VARIATION IN THE COSTS, BENEFITS, AND FREQUENCY OF NEST REUSE BY BARN SWALLOWS (*HIRUNDO RUSTICA*)

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ABSTRACT.—The frequency of nest reuse and the costs and benefits of this behavior were investigated in a population of Barn Swallows (*Hirundo rustica*) at Delta Marsh, Manitoba, during 1984-1986. Slightly less than half the clutches were laid in old nests, and this proportion did not change seasonally except in one late year when old nests were preferred by late-nesting pairs. The delay between nest and clutch initiation was greater for new vs. old nests, but only significantly so in June and July. Parasites (hematophagous mites) were common in old nests that had been used the previous year and significantly reduced chick survival. Swallows appeared to be able to assess parasite load and selected unparasitized old nests for the first nesting attempt. Nest instability did not appear to be a cost of nest reuse. The mean reproductive success per pair was equal for swallows using old vs. new nests, suggesting that birds can assess the costs and benefits of particular nests and nest sites. Nest reuse was, however, considerably less frequent than in other studies, presumably because the costs and benefits of this behavior vary geographically. In particular, the breeding season at Delta Marsh is extended, and the time delay caused by building a new nest is therefore less important than elsewhere. More birds have the option of avoiding the parasite costs of nest reuse while still successfully rearing two broods. Thus, individuals apparently maximize their reproductive success by adjusting their nesting strategy to account for the local costs and benefits of the two nesting options. *Received 2 March 1987, accepted 10 September 1987.*

THE nests of many species of birds are temporary structures that do not survive beyond one nesting attempt, and new nests must be constructed each year or even for each nesting attempt within a year. Other birds have more permanent nests that survive for considerable periods of time, providing the option of reusing an old nest instead of building a new one. The nests of raptors, for example, are often large, stable structures used consistently year after year (e.g. Wimberger 1984). Similarly, hole-nesting and burrowing birds have the opportunity to reuse nest sites because of the permanent nature of the cavities. Nest reuse is also common among swallows (e.g. Bent 1942). Hole-nesting species such as Bank Swallows (*Riparia riparia*) return to the same sites year after year (e.g. Bent 1942), while the mud nests of species such as Cliff Swallows (*Hirundo pyrrhonota*) (e.g. Samuel 1971, Brown and Brown 1986) and Barn Swallows (*H. rustica*) (e.g. Bent 1942, Samuel 1971, Shields 1984) survive and are reused.

Reuse of old nests entails a number of potential costs and benefits to Barn Swallows, as well as to other species. The most often mentioned benefits involve the time and energy savings realized by not constructing a new nest (e.g. Shields et al. in press). Old nests also may occupy the best sites in a territory (in terms of protection from wind, rain, and predators), and thus the benefits may not be related to reuse of the nest so much as to use of the optimal site. The major cost associated with nest reuse appears to be increased parasite load (Clark and Mason 1985). Nest parasites can reduce adult reproductive success and the fitness of chicks in Purple Martins (*Progne subis*; Moss and Camin 1970), Cliff Swallows (Brown and Brown 1986), and Barn Swallows (Shields and Crook 1987). The degree of parasitism and the type of parasites present vary geographically (Shields and Crook 1987), and not all parasites appear to have a detrimental effect on nestlings (Brown and Brown 1986). Nonetheless, it has been suggested that in response to nest parasites, species that reuse nests frequently incorporate green vegetation in their nests to reduce parasite loads through repellent or toxic chemicals in the plants (Wimberger 1984, Clark and Mason 1985). Nest instability may be another cost of nest reuse; falling nests contribute significantly to mortality of eggs and chicks in reused nests in the Barn Swallow (Shields and Crook 1987).

