EFFECTS OF PREDATION AND COMPETITOR INTERFERENCE ON NESTING SUCCESS OF HOUSE WRENS AND TREE SWALLOWS[1]

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Abstract. I examined the relationships among brood survival in House Wrens (*Troglodytes aedon*) and Tree Swallows (*Tachycineta bicolor*) and rates of nest-box use, species interference, and nest predation. Tree Swallows nested in boxes in one of three woodlands occupied by House Wrens. Over a 4-year period, clutch mortality rates in swallows were significantly higher than those in wrens, but wrens on swallow-free plots had lower failure rates than wrens that coexisted with swallows. Though conspecifics interfered at 9 of 99 (9%) wren nests, predation was the major cause of wren nest failure, accounting for 70% of 27 unsuccessful attempts. Increased nest failure in wrens was associated with increased rates of box use. In contrast, clutch mortality in Tree Swallows was related to nest interference by wrens. Of 29 swallow nests, 13 (45%) showed signs of interference by wrens, and eight of these 13 (62%) were initiated in boxes containing empty "dummy" nests built earlier by wrens. House Wrens are interference competitors because they exclude swallows from boxes by destroying swallow nests. Destroying nests of other species has advantages for wrens if high concentrations of empty nests, including dummy nests, inhibits search efficiency of predators. An experimental approach is recommended for testing the hypothesis that House Wrens build dummy nests and destroy heterospecific nests because empty nests deceive predators.

Key words: Interference competition; clutch mortality; nest predation; box-use rate; dummy nest; riparian woodlands; House Wren; Troglodytes aedon; *Tree Swallow;* Tachycineta bicolor.

INTRODUCTION

The availability of nest holes may limit abundances of secondary cavity-nesting birds (Von Haartman 1957; Holroyd 1975; Gustafsson 1988; Brawn and Balda 1987, 1988). House Wrens and Tree Swallows are secondary cavity-nesters whose abundances often increase after introduction of nest boxes (Low 1933, Drilling and Thompson 1984, Yahner 1983/1984). Male House Wrens build dummy nests and defend multiple cavities within their territory boundaries (Kendeigh 1941, Belles-Isles and Picman 1986a), thereby limiting breeding opportunities for other nesting pairs. In Tree Swallows, territorial defense in the form of aggressive attacks can prevent conspecifics from breeding even when unoccupied boxes are present (Harris 1979, Robertson and Gibbs 1982). Intraspecific competition for nest sites and mates in these species can apparently lead to nest usurpation (Leffelaar and Robertson 1985), floating

populations (Stutchbury and Robertson 1987a), brood parasitism and egg dumping (Lombardo 1988, Picman and Belles-Isles 1988, Price et al. 1989), bigamy and extra-pair copulations (Quinney 1983, Johnson and Kermott 1989), infanticide (Belles-Isles and Picman 1986b, Robertson and Stutchbury 1988), and killing of adult conspecifics (Lombardo 1986, Belles-Isles and Picman 1987).

Under conditions of nest-site limitation, the consequences of interspecific competition for nest boxes and natural tree holes may overshadow the effects of intraspecific competition (Van Balen et al. 1982, Gustafsson 1988, Ingold 1989), resulting in reduced reproductive success of the subordinate competitor (Gustafsson 1987, Ingold 1989). In House Wrens, both sexes puncture eggs and destroy nests of open-nesting birds (Belles-Isles and Picman 1986b) and other cavity-nesting species (Gardner 1925, Sherman 1925, Kendeigh 1941). Belles-Isles and Picman (1986b) speculated that interspecific competition for food or nest sites may explain nest-destroying behavior by House Wrens. If House Wrens dominate

[674]

interactions, then interference competition by wrens may result in lowered reproductive success in other species. Yet, no studies have compared reproductive success in House Wrens to success in hole-nesting species exposed to wren interference. Unfortunately, effects of predation on nest distribution and brood survival can mask or be mistaken for results of competition (Nillson 1984). To determine if interspecific competition is assymetrical, interference effects must first be isolated from nesting losses caused by factors like predation.

In the central Rocky Mountains, House Wrens and Tree Swallows frequently co-occur in foothill riparian woodlands (Finch 1989a); House Wrens numerically dominate cavity-nesting avifaunas in these habitats, with population levels that are two to three times higher than Tree Swallows (Finch 1987, Finch 1989b). During a study of nest-site selection by House Wrens (Finch 1989c), I observed that swallows and wrens were syntopic in one of three woodlands containing nest boxes. Here, I postulate that temporal, spatial, and interspecific differences in frequencies of box use influence reproductive success of wrens and swallows through effects on probabilities of nest destruction and competitive interference. For example, rates of nest predation were positively associated with densities of box-nesting Great Tits (Parus major) (Krebs 1971, Dunn 1977) but were unrelated to densities of other cavity-nesting species (Tompa 1967, Brawn 1987). Variation in the densities or spacing of box-nesters may also influence competition for nest sites, dictating rates of box intrusion (Kendeigh 1941, Muldal et al. 1985) and subsequent nesting success.

In this study, I predicted the following: (1) rates of nesting failure in wrens and swallows vary in relation to probabilities of nest predation or interspecific interference, (2) spatial and temporal changes in frequencies of nest destruction and interspecific nest intrusion are associated with differences in box availability and rates of box use, (3) in areas of syntopy, House Wrens outcompete Tree Swallows for boxes as reflected by interspecific differences in rates of interference and nesting success, and (4) wrens benefit by the absence or exclusion of nesting swallows such that wren productivity is higher in areas without swallows than in areas with swallows. These predictions were addressed by first assessing and then controlling for spatial and temporal vari-

ability in nesting productivity and focusing on correlative relationships among the residuals of rates of box use, interference, and nesting failure. To determine if availability and frequency of use of nest boxes influenced rates of nest destruction and competition, I used the ratio of used to total nest boxes as an index. If the number of potential sites that remain unused or empty is as informative to search-strategy predators or competitors as the number of used sites (e.g., Watts 1987, Martin and Roper 1988), then this ratio may be a more relevant predictor of "density-dependent" interactions than abundances of birds or nests.

