

Range expansion of the House Sparrow through Guatemala and El Salvador



House Sparrow (*Passer domesticus*). Photo/Allan D. Cruickshank/VIREO.

The hardy, adaptable *Passer domesticus* appears to be at home anywhere—from Manitoba through Central America.

Walter A. Thurber

ANYONE WHO HAS EVEN CASUALLY studied the House Sparrow (*Passer domesticus*) recognizes its capability for rapid range expansion. Bent (1958) provides the best documented account of the introduction and early spread of the species in the United

States; Robbins (1973) summarizes the spread and distribution in North America as of 1970. This species was introduced into eastern cities of the United States in the 1850s and 1860s and by 1886 it was broadly established east of the Mississippi River. By 1910,

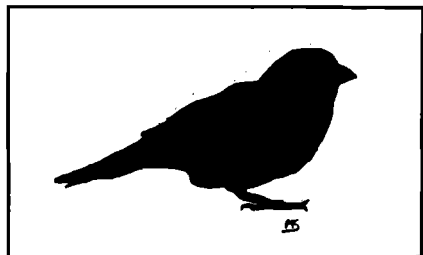
it was nearly everywhere in the States. By 1969, it had reached southern Canada and northern Mexico.

By comparison, the history of the House Sparrow in South America is less detailed. It was introduced in widely separated sites and few people kept rec-

ords of first appearances. Range expansion has continued since Summers-Smith (1963) first summarized the data from about 1960 on. The species was introduced at Buenos Aires in 1870 (Boucher and Bedano 1976), spreading rapidly throughout Argentina (Ulrog 1959). It reached Uruguay in 1900, colonizing it completely (Gore and Gepp 1978), and then moved up the Paraguay River (Smith 1973) into Mato Grosso, Brazil, where it was reported in 1952 (Sick 1959). Birds of the same origin went westward across Paraguay into southern Bolivia, appearing in La Paz in the 1950s (Summers-Smith 1963). A transplantation to Punta Arenas, Tierra del Fuego, in 1918, initiated a colony that spread to Ushuaia at the southern tip of the continent by 1957 (Humphrey *et al.* 1970). In 1904, House Sparrows were liberated in Santiago, Chile; they spread over the entire country (Johnson 1965), crossing into Peru in 1951 (Koepke 1964), and proceeded up the coast to Lima where they were reported in 1953 (Summers-Smith 1963).

An introduction at Rio de Janeiro in 1904, and another in Rio Grande do Sul in 1910, led to widespread colonization of southeastern Brazil, including the capital, Brazilia, where the species appeared in 1959 (Smith 1973). For a time it seemed that the hot, humid climate of the Amazon might be a barrier, but Smith (1973) found a flourishing colony at Maraba, Para. He suggested that the birds arrived *via* the new highway from Brazilia and that they might continue along the Transamazon Highway westward.

The demonstrated adaptability of House Sparrows indicates that the species will eventually inhabit most of the Western Hemisphere. When we first saw House Sparrows in western Guatemala (Thurber 1972), we did not doubt that their advance would continue through Central America. This presented an opportunity to trace the progress of the species and study its adaptations to new conditions. After some detailed study, the political situation



prevented further field work. But what we learned gave tantalizing glimpses of the species in a new environment.

SOURCES

Many early records of House Sparrows in Central America were provided for this study by knowledgeable birders who noted the species. Our own experience with House Sparrows in Guatemala were those of a traveling birder visiting a wide range of localities; but, in El Salvador, weekends from 1966 to 1969 were spent mapping species distribution, and from 1969 through 1979 a major portion of time was spent in the field. In 1977, along with 13 Salvadorans, an organized town-by-town census of El Salvador's House Sparrows was made. In 1978 and 1979, follow-ups were done with brief trips to check colony development and range expansion; other members of the team continued to add information.

From 1977 through 1979, visits to a few nesting colonies continued for additional data. The Christmas Bird Count (hereafter, CBCs) issues of *American Birds* from 1974 on include a site in Guatemala. The results of the CBCs clearly show the population build-up through the early years following invasion.

Prepared skins, skeletal and spirit material for possible future study of phenotypic changes has been deposited at the American Museum of Natural History.

INVASION AND COLONIZATION

Range expansion in Guatemala. House Sparrows were first recorded for this country May 1, 1970, at Quezaltenango (2350 meters elevation), (Thurber 1972). On January 15, 1971, Alden (*in litt.* 1977) observed 10 at Chichicastenango, Quiché (1800 meters). In 1972, Ewert (*in litt.* 1973) noted House Sparrows as follows: March 31, a pair in Guatemala City (1480 meters); April 2, several at Chichicastenango; April 3, common at Quezaltenango. From 1972 on, Leahy (*in litt.* 1978, 1980) saw the species in "all towns of any size" in the western highlands and in many lowland towns, considering them common to abundant. Leahy observed House Sparrows in 1972 at Lake

Atitlán, Sololá (1564 meters) Christmas Bird Counts at the lake show colony growth: 8 in 1974; 30 in 1975; 50 in 1976; 42 in 1977; 100 in 1978 (Hollinrake 1975; Brose 1976-1979). Leahy recorded the species on the Pacific slope 1975 at Esquintla (347 meters); 1979 at the nearby towns of Democracia and Taxisco; 1979 at Mazatenango, Suchitepequez; he noted the species in 1978 in El Petén at Flores (115 meters) and two nearby towns.

After the first sightings in Guatemala City in 1972, reports were frequent. Villeda (*pers. comm.*) noted the species in several parts of the city in 1974; it is now widespread and common there (*pers. obs.*). Villeda saw House Sparrows at Cabañas, Zacapa (280 meters), in August 1974, and learned that they were new arrivals. In early 1976, we found them abundant at Cabañas and present in nearby Zacapa.

