams, and lakes because birds require relatively large open areas for vertical flying space around nesting burrows (Hjertaas 1984). Larger colonies are located on longer banks, and these larger colonies tend to persist longer than smaller colonies (Josefik 1962, Freer 1977, B. Garrison unpubl. data).

Burrows are dug generally parallel to the ground surface and perpendicular to bank face. Nest cavities are located at the terminal end of burrows and enlarged upward and to the sides, and the nest cavity floor is level with burrow floor (Hickman 1979). Burrows are located in the upper portions of the bank or bluff, and burrow density decreases from top to bottom (Sieber 1980). Hjertaas et al. (1988) reported that burrows in Saskatchewan were an average of 111.2 cm (SD = 49.1, range 25-340, n = 545) from the base of the bank and 64.5 cm (SD = 45.5, range 10-320, n = 545) from the top of the bank, while Spencer (1962) found that burrows averaged 85.1 cm (SD = 80.4, range 18-320, n = 25) from the bank top in Pennsylvania and Vermont. The top burrows were an average of 70.0 cm (SD = 57.0, range 5-140, n = 32 colonies) from the top of the bank in California (Humphrey and Garrison 1987). Using average height of vertical banks, burrows were placed an average of 36% (Hjertaas et al. 1988), 27% (Spencer 1962), and 21% (Humphrey and Garrison 1987) from the top of the bank. Burrows placed in the upper third of the bank are less susceptible to many ground predators (Sieber 1980).

Lengths of nesting burrows generally are between 0.2-1.0 m. Average nest burrow lengths include 58.8 cm (SD = 11.1, range 10-40, n = 25 colonies) in Pennsylvania and Vermont (Spencer 1962), 64.4 cm (SD = 19.7, range 28-137, n = 512 nests) in Alaska (Hickman 1979), 90.0 cm (SD = 1.7, range 60-120, n = 34 nests) (Wickler and Marsh 1981), 63.6 cm (SD = 19.3, range 15-145, n = 545 nests) in Saskatchewan (Hjertaas 1984), 65.7 cm (SD = 11.8, n = 7 colonies) in Wisconsin (Petersen 1955), 65.6 cm (range 35-119, n = 29 nests) in England (Hickling 1959), 71.0 cm (range 38-119, n = 89 nests) in New York (Stoner 1936), 61.5 cm (SD = 1.7, range 10-105, n = 32 colonies) (Humphrey and Garrison 1987). In Ontario, length of 297 burrows ranged from 0.2-1.5 m (Peck and James 1987), and burrow length averaged 90.0 cm (range 42-180 cm, n = 39 nests) in British Columbia (Campbell et al. 1997). Burrow lengths in Illinois ranged from 46-183 cm (Graber et al. 1972), while burrows in New York averaged 59 cm (Freer 1977). Burrows in gravelly soils are longer than those in sandy, silty, loamy soils (Petersen 1955,

Hickman 1979), while Hjertaas (1984) found that burrows in sand and clay soils had similar lengths. Burrows in loose sand were deeper than those in compact sand, and deeper burrows had greater breeding success than shallow burrows (Sieber 1980). Burrows started later in the breeding period are shorter than those started earlier (Hickman 1979). Height and width of burrow entrances averaged 3.8 cm x 6.4 cm in Alaska (Hickman 1979), 5.5 cm x 7.2 cm in California (Humphrey and Garrison 1987), and 6 cm x 7 cm in British Columbia (Campbell et al. 1997).

Heights of the vertical banks at nesting colonies averaged 3.3 m (SD = 1.7, range 1.3-7.3, n = 32) in California (Humphrey and Garrison 1987), 1.8 m (range 0.5-6.6, n = 60) in Saskatchewan (Hjertaas 1984, Hjertaas et al. 1988), 3.2 m (SD = 1.9, range 0.9-6.4, n = 25) in Pennsylvania and Vermont (Spencer 1962). Nesting bank height ranged from 1.5-23.0 m in Illinois (Graber et al. 1972) and 1.2-15.0 m in Maryland (Saunders and Saunders 1996). In Saskatchewan, average height of vertical banks with nesting colonies (1.8 m) was taller than unused banks (1.4 m) (Hjertaas 1984). Lengths of banks at nesting colonies averaged 455 m (SD = 441, range 13-1900, n = 32) in California (Humphrey and Garrison 1987), 31 m (range 4-221, n = 60) in Saskatchewan (Hjertaas 1984, Hjertaas et al. 1988), 57 m (SD = 59, range 9-305, n = 25) in Pennsylvania and Vermont (Spencer 1962). Longer banks are found on banks along rivers and streams where water erosion can create more suitable nesting habitat. In Saskatchewan, average length of nesting banks (31 m) was longer than unused banks (22 m) (Hjertaas 1984). There appears to be no particular preference in compass orientation of colonies (Hjertaas 1984), although some directions will predominate along rivers and streams depending on the direction of water flow and meander patterns (B. Garrison unpubl. data).

Throughout much of North America except California, many Bank Swallow colonies are located in man-made sites such as sand and gravel quarries, road cuts, and construction sites (Erskine 1979, Hjertaas 1984). Hjertaas (1984) demonstrated that Bank Swallows may select man-made sites over natural sites. In Pennsylvania and Vermont, 13 of 25 (52%) colonies were in gravel and sand pits, 5 (20%) in road-cut banks, 1 (4%) in a pile of coal, and 1 (4%) in a river bank (Spencer 1962). In Ontario, 430 of 713 (60%) individual nest records were from natural banks, 266 (37%) records were from manmade sand and gravel pits, 9 (1%) records were from sand dunes, 5 (1%) records were from manmade piles of sand, gravel, and sawdust, and 3 (<1%) records were from plastic tubes in banks (Peck and James 1987). In British Columbia, 220 of 815 (27%) colonies were in roadcut banks, 139 (17%) colonies were in banks and cliffs of lakeshores, 65 (8%) colonies were in gravel pits, 57 (7%) were in river banks (Campbell et al. 1997). In California, however, 105 of 111 (95%) colonies were in banks along rivers, lakes, streams, and coastlines, with the remaining 5 (5%) colonies in earthen berms, quarries, road cuts, and a ground potato mound (Laymon et al. 1988). In England, 72 of 162 (44%) nests were in river banks, 65 of 162 (40%) nests were in quarries, and 25 of 162 (15%) nests were in miscellaneous sites (Morgan 1979). In North America, Bank Swallow colonies are also located in berms created from dredge spoil (Kiviat et al. 1985), iron ore tailings (Van Deusen 1947), and sawdust piles (Gross 1942, Greenlaw 1972). In Europe, Sand Martins are known to occasionally nest in artificial nest sites, including drain pipes or other artificial holes (Asbirk 1976, Cramp 1988). The use of artificial nest sites is not known from North America.

