NESTING PHENOLOGY AND COMPETITION FOR NEST SITES AMONG RED-HEADED AND RED-BELLIED WOODPECKERS AND EUROPEAN STARLINGS

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ABSTRACT.—I observed 96 pairs of Red-bellied Woodpeckers (*Melanerpes carolinus*) and 105 pairs of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) during three breeding seasons in urban and rural areas in Oktibbeha County, Mississippi. European Starlings (*Sturnus vulgaris*) and Red-bellied Woodpeckers initiated nests in late March and early April; Red-headed Woodpeckers nested during the first week of May. Most competition for freshly excavated nest sites was between starlings and Red-bellied Woodpeckers. Fifty-two percent of Red-bellied Woodpecker nest cavities and 7% of Red-headed Woodpecker nest cavities were usurped by starlings. Differences in nest-site parameters of the woodpecker species appeared to influence starling choice of cavities. Pairs of Red-bellied Woodpeckers unable to avoid starling competition suffered apparent reductions in fecundity. Ultimately, pairs able to avoid starling competition in March and April should be at a selective advantage. *Received 5 April 1988; accepted 12 October 1988.*

AN a priori assumption for interspecific competition is that a reduction in fitness occurs in individuals adversely affected (Roughgarden 1979). Studies on interspecific competition in birds demonstrate such reductions in fecundity (Dhondt and Eyckerman 1980, Hogstedt 1980, Minot 1981, Garcia 1983, Minot and Perrins 1986, Gustafsson 1987). Numerous authors report interactions between European Starlings (*Sturnus vulgaris*) and other cavity-nesting species (Wood 1924, Shelley 1935, Howell 1943, Kilham 1958, Polder 1963, Zeleny 1969, Reiler 1972, Troetschler 1976, Ingold and Ingold 1984), but few attempt to document competition using fitness as a measure. The fecundity of cavity-nesting birds is limited by the availability of nest sites (von Haartman 1957, Hilden 1965, Scott 1979, Mannan et al. 1980). Troetschler (1970, 1976) found that starlings successfully usurped Acorn Woodpecker (*Melanerpes formicivorus*) nest cavities which increased starling populations. Troetschler (1976) concluded that because Acorn Woodpeckers responded to starling competition by excavating more cavities or delaying nesting, their fecundity was not adversely affected and local populations remained stable. Conversely, van Balen et al. (1982) and Nilsson (1984) found reductions in the breeding success of both Great Tits (*Parus major*) and Nuthatches (*Sitta europaea*) from starling competition for nest cavities.

Red-bellied Woodpeckers (*M. carolinus*) and Red-headed Woodpeckers (*M. erythrocephalus*) are two common primary cavity-nesting species broadly sympatric with starlings in eastern North America. In the southeastern United States, starlings and Red-bellied Woodpeckers (Red-bellies) generally initiate nesting in late March and early April, and Red-headed Woodpeckers (Red-heads) begin in early May (Bent 1939, Imhof 1976, Dakin 1984). Double-broodedness is common in the three species (Coues 1903, Bent 1939, Short 1982, Dakin 1984, Smith and Layne 1986, Ingold 1987). Both woodpecker species lose cavities to starlings (Kilham 1958, Zeleny 1969, Reller 1972, Jackson 1976, Short 1979), but the short breeding season of starlings and the tendency for later nesting by Red-heads, coupled with their aggressive nature, could make them less vulnerable to starling competition.

I quantified the nesting phenology of the three species, and identified the degree of phenological overlap and timing of potential competition for nest sites among them. I also compared woodpecker nest-site parameters and the proportion of Red-belly nest cavities vs. Red-head nest cavities usurped by starlings. I discuss whether differences in proportions are related to nesting phenology or nest-site parameters of the woodpeckers, and whether a relationship exists between the timing of reproductive efforts in Red-bellies and Red-heads and their fecundity. Interspecific competition between starlings and native North American woodpeckers apparently reduces woodpecker fecundity.