We believe that the invasion of Guatemala began not long before 1970. Many sections of Guatemala were visited for several years without seeing the species. House Sparrows were not noted during the 1960s by Land (1970) or by Ibarra (*pers. comm.*). In 1969, the range of *P. domesticus* was not reported in the southern states of Mexico (Robbins 1973), except for an outlier at Tuxtla Gutierrez, Chiapas, where a small flock appeared in 1950 (M. Alvarez del Toro 1950; *in litt.* 1977).

Range expansion through El Salvador. Monroe (*in litt.* 1976) observed two males at La Herradura, La Paz (5 meters) January 7, 1972. Strauch (*in litt.* 1974) saw "about a dozen" on the outskirts of San Miguel (100 meters) May 14-15, 1973. On July 22, 1973, we found a flourishing colony of 35± birds and 11 active nests at San Marcos Lempa, Usulután (90 meters); local people had captured birds for sale during the preceding rainy season between May and September 1972. Hamel (*in litt.* 1976) saw a pair in the central plaza of Usulután (100 meters) June 24, 1974, and others (*pers. comm.*) at La Unión (5 meters), July 19-20, 1974. Airey (*pers. comm.*) found House Sparrows at San Francisco Gotera, Morazán (200 meters), in May 1975.

The House Sparrow census of 1977, described below, showed the species broadly but not uniformly distributed with major exceptions in the highland areas. Certain early colonies had doubled or tripled, and a few had multiplied

Table 1. Growth of House Sparrow colonies in El Salvador following first years reported.

Locality	First record	Status in 1977
La Herradura, La Paz	2 (1972) ¹	10± ²
San Miguel, San Miguel	12± (1973) ¹	99 est., 3 colonies, 9 nests
San Marcos Lempa, bridge Usulután	25-50 (1973) 11 nests	75 counted, 15 nests
Usulután, Usulután	2 (1974) ¹	250 est., 4 colonies, 62 tests
La Unión, La Unión	"some" (1974)	40 est., 2 colonies, 7 nests
San Francisco Gotera, Morazán	"several" (1976)	22 est., 2 colonies, 1 nest

¹ no effort made to determine actual population.

² heavily wooded conditions at La Herradura made counts difficult.

into three or four colonies (Table 1). There were unexpected gaps along possible invasion routes, some of which filled in during the following two years, notably at San Salvador (650 meters), where by 1980, small bands were seen in several parts of the city.

We doubt that House Sparrows were present in El Salvador much before the first sightings. During the preceding five years we had been mapping species distributions throughout the regions where the first colonies were found. Note also the pattern for both Guatemala and El Salvador, no records until suddenly a spate of sightings for a fairly large geographic area, as though the birds had moved in like a wave of migrants.

Range expansion beyond El Salvador. Stiles (*in litt.* 1977) reported that in Costa Rica, House Sparrows were present "in flocks" on the Central Plateau in February-March 1974, and were well-established in Guanacaste Province in early 1975; by 1977, the species was present in most major cities and towns of the northwestern and central parts of the country but had not arrived on the Caribbean slope.

The late E. Eisenmann (*in litt.* 1980) summarized recent records for Panama. The earliest record is in 1975, in David, Chiriquí. The species was also seen in Panama City in 1979.

Rate of range expansion. The first records for House Sparrows in Guatemala and El Salvador, respectively, span an interval of less than two years at sites some 360 kilometers (220 miles) apart. Thus the rate of advance may have been 180 kilometers/year (110 miles/year); less if the birds arrived in Guatemala before 1970. If the birds were in Guatemala in 1968, the rate would have been about 90 kilometers/year (55 miles/year). The higher rate is more consistent with the rate from El Salva-

dor to Costa Rica, 600 kilometers in two years (275 miles/two years), and the average rate for all of Central America, which may range from 160 kilometers/year to 240 kilometers/year. Smith (1973) noted an advance in Brazil of 800 kilometers in six years (500 miles/six years) from Brazilia to Maraba.

Robbins estimated a radial spread of *P. domesticus* from coastal cities of North America at about 8 kilometers/year (5 miles/year) during the early years. Judging from his maps, the rate did not change greatly during the spread of the species across North America and southward through Mexico. By comparison, the rate through Central America has been spectacular.

Topography's influence on range expansion. In North America, House Sparrows dispersed radially from sites of introduction, merging in a broad front across the continent relatively unhampered until they reached the Rocky Mountains. But in Chiapas, Guatemala, and El Salvador, the birds were channeled between the Pacific Ocean and inland mountains; the front was only 60-125 kilometers wide. Robbins (1973) estimated a radial spread from coastal cities as 160 kilometers in 15 years; the semicircular area thus colonized was about 40,000 km², a rate of about 2500 km²/year. In Central America, assuming a frontal width of 100 kilometers and a minimum speed of 90 km/year, the rate of colonization would be about 9000 km²/year or more.

Another factor to be considered as affecting the rate of expansion is the density of suitable colonization sites. Generally the density of sites in Central America is high.

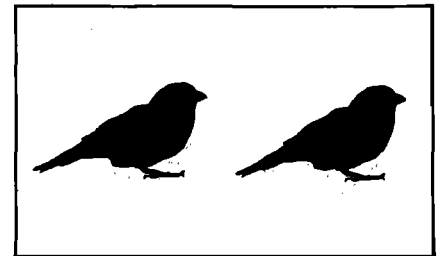
Introduction, deliberate or accidental, of House Sparrows into new areas is another factor. Deliberate introduction was important in the early spread

of the species across the United States (Robbins 1973) and South America (Summers-Smith 1963). Caged birds, often miles from their origins, are common in Central American markets. Escaped or released birds might form the nucleus for a local colony. Perhaps the colony at Tuxtla Gutierrez, Chiapas, first noted in 1950, far south of the main wave, was founded by escapees.

