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BENEFITS AND COSTS TO PLAIN-FRONTED THORNBIRDS (*PHACELLODOMUS RUFIFRONS*) OF INTERACTIONS WITH AVIAN NEST ASSOCIATES

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ABSTRACT.—From 1990 through 1993, I examined the interactions among a group of bird species in central Venezuela that use the multichambered stick nests of the Plain-fronted Thornbird (*Phacellodomus rufifrons*). Eleven species besides thornbirds, referred to as associates, used thornbird nests as nest sites and, in some cases, roost sites. During the 18-month study, 130 incidents of associates nesting in thornbird nests were recorded. More than 90% of thornbird territories observed for at least two breeding seasons (n = 33) had at least one associate nesting attempt. Four species accounted for over 86% of the attempts by associates: Cattle Tyrants (*Machetornis rixosus*), Stripe-backed Wrens (*Campylorhynchus nuchalis*), Saffron Finches (*Sicalis flaveola*), and Troupials (*Icterus icterus*). Sometimes thornbird and associate nesting attempts overlapped, taking place within the same nest in different chambers, or in different thornbird nests within a territory. Nine of 27 (33%) thornbird nesting attempts at the beginning of the 1991 breeding season overlapped associate attempts, and 5 of 26 (19%) overlapped in 1992. Nesting with associates involved benefits and costs for the thornbirds. In 1991, thornbird nesting attempts that overlapped Troupial nesting attempts were no more likely to succeed (33% successful, n = 6) than attempts with no associate overlap (28% successful, n = 18). Thornbird attempts that overlapped those of other species, however, were significantly more likely to succeed than attempts with no overlap (100% successful, n = 3). In 1992, patterns were similar (0% successful with Troupials, n = 2; 10% successful with no associates, n = 21; 33% successful with other associates, n = 3), although high thornbird nest mortality and small sample sizes precluded statistical analysis. Thornbird nesting attempts that overlapped two associate nesting attempts (n = 7, 1991 and 1992 combined) had a high success rate (71%). Rainfall in the month before fledging was positively associated with the number of fledglings produced in 1991, but not in 1992. Nest-guarding behavior by associates and enhanced mobbing of predators (demonstrated in predator-presentation experiments) were likely mechanisms of enhanced reproductive success when thornbirds nested with associates. Thornbirds often were treated with aggression by associates, and circumstantial evidence indicated that Troupials sometimes preyed on thornbird eggs and nestlings. Valuable nest sites may lead coexisting species to converge, rather than diverge, in their use of this resource. *Received 20 February 1995, accepted 26 July 1995.*

DIFFERENT TYPES of nesting associations among birds (described by Durango 1949) range from mixed colonies of seabirds (Burger and Gochfeld 1988) to passerine species nesting near and within larger nests of more aggressive species (Favaloro 1942, Parker 1981, Konrad and Gilmer 1982). The advantages of nesting associations include enhanced predator detection and defense (e.g. Pettingill 1942, Goransson et al. 1975, Slagsvold 1980, Post and Seals 1993), and some studies provide strong evidence that individuals nesting in interspecific associations have higher reproductive success than those nesting outside such associations (Clark and Robertson 1979; Wiklund 1979, 1982; Bijlsma 1984; Burger 1984). Possible costs to nesting in interspecific associations are similar to those for intraspecific associations, including reduced feeding rates (Hoogland and Sherman 1976, Gaston et al. 1983) and predation by associates (Wittenberger and Hunt 1985, Shields and Parnell 1986).

Nesting associations may be especially important in open tropical and subtropical habitats (Lindell 1996). Nest predation can be severe in tropical areas (Snow and Snow 1963, 1973, 1979; Skutch 1966; Ricklefs 1969; Fogden 1972), and the high species diversity and low structural heterogeneity of vegetation in open habitats like savannas may mean that avoidance of

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predation by nest-site partitioning (cf. Martin 1988a, b, c; 1993) is not possible. I examined a system in central Venezuela where several avian species converge, rather than diverge, in their choice of nesting sites, resulting in the formation of nesting associations. Such associations provide an opportunity to assess potential costs and benefits of this strategy.