STUDY AREA AND METHODS

From 15 March through 5 September 1985–1987, active Red-bellied and Red-headed woodpecker nest sites were located on the Mississippi State University (MSU) campus, the MSU south farm, and in the city of Starkville. The study area covered ca. 4,200 ha in Oktibbeha County, Mississippi. Starling boxes within this area from a previous study (Dakin 1984) were monitored, and other active starling nests were located in the study area. The campus and city are characterized by scattered hardwoods and pines surrounded by lawns, roads, buildings, and abandoned lots. The south farm consists primarily of pastures and hay meadows with scattered hardwoods and large snags.

Because starlings and Red-bellies initiated nesting concurrently, pairs of Red-bellies were categorized as either competitors or controls (competition-free). Pairs were considered controls if starlings were not detected at or near their nest sites (a circular area of ca. 0.5 ha around the cavity tree) throughout breeding. Although such a method of categorization did not preclude that some control birds would encounter starlings, the criteria used in defining such pairs made it unlikely.

Each active woodpecker nest was observed for at least 30 min each week between 0700 and 1900 to determine status and detect overt interactions between starlings and woodpeckers. I observed cavities where starlings were present up to 4 h/week. An interaction was recorded when two species, within sight of each other, responded mutually. Acknowledgments included vocalizations, aggressive pursuit flights, or attacks at the nest cavity. Nest sites that could be reached were climbed each week to confirm occupancy and nest status. Contents of nests were examined with a light and mirror.

At each cavity I measured height (m), horizontal and vertical diameter of cavity entrance (cm), facing compass direction of the entrance (degrees from north), angle of the cavity limb (from vertical), presence or absence of bark around the cavity entrance, living vs. dead cavity tree, number of trees (>2.5 cm DBH) in a circular area of $\frac{1}{25}$ ha around the cavity tree, height of ground vegetation ($\leq$1.5 m) around the cavity tree (values scored from 0 to 5: zero represented no ground vegetation and 5 represented maximum vegetation; following Nudds 1977), and the DBH of the cavity tree (cm). Differences in horizontal and vertical cavity diameter, cavity height, number of trees around the cavity tree, and tree DBH between Red-belly and Red-head nest sites were analyzed using two-tailed t-tests. State of tree, bark, cavity angle, compass direction, and vegetation height were analyzed using contingency table Chi-square tests.

I used Kolmogorov-Smirnov tests to determine whether differences existed in the timing of nesting in any species among years. Significant differences were detected ($P < 0.05$) for starlings and Red-bellies among years; these data are presented separately. No differences were detected among years for Red-heads ($P > 0.05$), and these data were pooled.

Differences in the number of interactions/h among starlings, Red-bellies, and Red-heads for the 3 yr were analyzed using a Kruskal-Wallis test because of their heterogeneous variances and the unequal sample sizes between years. I found no differences ($P > 0.10$), and these data were pooled. Between-year differences in numbers of cavity usurpations per cavities observed were minimal, and sample sizes were small; these data were pooled. Because of small unequal sample sizes between years, I used Kruskal-Wallis tests to analyze differences in Red-belly and Red-head clutch sizes, nestling numbers, and fledgling numbers among years. No significant differences were detected ($P > 0.25$), and these data were pooled.

RESULTS

Nesting phenology.—Nest starts by starlings and Red-bellies for all years occurred in late March and early April (Figs. 1, 2). Most active Red-belly nests in March were being excavated (94%), and in April at least 50% of active nests were still undergoing excavation.

Starling clutch starts, nests with nestlings, and nests producing fledglings followed a bimodal pattern similar to that reported by Dakin (1984; Fig. 1). Presumably some pairs were double brooded while others attempted a second nest after an unsuccessful first try. A resurgence of Red-belly nesting activity occurred in mid- to late June of all years, by which time starlings no longer started nests. The nesting period of Red-bellies extended into early August in all years, but starlings completed nesting by early to mid-July of each year.

