CAVE SWALLOW (*Petrochelidon fulvus*) NEST REUSE IN EAST-CENTRAL TEXAS

A Thesis

by

MARGARET ELIZABETH BYERLY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2004

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Keith A. Arnold (Chair of Committee)	Roel R. Lopez (Member)
Larry J. Ringer (Member)	Robert D. Brown (Head of Department)

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ABSTRACT

Cave Swallow (*Petrochelidon fulvus*) Nest Reuse in

East-Central Texas. (December 2004)

Margaret Elizabeth Byerly, B. S., Randolph-Macon Woman's College

Chair of Advisory Committee: Dr. Keith A. Arnold

Although nest reuse is most commonly associated with costs such as nest instability and increased ectoparasite loads, contrary evidence supports the possibility that nest reuse might provide an adaptive function in the form of time and energy savings. The Cave Swallow (*Petrochelidon fulva*), which nests under bridges and culverts in east-central Texas, chooses predominately to reuse nests when old nests are available. I conducted a field experiment involving bridge pairs and single bridges, in which I applied a treatment of nest removal to one bridge of each pair and one half of each single bridge in order to test whether control bridges and nests exhibited increased productivity from the availability of old nests. I found that a higher percentage of young fledged from control bridges and more fledged per clutch from control bridges. Small sample sizes diminished the ability to detect differences within the single bridge experiment. Results from this research support the time-energy savings concept and may be reconciled with conflicting research through fundamental differences between studies in immunity to ectoparasites, infestation type, and nest microclimate.

For Mom, Dad, and Trevor

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I would like to thank my major advisor Dr. Keith Arnold, and committee members Dr. Roel Lopez, and Dr. Larry Ringer for their help with this project. I would also like to sincerely thank Dr. Markus Peterson for all of his generous assistance, support, and good humor. I would not have been able to complete this work without his help.

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My hardworking field assistants also deserve praise: thanks to Will Henry, Megan Meier, Rick Rogers, Megan Russell, and Jason Sanford for their hard work in hot, muddy conditions.

Finally, I'd like to thank my family and friends, and especially, my fiancé Trevor Williams, who is a saint.

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INTRODUCTION

Many avian species build nests out of durable materials which can remain intact for several breeding seasons (Watts 1987, Cavitt et al. 1999). Long-lasting nests provide some species with the option to reuse nests, rather than building new nests. However, much of the empirical evidence suggests the costs that a bird might incur from nest reuse makes this practice unlikely. Nest instability (Shields and Crook 1987) and increased ectoparasite loads (Brown and Brown 1986, Shields and Crook 1987, Barclay 1988, Loye and Carroll 1991, Loye and Zuk 1991, Oppliger et al. 1994, Rendell and Verbeek 1996b, Rytkonen et al. 1998, Szep and Moller 2000) are associated with nest reuse, and the number of ectoparasites in a nest increases the more a nest is reused (Rendell and Verbeek 1996a). High ectoparasite volume in a nest can lead to reduced productivity by negatively affecting the survival and growth of nestlings raised in infected nests (e.g., Rothschild and Clay 1952, Moss and Camin 1970, Capreol 1983, Brown and Brown 1986, Moller 1990). It is, therefore, not surprising that some species remove old nests before nesting (Pacejka et al. 1996), some will abandon old colonies after ectoparasites accumulate over several years (Emlen 1986, Loye and Carroll 1991), and others will abandon infested colonies between clutches within the same year (Chapman 1973, Newman 1980). Some cavity-nesting species avoid old nest material altogether in favor of clean cavities or nest boxes (Loye and Carroll 1991, Oppliger et al. 1994, Rendell and Verbeek 1996a, Rytkonen et al. 1998, Mazgajski 2003). All of this evidence has lead to the hypothesis that old nest material increases ectoparasite loads

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and , therefore, decreases the productivity of birds that choose to reuse nests (Moller 1989).

Despite all of the evidence that associates nest reuse with reproductive costs, this practice is not always avoided. Some secondary cavity-nesting birds do not avoid old nests (Thompson and Neill 1991, Orell et al. 1993 Johnson 1996), while some prefer to nest in boxes that contain old nests (Davis et al. 1994, Mappes et al. 1994, Olsson and Allander 1995). Olsson and Allander (1995) reported that Pied Flycatchers (*Ficedula hypoleuca*) actually preferred nest boxes which contained old nests, despite the presence of ectoparasites. Mappes et al. (1994) also found that Pied Flycatchers preferred to use old nest boxes, and upon further investigation, discovered that only the new nests in their study harbored ectoparasites.

Because avian species sometimes choose nest reuse as an alternative to building a new nest despite the assumed costs, nest reuse may provide an adaptive function (Cavitt et al. 1999). Several hypotheses exist to predict the function of old nests. Some have suggested that old nests might serve as cues for nest-site selection (Erckmann et al. 1990, Thompson and Neill 1991, Mappes et al. 1994, Olsson and Allander 1995). However, in a test involving Red-winged Blackbirds (*Agelaius phoeniceus*), Erckmann et al. (1990) found little evidence to support this hypothesis. Likewise, Yahner (1993) found that varying the number of remaining nests from the previous season did not affect nest establishment in small, even-aged forest plots. An alternative hypothesis suggests that the accumulation of old nests might protect a species from search-strategy predators (Collias and Collias 1964, 1978, Watts 1987, Mazgajski 2003). Although Watts (1987) found evidence suggesting that existing old nests may protect new active Northern Cardinal (*Cardinalis cardinalis*) nests, others had different results. Cavitt et al. (1999) tested if the presence of old Brown Thrasher (*Toxostoma rufum*) nests could saturate the search cues of predators, thereby providing protection for the currently breeding Brown Thrashers. These authors detected no evidence to support this, but suggested a third hypothesis: nest reuse may help birds save time and energy (Pearson 1974, Ueda 1989, Moller 1990, Conrad and Robertson 1993, Johnson 1996, Cavitt et al. 1999).

