

POPULATION DYNAMICS AND MIGRATION ROUTES OF TREE SWALLOWS, *TACHYGINETA BICOLOR*, IN NORTH AMERICA

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Abstract.—Band recoveries and published accounts indicate that 79.1% of Tree Swallows (*Tachycineta bicolor*) die in their first year and 60.3% in each subsequent year. Tree Swallows live an average of 2.7 yr. The net reproductive rate (R_0) is 0.701 females/yr. At that rate a female that raises an average-sized brood in each breeding year more than replaces herself in an average life span. However, a second year (SY) female that fails to breed must raise an average-sized brood in each of the next three years to replace herself, but few females live that long. Tree Swallows use three migration routes east of the Rockies: (1) east coast and Great Lake populations migrate along the eastern seaboard to Florida, the Caribbean and Central America; (2) Canadian prairie and mid-west USA populations follow the Mississippi drainage basin to the Gulf Coast states and Central America; (3) populations along the east side of the Rockies migrate due south into Mexico. Migration routes of western populations are unknown, but a resident population may exist in southern California.

DINÁMICA DE POBLACIONES Y RUTAS DE MIGRACIÓN DE *TACHYGINETA BICOLOR* EN NORTE AMERICA

Resumen.—Tanto la literatura como el recobro de anillas indican que el 79.1% de los individuos de *Tachycineta bicolor* mueren durante el primer año y el 60.3% en años subsiguientes. En promedio estas aves duran 2.7 años. La tasa neta reproductiva de la especie (R_0) es de 0.71 hembras/año. A esta tasa reproductiva, una hembra que cría una camada de tamaño promedio durante sus años de vida, producirá una pequeña mayor cantidad de individuos que su remplazo. Sin embargo, una hembra de dos años (SY) que falle en reproducirse, debe criar una camada de tamaño promedio durante los próximos tres años para poder ser remplazada. No obstante las hembras por lo general no duran tanto tiempo. Estas golondrinas utilizan tres rutas de migración al este de las Rocallosas. Las poblaciones de la costa este y el Gran Lago migran a lo largo del borde este costero de la Florida, el Caribe y América Central. Las poblaciones de la pradera canadiense y el mediano oeste norteamericano, siguen la ruta del Mississippi hasta los estados del golfo y prosigue hacia América Central. Las aves al este de las Rocallosas migran hacia el sur hasta México. Las rutas de migración de las poblaciones del oeste son desconocidas, aunque al sur de California es probable que exista una población residente.

The Tree Swallow (*Tachycineta bicolor*) is a ubiquitous breeding species of temperate North American (AOU 1983). Its breeding behavior has received much attention (e.g., Chapman 1935, 1939, 1955; De Steven 1978; Forbush 1929; Harris 1979; Kuerzi 1941) and several authors have examined the rate of return of banded swallows (e.g., Chapman 1955; Houston and Houston 1987; Low 1933, 1934). However, I know of no

studies that have described the demographics and migration pattern of the Tree Swallow across its range in North America.

METHODS

The data used in this paper came mostly from band recovery records collected between 1929 and 1984 by the U.S. Fish & Wildlife Service, and published accounts of the breeding biology of the Tree Swallow across North America. A first-year (HY) mortality estimate was derived from the proportion of banded nestlings that survived from the date of nest departure to the beginning of the next breeding season (1 Apr.). Too few recoveries were available to derive a mortality estimate for swallows older than 12 mo (AHY). Instead I used the average (39.7%) percentage of adults that returned to their breeding site each year from two long term studies (Chapman 1955, Houston and Houston 1987) to derive a conservative estimate of annual adult mortality. I assumed that adult mortality rates were similar in subsequent years. These data were then used to construct a vertical life table and net reproductive rate. A vertical life table estimates the age structure of a population at a point in time and assumes that the population is constant and recruitment and mortality rates are equal (Moss, Watson, and Ollason 1982). The net reproductive rate (R_0) is a statistic of the number of female offspring produced by a cohort of females through their life span or:

$$R_0 = \sum_0^{\infty} l_x m_x \quad (1)$$

where l_x is the probability of surviving to year x and m_x is the number of female offspring produced per breeding female in year x (Krebs 1972). The number of female offspring that fledged per successful breeding attempt was estimated from the reproductive efficiency of adult females (ASY) in 13 studies across North America. Females that breed in their second year (SY) are less fecund than older (ASY) females so I used a value of 1.94 female offspring produced by SY females (De Steven 1978).