STUDY AREA

Three study plots were established in May 1982 in streamside habitats in Carbon County, southeastern Wyoming, at elevations ranging between 2,050 and 2,250 m. One plot was established at Rock Creek 5 km northeast of Arlington, and two plots, named Foote Camp and Treasure Island, were spaced 34 km apart along the North Platte River near Saratoga. House Wrens nested in boxes at all three plots, but Tree Swallows used boxes at Foote Camp only. Woodlands were dominated by narrowleaf cottonwood (Populus angustifolia), a variety of shrub species, especially willows (Salix spp.), and herbaceous species. Shortgrass prairie interspersed with sagebrush (Artemisia tridentata) bordered riparian woodlands. Vegetation composition of the study areas is described in greater detail in Finch (1987, 1989c).

METHODS

On each of the three plots, 21 to 22 nest boxes (n = 65 boxes) were mounted at heights of 2 m on live deciduous trees >10 cm dbh. The number of boxes on each plot was limited by habitat patch size. Boxes were spaced at intervals of 30–35 m in grids conforming to the shape and size of the riparian corridor. Nest boxes were built of cedar 1.7 cm thick, 14 × 14 × 28 cm in outside dimension, with latchable top doors and entrances 3.8 cm diameter. Boxes were labeled with grid coordinates. Although natural cavities were available, spot-map checks indicated that most cavity-nesters shifted to boxes after they were erected.

I determined status (empty or occupied) of box and progress of nesting attempts by checking all nest boxes early in the afternoon every 2–4 days

from mid-May to early August of 1983 through 1986. Because of the short period of temperate weather, only a few boxes were nested in more than once in a single breeding season, either by the same nesting pair, by different pairs, or by different species. Based on observations of entry by other species or additional conspecifics into occupied boxes, and records of egg destruction, followed by subsequent egg laying, it appeared that some "second" clutches were products of usurping birds. Therefore, to indicate competitive pressure for boxes, estimates of box-occupancy rates were based on all nests. Use rates of species were pooled because concurrent use of multiple boxes by both species (1) reduces availability of nest sites, fostering conditions that may favor interspecific and intraspecific competition, and (2) increases abundance of active box nests, possibly encouraging search-strategy predation. Occupancy rate, defined as the ratio of the number of nests to the total number of boxes available, was computed by plot and year for comparisons with rates of interspecific nest interference and nesting failure. Occupancy rate was also calculated using wren nests only. Boxes were cleaned out each September so that new twigs and nests were not confused with box contents from the previous year.

Because individual male House Wrens frequently stuff multiple cavities with twigs (Kendeigh 1941), the appearance of the first egg was used as an index to nesting. Nests were considered abandoned if adults no longer attended the nest, and nest contents failed to hatch or fledge. Predation was assumed if nest material was disturbed, whole clutches disappeared, eggs or nestlings were partially eaten, predator feces were found in the nest, boxes were damaged or unlatched, or nests were empty before nestlings were due to fledge. Partial losses resulted from egg puncturing by intruders, hatching failure, and nestling starvation. Reproductive outcome was classified as successful, even in reduced broods, if at least one offspring fledged from the nest.

House Wrens, which are known to destroy nests of their own and other species, may interfere at nests of nearest neighbors. Observations of behavioral interactions between species were recorded during nest checks. Because the materials used to construct nests differ between Tree Swallows and House Wrens, I inferred entry into an occupied box by another species when foreign nesting material appeared. Boxes were used by

Tree Swallows and House Wrens exclusively. Interference by House Wrens at Tree Swallow nests was determined if twigs were found in boxes after swallows constructed grass nests, or if wrens were observed at swallow nests. Pierced or cracked eggs, partial clutch losses, or emptied swallow nests were sometimes discovered at, or following, the time of box intrusion by wrens. Interference by swallows at wren nests was recorded if twig nests lined with feathers were built first, followed by construction of grass nests. Interference by conspecifics was assumed when three or more birds were observed simultaneously using an occupied box, when a singing male chased another singer from the box, or when, on the swallow-free plots, wren eggs were punctured or lost between successive nest checks from nests that otherwise remained unaltered and active. Some cases of destruction of entire clutches (Freed 1986a) were probably overlooked because I scored them as predation by mammals and snakes (see Finch 1989c); thus, my estimates of nest interference are conservative. If partial clutch losses were recorded prior to total loss, egg destruction by wrens or swallows was designated.

Interference rate was defined as the number of nests showing signs of interference divided by the total number of nests. The likelihood of interference at nests of wrens, swallows, or both species may be related to availability of nest sites, herein indicated by box-occupancy rate. I first assessed the influence of the factors PLOT (1–3) and YEAR (1983–1986) on occupancy rate and interference rate at nests of House Wrens or both species by applying two-way analysis of variance (procedure MANOVA, SPSS/PC+). Differences in occupancy rates between plots were detected using a Student-Newman-Keuls (SNK) test of multiple comparisons. To determine if interference rate was associated with occupancy rate, I controlled for the effects of the extraneous factors PLOT and YEAR by entering the casewise residuals listed by MANOVA in subsequent tests. Pearson's product-moment correlations were used to compare the residuals of occupancy rate with the residuals of either of the dependent variables, interference rate at wren nests or interference rate at all nests. Number of plots occupied by Tree Swallows was insufficient for statistical analyses of interference rates at swallow nests.