The Plain-fronted Thornbird (*Phacellodomus rufifrons*) nests in close association with several other avian species (Skutch 1969b, Thomas 1983). Skutch (1969b) referred to birds that use thornbird nests as "associated birds" and stated that some of them "are mild and inoffensive while others are mercilessly aggressive toward the industrious builders." Because the effects of these other species on thornbird reproductive success had not been systematically investigated before this study, I adopted Skutch's term "associate" because it makes no assumptions about the nature of the interaction. I categorized species as associates if they were observed to nest in thornbird nests while the territories were occupied by thornbirds.

Here, I describe the nature, extent, and temporal patterns of associations among Plain-fronted Thornbirds and the other species that use thornbird nests. I also describe the effects of nest associates on thornbird reproductive success. Mechanisms through which associates may affect thornbird reproductive success, including aggression (a possible cost) and antipredator behavior (a benefit), were investigated. Nest guarding by associates was measured, and predator-mobbing behavior was assessed through predator-presentation experiments.

METHODS

Study site and natural history.—Field work was carried out in the llanos of Venezuela, 7 km north of Corozo Pando (8°34'N, 67°35'W). The 9,000-ha study site, Hato Masaguaral, has been maintained as both a cattle ranch and wildlife preserve since the 1940s. The llanos are flat, warm, low-lying plains (ca. 65 m elevation) with a seasonal rainfall pattern characterized by a four-month dry season, a six-month wet season, and two transitional months. Hato Masaguaral encompasses a variety of community types including gallery forest, palm savanna, pasture with scattered trees, and shrub/woodland (Troth 1979). The avifauna has been described by Thomas (1979).

Thornbirds are small (ca. 25 g), insectivorous members in the family Furnariidae. They usually nest in monogamous pairs, although about 10% of nesting attempts occur in trios (Lindell 1994). Thornbirds occupy pasture and shrub/woodland habitats and nest throughout the wet season, from April to November. Thornbird nests are constructed of sticks, which often are thorny. The nests hang from the ends of branches and are sometimes well over 2 m in length, with the bottom of the nest 1.60 to 12.87 m above the ground ($\bar{x}$ = 4.70 ± SD of 2.18 m, n = 38). Nests often have numerous entrances leading to chambers that are not connected internally.

Determination of nesting activities, nest-site positions within thornbird nests, and thornbird reproductive success.—I and five assistants monitored 17 thornbird territories from May through September 1990 and January through February 1991, 38 territories from May through November 1991, and 36 from May through November 1992 and March through April 1993. Monitoring consisted of nest watches and/or spot checks of thornbird nests to determine the nesting status of thornbirds and associates, to record intra- and interspecific interactions near the nests, and to determine the fate of thornbird nesting attempts. Thornbirds and associates did not nest simultaneously within a nest chamber, but they often nested simultaneously in different chambers of the same nest.

Watches or checks were carried out on average once every three days at each territory. Watches lasted 30, 45, or 60 min per territory, depending on the amount of time required to determine the nest status of thornbird residents and any associates. Watches were supplemented with nest checks, which involved using a ladder to examine nesting chambers that were low enough to be accessible. It was difficult to determine the contents of thornbird nesting chambers because the tunnels leading to the chambers are twisted and inflexible. However, it usually was possible to see the eggs and chicks of associates, because associates often enlarged the nesting chambers or used nesting chambers enlarged by other species.

The distance from the thornbird chamber to the top of the nest, and the length of the nest, were measured at 28 randomly selected nests (with associates and without associates). These data were arcsine transformed because they were not normally distributed. Differences among the data were then analyzed using two-tailed t-tests. Two measurements of thornbird reproductive success were assessed. Nesting success described the success or failure of nesting attempts. A successful nesting attempt was one in which at least one bird fledged and was able to return to the nest with its parents the first few nights after fledging. The number of fledglings produced per successful attempt was the second measure of reproductive success. For analyses testing the effects of associates on nesting success, I used data from the first nesting attempt per territory each year that was observed from start to finish. For analyses testing the effects of associates on the number of fledglings produced, I used data from the first successful nesting attempt from each territory.