Generally, new burrows are generally dug each year especially if the bank or cliff face used the previous year collapsed from erosion or man's workings and no old burrows remain (Petersen 1955, Hickman 1979, Cramp 1988). Some old burrows are reused, and burrows are enlarged and deepened with excavation activities that are part of pair bond (Petersen 1955, Hickman 1979). Old nests are removed from reused burrows and new nests are constructed (Petersen 1955). Petersen (1955) observed one instance where a re-nesting occurred in a nest from which a brood recently fledged, while Peck and James (1987) reported a female laying in a nest with six partially incubated eggs. Reuse of old nests is probably avoided due to increased likelihood of infestation by fleas (*Ceratophyllus* spp.) in the nests (Haas et al. 1980). Males producing second broods within a breeding season reused first-brood burrows more often than females (Sieber 1980).

VEGETATION SURROUNDING THE NEST

Bank Swallow nests, because of their placement in vertical faces of banks and bluffs, are generally devoid of vegetation around the nest burrow. Vegetation on the top of the bank or bluff, however, is extremely variable depending on colony location. This variation occurs in almost all measures including vegetative cover, height, and species composition. There appears to be no selection for specific vegetation communities at most nest sites as selection is directed at the nesting bank or bluff itself where soil type, height, and slope are the primary factors determining whether the site will be used for nesting (Garrison 1989).

Throughout California, colonies are mostly located amidst lowland vegetation types including riparian forests dominated by willows (*Salix* spp.) and Fremont cottonwood (*Populus fremontii*). Many colonies along the Sacramento and Feather rivers occur under cultivated crops including deciduous orchards, irrigated row crops, and dryland grain crops. Colonies at coastal locations are located under coastal grassland and coastal scrub communities, while colonies in montane environments in Shasta, Lassen, and Plumas counties occur in coniferous forests where pines (*Pinus* spp.) and firs (*Abies* spp.) dominate. Colonies in northeastern California occur under irrigated pasture, riparian forests, and desert shrub habitats.

ELEVATION

In California, Bank Swallow nesting colonies occur from sea level at the coastal sites to over 2000 m at Crowley Lake, Mono County. This species, despite this elevational range, basically occurs as a nesting species in valleys and coastal areas where alluvial soils occur. Similar elevational ranges occur throughout the species largely Holarctic breeding distribution with a maximum elevation of 4500 m in the Himalayas (Cramp 1988).

NEST TYPE

Bank Swallows are open cup nesters in burrows dug into vertical faces of banks and bluffs. Plant species composition of nests is variable and indicative of materials available in the colony area. Nests in British Columbia were described as seamy, flat platforms composed of grasses, feathers (5 of 12 nests), twigs (2 of 12 nests), straw, rootlets, plant stalks, or leaves (Campbell et al. 1997), while nests in Ontario were described as scanty, flat platforms usually composed of grass stalks and straws, and less often twigs, plant stalks, leaves, and rootlets (Peck and James 1987). In Texas, nests were constructed on grasses, straw, and feathers (Oberholser 1974), while nests in Alaska were constructed of dried grasses, feathers, tissue paper, and shredded cigarette filters (Hickman 1979). Feathers are mostly from waterfowl (Petersen 1955, Hickman 1979), but feathers of domestic fowl and Rock Doves (*Columba livia*) also occur (Beyer 1938). Nests in California are very similar to those from other areas, and feathers from the Mallard (*Anas platyrhynchos*) are the most prevalent feather in Bank Swallow nests in California.

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

BREEDING BIOLOGY

TYPICAL BREEDING DENSITIES

The Bank Swallow shows some of the highest degree of coloniality of any swallow in the world. Bank Swallows typically nest in colonies up to 1500 nesting pairs, but they also nest solitarily (Hoogland and Sherman 1976, Cramp 1988, Turner and Rose 1989). Many complex social behaviors have evolved as a result of the species' highly colonial nature including coordinated foraging activities, territoriality, courtship, breeding, parent-offspring recognition, and predator avoidance (Emlen and Demong 1975, Windsor and Emlen 1975, Hoogland and Sherman 1976, Beecher et al. 1981, Turner and Rose 1989).

DISPLAYS

Most displays by Bank Swallows occur during the breeding period, and several types of display flights are associated with pair bonding. Unpaired males perform territory-circle flights during burrow excavation. The territory-circle flights consists of circular flights around the burrow entrance to advertise to unpaired females as they fly past. Invitation-flights are performed at the completion of burrow excavation. The males overtake

females in flight and land at the burrow entrance, apparently to entice females into the burrow (Kuhnen 1985). Guarding-flights occur when nest building is completed; the male accompanies (guards) the female in flight to the burrow. Mate-pursuit flights (sexual chases) occur between mated pairs 3-5 days before egg laying; paired males drive away intruding males (Kuhnen 1985). Males and females that have paired prior to arrival at the colony site sit close together at the burrow; the male digs the burrow while the female faces out and deters approaching males and females (Kuhnen 1985). Unpaired males conduct advertising-displays from the burrow where they face outward, sing, ruffle head and throat feathers, display their white throat, and vibrate closed wings (Kuhnen 1985, Turner and Rose 1989). Females flying by burrows cause males to fly out, sing, and perform territory-circle flights. If a female lands near the burrow, the male perches on the burrow ledge and displays his white throat patch (Kuhnen 1985).