Assuming that both old nests and new nest sites are available, a bird must decide whether to spend the time and energy necessary to build a new nest and avoid the costs of nest reuse, or to conserve time and energy and use an old nest, thereby risking increased parasite loads and nest instability. The strategy adopted by Barn Swallows should vary geographically, seasonally, and among individuals depending on the relative costs and benefits present. If energy savings are important, nest reuse should be highest in areas, or at times, of low prey abundance, whereas if time savings are important, nest reuse should be highest in late-nesting birds or in areas with short breeding seasons. Furthermore, if the increased energy required to build a new nest is an important factor, individuals with higher energy reserves should be better able to afford this cost and thereby avoid the risks of reusing an old nest. Finally, if parasites are a cost of nest reuse, birds should select old nests that are free of parasites. Cliff Swallows apparently can assess parasite loads and preferentially select parasite-free nests (Brown and Brown 1986).

I attempted to assess the various costs and benefits of nest reuse to Barn Swallows and determine how these affect reproductive success. Additionally, by comparing my data with that of other studies and testing the above predictions, I evaluated how the nesting strategy of Barn Swallows changes with changes in the relative costs and benefits of nest reuse.

METHODS AND MATERIALS

The study was conducted at the University of Manitoba Field Station, Delta Marsh, Manitoba (50°11'N, 98°23'W), during the summers of 1984–1986. The study area is on the southern shore of Lake Manitoba on a narrow, forested ridge separating the lake from Delta Marsh (see Mackenzie 1982 for details). The area is extremely productive, and insect abundance, particularly chironomids (Diptera, Chironomidae), is very high from mid- to late May through August. Chironomids form the basis of the diet for a number of passerines nesting at high density in the area (e.g. Busby and Sealy 1979, Sealy 1980).

Barn Swallows nested on and in the various buildings at the Field Station and the adjacent Portage Country Club. At the beginning of May each year, before swallows had arrived in the study area, all nests still present from previous years were censused, labeled, and their contents and condition noted. From the time swallows arrived until they left in early September, I made daily nest checks to record new nests and additions to old ones. Nest checks continued on active nests until the clutches had hatched, and one final check was made 16 days after the first hatch to record the number of "fledglings." Checks made later than this frequently caused chicks to flush. I considered the count on day 16 as the number of fledglings and used it as a measure of reproductive success (see Snapp 1976). Nests accidentally or purposely destroyed by humans were not included in reproductive success data.

In 1984 hematophagous mites (Dermanyssidae) were observed frequently in Barn Swallow nests. I assessed the presence of these parasites in nests before the arrival of swallows in early May 1985 and 1986. I placed my hand in each nest for 5 s and noted the presence or absence of mites crawling on my hand. Although this technique would not assess the presence of other common Barn Swallow parasites, such as blowflies (*Protocalliphora* spp.) or swallow bugs (Cimicidae), I never observed other parasites in nests or on nestlings. Swallow bugs and fleas have not been recorded in Barn Swallow nests in southern Manitoba (T. D. Galloway pers. comm.).

In May 1986, as the swallows were establishing territories, birds were captured in mist nets. Each bird was weighed to the nearest 0.1 g, its wing chord measured to the nearest 0.5 mm, and its fat reserve estimated by scoring the amount of fat visible in the claviculocoracoid region on a scale of 0 (none) to 3 (bulging) (see Morton et al. 1973 for details). The white tail markings of each bird were painted with various colors of enamel paint to allow later identification. The nesting behavior of these birds was followed through the summer.

Data on various aspects of reproductive success were compared using *t*-tests unless variances were unequal (*F*-ratio test), in which case Mann-Whitney tests were used (Zar 1984). Where no statistical differences existed between years, data were pooled. All tests employ a rejection level of 0.05, and data are presented as means ± SE.

RESULTS

Barn Swallows arrived in the study area in early May, and the first nest construction occurred in the third week of May. The first egg was laid in the last week in May. In 1984 the first egg was not laid until 2 June, the latest date of the three years.

