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Hirundo rustica

FRENCH:
Hirondelle des granges,
Hirondelle rustique,
Hirondelle de cheminee
SPANISH:
Golondrina ranchera,
Golondrina tijerela

Barn Swallow

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> *One hardly knows what quality to admire most in . . . the Barn Swallow. All the dear associations of life at the old farm come thronging up at sight of him. You think of him somehow as part of the sacred past; yet here he is today as young and as fresh as ever, bubbling over with springtime laughter.*
>
> William L. Dawson, 1923, *The Birds of California*

The Barn Swallow is the most widely distributed and abundant swallow in the world. It breeds throughout most of North America, Europe, and Asia and winters in Central and South America, southern Spain, Morocco, Egypt, sub-Saharan Africa, the Middle East, India, Indochina, Malaysia, and Australia. Originally nesting primarily in caves, the Barn Swallow has almost completely converted to breeding under the eaves of or inside artificial structures such as buildings and bridges. In North America, this shift in nest sites began before European settlement and was virtually complete by the mid-twentieth century; nowadays natural nestings are rarely seen and usually reported in print if they occur. As with other swallows that have shifted to nesting on human-made structures, such as the Purple Martin (*Progne subis*), Barn Swallows now sometimes nest in larger colonies than probably occurred in natural settings.

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

The Barn Swallow's close association with human habitations means that it is well known to the public, and in some parts of the world having Barn Swallows nest on one's property is

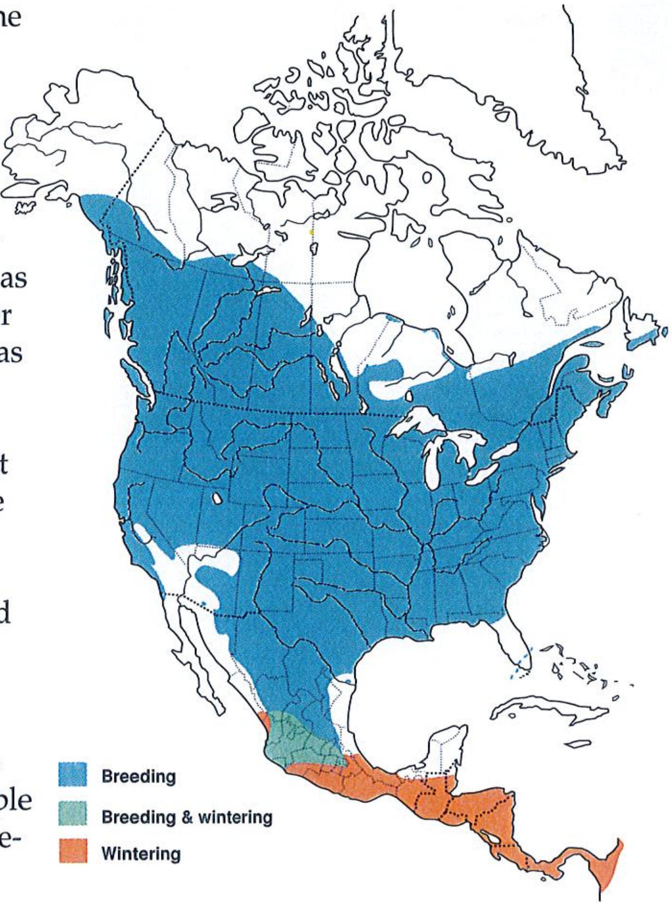

Figure 1.
Distribution of Barn Swallow in North America. This species also winters throughout South America and breeds in Europe, Asia, and Africa. See text for details.

Order PASSERIFORMES Family HIRUNDINIDAE

considered a harbinger of good luck. Legend has it that the Barn Swallow consoled Christ on the cross and got its forked tail because it stole fire from the gods to bring to people, losing its middle tail-feathers when a wrathful deity hurled a firebrand at it (Turner 1991). Another superstition is that cows will give bloody milk or go dry if anything happens to the Barn Swallows nesting on a farm. Barn Swallows have been closely associated with humans and their structures for more than 2,000 years in Europe (Møller 1994a).

As a consequence of both its wide distribution and its nesting on accessible artificial structures near people, the Barn Swallow has been studied extensively throughout the world and especially in Europe. More papers have been published on this species than on any other swallow, and it is one of the most thoroughly studied birds in the world. The Barn Swallow has figured prominently in studies on the costs and benefits of group living (Snapp 1976, Møller 1987a, Shields and Crook 1987), and it has served as a model organism for detailed studies on the mechanisms of sexual selection (Møller 1994a). Tail length and degree of asymmetry in the outer tail-streamers have been found to be reliable predictors of individual quality in both males and females, and individuals use these characteristics to select mates. Tail length tends to correlate with reproductive success, annual survival, propensity to engage in extra-pair copulation, parental effort, ability to withstand parasites, immunocompetence, and other measures of fitness. However, most of the research on sexual selection has been done on European populations, and relatively few similar studies have been done on the North American Barn Swallow.

Several species very similar to the Barn Swallow are found in sub-Saharan Africa, Malaysia, and Australia. The relationship among these forms and even the various subspecies within the Barn Swallow is unclear. The North American subspecies of Barn Swallow, *H. r. erythrogaster*, differs as much in morphology and behavior from the nominate race of Europe and western Asia as some closely related species of *Hirundo* from Africa (A. P. Møller pers. comm.). While a limited comparison of genetic variation was inconclusive, the level of differentiation found between Eurasian and North American populations suggests that more than one species may exist within the Barn Swallow as currently classified (Zink et al. 1995).

The Barn Swallow has the distinction of being perhaps the only northern temperate breeder that commonly winters in South America and occasionally also breeds there during the boreal winter; Barn Swallows have been reported nesting in small numbers in northern Argentina. In addition, these swallows—not the more famous egrets—have the distinction of having indirectly led to the founding of the conservation movement in the United States: the destruction of Barn Swallows for the millinery trade apparently prompted George Bird Grinnell's 1886 editorial in *Forest and Stream* that led to the founding of the first Audubon Society (G. Gladden in Pearson 1923).

DISTINGUISHING CHARACTERISTICS

Medium-sized swallow (17–20 g), with long forked tail. Adults (Definitive Basic plumage) have steely-blue upperparts, rufous underparts, and chestnut forehead. Tail is deeply forked, with white spots on inner webs. Sexes are similar, but males have longer outer tail-streamers than females (usually 79–106 mm in males and 68-84 mm in females; Pyle 1997) and tend to be darker chestnut on underparts. Adult plumages are similar throughout year. Juveniles (Juvenal plumage) are similar to adults but have paler underparts and less forked tails.

Distinguished in all plumages and ages from all other North American swallows by deeply forked tail with white spots on inner webs and extensive rufous or chestnut underparts. Length of outermost tail-streamers varies between sexes and ages but is always much greater than in any other North American swallow species. Some sex- and age-related variability in darkness of chestnut underparts, but averages much more rusty than next most similar species, Cliff Swallow (*Petrochelidon pyrrhonota*). The complete dark-blue breast-band characteristic of Barn Swallow races in Eurasia is reduced to nonconnecting patches on either side of the chest in North American birds. The North American race is also more chestnut on underparts, compared to most Eurasian birds, which average much whiter underneath.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. ALASKA AND CANADA. Breeds in se. and south-coastal Alaska (Armstrong 1995), and from s. Yukon Territory, s. Mackenzie, and n. Saskatchewan, south to U.S. border (Godfrey 1986, Smith 1996, Am. Ornithol. Union 1998), including Queen Charlotte Is. and Vancouver I. in British Columbia (Campbell et al. 1997). Farther east, breeds throughout Ontario but is absent from large portions of forested areas north of 50°N (Clark and Clark 1987), throughout s. Quebec (mainly south of 50°N), including Anticosti I. (Landry and

Bombardier 1996), s. Newfoundland, and throughout Maritime Provinces (Am. Ornithol. Union 1998). Manitoba range is poorly known, but recent information from Saskatchewan (Smith 1996) and Ontario (Clark and Clark 1987) suggests that species is widespread breeder in s. Manitoba but only very local breeder in n. Manitoba.

United States. Breeding range currently extends throughout most of U.S. and is expanding as bridges, houses, and other human-made structures continue to be constructed in areas where suitable nesting sites were previously lacking (deserts, extensive forests, etc.). Currently breeds from Canadian border south throughout U.S. to n. Florida (and locally south to s. Florida, with 1 breeding record from Florida Keys; Stevenson and Anderson 1994), Gulf Coast, and Mexican border, but largely absent from all but se. Arizona (Arizona Breeding Bird Atlas unpubl.) and southernmost Nevada (but breeds very locally in remainder of state). In California, absent from higher elevations of Sierra Nevada, and most of s. California south of Owens and San Joaquin Valleys, and east of coast range, but local breeding occurs within this area where suitable habitat exists (e.g., s. Salton Sea; Small 1994).

Mexico. Breeds in extreme nw. Baja California Norte, and in interior of Mexico from e. Sonora, Chihuahua, Coahuila, and Nuevo León, south to s. Nayarit, Colima, s. Michoacán, and Puebla (Phillips 1986, Howell and Webb 1995).

Argentina. From 5 to 11 breeding pairs found in e. Buenos Aires Province, Argentina, 1980–1982, during boreal winter (Martinez 1983), and subsequent breeding records from 3 other localities in that province (Paynter 1995).

Winter range. Winters uncommonly in Mexico on both slopes from Nayarit, Guanajuato, and s. Veracruz southward throughout Central America, but rare in Yucatán (Howell and Webb 1995). In Panama, most numerous on Pacific side (Ridgely 1976). Bulk of North American population apparently winters in lowlands throughout South America (including Galápagos Is.), with vagrants to Tierra del Fuego and Falkland Is., but rare in eastern quarter of Brazil and south of central Chile and n. Argentina (Ridgely and Tudor 1989, Paynter 1995). Primarily a transient throughout West Indies, although individuals occur every month (Raffaele et al. 1998). Nonbreeders also linger throughout year in most of Central and South America, including Galápagos Is. Stragglers occur regularly in Dec and Jan in California and Arizona, along Gulf Coast, and in Florida, and rarely as far north as Massachusetts (Veit and Petersen 1993).

Other records. Casual in n. Alaska (occasionally nesting; Childs and Maher 1960), n. Mackenzie, s. Keewatin, s. Labrador, and Revillagigedo and Clipperton Is.

OUTSIDE THE AMERICAS

Breeding range. Breeds from Iceland, British Isles, Faeroe Is., Scandinavia, n. Russia, and n. Siberia south to Mediterranean region, n. Africa, Near East, Arabia, Iran, Himalayas, China, Taiwan, and Japan (Am. Ornithol. Union 1998).

Winter range. Winters south to tropical Africa, East Indies, n. Australia, and Micronesia (Am. Ornithol. Union 1998).

Single record of North American race from Chukchi Peninsula in Siberia (Portenko 1989); accidental on Hawaiian Is. and s. Greenland.

HISTORICAL CHANGES

As humans have constructed more buildings, bridges, and culverts that provide suitable nesting sites, Barn Swallows have expanded their range into areas where they formerly did not occur; mo{‰ of these documented range expansions have occurred in second half of twentieth century. Range expansion in California's Central Valley occurred as irrigation structures were installed (Grinnell and Miller 1944). In Arkansas in first half of twentieth century, this species occurred only in Ozark Plateau region, where it was rare, but it had spread statewide by late 1960s, and it is now common there (James and Neal 1986). Rare in w. Tennessee in 1930s, but has since become common across the state (Nicholson 1997). Expanded breeding range into central and s. Louisiana, Mississippi, Alabama, and Florida Panhandle in mid-1960s and 1970s (Jackson and Burchfield 1975, Reid 1975). First confirmed nesting in Florida was in 1946, and breeding had extended throughout the state (to Florida Keys) by 1987 (Stevenson and Anderson 1994). Increased as breeder throughout N. Carolina, S. Carolina, and Georgia during mid-1960s; no known nesting in Georgia from 1904 to 1942 (Brown 1986). Breeding has increased in Colima, Mexico, beginning in 1950s (Phillips 1986). Breeding pairs decreased in parts of ne. U.S. in late 1800s, coincident with increase of House Sparrows (*Passer domesticus*) that usurp Barn Swallow nests (Brewster 1906). Breeding in Argentina may be relatively recent (Martinez 1983), and reports of birds spending boreal summers in South America seem to be increasing in recent years (Paynter 1995).

FOSSIL HISTORY

Little information; closest fossil is *Hirundo aprica*, an Upper Pliocene species described from Kansas (Feduccia 1967) that resembles modern *H. rustica*.

SYSTEMATICS

GEOGRAPHIC VARIATION

For species as a whole, slight clinal differences in size (mainly wing length and tail length), coloration of underparts, and width and pattern of breast-band. Coloration of underparts (adults in fresh plumage) varies from whitish to deep red-brown or rufous-chestnut; individual variation in this character is great in some populations, however, even when differences due to age and wear are taken into account. Completeness of dark breast-collar varies from broad (not invaded by color of throat) and complete to narrow or broken in center of breast.

Within North America, tail length increases clinally from south to north (Patterson 1981; see Measurements: linear, below); otherwise no geographic variation documented in linear measurements or plumage coloration for North America (but see discussion of *H. r. erythrogaster* under Subspecies, below). Variation among Eurasian populations is summarized by Vaurie (1959) and Cramp (1988), who noted cline of decreasing size from west to east both within Europe and between European and e. Asian populations; also generally decreasing in size from north to south. Geographic variation of tail length in European populations of *H. r. rustica* reported by Møller (1995).

SUBSPECIES

At least 6 subspecies recognized (Vaurie 1959, Phillips 1986, Cramp 1988). Only 1 subspecies breeds in the Americas (*H. r. erythrogaster*), and 2 others are rare visitors here (*H. r. rustica* and *H. r. gutturalis*). Am. Ornithol. Union (1998) divided subspecies into 2 groups, placing those breeding in the Old World under *rustica* group (5 subspecies: nominate *rustica, transitiva, savignii, tytleri,* and *gutturalis*) separate from North American *erythrogaster* group (1 subspecies: *erythrogaster*). Taxonomic status of several populations sometimes recognized as subspecies needs study—e.g., breeders on Gulf Coast islands ("*insularis*") and in extreme ne. Asia ("*saturata*"); also, breeding birds in South America are presumed to be *erythrogaster*, although their taxonomic status should perhaps be critically evaluated. Relationships among Old World and New World taxa needs study. For example, the e. Asian races (*gutturalis* and *tytleri*) show similarities to North American *erythrogaster* in pattern of breast-band and to some degree in underparts coloration, whereas the 3 races to the west in Eurasia and n. Africa (nominate *rustica, transitiva,* and *savignii*) are more similar to each other in breast-band pattern; areas of intergradation are found between all Eurasian subspecies, however. Comparison of mitochondrial DNA (mtDNA) restriction fragment profiles between Barn Swallows from ne. Asia and North America found a level of genetic differentiation that suggests a close relationship but one possibly worthy of species-level distinction (Zink et al. 1995). No conclusions regarding relationship between birds of these regions or among other taxa of Barn Swallow are possible, however, until samples from other parts of the species' range are analyzed.