As the pair bond is formed, both sexes sing twittering songs while perched side by side or facing each other at the burrow entrance. Behaviors that indicate the completion of pair bonds include: 1) regular visits by the female to a particular burrow where she engages in sporadic excavations; 2) both birds spending long periods of time together in the burrow (including at night); and the invitation and guarding-flights by the male (Kuhnen 1985). Copulations occur in burrows, but have also been seen on the ground, on wires, at the bank face, and in the air (Turner and Rose 1989). To copulate, a male sings while approaching the female, sometimes quivering his wings, then mounts and copulates with raised wings (Kuhnen 1985, Turner and Rose 1989).

MATING SYSTEM

The Bank Swallow is socially monogamous where only one male and one female tend the nest. Neither sex is known to establish ownership of multiple nests. Males settle into a fixed area of the nesting colony and begin attracting females once the burrow is about 30 cm long (Kuhnen 1985, Cramp 1988). Males apparently only attempt extra-pair copulations with females during their fertile period (Hoogland and Sherman 1976, Jones 1986a). Male Bank Swallows also attempt extra-pair copulations on the ground with dead birds (Petersen 1955, Hoogland and Sherman 1976). Males attempted to copulate with stuffed conspecific females during the burrow construction, egg-laying, and incubation periods (Hoogland and Sherman 1976). Competing females will visit burrows of breeding pairs, and paired females drive off intruders (Kuhnen 1985).

Sexual chases where extra-pair copulations by other males are the objective are prevalent (Petersen 1955, Beecher and Beecher 1979, Kuhnen 1985). Promiscuous copulations appear to be not as common as might be indicated based on the frequency of sexual chases, possibly due to the success of the guarding male and difficulty in observing the behavior (Beecher and Beecher 1979). Males selectively chase female Bank Swallows that are heavier than normal for extra-pair copulations because females are heaviest during laying and pre-laying periods when they are fertile (Beecher and Beecher 1979, Jones 1986a). The heavy females present cues during flight to males because they have heavier wing loading and a more labored flight.

CLUTCH SIZE

Clutch size typically ranges between 2-7 eggs with most clutches having 4-5 eggs. Limited field observations indicates that Bank Swallow clutches in California are within this range. Clutch sizes from areas other than California include: (1) Alaska, 4.09 (SD = 0.78, range = 2-6, n = 242; Hickman 1979); (2) Ontario 4.44 (range = 1-9, n = 261; Peck and James 1987); (3) Saskatchewan 4.87 (SD = 0.92, range = 2-7, n = 218; Hjertaas 1984); (4) British Columbia 3.51 (SD = 1.53, range = 1-7, n = 67; Campbell et al. 1997); (5) Michigan 4.98 (SD = 0.74, range = 3-8, n = 217; Hoogland and Sherman 1976); (6) Britain 4.78 (SD = 0.91, range = 2-6, n = 56; Morgan 1979); (7) New York 4.38 (SD = 1.04, range = 2-7, n = 170; Freer 1977) and 4.82 (SD = 0.66, range 3-6, n = 22; Bull 1985); (8) North Dakota 5.3 (range = 4-7, n = 6; Stewart 1975); (9) Maryland 5.1 (range = 4-7, n = 28; Saunders and Saunders 1996); and (10) Wisconsin 4.86 (SD = 0.81, range = 2-6, n = 125) (Peterson 1955). There appears to be a trend for more eggs in clutches laid earlier as Wisconsin clutches laid before 15 Jun averaged 5.03 eggs (SD = 0.69, range = 3-6, n = 104), while clutches laid after 15 Jun averaged 4.00 eggs (SD = 0.84, range = 2-5, n = 21; Peterson 1955).

Freer (1977) found no significant difference in clutch sizes at five different colony sites in New York, and there appeared to be a slight, albeit statistically insignificant, trend for larger clutches for nests initiated during the middle of the April to May egg-laying period. Svensson (1986) found considerable annual variation in the average clutch size of Sand Martins nesting in Swedish Lapland. Average clutch sizes between 1969 and 1985 ranged from approximately 3.85 eggs in 1977 to approximately 5.00 eggs in 1969 and 1985. This variation was largely due to a general decline in clutch size with median egg-laying date within the nesting colony.

INCUBATION

Females do the majority of incubation, while males participate primarily when the female leaves nest. Females primarily incubate at night as Petersen (1955) found females incubating alone in 21 of 32 (66%) nests, males alone in 2 of 32 (6%) nests, and both sexes in 9 of 32 (28%) nests. Turner and Rose (1989) reported that Bank Swallows incubate nearly 100% of the time, but Ellis (1982) found that Bank Swallows incubated eggs an average of 75.9% (SD = 8.7%, n = 4 nests) of the time. Ellis (1982) also found that incubation effort increased with decreased nest cavity temperature.

INCUBATION PERIOD

Bank Swallows begin incubation before the clutch is complete (Peck and James 1987). Females mostly spend nights on the eggs during egg-laying (Petersen 1955). A sustained incubating schedule is initiated by the female near the end of laying, usually at least 1-2 days before the clutch is complete (Peterson 1955, Turner and Rose 1989). A single medial abdominal brood patch develops in females during egg-laying; males lack brood patches. There is little variation with incubation periods within and between populations. In Wisconsin, incubation periods ranged from 13-15 days (n = 11) (Petersen 1955), while Stoner (1936) reported incubation periods of 14-16 days in New York. In Alaska, incubation periods were 14-15 days (Hickman 1979), while Peck and James (1987) found incubation periods ranging from 13-16 d in Ontario (n = 24). Sand Martin incubation periods in Europe are 14-15 days (Cramp 1988).