The probability of clutch mortality was calculated using Mayfield's (1961, 1975) method based on the number of days of exposure (EXP)

that a known nest is at risk. Estimates of daily mortality rate of whole clutches (clutch $\dot{m}$), probability of survival for one day (clutch $\hat{s}$), and probability of survival through the incubation and nestling phases of length t days (clutch $\hat{s}^t$) were calculated for each species by plot and year. I used Mayfield's formula based on egg or nestling days of exposure to compute the daily rate of partial losses (partial $\dot{m}$) and the survival probability of reduced clutches through the entire nest period (partial $\hat{s}^t$). Total probability of mortality for the entire nest period (total $\dot{m}^t$) is equal to 1 − (clutch $\dot{m}^t$ × partial $\dot{m}^t$ × hatching rate). Nests were visited frequently so I used Mayfield's midpoint assumption (Johnson 1979).

To obtain a large-sample estimate of the variance (V) of $\dot{m}$, I used Johnson's (1979) estimator EXP^3/((EXP − losses) × losses). To test for variation in daily mortality rates between species and study areas, I used the statistic $(\hat{s}_2 - \hat{s}_1)/(V(\hat{s}_1) + V(\hat{s}_2))^{1/2}$ (Johnson 1979), where the subscript specifies each treatment group (note that $\dot{m}_1 - \dot{m}_2 = \hat{s}_2 - \hat{s}_1$). If the resulting value is greater than the statistic, $z_{1/2}$, then the null hypothesis that $\dot{m}_1 = \dot{m}_2$ is rejected. I pooled wren nests from the two box grids that had no swallows because wren fledging success by year was similar between these grids (Finch 1989c). Using z-statistics, nesting mortality in this pool of wren nests was then compared by year to mortality of wren or swallow nests found on the grid shared by both species. Probability values obtained from independent tests by year were combined using Fisher's procedure (Sokal and Rohlf 1981) for deriving an overall significance test based on multiple outcomes. The first study year was regarded as a transitional period during which returning migrants learned the locations of nest boxes, and therefore, 1983 results were excluded from combined-year tests to reduce bias.

Effects of rates of box use and nest interference on nesting success of wrens or both species were assessed using partial correlational analyses. I first used two-way ANOVAs to remove the effects of PLOT and YEAR from each continuous variable and then correlated resultant residuals of clutch $\dot{m}$ and partial $\dot{m}$ to residuals of interference rate and occupancy rate entered concurrently. To evaluate the independent influences of interference rate and occupancy rate on nesting success, I separated out the effect of either variable and reported the resulting partial correlation coefficient (r_p). Numbers of swallow nests
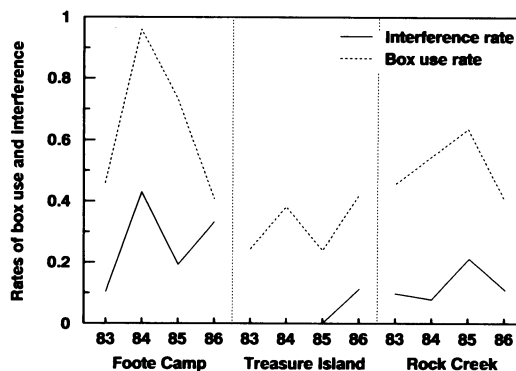

FIGURE 1. Rates of box use and rates of interference at pooled nests of House Wrens and Tree Swallows in three study areas from 1983 through 1986.

per plot were insufficient to analyze effects of occupancy rate and interference on swallow offspring survival. But if probabilities of interaction with predators or competitors are dependent on the total number of boxes occupied or empty, then occupancy patterns of swallows may not explain variation in swallow productivity. I pooled wren and swallow nests to determine if overall rates of box use or interference influenced probabilities of predation, competition, or overall nest failure.

RESULTS

BOX USE AND NEST INTERFERENCE

Of 128 nests found in 65 boxes from 1983 through 1986, 77.3% were initiated by House Wrens and 22.7% by Tree Swallows. Most nests (44%) were at the Foote Camp plot, while 35% were at Rock Creek, and only 21% at Treasure Island. Although Tree Swallows nested primarily at Foote Camp in all study years (86% of all swallow nests), the species built four nests in boxes at Rock Creek in 1985.

Box occupancy rates varied somewhat by PLOT ($F_{2,6} = 4.52, P = 0.064$), but not by YEAR ($F_{3,6} = 1.99, P = 0.272$) (Fig. 1); over the 4-year period, 64% of all boxes at Foote Camp were used, whereas 32% were occupied at Treasure Island, and 49% at Rock Creek. Total occupancy rate differed between Foote Camp and Treasure Island (SNK tests, $P < 0.05$), but not between other pairs of plots. Wren occupancy rate did not vary among plots or years ($P > 0.1$).

Rates of interference by House Wrens (estimated by direct observation, and from occurrences of punctured eggs and displaced or added

nest material) at active nests of conspecifics was similar among plots and years ($P > 0.10$ for all comparisons), but wren interference at nests of both species varied by PLOT ($F_{2,6} = 5.68, P = 0.041$) but not by YEAR ($F_{3,6} = 0.83, P = 0.522$) (Fig. 1). Over the 4-year period, interference was detected at 9 of 99 (9%) wren nests and 13 of 29 (45%) swallow nests. At Foote Camp, the plot shared by both species in all years, wren interference was evident at only 3 of 31 (10%) wren nests, whereas 12 of 25 (48%) nest boxes used by swallows were invaded, primarily by House Wrens depositing twigs. Although 5 of 41 (12%) of all House Wren nests at Rock Creek displayed signs of intrusion by conspecifics, only 1 of 27 (4%) of all wren nests at Treasure Island showed signs of interference.

At least 20 of 22 (90%) records of intrusion at nests of either species involved House Wrens. Of the nine wren nests that suffered conspecific intrusions, five were totally destroyed, probably by conspecifics. Circumstantial evidence (chasing of conspecifics; new twigs deposited onto feather-lined nest; and egg destruction, followed by the appearance of new eggs) suggested that wrens usurped at least one conspecific box at Rock Creek. In addition, an adult wren was found dead, but uneaten, in a failed Rock Creek nest with intact eggs, suggesting either conspecific killing (Freed 1986a, Belles-Isles and Picman 1987) or mortality for reasons other than predation.