I employed the Mayfield (1975) method to calculate daily mortality rates for the first nesting attempts of thornbirds, with and without associates, in 1991 and 1992. I also calculated daily mortality rates for the first nesting attempts of the second half of the nesting season (defined as beginning 1 September) for each territory under observation in both years. I confined mortality rate calculations to the incubation period because associates tended to begin nesting before thornbirds, resulting in a low number of days that associates overlapped with thornbird nestling periods. Relatively low numbers of nest days and nest losses with associates precluded statistical analyses to determine differences in mortality rates related to nesting overlap with associates.

Thornbird and associate nesting overlap.—When I examined the relationship between thornbird nesting success and associate overlap, I considered thornbird and associate nesting attempts to overlap when thornbirds and associates simultaneously had eggs and/or nestlings in different chambers of the same nest, or in thornbird nests within 12 m of each other. I chose 12 m because thornbirds and associates frequently interacted with each other and jointly mobbed predators at each others' nests when the nests were ≤12 m apart. When I examined thornbird nesting chamber position relative to associate overlap, I used only cases of associate overlap in which both species were nesting in the same nest.

Because nests were not visited every day, I was not able to determine exactly when nesting attempts began. I estimated the number of days of nesting overlap for thornbirds and associates by using data for incubation- and nestling-period lengths for the various species (Skutch 1969a, b; Harrison 1973; Skutch 1989; Rabenold 1990; pers. obs.) and backdating based on the number of associate eggs and/or chicks observed during nest checks and on known dates of fledging of thornbird offspring. I assumed that thornbirds and associates laid one egg per day because this is true for most passerines (Welty and Baptista 1988).

I used *G*-tests of independence with Williams' correction (Zar 1974, Sokal and Rohlf 1981) to analyze thornbird nesting success as it related to associate overlap. I tested Troupial (*Icterus icterus*) effects on thornbird nesting success separately because Troupials are the only obligate associate, and they are known predators of eggs and nestlings (Robinson 1985, Rabenold pers. comm.). Sample sizes for other associate species were small and, thus, pooled. Logistic regression models were used to determine whether the mean number of days of overlap with Troupials or other associates was a significant predictor of thornbird nesting success (Hosmer and Lemeshow 1989). Data from nesting attempts throughout the 1991 and 1992 seasons were pooled for the logistic regression analyses, although no more than one attempt from any particular territory was used.

Rainfall may influence food availability for breeding birds. For example, Poulin et al. (1992) documented increased arthropod abundance at the beginning of the wet season (when most birds breed) for four habitats in Venezuela. Rainfall data usually were collected daily at the field site. Analyses using these data were restricted to months in which there were no missing data. I used simple linear regression (Sokal and Rohlf 1981) to determine whether rainfall in the month before fledging or failure was a significant predictor of the number of young fledged from successful attempts in 1991 and 1992. Territory quality, measured as the total number of successful attempts in 1991 and 1992, was not a significant predictor of the number of fledglings produced per successful attempt. Hence, in the models described above, I used all successful attempts per year, including multiple attempts from the same territory.

Nest guarding and measures of aggression.—I assumed that nest guarding was taking place when an adult thornbird or associate was perched near the nest during incubation or feeding of nestlings (and was not obviously engaged in other activities such as foraging; Slack 1976). To determine the mean number of min/h that thornbirds or associates guarded nests, 45 1-h nest watches were conducted in 10 randomly selected territories in the early wet season of 1991, when either thornbirds or one of the associate species were nesting. The total time an adult bird was within 5 m of the nest was recorded (adults guarding a nest usually perched within this distance), and the average number of min/h that an adult bird was within 5 m of the nest was calculated for each territory. Differences in time spent nest guarding between thornbirds and associates (all species pooled) were tested using a Mann-Whitney *U*-test.