H. r. erythrogaster Boddaert, 1783: Breeds in North America and occasionally in South America; winters in the Americas as described in Distribution, above. Distinguished from nominate *rustica* of Eurasia by breast-band normally thin, often interrupted medially (bluish black restricted to sides of chest and usually limited there), and underparts usually dark chestnut or rufous (see Distinguishing characteristics, above). Birds breeding on islands off n. Gulf Coast were named *H. r. insularis* by Burleigh (1942), who described them as having upperparts of Juvenal plumage dark brown (with hue near olive-brown rather than black), rear of head lacking blue-black, and adults having paler underparts (similar in some respects to nominate *rustica*). This race was not recognized by Am. Ornithol. Union (1957) and was listed only provisionally by Phillips (1986). Because juveniles and worn adults are paler on the underparts, assessment of this character needs to be made with care (Samuel 1971b, Patterson 1981); critical evaluation of upperparts coloration in juveniles needed. Also included under *erythrogaster* as a synonym is *H. r. palmeri* Grinnell, 1902, named from birds taken on Amaknak I., AK.

H. r. rustica Linnaeus, 1758: Breeds from w. Eurasia east to Yenisey Basin south to nw. Africa and s.-central Asia; winters mainly in sub-Saharan Africa; accidental in Alaska and s. Greenland. Continuous, broad, bluish-black breast-band contrasts with maroon throat and (in adults) pale breast and belly varying from pale buff or whitish to dull pinkish.

H. r. transitiva Hartert, 1910: Breeds in s. Syria, Lebanon, nw. Jordan, and n. and central Israel; partially migratory, some apparently wintering in ne. Africa (reports southward doubted by Clancey 1970). Similar to nominate *rustica*, but breast and belly of adults darker, more consistently reddish buff; averages slightly larger than nominate *rustica* in wing (male 125 versus 123 mm) and tail (102 versus 103 mm), but there is broad overlap in range of measurements (Shirihai 1996). Many intermediates between this and nominate *rustica* occur, and this race is intermediate to *savignii* (see below).

H. r. savignii Stephens, 1817: Resident in ne. Africa in Egypt (e.g., Nile Delta). Underparts dark maroon or rufous-chestnut, except for blue-black breast-band; averages slightly smaller than nominate *rustica* and *transitiva* (male wing averages 120 mm, tail 93 mm; Shirihai 1996).

H. r. tytleri Jerdon, 1864: Breeds from central Siberia south to n. Mongolia; winters in se. Asia. Underparts rufous to red-brown, with breast-band narrowed and sometimes broken by maroon color of throat.

H. r. gutturalis Scopoli, 1786: Breeds east of nominate *rustica* and south of *tytleri* from central Mongolia, middle Amur Basin, Korea, Kuril Is., Sakhalin, some of Japanese islands south to Philippine Is. and China, India, and Malaysia, wintering in se. Asia, islands of n. Australia, and parts of e. and s. Africa (Clancey 1970); accidental or casual in w. Alaska, Queen Charlotte Is. (British Columbia), and nw. Hawaiian Is. (Kure Atoll and Midway I.; Phillips 1986). Underparts pale as in nominate *rustica*, but breast-band broken or narrowly complete. Birds with highly variable underparts from ne. Asia sometimes given name *H. r. saturata* Ridgway, 1883, but these included under *gutturalis* by Cramp (1988). Some "*saturata*" closely resemble *erythrogaster*, and this was used by Dement'ev and Gladkov (1968) to merge "*saturata*" under *erythrogaster*, a decision not followed by Am. Ornithol. Union (1957) or Cramp (1988).

RELATED SPECIES

The Barn Swallow is closely related to several Old World taxa that closely resemble it in morphology, behavior, and ecology; these include the tropical African species Red-chested Swallow (*Hirundo lucida*), Angolan Swallow (*H. angolensis*), White-throated Swallow (*H. albigularis*), and Ethiopian Swallow (*H. aethiopica*), and the Australasian species Pacific Swallow (*H. tahitica*) and Welcome Swallow (*H. neoxena*). These taxa, along with Barn Swallow, may constitute a superspecies (Mayr and Short 1970). Genetic data and reassessment of morphological characters are needed to help define species limits in this group. The Barn Swallow belongs to a group of swallows that build mud nests (*Hirundo* and allies) that are sister to a "core martin" clade consisting of mainly New World taxa (e.g., *Progne*, *Stelgidopteryx*, and *Tachycineta*) that adopt existing holes for nests (Sheldon and Winkler 1993, Sheldon et al. 1999).

Hybridization. Barn and Cave (*Petrochelidon fulva*) swallows are reported to have hybridized in sw. Texas, where both species now breed together in highway culverts (Martin and Selander 1975, Martin 1980). Contact between the 2 species is thought to be recent, brought about by Cave Swallow's recent shift in nest sites from sinkhole caves to culverts and bridges. Hybridization has not been studied behaviorally, but limited observations suggest that hybrids usually occur in nests attended by "pure" Barn Swallow parents; most likely hybrids result from forced extra-pair copulations between male Cave Swallows and female Barn Swallows. At least 3 known Barn Swallow × Cliff Swallow hybrids from various parts of North America; little is known about how the hybridization occurred, but it probably also involved extra-pair copulation. Several cases of hybridization reported between nominate *rustica* and Common House-Martin (*Delichon urbica*) from Eurasia; possible hybrid Barn Swallow × Red-rumped Swallow (*Hirundo daurica*) also reported (Flumm 1975).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Long-distance migrant between breeding range in North America and wintering range in Central and South America. No overlap between breeding and winter ranges except in portions of central Mexico. Bulk of migrants apparently follow Central American isthmus, although there are records of trans-Gulf and trans-Caribbean migrants (Hailman 1962, Yunick 1977). Migrants are reported commonly in West Indies and Bermuda. Migration in both directions spans several months but is complex because one population or another is evidently migrating at all times except mid-Dec–early Jan and possibly between early or mid-Jun and early Jul (Phillips 1986). Presence of wintering populations in Mexico and Central America, and of boreal-summer residents in South America, complicates determination of timing.

TIMING AND ROUTES OF MIGRATION

Spring migration. Main Central American passage seems to occur Mar through May. Apparent spring migrants recorded in Mexico 15 Feb–20 Jun (see Phillips 1986). First arrivals on breeding grounds typically appear by late Jan in s. California (peak spring passage 15 Apr–10 May; Small 1994), 8 Feb in Texas (Oberholser 1974), 25 Feb but usually late Mar in Oklahoma (Baumgartner and Baumgartner 1992), second week of Mar in Arkansas (James and Neal 1986), 5 Mar in Tennessee (Robinson 1990), 23 Apr in Idaho (Burleigh 1972), late Mar–1 Apr in British Columbia (Campbell et al. 1997), 14 May in Alaska (Gabrielson and Lincoln 1959), 12 Apr in Nebraska, 28 Mar–5 Apr in Ohio (Peterjohn 1989), 5–10 Apr in Pennsylvania (Samuel 1972), and early Apr in Massachusetts (peak spring passage 11–26 May; Veit and Petersen 1993). Migration occurs primarily Apr–May in West Indies (Raffaele et al. 1998) and begins mid- or late Mar in

Bermuda, peaking mid-Apr through third week in May (Amos 1991). In South America, reported in Colombia as late as 15 Jun, French Guiana 7 Jun, Suriname 5 Jun, Brazil 10 May, Bolivia 22 Jun, and Paraguay 17 Apr, although some of these reports could represent boreal-summer residents (Haverschmidt 1954, Hayes 1995, Paynter 1995). In Honduras, latest date is 13 May (Monroe 1968); in Belize, 24 May (Russell 1964). Arrival at nesting sites usually follows several days of warm weather (Samuel 1971a).

Fall migration. Fall migration begins very early. Migrants noted flying along beaches in Cape May, NJ, as early as 10 Jul; large numbers usually by late Jul. Numbers peak in Cape May late Aug–early Sep; smaller numbers through mid-Oct, and occasional records through Dec (Sibley 1997). In Ohio, migration has been recorded third week of Jul through early Oct, with stragglers through late Oct or early Nov (Peterjohn 1989). In British Columbia, migration has been noted by early Aug, peaking late Aug–early Sep, with most birds departing by late Sep (Campbell et al. 1997). In Florida, migrants noted flying south as early as 28 Jun at Ft. Lauderdale; migration is continuous through Nov and well into Dec, with stragglers reported into Jan and Feb, but these reports may represent birds attempting to winter (Stevenson and Anderson 1994). In California, migration recorded late Jul–mid-Oct, with stragglers into Nov (Small 1994). Late dates of fall departure include 20 Sep in Alaska (Gabrielson and Lincoln 1959), 9 Oct in Idaho (Burleigh 1972), late Oct in Arkansas (James and Neal 1986), 19 Nov in Tennessee (Robinson 1990), 8 Nov in Oklahoma (Baumgartner and Baumgartner 1992), 7 Dec in Texas (Oberholser 1974), 25 Sep–5 Oct in Ohio (Peterjohn 1989), and 23 Nov in Massachusetts (Veit and Petersen 1993). Stragglers routinely remain as far north as Massachusetts well into Nov and early Dec (Veit and Petersen 1993). Migration occurs primarily Sep–Oct in West Indies (Raffaele et al. 1998), and late Jul (occasionally mid-Jul) through late Nov in Bermuda, where species reported more often in fall than during spring (Amos 1991). Apparent fall migrants recorded in Mexico 29 Jun–9 Dec (see Phillips 1986). In Honduras, recorded as early as 16 Aug (Monroe 1968); in Belize, 20 Aug (Russell 1964). In South America, fall transients recorded in French Guiana as early as 5 Aug, in Colombia 20 Aug, in Suriname 22 Aug, in Brazil 4 Sep, in Bolivia 3 Oct, in Paraguay 3 Sep, and in Argentina 20 Sep (Haverschmidt 1954, Paynter 1995).

MIGRATORY BEHAVIOR

Diurnal migrant, foraging as it moves. Cold and rainy weather forces migrants to search for food over lakes and ponds; hundreds often concentrate at lakes and rivers in Nebraska during spring cold snaps, sometimes remaining for several days or as long as bad weather lasts (CRB, MBB). Flocks with other swallows during migration, roosting in large flocks in marshes and grainfields. Often seen along lakeshores and coastlines, where groups may pass continuously for several days to weeks, always moving parallel to coast (Slud 1964). On trans-Gulf and trans-Caribbean crossings, lands on ships; many such birds are weak and die (Yunick 1977). A juvenile banded in New York was recovered 44 d later in the Caribbean off Panama, having averaged about 89 km/d (Yunick 1977). In European *H. r. rustica*, juveniles tend to begin migrating earlier in the day and continue flying until closer to dusk than adults (Gatter and Behrndt 1985). Migrating Barn Swallows in Britain went as far as 194 km/d, although some birds traveled as little as 2–26 km/d; daily distance covered increased later in fall (Ormerod 1991).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Ancestral breeding habitat presumably was mountainous areas and seacoasts that provided caves and rock crevices for nesting; birds also used hollow trees. Presently found in various habitats up to 3,000 m, mostly in Upper Sonoran and Transition Zones, including agricultural areas, cities, and suburbs, and along highways. Breeding habitat usually contains open areas (fields, meadows) for foraging, nest site that includes a vertical or horizontal substrate (often enclosed) underneath some type of roof or ceiling, and a body of water that provides mud for nest-building. See also Breeding: nest site, below.

SPRING AND FALL MIGRATION

Probably migrates over wide variety of habitats: open water, freshwater marsh, savanna, farmland, cities, and towns. Often seen in open coastal lowlands and seems to avoid forested regions and high mountains, although transients recorded to 3,700 m in South America (Ridgely and Tudor 1989). Often gathers to sleep in marshes. Migrants concentrate over water surfaces and marshes when poor weather reduces abundance of flying insects.

WINTER RANGE

Little information for North American race. Often found roosting and foraging in sugarcane or other grain fields, reed beds, or marshes. In Africa, closely associated with wetlands.

FOOD HABITS

FEEDING

Main foods taken. Flying insects at all times of year. Beal's (1918) analysis of 467 stomachs from across North America revealed 99.8% animal matter; plants included seeds of elderberry (*Sambucus*), red osier dogwood (*Cornus sericea*), croton (*Croton texensis*), and buckwheat (*Fagopyrum*). Some of these seeds may have been ingested accidentally or as grit. Often picks up grit or small pebbles, apparently to aid digestion of insects and possibly also for calcium; 80% of nestlings in Washington had grit in their stomach (Barrentine 1980). Occasionally eats eggshells or oyster (Ostreidae) shells provided by humans (Forbush 1929, Merrill 1976).

Microhabitat for foraging. Feeds above ground but at lower altitudes than most other North American swallows; usually not >10 m and often <1 m above ground. Prefers to feed in open areas over grassy pastures, in plowed fields, and around farmyards and domestic animals. Island-nesting birds off California coast feed over inshore waters (Small 1994). Foraging low to the ground may enable these birds to find more food and thus survive late-spring cold snaps better than species that forage higher (e.g., Cliff Swallow, Purple Martin, Chimney Swift [*Chaetura pelagica*]).

Food capture and consumption. Diurnal forager, pursuing insects in flight. Often feeds on insects flushed by farm implements, grazing mammals, humans, and flocks of other bird species. During breeding season, usually feeds singly or in groups of 2 (mated pairs), with no coordinated group foraging (Snapp 1976), although birds may occasionally cue on foraging activities of conspecifics through local enhancement (Hebblethwaite and Shields 1990). No evidence that colonies serve as information centers (Hoskyn 1988, Hebblethwaite and Shields 1990). During egg-laying and incubation in British Columbia, spent mean 7.9 min ± 0.8 SE on foraging trips away from nest and made 2.4 trips/h ± 0.2 SE (Brigham 1989). Occasionally lands on ground and picks up dead insects or picks insects off plant, artificial, or water surfaces in flight. During bad weather, may pick flies off walls of barns (A. P. Møller pers. comm.). Feeds at night in artificially lit areas (Knox 1990). Changes in mass of parents suggest that adults feed themselves on at least 42% of trips from nest while foraging to feed nestlings (Jones 1987b). In cold weather, birds concentrate at ponds and lakes and feed a few centimeters above water surface, often picking insects out of water. No information on foraging behavior during winter, but birds may concentrate in larger groups while feeding.

DIET

Major food items. Almost exclusively flying insects, although during adverse weather occasionally collects dead or moribund insects on ground. Probably very opportunistic, with diet reflecting local insect availability; 21 families were found in diet analysis of nestlings at a single Nebraska colony (Hoskyn 1988) and >80 families were recorded for *H. r. rustica* in Europe (Kozena 1979). Often feeds on single, large insects rather than on swarms; mean number of insects per bolus fed to nestlings in Nebraska was 3.5 ± 0.9 SE ($n = 26$), and 38.5% of boluses consisted of a single insect (Brown and Brown 1996).

Quantitative analysis. From Beal 1918, across North American range. Flies (Diptera)—including crane flies (Tipulidae), horseflies (Tabanidae), and robber flies (Asilidae)—are the most common food in diet (39.5% of food in 467 samples), especially in Mar (82%), declining in Sep (18%). Other insects represented included beetles (Coleoptera, 15.6%); true bugs (Hemiptera) and leafhoppers (Homoptera, 15.1%); bees, wasps, and ants (Hymenoptera, 12.8%); dragonflies and damselflies (Odonata, 4%); butterflies and moths (Lepidoptera, 2.4%); and grasshoppers and crickets (Orthoptera, 0.5%). Although Barn Swallows seem to prefer larger, single insects (Brown and Brown 1996; see above), stomach of 1 bird in Beal's study contained about 1,000 ants (Formicidae).