DEVELOPMENT AT HATCHING

Bank Swallows are altricial and nidicolous at hatching. Young are naked, bright reddish pink, and weigh approximately 1.6 g at hatching (Beyer 1938, Peterson 1955). A scanty covering of pale gray or gray-brown down occurs on the nape, back, and base of wings, and the eyes are large and black through closed lids. The inside of the mouth and bill flanges are lemon-yellow, the bill is yellowish-gray, and the feet pinkish-gray (Beyer 1938).

Mass increase is most rapid between 2-10 days of age; mass peaks at 12-14 days then gradually decreasing until fledgling (Peterson 1955, Marsh 1979). The beginning of the outer (9th) primary is evident by day 7 after hatching (Peterson 1955, Marsh 1979, Turner and Bryant 1982), and feather tips sprout on days 9-10. The length of the primary feathers increases linearly with age (Turner and Bryant 1982) at a rate of approximately 0.062 cm/day. By 10 days, the nestling appears spiny due to growth of closed feather sheaths with an almost full coat of dense, short gray-brown down between sheaths (Cramp 1988).

Tarsus length is approximately 6 mm at day 2 , finally reaching a length of approximately 12 mm at fledging. Tarsi grow rapidly for the first 6-8 days, by which the time tarsi reach 77% of the adult length; growth slows down considerably after that (Turner and Bryant 1982). Early tarsus growth facilitates an upright posture during begging, and allows nestlings to move along the burrow towards their parents to be fed. The bill also grows most rapidly during the first 7-8 days, with gape width reaching a maximum at about the middle of the nestling period, and then decreasing rapidly (Turner and Bryant 1982). Fat is added rapidly during the first 2-8 days coinciding with the period of most rapid weight gain. Once peak weight has been reached around 12-14 days, a high, although variable proportion of the nestling's weight is fat (Marsh 1979, Turner and Bryant 1982).

During the first few hours after hatching, the head is normally forward resting close to breast. The nestlings remain in a sprawled position for several days. At 5-7 days, they can crouch temporarily with head erect. By 8-10 days, they can sit erect and use shuffling walk to move out of the nest (Hickman 1979), and at 9 days, nestlings rush adults in burrow to be fed (Petersen 1955). Begging is confined to movements of head and neck until 13-15 days, when young begin to quiver wings during begging. Young move to burrow entrances at 15-17 days, but Petersen (1955) reported that nestlings at 12 days wait 6 inches from burrow entrance to be fed by adults. The fear response is well developed by day 15. Young exercise by stretching and flapping wings before fledging, and young can fly when leaving nest for first time.

NESTLING PERIOD

Young remain in the nest for 18-22 days before fledging. Nestling periods reported include: (1) an average of 22.3 days (SD = 2.1 d, n = 30) in Scotland (Turner and Bryant 1979); (2) 18-21 days in Pennsylvania (Beyer 1938); (3) 18-21 days in California (B. Garrison unpubl. data); and (4) 20 days in Wisconsin (Petersen 1955). Nestlings are capable of labored flight a few days prior to fledging. Adults reduce feeding rates and use vocalizations to motivate nestlings to fledge (Petersen 1955). Fledglings return to the burrow for 4-5 days after first flight landing in neighboring burrows or perching on roots, twigs, and branches around nesting banks (Bryant and Turner 1982), and juveniles as old as 28 days roost in their own burrows (Petersen 1955). Juveniles are basically independent at 30 days of age (Cramp 1988), and juveniles leave the colony area soon after fledging (Emlen and Demong 1975, Freer 1977). The birds join other juveniles and adults in flocks which remain in the colony area for approximately 1 week after fledging (Freer 1977). Juveniles must begin foraging during their first few hours of independence because parents feed them only irregularly after fledging (Emlen and Demong 1975).

FLEDGLING PERIOD

Once independent, juveniles spend much time foraging, usually in intraspecific flocks of juveniles and adults in the general area around the 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). Post-breeding flocks of juveniles and adults regularly land on ground to sunbathe, dust-bathe, and preen (Petersen 1955, Barlow et al. 1963, Cramp 1988). Juveniles also engage in attempted copulations, incipient excavation, nest-building, and brooding (Petersen 1955). Once migration occurs, however, little is known about their activities. Juveniles, once independent, wander extensively throughout a large area moving among several communal roosts over a longer period of time than adults. This wandering may serve to familiarize juveniles with their natal area and its landmarks for the subsequent spring return, as well as possibly 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.

PARENTAL CARE

Brooding begins at hatching and is largely continuous for first 2-3 days of nestling life. Brooding gradually begins to diminish until ceasing completely by about day 7-10 (Beyer 1938, Peterson 1955). Brooding decreases by shortening duration of brooding period. Nestlings are brooded at night by adults until day 10, and females do most brooding at night, with both sexes and males alone less prevalently (Petersen 1955). Feeding begins at hatching and continues until 3-5 days after fledging. Both sexes feed nestlings (Petersen 1955, Hickman 1979, Westerterp and Bryant 1984), but males tend to make more feeding visits than females (Petersen 1955, Westerterp and Bryant 1984). The parent bird compresses multiple insects into tight bolus before giving it to the young. The bolus is placed directly into nestlings' mouths with quick jabs of the adult's bill. Both parents remove fecal pellets from the burrow until young have fledged (Beyer 1938, Petersen 1955, Hickman 1979).

POST-BREEDING SOCIAL BEHAVIOR

After fledging and prior to fall migration, juveniles and adults roost together on trees, exposed roots on banks, shrubs, and logs on sand and gravel bars (Petersen 1955, Cramp 1988). Post-breeding flocks in California remain in the general area of the breeding colony for 1-2 wk after all the young have fledged and the colonies are abandoned. Bank Swallows are absent from the breeding areas once they disperse. During migration, birds roost communally in groups as large as 50,000-2 million birds in England (Cramp 1988) and several thousand in Utah (Paton et al. 1994). Migration roosts include vegetation at wetlands and marshes (Cramp 1988, Paton et al. 1994). During the post-breeding periods and fall migrations, Bank Swallows occur in mixed-species flocks with Barn (*Hirundo rustica*), Cliff (*H. pyrrhonota*), and Tree (*Tachycineta bicolor*) swallows.