Many swallow studies have addressed the time and energy savings hypothesis in swallow nest reuse, as Cliff Swallows (*Petrochelidon pyrrhonata*) (Brown and Brown 1986), Barn Swallows (*Hirundo rustica*) (Samuel 1971, Shields 1984, Barclay 1988), and Cave Swallows (*P. fulva*) (Kosciuch 2002) all may reuse their mud nests. Collias and Collias (1971) maintained that nest building may account for a substantial amount of total breeding costs, which nest reuse avoids. According to Withers (1977), a major cost of nest construction was time loss. Completion of a new Cliff Swallow nest requires 5–15 days and 1,400–1,800 trips to a mud source (Withers 1977). Gauthier and Thomas (1993) agreed with this, reporting that Cliff Swallows preferred to build nests that were attached to other nests. This allows Cliff Swallows, whose attached nests require fewer mud pellets, to save about 18 minutes per day. Gauthier and Thomas (1993) suggested this extra time might be used for foraging and nest protection. Extra foraging time might enable the birds to build up more energy stores. Upon further investigation, Gauthier and Thomas (1994) did find that Cliff Swallow parents reusing nests started the nestling period with higher fat reserves than those that built new nests. Cliff Swallows that reused nests also provided more food for their nestlings than those that built new nests (Gauthier and Thomas 1994).

In his thesis research, Kosciuch (2002) found that Cave Swallows breeding in Brazos County, Texas, reuse nests significantly more often than they built new nests: 83% of Cave Swallows in Kosciuch's (2002) study reused old nests (n = 156). Koschiuch (2002) also found that Cave Swallows even modified Barn Swallow nests by adding a small rim of pellets to the preexisting structure more often than they built new nests. If such nest reuse enables these Cave Swallows to save time and energy, this practice should lead to enhanced productivity. However, Kosciuch (2002) found few differences in reproductive success between Cave Swallows that built new nests and those that reused nests. But, because his sample size was low (only 9 new Cave Swallow nests existed), the ANOVA lacked the statistical power needed to detect differences between reproductive success of new and used nests (Kosciuch 2002). In order to understand its relationship to reproductive success, these findings suggest the need for further studies of swallow nest reuse.

The Cave Swallow, which nests colonially under bridges and culverts with other swallows in east Texas (Martin and Martin 1978), exhibits a strong predisposition for nest reuse and modification in and around Brazos County, Texas, and thus provided a good opportunity to retest the time and energy savings concept. I hypothesized that, in order to increase reproductive success, Cave Swallows preferentially chose to reuse nests in place of building new nests. To test this, I investigated eight pairs of bridges, which contained old Barn Swallow and Cave Swallow nests and were relatively homologous in regard to several landscape characteristics. Each pair consisted of an untreated control bridge and an experimental treatment bridge, which was stripped of old nests. In order to account for extraneous landscape effects, I also investigated three single bridges in which half of all preexisting swallow nests were removed before the breeding season. All nests that were then built where the treatment had been applied were considered treatment nests, and all nests that occurred where nests were not removed were considered control nests. If the data supported the research hypothesis, then:

1. More nestlings per clutch would fledge from control nests and control bridges.
2. A higher percentage of nestlings would fledge from control nests and control bridges.

METHODS

Study area and bridge information— I conducted this study throughout Brazos County, Texas, and in south Robertson County, Texas, where all bridges were surrounded by post-oak savannah (Gould 1962) (Fig. 1). Because previous studies lacked the statistical power to detect differences between reproductive success of new and old swallow nests, the bridge sample size in this study was as high as time and resources permitted in an effort to amplify statistical power. In January 2003, I searched throughout Brazos County and south Robertson County for bridges and culverts with preexisting Cave and Barn Swallow nests. Of the 55 structures investigated throughout these counties, 14 bridges contained a sufficient number of old swallow nests for inclusion, along with five of the structures Koschiuch (2002) examined.

Sixteen of these bridges were organized into eight pairs according to the following six landscape characteristics (Table 1). Because large colony size is associated with better access to foraging information (Brown and Brown 1996), increased water availability (Brown et al. 2002), and greater ectoparasite abundance (Brown and Brown 2002) within Cliff Swallow colonies and is linked with increased egg hatchability (Brown and Brown 2001), I used both bridge area and the number of preexisting nests as criteria for pairing bridges. I also considered foraging habitat, another important factor, while pairing bridges. The Cliff Swallow's foraging habitat occurs within a 1 km radius of its colony (Brown et al. 1992, Brown and Brown 1996), and food abundance might affect reproductive effort (Orians 1969, Emlen and Oring 1977, Dunn and Hannon 1992, Richner 1992). Therefore, I attempted to