Of 96 Red-belly pairs observed, 25 did not encounter starling competition. The pattern of nesting phenology of these pairs appears bimodal (Fig. 3), which suggests that some pairs were double brooded. During the 3 yr, 68% of control Red-belly pairs incubated eggs either in April or June. The proportion of competition-free Red-belly pairs with eggs before 1 May was significantly greater than that for competing pairs with eggs before this date in 1985 ($\chi^2 =$

4.3, df = 1, $P < 0.05$), 1986 ($\chi^2 = 3.9$, df = 1, $P < 0.05$), and 1987 ($\chi^2 = 6.52$, df = 1, $P < 0.05$).

Red-heads did not start excavating nests until late April and early May (Fig. 4) in any year. By the end of April of each year, starlings were rearing initial broods. Consequently Red-heads avoided most starling competition because starlings were preoccupied with rearing nestlings and not actively seeking nest cavities. Unlike starlings and Red-bellies, the nesting period of Red-heads extended through August of each year. Successful first and second broods were produced by at least 33 of 105 pairs (31%).

Interactions.—Ninety-five of 105 (91%) interactions between starlings and Red-bellies occurred from March through May (Fig. 5), when both species were starting nests. Most interactions (96%) occurred near freshly excavated cavities. The number of interactions was negatively associated with the progression of time during the nesting season ($F = 16.85$, $P < 0.01$, df = 1, 14; $r^2 = 0.53$). Forty-two of 62 (68%) interactions between starlings and Red-heads occurred from late April to late May. Associations between the number of starling/Red-head interactions and time, and Red-belly/Red-head interactions and time were not significant ($F = 1.02$, $P > 0.10$, df = 1, 11; $F = 0.11$, $P > 0.10$, df = 1, 15).

During the period when most Red-heads reared first broods, at least 22 of 42 (52%) starling pairs began second nests. This asynchrony of nest initiation for starlings and Red-heads reduced interactions between them. Interactions between the woodpecker species were most frequent from late April through early June, which coincided with a period of nesting overlap. Nesting delay by Red-bellies in response to starling competition in March and April may have increased competition between Red-bellies and Red-heads for nest sites in May and early June.

I found distinct differences in aggressive behavior of the woodpecker species. In 105 interactions between starlings and Red-bellies, Red-bellies were aggressors 31% of the time. In 62 interactions between starlings and Red-heads, Red-heads were aggressors 82% of the time. In 75 interactions between Red-bellies and Red-heads, Red-heads were aggressors 88% of the time. Thus Red-bellies were aggressors in only 42 of 180 interactions (23%), Red-heads in 117 of 137 interactions (85%), and starlings in 83 of 167 interactions (50%). Significant differences (contingency table Chi-square tests, $P < 0.005$) occurred between the total number of aggressive encounters among species.

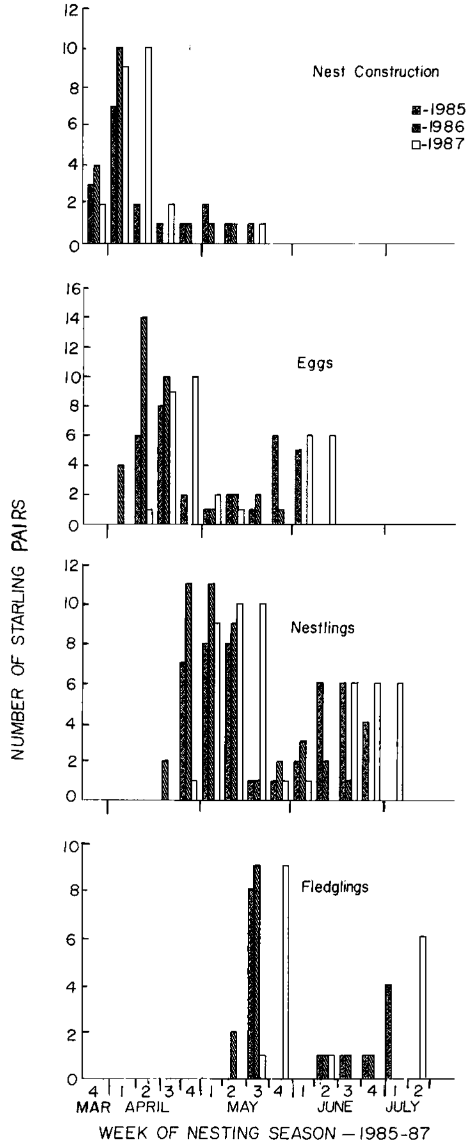

Fig. 1. Nesting phenology of European Starling pairs during 1985–1987 (n = 15, 17, and 10 pairs).