Results of the 1977 census. We surveyed 86 "municipios" of the 261 listed in the official registry of El Salvador (Fig. 1); those not visited were hamlets, most accessible only by 4-wheel drive vehicles. We found 35 colonies of House Sparrows in 26 towns (Table 2). The total counted for the country was 499, with an estimated population of 1100 birds.

The total of our counts underestimates the actual population because: 1) not all towns were visited; 2) we may have missed colonies in the larger towns; 3) we did not look for colonies outside town limits; 4) some colonies were visited during hot midday hours when birds are less active; 5) foraging birds may have been outside their colonies; 6) incubating and brooding birds may have been missed. We returned to four colonies for comparison counts, our estimates were about the same, but actual leisurely counts were higher. Taking into consideration these factors, we believe that the population of the areas studied was no fewer than the estimate of 1100 birds, and was 1500+ for the entire country.

Distribution in El Salvador in 1977. The eastern lowlands, sea level up to 300 meters, provided *P. domesticus* with conditions satisfactory for rapid and widespread colonization; nearly all colonies, including the largest, were found there. We had no reports of colonies in the northern highlands. The western half of the country, topographically diverse, was spottily colonized at four well-separated sites; House Sparrows were unaccountably absent from



EL SALVADOR

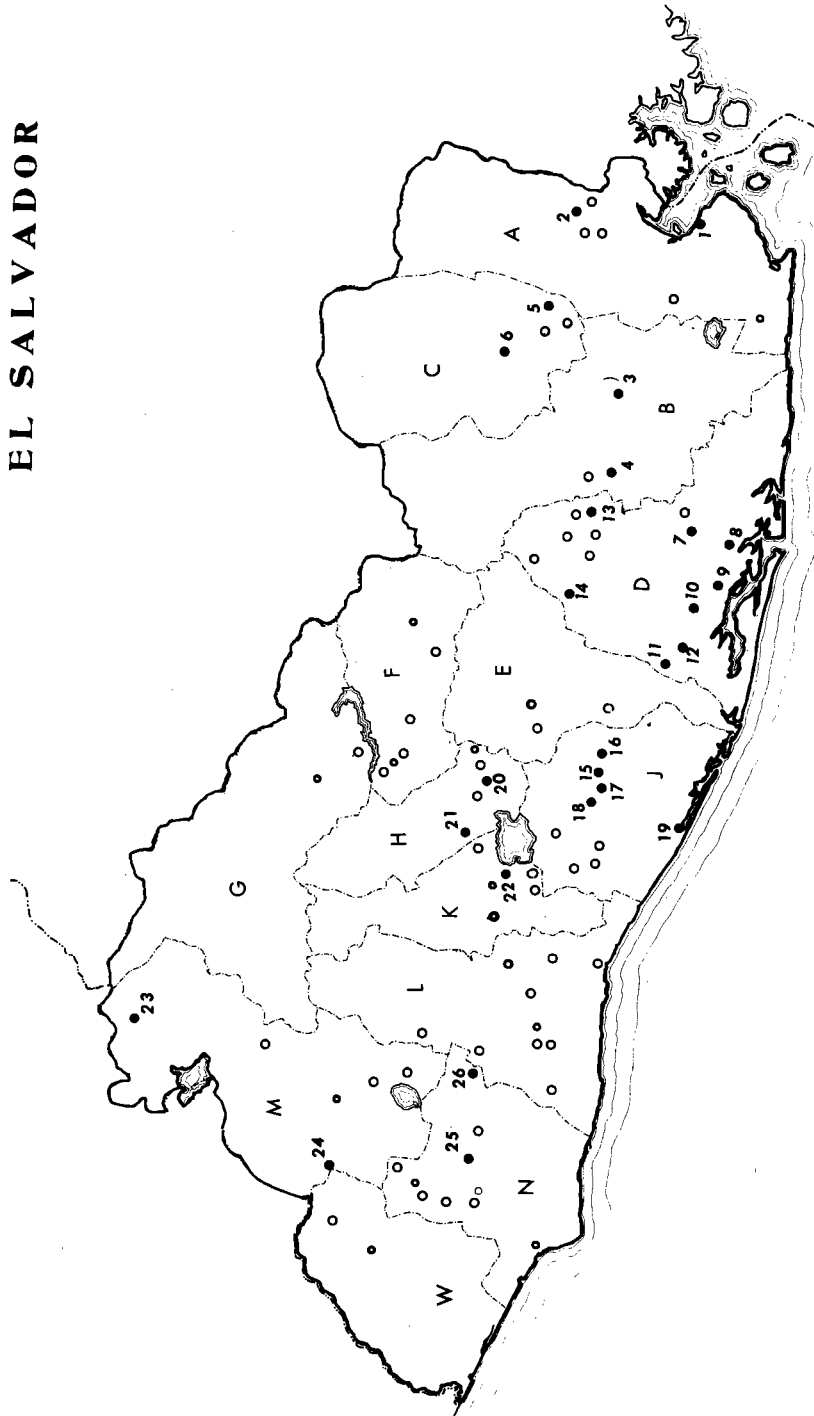


Figure 1. Locations of towns surveyed during the 1977 census of House Sparrows in El Salvador. **Solid circles:** House Sparrow colonies. **Open circles:** no House Sparrows seen. **Capital letters:** names of departments. A) La Unión; B) San Miguel; C) Morazán; D) Usulután; E) San Vicente; F) Cabañas; G) Chalatenango; H) Cuscatlán; J) La Paz; K) San Salvador; L) La Libertad; M) Santa Ana; N) Sonsonate; W) Ahuachapán. **Numbers:** names of towns having House Sparrow colonies. 1) La Unión; 2) Santa Rosa de Lima; 3) San Miguel; 4) Chinameca; 5) Jocoro; 6) San Francisco Gotera; 7) Usulután; 8) Puerto Parada; 9) Puerto Triunfo; 10) Jiquilisco; 11) San Marcos Lempa; 12) Tierra Blanca; 13) Jacuapa; 14) Puente Cuscatlán; 15) Zacatecoluca; 16) San Juan Nonualco; 17) San Rafael Obrajuelo; 18) Santiago Nonualco; 19) La Herradura; 20) Cojutepeque; 21) Perulapúa; 22) Ilopango; 23) Metapán; 24) Chalchuapa; 25) Izalco; 26) Armenia

Table 2. Populations and nests of House Sparrows recorded during the 1977 census of this species in 86 municipios of El Salvador.