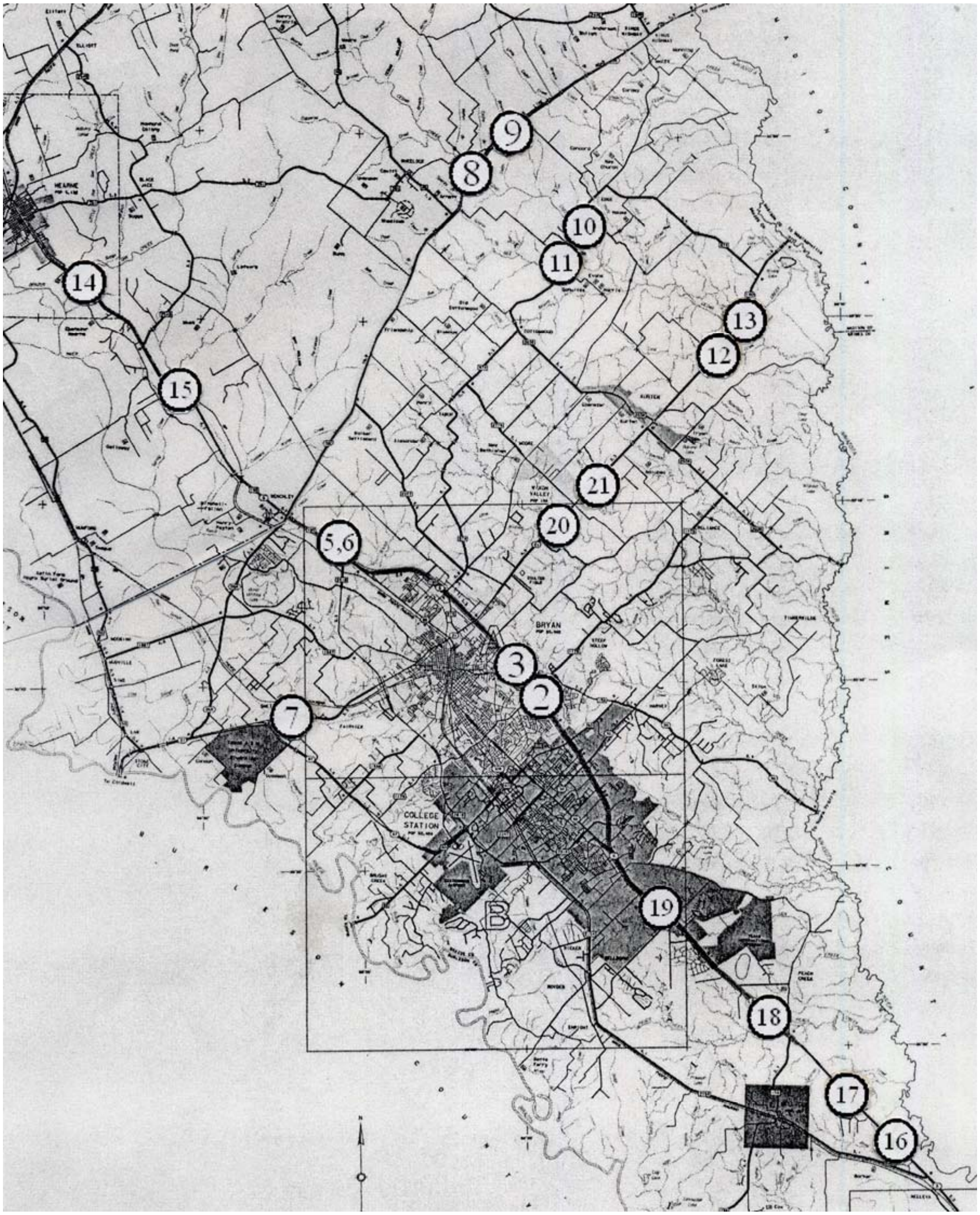

FIG. 1. Location of study bridges in Brazos County, Texas, and south Robertson County, Texas, for 2003 breeding season. Texas county highway maps used by permission of Texas Department of Transportation.

TABLE 1. Bridge locations, identification numbers, and landscape characteristics, which were used to pair the eight bridge pairs and designate the three single bridges in this study.

Bridge number	Bridge road	Stream or road traversed by bridge	Pair	Treatment type	Bridge orientation	Bridge area (m^2)	Traffic (AADT)	No. nests present before treatment
8	OSR	Cedar Creek	1	nests removed	east/west	3775	1975	25
10	FM 974	Cedar Creek	1	nests intact	east/west	2223	790	32
16	SH 6	Jones Creek	2	nests removed	north/south	9415	20850	125
19	SH 6 ML	Spring Creek	2	nests intact	north/south	9212	31000	111
7[a]	SH 21	Thompson Creek	3	nests intact	east/west	11476	8100	55
17	SH 6	Millican Creek	3	nests removed	north/south	6497	19700	58
12	US 190/SH 21	Sand Creek	4	nests intact	east/west	77088	7000	12
13	US 190/SH 21	Cedar Creek	4	nests removed	east/west	14176	7000	45
2[a]	Briarcrest Dr.	SH6	5	nests intact	north/south	6400	26900	23
3[a]	Booneville Rd.	SH6	5	nests removed	north/south	9900	21650	26

TABLE 1. Continued.

Bridge number	Bridge road	Stream or road traversed by bridge	Pair	Treatment type	Bridge orientation	Bridge area (m²)	Traffic (AADT)	No. nests present before treatment
20	US190/SH 21	Brazos Creek	6	nests removed	east/west	3544	9000	40
21	US 190/SH 21	Mathis Creek	6	nests intact	east/west	7088	9000	36
14	US 90/SH 6	Pin Oak Creek	7	nests intact	north/south	10290	14900	195
15	US 190/SH 6	Spring Creek	7	nests removed	north/south	12530	14900	204
9	OSR	Skubal Branch	8	nests intact	east/west	1482	1050	11
11	FM 974	Bee Creek	8	nests removed	east/west	2223	790	14
5[a]	US 190, west	Thompson Creek	—	half nests removed	north/south	3066	1775	31
6[a]	US 190/SH 6	Thompson Creek	—	half nests removed	north/south	10392	21000	53
18	SH 6	Peach Creek	—	half nests removed	north/south	39950	21000	119

[a] Five structures previously studied in Kosciuch (2002).

keep the distance between two paired bridges as close to 1-2 km as possible within the same general habitat so that the foraging ranges of those colonies might overlap. Because Cave Swallows historically only nested within the twilight zone in the caves and sinkholes of the Edward's Plateau, Texas (Selander and Baker 1957), bridges were also paired according to general bridge orientation, which affects how much sunlight and moonlight nests receive. Bridge type (over road or stream) and the amount of traffic on a bridge, measured by the Texas Department of Transportation as Annualized Average Daily Traffic (AADT), both were also used as criteria for matching bridge pairs because I hypothesized that close proximity to an available water source and disturbance might also affect swallow productivity. The experimental treatment was then randomly assigned to one structure from each pair. Once designated, all preexisting swallow nests were removed from each experimental structure prior to the 2003 breeding season using a painter's pole, which extended to 4.5 m.