Cavity usurpations.—Fifty-five of 105 (52%) freshly excavated Red-belly nest cavities were usurped by starlings. Forty-five occurred before 1 May (Fig. 6) when both species were initiating nesting. A few occurred at the end of May which coincided with final nest initiation attempts by starlings. Red-belly cavity usurpation by starlings was a negative function of time ($F = 19.26$, $P < 0.01$, df = 1, 6; $r^2 = 0.74$). Red-bellies also

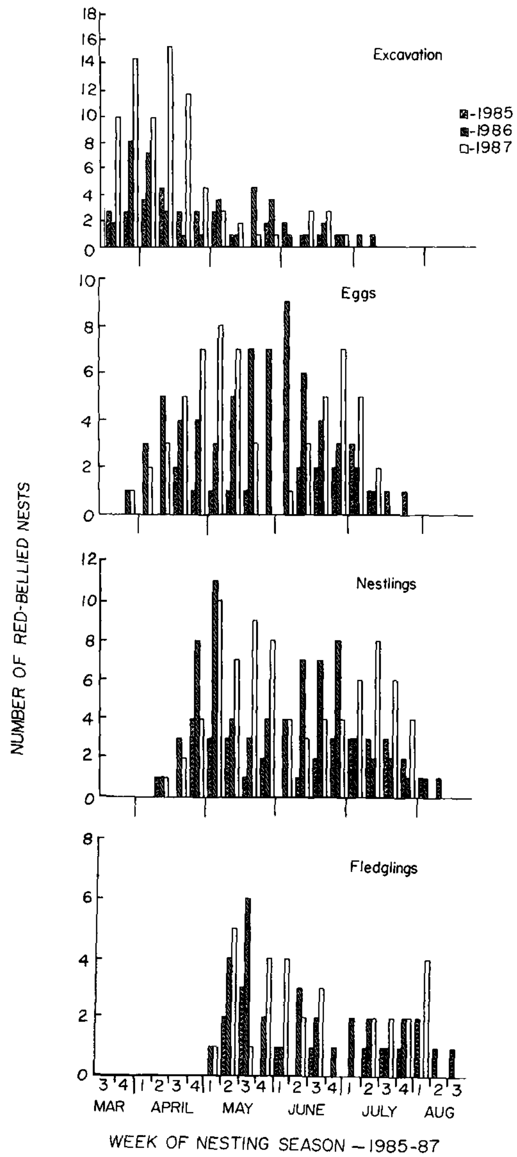

Fig. 2. Nesting phenology of Red-bellied Woodpecker pairs during 1985–1987 (n = 17, 39, and 40 pairs).