DELAYED BREEDING

Delayed breeding has not be demonstrated with the Bank Swallow. Birds begin breeding as second-year birds the first summer after they were born.

NUMBER OF BROODS

Bank Swallows are mostly single-brooded throughout much of their worldwide distribution, and with only one brood per breeding season likely in North America. Several authors for North American populations report one brood per year including Beyer (1938), Hickman (1979), Humphrey and Garrison (1987), while two broods per year were reported by Stoner (1936). Any reports of two broods in North America are questionable due to the difficulty in unequivocally determining if the second brood follows a successful first brood. Reports of two broods for North America probably are renesting attempts after failed first nesting efforts. Two broods per season are known for much of the western Palearctic except the north and eastern part of the range (Cowley 1983, Cramp 1988) which corresponds to the reports of Sand Martins being single brooded in Russia (Dementev and Gladkov 1968).

BROOD PARASITISM

Intraspecific brood parasitism is not known to occur with Bank Swallows. Their colonial breeding habits result in considerable extra-pair copulations and mate competition, but these behaviors do not appear to limit species occurrence or viability because these behaviors are typical in colonial swallows. Interspecific brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) is essentially non-existent with Bank Swallows as only one record was reported by Friedmann and Kiff (1985).

LANDSCAPE FACTORS

FRAGMENTATION

Fragmentation as defined as the breaking up of intact, homogeneous blocks of habitat does not readily apply to the Bank Swallow for its California breeding habitats. However, fragmentation of wetlands, grasslands, and other open habitats used while Bank Swallows migrate and winter may adversely affect them by reducing insect food resources and roosting habitat. Throughout its worldwide breeding distribution, Bank Swallow nesting habitat is extremely ephemeral due to the interaction between the friable soils needed for burrow excavation and the erosive forces needed to maintain the vertical faces at colony sites. Without some erosion, human-caused or otherwise, the vertical faces quickly collapse and break down, thereby becoming unsuitable for nesting. Also, Bank Swallow colonies typically do not occur in every bank or bluff that is suitable, nor do burrows occupy all suitable locations within an individual colony site. Furthermore, there is considerable turnover in colony sites from year to year. On the Sacramento River, Bank Swallows generally nest in 40-60% of the total number of banks that are suitable for nesting in any given year. Bank Swallow populations apparently require some habitat surplus in order to remain viable over the long-term.

The most significant fragmentation threat is the direct loss of suitable colony sites through bank protection and flood control projects. These projects destroy suitable nesting habitat by engineering eroding banks to a 2:1 or 3:1 slope of length to height and placing boulder-sized rock (riprap) on the new slope. Most erosion is stopped and nesting habitat is directly lost. When large amounts of eroding banks are protected in this way, the amount of suitable nesting habitat available to Bank Swallows is reduced. There are some reaches on the Sacramento River, particularly in Colusa, Sutter, Yolo, and Sacramento counties, where very few suitable banks remain due to extensive bank protection and channelization efforts. Populations in these reaches are extremely small and prone to localized extinctions. Localized population extinctions have occurred with other Bank Swallow populations as habitats disappear through human and natural causes (Cramp 1988, Brewer et al. 1991, Palmer-Ball 1996, Robbins and Blom 1996). The number of colonies and the number of nesting burrows per colony on the River Tisza, Hungry, are directly related to total area of suitable nesting habitat (Szep 1991b), so loss of suitable habitat will affect populations.

PATCH SIZE

Nesting colonies occur on banks ranging in length from 10-2000 m and height from 0.5-20 m indicating that Bank Swallow colonies can occur in banks and bluffs of various sizes. There is little indication that larger colonies have greater nest success than smaller colonies (Hoogland and Sherman 1976), but observations from the Sacramento River indicate that colonies in larger banks tend to be more consistently used on an annual basis than smaller colonies (B. Garrison unpubl. data). Larger colonies tend to occur on larger banks (Humphrey and Garrison 1987). The effect of predation is slightly greater at smaller colonies as proportionately more nests can be predated.

DISTURBANCE

The Bank Swallow is most affected by flooding and erosion disturbances. Flooding and associated erosion events can have positive and negative effects to this species. Other disturbances such as fire, wind throw, insect infestations of terrestrial vegetation, landslides, and earthquakes have little direct effect on Bank Swallows. Flooding in freshwater environments causes erosion and soil deposition. Erosion creates the vertical banks needed for nesting, while the alluvial soils (e.g., clays, silts, and loams) deposited during flood events are the friable soils needed for the burrows. Lack of erosion results in banks and bluffs becoming more gently sloped and unsuitable for nesting. Flooding and erosion, however, can also result in the need for bank protection, channelization, and flood control projects thereby reducing the amount of nesting habitat. Wave wash from boats, high winds, and rapidly fluctuating water levels from reservoirs and storms can cause bank undercutting during the breeding season possibly causing mortality to eggs and young in Bank Swallow colonies.

Bank Swallows appear relatively insensitive to moderate levels of human-induced disturbance. In California, colonies occur on banks under actively farmed irrigated row crops and orchards. Several colonies occur in coastal locations at public seashores where human activity can be substantial. The colony in the town of Fall River Mills, Shasta County, occurs in a bluff along the major road through town amidst several businesses. Other Bank Swallow colonies occur on river banks and bluffs at several reservoirs where recreational boat traffic occurs. These colonies appear to be reproducing successfully. Bank Swallows are most susceptible to habitat losses that may be human-induced or naturally occurring. Bank undercutting from boat wakes or fluctuating water levels has the potential to cause collapse of nesting banks.