The 15 most common families (from most to least abundant) in diet samples taken from nestlings using ring collars at 1 Nebraska colony (Hoskyn 1988) were Empididae (dance flies), Dolichopodidae (long-legged flies), Calliphoridae (blowflies), Syrphidae (syrphid flies)—all Diptera; Pyralidae (pyralid moths)—Lepidoptera; Rhagionidae (snipe flies)—Diptera; Formicidae (ants)—Hymenoptera; Scarabaeidae (scarab beetles)—Coleoptera; Sesiidae (clear-winged moths)—Lepidoptera; Sarchophagidae (flesh flies)—Diptera; Fulgoridae (fulgorid planthoppers)—Homoptera; Muscidae (muscid flies), Asilidae (robber flies), Stratiomyidae (soldier flies), and Otitidae (picture-winged flies)—all Diptera.

FOOD SELECTION AND STORAGE

Little information on North American race. *H. r. rustica* of Britain selects prey primarily by size, and inclusion of an item in diet depends on absolute abundance of high-ranking prey and not of low-ranking ones (Turner 1982). Small items of low profitability are included when food is abundant;

prey selection seems to maximize net energy gain (Turner 1982). Not known to store food.

NUTRITION AND ENERGETICS

Little information on North American race. In Britain, mean field metabolic rate determined for *H. r. rustica* was 104–112 kJ/d (*n* = 12 birds), dependent on assumptions used in the calculations; water turnover rate of laying females was 18.4 ml/d (*n* = 12); and energy content of egg material deposited in 24 h averaged 4.9 kJ (*n* = 11; Ward 1996). Energy expenditure for females did not differ significantly in egg formation, incubation, and brood-rearing periods, and costs of egg synthesis appeared to be small in relation to routine energy requirements (Ward 1996). Mean flight cost for *H. r. rustica* estimated at 0.3698 kJ/g/h ± 0.0854 SD (Turner 1983).

METABOLISM AND TEMPERATURE REGULATION

No data for North America. Barn Swallows cluster together during late-spring cold snaps when food is scarce in apparent attempts to conserve heat; 8 adult birds packed themselves into a nest during cold weather in Manitoba (Weatherhead et al. 1985), and dozens clustered together during 1974 swallow die-off in Europe (Bruderer 1975).

DRINKING, PELLET-CASTING, AND DEFECATION

Drinks exclusively on the wing, by skimming water surface and lapping up water with lower mandible. Adults fly out from nest several meters to defecate.

SOUNDS

VOCALIZATIONS

Development. Faint vocalization ("squeak") begins on third day after hatching (Wood 1937). Juvenile Call develops as nestlings grow and is well developed by fledging. No evidence for vocal learning, sensitive periods, or vocal mimicry. Juvenile Call probably develops into *Chirp* Call of adult.

Vocal array. See Samuel 1971c; following is from Brown 1985 unless noted. More vocalizations than in more colonial swallows.

JUVENILE CALL. Frequency 5–6 kHz; duration 75 ms. Given by nestlings and juveniles after fledging (light chirp call of Samuel 1971c).

CHEEP *CALL.* Figure 2A. Frequency 3–7 kHz. Given singly or in sequences with about 1-s intervals (plain sharp call of Samuel 1971c).

CHUREE *WHISTLE.* Frequency 2.5–5 kHz; duration 160–330 ms. Given singly or in series with 40-ms to 1-s intervals between calls; interspersed with and closely related to *Cheep* Call (high sharp call of Samuel 1971c).

CHIRP *CALL.* Figure 2B. Frequency 2–6 kHz; duration 75 ms. Given singly or in sequences with 150-ms to 1-s intervals between calls.

CHEET *CALL.* Frequency 3–7 kHz; duration 125 ms. Given in sequences lasting about 2 s.

STUTTER CALL. Frequency 2–7 kHz, duration 75–125 ms. Given in sequences with variable intervals; 2 types distinguished by Samuel (1971c).

WHISTLE CALL. Frequency 2–4 kHz; duration about 250 ms. Given in sequences (Samuel 1971c).

WHINE CALL. Frequency 2.5–4.5 kHz; duration 0.50–0.75 s. Repeated 2-6 times, often preceded and followed by part of Twitter-Warble Song (see below; Samuel 1971c).

TWITTER-WARBLE SONG. Figure 2C. Frequency 2–7 kHz; total song duration 4–20 s or longer. Long series of continuous warbling sounds constitutes about 85% of song; followed by 9–12 rapid, guttural gratings. Extended songs are composed by alternate repetition of the 2 parts. *Chirp* Calls often precede and follow songs and are incorporated into them.

SUBSONG. Frequency 2.5–6 kHz; variable duration of 1.5–10 s. Consists of partially recognizable components of Twitter-Warble Song, but of lower intensity and less structure.

Phenology. Juveniles give Juvenile Call until they become independent, at which time call probably transforms into *Chirp* Call. Subsong is given mostly at end of nesting season; juveniles 20–25 d old occasionally give it (A. P. Møller pers. comm.). All other vocalizations may be used at any time during breeding season, depending on a bird's nesting stage; little is known about vocal behavior during migration or winter.

Daily pattern. No obvious circadian influence on vocalizing.

Places of vocalizing. May vocalize virtually anywhere around a nesting site; all calls and songs may be given both in flight and when perched, as well as both at nest and away from it.

Repertoire and delivery of songs. No information on repertoire size or variability among individuals in use of Twitter-Warble Song in North American population; in Italian *H. r. rustica*, males have large song repertoires: up to 230 different song types were counted in 33 individuals (Galeotti et al. 1997). Songs may be given anytime during breeding season but are most frequent during pair formation and egg-laying. In *H. r. rustica* of Italy, song rate is maximal about 4 d before first egg is laid (Saino et al. 1997).

Social context and presumed functions. From Brown 1985, unless noted. Juvenile Call is given frequently by nestlings in nest, probably to enhance begging intensity, and by juveniles after fledging,

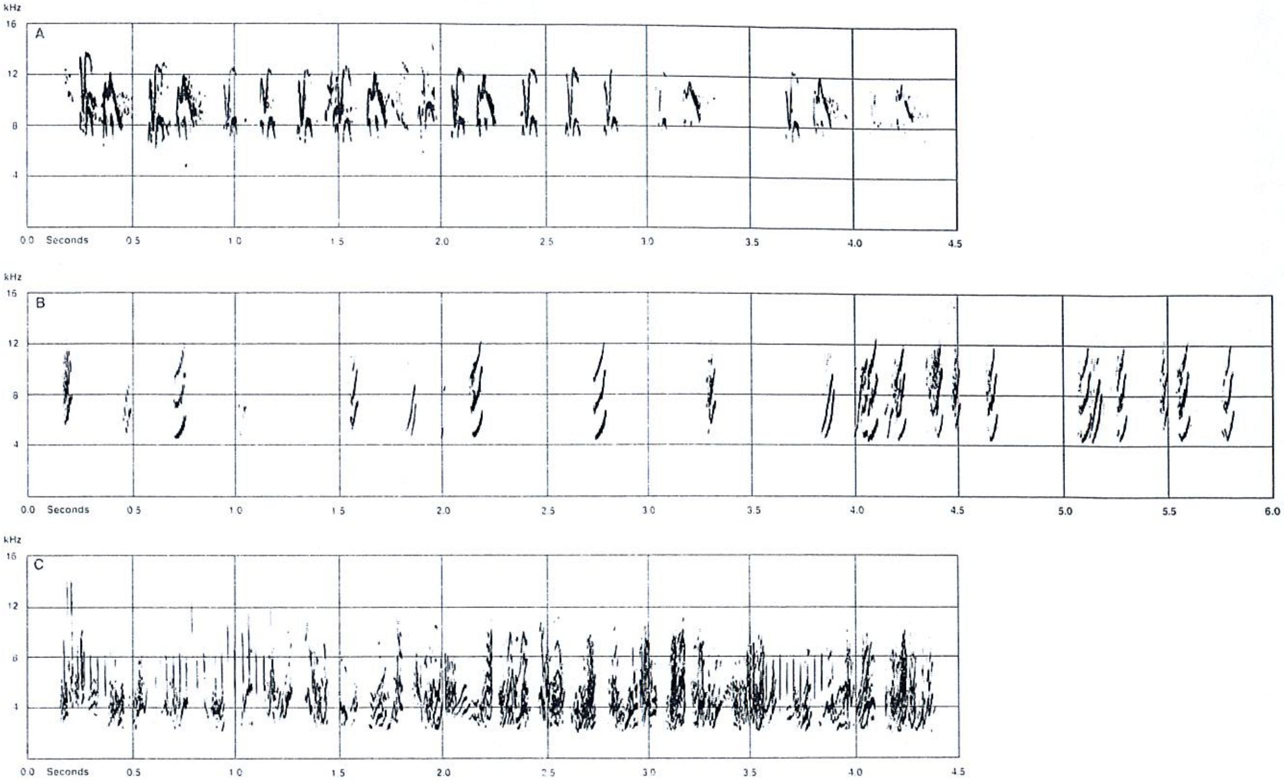

Figure 2. Vocalizations of the Barn Swallow. A. *Cheep* Call (BLB no. 6018, recorded 3 Jul 1962, Lincoln Co., ME). B. *Chirp* Call (BLB no. 7750, recorded 25 Jun 1965, Benton Co., OR). C. Twitter-Warble Song (BLB no. 5334, recorded 2 Jul 1961, Lincoln Co., ME). Prepared by staff of Borror Laboratory of Bioacoustics (BLB), The Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with an effective frequency resolution of 150 Hz [for A and B; 300 Hz for C] and a 200 point FFT transform size).

possibly to aid parents in finding them. Juvenile Call is not used by parents to recognize their own young (Medvin and Beecher 1986). Information content of Juvenile Call, on basis of the complexity of its structure, is much less than that of more colonial swallows (e.g., Cliff Swallow), which have highly developed parent-offspring recognition (Medvin et al. 1993). Juvenile Calls are less similar among siblings in Barn Swallows than in highly colonial swallows such as Cliff Swallow, presumably because Barn Swallow call does not have a "signature" function in recognition (Medvin et al. 1992). Adult's *Cheet* Call, given only when parents feed fledged juveniles, may be used to some degree by juveniles to recognize their own parents, although this recognition is weaker than in the more colonial swallows (Medvin and Beecher 1986). *Cheep* Call and *Churee* Whistle are both alarm calls, former used in virtually all alarm situations and latter when predator approaches a nest closely. *Churee* Whistle is given when predators are close enough to elicit high-risk diving by extremely agitated adults. Alarm calls given by any bird in a colony usually flush all birds from nests, and residents circle above predator. Males in *H. r. rustica* apparently give deceptive alarm calls—calls given when no predator is present—to thwart extra-pair copulation attempts by their mates (Møller 1994a). *Chirp* Call is a highly generalized vocalization given in virtually all contexts; function is unclear, but it is the primary vocalization given during nonbreeding season. Stutter Call is given during intraspecific chases and fights around nesting sites and mates and probably indicates excitement or agitation. Whistle Call is thought to be a pair-bond call (Samuel 1971c), given by both members of mated pairs when perched or flying together. Whine Call is possibly a precopulatory signal used only by females; call preceded 21 of 23 (presumably intrapair) copulation attempts (Samuel 1971c). Twitter-Warble Song is a courtship signal, given mostly during pair formation and egg-laying; often given by males, but females also sing it. The song is important in male-male interactions; females prefer males with more complex songs (Galeotti et al. 1997). Males whose nests are heavily parasitized by mites (*Ornithonyssus bursa*) sing less than lightly parasitized males (Møller 1991d); male singing rate is positively correlated with level of testosterone (Saino and Møller 1995). Apparently healthier males, as measured by immune responses, tend to sing more, and song may be given by females to select high-quality mates (Saino et al. 1997). Neighbors tend to sing similar songs; males give longer songs when they have few or no neighbors (Galeotti et al. 1997). Subsong is given by independent juveniles in late summer, often in company of adult males that sing Twitter-Warble Songs.

NONVOCAL SOUNDS

May snap mandibles together to produce clicking noise during intraspecific interactions.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. When on ground, walks exclusively. Goes to ground only to collect mud, grass, or feathers for nest, to pick up bits of gravel or (rarely) moribund insects, to sunbathe, or to seek refuge from strong winds. Sidles along a wire, tree branch, or other perching substrate using a sideways walk.

Flight. Flies at various heights from just above ground to ≥25 m. Flight consists of bursts of straight flight longer than those of other swallows; birds frequently alter course slightly to left or right, and these shifts cancel each other, leading to a straight course (Blake 1948). Often alters course dramatically when encountering an obstacle as small as tallgrass stems. Flight may be circular when feeding over an insect concentration, such as around cattle (Blake 1948). Birds are capable of sharper turns and dives than other swallows. Increased maneuverability is a consequence of the highly forked tail; outer tail-streamers deflect leading edge of tail, resulting in higher aerodynamic lift and allowing tighter turns (Norberg 1994). Maneuverability also increases as the symmetry in length of the outer tail-streamers increases (Møller 1991f). Long tails, along with high levels of symmetry in wing and outer tail, may improve foraging efficiency during extreme weather conditions (Brown and Brown 1999). Glides rarely, and when gliding, pulls wing-tips well back; glides usually last only 1–2 s, rarely 3 (Blake 1948). Carries tail nearly closed, except when turning or braking on landing. Flight speed is not much greater than that of other swallows, but with straighter flight this species covers ground more rapidly (see Blake 1948). Speed estimated at 8.0 m/s ± 2.0 SD (range 5–17), which matches the speed predicted if birds were flying to maximize rate of food delivery to nestlings (de la Cueva and Blake 1997).

Swimming and diving. Swims when falls into water by accident, simultaneously moving both wings up, forward, down, and backward in circular motion, each backstroke thrusting body forward; does this until reaching shore or other object on which to climb out of water (Jackson 1970). Does not routinely swim, however. No diving.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. From Møller 1991e, except as noted. Usually preens at perch sites near nest; preening peaks in early morning and evening and consists of quick movements through feathers, especially of wing and tail, ending with bird's shaking entire body. Only about 3.1% of preening bouts involve contact with uropygial gland. Total time spent preening varies among individuals (0–14.6%); nestlings preen more when their nests are infested by mites, but there was no such effect for adults. Preening declines during breeding cycle. Scratches head over wing. Stretches by extending one wing at a time below feet; then extends both in a V over back. This stretching sequence often immediately precedes flight. Yawns sometimes accompany stretches. Bathes by skimming water surface and "hitting" surface briefly in violent collision, sometimes several times in succession. In heavy rain, points bill straight up and holds position without moving. Birds in Europe seen dust-bathing in cinders, rolling and flapping wings in same manner as House Sparrows do (Tubbs 1954). Anting not known to occur.

Sleeping, roosting, sunbathing. Pairs often sleep together in nest or on rim, or on adjacent part of structure (e.g., nearby beam), for much of breeding season, but will begin roosting elsewhere by the time young approach fledging (Smith 1937). During premigratory periods in late summer, migration, and winter, birds often gather in large roosts to sleep in marsh vegetation; assemble over a roost site before landing, forming in some cases dense clouds that gradually circle lower and lower until birds finally start dropping down to perch, with many birds flushing and repeating the performance before finally settling for the night (Bates 1895). During sunbathing, birds partly spread their wings, erect body-feathers, tilt tail upward, contort one side of body skyward, and gape; often uses hot metallic roofs for sunbathing, especially on days with high ambient temperatures (Blem and Blem 1992). Specific function of sunbathing for Barn Swallows is unknown, but may aid in ectoparasite control.

Daily time budget. Little information for North American race. For adult *H. r. rustica* in Britain during brood-rearing period, 33.3% of birds' time was spent roosting, 15.8% resting, and 50.9% flying (foraging; Turner 1983).