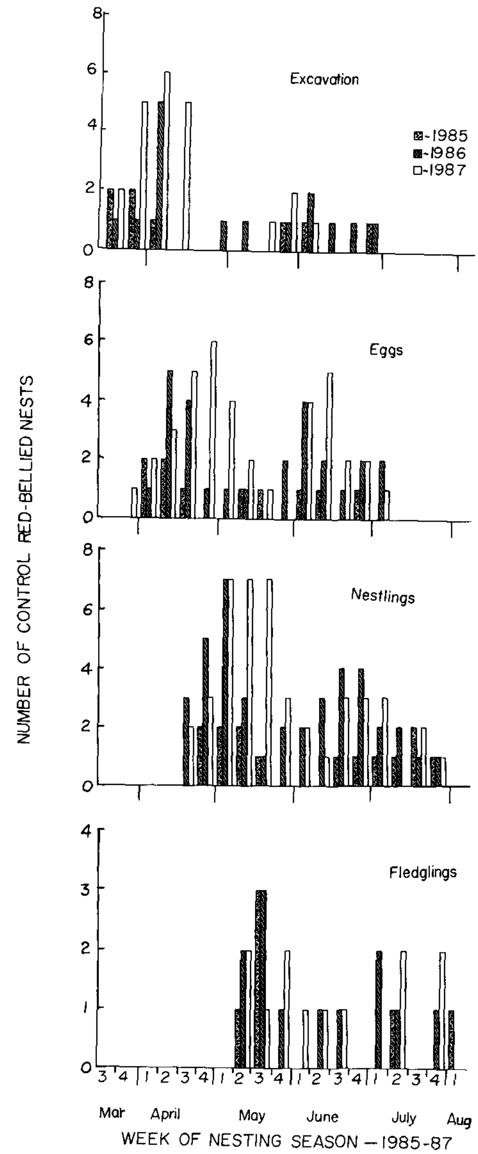

Fig. 3. Nesting phenology of Red-bellied Woodpecker pairs in the absence of European Starlings during 1985–1987 (data are a subset of the data presented in Fig. 2; n = 5, 8, and 12 pairs).

lost 6 nest cavities to Red-heads from late April through early May as a result of competitive encounters between these species.

Seven percent of 113 freshly excavated Red-head cavities were usurped by starlings; 75% of these occurred in late May. Because the sample sizes for starling/Red-head and Red-head/Red-belly cavity usurpations were small, I did not perform regression analyses.

Nest-site parameters.—I found significant differences ($P < 0.05$) between Red-belly and Red-head nests in vertical diameter of cavity entrance, angle of cavity limb, use of a living vs. dead tree, presence or absence of bark around

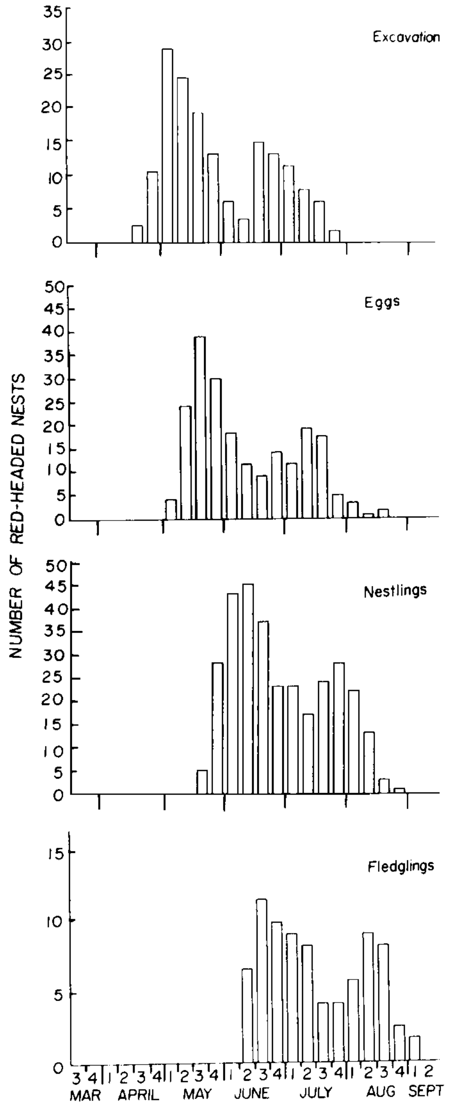

Fig. 4. Nesting phenology of 105 Red-headed Woodpecker pairs during 1985–1987.

cavity entrance, amount of ground vegetation around cavity tree, and number of trees in a $\frac{1}{25}$ ha circle surrounding the cavity tree. Red-bellies excavated cavities with small entrances surrounded by bark, that angled downward in living trees, and showed a proclivity for nesting in wooded areas with moderate to dense ground vegetation. Red-heads excavated more vertical facing cavities with larger entrances in dead trees without bark, and they nested most often in open areas with little ground vegetation.