Migration routes were determined from recoveries of banded birds during the non-breeding season (1 Aug.–31 Mar.). Some swallows that died during the breeding season could have been recovered later in the year near their nests. To separate these records from those of true migrants I arbitrarily chose a boundary of two degree blocks (120 km) as a dividing line beyond which records were considered to be from migrating swallows.

RESULTS AND DISCUSSION

Causes of mortality.—There were 802,662 Tree Swallows banded as nestlings or adults by 31 May 1984 and 293 recoveries in which the cause of death was reported. Sixty swallows (20.5%), of which 23 were in their first year of life (HY), were caught by other birds. Fifty-four (18.4%) died on highways or in collisions. The remaining 179 (61.1%) causes of death included being shot, caught by rodents, cats and dogs, trapped in buildings, electric shock, entanglements, and unspecified injuries.

TABLE 1. Percentage of Tree Swallows banded as nestlings and adults that were recaptured at the banding site one year later.

Banding location	Percent recaptured		Reference
	Nestlings	Adults	
Pennsylvania	5.4	51.3	Stahura 1982
New Jersey	3.1	39.6	Chapman 1955
Massachusetts	12.0	34.0	Low 1933
Connecticut	—	26.7	Kuerzi 1941
Alberta	1.3	13.7	Pinel 1980
Saskatchewan	0.8	12.8	Houston and Houston 1987

Mortality estimates.—Of 320 recoveries from swallows banded as nestlings that successfully left the nest, 253 (79.1%) occurred in their first year of life (HY code). Fewer bands were recovered from second-year (SY) ($n = 2$, 0.6%) and older (ASY) birds ($n = 65$, 20.3%).

To examine whether the estimate of 79.1% mortality in the first year of life is a reasonable approximation of mortality I examined the percentage of banded nestlings reported to have returned one year later, across the Tree Swallow's range (Table 1). Two authors have shown that most surviving nestlings return to their natal site the following year (Cohen 1981, Houston and Houston 1987). Banding data showed that only 37 of 1479 (2.5%) SY females recovered dead or alive during the breeding season occurred more than 10 km from their banding site. This result partly reflects the distribution of bird banders, but also supports Cohen's (1981) and Houston and Houston's (1987) findings. Therefore, the recapture percentages should approximate, but not exceed the survival estimate. For nestlings, those estimates ranged from 0.8 to 12.0% (Table 1) all below the band recovery estimate of 20.9%.

The recapture values for adults also varied from site to site (Table 1) and between years (Chapman 1955, Houston and Houston 1987). Two long term studies (Chapman 1955, Houston and Houston 1987) spanning 14 and 17 yr, respectively, had very similar mean rates of return by adults one year after banding. Chapman (1955) found a mean of 39.7% for all banded adults that returned the following year and Houston and Houston (1987) found a value of 38.7%. These values indicate that annual adult mortality is about 61%, nearly three times the value estimated from band recovery data (SY + ASY = 0.6% + 20.3% = 20.9%). The reason for this discrepancy is unclear except that very few recoveries occurred in the winter quarters where presumably most adult mortality takes place.

Recapture rates and annual survival estimates of other species of swallows also vary between years but approximate my estimates for Tree Swallows. For example, return rates of adult Cliff Swallows (*Hirundo pyrrhonota*) ranged from 27% (Sikes and Arnold 1984) to 50% (Mayhew 1958). Estimates of Bank Swallow (*Riparia riparia*) annual survival estimates from band recovery data were 35–40% for adults and 20–23%

TABLE 2. Vertical life table for the Tree Swallow beginning with 1000 individuals.

Year	Number alive at start of year	Number dying in the year	Mortality rate
0	1000	791	0.791
1	209	126	0.603
2	83	50	0.603
3	33	20	0.603
4	13	8	0.603
5	5	3	0.603
6	2	1	0.603
7	1	1	1.000

for juveniles (Hardwood and Harrison 1977, Mead 1979). The survival estimates for Barn Swallows (*H. rustica*) were 43% for adults (Henny 1972) and 35% for juveniles (Samuel 1971).