As elsewhere (e.g. Samuel 1971, Snapp 1976, Shields 1984) there were two nesting cycles each year at Delta Marsh, with mean hatching dates ranging from 20 to 24 June and 31 July to 5 August for the two clutches. Most pairs attempted to raise two broods a year, and many were successful. In 1984 and 1986 the peak number of active nests was the same in the first and second nesting periods, while in 1985 there were 25 and 23 active nests, respectively. Of 21 pairs in which at least one member was marked or whose nests could be documented by their timing and location, 19 attempted and 15 were successful in rearing a second brood, and 13 of the 21 were successful with both broods (i.e. fledged at least 1 chick/brood). For these birds the mean number of fledglings per pair for the entire season was 6.86 ± 0.54 (range 3–11). In 1986 two marked pairs each built three new nests and successfully reared two broods; the initial attempts failed in the egg stage. Thus, two broods per year was the norm in this population, and most pairs appeared to be successful in rearing both, on occasion even after an initial nesting attempt failed.

I divided the breeding season into two nesting periods, the first ending when the first young fledged (late June or early July). The first period thus included early renestings following egg or chick loss. The last nests were still active in late August, and each year one or two broods were still being fed in early September.

Each spring 58–70 old nests remained intact. Natural nest loss occurred during the winter because of strong winds, and some nests were purposely removed during repainting of buildings in the fall. Thus, every year on all buildings both old nests and new nest sites were available.

During 1984 and 1985 a maximum of 25 pairs of Barn Swallows was active in the study area based on the number of nests active simultaneously. In 1986 only a maximum of 17 pairs was active at any one time.

In all three years almost half of the nests reaching the egg stage were old nests (Table 1), and 65 of 136 nests with eggs were old. In 1985 and 1986 the proportion of old nests used increased from the first to the second nesting period, and in 1984 it decreased. None of these changes was statistically significant, however, nor was the change using the pooled data (Table 1). The availability of mud could restrict the nesting options of swallows, but in the study area mud was always available along the banks of channels in the marsh, a maximum of 200 m from any nest.

There was no preference early in the year for new or old nests. The initiation dates of early nests (to the end of the first week of June) were no different for old and new nests (Mann-Whitney test; 1984: $U = 32$, $n = 7, 8$; 1985: $U = 82$, $n = 12, 13$; 1986: $U = 39.5$, $n = 8, 8$; $P > 0.05$). Similarly, there was no preference late in the year, and initiation dates of old and new nests were no different in the second nesting period

TABLE 1. Comparison of the number of old and new nests used by Barn Swallows during the first and second nesting cycles of each year and for the pooled data. None of the χ^2 values is significant ($P > 0.05$).

		First	Second	χ^2_c
1984	New	14	13	0.93
	Old	14	6	
1985	New	19	5	1.97
	Old	14	11	
1986	New	14	6	0.43
	Old	11	9	
Total	New	47	24	0.33
	Old	39	26	

in 1985 or 1986 (1985: $U = 47.5$, $n = 6, 13$; 1986: $U = 11.5$, $n = 6, 9$; $P > 0.05$). In 1984 when the season was late, old nests had significantly later initiation dates than new nests in the second nesting period ($U = 66$, $n = 13, 6$; $P = 0.02$), indicating that old nests were preferred late in the year. Individuals may prefer one nesting strategy, although I marked birds only in one year and the sample size is small. Of 12 pairs that laid two clutches, 9 either built new nests both times or used old nests both times.

A total of 17 nests was used in at least two consecutive years, including 2 that were used in all three years. In 1985 and 1986, when the past history of each nest was known, old nests were used at random relative to their use the year before (1985: $\chi^2_c = 0.65$, 1986: $\chi^2_c = 0.0$, $P > 0.25$). Swallows thus showed no preference for nests used or not used the year before. Between nesting periods within each year, nest reuse was extremely low, and only 6 of 50 nests used in the second nesting period had also been used in the first nesting period.