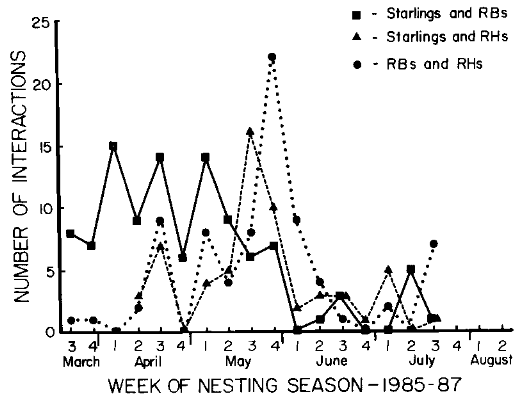

Fig. 5. Interactions among European Starlings, Red-bellied (RB) Woodpeckers, and Red-headed (RH) Woodpeckers during 1985–1987.

Of 55 Red-belly cavities usurped by starlings, most possessed bark around the cavity entrance and were located in limbs angling downward in living trees (Table 1). Five of 8 Red-head cavities usurped by starlings possessed these characteristics (Table 1). There were no significant differences (χ^2, $P > 0.05$) between the total number of Red-belly cavities with these characteristics and the 55 Red-belly cavities usurped by starlings with the characteristics. In addition, there were no significant differences (χ^2, $P > 0.05$) between the total number of Red-head cavities with the characteristics and the 8 Red-head cavities usurped by starlings with them (although this was likely the result of a small sample size).

Nest success vs. timing of nesting.—I recorded clutch size for 50 Red-belly clutches produced by 41 nesting pairs from the second week of April through the fourth week of June. I divided the data into clutches completed before 21 May (the date by which 96% of uninterrupted Red-belly pairs had laid initial clutches; Fig. 3) and those completed after 21 May, by which time second nesting efforts were common (following either successful or unsuccessful first attempts). Mean clutch size before 21 May was significantly larger than mean clutch size after this date (4.1 vs. 3.6; $t = 2.78$, df = 20, $P < 0.01$). A negative association existed between clutch size and time ($F = 17.12$, $P < 0.01$, df = 1, 10; $r^2 = 0.63$) (Fig. 7). There were also significant negative associations between mean Red-belly

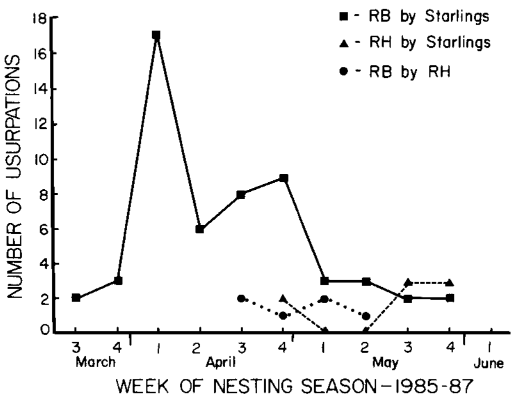

Fig. 6. Cavity usurpations among European Starlings, Red-bellied (RB) Woodpeckers, and Red-headed (RH) Woodpeckers during 1985–1987.

nestling and fledgling numbers and time (nestlings: $F = 34.31$, $P < 0.005$, df = 1, 10; $r^2 = 0.77$; and fledglings: $F = 18.11$, $P < 0.01$, df = 1, 10; $r^2 = 0.64$).

At least 13 of 25 Red-belly pairs (52%) that did not encounter starling or Red-head competition attempted second broods after successfully fledging first broods. Nine of the 13 pairs succeeded and fledged young from second broods. Of 71 Red-belly pairs that encountered either starling or Red-head competition, at least 44 (62%) reared first broods. However, only one of these 71 pairs (1.4%), attempted a second brood after fledging a first brood. Nineteen of these 71 pairs (27%) did not incubate first clutches until after 15 May, which minimized the possibility of raising second broods after late successful first ones.