Clear signs of interference by Tree Swallows at nests of conspecifics or wrens were not observed, possibly because they were obscured by effects of wren intrusions. Of the 13 swallow nests having signs of wren interference, 12 failed, either at the time of interference or later. At Foote Camp, wrens apparently usurped two boxes settled by Tree Swallows by first depositing twigs, then laying eggs in new nests after the swallow nests were destroyed. On four occasions, Tree Swallows were observed chasing House Wrens away from swallow-occupied boxes. Tree Swallows built nests and laid eggs in eight boxes that contained twigs or dummy nests placed by wrens, and four additional swallow nests had twig nests constructed over them. Eleven of these 12 swallow nests failed, and six failed during the egg-laying stage. A second swallow clutch laid in one of these twig nests was also destroyed after failure of an earlier incomplete clutch. At Rock Creek, wren(s) intruded at one unsuccessful swallow nest also.

After effects of PLOT and YEAR were removed, correlational analysis showed a significant positive relationship between residuals of interference rate (both species) and total occupancy rate ($r = 0.66, P = 0.020$). That is, interference rates increased at nests of both species as more boxes were occupied. At House Wren nests only, interference rate was not related to total occupancy rate ($r = -0.013, P = 0.969$) or wren occupancy rate ($r = -0.34, P = 0.273$), nor was interference rate at nests of both species related to wren occupancy rate ($r = 0.014, P = 0.964$).

NESTING FAILURE IN WRENS AND SWALLOWS

Of 99 nesting attempts by House Wrens, 70 (71%) fledged one or more offspring, two had unknown outcomes, and 27 failed. Predation accounted for 19 (70%) of the 27 failures, while five (19%) were destroyed by conspecifics, and three (11%) were deserted during the egg-laying or incubation stages for reasons unknown. Fifty successful nests (71% of 70) lost one to four eggs or nestlings before fledging. The mean ($\pm$SE) number of losses from successful nests was 1.2 ± 0.1 young/nest. Tree Swallows lost 20 of 29 nests (71%), 10–12 (50–60%) due to wren destruction (two nests were abandoned after interference), and eight (40%) by predation. The outcome of one swallow nest was unknown. Of eight successful swallow nests, four lost one to four eggs ($\bar{x} \pm$ SE $= 1.00 \pm 0.35$ losses/nest).

In House Wrens at the shared plot, the probability of clutch mortality over the entire nesting period (i.e., partial $\hat{m}^t \times$ clutch $\hat{m}^t$) ranged from a low of 50.3% in 1983 to a high of 89.1% in 1984 (Table 1). The overall $\hat{m}^t$ of Tree Swallows ranged from 31.6% in 1983 to 99.3% in 1986. Although daily mortality rates of whole clutches (clutch $\hat{m}$) were statistically similar between species at the shared plot in the first three study years, Tree Swallow young suffered higher daily mortality than House Wrens in 1986 (Tables 1 and 2). Daily rates of partial clutch losses (partial $\hat{m}$) in wrens were similar to those in swallows in each year except 1986, a year in which partial losses were lower in swallows only because no swallow clutches survived. Considering nests pooled over all years, overall $\hat{m}^t$ at the shared plot was 87.3% in swallows and 67.1% in wrens (Table 1). Results of combined-probability tests demonstrated that daily clutch $\hat{m}$ in swallows

TABLE 1. Mean daily rates ± SE of whole clutch and partial clutch mortalities ($\hat{m}$), numbers of days of exposure (EXP), and probabilities of clutch mortality through the nesting period ($\hat{m}^t$) in 1983, 1984, 1985, and 1986 in House Wrens and Tree Swallows using the same (shared) or separate (unshared, swallow-free) box areas.[a]

| Mortality rate | Shared area | | Unshared area |
	House Wren	Tree Swallow	House Wren
1983			
Clutch EXP	125	116	430
Partial EXP	758	464	2,219
Clutch $\hat{m}$	0.008 ± 0.008	0.000 ± 0.000	0.005 ± 0.003
Partial $\hat{m}$	0.012 ± 0.004	0.011 ± 0.005	0.005 ± 0.001
Total $\hat{m}^t$	0.503	0.316	0.286
1984			
Clutch EXP	127	94	529
Partial EXP	607	394	2,361
Clutch $\hat{m}$	0.055 ± 0.020	0.106 ± 0.032	0.006 ± 0.003
Partial $\hat{m}$	0.007 ± 0.003	0.003 ± 0.003	0.010 ± 0.002
Total $\hat{m}^t$	0.891	0.983	0.427
1985			
Clutch EXP	239	102	313
Partial EXP	1,393	479	2,038
Clutch $\hat{m}$	0.017 ± 0.008	0.039 ± 0.019	0.013 ± 0.006
Partial $\hat{m}$	0.004 ± 0.002	0.002 ± 0.002	0.006 ± 0.002
Total $\hat{m}^t$	0.524	0.771	0.473
1986			
Clutch EXP	86	30	493
Partial EXP	433	121	2,642
Clutch $\hat{m}$	0.023 ± 0.016	0.133 ± 0.062	0.006 ± 0.004
Partial $\hat{m}$	0.009 ± 0.005	0.000 ± 0.000	0.006 ± 0.001
Total $\hat{m}^t$	0.683	0.993	0.338
Total years			
Clutch EXP	577	342	1,765
Partial EXP	3,191	1,458	9,260
Clutch $\hat{m}$	0.024 ± 0.006	0.053 ± 0.012	0.007 ± 0.002
Partial $\hat{m}$	0.007 ± 0.002	0.005 ± 0.002	0.007 ± 0.001
Total $\hat{m}^t$	0.671	0.873	0.375

[a] The standard error (SE) of $\hat{m}$ is computed using EXP, the number of days of exposure that a clutch or individual egg/nestling risks mortality.

was significantly higher than that in wrens, but partial $\hat{m}$ was similar between species (Table 2).