Reproductive success (fledglings/nest with eggs) was equal for new and old nests (Table 2). In two years birds building new nests averaged more fledglings than birds in old nests, but the reverse was true in 1986, and the differences were not statistically significant. Clutch size was also similar in old and new nests (1984: $t = 1.40$, df = 43; 1985: $t = 1.17$, df = 47; 1986: $t = 0.96$, df = 33; $P > 0.05$), and the pooled data showed no significant difference (old: $\bar{x} = 4.70 \pm 1.00$, $n = 64$; new: $\bar{x} = 4.70 \pm 0.80$, $n = 66$). Although the sample size is small, pairs followed for an entire summer did not differ in their total seasonal reproductive success whether they used old nests or built a new one initially (old: $\bar{x} = 6.63 \pm 0.78$, $n = 8$; new: $\bar{x} = 7.00 \pm 0.75$, $n = 13$; $t = 0.32$, $P > 0.50$). Of 7

TABLE 2. Reproductive success (fledglings/nest) for Barn Swallows using new vs. old nests. None of the t-values is significant ($P > 0.05$).

		n	$\bar{x}$ (SE)	t
1984	New	23	3.65 (0.35)	1.72
	Old	15	2.60 (0.54)	
1985	New	17	3.41 (0.45)	0.67
	Old	25	3.00 (0.40)	
1986	New	12	3.25 (0.44)	1.24
	Old	19	4.00 (0.39)	

pairs that built two new nests, 5 successfully reared at least 1 chick in each. Five of 6 pairs that used one old and one new nest were successful, while 3 of 6 that used two old nests were successful. Two pairs that built a new nest initially, and were successful, were not seen in the second breeding period.

Dermanyssid mites were present in some old nests in the spring before the swallows returned. The parasites were found almost exclusively in nests that had been used the year before (1985: $\chi^2_c = 28.2$, $n = 59$; 1986: $\chi^2_c = 20.0$, $n = 58$; $P < 0.001$). Only 5 of 59 nests that had not been used the previous year contained parasites, whereas 43 of 58 used nests were parasitized.

Barn Swallows used old nests at random with respect to the presence of parasites when the entire summer was analyzed (Table 3). This was not true, however, when nest choice was analyzed for separate nesting periods. In 1985 none of the old nests used in the first nesting period was parasitized, but 10 of 14 used in the second period were ($\chi^2_c = 9.65$, $n = 24$, $P < 0.005$). The sample size in 1986 was too small to permit statistical analysis, although the trend was the same and overall unparasitized nests were selected more often in the first period (Fig. 1).

Reproductive success was significantly lower in parasitized old nests than unparasitized ones

TABLE 3. Use of parasitized vs. unparasitized old nests by Barn Swallows. Neither χ^2 value is significant ($P > 0.05$).

		Used	Not used	χ^2_c
1985	Parasites	9	23	1.10
	No parasites	14	18	
1986	Parasites	5	14	0.06
	No parasites	13	26	

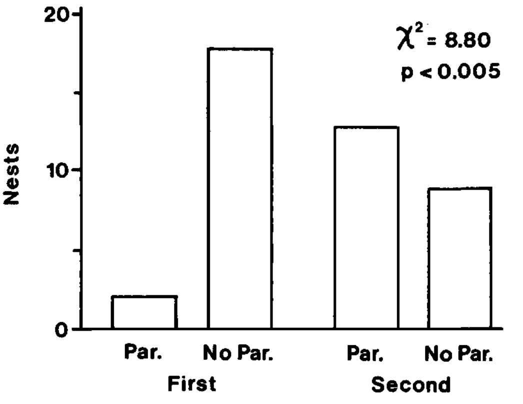

Fig. 1. Number of parasitized and unparasitized nests used by Barn Swallows in the first vs. the second nesting periods of 1985 and 1986.