All inter- and intraspecific aggressive interactions that occurred within 2 m of the nests were recorded. An aggressive interaction was defined as one individual chasing, pecking, grabbing or making an aggressive intention movement toward another individual. I limited the number of aggressive interactions recorded for any species-pair during a particular nest watch to five to avoid skewing the data as a result of any particularly aggressive individuals. I analyzed the asymmetries in initiation of aggressive interactions within species pairs with *G*-tests of goodness of fit. A *G*-test of independence was used to examine the relationship between the species initiating Troupial-Saffron Finch (*Sicalis flaveola*) interactions and time of year, because the two species use thornbird nests at different times during the breeding season.

Predator-presentation experiments.—These experiments were conducted at eight territories in 1991 and eight different territories in 1992 and included: (1) thornbirds that nested without associates, and (2) thornbirds and Troupials that nested simultaneously in one nest or in different nests less than 12 m apart. Also in 1992, experiments were conducted at three territories where Troupials nested alone and in two territories where thornbirds and Troupials nested simultaneously in territories that also were used for experiments in 1991. Thus, results from these two

TABLE 1. Number of nesting attempts by nest associates of Plain-fronted Thornbirds, and whether they exhibited aggression toward thornbirds at thornbird nests. Observations of 130 associate nesting attempts at 52 thornbird nests over 18 months, 1990 to 1993.

Species	No. nesting attempts (% of total)	Aggression toward thornbirds[a]
Troupial (*Icterus icterus*)	49 (37.7)	Yes
Saffron Finch (*Sicalis flaveola*)	38 (29.2)	Yes
Cattle Tyrant (*Machetornis rixosus*)	14 (10.8)	Yes
Stripe-backed Wren (*Campylorhynchus nuchalis*)	11 (8.5)	Yes
Blue-gray Tanager (*Thraupis episcopus*)	7 (5.4)	Yes
Great Kiskadee (*Pitangus sulphuratus*)	4 (3.1)	Yes
Gray Seedeater (*Sporophila intermedia*)	2 (1.5)	No
Rufous-vented Chachalaca (*Ortalis ruficauda*)[b]	2 (1.5)	No
Rusty-margined Flycatcher (*Myiozetetes cayanensis*)	1 (0.8)	Yes
Glaucous Tanager (*Thraupis glaucocolpa*)	1 (0.8)	Yes
Unidentified[c]	1 (0.8)	No

[a] Includes chasing and other harassment of thornbirds approaching their nests.

[b] No aggression seen, although a chachalaca was incubating eggs in section of nest that had been under construction by thornbirds the previous day.

[c] Probably Yellow-chinned Spinetail (*Certhiaxis cinnamomea*); two eggs discovered one day but gone the next.

experiments were not included in the statistical analyses of the effects of association on the number of species and individuals mobbing the introduced predator, although they were used to compare the number of attacks on the introduced predator when thornbirds nested alone, when Troupials nested alone, and when the two species nested simultaneously. During each experiment, we recorded the number of species and individuals within 3 m of the nest each minute during 20-min periods before, during, and after introducing a caged Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) to within 1 m of the nest. We placed the pygmy-owl next to the nest where the thornbirds were nesting if the thornbirds and Troupials were using different nests. Pygmy-owls are diurnal, as well as nocturnal predators of birds. We twice observed them fly to thornbird nests in apparent predation attempts after thornbirds had returned to the nest for the night. During one of these incidents, several thornbirds emerged from the nest and scolded the pygmy-owl for several minutes until it left. During the other incident, the thornbirds never emerged from the nest and the pygmy-owl eventually left.

The numbers of species and individuals observed each minute within 3 m of the nest during the prepresentation, presentation, and postpresentation periods were tallied. I refer to the data on the numbers of individuals as individual-minutes because it is the sum of individuals sighted during each minute of the three 20-min periods of the experiment. It is not equivalent to individuals because, for example, one Troupial present during both the first and second minutes of the presentation would be counted as two individual-minutes. Date were square-root transformed to meet the assumptions of ANOVA. I then performed two-factor repeated-measures ANOVAs (Sokal and Rohlf 1981) to compare the mean number of species and individual-minutes among the prepresentation, presentation, and postpresentation periods, for situations with only thornbirds nesting, and for those with thornbirds and Troupials nesting simultaneously. For the experiments conducted in 1992, the number of attacks by any species on the pygmy-owl was recorded. An attack was defined as an individual swooping to within 1 m of the pygmy-owl's cage.