Survival estimates based upon the number of marked birds that return to the banding site underestimate the true survival value because they fail to account for birds that survived, but bred elsewhere. However, Cohen (1981), Chapman (1955), and Houston and Houston (1987) showed that although a small number of SY females bred in nearby populations they nested closer to their natal sites in succeeding years, sometimes reoccupying the nest box where they were raised. Therefore, long term studies such as Chapman's (1955) and Houston and Houston's (1987) should account for most breeding females although a small bias against younger age-classes exists. Since Chapman's (1955) and Houston and Houston's (1987) studies spanned the greatest number of years and were so similar, their average values probably most accurately estimate adult Tree Swallow survival. In addition, Houston and Houston (1987) showed that the percentage of adult females that returned one, two, three, four, five, and six years after banding declined at a relatively constant rate per year suggesting that adult female mortality was relatively constant between classes.

A life table constructed with annual mortality probabilities of 0.791 in the first year of life and 0.603 (1.00-0.397 annual survival probability for adults) in subsequent years shows that Tree Swallows live an average of 2.7 yr and a maximum of 8 yr (Table 2). The net reproductive rate (R_0) requires knowing the number of female offspring produced per breeding female each year. Thirteen studies across North America indicate that the mean clutch size is 5.6 eggs which produce 4.3 (76%) fledglings (Table 3). Assuming equal sex ratios, then an average of 2.15 female fledglings were produced per clutch. By multiplying the mean life span (2.7 yr) by the net reproductive rate (0.701 females/yr, from eq. 1) results in 1.89 females being produced in an average life span if all breeding females successfully raised an average brood size each year. In fact, all females are not successful in raising a brood each year and not all SY

TABLE 3. Reproductive efficiency of Tree Swallows in North America.

Mean clutch size	Number of young fledged/egg laid	Number of nests	Location	Reference
6.2	0.80 ^a	62	Ontario	Quinney 1983
6.2	0.95	52	Montana	Wedemeyer 1935
6.1	0.65	127	British Columbia	Butler, unpubl. data
6.0	0.89	119	Ontario	De Steven 1978
5.9 ^b	0.87 ^b	41	Manitoba	Zach 1982
5.7	0.78	1257	Alberta	Pinel 1980
5.7	0.87	111	Alberta	Stiles 1980
5.6	0.71 ^a	52	Ontario	Quinney 1983
5.6	0.74	30	New Brunswick	Paynter 1954
5.2	0.87	22	New Brunswick	Winn 1949
5.2	0.60	1477	New Jersey	Chapman 1955
5.2	0.71	68	Connecticut	Kuerzi 1941
4.7	0.49	290	Massachusetts	Low 1934
Mean	5.6	0.76		

^a Values are from two populations in different habitats.

^b Values are from the most productive clutch size.

females breed (Lombardo 1987, Stutchbury and Robertson 1985). A SY female that fails to raise an average sized brood reduces her net reproductive rate to 0.295 ($R_0 - l_1m_1 = 0.701 - 0.406$). That means she must successfully raise a brood in each of the next three years to replace herself (0.295 females/yr \times 3 breeding seasons \approx 1.0 female) but the probability of surviving to four years of age is only 1.3% (Table 2). It is no wonder that SY females vigorously attempt to usurp occupied nest sites (Leffelaar and Robertson 1985).

Migration routes.—Only 41 recoveries of banded swallows occurred outside the breeding season and greater than two degree blocks (120 km) from the banding site (Fig. 1). During the winter non-migratory period (November–January) (Tyler 1942) 14 bands were recovered from first (HY) and second year (SY) Tree Swallows and seven from older (ASY) swallows. Those records indicate that Tree Swallows spend the winter from southern USA to Honduras. There appear to be three patterns of migration east of the Rocky Mountains.

1. Tree Swallows from southern Ontario and the eastern seaboard migrate along the Atlantic Coast of the USA to winter in Florida, Cuba, and Honduras. Early reports support my interpretations. Tyler (1942) and Forbush (1929) mention Tree Swallows in those areas in winter. During the winter of 1895 severe winter weather and scarcity of food caused high mortality among Tree Swallows in Florida (Smith 1895). The following spring Forbush (1904) noted that the breeding population of Tree Swallows in New England was far below normal.