I monitored 33 Red-belly pairs over three seasons to determine accurately the number of nestlings each fledged in a season. Seventeen pairs encountered starling competition; 16 were competition-free. The competing pairs fledged at least 38 nestlings, but none fledged both first and second broods. Conversely, the 16 noncompeting pairs fledged at least 53 nestlings, and six pairs successfully reared both first and second broods. Mean number of fledglings per pair for control birds was significantly greater than that for competing birds (3.3 vs. 2.2; $t = 2.22$, df = 31, $P > 0.05$).

Eighty-eight Red-head clutch sizes were recorded from 56 nesting pairs from the second

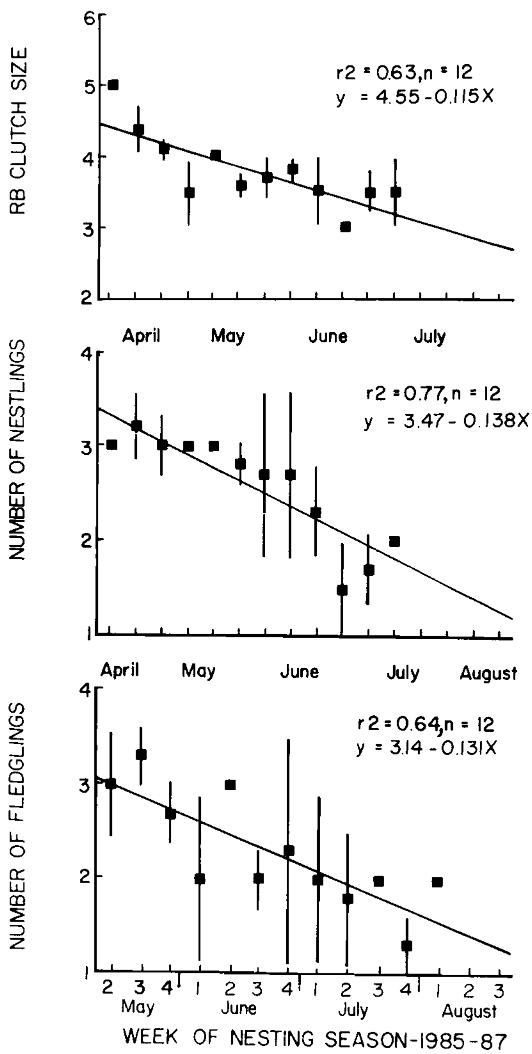

Fig. 7. The relationship between time (in weeks) and mean clutch size, number of nestlings, and number of fledglings for Red-bellied Woodpeckers. Vertical lines represent standard errors.

TABLE 1. Comparison of nest-site parameters of cavities usurped by starlings (S) from Red-bellied (RB) and Red-headed (RH) woodpeckers.

Parameter	% RB nests (n = 94)	% RB nests usurped by S (n = 55)	% RH nests (n = 105)	% RH nests usurped by S (n = 8)
Bark present	79	89	47	63
Living tree	73	85	45	63
Cavity limb angled down	63	67	34	63

week of May through the third week of August. Clutch data were divided into two groups. Fifteen June was the date that partitioned first and second broods (the date by which 92% of Red-head pairs with clutches were still attempting first broods; Fig. 4). Mean Red-head clutch size before 15 June was not significantly different from mean Red-head clutch size after this date (4.5 vs. 4.3; $t = 1.13$, df = 41, $P > 0.10$).

Fifteen July was the date that best separated Red-head pairs with fledglings into those pairs engaged in first vs. second nesting efforts (the latest date by which 100% of Red-head pairs with fledglings were completing initial broods; Fig. 4). Mean number of Red-head fledglings per pair did not differ in the two groups (2.1 vs. 2.3; $t = 0.719$, df = 31, $P > 0.10$). In addition, 8 of 46 Red-head pairs with nestlings (17%) before 15 July failed to fledge any offspring compared to 4 of 13 pairs with nestlings (31%) after 15 July. This difference was not significant ($\chi^2 = 1.12$, df = 1, $P > 0.10$).