<i>Department and municipio</i>	<i>Population</i>	<i>Nests found</i>
La Unión, La Unión	16 (40)*	7
Santa Rosa de Lima	6 (15)	1
San Miguel, San Miguel	36 (100)	9
Chinameca	2 (2)	0
Morazán, Jocoro	10 (25)	5
San Francisco Gotera	12 (20)	1
Usulután, Usulután	152 (220)	62
Puerto Parada	6 (20)	0
Puerto Triunfo	7 (15)	0
Jiquilisco	31 (110)	18
San Marcos Lempa	75 (110)	25
Tierra Blanca	8 (10)	0
Jucuapa	9 (20)	0
Puente Cuscatlán	1 (2)	0
La Paz, Zacatecoluca	— (26)	7
San Juan Nonualco	8 (25)	1
San Rafael Obrajuelo	6 (15)	0
Santiago Nonualco	— (25)	0
La Herradura	10	0
Cuscatlán, Cojutepeque	4 (10)	0
Perulapia	14 (25)	1
San Salvador, Ilopango	25 (60)	0
Santa Ana, Metapán	15 (25)	0
Chalchuapa	12 (15)	2
Sonsonate, Izalco	14 (20)	0
Armenia	20 (40)	1

* Numbers outside parentheses are actual counts; numbers in parentheses are estimates.

the coastal strip and inland hills. Superficial acquaintance with population centers does not suggest differences that explain such discontinuous distribution.

Invasion patterns in El Salvador. During the 1977 census we tried to identify a town-by-town invasion route from Guatemala. There are three reasonable routes: 1) along the coast from Esquintla through a region of large haciendas and few towns; 2) along the Panamerican Highway with its many towns from Guatemala City through the western hill region; 3) from Zacapa through a pass in the northern cordillera. The census teams checked the towns along these routes with special care, some were double checked. We found no House Sparrows in Acajutla, Sonsonate or La Libertad along the coastal route. We found one small colony at Chalchuapa along the Panamerican Highway. We found a colony at Metapán on the route from Zacapa, but it is unlikely that this was the source of the eastern populations unless House Sparrows had been present in the Zacapa region long before the 1974 report.

An hypothesis that explains the discontinuous colonization suggests that the earliest colonies derived from captive birds. This is not unreasonable

considering the size of the wild bird trade, but requires the almost simultaneous liberation of captive birds in several well-separated places.

A third hypothesis proposes that House Sparrow colonies built up to insupportable levels. Excess birds, especially immatures which show little attachment to natal sites (North 1973), tended to disperse and were carried away by the long-lasting, violent wind storms that frequently lash the region. Occasionally a pair arrived at a favorable site far from the source.

Colony growth. Table 1 presents data on the growth of the earliest colonies. The earliest data was obtained in passing except at San Marcos Lempa where we spent more time on successive days. A pattern of colony growth and dispersion can be inferred from the data for Usulután. In June 1974, Hamel observed a pair of House Sparrows in the central plaza. In May 1977, the census team counted 52 birds (100 estimated) and 29 active nests in the plaza. We found another colony at 84 birds (120 estimated) and 32 nests in a cemetery at the western edge of the city. Two kilometers west of the city we found a colony of 16 birds and one nest. A month later we found a colony of 6–8

birds and one nest on the eastern edge of the city. In 1978, we saw a small flock but no nests. Seemingly the original colony expanded until the carrying capacity of the plaza was reached. At least one pair left and found suitable conditions in the cemetery. Excess birds from this and/or the mother colony colonized adjoining sites. Multiple colonies in other towns may have been established in the same way.

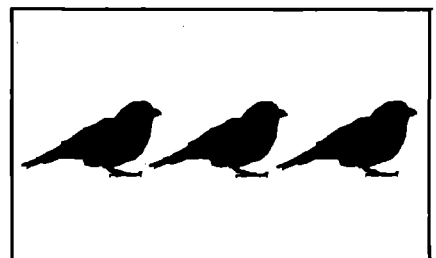
Changes in El Salvador after 1977.

Scattered reports show that House Sparrows continued to multiply and colonize new areas. Most reports are for San Salvador for which we had no records through 1977. In December 1978, Andino (*pers. comm.*) reported House Sparrows in a small plaza near the city center; Villeda (*pers. comm.*) verified the report January 29, 1979, finding eight birds in this barren and busy plaza. Villeda also observed a pair in the eastern part of the city May 24, 1979. In December 1979, Wall (*pers. comm.*) saw 4–5 birds at the Ilopango airport, and in January 1980, 10–12 in Colonia San Cristóbal, a suburb near the airport.

On August 3, 1979, we saw 5–10 House Sparrows at Usulután but found no nests.

We traveled the Panamerican Highway from San Salvador to the Guatemalan border February 29, 1979. At Chalchuapa, where 12–15 birds and one nest were seen June 25, 1977, we now saw 50 birds (estimated) and 10 nests. At Ahuachapán, where no birds were seen in 1977, we saw five birds but no nests. At Santa Ana, we saw one male and heard one other bird in the central plaza, but found none in other parts of the city.