Since no bridge pair satisfied all criteria perfectly, differences, which may affect reproductive success, remained between the two bridges of each pair. To avoid these landscape effects, I chose bridges 5, 6, and 18 as single bridges from which half of all preexisting nests were removed prior to the 2003 breeding season (Table 1). Because nests do not generally occur uniformly throughout a bridge, I inspected each single bridge to assess where nests were congregated. I then bisected the body of nests for each single bridge into equal halves according to nest congregation and randomly chose one half to be removed using the painter's pole. Under bridge 5, the eastern most nests were removed, and under bridge 6, the southern most nests were removed. In bridge 18 all preexisting nests were assembled towards the northeast side of the bridge. Because bridge 18 is so large, comprised of five sections each with an area of 7,990 m^2, the northern most nests were removed from each of these sections.

Data collection and analysis—In mid March 2003 at the beginning of the breeding season, I mapped the nests at each bridge. I assigned each nest a location and number, and new nests were added to the maps as they were built. Maps from previous summers were used to track any old nests remaining at bridges 2, 5, 6, and 7, as Koschiuch (2002) investigated these bridges during the 2000 and 2001 breeding seasons, and I examined them during a pilot study in 2002.

Once the swallows returned and began nesting in mid March 2003, I assembled a field crew of six interns, and we visited each bridge every three to seven days and recorded date, time, and contents of each nest (eggs, nestlings, fledglings). Data were obtained using painter's poles with attached auto-inspection mirrors. I followed the methods for determining incubation and nestling periods used by Kosciuch (2002). If eggs were laid between checks, I determined lay date by back-dating one egg per day. The incubation period started on the day the last egg was laid and continued until the hatching of the last egg. Nestling period began the day the last egg was hatched and continued until the last nestling fledged. If hatching or fledging occurred between checks, I assumed the mid-point between checks as the exact date of hatching/fledging. Cave Swallow nestlings that fledged after 18 days were considered successful. The first successful clutch to fledge at a nest was considered the first brood, and the second successful clutch was considered second brood and so on.

Upon completion of data collection, I computed fledged/clutch and percent fledged for each of the bridge pairs and all three single bridges in order to create standardized response variables. This was necessary to account for differences between and among bridge pairs. I also tallied total eggs laid, total clutches laid, and total fledged for each of the 19 bridges. Because the resulting data were both non normal and had unequal variances, I then performed the statistical analysis using the Wilcoxon Signed Ranks test in SPSS version 11.5 (SPSS 2002) to examine for differences in the response variables between the control and treatment bridges of the bridge pairs and the control and treatment nests of the single bridges.

RESULTS

Bridge pairs. —All Cave Swallow colonies in this study existed in the presence of Barn Swallow colonies, and some also in the presence of Cliff Swallow colonies (Table 2). I collected data from 681 Cave Swallow nests within the bridge pairs, which were both active (contained at least one clutch) and accessible with the nest pole. Of these, 309 nests were used for data analysis (Table 2). The remaining nests were not used due to road construction at bridge pair 6, a House Sparrow (*Passer domesticus*) infestation at bridge 14 of pair 7, and insufficient data for the three accessible Cave Swallow nests located at bridge 11 of pair 8. Some nests from each bridge were inaccessible because they were too high or had very narrow openings. These and other nests were excluded because they were missed altogether by the field crew (Table 2).

Mean fledglings/clutch was 2.53 ± 0.08 and 3.06 ± 0.20 (SE, n = 5) for treatment and control bridges, respectively. Median fledglings/clutch for treatment and control bridges was 2.57 and 3.32, respectively. Mean percentage fledged was 72.73 ± 3.05 and 85.48 ± 2.39 (SE, n = 5), for treatment and control bridges, respectively. Median percentage fledged for treatment and control bridges was 70.71 and 86.06, respectively. Both fledglings/clutch and percent fledged were significantly lower for the treatment bridges (Wilcoxon, $P < 0.05$, n = 5; Figs. 2, 3). Total fledged, total eggs laid, and total clutches laid did not differ significantly between treatment and control bridges (Wilcoxon, $P > 0.10$, n = 5; Table 3). However, with the exception of bridge pair 3, there is a slight trend of more individuals fledging at control bridges as compared to their paired treatment bridges (Fig. 4).

TABLE 2. Number of Cave Swallow nests from each bridge used in analysis along with types and quantities of Barn, Cave, and Cliff Swallow nests present at all 19 study bridges during the 2003 breeding season.

Bridge number	Pair	Number of Barn Swallow nests[a]	Number of Cave Swallow nests[a]	Number of Cliff Swallow nests[b]	Number of Cave Swallow nests used in study[c]
8	1	1/2	20/8	0	19
10	1	4/6	22/8	0	21
16	2	21/1	89/3	0	72
19	2	43/2	94/5	0	80
7	3	8/6	26/19	0	18
17	3	16/1	53/1	0	48
12	4	2/0	17/3	36	13
13	4	10/7	18/12	80	16
2	5	4/1	14/3	12	13
3	5	3/2	10/2	1	9

TABLE 2. Continued

Bridge number	Pair	Number of Barn Swallow nests[a]	Number of Cave Swallow nests[a]	Number of Cliff Swallow nests[b]	Number of Cave Swallow nests used in study[c]
20	6	0/2	22/0	0	—
21	6	12/0	30/4	0	—
14	7	59/6	98/9	40	—
15	7	22/6	157/6	0	—
9	8	7/0	8/0	0	—
11	8	4/4	3/3	0	—
5	—	7/11	13/1	0	10
6	—	10/7	15/15	66	15
18	—	89/0	152/2	70	128

[a] active nests/ inaccessible or accidentally missed nests that were not monitored.

[b] number of intact nests; these were never monitored.