(parasitized: $\bar{x} = 2.60 \pm 0.60$ fledglings/nest, $n = 15$; unparasitized: $\bar{x} = 3.96 \pm 0.30$ fledglings/nest, $n = 26$; $t = 2.28$, $P < 0.025$). Because most parasitized old nests were used in the second nesting period when reproductive success might be reduced for other reasons, second-period nests were analyzed separately. Reproductive success was still higher for unparasitized nests (parasitized: $\bar{x} = 2.15 \pm 0.60$ fledglings/nest, $n = 13$; unparasitized: $\bar{x} = 3.70 \pm 0.45$ fledglings/nest, $n = 10$; $t = 1.97$, one-tailed $P < 0.05$). Reduced success of parasitized nests appeared to be due to increased nestling mortality, which was significantly higher (parasitized: $\bar{x} = 1.23 \pm 0.51$ nestlings lost/nest, $n = 13$; unparasitized: $\bar{x} = 0.36 \pm 0.22$ nestlings lost/nest, $n = 25$; $t = 1.85$, one-tailed $P < 0.05$). Of 3 nests that were used and that had particularly heavy mite infestations, 2 failed completely because of chick mortality; the young were found covered with mites in the nest.

Birds that used old nests varied considerably in their nesting behavior. Early in the year new mud was added to old nests so that up to several centimeters' depth was added to the rim. The number of days of new mud construction per old nest was significantly lower in June and July compared with May (May: $\bar{x} = 1.57 \pm 0.28$ days, $n = 21$; June/July: $\bar{x} = 0.79 \pm 0.21$ days, $n = 29$; $t = 2.29$, $P < 0.05$). Throughout the breeding season most reused old nests had old feathers removed and replaced by new feathers. Occasionally, a clutch was initiated in a nest without any apparent construction or addition of feathers. Green vegetation was not observed in any nest.

The change in behavior of birds using old nests meant that the delay between the initiation of nest construction and the first egg varied during the year (Fig. 2). In May new and old nest users had equal and relatively long delays, but in June and July delays were significantly shorter in both groups, and birds using old nests had half the delay of new nest builders (Fig. 2).

Falling nests were not common during the breeding season. I recorded only 4 nests with eggs or chicks that fell of natural causes; 2 were old and 2 new. Virtually all nest loss occurred during the winter.

Heavier birds did not preferentially build new nests in the first nesting period. There was no significant difference in male mass or wing chord between new and old nest users (Table 4), and, although the sample is small, the mean fat index was similar. Females that built new nests were the same size (wing chord) as those that used old nests, but they were significantly lighter and tended to have a lower fat index, contrary to the prediction.

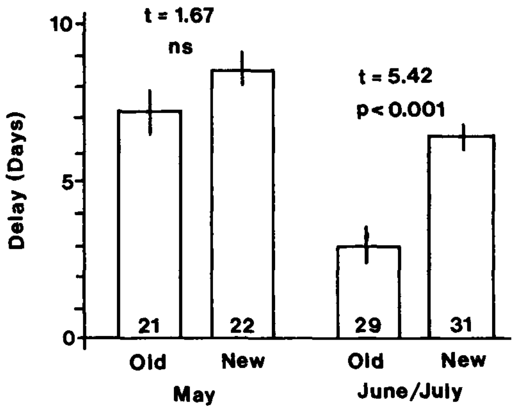

Fig. 2. Mean (±SE) delay (in days) between start of nest construction and first egg for old vs. new nests early in the year (May) and later (June/July). Number of nests is given at the bottom of each bar. *t*-values are given for comparison within each time period (ns = $P > 0.05$).

Discussion

Barn Swallows at Delta Marsh, as elsewhere (e.g. Samuel 1971, Shields 1984), used two nesting strategies: reuse of old nests and construction of new ones. Shields et al. (in press) predicted that because nest reusers save time and energy, in the absence of balancing costs they should realize a greater reproductive success than new nest builders. My results indicate that the two strategies result in equal reproductive success, both per nesting attempt and per season. This can be explained if the birds can assess accurately the various costs and benefits of each strategy in a particular territory before they nest, are not limited (e.g. by other individuals) in the ultimate choice they make, and thus settle in an ideal free manner (Shields et al. in press).

The costs and benefits a swallow must assess are many and probably vary geographically as well as temporally. New nests require more energy to build than an old one. There is also a cost in the added construction time required (Shields et al. in press), although at Delta this cost was apparent only late in the season. Early in the year there was no difference in the delay between nest and clutch initiation in old and new nests, presumably because low insect abundance and poor weather conditions delayed clutch initiation for all birds. The prediction that the increased time expenditure required to build a new nest would cause a shift toward greater old-nest use late in the season, when time becomes more important, was not supported. Evidently, the time difference is not important to the birds.