Habitats colonized. Thus far, records of *P. domesticus* in Guatemala and El Salvador are confined to populated places. Alvarez del Toro (*in litt.* 1977) emphasized the same for Chiapas, Mexico. Within towns and cities most colonies have been found in the central plazas. Spanish American towns were



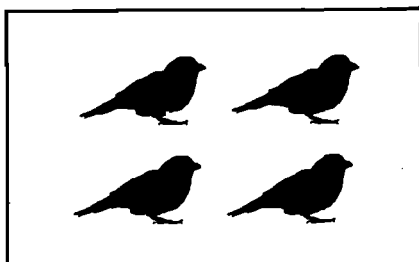
laid out on a rectangular grid with four or more blocks left at the center for a plaza. Buildings outside the plaza abutted the streets closely, leaving little space for grass and trees. The central plaza usually became a small park, with either just a few palms or fully developed with ornamental plantings and crisscrossing walks. As a town grew, secondary plazas might be left by churches, and open spaces were provided at schools, clubs and cemeteries. One feature common to all, and this is important to House Sparrows, was the presence of benches where people congregate and eat at all hours. Typically discards are thrown on the ground. House Sparrows have an unending supply of food, though rarely plentiful. The scavenged food is supplemented with seeds and insects gleaned from grassy and/or weedy plots.

Within the plazas House Sparrows face little competition except from the ubiquitous starving dogs ready to snatch up any crumb, and in some plazas from a few Rock Doves (*Columba livia*). Predation is limited, mostly to boys with slingshots. Nesting sites are plentiful: palms, Casuarinas (*Casuarina equisetifolia*), bell and clock towers, niches in church walls. But strictly residential areas have little to offer House Sparrows.

Colony sites outside the plazas have similar features. The cemetery at Usulután has a row of Casuarinas with benches; Usulután serves snacks in its patio beneath Casuarinas; San Marcos Lempa has a bridge adjacent to a strip of roadside markets where transients refresh themselves. The port towns of La Herradura, Puerto Parada, and Puerto Triunfo have no plazas but people congregate and eat at the docks to wait for the tides.

ADAPTATIONS IN REPRODUCTIVE BEHAVIOR

Nest sites and nests. Most of the nests seen were in Casuarina trees, the close-



set, rough twigs firmly anchor the loosely compacted nests of House Sparrows. Palms probably serve as nesting sites more often than records indicate; nests are rarely visible in the elevated, compact crowns although nesting can be inferred when birds bring nesting materials and food. Villeda (*pers. comm.*) saw extensive nesting activity in a grove of Coconut Palms (*Cocos nucifera*) at Cabañas, Guatemala. Of man-made structures, churches with clock and bell towers were most notable: nests were built on cross members beneath the roofs; in niches in the walls of old churches; under traditional curved roofing tiles that leave arched spaces at the eaves; within arched spaces between corrugated asbestos roofing sheets and the side walls. Nests were also found on roof trusses and beams and in cavities in walls of buildings. A few were found in natural cavities and woodpecker holes in tree trunks. Hangers supporting the cables of the suspension bridge at San Marcos Lempa provided sites for many nests.

Of the 60± nests examined, most were loosely compacted masses of straws with a few fine twigs, occasional plant fibers and bits of string. The chambers within were always lined with chicken feathers. Nests not constrained

by their supports were globular, 25 to 35 centimeters in diameter.

Nesting phenology. Figure 2 provides a monthly summary of data on reproductive activity of House Sparrows in El Salvador. Visits to the lowlands were infrequent in December and January. Data then are scant. Approximate egg-laying dates were obtained by extrapolation, assuming that sparrow development in El Salvador proceeds as in New York State: 12 days for incubation (Weaver (1943); 15 days as nestlings, and 4–6 weeks between fledging and full molt (Weaver 1942). The data for Chalchuapa (600 meters elevation) are separated from data obtained near sea level although there is no firm evidence that altitude affects breeding schedules. Meteorological Service tables show that the rainy season in the lowlands begins slightly later, produces more rain, and lasts a month longer than at Chalchuapa, and that average monthly temperatures are about 6° higher.

Molting juveniles of May 27, probably hatched from eggs laid about the beginning of March. Juveniles seen April 26, indicated nesting as early as late February. Non-molting juveniles from October 26, indicated nesting in September, possibly earlier. A sexually