[c] active nests for which sufficient data exists; used in this study's analysis.

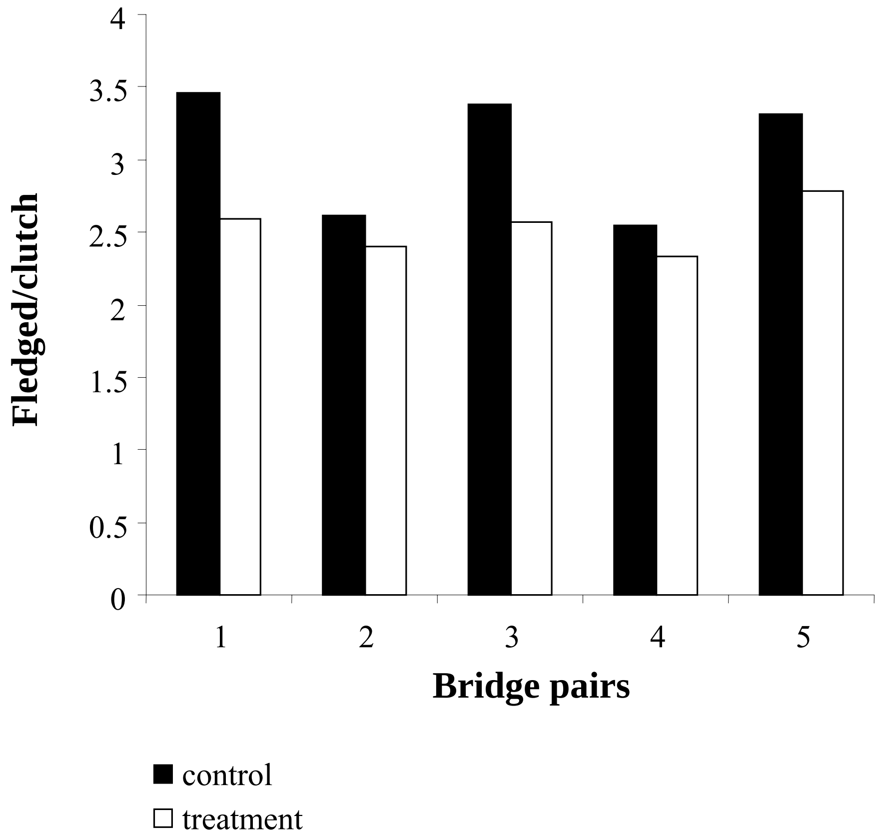

FIG. 2. Total number of birds fledged per total number of clutches laid for both control and treatment bridges of bridge pairs one through five.

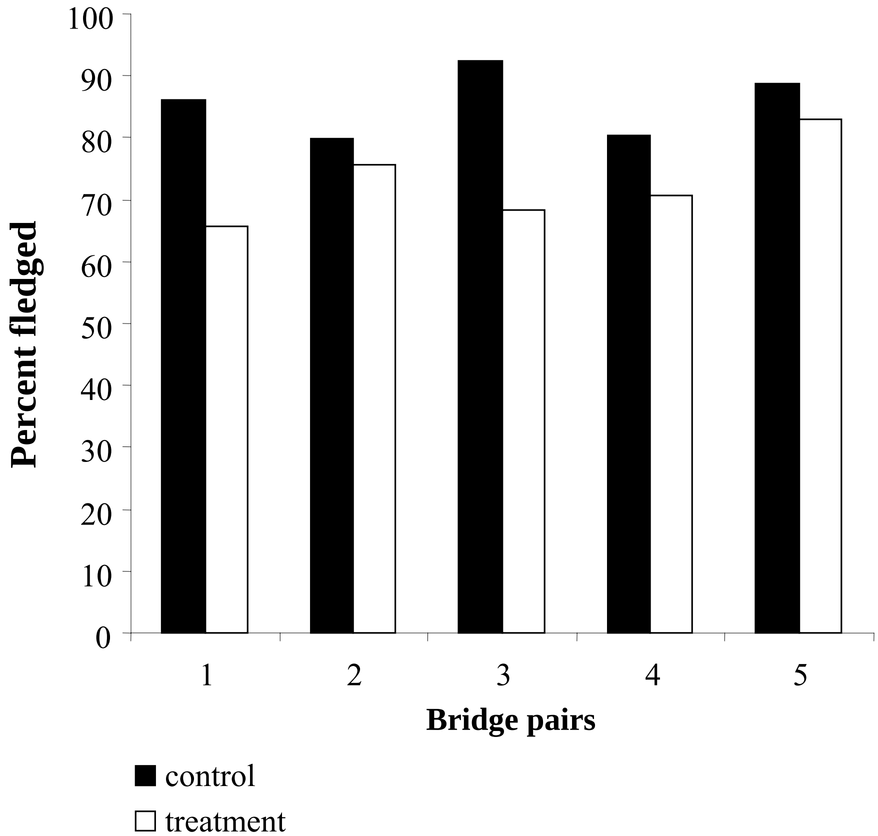

FIG. 3. Percent fledged from each treatment and control bridge of bridge pairs one through five.

TABLE 3. Reproductive success of Cave Swallows nesting at treatment and control bridges for bridge pairs one through five. Values are means ± SE and medians with upper and lower 95% CI.

Reproductive variable	Treatment bridges				Control bridges			
			95% CI				95% CI	
	$\bar{x} \pm SE$	median	Upper	Lower	$\bar{x} \pm SE$	median	Upper	Lower
Fledged/clutch[a]	2.53 ± 0.08	2.57	2.79	2.33	3.06 ± 0.20	3.32	3.46	2.55
Percent fledged[a]	72.73 ± 3.05	70.71	82.98	65.75	85.48 ± 2.39	86.06	92.31	79.85
Total fledged	165.80 ± 64.97	96	388	39	163.80 ± 68.46	108	432	63
Total clutches	67.00 ± 27.14	37	162	14	57.20 ± 27.18	32	165	19
Total eggs laid	229.80 ± 86.73	146	512	47	197.20 ± 87.37	117	541	71

[a] Wilcoxon Signed Ranks test, frequency distributions of treatment and control bridges are significantly different, $P < 0.05$.