One cost of reusing an old nest is the added parasite load commonly found in them (Brown and Brown 1986, Shields and Crook 1987, this study). As pointed out by Brown and Brown (1986) and Shields and Crook (1987), the specific identity of nest parasites varies geographically, but they are invariably detrimental to birds using old nests. Mites in the nests at Delta were associated with a significant increase in nestling mortality. Whether they also reduced the fitness of chicks that survived to fledging (Moss and Camin 1970, Brown and Brown 1986, Shields and Crook 1987) could not be determined because I did not weigh nestlings, but it is not an unreasonable assumption.

One way birds can reduce the parasite cost of nest reuse is to use nests intermittently (Shields et al. in press) because many parasites, including mites, suffer high mortality if a nest is not used each year (Brown and Brown 1986, T. D. Galloway pers. comm., this study). Cliff Swallows accomplish this by occasionally switching colonies from year to year (Brown and Brown 1986). Barn Swallows need only switch nests, not entire colonies, because their dispersed nests reduce the possibility of para-

TABLE 4. Comparison of mean (±SE) wing cord, mass, and fat index for male and female Barn Swallows using old vs. new nests in 1986. Sample sizes are given in parentheses. $P < 0.02$ for female mass; for all other comparisons, $P > 0.05$.

		Wing (mm)	Mass (g)	Fat
Males	Old	117.9 ± 1.00 (8)	19.51 ± 0.44 (8)	1.7 ± 0.4 (6)
	New	118.5 ± 1.20 (7)	19.86 ± 0.39 (8)	1.6 ± 0.4 (5)
Females	Old	117.0 ± 1.26 (9)	21.34 ± 0.71 (9)	2.1 ± 0.3 (7)
	New	114.8 ± 1.34 (8)	19.03 ± 0.39 (8)	1.7 ± 0.5 (6)

sites migrating from one nest to another. I found that Barn Swallows selected nests at random with respect to their use the previous year. This still reduces the risk of using a parasitized nest, and at Delta a bird using an old nest had a 41% chance of selecting a parasitized one.

Barn Swallows do not use green vegetation in their nests (Bent 1942, this study), unlike some other species (e.g. Wimberger 1984, Clark and Mason 1985), and thus do not take advantage of the potential toxic qualities of compounds in the vegetation. I believe, however, that the swallows can recognize parasitized nests and avoid them, as Cliff Swallows appear to do (Brown and Brown 1986). Unparasitized nests were selected in the first nesting period. This option may be less available in the second nesting period because most nests used in the first period become parasitized, and the number of unparasitized nests per territory may initially be limited. In addition, there are probably fewer parasites in nests used the previous year compared with those used in the first nesting period. Another option might be to build a new nest for the second nesting period, a strategy some birds adopt, but nest-site quality may suffer. Another cost of nest reuse can be nest instability (Shields et al. in press), although at Delta this was less apparent. The strong winter winds undoubtedly removed most unstable nests before the beginning of the breeding season.

If nest instability is not a problem and Barn Swallows can assess nest parasite load and select unparasitized nests for the first nesting attempt, then there are no costs involved in using an old nest. Although there is also no benefit in terms of time early in the year, there is an energetic benefit, and old nests should be preferred, particularly by birds for which the cost of building new nests is more significant (those with low energy reserves). Because both sexes participate in nest construction (Bent 1942, Samuel 1971), fat-reserve differences might be expected in one or both. Although sample sizes were small, I found no such differences or (in females) the differences were opposite to that predicted. This may be related to the observation that yearling females more frequently build new nests (Shields et al. in press).