RESULTS

Nest associates.—In addition to thornbirds, 11 other bird species attempted to nest in thornbird nests (Table 1). Eight of these were observed to chase and/or harass thornbirds as they tried to approach their nest(s). Two additional species, the Bicolored Wren (*Campylorhynchus griseus*) and the Carib Grackle (*Quiscalus lugubris*), were seen bringing nest material into thornbird nests, and Bicolored Wrens were found roosting in thornbird nests on four occasions. Scaled Doves (*Scardafella squammata*) also were observed walking and sitting on thornbird nests, possibly prospecting for nest sites. I observed 8 of 11 associate species carrying nest material into thornbird chambers where they nested. For two species, the Rufous-vented Chachalaca (*Ortalis ruficauda*) and the Glaucous Tanager (*Thraupis glaucocolpa*), I was not able to confirm their bringing material into nests.

The two most common associate species, Troupials and Saffron Finches, accounted for

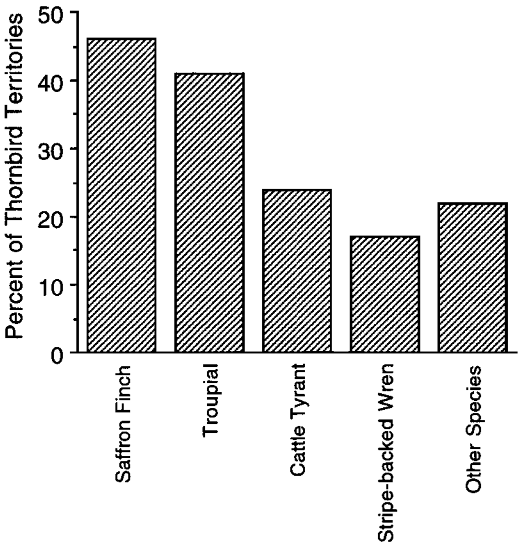


FIG. 1. Percent composition of nest associates with at least one nesting attempt in Plain-fronted Thornbird territories in 1991 and 1992 ($n = 41$, including territories observed in only one year).

67% of total associate nesting attempts (87 of 130), and the four most common species, which also included Cattle Tyrants (*Machetornis rixosus*) and Stripe-backed Wrens (*Campylorhynchus nuchalis*), comprised 86% of all nesting attempts by associates (112 of 130; Table 1). All associate species except Troupials used thornbird nests facultatively. Troupials nested only in thornbird nests and also roosted in thornbird nests throughout the year.

Associate nesting attempts were made in thornbird nests at 30 of 33 thornbird territories that were observed during at least two nesting seasons. Associate species varied in the frequency with which they used these nests (Fig. 1). Associates were recorded nesting in thornbird nests in every month from March through November during this study (Figs. 2 and 3). It is likely that associates nested in thornbird nests in December as well, because I recorded several associate nesting attempts beginning at the end of November. Thornbirds were observed nesting in all months from April through November, and they probably continued nesting through December.

A striking pattern in the phenology data is the temporal division of thornbird nest use by the two most common associate species (Fig. 2). In both 1991 and 1992, Troupials nested in thornbird nests from April through September, and Saffron Finches used them from September through November, and probably occasionally throughout the dry season from December through March. Two Saffron Finch nesting attempts at sites other than thornbird nests were observed by a local worker in late December or