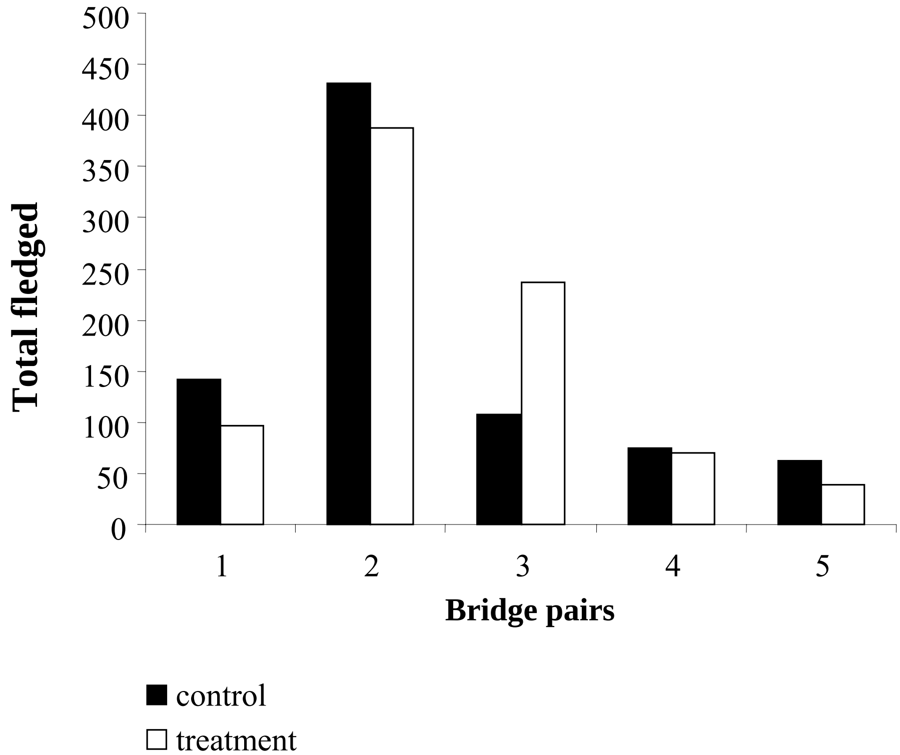

FIG. 4. Total number of young fledged from both treatment and control bridges of bridge pairs one through five.

Single bridges—Of the 180 accessible active Cave Swallow nests within bridges 5, 6, and 18, 153 nests had sufficient data for data analysis (Table 2). None of the reproductive variables differed significantly between treatment and control nests (Wilcoxon, $P > 0.10$, n = 3; Table 4). Even so, the control nests at each of these three bridges seem to show a trend of more eggs laid, clutches laid, and individuals fledged from (Figs. 5, 6, 7).

TABLE 4. Reproductive success of Cave Swallows nesting in treatment and control nests at the three single bridges: 5, 6, and 18. Values are means ± SE and medians with upper and lower 95% CI.

Reproductive variable	Treatment bridges				Control bridges			
			95% CI				95% CI	
	$\bar{x}$ ± SE	median	upper	lower	$\bar{x}$ ± SE	median	upper	lower
Fledged/clutch	2.23 ± 1.15	2.83	3.86	0	3.12 ± 0.29	3.21	3.56	2.57
Percent fledged	55.67 ± 28.37	74	93	0	82.00 ± 7.02	88	90	68
Total fledged	65.67 ± 52.75	27	170	0	178.00 ± 127.05	57	432	45
Total clutches	22.67 ± 18.75	7	60	1	66.00 ± 51.00	16	168	14
Total eggs laid	87.00 ± 71.40	29	229	3	250.00 ± 193.03	63	636	51

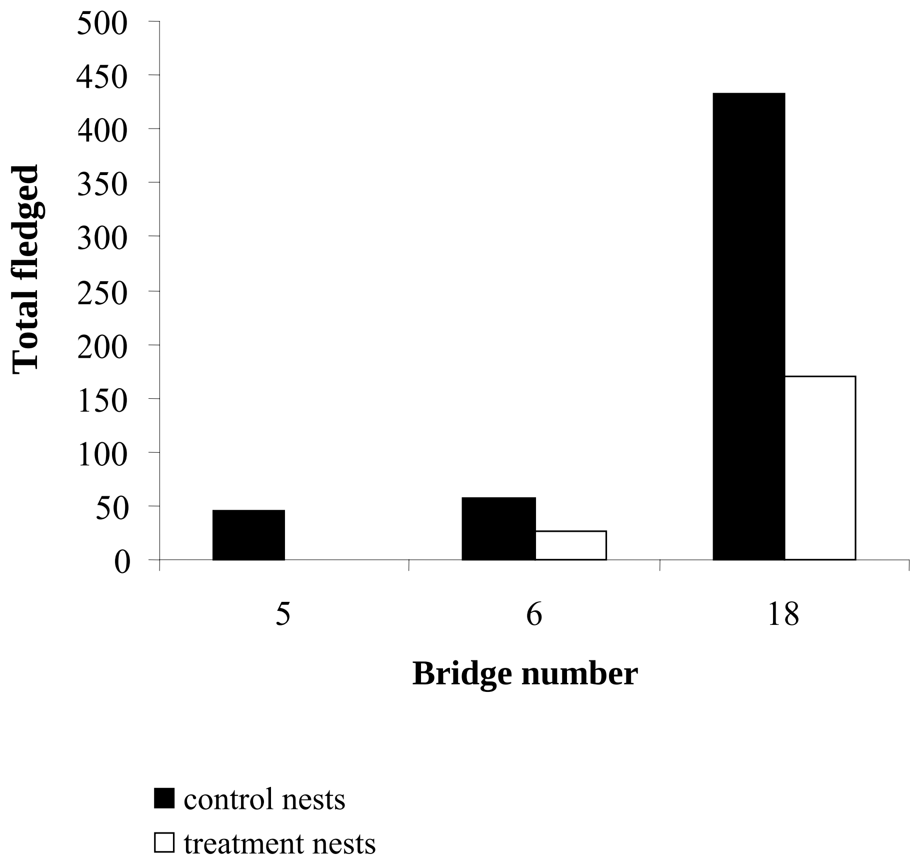

FIG. 5. Total young fledged from control nests and treatment nests at single bridges 5, 6, and 18.