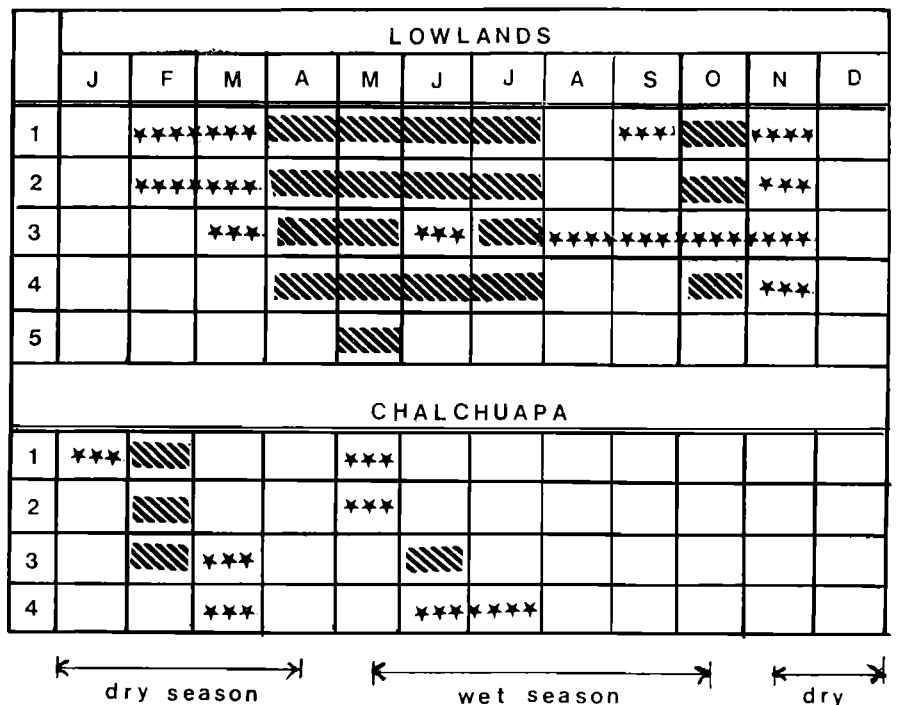


Figure 2. Phenology of reproductive activities of *Passer domesticus* in El Salvador: lowlands, 0–100 meters elevation; Chalchuapa, 600 meters elevation 1) nest building and/or copulation, 2) eggs and/or incubation; 3) nestlings and/or food delivery at nest; 4) juveniles and/or feeding of fledglings; 5) juveniles in molt. Bars: observed activities; stars: activities inferred by extrapolations from dates of observed activities.

active female with eggs ready to lay was examined October 26; she might have nested in early November and fed nestlings in mid-November, possibly later.

On May 27, we examined two sexually active females in juvenal plumage, one with an incompletely ossified skull (Stage B, *North American Bird Banding Manual*, 1977). Extrapolation to their hatching dates is complicated because nesting interrupts or defers molting in some species, and possibly affects skull ossification. Assuming no interruptions, these females could have come from eggs laid between February and April; otherwise they might have been six months older, hatched from eggs laid between November and February.

Feeding of nestlings was noted at Chalchuapa June 25; nest building, incubation, and feeding of nestlings in February. The nesting season there thus extends from January at least through June.

In Guatemala, Villeda (*pers. comm.*) saw House Sparrows carrying nesting materials and food at Cabañas in mid-June and the beginning of November. We observed nest building May 1, at Quezaltenango.

In Costa Rica, Fleischer (1982) saw House Sparrows feeding fledglings February 17; extrapolation puts egg-laying dates in mid-January or earlier. He cites a personal communication from Stiles that House Sparrows nest in San José through October and may nest year-round.

This evidence suggests year-round breeding of *P. domesticus* in Central America, which is not especially surprising if we consider that nestlings are reported every month in North America, including winter months (Cottam 1929; Snow 1955; Wessels 1976). But in North America, the cycle of reproduction of *P. domesticus* is generally linked with the photoperiod (Burger 1949). Day length in Central America changes so slightly that it is possible that the reproductive cycle is free-running. Only color-banding studies can answer the many intriguing questions raised.

Clutch size. Table 3 gives data for 22 nests. Clutches with one egg may have been incomplete. A nest with two eggs and a hatchling is included with eight nests having three eggs each. Two nests each containing very young nestlings were probable 3-egg clutches. Nine nests with two older nestlings each may have lost third nestlings. Relevant to this dis-

Table 3. Numbers of eggs and/or nestlings in 22 House Sparrow nests found in the lowlands of El Salvador 1977.

Number/nest	1	2	3
Eggs	2	0	9 ¹
Nestlings	0	9	2 ²

¹ includes 1 nest with 2 eggs and 1 hatchling.

² nestlings were 1-3 days old.

cussion was a female with one ovum in her oviduct and two almost ready to enter, and another with three ova of three, two plus, and two millimeters respectively.

The limited evidence suggested a clutch size of three for *P. domesticus* in El Salvador, smaller than the 4-5 reported for more northern latitudes. Latitude seems to be a constraint on clutch size in many species (Skutch 1976). Cody (1971) plotted clutch size vs latitude for genera present in both temperate and tropical zones; interpolation for 13°N on his curves predicts a clutch size of two plus for El Salvador. Murphy (1978) plotted clutch size of House Sparrows vs latitude between 35°N and 51°N; extrapolation for 13°N on his plot predicts a clutch size of 3.5 for El Salvador.

In Costa Rica, Fleischer (1982) obtained data on seven nests: one with one egg (possibly an incomplete clutch); one with one nestling about to fledge; three with two eggs (one nest judged with a complete clutch because nestlings were being fed 10 days later); one with two nestlings (ages not given); one with three eggs. He also found a "dump" nest with 10 eggs and an incubating female, a rarity. Assuming all clutches complete and ignoring the dump nest, Fleischer's nests average slightly fewer than two eggs/nest, an absolute minimum that does not consider possible incomplete clutches or nestling fatalities. Extrapolation from Murphy's (1978) plot predicts a clutch size of 3.3 for Costa Rica.

It has been proposed that latitude operates on clutch size through day length. Lack suggests that shorter daylight hours (11-13 in El Salvador, 15+ during the breeding season in North America), reduces the time available for obtaining adequate food for large clutches. Ashmole (1963) proposes that in higher latitudes there are flushes of available food during the summers. The presence of runts and probable runt mortality in El Salvador suggest insufficient food or insufficient time for food gathering, but three prelaying females

were extremely fat, suggesting adequate supplies of food for egg production.

Nestlings and nestling success. Table 4 gives data on nine nestlings from four nests, plus two siblings that were photographed but not measured, and a trio of nestlings that were hurriedly examined. These last showed differences in size and development similar to the first trio in the table.

The smallest of three siblings in each of two nests was about one-half the size of its nest mates and seemed very weak. These runts (barely able to sit up) could not compete vigorously with their siblings. Incubation might have begun before the third eggs were laid. Murphy (1978) noted 26 cases of incubation before completion of clutches, although he believed that the initial disadvantage of late hatching was compensated for by other factors. However, in the instances described for El Salvador, the runts seem to be increasingly disadvantaged, perhaps because the diet was inadequate in quantity and/or quality.