ADJACENT LAND USES

A wide variety of land uses occur around Bank Swallow colonies including hydroelectric power generation, irrigation water conveyance, recreational boating, commercial agriculture, vehicular and pedestrian traffic, and domestic livestock grazing. These land uses appear relatively benign as long as the integrity of the nesting bank remains. Any land use has the potential for adverse effects if it causes fluctuating water levels and increased erosion during the nesting period whereby banks with active colonies collapse. Mortality to eggs and nestlings can occur if banks collapse. Adjacent land uses that retain nesting bank integrity, allow bank erosion to occur, and provide insect food resources are unlikely to have substantive adverse impacts to Bank Swallows.

CLIMATE

Bank Swallows are found in a variety of temperature climates throughout their worldwide distribution. They generally do not occur in tropical or subtropical climates. Most of their breeding range occurs in the more northerly latitudes where temperature ranges are extreme, but their migratory habits allow them to avoid extreme winter weather conditions. In California, Bank Swallows nest throughout the central and northern part of the state including cool, moist coastal zones and hot, dry inland valleys and high elevation interior deserts.

PESTICIDE USE

Pesticide use appears not to be a problem with Bank Swallows. Eggshell thinning has not been found, and an analysis of three eggs from a Sacramento River colony found no detectable levels of any harmful pesticides (R. Schlorff pers. comm.).

PREDATORS

Bank Swallows at nesting colonies are predated by many animals, including mammals, birds, and snakes. No information exists on predators during migration and on the wintering range. In California, American Kestrels *(Falco sparverius*) and Peregrine Falcons (*F. peregrinus*) take birds on the wing, while Great Blue Herons (*Ardea herodias*), Great Egrets (*A. albus*), and Gopher Snakes (*Pituophis melanoleucus*) feed on nestlings and adults in burrows at colonies. In other parts of the Bank Swallow's North America range, predators include American Kestrels in New York (Freer 1973, Windsor and Emlen 1975), Michigan (Hoogland and Sherman 1976), and Alaska (Hickman 1979); Black Rat Snakes (*Elaphe obsoleta*) in Kansas (Plummer 1977) and Virginia (Blem 1979); Eastern Chipmunks (*Tamias striatus*) in Massachusetts (Ginevan 1971); Western Plains Garter Snakes (*Thamnophis radix*) and Deer Mice (*Peromyscus maniculatus*) in Saskatchewan (Hjertaas and Hjertaas 1990); Blue Jays (*Cyanocitta cristata*) in Michigan (Hoogland and Sherman 1976); Striped Skunks (*Mephitis mephitis*) in New York (Stoner 1936); Norway Rats (*Rattus norvegicus*) in New York (Stoner 1938); American Badgers (*Taxidea taxus*) in Saskatchewan (Potter 1924); Barred Owls (*Strix varia*) in Wisconsin (Errington 1932); Mink (*Mustela vison*) in Massachusetts (Brewster 1903); and Northern Shrikes (*Lanius excubitor*) and Brown Bears (*Ursus arctos*) in the Yukon Territory (Morlan 1972). American Badgers, Brown Bears, and Mink dig up burrows trying to get at the nest contents (Brewster 1903, Potter 1924, Morlan 1972).

Snakes climb into burrows from the bottom or top of nesting banks (Hjertaas and Hjertaas 1990, B. Garrison pers. observ.). Snakes can spend several days in a colony, feeding on an entire brood, coiling inside a nest, digesting their food, defecating, shedding, 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 snake access and foraging success. American kestrels take Bank Swallows in the air and in their burrows. At burrows, kestrels fly to burrows from nearby perches taking nestlings from burrow entrances or reaching into the burrow with one of their feet (Windsor and Emlen 1975). In the air, American Kestrels take Bank Swallows by flying into mobbing flocks or chasing birds singled out from aerial groups. Most aerial predation by American Kestrels and raptors such as the Hobby (*F. subbuteo*) take place during the fledging period (Windsor and Emlen 1975, Szep and Barta 1992), so it appears likely that aerial predators take fledglings because adults would be extremely difficult prey to catch in the air.

Szep and Barta (1992) found that the number of attacks and the number of Sand Martins caught by Hobbies at martin colonies in Hungary increased with larger colonies. During the July fledgling period over a 2-yr period, the number of attacks per d averaged between 16.8 (SD = 12.3, n = 7 d) and 27.0 (SD = 11.9, n = 7 d), while the number of birds caught averaged 0.7/d (SD = 0.8, n = 7 d, 4 martins caught) and 1.4/d (SD = 1.4, n = 7 d, 10 martins caught).

Colony sites have been deserted as habitat suitability decreased and Black Rat Snake predation increased (Blem 1979). Mead (1979b) found that predation accounted for 11.9% of the known causes of death for banded Sand Martins from Britain, which was the third greatest source of mortality behind deaths due to motorized vehicles (45.2%) and humans (15.5%). Predators affect the occurrence and viability of Bank Swallows at localized levels where colony sites become abandoned if subjected to abnormal levels of predation. However, predation levels appear to be influenced more by habitat conditions as snake predation likely increases as habitat quality decreases. Yet, colony sites can be abandoned quickly

if habitat conditions become unsuitable regardless of predation levels. Furthermore, the Bank Swallow's colonial nesting habits attract predators (Windsor and Emlen 1975, Hoogland and Sherman 1976, Szep and Barta 1992).

DEMOGRAPHY AND POPULATION TRENDS

Bank Swallow demographics are extremely variable due to several factors. Published information and observations from California indicate that the number of colonies and, hence, the total population size for a given area fluctuates greatly. Furthermore, demographic parameters within populations can vary. For example, sex ratios of captured Sand Martins in Sweden were highly variable ranging from 1.95 males: 1 female to 1 male: 1.30 females over a 4-yr period (Persson 1987a). Sex ratios changed due to population dynamics resulting from differential mortality, and biased sex ratios occurred in different age classes during different years. Sex ratios were 1 male:1 female when breeding populations grew, and > 1 male:1 female when the population declined. Mortality-inducing events such as bank collapse and predation that differentially affected males and females caused biased sex ratios (Persson 1987a).