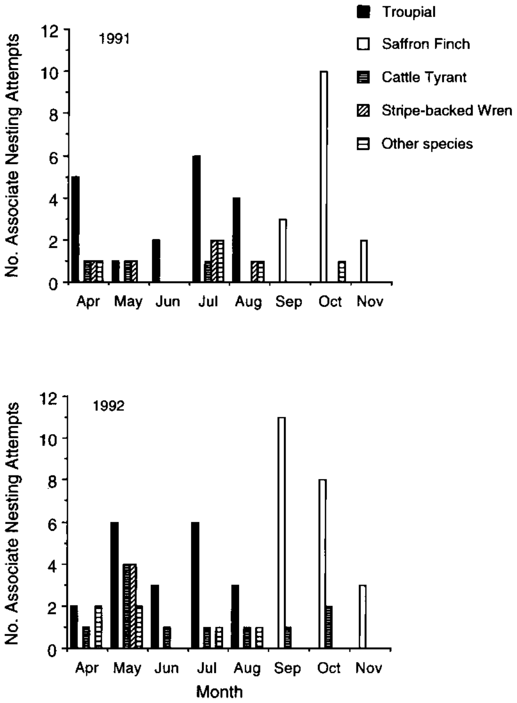


FIG. 2. Seasonal distribution of associate nesting attempts in Plain-fronted Thornbird nests in 1991 (38 territories) and 1992 (36 territories).

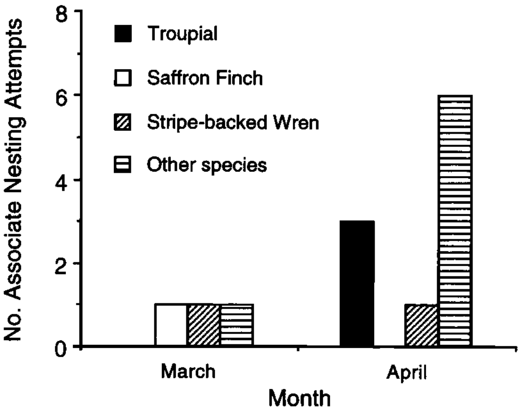


FIG. 3. Seasonal distribution of associate nesting attempts in Plain-fronted Thornbird nests in 1993 (36 territories).

TABLE 2. Aggressive interactions[a] among Plain-fronted Thornbirds and the six most common nest associates, 1991 and 1992.

	Aggressor						
Recipient	Plain-fronted Thornbird	Saffron Finch	Troupial	Cattle Tyrant	Stripe-backed Wren	Blue-gray Tanager	Great Kiskadee
Plain-fronted Thornbird	196	148	138	30	80	20	13
Saffron Finch	28	7	12	16	3	0	3
Troupial	0	26	17	4	18	3	0
Cattle Tyrant	4	10	11	5	2	0	0
Stripe-backed Wren	8	0	9	0	3	0	0
Blue-gray Tanager	3	0	2	1	1	0	0
Great Kiskadee	2	1	4	5	2	0	1

[a] Within 2 m of thornbird nests.

early January of 1992-93 (K. Rivera pers. comm.), and I recorded one Saffron Finch nesting attempt in a thornbird nest in March 1993 (Fig. 3). In both years, the temporal distributions of Troupial nesting attempts were significantly different from those of Saffron Finch attempts (Kolmogorov-Smirnov tests; 1991, $n_1 = 18$, $n_2 = 15$, $D = 270$, $P < 0.001$; 1992, $n_1 = 20$, $n_2 = 22$, $D = 440$, $P < 0.001$). The behavioral interactions of Troupials and Saffron Finches reflected the temporal division of thornbird nest use. From May through August, Troupials initiated more aggressive interactions toward Saffron Finches than vice versa (7 vs. 2), whereas from September through November, Saffron Finches initiated more aggressive interactions toward Troupials than vice versa (24 vs. 5; $G = 10.5$, df = 1, $P < 0.005$).

Within 2 m of thornbird nests, associates were much more aggressive toward thornbirds than thornbirds were toward associates (Table 2). Saffron Finches and Troupials initiated these types of aggression toward thornbirds significantly more often than thornbirds did toward them (Saffron Finch, $G = 89.5$, df = 1, $n = 176$, $P < 0.0001$; Troupial, $G = 191.3$, df = 1, $n = 138$, $P < 0.0001$). Aggressive interactions, however, were not limited to these types of direct confrontations. Once I observed a Troupial remove another Troupial's egg from a thornbird nest and destroy it. I also observed a resident thornbird enter the nesting chamber where Troupials were incubating, return to the chamber entrance with a Troupial egg in its beak, and fly away with it. Thornbird nesting attempts failed as a result of several factors, including nest predation by associates, although for the majority of nest failures, the cause could not be determined (Table 3). Sometimes associates tolerated each other. In one instance, a pair of Troupials and a pair of Cattle Tyrants nested within the same nest, overlapping 33 days. Both pairs fledged young. In six other cases, two associates overlapped within a thornbird territory using thornbird nests for at least two weeks.