The nestlings in four broods of two were estimated at about 2, 4, 8+, and 8+ days old, respectively. In each duo, one nestling was somewhat smaller and less developed than its sibling, but obviously not enough to prevent survival. Our limited data suggest that the differences continue through the nestling stage and that the initial disadvantage is not compensated for.

Age at first breeding. A female in juvenal plumage, not molting, on May 18, had an incompletely ossified skull with a large "window" on each side; this suggested an age of six months or less

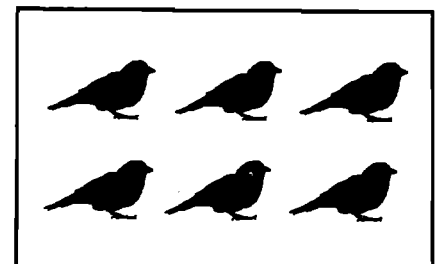
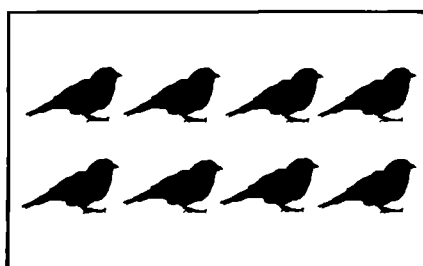


Table 4. Data on 14 nestlings from 6 nests of *Passer domesticus*, El Salvador, 1977. Ages are estimated using Weaver (1942).

Nest No.	Weight (g)	Length (mm)	Ulna or wing (mm)	Age (days)
#77-5-18D	9	62	11	4+
	6¼	60	10	4
	4	50	6	2+
#77-5-18E	6¾	63	9	2+
	4½	53	6	1-2
#77-5-18C	22	92	33	8+
	18¼	80	26	7+
#77-5-18B	20¼	85	32	8+
	18	80	28	7+
#77-4-26B	—	—	—	4+
	—	—	—	4-
#77-4-26C	—	—	—	4
	—	—	—	4-
	—	—	—	2+

(Nero 1951) if ossification proceeds at the same rate in the tropics as in higher latitudes. This female had no incubation patch and was extremely fat. She was nearly ready to lay; one ovum was 12 millimeters in diameter and almost free, two others, 8 millimeters and 7 millimeters, respectively, were almost free. A female on May 17, had an unossified skull, possibly less than four months old, with an active ovary with ova 3, 2+ and 2 millimeters, respectively. She was very fat and not molting, and still in juvenal plumage. We believe that both birds were nesting or about to do so.

We find no reference to proven nesting by very young House Sparrows as confirmed by color banding studies; most such studies have been carried out in temperate zones where winter interposes a hiatus in the sexual cycle. A few individuals with active gonads but in juvenal plumage and with incompletely ossified skulls, have been reported from the mild climate of southern California: two females, in March and April, respectively, skulls partly ossified, the first in a low stage of sexual development, the second in full breeding condition



(Davis and Davis 1954); three males, in June, July, and August, respectively, skulls unossified to one-quarter ossified, juvenal plumage with a few adult feathers, bills black to very dark brown (Davis 1953). Early breeding has been noted in other species (Miller 1959a; Miller 1959b; Immelman 1971; Johnson (1962).

DISCUSSION

The rapid expansion of *P. domesticus* through Central America appears to be a simple case of an r-selected species invading a region where K-selection is appropriate (Mac Arthur and Wilson 1967). In simpler but less concise language: a species of northern Europe adapted for high reproductive potential in order to recuperate quickly from catastrophic winter losses, has moved into a region where conditions are favorable and relatively stable; with high fecundity and low mortality an excess of young is produced, more than can be accommodated at any one site, and the excess is forced to emigrate. However, the matter is not that simple.

The full effect of latitude change is yet to be discovered. Our data and that of Fleischer in Costa Rica suggest that clutch size is affected, but this may be an indirect effect, possibly owing to differences in quality and availability of food, or to release from photoperiodic and/or seasonal control, permitting more but smaller clutches/year.

The change in climate was probably

beneficial though not entirely so. Certainly birds that can colonize Death Valley, California, and Churchill, Manitoba, would find nothing insupportable in the temperatures of Central America. Especially beneficial was the liberation from heavy winter mortality which sometimes takes up to 50% of a population, especially among young birds (Will 1973). The effect of long dry seasons is undetermined. A House Sparrow drinks up to 30% of its weight daily, more if heat stressed (Bartholomew and Cade 1963). In most of El Salvador and much of Guatemala there is little free water in rural areas from mid-November to mid-April; all but the largest streams go dry midway through the period. This may be a factor that limits House Sparrows to towns where free water is found.

Possibly the most adverse factor limiting the spread of this species has been the presence of already well-established species. Conditions in Central America have long been relatively stable; native birds have partitioned the resources and occupied the niches. These native birds are K-selected and so make exceptional competitors in the environments to which they are adapted (Meyers 1977). However, the native birds rarely invaded the compact, comparatively barren towns of Spanish design. There the House Sparrows, already adapted to live close to man, found the plazas and parks almost free of competitors. Food, though inferior in quality and quantity, was dependable. Nest sites were plentiful. Native predators were too timid to live in the towns.

And so the House Sparrows flourished in towns. When they tried to disperse into open country they met with the full force of competition and with predators for which they had no defense. Adaptable as they are, House Sparrows have not yet been able to find, open, and exploit niches outside the towns in Guatemala and El Salvador.

This explains the small absolute numbers of House Sparrows in El Salvador where we estimated fewer than 2000 in 1977. This number is trivial compared with 15,000 breeding birds in McLeansboro, Illinois (Will 1973), 20,000 birds feeding in one square mile near Stillwater, Oklahoma (North 1973), and 330 pairs/100 acres of suburban Pinellas County, Florida (Woolfenden and Rohwer 1969). However, North American House Sparrows are

not confined to a few hundred meters² of a very compact town; they can forage widely on lawns, gardens, livestock feeding lots, grainfields, and at grain elevators and feed stores. House Sparrows of Central America do not have these resources.