Overall $\hat{m}^t$ in wrens over all 4 years was 37.5% at the swallow-free plots compared to 67.1% at the swallow-used plot (Table 1). The greatest within-year difference was in 1984 when clutch $\hat{m}^t$ through the entire nesting period was 89.1% in wrens on swallow-used plots and only 42.7% in wrens on swallow-free plots (Table 2). The outcome of the combined-probability test indicated that daily clutch $\hat{m}$ in wrens on the shared plot was significantly greater than that in wrens on the swallow-free plot. In comparisons between swallows at Foote Camp and wrens occupying the swallow-free plots, daily clutch $\hat{m}$ differed significantly in 1984 and 1986, as well as in the combined-year test, while partial $\hat{m}$

differed in 1984 and 1986, and in the all-year test.

RELATIONSHIPS AMONG RATES OF BOX USE, INTERFERENCE, AND MORTALITY

The daily mortality rate ($\hat{m}$) of House Wren clutches was positively associated with total occupancy rate (partial $r_p = 0.67$, $P = 0.025$) (Fig. 2), but was unrelated to interference rate at wren nests ($r_p = 0.32$, $P = 0.335$). That is, wren nests were more likely to fail as box-occupancy rates, rather than interference rates, increased. Daily clutch $\hat{m}$ was not associated with wren occupancy rate ($P > 0.05$). Incomplete clutch losses (partial $\hat{m}$) in wren nests were negatively related to total occupancy rate ($r_p = -0.80$, $P = 0.003$) and unrelated to interference rate at wren nests ($r_p =$

TABLE 2. Z-statistics and combined-probability tests comparing daily mortality rates (ṁ) between nests of (1) House Wrens and Tree Swallows in the area shared by both species, (2) wrens on areas used by swallows and wrens on swallow-free areas, and (3) wrens on swallow-free areas and swallows.[a]

Comparison[b]	z-values				Combined-P test[c]
	1983	1984	1985	1986	
Shared area					
Wren vs. swallow					
Clutch ṁ	1.01	1.36	1.07	1.72*	11.14*
Partial ṁ	0.18	0.98	0.84	2.02*	10.34
Shared vs. unshared					
Wren vs. wren					
Clutch ṁ	0.39	2.41*	0.38	1.03	12.09*
Partial ṁ	1.68*	0.92	0.44	0.74	5.80
Wren vs. swallow					
Clutch ṁ	1.40	3.15**	1.31	2.05*	22.45***
Partial ṁ	1.16	2.41*	1.25	4.01***	30.39***

[a] * $P \le 0.1$, ** $P \le 0.01$, *** $P \le 0.001$.
[b] Clutch ṁ means daily mortality rate of whole clutches; partial ṁ means daily rate of clutch reduction at nests that remain active.
[c] Comparisons were made between groups by combining probabilities across years using Fisher's procedure (Sokal and Rohlf 1981). The test statistic is distributed as χ^2 with 6 degrees of freedom ($2k$, where k = the number of years and probabilities). Probabilities computed for 1983 were excluded from these tests because 1983 was a transition year for nesting birds.

-0.01, $P = 0.973$). In sum, wren clutches were more likely to be totally destroyed than partially lost as box-occupancy rates increased.

Although Tree Swallow nesting was primarily on one plot, preventing statistical comparisons of rates of interference and nesting failure, the positive relationship between wren interference rates and clutch mortality at swallow nests is clear (Fig. 3). I combined Tree Swallow nests with wren nests to determine if the addition of swallow nests influenced relationships among clutch mortality, interference rate, and total occupancy rate. Daily clutch ṁ of pooled species was positively related to interference rate ($r_p = 0.92$, $P = 0.0001$) (Fig. 4) but was unrelated to total occupancy rate ($r_p = -0.50$, $P = 0.117$). Partial ṁ at all nests was not associated with either interference rate ($r_p = -0.19$, $P = 0.569$) or occupancy rate ($r_p = -0.53$, $P = 0.093$). Thus, due to the strong effect of interference at swallow nests, the independent variable affecting survival of whole broods shifted from box-occupancy rate (wren nests only) to interference rate at pooled nests of swallows and wrens.

Factors related to failure appeared to affect probability of partial losses and mortality rates of whole clutches in opposite directions. In a partial correlational analysis of these two mortality components with interference rate at all nests, interference rate increased as daily clutch ṁ increased ($r_p = 0.98$, $P = 0.0001$), and partial

ṁ correspondingly declined ($r_p = -0.94$, $P = 0.0001$). Because variation in partial-loss rates may be contingent on variation in failure rates of whole nests, effects of interference rate and occupancy rate on partial losses should probably be interpreted with caution.

DISCUSSION

EFFECTS OF CONSPECIFIC INTERFERENCE AT WREN NESTS

Conspecifics, rather than swallows, were primarily responsible for interference at boxes occupied by wrens. Some wren nests lost one or more eggs due to interference, but were successful in producing fledglings. House Wrens achieved highest rates of brood survival on the plots where box use by swallows was absent or rare. Predation, rather than nest interference, explained high rates of total nest failure in House Wrens at the swallow-used plot. In contrast, Freed (1986a) reported that conspecific destruction of whole clutches by tropical House Wrens was common.

