

FACTORS AFFECTING SITE TENACITY IN NEW YORK BANK SWALLOWS

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Attachment to a former nesting location (site tenacity) has been shown to be affected by several factors. In long-term studies on site attachment in larids, for example, Austin (1949) examined the effects of age in Common Terns (*Sterna hirundo*), Coulson and White (1958) studied the effects of age in Kittiwakes (*Rissa tridactyla*), and Southern (1977) worked on the effects of both age and site stability in Ring-billed Gulls (*Larus delawarensis*). A small number of similar studies have been done on passerines. Site attachment has been shown to be affected by sex in Song Sparrows (*Melospiza melodia*) (Nice, 1937) and in Gray Catbirds (*Dumetella carolinensis*) by Darley et al. (1977). Others have found a relationship between reproductive success and the tendency to return to a former breeding site (von Haartman, 1949; Nolan, 1978). Most studies have not shown an increase in site attachment with age in passerines.

The Bank Swallow (*Riparia riparia*) is a suitable species for the study of site fidelity because of the ease with which substantial numbers can be captured for banding. Furthermore, since Bank Swallow nesting sites are easy to locate and are limited in number, the likelihood of capturing returning birds may be greater than in passerines having scattered single nests. Several studies have reported the tendency of the Bank Swallow to return to former nesting places (Stoner, 1941; Bergstrom, 1951; Leys, 1970; MacBriar and Stevenson, 1976), but factors that affect site tenacity have not been analyzed in this species. The present study considers the effects of age, sex, breeding success, and site stability on breeding site tenacity in Bank Swallows. In addition, site tenacity in several species of North American swallows is compared, and a possible explanation for a lesser attachment in Bank Swallows is offered.

METHODS

Bank Swallows nesting in seven sand and gravel banks were banded over a 13-yr period in southeastern New York State. The study area was located in and near the village of Ellenville, Ulster County, in a valley between the southern foothills of the Catskill Mountains and the Shawangunk Mountain. All of the colonies were located in sand and gravel banks that had been excavated for commercial purposes, and all were within 11 km of the village of Ellenville. The three largest colonies (up to 250 pairs) were about 6 km apart; the shortest distance between any two active colonies was 2.4 km.

Small numbers of Bank Swallows were banded each year from 1965 to 1969. More than 250 new birds were banded each year from 1970 through 1973, and more than 400 new birds were banded yearly from 1974 to 1976. A total of 2,816 Bank Swallows were banded, and 292 birds returned in at least one subsequent breeding season through 1977.

TABLE 1.

Bank Swallows banded (through 1976) and returns (through 1977) by age and sex.

	Juvenile	Adult male	Adult female	Adult U	Total adults	Total all classes
Number banded	432	1,093	1,250	41	2,384	2,816
Returns ¹	35 ²	147	163	0	310	345
Percent returns	8.1	13.4	13.0	0	13.0	12.3

¹ A return is a bird recaptured in any later breeding season at any of the local colonies.

² This table includes multiple returns of 292 individuals birds. There were 33 juveniles returning a total of 35 times, 123 males returning 147 times, and 136 females returning 163 times.

Most of the birds were captured in mist nets placed across the bank face. Young birds were captured as they left their burrows, often on their first flights. Adults were sexed by examination for the presence of a brood patch. A small number caught early in the nesting season could not be sexed.

RESULTS

Table 1 summarizes the banding and return data for Bank Swallows captured in this study. Birds recaptured in a subsequent nesting season at any of the local colonies are here lumped together as "returns."

The return rates (stated as a percentage of those banded) obtained in this and other studies are compared in Table 2. Much of the variation in return rates found by these authors reflects the intensity of recapture effort at each colony as well as the extent of coverage of other nearby colonies. My overall return rate for birds banded as adults (13%) is most similar to the rate obtained by Bergstrom (1951) who recaptured 12.5% of the adult Bank Swallows he had banded along the banks of the Connecticut River. The birds nested in a one-half-mile-long section of the river bank, and Bergstrom's recapture effort there appeared to be consistent over the six-year period of his study. The lower return rates recorded by other authors were undoubtedly because their work was done in locations where the colonies were too numerous, large, or scattered to be as thoroughly sampled. MacBriar and Stevenson (1976), for example, banded swallows at 28 separate locations, and Leys (1970) used data from more than 50 colonies. The small number of colonies in the Ellenville area, their relatively small size, and their proximity to each other enabled me to capture swallows on at least two different dates at each colony during each breeding season.