Paradoxically, the factors that limit population growth may have been responsible for the rapid range extension of the species. Consider the situation in which a pair of House Sparrows makes its way into a suitable town plaza. Their reproductive rate is high, their mortality rate low; they increase geometrically. Within a few generations the colony will have reached the carrying capacity of the site. There are few or no outside sources of food for additional birds. Another generation results in an excess. Some of the immatures leave without aim or direction, perhaps being borne on the strong north winds that frequently occur. They wander, many succumb, some make their way into another town which may be far from the mother colony. Thus the rapid advance and saltatory progression.

This amazingly adaptable species may find ways to invade the rural areas, repeating its North American history, but by means of entirely different adaptations. The species will probably continue to make adaptations to the climate, photoperiod, latitude, competitors, predators, and diseases. Summers-Smith (1963) considered that *P. domesticus* was of tropical origin and that it took some of its tropical adaptations with it when it spread into northern Europe. It will be interesting to learn if any of its tropical heritage will assert itself now that it has reinvaded the tropics. We have been presented with a natural experiment which, if we hurry, we can use to test many of the theories and models that have been devised to explain some of the adaptations of birds.

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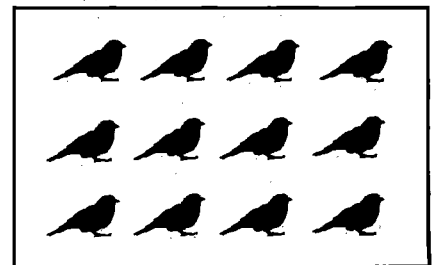
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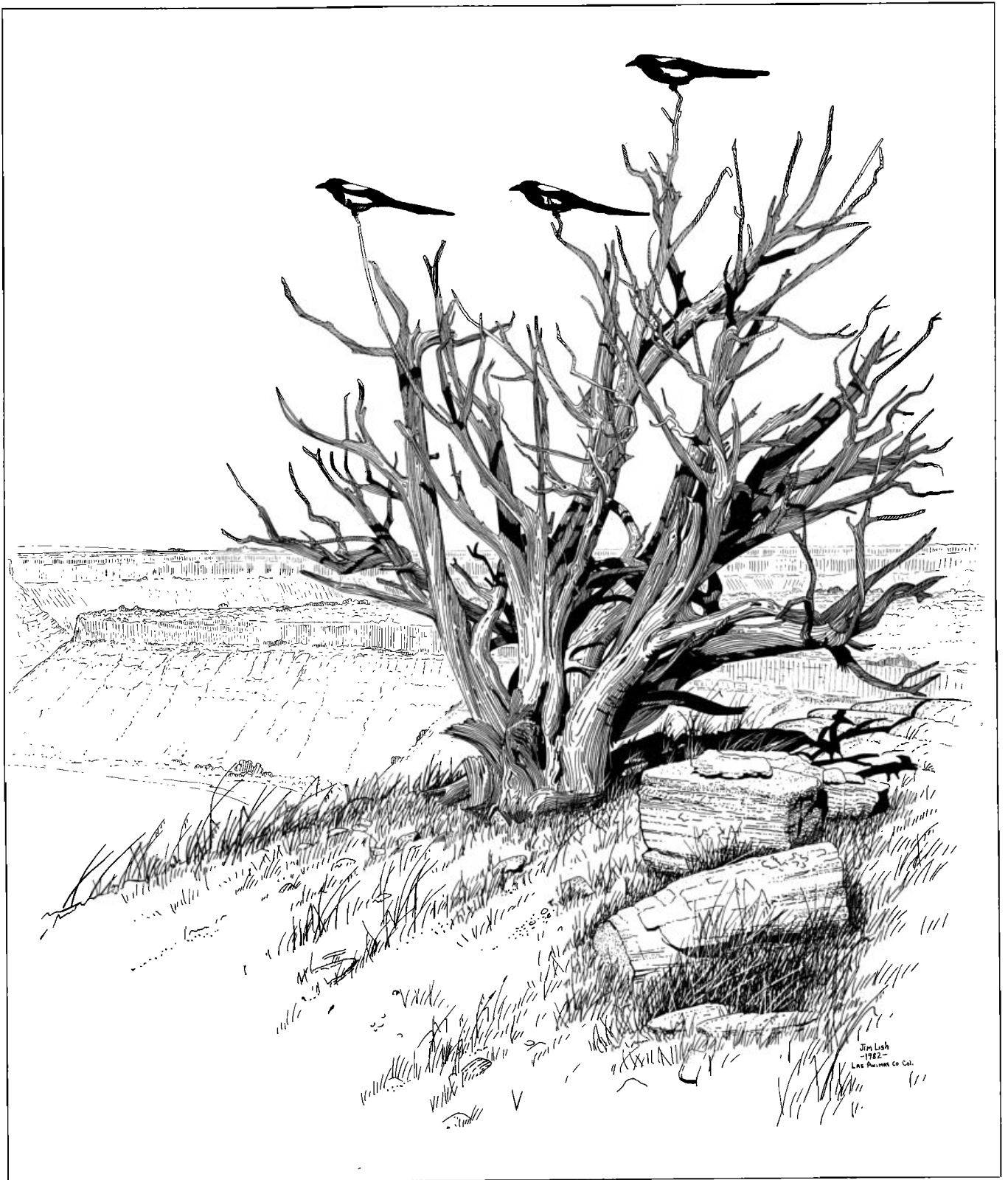
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Northern Hawk-Owl (Surnia ulula). Illustration/James Coe.



Black-billed Magpies (Pica pica). Illustration/James Lish.