Although box-use rates were higher at Foote Camp than at the swallow-free plots, interference rates at wren nests did not vary among plots, suggesting that interference was not directly explained by reduced availability of nest sites. In dense populations of tropical House Wrens, mates rather than nest sites per se are in short supply; unmated wrens vigorously compete for mates by destroying eggs, usurping territories, and mating
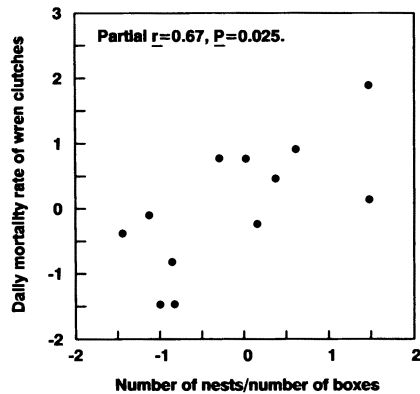
FIGURE 2.   Standardized partial regression plot for daily mortality rate of House Wren clutches and ratio of the number of all nests to the number of boxes. Residuals of the two variables were plotted after removing the effects of PLOT, YEAR, and interference rate at House Wren nests.
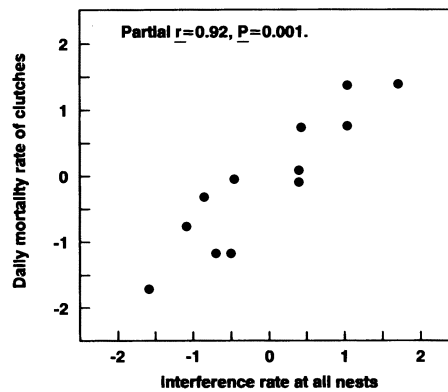

FIGURE 4.   Standardized partial regression plot for daily mortality rate in nests of both species and interference rate at all nests. Residuals of the two variables were plotted after removing the effects of PLOT, YEAR, and box occupancy rate.

with territory owners (Freed 1986a, 1986b). In this study, not all box-nesters were conspecifics which may explain the lack of relationship between box-use rates and wren-nest interference. I found little evidence that swallows intervened at wren nests, and therefore, I did not expect increased rates of box use (due in part to presence of swallows at Foote Camp) to result in increased interference at wren nests. Interference effects on wrens may be more important when wrens alone occupy a high percentage of boxes, resulting in increased opportunities for intraspecific interactions like infanticide, brood parasitism, extra-pair copulations, bigamy, nest confiscation, and mate theft.
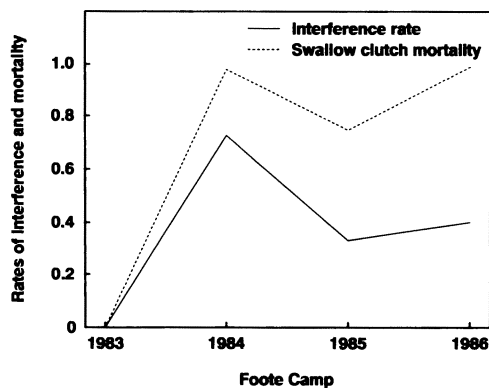

FIGURE 3.   Interference rates and probability of overall clutch mortality of Tree Swallows at Foote Camp.

Nor was the probability of partial wren losses related to interference rates, possibly because interference occurred at failed whole nests as well as at nests that remained active after clutch reduction. In addition, partial losses were caused by multiple factors (e.g., nestling starvation, egg and nestling mortality at hatching, predation) so that the effects of any single factor were obscured.

RELATIONSHIP BETWEEN BOX-USE
RATE AND PREDATION AT
WREN NESTS

Total nest failure in House Wrens was strongly associated with rates of box occupancy. Clutch mortality rates in wrens were especially high, ranging from 50–89% over the 4-year period, at the box-plot with highest nest densities. Nests that may have survived with partial losses caused by interference or starvation at low box-use rates were likely to be totally destroyed by predators at high occupancy rates. Predators usually destroy whole clutches rather than leave any surviving offspring (Brown and Brown 1988). Predation was the major cause of nest failure, accounting for 70% of all unsuccessful nesting attempts by wrens. I detected signs of nest predation by red squirrels (*Tamiasciurus hudsonicus*), raccoons (*Procyon lotor*), and small rodents (unknown species) (Finch 1989c). Weasels (*Mustela frenata*) and bullsnakes (*Pituophis melanoleucus sayi*), other predators that destroy House Wren nests in riparian woodlands of Wyoming (L. Scott Johnson, pers. comm.), were also observed in my study areas.

Field experiments have demonstrated that high nest densities resulted in heightened predation rates (Tinbergen et al. 1967, Goransson et al. 1975, Page et al. 1983). Andersson and Wiklund (1978) suggested that spacing out of nests was a predator avoidance strategy, but Picman (1988) concluded that dispersing nests widely apart was only advantageous in habitats with high predation rates. Because deciduous riparian woodlands typically have higher bird densities than surrounding habitats (Hehnke and Stone 1978, Johnson and Haight 1985), rates of nest predation may be high. For instance, Janzen (1978) reported higher rates of egg mortality in deciduous woodlands of Costa Rica than in other habitat types. Thus, spacing nests out by minimizing occupancy rate of boxes could have adaptive value in the cottonwood woodlands of this study.

Reduced predation rates are associated with increased numbers of empty nests in Northern Cardinals (*Cardinalis cardinalis*) (Watts 1987) and Marsh Wrens (*Cistothorus palustris*) (Leonard and Picman 1987). Likewise, a high proportion of empty boxes may inhibit predator search efficiency. In this study, destruction rates of House Wren nests declined as the proportion of vacant boxes increased. If predators use nest boxes as search images based on previous rewards, then risk of predation may be highest when the ratio of empty-to-occupied boxes is low. Martin and Roper (1988) similarly concluded that the predation rate on open nests of Hermit Thrushes (*Catharus guttatus*) was influenced by the association between unused sites and used sites.