Little quantitative information on population regulation exists for North America. Breeding populations are affected by weather in various ways, and BBS data from 1966 to 1979 (Robbins et al. 1986) indicated a 30% decline in the combined populations of Bank, Barn, Cliff, and Tree swallows in Nova Scotia, Maine, and New Hampshire possibly resulting from an abnormally cold, rainy period during migration in late May 1974. Drought conditions in north African wintering grounds were cited as the cause of decreases in Sand Martin breeding populations in Britain (Cowley 1979), Scotland (Jones 1987a), and Hungary (Szep 1993), although Svensson (1986) felt that winter range weather conditions were not an adequate explanation for Sand Martin breeding population changes in Swedish Lapland. Reduced body size (measured by keel length) in Sand Martins in Britain and Scotland coincided with reduced breeding populations and the African drought indicating that winter range weather profoundly affects breeding populations by selecting for smaller birds that are better able to survive periods of reduced insect prey populations (Jones 1987b, Bryant and Jones 1995).

The size of individual colonies varies from year to year due to predation, habitat changes, and wintering ground weather conditions. A single colony in Virginia varied in size from 40-435 burrows between 1975 and 1987, and the site was abandoned in 1988 and 1989 due to increased snake predation and habitat degradation (Blem and Blem 1990). In Connecticut, a single colony varied from 285-910 burrows from 1945-1950 due to summer weather and habitat changes (Bergstrom 1951). In Saskatchewan, a population of Bank Swallows varied from 39-40 colonies and 293-318 nests from 1980-1981 (Hjertaas et al. 1988). A single Sand Martin colony in Swedish Lapland ranged from 8-80 nesting pairs from 1968-1985, and the site was inactive one yr (1979) (Svensson 1986). Over a 14-yr period, a single colony in Britain varied from 35-772 pairs, and the site was inactive one yr (1962) (Harwood and Harrison 1977). Jones (1986b) found considerable annual variation over a 3-yr period for 27 Sand Martin colonies in Scotland, while Sieber (1982) found a 37% reduction in a Sand Martin population over a 21-yr period (1960-1980) in Sweden. A Sand Martin population in England varied from 150-700 pairs over a 11-yr period with changes between yrs ranging from 45% to +27% (Cowley 1979).

POPULATION TREND

For Bank Swallows, atlasing is a good monitoring technique because colony sites can be sought out and documented more readily. The population on a portion of California's Sacramento River averaged 2082 pairs (SD = 1064 pairs, range 1044-4326 pairs, n = 12) and 14.8 colonies (SD = 5.3, range 10-28, n = 12) between 1986-97 (B. Garrison unpubl. data). The population trend over the last 12 yr on the Sacramento River included a decline from a large population between 1986-1990 to a relatively small, fluctuating population from 1991-1997. Breeding Bird Surveys (BBS) are not the best long-term population monitoring techniques because the birds colonial nesting habits and ephemeral nature of colony sites make it difficult to consistently detect at many points. However, examining BBS data showed stable breeding populations between 1966 and 1991 for the North American continent. Significant increases between 1966 and 1991 appear to have occurred in the Upper Coastal Plain and Great Lakes Plain physiographic strata, while significant decreases appear to have occurred in the Driftless Area, Adirondack Mountains, Closed Boreal Forest, and Till Plains strata. DeSante and George (1994) reported a weak decreasing trend in BBS counts of Bank Swallow

populations west of the Rocky Mountains between 1966 and 1991. Statistically significant trends in BBS data for this species must be interpreted cautiously, as abandonment or recent colonization of nesting sites along survey routes may greatly bias relative estimates of abundance. Nesting populations reported to be declining include those in California (Garrison et al. 1989) 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 declines and continuing threats to existing colony sites (Garrison et al. 1989) have resulted in the Bank Swallow being listed as a threatened species in California. In Oregon, the Bank Swallow is listed as a sensitive species due to the small population and susceptibility to habitat loss (Oregon Dept. of Fish and Wildlife 1996). The Bank Swallow is also considered a species of special concern in Kentucky due to its restricted distributed and population declines (Palmer-Ball 1996). In Maryland, Bank Swallow populations appear stable, but the breeding distribution has shifted from the Chesapeake Bay shoreline to gravel pits and river banks in the interior part of the state (Saunders and Saunders 1996). Shifting distribution away from coastal locations to inland breeding sites has also been noted in New York (Andrle and Carroll 1988) and Connecticut (Bevier 1994).

MANAGEMENT ISSUES AND OPTIONS

EXOTIC SPECIES INVASION/ENCROACHMENT

The Bank Swallow, compared to other species of small-bodied landbirds, appears to be little affected by exotic species. This is largely due to its strict and relatively unique nesting habitat requirements. Nesting colonies are usually located in extremely rural or wildland environments where exotic species are less prevalent. Instances where exotic species can potentially cause problems to Bank Swallows do occur, however, as European Starlings (*Sturnus vulgaris*) have apparently supplanted Bank Swallows from some burrows at the colony at Fort Funston, San Francisco County.

HABITAT LOSS

The most significant management issue affecting the Bank Swallow in California is the direct loss of suitable colony sites through bank protection and flood control projects, particularly on the Sacramento River (Garrison et al. 1987). These projects destroy suitable nesting habitat by resloping the bank and placing riprap rock on the bank. Erosion is stopped and nesting habitat is destroyed. Loss and modification of wetlands, grasslands, and other open habitats used during migration and wintering has the potential to adversely affect Bank Swallows by reducing insect food resources and roosting habitat.