The Effect of Age on Site Tenacity

Return rates for Bank Swallows banded as juveniles are substantially less than those for birds banded as breeding adults (Table 2). This is as expected, and is undoubtedly due to higher mortality in first-year birds

TABLE 2.
Summary of published rates of return in Bank Swallows.

Author	Location of study	Length of study (yr)	Total banded	Percentages returning ¹	
				Adults	Young
Stoner (1941)	Iowa, New York	17	7,318	4.4	1.1
Bergstrom (1951)	Connecticut	6	2,024	12.5	4.8
Leys (1970)	Netherlands	10	8,444	6.0	4.7
MacBriar & Stevenson (1976)	Wisconsin	13	6,781	5.0	2.0
Freer (present study)	New York	13	2,816	13.0	8.1

¹ Percentages taken directly from papers cited or calculated from data therein.

and to dispersal of the survivors for their first breeding season. Harwood and Harrison (1977) have calculated the postfledging mortality in young Bank Swallows to be 80% during the first year. When this very high mortality is taken into account, the numbers of survivors returning to their birthplace is actually substantial. Of the 432 juvenile Bank Swallows banded in this study, only 86 can be expected to be alive to breed for the first time. I recaptured 33 of these birds in subsequent seasons; this is 38% of those expected to survive. It indicates a rather strong attachment to the natal region.

Of the yearling swallows, 15 returned to the same colony site where they had been reared, and 18 returned to some other nearby colony (Table 3). This is similar to results obtained by Leys (1970), who found that half of his returning young Sand Martins were recaptured at the banding colony and half were recaptured at other colonies from 11 to 50 km from the natal colony. MacBriar and Stevenson (1976) also recaptured half of their returning young Bank Swallows at the original banding site and half at other locations up to 14.5 km away.

TABLE 3.
Returns of Bank Swallows banded as fledglings.

Age at first return	Returns to the natal colony		Returns to other colonies	
	Male ¹	Female	Male	Female
1	8	2	11	2
2	3	2	1	
3			3	
4			1	
Total	11	4	16	2

¹ Sex was determined at the time of return.

TABLE 4.
Multiple returns of individual adult Bank Swallows.

	Same colony ¹	Different colony
First return	195 (67) ²	97 (33)
Second return	36 (73)	13 (27)
Third return	3 (100)	
Fourth return	1 (100)	
Total	235 (68)	110 (32)

¹ Returned in a subsequent breeding season to the colony where last captured.

² Numbers in parentheses are percentages of the total.

Only six of the 33 returning young birds were females (Table 3). Sex cannot be determined at the time of fledging, but if it is assumed that half of the 432 banded fledglings were female, only 3% of these females were ever recaptured at any of the local colonies, whereas 12.5% of the males were recaptured. This could indicate that young females have a higher mortality rate, a wider dispersal for their first breeding, or perhaps a tendency not to breed as yearlings. More data are needed in order to determine which is the case. Mason (1953) reported similar data from banded young Barn Swallows (*Hirundo rustica*); 20 of the returning birds were male and only 1 was female. He believed that this was due to wider dispersal of the females.

In his long-term study of Common Terns, Austin (1949) found that site attachment increased with age. Some of his terns switched colonies during their early years, but as they became older they tended to return more faithfully to a single location. Bank Swallows are short-lived as compared with terns, but I attempted to determine if any increase in site attachment could be observed as the birds aged. An indication of such an increase might be apparent in multiple returns of individual birds banded as adults (Table 4). The data shown here suggest that site attachment does tend to increase with age; on their first return, 67% of the Bank Swallows were captured in the colony where they had been banded, and on their second return, 73% were found in the colony of their last capture. The few birds returning for their third and fourth times were all recaptured in the same colony as their last capture.

The Effect of Sex on Site Tenacity

Other studies have shown that male passerines have greater site fidelity than females (e.g., Nice, 1937; Darley et al., 1977; Nolan, 1978). This greater attachment is presumably related to the earlier spring arrival and territory selection by the male. Mayhew (1958), however, found that female Cliff Swallows (*Petrochelidon pyrrhonota*) show greater faithfulness to their nesting sites than do the males. This point has not been addressed in earlier Bank Swallow studies.

The percentage of banded adult male and female Bank Swallows that subsequently returned is about the same (13.4% vs. 13.0%) (Table 1). Of 147 adult males that returned, 97 (66%) were recaptured at the original banding colony, and 50 (34%) were recaptured at some other colony. Of 163 returning adult females, 121 (74%) returned to the banding colony, and 42 (26%) were recaptured at some other colony location. Both sexes, therefore, show rather strong attachment to places where they have nested before, and the difference between them is not significant ($\chi^2 = 2.52$, $P > 0.05$). It is not known if males arrive earlier in the spring than the females or if males select the colony or burrow locations.