In this study, I detected signs that a predator(s) sequentially destroyed nests in multiple years at the plot shared by both species. Its dexterity in unlatching boxes, ripping off box lids, and tearing up nests implicates the raccoon, a known search-strategy predator (Bowman and Harris 1980). Raccoon tracks were observed along the river banks bounding the box grid, and claw marks were visible on some nest boxes. Serial predation in response to high reward rate set by the high density of box nests may explain increased nesting mortality in wrens at Foote Camp. Following 1984, the year of peak mortality, fewer boxes had nests at Foote Camp, suggesting either that box-nesters adopted a predator-avoidance strategy (i.e., shifting to new cavities, Sonerud 1985) or that bird populations were lower due to high nest failure the year before.

EFFECTS OF WREN INTERFERENCE AT SWALLOW NESTS

Male House Wrens build and guard multiple empty nests within their territories, but each female selects one site for egg laying (Kendeigh 1941). Multiple-nest defense by males may be a tactic for attracting mates (Kendeigh 1941), for increasing opportunities for bigamy (Freed 1986b), or for ensuring the availability of surplus nest sites if the first nesting attempt fails. But high densities of dummy nests may also protect actual nest sites from search-strategy predators, as is evident in Marsh Wrens (Leonard and Picman 1987). If Tree Swallows nest in boxes defended by male House Wrens, then a dummy-nest strategy is negated by the presence of swallow eggs. Wrens began building nests in boxes on my study areas 6 days earlier on average than swallows (two-way ANOVA with factors year and species; species effect: $P < 0.05$). Although Tree Swallows generally arrive on North American breeding grounds earlier than House Wrens (G. Holroyd, pers. comm.), territory-settlement dates in swallows are not related to timing of egg laying (Stutchbury and Robertson 1987b). Late-breeding swallows nested unsuccessfully in seven of eight boxes that contained dummy nests built by wrens. If swallows nest in an "empty" box that is defended by a multiple-nest House Wren, then the wren may interfere with the swallow nest during a territorial visit. If some or all eggs are destroyed by wrens, swallows may abandon the nest site, and then the box will return to its original condition, that of a dummy nest.

In this study, wren interference at swallow nests often preceded or accompanied whole-clutch failure. Destroying active swallow nests has advantages for wrens if the function of a dummy nest is to deceive predators. Just as predation rates are reduced in areas where old nests have accumulated (Watts 1987), so too might search efficiency of predators be inhibited by high concentrations of empty swallow nests and wren dummy nests. Because cavity-nest predators are also likely to prey upon the contents of open nests, high densities of empty nests of any type may benefit House Wrens. By destroying the eggs of open-nesting and cavity-nesting birds (Kendeigh 1941, Belles-Isles and Picman 1986b) and forcing pairs to nest further away, House Wrens may cause reduced predation rates in the locality of their own nest sites.

Other possible advantages to destroying eggs in hole nests include: (1) cannibalism and diet augmentation (Belles-Isles and Picman 1986b, Brown and Brown 1988), (2) freeing the cavity so that a House Wren pair can readily renest in a surplus site if their first attempt fails; (3) for males, attracting females by displaying superior mate quality as advertised by his ability to defend surplus cavities (Kendeigh 1941); (4) reducing risks of nest usurpation by spacing nests of secondary cavity-nesters more widely apart; (5) reducing risks of egg destruction, egg dumping (Price et al. 1989), extra-pair copulations (Johnson and Kermott 1989), and mate theft by increasing distances between conspecific pairs (e.g., Tree Swallows, Muldal et al. 1985); (6) reducing nest-mate competition in broods parasitized by conspecifics (sensu Brown and Brown 1988, see also Lombardo et al. 1989), and (7) reducing local competition for other resources like food or foraging substrate (Belles-Isles and Picman 1986b). The seventh point is also an alternative explanation for destruction of open nests (Belles-Isles and Picman 1986b). Unlike the empty-nest hypothesis, however, the food-competition hypothesis does not account for indiscriminate destruction of open nests by House Wrens regardless of whether their diet or foraging habits are similar to that of the "competing" species. Nor does it explain why nest-destroying behavior is suppressed in males after pairing and in females after egg laying when energy requirements should be higher (Belles-Isles and Picman 1986b).

As no wrens have ever been observed to eat the eggs that they punctured or ejected (Belles-Isles and Picman 1986b), it is safe to rule out diet supplementation as a major reason for egg destruction. Though House Wrens may benefit from the destruction of hole nests for the other six reasons listed, these reasons do not readily explain the evolution of egg destruction because they do not account for the destruction of open nests. Factors two, four, and five explain intraspecific interactions only. Nor does factor two explain why female wrens (not just males) destroy nests. And factor six does not answer why wrens destroy the nests of Tree Swallows, a species that forages in the air on a different food supply.

Perhaps House Wrens are genetically "programmed" to destroy a neighbor's eggs on sight even when there is no immediate advantage. Indiscriminate destruction of open and hole nests

may be naturally selected if the trait results in fewer behavioral errors than one involving a reasoning process (i.e., deciding to destroy or not). In other words, harming others may benefit wrens more often than not. But, if harming others does not render manifest or potential benefits to the harmer, it can be interpreted as spiteful behavior (sensu Hamilton 1970). Though spiteful behavior is feasible in interspecific relationships where kinship is zero (Hamilton 1970), it is an unlikely reason for nest destroying behavior by wrens because destruction is nonselective, i.e., directed at conspecifics and heterospecifics who may or may not possess the trait; it seems to be inherent to all wrens (Belles-Isles and Picman 1986b); it carries the potentially high cost of retaliation; and it affords many plausible advantages. Possibly, no single factor or advantage is responsible for the selection of egg puncturing by male and female wrens.