For first nesting attempts in 1991, thornbirds initiated nesting before associates as often as associates initiated nesting before thornbirds in

TABLE 3. Likely causes and evidence for 76 Plain-fronted Thornbill nesting failures, 1991 and 1992.

Unknown ($n = 47$).
Predation by species other than associate (10).—Severe nest damage, predators on nest near time of failure, or predation event observed.
Troupials (6).—Troupials observed removing sticks from nest near time of failure, seen severely harassing thornbirds, or predation event observed.
Other associate predation (2).—Associates observed severely harassing thornbirds near time of failure.
Predation by associates or by species other than associates (3).—Sticks and/or eggs on ground beneath nest.
Intraspecific competition for territories (3).—Failures following intraspecific interactions at nest and recent resident turnover.
Premature fledging (2).—Recent fledgling disappears after not being able to return to nest.
Nest support branch breaks and nest falls to ground (2).
Brood parasitism (1).—Thornbird adults fed young of brood parasite, Striped Cuckoo (*Tapera naevia*).

situations in which thornbirds and associates overlapped (six times thornbirds nested first, six times associates nested first). In 1992, associates initiated nesting before thornbirds more often than thornbirds initiated nesting before associates ($G = 9.4$, df = 1, $n = 12$, $P < 0.005$). Data from five nesting attempts in which I was unable to determine which species initiated nesting, as well as three nesting attempts in which two associate species were involved, were excluded from the analyses. My data indicate that the majority of overlap between thornbirds and associates occurred during the thornbird's incubation period.

When thornbirds and associates overlapped within a nest, thornbirds used a higher chamber in the nest (closer to the support branch) 27 of 28 times ($G = 29.6$, df = 1, $n = 28$, $P < 0.001$). The distance from the thornbird chamber to the top of the nest at 28 randomly selected nests did not differ between thornbird nests with and without associate overlap (with associate overlap, $\bar{x} = 29.2 \pm 18.4$ cm, $n = 17$; without associate overlap, $\bar{x} = 30.7 \pm 19.6$ cm, $n = 11$; $t = -0.21$, $P > 0.8$). The relative height of the thornbird chamber (distance from top of the nest/length of nest) was not significantly different for thornbirds nesting with and without associates in the nest (with associates, 28.5%; without associates, 38.1%; with arcsine transformation, $t = 1.5$, $n = 28$, $P = 0.15$). Nests where thornbirds nested alone were significantly shorter ($\bar{x} = 76.1 \pm 20.4$ cm, $n = 17$) than nests in which thornbirds and associates overlapped ($\bar{x} = 103.5 \pm 34.0$ cm, $n = 11$; $t = -2.7$, $P = 0.01$).

Thornbird reproductive success.—In 1991, thornbird nesting success with Troupial overlap was not significantly different from that with no associate overlap (2 of 6 nests vs. 5 of 18; $G = 0.07$, df = 1, $n = 24$, $P = 0.77$). In contrast, thornbird nesting success with associates other than Troupials was significantly higher than with no associate overlap (3 of 3 vs. 5 of 18; $G = 5.6$, df = 1, $n = 21$, $P = 0.02$). Nesting began earlier in 1992 than in 1991. Consequently, a substantial number of nesting attempts had already begun when I began my observations and thus were not used in the 1992 analysis. The thornbird nesting attempts in 1992 that I did observe from start to finish experienced high mortality and low association rates (with Troupial overlap, 0 of 2 nests successful; with associate overlap other than Troupials, 1 of 3 nests; with no overlap, 2 of 21 nests), making statistical analyses inappropriate. Using the Mayfield (1975) method, I employed data from the nesting attempts initiated before I arrived to determine average daily mortality rates during the incubation period in 1991 and 1992. The rates were lower in both years when thornbird attempts overlapped associate attempts by any species compared with when thornbirds nested alone (Table 4).