Although sex does not apparently play an important role in the degree of site fidelity in adult Bank Swallows, it is a factor in the rates of return of yearling birds, as mentioned earlier. Of 33 returning birds banded as juveniles, 27 were male and only 6 were female.

The Effect of Breeding Success on Site Tenacity

It has been shown that breeding success increases the likelihood of return to the nesting site (Delius, 1965; Darley et al., 1977; Nolan, 1978). Breeding success was recorded in several Bank Swallow colonies in 1975 and 1976 as part of a study of the effects of position within the colony on reproductive success (Freer, 1977). At least one young was known to be fledged successfully from each of 135 burrows (out of 197 active burrows) at Kelly's colony in 1975, and from each of 183 burrows (out of 218 active burrows) at the same location in 1976. Examination of the return rates to this successful colony showed that 19% of the 1975 adults were recaptured there in 1976 and 15% of the 1976 adults were recaptured there in 1977 (Table 5). Only 3% and 1%, respectively, were recaptured at other colony sites in 1976 and 1977.

In contrast, colony sites that produced few or no young were not usually reoccupied by Bank Swallows in the following breeding season. In the few cases where these sites were reoccupied, banding data suggested that the new occupants were birds that had not nested there in the unsuccessful season. One location called Rock Bank was extensively preyed upon by one or more American Kestrels (*Falco sparverius*) in 1972 (Freer, 1973), when at least 25 young were known to have been taken within a few days. This sand bank was not used by Bank Swallows in 1973, although it appeared to human eyes to be as suitable as before. In 1976, the same location was again inhabited by about 30 pairs of swallows, but a mammal dug down through the top of the bank to the nest chambers and destroyed the eggs or young from more than half of the nests. All of the swallows subsequently abandoned the colony. This site was not reused in 1977, but was again occupied in 1978. Another colony location (Napanoch) was believed to have very poor nesting success in 1973, apparently due to the instability of the sand bank. Frequent landslides and collapses of small sections of the bank destroyed many of the burrows, and no young were seen or captured,

TABLE 5.

Returns of banded adult Bank Swallows to sites where breeding success was known.

	Sites where breeding was successful ¹			
	Kelly's 1975		Kelly's 1976	
Adults banded	129		158	
Returns in the following year	24 (19) ²		24 (15)	
Recaptured elsewhere in the following year	4 (03)		2 (01)	
	Sites where breeding was unsuccessful			
	Rock Bank 1972	Rock Bank 1976	Napanoch 1973	Fallsview 1976
Adults banded	96	24	32	32
Returns in the following year	0	0	0	0
Recaptured elsewhere in the following year	0	6 (25)	7 (22)	7 (22)

¹ See text for a discussion of successful and unsuccessful breeding.² Numbers in parentheses are percentages of the total banded.

despite efforts to do so. Bank Swallows did reoccupy that sand bank in the following year (1974), but none of the 1973 birds was recaptured. However, seven of the 1973 birds were recaptured in other breeding colonies in the region in 1974. A third colony site (Fallsview) was abandoned after wind and rain eroded the fine sand so extensively that some nests were exposed. No young were seen at this location, and this site was not utilized the following year.

These observations indicate that Bank Swallows are more likely to return to a location where they have nested successfully than to a site where nesting was unsuccessful.

The Effect of Site Stability on Site Tenacity

McNicholl (1975) reviewed the subject of site tenacity in gulls and terns in relation to the stability of the breeding site. He hypothesized that nest site tenacity is particularly well developed in those that breed in highly stable habitats. Site stability (the year-to-year suitability of a breeding location) is clearly not a characteristic of sand banks. I have described elsewhere (Freer, 1977) the stages in weathering and collapse of sand banks that are no longer being excavated by men. Bank Swallows prefer freshly exposed clean vertical bank faces for their nesting sites; in time, natural weathering processes cause a gradual collapse of the bank, and the bank becomes less suitable as a nesting location. This can be illustrated by comparison of the return rates to a location that was

gradually weathering and slumping with the return rates to a location that continued to present a vertical bank face.