AGONISTIC BEHAVIOR

Physical interactions. Males defend nest sites and mates by attacking intruders, chasing them, and pecking them, and sometimes grappling together in physical combat and falling to the ground. Approaches intruders in flight or by sidling along a perch; feathers are sleeked and carpal joints exposed, and bird sings repeatedly in threat before attacking (Møller 1994a). In birds at perching sites away from nests, spatial positions are adjusted by flight approaches by one bird at another, hovering, and displacements (Hutton 1978). New arrivals remain motionless for a few seconds before initiating preening or aggression toward adjacent birds; head orientation is apparently important in setting distances between birds (Hutton 1978). Birds may peck at an adjacent bird if neighbor's head is turned toward it; birds gape at conspecifics during threat displays (Hutton 1978). Conflicts at perch sites arise when an approaching bird lands and sidles close to an incumbent preoccupied with preening or sleeping; incumbent may be chased away by pecks from new arrival, or vice versa. Early in nesting season, groups of 2–6 Barn Swallows often engage in chases near nesting sites, with birds singing profusely; female can be pursued by several males. Leucistic individual was repeatedly chased in flight by conspecifics (Withgott and McMahon 1993).

Communicative interactions. When perched near a female, male sometimes holds body horizontal, head stretched forward, beak pointing straight ahead, tail prominently spread, and all feathers drawn in sleekly except for those on throat, which are fluffed out. Male sings profusely and sidles toward female, which then usually attacks him; function of display unknown (Hartley 1941). White spots of tail may allow visual communication in dark caves, where birds historically nested; during pair formation, male often spreads tail (Møller 1994a).

SPACING

Territoriality. Birds defend small space around nest and favor perch sites near nest; territory size among European birds usually averages 7-8 m^2 during pair formation, nest-building, and egg-laying, declining to about 4 m^2 during incubation and brood-rearing and increasing again when second clutch is started (Møller 1990a). Defense usually is directed against neighboring pairs, but also against unmated birds looking for nest sites or mates. Males usually defend against males and females against females. Polygyny may occur when 2 females settle within a single male's defended area. Active nests can be as close together as 0.1 m; mean distance apart was 3.7 m ± 1.9 SD in Mississippi (Lohoefener 1980), 3.7 m ± 3.1 SD ($n = 84$) in Oklahoma (Grzybowski 1979), 2.3–3.7 m in Nebraska (Hoskyn 1988), and 1.7 m ($n = 7$) in British Columbia (Campbell et al. 1997). In *H. r. rustica* of Europe, territorial aggression by a pair against intruders is greater during egg-laying than in pre-laying or brood-rearing periods, possibly as defense against intraspecific brood parasitism (Møller 1989a; see Breeding: brood parasitism, below).

Individual distance. At perching sites, mean distance between birds 11.7 cm ± 3.9 SD (range 5–150); in mixed-species flocks, distance to nearest heterospecific is usually larger (mean 48.6 cm ± 25.5; Hutton 1978). Juveniles that have just left the nest may perch more closely; in cold weather, Barn Swallows observed sitting tightly against Bank Swallows (*Riparia riparia*) in attempts to huddle (Meservey and Kraus 1976), and they cluster closely with conspecifics when inclement weather lasts 2–3 d (see Food habits: metabolism and temperature regulation, above).

SEXUAL BEHAVIOR

Mating system and sex ratio. Usually socially monogamous but genetically polygamous (see discussion of extra-pair copulations, below). Polygyny is known, with male devoting most of his parental care to first mate (Wolinski 1985, Medvin et al. 1987). Experimental studies in Ontario showed that females prefer males with longer tails; result is that long-tailed males attract mates sooner and their mates initiate egg-laying earlier than do mates of shorter-tailed males, but reproductive success does not differ between long- and short-tailed males (Smith and Montgomerie 1991). Sex ratio is apparently male-biased: in Kansas, 63% males (Anthony and Ely 1976); in Massachusetts, 54% males (Mason 1953).

Unmated males known to commit sexually selected infanticide, killing nestlings 1–4 d old, in apparent attempts to incite divorce in pair and establish pair bond with female, or after disappearance of male for other reasons (Crook and Shields 1985, Møller 1994a, Banbura and Zielinski 1995a). Infanticidal males do succeed in breaking up pairs after killings and pairing with female. Males switch from infanticidal to noninfanticidal strategies between years (Crook and Shields 1985). Infanticide is more common in large colonies, which apparently attract unmated males: at a colony of >50 nests in Nebraska, 78.3% ($n = 69$) of nests failed; most failures presumed to be due to infanticide or conspecific egg destruction (Hoskyn 1988).

Mate choice and sexual selection have been studied extensively in *H. r. rustica* of Europe (Møller

1994a, Saino and Møller 1996). Male tail length is correlated with many components of mating success: for example, males with longer tails had higher probability of obtaining mate, shorter time to get one, greater success at extra-pair copulations, better-quality mates that invested more in offspring, and fewer ectoparasites (Møller 1994a). Tail length appears to be reliable signal of individual quality in both males and females. Females also apparently use degree of asymmetry in outer tail-streamers to choose mates, preferring more symmetric individuals (Møller 1994b).

Pair bond. Most birds establish pair bonds after arrival on breeding grounds. Pairs form anew each season, but members of a pair often remain together for 2 consecutive seasons if successful the first season (Shields 1984b). Male displays spread tail and often sings when trying to attract female; if she repeatedly perches with him or at his nest, pair bond forms (Møller 1994a). Unmated males perform song choruses, flying overhead, attempting to attract females; they swoop down to nest site if female appears. Females occasionally desert their first mate after 1–16 d (Møller 1994a). Male frequently chases his mate; chases continue through egg-laying. Males guard their mates by closely following them during the time they are fertile, preventing them from engaging in extra-pair copulation attempts. Mate-guarding is less intense later in season and among solitarily nesting birds or in small colonies, presumably because risk of cuckoldry is lower in these situations (Møller 1985). Mate-guarding by male increases with his level of testosterone (Saino and Møller 1995). Intra-pair copulation often occurs on perching site away from nest, continuing until late into egg-laying; male hovers above and slightly behind female, tail widely spread, outer streamers uplifted, and legs dangling (Nethersole-Thompson and Nethersole-Thompson 1940). Female reported to hold wings low, below tail, as apparent invitation to mount (Hartley 1941).

Extra-pair copulations. Extra-pair copulations probably occur commonly, but little studied in North American race. Extra-pair copulation behavior in *H. r. rustica* of Europe is described in detail by Møller (1994a). DNA-fingerprinting analyses revealed that 22% of nestlings in an Ontario study (n = 45) were sired by extra-pair fertilizations (≥1 illegitimate young in 5 of 11 nests). Longer-tailed *H. r. rustica* males in Europe have greater certainty of paternity than shorter-tailed males (Møller 1994a, Møller and Tegelstrom 1997); in contrast, in Ontario, more illegitimate young occurred in nests of males whose tails had been experimentally lengthened (Smith et al. 1991). Because males in North America incubate more than males in Europe, their opportunities for extra-pair copulations may be reduced. Unmated, extra males that attend nests try to copulate with female of the pair (Crook and Shields 1985), and paired males attempt to copulate with neighboring females (Møller 1994a). Females paired to shorter-tailed males in Europe are more likely to seek extra-pair copulations than are those paired to long-tailed males, and extra-pair copulations increase with population density (Møller 1994a).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. When found nesting in caves, usually only 1–2 pairs at a site (Baird et al. 1875, Speich et al. 1986), although occasionally nesting colonies of 3–30 nests have been reported in natural sites. With switch to artificial nesting sites, birds are now sometimes found in colonies consisting of several nests on a single nesting structure. These nesting groups are probably on average larger than what the birds historically experienced, although many solitary pairs continue to occur. In Mississippi, average colony size on bridges was 2.3 nests (n = 44 nests; Jackson and Burchfield 1975), with numerous nesting groups of ≥6 nests (Lohoefener 1980); colony size varied from 1 to 14 nests in Kansas, mostly on buildings (Anthony and Ely 1976); 1–30 (n = 34 colonies) and 1–22 nests in New York, also on buildings (Snapp 1976, Shields and Crook 1987); and 3–83 nests in British Columbia, with 56% between 5 and 14 nests (n = 135 colonies; Campbell et al. 1997). Any colony of >35 nests is unusual; one of largest colonies known had 90 nests under decking of a building in coastal New Jersey (Ball 1983). During migration and winter, Barn Swallows roost in enormous flocks, spreading out to forage over nearby areas during the day. Some roosts of *H. r. rustica* in e. and s. Africa reportedly reach ≥1 million individuals (Bing 1993). Although this species is clearly quite gregarious during winter and migration, the inability of parental Barn Swallows to recognize their own young (Medvin and Beecher 1986) and their high degree of risk-taking in mobbing predators (Brown and Hoogland 1986) both suggest that the species historically has been largely a solitary nester.

Studies of coloniality in Barn Swallows have revealed few advantages of grouping, consistent with the interpretation that colonies form mostly because suitable nesting sites are limited and birds are forced into colonies in some areas (Snapp 1976, Shields and Crook 1987). Also consistent with this interpretation, colony size increased with size of nesting structure (building) in *H. r. rustica* (Møller 1987a). Colonial pairs fledged more young than solitary pairs in Mississippi, but the higher rate of fledging success was attributed to larger clutch sizes of colonial birds, possibly because older females settled in colonies (Lohoefener 1980). In New York, fewer young fledged from nests in larger groups than from solitary nests or nests in small groups, suggesting a net reproductive cost to coloniality (Shields and Crook 1987); in another New York study, reproductive success did not vary with colony size (Snapp 1976). In *H. r. rustica* in Denmark, costs of coloniality were more obvious than benefits: birds nesting in larger colonies found less food, experienced more extra-pair copulations, more ectoparasitism, more predation, more infanticide, and more brood parasitism, and spent more time guarding their mates and nests (Møller 1987a).

Play. In Britain, 3 juveniles were observed apparently playing with large white feather in flight, repeatedly dropping it and catching it before it reached the ground (Thompson 1990).

Nonpredatory interspecific interactions. Eastern (*Sayornis phoebe*) and Say's (*S. saya*) phoebes, Cliff and Cave swallows, House Wrens (*Troglodytes aedon*), House Sparrows, and *Myotis* bats usurp Barn Swallow nests, sometimes destroying eggs in the process; Cliff Swallows create dome over nest with mud to make characteristic jug shape, and sparrows fill interior with grass. Cliff Swallows (and probably Cave Swallows) are dominant over Barn Swallows in nest-site interactions, and in mixed colonies Barn Swallows often occupy only the darkest interiors of culverts, which Cliff Swallows seem to like least (Brown and Brown 1996). House Sparrows destroy Barn Swallow eggs and nestlings in nest takeovers and steal nesting material from Barn Swallows (Weisheit and Creighton 1989). Pair of Barn Swallows and pair of Say's Phoebes occupied same nest in New Mexico; both species laid eggs, incubated, fed each other's nestlings, and eventually fledged young (Kozma and Mathews 1995). Each exhibited aggression toward each other upon encounters at nest. Birds occasionally build nests adjacent to wasp nests (see Breeding: nest site, below), but they do not seem to interact obviously with the wasps (Jackson and Burchfield 1975). Male Barn Swallow seen copulating with female Violet-green Swallow (*Tachycineta thalassina*) in Oregon (Gullion 1947). Barn Swallow in Illinois chased a flying Dickcissel (*Spiza americana*) for no apparent reason (Beason 1974); nominate race of Europe often chases other species encountered during foraging—e.g., Common Sandpiper (*Actitis hypoleucos*; Root 1991), Kingfisher (*Alcedo atthis*; Hamzij 1991), and bats (Rosair 1975).

PREDATION

Kinds of predators. Includes accipiter hawks (*Accipiter* spp.), American Kestrel (*Falco sparverius*), and other hawks; screech-owls; Parasitic Jaeger (*Stercorarius parasiticus*); California Gull (*Larus californicus*); Great-tailed (*Quiscalus mexicanus*), Common (*Q. quiscula*), and Boat-tailed (*Q. major*) grackles; rats (*Rattus* spp.); squirrels; weasels (*Mustela* spp.); raccoon (*Procyon lotor*); bobcat (*Lynx rufus*); domestic cats (*Felis domesticus*); snakes; bullfrogs; and fish. Fire ants (*Solenopsis geminata*) observed attacking nests in Texas, killing young and carrying them away (Kroll et al. 1973). Nominate race has been found trapped in burrs of greater burdock (*Arctium lappa*) plant (Burton 1994).

Manner of predation. Large mammals such as bobcats reach and/or jump up to knock nests off walls in culverts with low (<2 m) ceilings (Lohoefener 1978). Avian predators (hawks, jaegers, gulls, grackles) pursue, catch, and kill adults in flight; some (grackles) walk toward swallows on ground and attack them. Kestrels occasionally enter culverts in pursuit of adults (Lohoefener 1980), and grackles raid nests in culverts. Predators were attracted to larger Barn Swallow colonies in Kansas (Lohoefener 1980).

Response to predators. Mobs predators near nest sites by circling, giving alarm calls repeatedly, and diving toward predator, sometimes coming within a few centimeters of or physically striking predator. Approaches predators more closely (more likely to dive) than more colonial swallows do (Brown and Hoogland 1986). Mobbing is most intense when young are in nest (Smith and Graves 1978, Shields 1984a); birds still direct alarm calls at predators, but they do not dive if young are not present. Mobs may consist of 1–19 birds, depending on number of active nests nearby (Shields 1984a). Adults with young whose nests are directly threatened mob more vigorously. Other mob members are birds at earlier nesting stages (including nonbreeders) or others whose nests are not directly attacked; these birds remain on periphery of mob and do not dive or take high risks (Shields 1984a). Barn Swallow mobs predators that are perched and follows those in flight, diving at back. Mobbing can be directed at virtually any species that approaches nest or colony site when birds have young—e.g., Snowy Egret (*Egretta thula*), Eastern Kingbird (*Tyrannus tyrannus*), Bank Swallow, Cliff Swallow, Northern Mockingbird (*Mimus polyglottos*), Loggerhead Shrike (*Lanius ludovicianus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Boat-tailed Grackle (Hailman 1960, Guillory and LeBlanc 1975). In European birds, some evidence that males that are less certain of paternity of their broods are less vigorous in their mobbing of predators (Møller 1991a).

BREEDING

PHENOLOGY

Pair formation. Figure 3. Begins on or very soon after arrival on breeding grounds. In W. Virginia, birds were usually paired within 2 wk of arrival (Samuel 1971a). In *H. r. rustica* of Denmark, males arrive on average 4.8 d ± 0.3 SE before their mates ($n = 198$; Møller 1994a). For representative arrival dates, see Migration: timing and routes of migration, above.

Nest-building. Begins about 2 wk after arrival in Manitoba (Barclay 1988); pair in Vermont began nest-building 5 d after arrival (Smith 1933). Birds nesting solitarily in Mississippi tend to nest slightly later than those breeding with at least one other pair (Lohoefener 1980), but in New York, solitaries nest earlier than birds in colonies (Shields and Crook 1987). In Pennsylvania, nest-building occurs 8 May–10 Jul (Brauning 1992).