Interspecific competition for limited numbers of nest sites is yet another factor that might cause House Wrens to interfere with Tree Swallow nests. If swallows occupy a high proportion of boxes, then wrens have fewer nest sites from which to choose. Male House Wrens have high return rates to breeding sites that they occupied the year before (Drilling and Thompson 1988). Returning wrens may try to usurp occupied boxes within their territories. Despite intrusions at swallow nests, however, only a few swallow boxes were actually confiscated by nesting wrens, suggesting that wrens did not destroy most swallow nests for purposes of unsurpation. By building nests earlier, House Wrens seemingly avoided agonistic interactions with swallows. Wrens may build nests earlier than swallows to reduce competition for nest cavities among conspecifics or among species. Stutchbury and Robertson (1987b) suggested that swallows in Ontario timed their egg laying for mid-May to benefit from synchronous breeding and favorable environmental conditions. Also, because swallows typically choose nest sites in open meadows and woodland edges (Munro and Rounds 1985), interior woodlands may be less preferred by them. Hence, swallows that breed later than average in woodlands may be floaters using suboptimal sites (e.g., Stutchbury and Robertson 1987a). Lack of swallow nesting on two of three study areas supports the interpretation that swallows avoided nesting in interior woodlands where wrens were abundant,

even though they were observed in adjacent open areas.

In conclusion, interference by House Wrens at Tree Swallow nests may be more related to territorial defense of dummy nests and nest-protection tactics than to attempts to usurp nest sites. Although I have listed numerous possible explanations, an experimental approach is needed to factor out the underlying reason(s) for wren interference and egg destruction. To test the hypothesis that high concentrations of empty nests discourage predation at active nests, I recommend that densities of empty nests (in boxes or in the open) be experimentally increased in study areas containing multiple active nests of House Wrens or an alternate species. The null hypothesis of no effect on predators is rejected if nest predation is (1) higher in study areas with no treatment (spatial control) than in treatment areas, and (2) higher in the same areas in year(s) prior to treatment (temporal control) than in treatment year(s). Both temporal and spatial controls are recommended to account and adjust for natural variation in nesting success by area and year. Testing the reverse hypothesis, that predation at wren nests is increased in areas having high densities of nests with prey, will not support or refute the empty-nest hypothesis. But, if this second hypothesis is also supported, then nest-destroying behavior has two advantages for House Wrens, i.e., creating empty nests that deter predators and eliminating active nests that facilitate predation. The ratio of empty to active nests may then act as a dynamic continuum that selects for the evolution of egg destruction by House Wrens. The study design for the active-nest hypothesis would parallel that used for the empty-nest hypothesis, expect that real eggs (e.g., quail eggs) would be added to experimental nests.

ASYMMETRICAL COMPETITION BETWEEN WRENS AND SWALLOWS

By destroying swallow nests and controlling surplus nest sites, House Wrens prevent access and successful breeding by swallows; such interactions are usually considered competitive (Dhondt and Eyckerman 1980). Asymmetrical competition occurs when one species is more negatively affected than the other (Connell 1983, Schoener 1983, Persson 1985). In this study, House Wrens dominated interactions with swallows by (1) destroying eggs and nests of swallows, (2) having few or no nests damaged or usurped by swallows,

and (3) having higher nesting success. Interference competition, defined as immediate exclusion of a competing individual from a resource (Ricklefs 1979), was the most obvious type of interspecific competition in this study. House Wrens excluded Tree Swallows from nest boxes by destroying swallow nests, forcing them to nest elsewhere (see also Belles-Isles and Picman 1986b).

After the first year, interference rates were greater at swallow nests than at wren nests and were associated with low survival of swallow clutches. This evidence suggests that swallows were less successful than nesting wrens at defending nests from intruders (but see Kuerzi 1941), or were less likely or less able to invade wren nests. Although Tree Swallows destroy eggs and usurp territories of conspecifics (Harris 1979), they have not been reported to regularly destroy the nests of other species (but see Butler and Campbell 1987). Furthermore, swallows apparently do not defend multiple surplus nests from other species (Robertson and Gibbs 1982, but see Rendell and Robertson 1989), although they can prevent conspecific access to empty boxes through territorial defense of active nests (Robertson et al. 1986). By generalizing nest-destroying behavior to include other species (Belles-Isles and Picman 1986b), possibly in relation to multiple nest control, House Wrens outcompete swallows for boxes.

Exploitation competition, in which resource availability is diminished for some animals through use by others (Alatalo et al. 1987), may operate secondarily in wren-swallow relationships. For example, by occupying boxes earlier and by having higher population levels than swallows (Finch 1989b), House Wrens may indirectly reduce the availability of nest sites for Tree Swallows. Establishment of dummy nests by wrens also may deter swallows from nest-box settlement. Results from this study cannot support or refute the concept of exploitation competition because they are subject to other interpretations; however, the results from this study do offer new directions for future experimental tests.

MANAGEMENT IMPLICATIONS

Interspecific competition may be minimized when cavity resources are partitioned in space. When boxes are distributed in a wide variety of habitats, Tree Swallows readily choose those that

are in or adjacent to open areas (Rustad 1972, Munro and Rounds 1985), whereas House Wrens prefer boxes that are in tree and shrub habitats (Willner et al. 1983, Munro and Rounds 1985). House Wrens also select natural cavities in shorter trees and snags than those preferred by Tree Swallows (Stauffer and Best 1982). By introducing nest boxes, competitive interactions between species may be artificially increased, particularly when boxes are placed at the same height or in habitats where both species coexist. Boxes may be more attractive or more easily found than natural nest sites, resulting in shifts away from use of natural cavities (Gustafsson 1988). Moreover, population densities of secondary cavity-nesters often increase after introduction of nest boxes (Gustafsson 1988). Thus, establishment of nest-box plots is an excellent means of experimentally inducing interspecific competition. On the other hand, if the purpose of nest-box establishment is to enhance habitats for cavity-nesting species, then standardized placement of boxes may not provide suitable nest-site resources for targeted species, especially if some species exclude boxes from others. By spacing boxes widely apart in a broad range of habitat patches and heights, managers may increase box access and species use.

ACKNOWLEDGMENTS

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