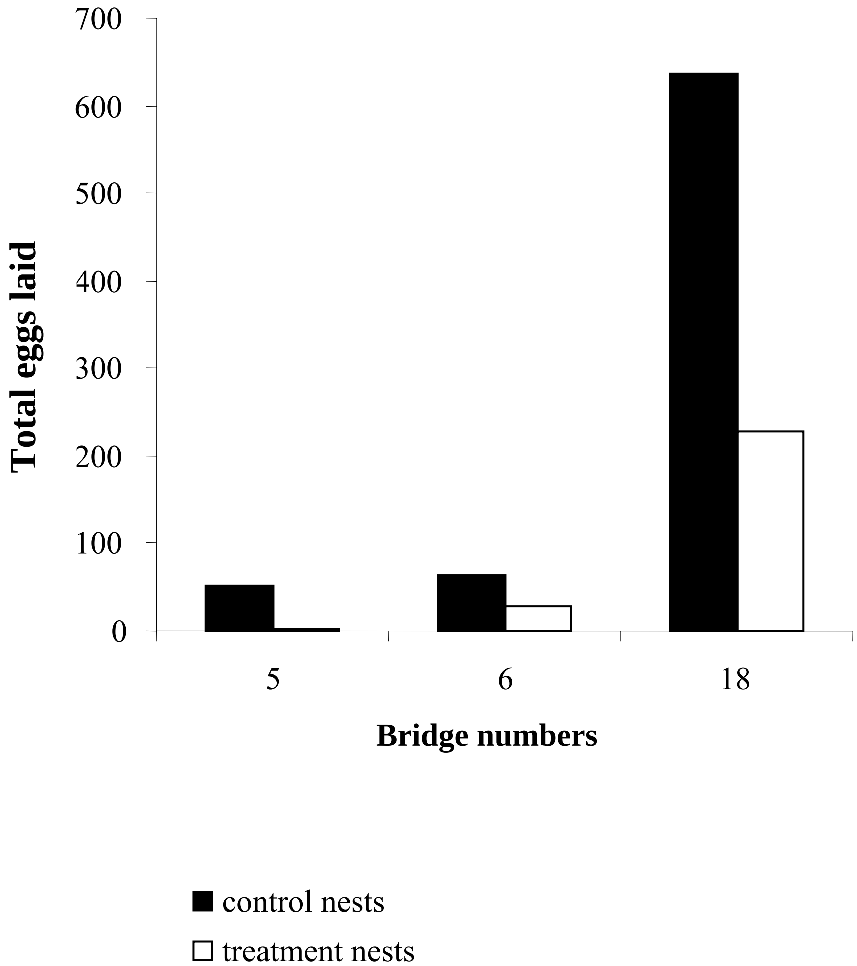

FIG. 6. Total eggs laid in control nests and treatment nests at single bridges 5, 6, and 18.

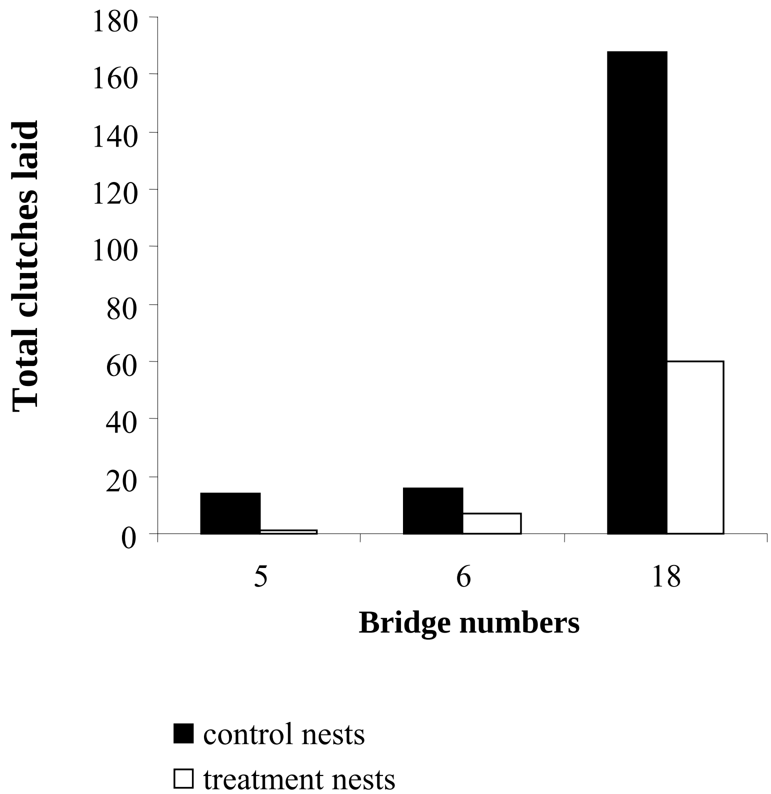

FIG. 7. Total number of clutches laid in control nests and treatment nests of single bridges 5, 6, and 18.