First brood per season. Time between pair formation and clutch initiation in Ontario was 7–20 d (Smith and Montgomerie 1991). In British Columbia, first clutches initiated as early as 30 Apr (Campbell et al. 1997). In Kansas, clutch initiation dates spanned 1 May–10 Aug in one study, with most first clutches started 15–25 May ($n = 104$ nests; Johnston 1964); peaked 1–5 Jun in another study (Anthony and Ely 1976); this species lays earlier than other swallows (Robins 1970). In Oklahoma, earliest clutch initiation date about 31 Mar (Baumgartner and Baumgartner 1992). A month may elapse between arrival on breeding grounds and first egg-laying (Anthony and Ely 1976); average interval between pairing and egg-laying in *H. r. rustica* in Denmark was 16 d ($n = 210$; Møller 1994a).

Second brood per season. Modal clutch initiation date for second clutches in Kansas was 5 Jul in one study (Johnston 1964) and 15–16 Jul in another ($n = 68$ clutches; Anthony and Ely 1976); latest date for Oklahoma 2 Aug (Baumgartner and Baumgartner 1992). Average interval between initiation of first and second clutch is poorly known for North American race, but interval of about 51 d was recorded for birds in British Columbia ($n = 25$; Campbell et al. 1997).

NEST SITE

Selection process. Birds investigate many potential nesting sites upon arrival on breeding grounds, spending relatively little time at each initially but gradually confining their attention to the chosen one. Suitable old nests from previous years are occupied as soon as birds arrive (Mason 1953). Birds appear to assess parasite (mite) load of existing nests and avoid heavily parasitized ones (Barclay 1988, Møller 1990b). Birds that build new nests select sites by flying up to sections of wall or rafters, hovering briefly, then flying to another spot. Nest-building begins soon after apparent choosing of site (CRB, MBB).

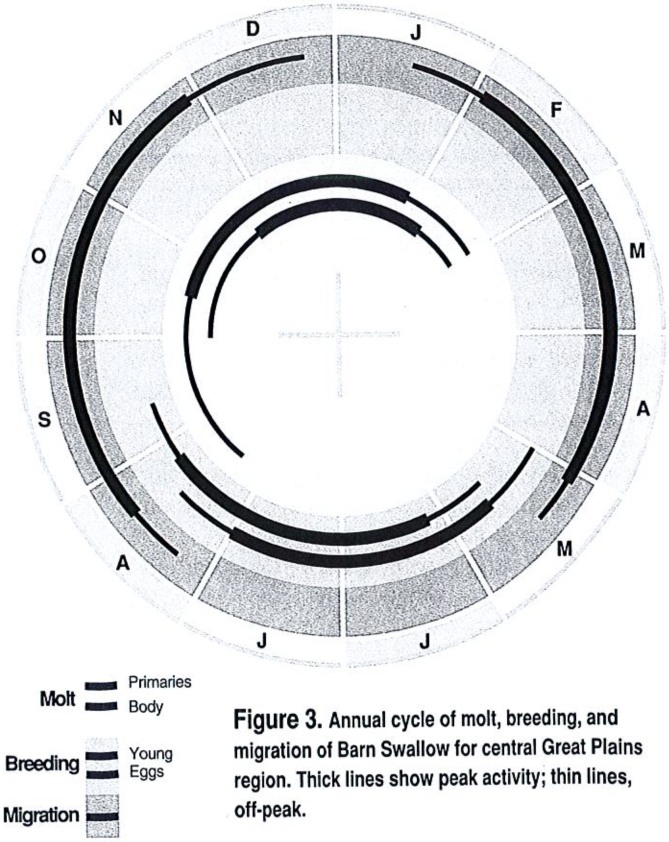

Figure 3. Annual cycle of molt, breeding, and migration of Barn Swallow for central Great Plains region. Thick lines show peak activity; thin lines, off-peak.

Microhabitat. Mud nest is either fastened to a vertical wall underneath a horizontal overhang, often near juncture of wall and ceiling, or built on top of a horizontal ledge or other substrate underneath an overhang. Nests are sometimes built on top of curled wires or rods. Reportedly uses cavities and crevices in rock faces, in which case typical mud nest is not built. In Mississippi, 20 nests were attached to flat, relatively smooth vertical walls; 28 nests to walls on a crack; 4 to masonry bolts protruding from a wall; 36 to mud nests of wasps (*Trypoxylon politum*) or mud daubers (*Sceliphron caementarium*) that were in turn attached to flat vertical walls; 9 to wasp nests in a corner between walls and beams; and 1 to a wasp nest in a crack on a corner (Jackson and Burchfield 1975). Solitary Barn Swallow nests were more likely to be attached to wasp nests than were Barn Swallow nests in colonies (Lohoefener 1980). In British Columbia, 46% of 2,537 nests were attached to rafters or beams of buildings, 18% under eaves, 11% on ledges or projections, 9% on vertical walls, and 5% over light fixtures (Campbell et al. 1997). No systematic differences in compass directions in which nests are oriented. Heights of 2,563 nests in British Columbia ranged from 0.3 to 30 m (57% between 2.4 and 3.5) above ground (Campbell et al. 1997).

Site characteristics. Before widespread introduction of European culture into North America in nineteenth century, Barn Swallows used mostly caves as nesting sites. Occasionally nests were built in holes or crevices in cliff faces; birds did not apparently use exposed cliff walls (under overhangs) as Cliff Swallows do. Natural nesting sites, mostly in caves, were reported in 1800s and early 1900s from California, Washington, Nevada, Dakota Territory, Kansas, Minnesota, Wisconsin, Michigan, Maine, and Massachusetts (Betts 1916, Speich et al. 1986). The birds no longer nest at most of these sites; since 1960s, natural nestings, again mostly in caves, have been reported only from Channel Is. of California, Oregon, Washington, British Columbia, Nebraska, Arkansas, W. Virginia, New York, and Canadian Maritime Provinces (McDaniel and Gardner 1977, Speich et al. 1986, Erskine 1992, CRB). In Maritime Provinces, 5 of 1,093 nests were in natural settings, usually in caves or underneath cliffs close to water (Erskine 1992), and 1% of 2896 nests in British Columbia were in natural sites (Campbell et al. 1997). Only in Channel Is., CA, can birds still be found regularly nesting in caves (Speich et al. 1986). In caves, nests are attached to roofs on small irregular ledges 3–7 m inside opening. A nest in Nebraska was built on top of a small, narrow earthen ledge on side of cliff underneath an overhang (CRB).

The birds' conversion to artificial sites must have started well before European settlement of North America. Birds were nesting on Native American habitations in early 1800s (Macoun and Macoun 1909). This species now nests in virtually any sort of building, shed, bridge, culvert, or other structure that provides a wall with overhang and/or flat ledge. Willing to go into and out of small windows and other openings to reach nests inside structures, sometimes in very dimly lit areas. Seems to avoid wooden nesting structures in some areas (e.g., Mississippi; Jackson and Burchfield 1975), but in other areas does not obviously avoid wooden sites (e.g., Nebraska; CRB, MBB). In remote parts of Maritime Provinces (also Nebraska; CRB, MBB), birds use circular corrugated-metal culverts, placing nests on top of large bolts on culvert walls (Erskine 1992); reported to nest on moving oil pumps (Hjertaas 1991) in Saskatchewan, moving boats in Minnesota (Lesher 1988), and trains in British Columbia (Swarth 1935), and many other types of sites throughout North America. In Mississippi, where birds use exclusively bridges, seems to prefer sites with water running through them and utility wires nearby and constructed of metal or concrete; bridges used had shorter spans, higher end walls, and wider entrances than unused sites (Jackson and Burchfield 1975). Culverts with >1 nest in Mississippi tended to be slightly larger in physical dimensions than those with solitary nests; minimum culvert size that the birds will use is apparently 0.9 m in length and width (Lohoefener 1980). In Kansas, 8% of nests ($n = 199$) were under bridges or in culverts; remainder in farm buildings (Anthony and Ely 1976). Apparently there are extensive geographic differences in type of artificial structure typically used.

European *H. r. rustica* also used caves (and hollow trees) historically but has converted almost entirely to artificial structures.

NEST

Construction process. Both sexes build nest, but female seems to take more active role, especially in shaping nest (Smith 1933, 1937, Anthony and Ely 1976); in *H. r. rustica*, proportion of nest-building by males varies from 0 to 68% (Møller 1994a). Birds land at mud source and collect mud in beak, often mixing it with grass stems, and attach mud pellets to vertical wall or on top of flat object (see Fig. 4). Birds seem to prefer building on top of ledge or other object protruding from substrate, probably to give nest more support, but often have nothing underneath, with nest attached to wall solely by its sides. Begins construction by making narrow mud shelf, large enough for bird to sit on, and then builds up sides. If attached to vertical wall, nest has semicircular half-cup shape; if built on bottom support, can be circular full cup. In European *H. r. rustica*, rate of nest-building varies from 5 to 42 collecting trips/h (mean 29.9 ± 1.9 SE, $n = 168$; Møller 1994a). There are 4 stages of nest construction: (1) building a base from which to work, usually taking 1–4 d; (2) construction of mud shell, usually taking 3–14 d; (3) addition of grass lining, usually taking 1–5 d; and (4) addition of feather lining, usually taking 1–3 d (Anthony and Ely 1976, Lohoefener 1980). Average building time for new nests in W. Virginia was 6.4 d (range 3–10; Samuel 1971a); in British Columbia, 15 d ($n = 10$; Campbell et al. 1997). Delays of up to 10 d are common, depending on weather conditions. In colonies, birds steal nest-lining materials from unattended neighboring nests (Lohoefener 1980). Birds apparently use both position on wall and features of nest itself to locate their own nest within a culvert (Grzybowski 1979).

When reusing old nest from a previous year, birds add new mud to rim and toss out old feathers; some nests in Nebraska that have lasted intact for at least 17 yr have had mud added each year, becoming >70 cm deep (CRB, MBB). In Manitoba, more mud is added to old nests reused in May than those

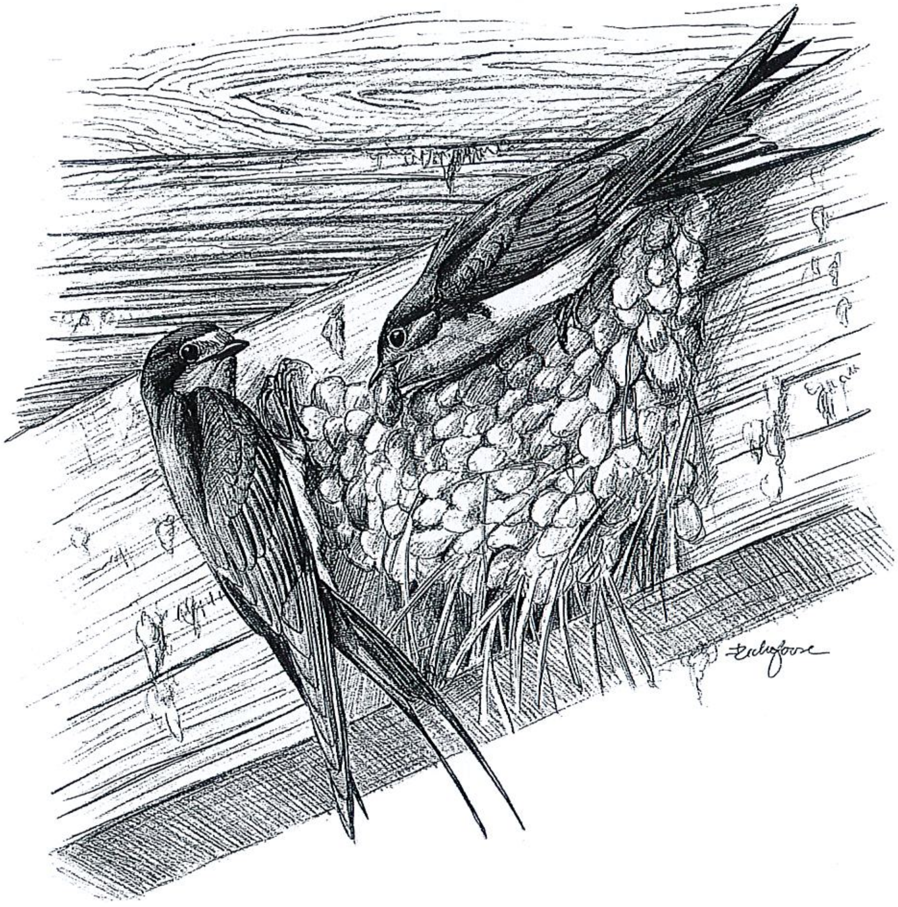

Figure 4. Male (left) and female (right) Barn Swallows building nest. Drawing by J. Zickefoose.

occupied in Jun or Jul (Barclay 1988). Nest renovation in Kansas typically lasts 2–5 d (Anthony and Ely 1976). In New York, birds reusing an old nest spent mean of 4.8 d refurbishing it ($n = 45$), compared to 11.0 d building new nests ($n = 15$; Shields et al. 1988). Some new mud and new feathers are often added to nest between broods if it is reused within a season (Samuel 1971a).

Structure and composition matter. Nests often have distinct layers of mud, reflecting different mud sources; sometimes mud layers are interspersed with layers of grass stems. Mud has more grass mixed into it than in nest of Cliff Swallow. Mud composition of nests in Montana was 56.4% sand, 31.5% silt, and 11.9% clay ($n = 33$ nests; Kilgore and Knudsen 1977), with no differences in composition between different parts of nest. Interior of nest is lined with fine grass stems, horsehair, strands of algae (Duffin 1973), and often profusely with feathers, often large poultry feathers. Presence of feathers coincides with egg-laying and incubation periods. Nests of *H. r. rustica* may contain 750–1,400 mud pellets (Møller 1994a). In rare circumstances in which birds nest in rock cavities, nest contains little or no mud.

Dimensions. Walls of nest are reported to be about 2.5 cm thick; total length and breadth of nest about 13 cm, interior 5 cm deep, and 7.5 cm wide at rim (Baird et al. 1875). Nests can sometimes be quite close to a ceiling; clearance between nest and ceiling is usually 2.5–6 cm, sometimes up to 58 cm (Grzybowski 1979, Lohoefener 1980). In Michigan, nest cup depth varied from 2.3 to 4.5 cm, with inside volume of 41–162 cm^3 ($n = 17$ nests); nest volume had no apparent effect on clutch size or reproductive success (Goodman 1982).

Microclimate. No information.

Maintenance or reuse of nests, alternate nests. Commonly reuses old nests from a previous year; in Manitoba, 45.3% of first clutches ($n = 86$) and 52.0% of second clutches ($n = 50$) were in old nests (Barclay 1988); in Kansas, 62% of first clutches ($n = 105$) were laid in old nests (Anthony and Ely 1976); in W. Virginia, 56% of nests used one year were reused the next ($n = 62$; Samuel 1971a). In Mississippi, birds nesting solitarily were more likely than those in colonies (≥6 pairs at a site) to build new nests (Lohoefener 1980). Reuse of nests used earlier in same year varies; only 6 (12%) of 50 nests used for second clutches in Manitoba had been used for first clutch in same year (Barclay 1988), but 81.3% of females ($n = 16$) in Oklahoma used same nest for both first and second clutches (Iverson 1988), and 45.2% of nests ($n = 137$) in Kansas were used for 2 broods (Anthony and Ely 1976). Studies of marked birds in New York showed that 53% reused same nest for second nesting attempt (Shields 1984b). Within a season, successful nesters in New York were more likely to change nests for second clutch; between seasons, birds were more likely to return to same nest if they had been successful (Shields 1984b). Clutch size and reproductive success did not differ between birds using old nests or building new ones (Barclay 1988).

Nonbreeding nests. Birds occasionally reported to construct mud platform contiguous with nest (rarely separate) for sleeping (Baird et al. 1875), but no nonbreeding nests are known.

EGGS

Shape. Ovate to elliptical ovate and variable (Oberholser 1974).