Bank Swallows occupied a sand bank along Route 209 during every nesting season since 1969, and the owners of the land excavated some sand every year, resulting in fresh vertical surfaces in the bank. However, the commercial excavating operations ceased in 1974, and the bank gradually began to erode and collapse. Enough vertical sections remained to allow a colony of about 125 pairs to occupy the site in 1975, but by the time the nesting season began in 1976, few areas of the bank were suitable for the birds. The number of nesting birds was reduced to about 40 pairs. Only about 12 pairs nested there in 1977. Banding operations were consistent at the 209 colony from 1969 to 1977. Between 1969 and 1975, an average of 7% of the swallows banded in this colony each year were recaptured there in the next year, and only about 2% were recaptured at other colony locations. However, 15% of the birds banded there in 1976 were found nesting elsewhere in 1977, suggesting that an increasing number of birds had not been able to locate suitable nesting space in the slumping sand bank.

At another colony location (Kelly's), truckloads of sand were regularly removed throughout the study period. This provided newly suitable bank faces for the nesting birds, and colonies of up to 200 pairs were found every year since 1973. From 1973 to 1976, an average of 10.4% of the birds banded at Kelly's each year were recaptured there in the following year, while an average of only 2.1% were recaptured in other colonies.

DISCUSSION

Sex appears to be the least important of the factors affecting site attachment in Bank Swallows. Adult males and females have nearly equal degrees of site tenacity; the only apparent difference between the sexes is in the differing returns of one-year-old males and females. As in other bird species, however, site attachment is influenced by age, especially with regard to first-time breeders vs. older birds. Some tendency exists for an increase in site attachment with increasing age in adult Bank Swallows. In addition, prior reproductive success is clearly important as a factor affecting site tenacity. This is surely an important adaptation serving to maximize the reproductive potential of the returning birds, and it can be expected to exist in most avian species.

The less usual factor influencing site attachment in Bank Swallows is their requirement of a disturbed sand bank for burrow locations. In natural river bank sites, water undermines the banks, causing their collapse, and leaving fresh vertical exposures. Man-made sand banks that are suitable for nesting in one season do not usually remain suitable unless they are excavated again. Since Bank Swallows require these types of disturbed sites, a very highly developed site attachment would be disadvantageous to them. Lesser attachment to previously used sites allows for the rapid pioneering of newly suitable locations.

In general, site tenacity undoubtedly has selective advantage in familiarizing the bird with its surroundings. This may serve it well in avoiding predators, finding food, and in locating sites having the proper characteristics needed for nesting. One might expect to find such an advantageous trait in all of the swallows. However, examination of the return rates of other North American swallows reveals that some exhibit a higher degree of site faithfulness than do Bank Swallows. Comparison of their nest locations with that of Bank Swallows suggests that the differences in breeding site tenacity may be related to differences in nest site stability, as suggested for larids by McNicholl (1975).

The natural and man-made nesting sites used by Cliff Swallows are highly stable locations which could be available for many years. It would therefore be adaptive for Cliff Swallows to have well developed site tenacity, which should be reflected in a high banding return rate. Mayhew (1958) found that to be the case; 48% of his banded adults returned in subsequent years. Barn Swallows also nest in stable locations; Mason (1953) reported that 34% of his banded adults subsequently returned. Tree Swallows (*Iridoprocne bicolor*) and Purple Martins (*Progne subis*) both nest in relatively stable situations, and the degree of site tenacity reported for each is correspondingly high. Chapman (1955) found that 40% of his breeding adult Tree Swallows returned the next year, and Allen and Nice (1952) reported that 77 of 79 returning adult martins were found at the banding location.

It seems reasonable to assume that the effects of age and prior breeding success on site attachment are similar for most of the swallow species mentioned. Sex may well have more importance in those species in which the males arrive at the breeding location earlier than the females, and where the males select the breeding territory. In those species in which territoriality is not well developed, as in the Cliff and Barn swallows, sex is probably not a major factor in the development of site attachment. The differences in the high rates of return in these species (48% and 34% of adults banded) and the relatively low rate found here in Bank Swallows (13% of adults banded) may well be attributable to differences in stability of their nesting sites.

SUMMARY

The returns of 292 Bank Swallows to sand and gravel banks in southeastern New York State were examined to determine factors influencing site tenacity in this species. As in other species, it was found that the return rate of banded fledglings was low; but when their high mortality was taken into account, a large percentage of the survivors were shown to return to the banding site or other nearby sites to breed as adults. Some increase in site tenacity with increase in age was found. No difference in site attachment occurred between adult males and females, but more one-year-old males returned to the area than did one-year-old females. Adults returned more faithfully to sites where they had successfully produced young than to sites where few or no young were

produced. Return rates in certain other species of swallows were compared with those of Bank Swallows. It is suggested that the much lower rate in Bank Swallows is an adaptation to the instability of its nesting locations.

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