Discussion

I believe that interference competition (Schoener 1974, Levine 1976, Maurer 1984) between starlings and Red-bellied Woodpeckers for freshly excavated nest cavities in east-central Mississippi is intense. Furthermore, Red-bellies that competed with starlings were less fecund than competition-free individuals. Two reasons that Red-bellies lost cavities to starlings at a higher rate than did Red-heads were that starlings and Red-bellies initiated nesting at the same time, but Red-heads began to nest later and Red-bellies tended to defend their cavities less vigorously than Red-heads (Nichols and Jackson 1987). Starlings frequently reused the same nest cavities when attempting second broods (Dakin 1984). If breeding starlings in this study behaved similarly, they would not have been seeking new nest cavities in early May, and would not compete with the later nesting Red-heads. Conversely, those starlings that sought fresh nest cavities for renesting or to raise a second brood, potentially competed with Red-heads for such cavities.

Cavity-site parameters between Red-heads and Red-bellies were similar to those reported previously (Reller 1972, Jackson 1976). These differences are potential factors that influence starlings in nest-site choice. The records of starlings nesting in cracks and crevices of houses and buildings, nest boxes, natural cavities in trees, and in old woodpecker cavities (Bent 1948, Kessel 1957, Zeleny 1969, Dakin 1984) are evidence of generalized requirements for nest sites, but provide little evidence about choice. Of 8 Red-head nest cavities usurped by starlings, 63% were more similar to typical Red-belly nest cavities (surrounded by bark in limbs angling down in living trees) than to typical Red-head nest cavities. I consider this evidence that starlings may prefer certain nest-site characteristics when choosing woodpecker nest cavities for nest sites. However, the extent to which starlings are influenced by differences in these characteristics is unclear and warrants further investigation.

There are advantages of a one-month separation of nest initiation in Red-heads and Red-bellies, and selection could act on these species in response to starling competition. Red-heads and Red-bellies resemble each other in size and behavior (Bent 1939, Selander and Giller 1959, Mayr and Short 1970, Jackson 1976, Williams and Batzli 1979) and exhibit a wide range of niche similarities. Despite differences in nest-site preferences of the two species (Selander and Giller 1959, Reller 1972, Jackson 1976, Kilham 1977), they competed for nest sites, but almost always after the first of May, when many Red-bellies were completing initial nesting efforts. One consequence of early nesting by Red-bellies is the avoidance of competition with Red-heads for cavity sites. However, Red-bellies must compete with the early-nesting starlings. Red-belly pairs that can avoid starling competition completely should have a strong advantage, especially if they rear two broods. Only a few pairs (18%) of early nesting Red-bellies avoided direct competition with starlings. Many of these pairs nested in densely vegetated areas that were apparently less attractive to breeding starlings. A few pairs, however, nested in relatively open areas surrounded by lawns or fields, suggesting that not all Red-belly nest cavities located in areas of starling overlap are certain to be discovered by breeding starlings. Conversely, Red-bellies that nested in rural locations did not necessarily escape competition. Of 6 Red-belly pairs observed on the south farm, 4 (67%) lost their cavities to starlings.

A frequent consequence of interspecific competition is a shift in the niche of one or more of the competing species (Diamond 1978). When competition with starlings is unavoidable, Red-bellies may be more successful by delaying nesting until starlings have finished nesting (selection could favor delayed nesting). However, this strategy has weaknesses. For instance, Red-bellies that delay nesting (and avoid starling competition) will compete more frequently with Red-heads. Red-bellies that delay nesting may encounter suboptimal factors and a loss of fecundity. Van Balen and Cave (1970) and Mertens (1977) suggest that hole nesting by Great Tits in June or later is a poor strategy because nestlings potentially have a greater risk of incurring hyperthermia. Finally, delayed nesting could prevent fecundity enhancements from second and third broods. Behavioral responses of Red-bellies to competition with starlings and Red-heads for nest sites are potentially numerous and complex. Because starling competition for nest sites could reduce Red-belly fecundity, selection may favor individuals able to completely avoid starlings during the early breeding season, or more aggressive individuals better able to compete for nest sites. Thus as starling/Red-belly nest-site competition continues, Red-belly populations should use urban habitats less frequently and should use rural forested habitats relatively more frequently.

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