Size. From Western Foundation of Vertebrate Zoology (means based on clutch averages, extremes based on individual eggs; $n = 22$ clutches, 101 eggs): length 19.26 mm (range 16.30–21.68), breadth 13.75 mm (range 12.44–14.84), empty shell weight 0.100 g (range 0.075–0.136). In European *H. r. rustica*, mean length 1.96 cm ± 0.08 SD (range 1.76–2.18), mean breadth 1.37 cm ± 0.04 SD (range 1.28–1.49, $n = 231$ clutches; means calculated from means per clutch; Ward 1995). Generally no correlation between egg size and laying order, although occasionally last egg is largest (Banbura and Zielinski 1995b).

Mass. For North American race, mean for fresh eggs was 1.9–2.0 g (range 1.4–2.1, $n = 18, 44$; Stoner 1935, Manning 1979). Mean 2.0 g ± 0.1 SD (range 1.7–2.3) for *H. r. rustica* ($n = 231$ clutches; Ward 1995). Fresh-egg mass was unrelated to clutch size, skeletal size and wing length of female, female age, position of egg in clutch, hatchability, or whether clutch was a first or second clutch; fresh-egg mass was positively related to hatchling mass and wing and tarsus length of hatchlings (Ward 1995). Lipid content of whole eggs and of yolk increased with food availability during the 6 d before laying but was unrelated to temperature or rainfall (Ward 1995). An egg contains mean 10 kJ ± 0.9 SD ($n = 20$) of energy, requiring investment of about 14.3 kJ/egg by female (Ward 1995).

Color. Ground color creamy white or pinkish white and slightly glossy, with small spots and dots of reddish brown, dark brown, purplish brown, and cinnamon; also sparingly marked with lilac, lavender, and vinaceous gray (Oberholser 1974). Color pattern, size, and shape of eggs in European *H. r. rustica* are claimed to be individually distinctive enough to allow humans to recognize eggs of specific females (Møller 1987b), but in North America this is not the case (Brown and Sherman 1989).

Surface texture. No information.

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

Clutch size. In 1 Kansas study, mean 4.7 eggs (mode 5, range 3–7, $n = 43$), with average clutch size declining by about 0.6 egg from 1 May to 10 Aug (Johnston 1964); in another study, first clutch averaged 4.6 eggs (range 4–7, $n = 105$) and second clutch 4.1 eggs (range 3–6, $n = 68$; Anthony and Ely 1976). Similar figures reported from Mississippi, where birds nesting in colonies had larger overall clutches than those nesting solitarily (Lohoefener 1980). In Michigan, mean overall clutch size was 4.7 eggs ± 0.9 SD (range 3–6, $n = 17$; Goodman 1982). In W. Virginia, mean size for first clutches was 4.6 eggs ± 0.1 SD ($n = 94$); for second clutches, 4.1 eggs ± 0.3 SD ($n = 33$; Samuel 1971a). Clutches of 6 or 7 seldom have 100% survival, but surviving broods of 6 or 7 do occur (Mason 1953). In *H. r. rustica* of Europe, clutch size generally increased with overall nest size as measured by nest volume (Møller 1982).

Egg-laying. Egg-laying followed completion of feather lining by 1–3 d in Kansas; 1 egg laid per day, usually between 05:30 and 07:30 (Anthony and Ely 1976). Determinate layer; removal of eggs during laying has no influence on clutch size (Davis 1955). In Europe, some females are intraspecific brood parasites (see Brood parasitism, below); females visit neighboring nests apparently to assess their suitability as host nests and lay in them when host female is absent. Egg-laying within a colony is largely asynchronous, and females do not seem to actively cluster egg-laying times.

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation is thought to begin after laying of penultimate egg in Vermont (Smith 1933) and Kansas (Thompson 1961), and after third egg of 5 in Kentucky (Tabler 1956); begins after laying of last egg in European *H. r. rustica* (Kuzniak 1967).

Incubation patch. Single medial abdominal patch in female only. Although they incubate, North American males do not have brood patches.

Incubation period. Reported as 13.8 (range 13–15, $n = 20$) and 13.7 d ($n = 118$) in Kansas (Thompson

1961, Anthony and Ely 1976); 14.6 d (range 12–17, *n* = 42) in British Columbia (Campbell et al. 1997); and 14.6 d in European *H. r. rustica* (Kuzniak 1967). Few other data, except for single nests from elsewhere in North America.

Parental behavior. In North America, both sexes incubate, but females do more. Males in Ontario incubated on average about 9% of total time that eggs were covered, although there was considerable variation among individuals (Smith and Montgomerie 1992). Temperature measurements of eggs show that the male, despite lacking brood patch, is as effective as female in keeping eggs warm; incubation temperature usually kept at about 35°C (Ball 1983). Incubation bouts averaged 6.9 min (range 0.7–57.6, *n* = 178); total nest attentiveness higher for first clutches (63.9%, *n* = 16) than for second clutches (48.1%, *n* = 15; Smith and Montgomerie 1992). Incubation declines during a day, with clutches incubated only about 25% of the time by late afternoon; nest attentiveness does not vary across incubation period (Smith and Montgomerie 1992). As temperature inside nest rises, adults incubate less (Smith and Montgomerie 1992). Incubation attentiveness varies inversely with amount of feathers that line nest (Møller 1991c). Females spend the night on eggs (Ball 1983). Adults turn eggs with bill at start of incubation bout. Incubation by males in North American race is believed to be partly responsible for shorter outer tail-streamers than in European birds; breakage of streamers when rubbing against nest and substrate while incubating may select against tail elongation (Smith and Montgomerie 1991). Males do not feed females during incubation. Brood-enlargement experiments on *H. r. rustica* showed that females increased the length of time they incubated when given larger clutches (Jones 1987c). Detailed observations on incubation attentiveness are presented by Smith and Montgomerie (1992).

Hardiness of eggs against temperature stress; effect of egg neglect. No information on hardiness of eggs or effect of egg neglect. Under apparently normal conditions, 10 and 23.2% of eggs laid in first (*n* = 13) and second (*n* = 9) clutches, respectively, did not hatch in Kansas (Thompson 1961); mean number of unhatched eggs/clutch in Michigan was 0.1 ± 0.3 SD (*n* = 17; Goodman 1982), and 5.2% of 1,750 eggs in New York did not hatch (Snapp 1976).

HATCHING

Preliminary events and vocalizations. No information.

Shell-breaking and emergence. Hatching period usually about 24 h in Kansas, with last-hatched young smallest and often succumbing (Thompson 1961). In *H. r. rustica* in Britain, eggs hatched in the order laid and usually within 24-h period (McGinn and Clark 1978); but in Poland, hatching order was independent of laying order, and only 60% of clutches hatched within 24-h period (Kuzniak 1967).

Parental assistance and disposal of eggshells. Not known to assist, but in Poland females remained continuously at nest during hatching (Kuzniak 1967). Adults carry broken eggshells away from nest, dropping them several meters away.

YOUNG BIRDS

Condition at hatching. Mean mass at hatching reported as 2.2 g ± 0.5 SD (*n* = 29 young from 7 nests) in Kansas (Anthony and Ely 1976) and 2.4 g (range 1.5–3.5, *n* = 31) in Iowa and New York (Stoner 1935). Temperature (for birds brooded by adults immediately before measuring) averaged 36.4°C (range 33.3–38.7, *n* = 31 birds; Stoner 1935). Mean ulna and tarsus lengths were 5.2 mm ± 0.6 SD and 4.6 mm ± 0.5 SD, respectively, in Kansas (Anthony and Ely 1976) and 5.0 mm (range 4.0–5.5, *n* = 7) and 3.5 mm (*n* = 31), respectively, in Iowa and New York (Stoner 1935). Bill length reported as 6.0 mm for *H. r. rustica* (George and Al-Rawy 1970). Young hatch naked except for pale smoke-gray tufts of natal down about 5 mm long on forehead, scapulars, occiput, and middorsal region; bill cream-colored (Wood 1937, Anthony and Ely 1976).

Growth and development. On day 2, skin of femoral, alar, and dorsal tracts begins darkening; on day 4, bill darkens and pin-feathers first become noticeable along ulnar side of wing (Wood 1937, Anthony and Ely 1976). By day 8, pectoral pin-feathers begin to show, and brown forehead-feathers appear by day 14 (Wood 1937). Eyes open gradually from days 5 to 8 and are completely open by day 11; rectrices appear on days 5–6, and primaries and rectrices emerge from sheath on day 8 or 9 (Stoner 1935, Wood 1937, Anthony and Ely 1976). Wing measured as 8.1 cm on day 19, when birds fledged (for comparison, same observer measured wing of adults as 12.0 cm; Wood 1937). Mass gain greatest between days 4 and 10; average mass 19.5 g (*n* = 18) at day 10; maximum mass (about 21 g) attained at day 12 and diminished to mean 17.5 g at fledging (Stoner 1935). Temperature increased daily over first 10 d as birds became homeothermic; mean on day 5 was 39.8°C (*n* = 10) and 40.9°C (*n* = 18) on day 10; by day 17, mean was 42.2°C (*n* = 15), very similar to that of adult (Stoner 1935). Length of ulna shows greatest increase during first 10 d, averaging about 2.4 mm/d until full length attained on day 12 (mean 25.4 mm; Stoner 1935). Tarsus grows most rapidly during first 6 d, growth diminishing markedly between days 6 and

10; final length attained on days 11–12 (Stoner 1935). Average length of outer primary at day 5 was 1.3 mm, increasing by average 21.7 mm ($n = 18$) during next 5 days; outer primary growth shows extensive variation within broods (Stoner 1935). At day 15, average length of outer primary was 46.1 mm; overall growth throughout nestling period is about 4 mm/d. Outer tail-feathers averaged 1.2 mm at day 5 ($n = 10$), increasing to 13.7 mm at day 10 ($n = 18$) and 31.4 mm at day 15 ($n = 18$; Stoner 1935). Middle tail-feather averaged 1.0 mm at day 5, 2.1 mm at day 6, 11.7 mm at day 10, and 27.5 mm at day 15 (Stoner 1935). Growth curves are presented graphically in Stoner 1935 and Anthony and Ely 1976, and rates of change in lipid and water content of different body components during nestling growth are given by Ricklefs (1967). Detailed developmental studies of alimentary canal in nestlings in *H. r. rustica* are presented by Przystalski (1988) and of temperature regulation by Al-Rawy and Kainady (1976).

Nestlings begin flapping wings by day 9, begin preening by days 12–15 by drawing open bill along feather-shafts to remove pieces of white feather-sheaths, and stand on nest rim by day 14 (Smith 1933, Wood 1937, Tabler 1956). Starts to show fear response by day 9, retreating from nest rim and hunkering down at alarm call of adult (Smith 1933). May fledge prematurely by day 14 if handled (Anthony and Ely 1976).

Energy requirements for nestlings in broods of different sizes for *H. r. rustica* in Britain are discussed in detail by Turner (1983).

PARENTAL CARE

Brooding. Little information for North American race; brooding largely ceases by day 15, although female continues to spend night on nest, with male often roosting nearby (Samuel 1971a). In *H. r. rustica* in Britain, females reported to brood for ≥10% of time when nestlings were 1–7 d old and <10% after day 7; females with larger broods brooded less (Jones 1987a). Females brooded almost continuously for first 3 d after hatching in Poland (Kuzniak 1967); detailed observations on brooding by *H. r. rustica* in Germany are presented by Purchon (1948).

Feeding. Both parents feed nestlings, largely equally in North America. Feeding is directed toward young in relation to begging intensity; those that open mouth widest and reach forward farthest are fed. All nestlings in a brood tend to receive relatively equal amounts of food, in part because each nestling turns around to defecate over nest rim after being fed and remains in this position for several minutes, during which time other brood members are fed (McGillivray and Levenson 1986). No active apportionment of food among brood; parents usually feed only 1 nestling per visit. Feeding rates averaged about 29 visits/h/nest (range 21–38) in New York (Snapp 1976). Small nestlings beg in response to decreased light intensity at nest (Jackson and Burchfield 1975). In *H. r. rustica* in Britain, 52% ± 21 SD of food deliveries were by females (Jones 1987b). Feeding rates rise steadily until peaking at day 13, then decrease and are greater for larger broods (Jones 1987a, 1987b). Mean prey size taken by birds feeding young was 6.0 mg ± 5.6 SD ($n = 4{,}960$); number of insects per bolus was 18.1 ± 14.1 SD ($n = 92$); bolus dry weight was 73.4 mg ± 31.9 SD ($n = 432$); distance from nest to foraging patch traveled by adults was 0.17 km ± 0.12 SD ($n = 118$); and total duration of foraging trip was 2.8 min ± 1.7 SD; amount of food brought back is unrelated to distance flown to forage (Bryant and Turner 1982) but increases steadily with nestling age (Jones 1987a, 1987b). Female parents lose mass steadily while feeding young (up to 19.3% of body mass); male parents show no consistent pattern (Jones 1987a). Males deliver significantly smaller food loads than females: for males, mean 0.115 g ($n = 281$); for females, mean 0.137 g ($n = 425$; Jones 1987b). Maximum nestling mass is higher in nests of older parents than in nests of yearlings, suggesting that older parents provision young better (Languy and Vansteenwegen 1989). Female *H. r. rustica* in Germany observed begging for food from male at nest by fluttering wings, then feeding those items to young (Purchon 1948).

Nest sanitation. By day 12, nestlings back up to nest edge and defecate over rim, and as a result feces often accumulate below nest. Before then, adults swallow or carry fecal sacs from nest.

Carrying of young. Not known to occur.

COOPERATIVE BREEDING

Helpers. Nests often attract attention of extra adults that associate with a pair for up to an entire breeding season; these extra birds are sometimes tolerated and occasionally lead to polygyny (Medvin et al. 1987). Extra birds were predominantly males in New York (Crook and Shields 1985, 1987) and yearling females in Washington (Medvin et al. 1987). Extra adults contribute relatively little to feeding young, but they are known to mob predators and assist in nest-building, incubation, and brooding young (Crook and Shields 1985, 1987, Medvin et al. 1987). Extra adults may be using nest attendance as breeding strategy either to replace one pair member should something happen to it (Medvin et al. 1987) or to commit sexually selected infanticide (Crook and Shields 1985, 1987), providing opportunity for males to take over breeding female (see Behavior: sexual behavior, above). Nests that are attended often are ones occupied by older females (Crook and Shields 1987), consistent with interpretation that male attendants are trying to secure high-quality birds as mates.

Juveniles from first brood have been reported to feed siblings of second brood (Mackay 1899, Forbush 1929, White 1941), in some cases providing substantial amounts of food (Williamson 1941); older siblings provided 6-28.5% of total feedings at 8 nests in Ohio (Myers and Waller 1977). Unrelated juveniles also feed broods, contributing up to 19% of total feedings (Myers and Waller 1977).

Results of helping. Generally adult nest attendants probably do not provide enough food to be meaningful, but being tolerated by breeding pair presumably provides opportunities for attendant to become a breeder itself by replacing one member of pair. Not all extra adults are tolerated, however; many are chased from vicinity of nest whenever they appear (Crook and Shields 1985). Reproductive success does not differ between nests attended by extra adults and those without attendants (Crook and Shields 1987). Attendance at nest may be most frequent when a biased sex ratio (see Behavior: sexual behavior, above) or late arrival on breeding grounds reduces an individual's chances of finding a mate or preferred nest site. Advantages of helping to feed broods for juvenile birds are presumably kin-based in cases of feeding siblings, but reasons are unclear for help by unrelated juveniles.