MANAGEMENT

Local breeding populations benefit greatly from annual erosion and maintenance of the suitability of banks, cliffs, bluffs, and quarries where nesting colonies occur. Human activities creating sand and gravel quarries, road cuts, and other vertical banks in friable soils has directly benefited the Bank Swallow by increasing its distribution in Canada (Erskine 1979). However, Bank Swallows were often unintentional benefactors of these activities. Outside of California, several active sand and gravel quarries avoid extraction activities around active nesting colonies to minimize disturbance to nesting birds. Maintenance of suitable habitat is ensured if actions creating vertical faces such as moving water or sand and gravel extraction activities continue. In California, few colonies are located in quarries, so active management of quarries will unlikely have any widespread benefit for Bank Swallows in the state.

There are few cases documenting management efforts taken specifically to benefit Bank Swallows. A recovery plan has been written for the Bank Swallow in California (Schlorff 1992). Two artificial banks and six enhanced natural banks were built along the Sacramento River as mitigation for loss of colony sites from flood control projects (Garrison 1991). Bank Swallows occupied one of the two artificial sites and five of the six 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 within 3 yr as no maintenance was conducted thereby rendering the sites unsuitable because the vertical banks sloughed off, banks became overgrown with vegetation, and/or the soils became very hard (Garrison 1991). This short-term response indicates that habitat

enhancements can be done, but the high cost of construction and maintenance and the small area involved makes artificial habitat enhancement not very cost-effective.

One hundred nesting burrows dug in 1986 with a hand auger on the Sacramento River were not used by Bank Swallows (R. Schlorff pers. comm.). Construction of these artificial burrows was probably not effective due to the ephemeral nature of the nesting colony and the fact that a colony had not previously occupied the bank. Garrison (1991) proposed that meander loops could be created off the mainstem of rivers by diverting water through extensive areas of alluvial soils. Vertical banks would be created as the water erodes the soil. This is essentially the same process that creates new Bank Swallow nesting habitat on the Sacramento and Feather rivers. To date, this management action has not been attempted. Habitat enhancements, however, may not be necessary in areas where considerable amounts of suitable habitat exists.

Listing as the Bank Swallow as a threatened species in California has protected some nesting sites from proposed flood and erosion control projects. Since listing, a few sites have been destroyed when emergency projects were allowed. In general, the species population dynamics makes it difficult to achieve success with any management action other than conservation of extensive amounts of suitable nesting sites throughout large areas. Integrating Bank Swallow habitat protection with larger scale riparian ecosystem conservation efforts, as is occurring along the Sacramento River, appears the most promising. Successful conservation of Bank Swallow nesting habitat needs with riparian ecosystem management will have the greatest success if cycles of flooding and erosion are allowed to continue in as natural cycle as possible. Management actions designed to maintain and improve the functioning of riparian ecosystems will benefit all wildlife associated with these systems, as well as reduce the societal costs for ongoing flood control projects.

ASSOCIATED BIRD SPECIES

Birds that will benefit from management actions directed at the Bank Swallow include those species that nest in eroding banks and bluffs along California's waterways. However, management actions should more appropriately be directed at allowing fluvial geomorphological processes such as erosion, deposition, and meandering to occur along the state's rivers, streams, lakes, and coastal areas. The Bank Swallow and all other fish and wildlife associated with these ecosystems will benefit. Riparian ecosystems will have greater levels of integrity if fluvial geomorphological processes occur. Species specifically associated with eroding banks and bluffs along many of the state's lowland rivers and streams include the Bank Swallow, Northern Rough-winged Swallow, Cliff Swallow, Black Phoebe (*Sayornis nigricans*), Barn Owl (*Typo alba*), and Belted Kingfisher (*Ceryle alcyon*). These species will directly benefit from management actions directed at the Bank Swallow.

HABITAT AND POPULATION OBJECTIVES

Establishing habitat and population objectives for the Bank Swallow in California will be difficult. The ephemeral nature of nesting habitat, fluctuations in breeding populations, patchy California breeding distribution, and existence of unoccupied habitat must all be considered when establishing these objectives. The Bank Swallow is affected by factors outside of its breeding grounds, particularly drought and habitat conditions on the wintering grounds, thereby population objectives may not be under the control of wildlife managers in California. However, management objectives should be established for population centers on the Sacramento and Feather rivers, Pit River area, Lower Klamath/Tule Lake area, Fall River area, Hat Creek/Lake Briton area, Honey Lake area, and rivers and lakes in Mono and Inyo counties. Concentrating management activities at known population centers is a biologically prudent approach to conserving the Bank Swallow population in California. Baseline information on population levels combined with habitat inventories will be needed to establish habitat objectives. A feasible approach would be to identify all areas of currently and potentially suitable nesting sites in a management area.

Individual colonies will likely continue to appear sporadically throughout the state in areas away from major population centers and areas supporting long-standing colonies. Because of the unpredictable nature of these particular colonies, it seems infeasible to direct any disproportionate management emphasis. Nevertheless, any area where Bank Swallow colonies are found should receive some management action to allow the birds an opportunity to establish nesting colonies.

MONITORING METHODS AND RESEARCH NEEDS

Annual surveys of population centers along the Sacramento and Feather rivers is essential to monitor population trends. Annual monitoring efforts should also include known colony areas in the larger population centers including: (1) Cache and Hat creeks; (2) the American, Cosumnes, Fall, Pajaro, Pit, Salinas, Scott, Smith, and Susan rivers; (3) Tule Lake, Lake Briton, Clear Lake (Modoc County), and Lower Klamath Lake; and (4) coastal areas at Ano Nuevo and Fort Funston. Population surveys should also include habitat inventories. These surveys will likely include 80-90% of the known colony areas in the state. Nesting productivity should also be determined annually at a subset of colonies throughout California, particularly along the Sacramento and Feather rivers. These monitoring efforts should be integrated with data gathering on water flows, erosion rates, and flood control and bank protection efforts so that adaptive management efforts can occur.

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