DISCUSSION

Bridge pairs—Treatment bridges fledged a lower percentage of young and had significantly lower fledglings/clutch as expected. Bridge colonies in which Cave Swallows had access to preexisting nests from the beginning of the breeding season fledged a higher percentage of young and fledged more young per clutch than colonies where all nests were new. Because of the extraneous differences within each bridge pair, it is not surprising that total fledged, total eggs laid, and total clutches laid did not differ significantly among the treatment and control bridges. However, the treatment bridges for pairs 1, 2, 4, and 5 all fledged slightly less young than the control bridges, which was expected (Fig. 4). Pair 3 did not follow this trend, but the bridges within this pair (7, 17) were not paired as appropriately as the rest. Bridges 7 and 17 differed greatly by bridge area, orientation, and surrounding habitat, thus accounting for such a disparate treatment effect (Table 2).

Single bridges—Low sample size most likely affected the ability to detect differences between productivity of treatment and control nests at bridges 5, 6, and 18. At all 3 of these bridges, total fledged, total eggs laid, and total clutches laid were much higher for control nests that had been reused. However, the power to detect these differences was very low.

In this study, results from the bridge pair experiment indicate that nest reuse benefits Cave Swallows in east-central Texas. These results agree with several swallow studies previously mentioned (Withers 1977, Gauthier and Thomas 1993, Gauthier and Thomas 1994) and support the hypothesis that nest reuse does allow time or energy savings, which are then manifested in higher productivity at colonies where previously existing nests are available. These results conflict with the outcomes of other swallow studies, which also examine the effects of nest reuse (Barclay 1988, Moller 1990, Loye and Carroll 1991, Rendell and Verbeek 1996a). However, Barclay (1988) found evidence to suggest that costs and benefits of nest reuse can vary spatially and temporally. Nest reuse costs and benefits that change depending on location or time might explain the discrepancies between these different results.

Barclay (1988) also suggested that "individuals compensate for local costs and benefits and adopt a strategy that maximizes their reproductive success." Cave Swallows in this study benefit from nest reuse. Therefore, the costs typically associated with this practice must be somehow diminished or not exist at all in this location. This could occur in several ways. First, both Barn Swallows and Cliff Swallows exhibit the ability to assess a nest's parasite load (Brown and Brown 1986, Barclay 1988). Cave Swallows may possess this same quality, allowing them to avoid old nests in which ectoparasite costs would outweigh any benefits of nest reuse. The type of nest infestation may also help explain this study's results. Second, according to Rendell and Verbeek (1996b) parasites that require over-winter survival in a nest are more prevalent among old nests. Various unidentified ectoparasites were visible in and out of the Cave Swallow nests throughout the 2003 breeding season, but if none of these parasites over-winter in nests, this cost would be eliminated, thus possibly explaining this study's results.

Third, it is also possible for few or no ectoparasites to exist in reused nests. Microclimate variability exists in nest sites (Erbelding-Denk and Trillmich 1990) and influences parasite development (Holland 1985). Eeva et al. (1994) found that the flea populations in nests of Pied Flycatchers and Great Tits (*Parus major*) correlated negatively with nest moisture. Sikes and Chamberlain (1954) discovered that changes in temperature and humidity affects the generation time of fowl mites. Fourth, parasites are often associated with predators, which may check their population numbers (Gold and Dahlsten 1989, Burtt et al. 1991). Davis et al. (1994) found the predatory parasitoid wasp larvae (*Nasonia vitripennis*), which feeds on blowflies, in old nests found in Eastern Bluebird (*Sialia sialis*) nest boxes. If such hostile nest conditions existed for ectoparasites in this study, this might also explain the observed results.

Fifth, even if ectoparasites thrived in the Cave Swallow nests, it is possible for hosts to develop immunity to this. According to Moller and Erritzoe (1996), host/parasite coevolution occurs when a large group of birds reuses nests, thus increasing transmission of the parasite and pressure on the host. These authors discovered that avian "species that reused their nest sites consistently had larger immune defense organs than species that did not re-use their nests or did so to a smaller extent" (Moller and Erritzoe 1996). In this study 95.3% of the nests were reused at the control bridges (n = 172), and 75% of the nests were reused in the single bridges (n = 180). These results are similar to a previous study involving Cave Swallows in east-central Texas (Kosciuch 2002). Because nest reuse is so prevalent among the Cave Swallows in this study and has been prevalent in the past, these colonies may have developed immunity to ectoparasites associated with reused nests, thus making nest reuse a very effective strategy.

In order to further understand Cave Swallow nest reuse, future studies should focus on how Cave Swallows in east-central Texas avoid nest reuse costs. Because Cave Swallows here reuse nests so frequently and enhance productivity via nest reuse, future investigations of these birds should examine their immune defense organs, nest microclimates, and ectoparasite types and life histories to see if any of these effectively decrease ectoparasite loads. It would also be beneficial to compare this information to a separate population of swallows that avoids nest reuse. Any differences in immunity, nest microclimate, and/or ectoparasites between the two populations would help explain why nest reuse is such a strategic practice for Cave Swallows nesting in east-central Texas.

CONCLUSIONS

Cave Swallows in east-central Texas enhance their productivity by reusing nests. Traditional costs associated with nest reuse are either effectively avoided or do not exist for birds in the study colonies. Some evidence suggests that Cave Swallows in this study may have developed immunity to ectoparasite infestations associated with nest reuse.

Scientists have reported various swallow species and other cavity-nesters both avoiding old nests and choosing to reuse nests. The attractiveness of old nests varies among studies and seems to hinge on ectoparasite loads or the ability of birds to deal with this cost. Many factors other than nest age affect whether nest reuse is an effective breeding strategy for avian species. Nest microclimate, ectoparasite type, an individual's ability to assess a nest's ectoparasite load, the presence of parasite predators, and enhanced parasite immunity all play a part in determining whether nest reuse is strategic. When the costs of nest reuse are eliminated, swallows and other cavity nesters should choose to enhance reproductive success by reusing nests.

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