BROOD PARASITISM

Identity of parasitic species. North American race is parasitized rarely by Brown-headed Cowbird (*Molothrus ater*). Occasional records of parasitism of *H. r. rustica* by Common Cuckoo (*Cuculus canorus*) in Britain (Wolley-Dod 1892, Young 1974). Intraspecific brood parasitism apparently occurs rarely in North American race—not detected by Shields and Crook (1987) or Hoskyn (1988)—but regularly in *H. r. rustica*; studied thoroughly in Denmark (Møller 1987b).

Frequency of occurrence, seasonal or geographic variation. Single records of cowbird parasitism from Iowa, Manitoba, and Maryland; 2 reports from Ontario; 3 from Oklahoma and Pennsylvania; undetermined number from Kansas; none observed in 322 nests in Louisiana, 185 nests in Iowa, 284 nests in Kansas, or 3,776 Cornell University nest records (reviewed in Wolfe 1994). Intraspecific parasitism occurred in 16.5% of 261 nests in Denmark and is more frequent in larger colonies, where individuals have greater opportunities for parasitism, and is perpetrated largely by residents living near host's nest (Møller 1987b).

Timing of laying in relation to host's laying. No information on interspecific parasitism. Intraspecific parasitism in Denmark tends to occur during and immediately after laying by host female (Møller 1987b).

Response to parasitic mother, eggs, or nestlings. No information on interspecific parasitism, but eggs are presumably accepted if added during or after host female starts laying. Eggs of other Barn Swallows are accepted if added during laying or incubation, but birds reject eggs if placed in their nest before host's laying (Møller 1987b). Birds recognize eggs only by time in nesting cycle and do not discriminate on basis of color pattern or other physical characteristics (Grzybowski 1979). Part of the reason for nest-guarding may be to prevent intraspecific parasitism; parasitized nests in Denmark were ones whose owners had guarded less (Møller 1987b). North American race apparently guards nests less than European *H. r. rustica*; birds in Nebraska guarded nests a mean 29.3% ± 4.0 SE (*n* = 33; Brown and Brown 1996) of the time during egg-laying, versus 55.3 ± 3.7 SE to 74.9% ± 2.3 SE of the time in Denmark (Møller 1987b), suggesting that intraspecific parasitism is less likely in North America.

Effects of parasitism on host. No apparently negative effects in 2 cases of cowbird parasitism studied in Oklahoma (Wolfe 1994). Females parasitized intraspecifically in Denmark had smaller clutches of their own than nonparasitized females, but it is unclear whether this difference was directly related to being parasitized (Møller 1987b).

Success of parasite with this host. In 1 nest in Oklahoma, cowbird chick survived to fledging but disappeared and was not seen outside nest; in second case, cowbird egg never hatched (Wolfe 1994). Intraspecific parasitism in Denmark is often successful, with hosts rearing parasitic offspring; results in greater annual reproductive success for parasitic females (Møller 1987b).

FLEDGLING STAGE

Departure from nest. Young reported to fledge at mean of 20.4 and 20.7 d (first and second broods, respectively) of age in Kansas (range 15–24 d; Anthony and Ely 1976); in W. Virginia, 20.7 d (range 18–27, *n* = 10; Samuel 1971a); in British Columbia, 19.5 d (range 19–24, *n* = 12; Campbell et al. 1997). Nestling period reported to be 19–23 d for *H. r. rustica* in Poland, with all brood members leaving nest on same day (Kuzniak 1967). Adults escort juvenile when flying from nest, seeming to lead it to perch site (Smith 1937).

Association with parents or other young. Parents lead young back to nest to sleep for up to several days after fledging. Broods in Washington traveled mean of 0.48 km (*n* = 11) from nest site, where they usually stayed in same general area for several days, often perching on wires or other exposed perches;

broods typically remain segregated from others, and juveniles do not mix between broods until independent (no creches form; Medvin and Beecher 1986). Parents do not recognize their own young (Grzybowski 1979) and thus do not discriminate against conspecific juveniles if any join the brood.

Ability to get around, feed, and care for self. Juveniles are fed by their parents for several days, possibly up to a week, after fledging; family groups have broken up entirely by 2 wk after fledging (Smith 1937, Medvin and Beecher 1986). At first juveniles are usually fed while perched, but eventually they begin taking food from their parents in flight, flying to meet incoming adult, and food is transferred in midair.

IMMATURE STAGE

Once independent, juveniles travel widely, often visiting other active nests or colonies; banded juveniles have been recaptured at other colonies 5–8 km from fledging site (Bell 1962). Recently fledged juveniles intrude into nests that contain smaller nestlings, and in some cases are fed by parents of the smaller nestlings; the juveniles are apparently unrelated to the small nestlings in these cases (Ball 1982, Zielinski and Banbura 1995). This food-stealing represents kleptoparasitism as described for other swallows (Brown and Brown 1996).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Yearlings of both sexes typically breed, although many unmated males in some populations are first-year birds.

Clutch. First-year females lay smaller clutches than older birds. In New York in small colonies, pairs in which female was a yearling had mean seasonal egg production of 5.7–6.2 eggs (counting both clutches), compared to 6.8–7.5 eggs for those in which female was an older bird; in large colonies, seasonal means were 6.2–6.4 eggs for yearlings and 7.9–8.3 eggs for older birds (Shields and Crook 1987). Clutch size increases with latitude in *H. r. rustica* (Møller 1984).

Annual and lifetime reproductive success. In Ontario, first broods averaged 3.1 surviving fledglings ($n = 20$); annual reproductive success, counting young fledged from second brood, if any, was 4.2 fledglings/male ($n = 20$; Smith and Montgomerie 1991). In Manitoba, mean annual reproductive success for birds attempting 2 broods was 6.9 ± 0.5 SD (range 3–11) fledglings/pair (Barclay 1988). In Kansas, first broods produced mean of 2.7 young/nest, compared to 2.9 young/nest for second broods (Anthony and Ely 1976). Among nests producing ≥1 fledgling, first broods averaged 4.3 young ($n = 374$), second broods 3.3 ($n = 101$) in Massachusetts (Mason 1953). Averaged over both broods, mean of 3.4 fledglings/nest ($n = 222$) in one year and 3.1 ($n = 235$) in another in Mississippi (Lohoefener 1980), and 4.0 ± 1.3 SD (range 0–5, $n = 17$) in Michigan (Goodman 1982). In New York, mean of about 2.8 fledglings/nesting attempt for solitarily nesting birds and those in small colonies, and about 1.5 for birds in larger colonies (Shields and Crook 1987); in Nebraska, 3.0 fledglings/nest for solitary nesters, 3.3 fledglings/nest in colonies of 3–9 pairs, and 2.9 fledglings/nest in colonies of ≥10 nests (L. Smith pers. comm.). Nesting success measured as percentage of eggs laid that produced fledglings for first and second clutches: 58.3–82.5 and 71.1–73.2%, respectively, in Kansas (Anthony and Ely 1976) and 81.2 and 85.1%, respectively, in W. Virginia (Samuel 1971a). In British Columbia, 70% of nests ($n = 609$) produced ≥1 fledgling (Campbell et al. 1997).

Number of broods normally reared per season. Often 2. In Ontario, 30% of females initiated second clutch (Smith and Montgomerie 1991); in Manitoba, 90% (Barclay 1988); in Massachusetts, 67% ($n = 52$; Mason 1953); in New York, 49% ($n = 301$; Snapp 1976). In Denmark, 60% of birds ($n = 812$) initiate second nestings (Møller 1994a). Third and fourth broods reported in Mississippi (Loehoefener 1980), although these may have represented mostly birds whose earlier attempts had failed. No observations of color-marked birds successfully raising 3–4 broods anywhere in North America.

Proportion of total females that rear at least one brood to nest-leaving or independence. Unknown because fraction of females that are nonbreeders is unknown.

LIFE SPAN AND SURVIVORSHIP

Longevity record in North America is 8 yr 1 mo for bird in Massachusetts (Clapp et al. 1983). Only survival estimates using appropriate statistical methodology (SURGE; Lebreton et al. 1992) are for birds in Nebraska, where mean annual adult survival probability over 15-yr period was 0.350 ± 0.054 SE ($n = 300$); survival probabilities for males and females did not differ significantly (CRB, MBB). This estimate should be viewed cautiously, however, because it is based largely on data for birds at only 1 large colony.

DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. Fleas (Siphonaptera: Ceratophyllidae) include *Ceratophyllus idius* from New Brunswick, Newfoundland, and Ontario; *C. niger* from

British Columbia; *C. scopulorum* from New Brunswick (Wheeler and Threlfall 1989); and *C. garei, C. rusticus, C. affinis, C. hirundinis, C. farreni*, and *C. gallinae* from unspecified locales (Hicks 1962). Mites (Acari: Dermanyssidae) include *Dermanyssus gallinae* from British Columbia, Michigan, and Massachusetts; *D. hirundinis* from British Columbia; and *Ornithonyssus sylviarum* from Ohio, New Hampshire, Vermont, and Quebec (Peters 1936, Wheeler and Threlfall 1989). In California, dermestid beetles (Dermestidae: *Anthrenus lepidus, Anthrenus occidens*, and *Attagenus nigripes*) were found in nests (Linsley 1944). At least 5 species of blowflies (*Protocalliphora halli, P. aenea, P. hirundo, P. sialia*, and *P. metallica*) recorded in Barn Swallow nests in Ontario and New York, with infestation rates ranging from 4.6 to 50% of nests at different sites (Shields and Crook 1987, Bennett and Whitworth 1992). Blood parasites (Hematozoa) *Trypanosoma* recorded in Ontario (Bennett and Fallis 1960) and *Plasmodium* in New Jersey and Maryland (Williams and Bennett 1978). Feather lice (Mallophaga) include *Brueelia domestica, B. longa, Philopterus excisus*, and *P. domesticus* (Ischnocera: Philopteridae), and *Machaerilaemus malleus, Myrsidea rustica*, and *Myrsidea dissimilis* (Amblycera: Menoponidae; Kellogg and Chapman 1899, Peters 1936, Emerson 1972). The cliff swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) has been found on Barn Swallow nestlings in nests that occur in same culvert as Cliff Swallows in Nebraska (CRB, MBB) and at sites without Cliff Swallows in Oklahoma (C. E. Hopla in Sutton 1986). Nematodes include *Splendidofilaria algonquinensis* (Nematoda: Dipetalonematidae) from Ontario (Wong et al. 1990). Trematode *Collyriclum faba* (Trematoda: Troglotrematidae) was found in a bird in Michigan (Wolinski 1979). Many other parasites have been identified for *H. r. rustica* (see Hicks 1959, Møller 1994a).

Birds occupying nests infested with dermanyssid mites in Manitoba had significantly lower reproductive success than birds using unparasitized nests in both first and second nestings; reduced success of parasitized nests appeared to result from increased nestling mortality due to mites (Barclay 1988). Infestations of *Protocalliphora hirundo* in New York increased in larger colonies and later in season; these ectoparasites caused mortality among young, slowed growth rates of those that survived, and largely accounted for reduced reproductive success of Barn Swallows nesting in larger colonies (Shields and Crook 1987). Effects of fowl mite *Ornithonyssus bursa* on European race (Møller 1990b) largely parallel those of mites and blowflies in North America; fowl mites also cause reduced clutch sizes and greater asymmetry in outer tail-streamers in Barn Swallows (Møller 1991b, 1992).

CAUSES OF MORTALITY

Exposure. Cold and rainy weather occurring in late spring and early summer causes mortality among both adults (Brown and Brown 1999) and nestlings (Mason 1953, Anthony and Ely 1976) as result of starvation. Extreme heat during summer may also lead to nestling mortality (Mason 1953, Anthony and Ely 1976). Cold and rainy weather kills large numbers of birds on wintering grounds, as found for *H. r. rustica* wintering in Africa (Rowan 1972); drought in winter can also cause substantial mortality by reducing insect food supply (Møller 1994a). Record cold in Sep 1974 in Europe (Bruderer 1975) killed at least a million migrating swifts and swallows (a large fraction were Barn Swallows), many of them juveniles. Similar cases of mass mortality occurred in 1740, 1770, 1829, 1855, 1881, 1931, and 1936 (U. N. Glutz von Blotzheim and K. M. Bauer in Møller 1994a).

An unusually cold and rainy 6-d period in sw. Nebraska in May 1996 resulted in natural selection on beak and tail morphology in Barn Swallows (Brown and Brown 1999). Surviving males had significantly longer culmens and significantly less variance in asymmetry of outer tail-streamers than nonsurvivors. Surviving females had significantly longer outer tail-streamers and significantly less variance in outer tail-streamer length, overall body size, and outer tail-streamer asymmetry than nonsurvivors. Larger birds in general and those with less asymmetry in wing and outer tail tended to be favored. Larger size probably allows more fat to be stored and may confer thermal benefits to swallows during late-spring cold snaps. Similar mortality events apparently occurred in study area on only 1 other occasion since 1875.

Predation and parasitism. Predation can be locally important; a bobcat destroyed at least 40 nests in culverts in Kansas (Lohoefener 1978). Predation at nests is generally rare, however, and probably not a significant source of mortality (Shields and Crook 1987). Ectoparasitism by mites and blowflies is a more important cause of nest failure. Loss of nests by their falling from substrate can be frequent at times (CRB, MBB).

Competition with other species. House Sparrows can be serious nest-site competitors, apparently extirpating Barn Swallows from parts of New England in 1800s (Brewster 1906); sparrows reduced Barn Swallow fledging success by 45% at 1 site in Maryland (Weisheit and Creighton 1989). Other species that occasionally usurp nests (see Behavior: social and interspecific behavior, above) probably do not affect Barn Swallows significantly, although in Nebraska, reproductive success of Barn Swallow at sites also containing Cliff Swallows was about half that at sites without Cliff Swallows (L. Smith pers. comm.).

RANGE

Initial dispersal from natal site. Young seldom return to vicinity of their birthplace: among birds banded as nestlings, 0.44% (n = 679) in Kansas (Anthony and Ely 1976), 0.57% (n = 524) in Oklahoma (Iverson 1988), 0.0% (n = 157) in Nebraska (CRB, MBB), 1.0% (n = 1,008) in Pennsylvania (Bell 1962), 2.0% (n = 331) in New York (Shields 1984b), and 2.0% (n = 1,718) in Massachusetts (Mason 1953) returned to study area. Among 21 returns of first-year birds in Massachusetts, 20 (95%) were males, suggesting greater natal philopatry among males than among females (Mason 1953; see also Shields 1984b). One nestling banded in Kansas was recaptured 41 d later about 115 km southeast of banding site (Anthony and Ely 1976).

Fidelity to breeding site and winter home range. In Oklahoma and Massachusetts, 19.6% (n = 225) and 34.0% (n = 381) of birds banded as adults returned to study area in a subsequent year, with no significant difference between males and females in return rates (Mason 1953, Iverson 1988); comparable percentage in Kansas was 21% (n > 400; Anthony and Ely 1976), in Nebraska 12.3% (n = 300; CRB, MBB), in Pennsylvania 13% (n = 185; Bell 1962), and in New York 41.6% (n = 216; Shields 1984b). In Oklahoma, 16.6% of birds that returned to same colony site the next year (n = 12) used same nest; most returning birds stayed within same part of the highway culvert they had previously used, moving a mean 12.1 m from previous year's nest (Iverson 1988). In New York, 36% of birds returning to same colony site the next year reused the same nest; breeding-site fidelity was not influenced by adult age (Shields 1984b).