The fact that parasitized nests were used in the second nesting period and old nests were not preferred despite the energetic benefits may be explained by variable nest-site quality. Although there are usually several potential nest sites available in each territory, the quality of these sites in terms of shelter from sun, wind, and rain and protection from predators probably varies (Shields 1984). Presumably, the decision whether to build a new nest or use an old one takes into account the costs and benefits of each strategy and the quality of the sites available for a new nest vs. that of sites occupied by old ones.

Whatever criteria Barn Swallows use to choose nests, at Delta they opt to reuse nests (both between and within a season) much less often than has been found in other studies. Samuel (1971) found that 78% ($n = 59$) of clutches were laid in old nests in a study in West Virginia, and 19 of 33 pairs that raised a second brood did so in the same nest as their first brood. In New York 82% ($n = 188$) of active nests were old (Shields et al. in press), 36% of returning birds used the same nest as the year before, and 53% of renests were in the same nest (Shields 1984). This contradicts my prediction that shorter breeding seasons should correlate with greater nest reuse if latitude is taken as an indicator of the length of the breeding season. Latitude appears to be a poor indicator of the breeding season at Delta, however.

The Delta Marsh area is extremely productive, and insect abundance is very high, supporting high densities of nesting passerines (e.g. Busby and Sealy 1979, Sealy 1980) and roosting insectivorous bats (e.g. Barclay 1984). Swallows in this area therefore may not be stressed energetically during the latter stages of rearing their first brood and may have the energy reserves required to build a new nest for their second nesting attempt. Although insect abundance drops late in the summer (e.g. Busby and Sealy 1979), the decrease may not be as relevant as elsewhere if insect abundance is high initially, so the breeding season at Delta may be effectively extended. Comparative insect data are not available, but at Delta insect abundance starts to decline only in mid-August, and at the end of August it is still as high as at times during the middle of the summer (Busby and Sealy 1979).

My results suggest that the breeding season is extended at Delta. Snapp (1976) concluded that the length of the breeding season in New York limited the ability of Barn Swallows to rear a second brood and felt that birds hatching their first brood after 23 June could not raise a second brood successfully. The mean hatching dates in her study were 13 June and 23 July for the first and second broods. Equivalent dates at Delta were 7–10 days later, yet the success of second broods was high; 21 (78%) of 27 clutches hatched in August were successful.

A longer breeding season is also indicated by the fact that most birds reared a second brood, some even after losing an initial attempt. In other studies only 35–50% of pairs even attempted a second brood (Samuel 1971, Snapp 1976, Shields 1984). The result is that the seasonal reproductive success per pair at Delta is twice that of pairs in New York (Shields et al. in press). The longer breeding season at Delta means that the time-delay cost of building a new nest was not as critical as in New York. Swallows can afford to build new nests, avoiding the costs of using an old nest, and still rear two broods. Only in 1984, when the season was particularly late, did time appear to constrain the nesting of late-nesting pairs.

Shields et al. (in press) suggested that the benefits of nest reuse should be the same everywhere, but it appears that both the costs and benefits vary spatially and temporally in both relative and absolute terms. The time cost of building a new nest is relatively less important when the breeding season is extended. The actual number of days used to build a new nest also varies. It was shorter at Delta than in New York (Shields et al. in press) and can be as long as several weeks in Alberta (pers. obs.). Nest construction presumably can proceed faster in areas of high prey abundance, and the availability of mud also may contribute to variation in construction time. Mud is continuously available at Delta but may be available only after periods of rain in other areas, causing construction delays. The energetic cost of building a new nest probably does not vary much, but variable distance to sources of mud may be important. Environmental conditions affect the stability of old nests, and the risk of an old nest falling while in use may therefore vary. The types and numbers of parasites in reused nests varies, and the magnitude of the resultant cost probably also varies.

From the comparison of the nesting strategies adopted by Barn Swallows at Delta with those of swallows elsewhere, I conclude that individuals compensate for local costs and benefits and adopt a strategy that maximizes their reproductive success. By testing nesting strategy predictions at other sites, it may be possible to determine how Barn Swallows assess the costs and benefits of nest construction and reuse and the quality of nest sites.

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