2. Swallows from the Canadian prairies and American states near the

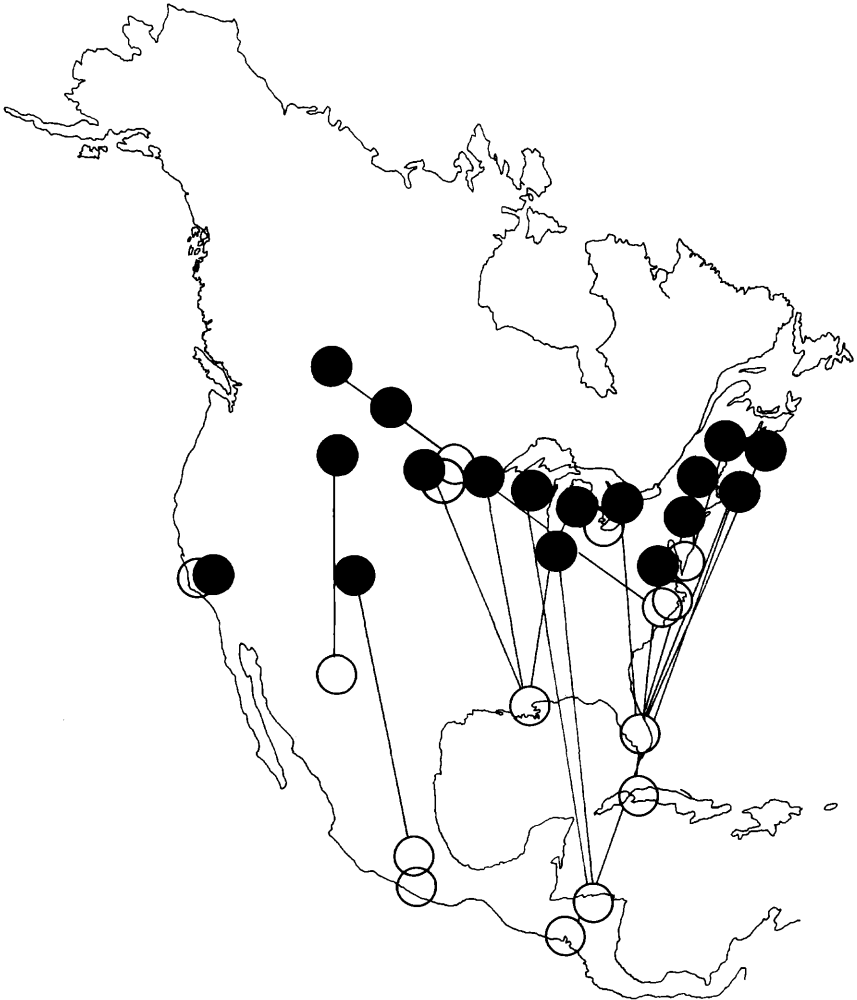


FIGURE 1. Banding locations (solid symbol) and recovery sites (open symbol) of Tree Swallows. Some symbols represent more than one banding location and recovery site.

eastern Great Lakes appear to migrate mostly along the Mississippi River Valley to their winter quarters in the southern USA and Central America. Houston and Houston (1987) reported that four nestlings banded in Saskatchewan were recovered to the southeast in southern Manitoba and North Dakota and Roberts (1932) reported large flocks of Tree Swallows migrating along the Mississippi River.

3. Migration routes along the eastern and western sides of the Rocky Mountains are poorly known. One recovery of a bird banded in Montana

and recovered in New Mexico and two banded in Colorado recovered in southern Mexico suggest a possible north-south migration route along the eastern slope of the Rocky Mountains (Fig. 1). The spring migration routes west of the Rocky Mountains may follow the Pacific Coast and river valleys. Tree Swallows arrive in Montana (Wedemeyer 1973) and southeastern British Columbia (Butler et al. 1986) in early to mid-March about one month ahead of those in Colorado (R. R. Cohen, pers. comm.). Wedemeyer (1973) proposed a spring route along the mild west coast of the USA, and upstream along the Columbia and Kootenay River valleys to Montana. Some of those birds may fly south along the east side of the Rockies but more western populations presumably retrace their spring routes. Two swallows banded in central California and recovered nearby are the only returns west of the Rockies. Those California recoveries occurred on 21 Feb. 1935 and 31 Oct. 1932 which might indicate a resident population there. Garrett and Dunn (1981) reported that Tree Swallows were commonly seen in some areas of southern California the year round.

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