Dispersal from breeding site or colony. In Oklahoma, 87.5% of banded birds recaptured the next year (n = 40) settled at same colony site (culvert) as in the previous year; those dispersing (all females) moved an average 1.6 km from previous colony site (n = 5; Iverson 1988), although observed dispersal distances were clearly biased by size of study area monitored. No properly reported data to calculate average breeding or natal dispersal distance. Extensive data on migratory movements and dispersal of *H. r. rustica* in Eurasia are available (see, for example, Davis 1965, Zink 1969, Medway 1973).

Home range. In Pennsylvania, 96 birds were transported 16–96 km from their nests and released; 55% of birds returned to their nests (Nastase 1982). Distance and direction from nest site did not significantly affect homing ability, at least within 100 km. Studies in Europe over longer distances (up to 1,875 km) show that homing ability declines with distance from nest site; birds released up to 153 km away returned the same day, and maximum speed of return was 412 km / d (reviewed in Nastase 1982). Birds in W. Virginia foraged within 1.2 km of nest site (Samuel 1971a); those in Europe generally confine their foraging to radius of 500 m from nest site (Møller 1987a).

POPULATION STATUS

See Figure 5. Breeding Bird Survey (BBS) data show areas of greatest abundance to be s. and e. Texas, central Kansas, e. Nebraska, most of Iowa, s. Minnesota, e. South Dakota, n.-central North Dakota, e. Wisconsin, and w.-central Kentucky. BBS data show significant overall increase in U.S. from 1966 to 1994 and significant decrease in Canada during same period. Largest increases in population have been in Georgia, Alabama, Louisiana, Arkansas, Texas, New Mexico, Colorado, N. and S. Dakota, Wisconsin, Illinois, and Alberta. Significant declines have occurred in California, Oregon, Washington, Missouri, Kentucky, Tennessee, ne. U.S., and most of Canadian provinces.

POPULATION REGULATION

Although natural nest sites in caves were probably limited and may have historically regulated population size, with conversion to artificial structures there now appears to be an abundance of suitable nesting sites; local numbers of breeding pairs often remain stable even with increases in suitable nesting sites (Holroyd 1975), so population now is probably not regulated by nest-site availability. Weather-related mortality during cold snaps in spring (see Brown and Brown 1999) probably regulates population size at least in n. North America and may help define northern limit of the bird's range. In *H. r. rustica*, winter mortality is thought to be the primary factor regulating population (Møller 1989b), but there is no information on winter mortality for North American individuals.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

On balance, human activity has had strongly positive effects on this species: construction of artificial structures has provided abundant nesting sites, leading to population size that is probably several orders of magnitude greater than before European settlement of North America. Barn Swallows are popular with people, and farmers often protect (rarely persecute) the birds on their property. The species seems to have adapted well to nesting in human-altered habitats in North America and worldwide.

Shooting and trapping. Birds were hunted by humans for millinery trade in 1800s (G. Gladden in Pearson 1923), although impact on population is

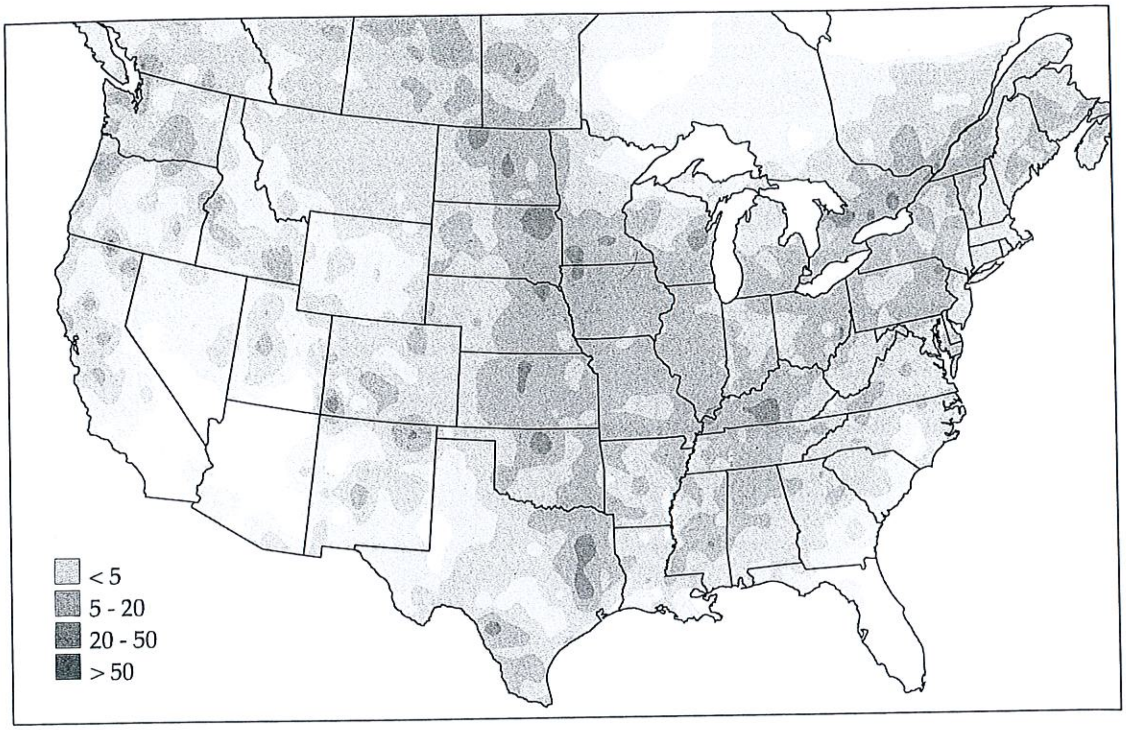

Figure 5. Relative abundance of the Barn Swallow in eastern North America, 1966–1991, based on Breeding Bird Survey data. Numbers shown are the average number of individual birds detected per route per year. Map from Price et al. 1995; used with permission.

unknown. Illegal hunting in North America now is negligible. Birds are harvested at winter roosts for food in Africa and possibly in South America and Asia.

Pesticides and other contaminants/toxics. Little information for North American race; declines of *H. r. rustica* in Israel in 1950s were attributed to pesticides (Turner 1991).

Ingestion of plastics, lead etc. Lead concentrations in carcasses, stomach contents, and feathers of adults nesting along major highway in Maryland were greater than those of birds nesting in rural areas away from highway, but there were no differences in clutch size or reproductive success near to versus far from highway (Grue et al. 1984). Lead contamination from automotive emissions is probably not a serious hazard to aerial foragers like Barn Swallows.

Collisions with stationary/moving structures or objects. Birds sometimes become tangled in fishing line or horsehair that is gathered to line nest (Knight 1980, Bartel 1985). Usually do not hit buildings or TV towers during migration. Proximity of nests on bridges and culverts to automobile traffic means that adults and juveniles are sometimes hit by passing cars.

Degradation of habitat. Use of vinyl and metal siding on buildings has reduced nesting sites in some areas (Erskine 1992), but in other areas widespread construction of concrete bridges and culverts has apparently led to major population increases and range expansion (Jackson and Burchfield 1975). Conversion to modern buildings and farming practices was cited as reason for Barn Swallow declines early in twentieth century in New England, where nesting sites were altered in ways that made them less suitable (Forbush 1929). With more bridges and culverts, however, there has been net gain in nesting sites within last 50–60 yr.

Disturbance at nest and roost sites. Nests on human buildings are sometimes considered a nuisance and removed, but most people encourage nesting. Fall and winter roosts tend to be located in marshes and other sites away from people, so birds are not subject to same kind of harassment at roosts as swallows that roost in cities.

Direct human/research impacts. Repeated banding activities at colony sites seem to have no impact on reproductive success (Iverson 1988). Birds become wary with repeated netting and visits to nests, however, and can be difficult to study (L. Smith pers. comm., CRB).

MANAGEMENT

Conservation status. Not considered endangered or threatened anywhere.

Measures proposed and taken. All measures in North America are very local in scope. Farmers in some areas nail narrow wooden ledges to walls or under eaves to give birds support for their nests. Birds can sometimes be enticed to relocate their nests to more desirable sites if intact nest with nestlings is moved slowly and then reattached (Winkler and McCarty 1990, CRB, MBB). Adults will continue nesting at the new site. Massive effort by 2,250 people during autumn swallow kill in Europe in 1974 rescued, fed, and then transported by air, train, and car approximately 500,000 migrating swallows (many Barn Swallows) and swifts to destinations south of Alps (Bruderer 1975).

Effectiveness of measures. Attempts to improve stability of nests and to relocate nests (see above) are usually successful. About 75% of swallows rescued in the 1974 kill survived to be released (Bruderer 1975).

APPEARANCE

MOLTS AND PLUMAGES

Molt in North American race (Pyle 1997) is similar to that of the better-studied *H. r. rustica*. European birds have single annual molt, starting in autumn just before or immediately after migra-tion, and continuing 4.5–6 mo (Møller 1994a). Some birds are completing molt on their return to breeding grounds in spring. Body- and wing-feathers are replaced first, tail-feathers last (Broekhuysen and Brown 1963, Møller 1994a). Juveniles begin molt of feathers on forehead well before migration but take longer than adults to complete molt of other feathers (Broekhuysen and Brown 1963, Møller 1994a). For North American race, flight feathers are replaced in Oct–Feb for birds ≥1 yr old and Nov–Apr for juveniles (Pyle 1997).

Hatchlings. See Breeding: young birds, above.

Juvenal plumage. From Oberholser 1974. Sexes similar. For timing and sequence of Prejuvenal molt, see Breeding: young birds, above. Similar in general appearance to Definitive Basic plumage (see below), but tail very slightly forked; colors much duller; crown and nape fuscous black or chaetura black, with faint metallic greenish sheen; remainder of upperparts much duller and sheen more greenish; upperwing-coverts edged with reddish brown; forehead brownish buff or fawn color; chin and throat vinaceous cinnamon; blackish breast-band mixed with vinaceous cinnamon; light spots of tail smaller than those of adult and strongly tinged with buff.

Basic I plumage. Prebasic I molt complete. Molt occurs primarily after species has departed North America (Oct–Apr) but may begin on forehead well before migration; flight feathers replaced Nov–Apr (Broekhuysen and Brown 1963, Møller 1994a, Pyle 1997).

Basic I plumage similar to Definitive Basic plumage for each sex, but tail shorter (outermost rectrices [R6] project only 14–21 mm beyond central pair [R1] on closed tail; Pyle 1997) and tail-spots tinged with pinkish buff (both sexes), and forehead paler (female).

Definitive Basic plumage. From Oberholser 1974. Definitive Prebasic molt complete; occurs primarily after species has departed North America (Aug–Feb), but may begin on breeding grounds; flight feathers replaced Oct–Feb (Pyle 1997).

MALE. Forehead chestnut; remainder of upperparts metallic indigo blue to slightly purplish blue; wings chaetura black to chaetura drab or fuscous on inner webs, exposed surface with metallic green sheen, except lesser-coverts, which are similar to back (no reddish-brown edgings); tail deeply forked, outermost rectrices (R6) projecting 35–53 mm beyond central pair (R1) on closed tail (Pyle 1997); rectrices chaetura black, glossed with metallic green, all feathers except middle pair with conspicuous large white or buffy white spot on inner web, largest and oblong on outer pair; lores and cheeks fuscous or fuscous black; sides of neck like crown; chin and throat chestnut to cinnamon rufous, separated from remainder of underparts by incomplete breast-band of dull metallic blue or greenish feathers; remainder of underparts, including wing-lining, varies from chestnut to pale pinkish buff.

FEMALE. Similar to male, but tail less deeply forked, outermost rectrices (R6) projecting 26–38 mm beyond central pair (R1) on closed tail (Pyle 1997); upperparts slightly more greenish, and underparts on average paler.

Aberrant plumages. Albinism, partial albinism, and leucism occur uncommonly in Barn Swallows under natural conditions (Withgott and McMahon 1993); incidence of partial albinism increased significantly among birds exposed to radioactivity release at Chernobyl, Ukraine (Ellegren et al. 1997).

BARE PARTS

Bill and gape. Bill black or slate black. Gape dull pinkish.

Iris. Dark brown to black.

Legs and feet. Reddish brown in juvenile; clove brown, seal brown, or light seal brown in adult (Oberholser 1974).

MEASUREMENTS

LINEAR

Bill length. In Nebraska, mean for males 6.9 mm ± 0.3 SD (n = 16); for females, 7.1 mm ± 0.3 SD (n = 28; CRB, MBB).

Bill width. In Nebraska, mean for males 5.5 mm ± 0.4 SD ($n = 16$); for females, 5.6 mm ± 0.3 SD ($n = 28$; CRB, MBB).

Wing length. In W. Virginia (Samuel 1971b), mean across both sexes 119.5 mm ± 1.7 SD ($n = 91$); in Nebraska (CRB, MBB), mean for males 116.2 mm ± 3.3 SD ($n = 16$); for females, 113.9 mm ± 2.7 SD ($n = 29$).

Outer tail length. From Patterson 1981, except data for Nebraska. In Canada and Alaska, mean for males 88.3 mm ± 6.3 SD ($n = 18$), for females 78.4 mm ± 5.5 SD ($n = 18$); from 42°N to Canadian border, for males 88.0 mm ± 6.0 SD ($n = 41$), for females 77.2 mm ± 5.3 SD ($n = 24$); from 37 to 42°N, for males 86.3 mm ± 6.4 SD ($n = 54$), for females 74.4 mm ± 4.4 SD ($n = 39$); in Maryland, for males 85.5 mm ± 5.4 SD ($n = 73$), for females 73.2 mm ± 4.6 SD ($n = 63$); in Nebraska, for males 84.6 mm ± 11.6 SD ($n = 16$), for females 73.4 mm ± 12.0 SD ($n = 29$; CRB, MBB); from Mexican border to 37°N, for males 82.9 mm ± 6.2 SD ($n = 38$), for females 73.2 mm ± 4.3 SD ($n = 11$); in Mexico, for males 79.2 mm ± 1.9 SD ($n = 9$), for females 73.0 mm ($n = 2$).

Middle tail length. In Nebraska, mean for males 42.9 mm ± 2.4 SD ($n = 16$); for females, 42.3 mm ± 1.8 SD ($n = 29$; CRB, MBB).

Tarsus length. In Nebraska, mean for males 9.9 mm ± 0.5 SD ($n = 16$); for females, 9.7 mm ± 0.5 SD ($n = 29$; CRB, MBB).

MASS

In Nebraska across entire breeding season, mean for males 18.1 g ± 1.1 SD ($n = 106$); for females, 19.2 g ± 1.5 SD ($n = 130$).

PRIORITIES FOR FUTURE RESEARCH

Major priorities should be to resolve the systematics of the *Hirundo rustica* group and its sister species from Africa, Asia, and Australia. We need additional genetic analyses to determine how divergent the North American Barn Swallow is from the nominate race of Europe and the Siberian subspecies. There are clear differences in morphology and behavior between North American and Eurasian birds, and the significance of these differences is unknown. For example, incubation by males in North America is thought to influence the evolution of ornamental traits (the length of outer tail-streamers) and the development of mixed reproductive strategies such as extra-pair copulation. Further work is needed to determine whether male incubation indeed constrains sexual selection in these ways. Why does intraspecific brood parasitism apparently occur commonly in Europe but rarely or not at all in North America? The extensive work on sexual selection and mate choice in European birds has hardly been repeated in North America, and it is not clear that the same mechanisms of sexual selection necessarily operate in the North American race. North American investigators should capitalize on the suitability of the Barn Swallow for studies of sexual selection.

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