TABLE 4. Daily nest mortality rates (Mayfield 1975) during incubation period for first nesting attempts per territory of first and second halves of nesting season, 1991 and 1992.

	Daily mortality rate (no. nest days)	
Portion of nesting season	Without associates	With associates
	1991	
First half	0.029 (280)	0.000 (64)
Second half	0.039 (128)	0.000 (42)
	1992	
First half	0.020 (204)	0.014 (71)
Second half	0.035 (255)	0.017 (60)

Seven thornbird nesting attempts from 1991 and 1992 overlapped two associate attempts. Five of these attempts were successful, yielding a 71% success rate. When thornbirds overlapped with Troupials, the number of days overlap was not a significant predictor of nesting success. However, when thornbirds overlapped with species other than Troupials, the number of days overlap was positively associated with the probability of nest success (Table 5). Thornbird nesting attempts that overlapped two associate nesting attempts were not included in these analyses because of small sample sizes.

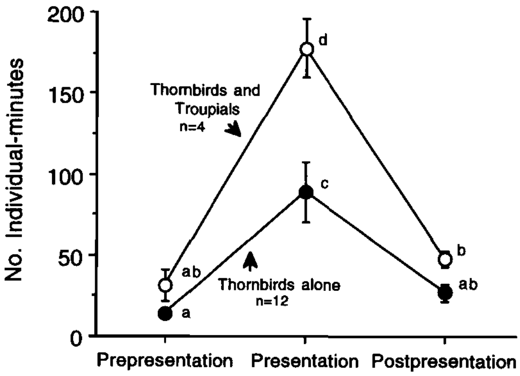
In 1991, successful thornbird attempts that overlapped associate attempts produced no more fledglings ($\bar{x} = 1.9 \pm 0.9$, $n = 7$) than attempts with no associate overlap ($\bar{x} = 2.1 \pm 1.0$, $n = 8$; Mann-Whitney U-test, $Z = -0.56$, $P = 0.58$). However, rainfall in the month before fledging or failure was a significant positive predictor of fledgling number in 1991 ($F = 19.77$, $n = 22$, df = 1, $P < 0.001$), explaining 47.2% of the variance. In 1992, thornbirds fledged more young from attempts that overlapped associate attempts ($\bar{x} = 2.4 \pm 0.8$, $n = 7$) than from attempts with no overlap ($\bar{x} = 1.6 \pm 0.6$, $n = 5$; $Z = -1.82$, $P = 0.07$), but the difference was only marginally significant. Rainfall was not a significant predictor of fledgling number in 1992 ($F = 0.75$, $n = 22$, df = 1, $P = 0.40$).

TABLE 5. Maximum likelihood analyses from logistic regression models of Plain-fronted Thornbird nesting success (1, success; 0, failure) as a function of number of days of nest associate overlap. Degrees of freedom = 1 for both analyses.

	n	β^a	G^b
Troupials	12	−0.038 ± 0.104	0.14^{ns}
Other associates	11	0.527 ± 0.365	7.50**

[a] $\bar{x}$ ± SE. $\bar{x}$ is maximum-likelihood estimate, with asymptotic value given for SE. β is coefficient of variable "number of days overlap."

[b] Likelihood ratio; viz. difference in log likelihoods of equations describing thornbird nesting success with only one parameter (a constant) vs. equation with "no. days overlap" as second parameter. **, $P < 0.01$.



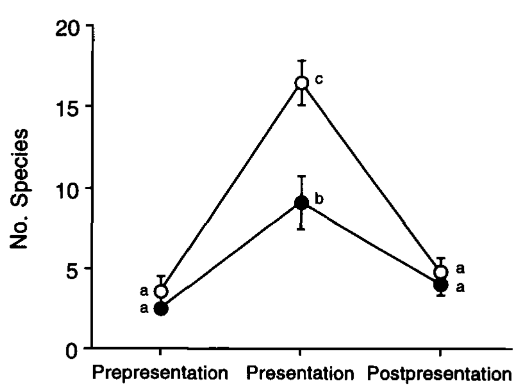


FIG. 4. Number of individual-minutes ($\bar{x}$ ± SE) recorded within 3 m of nest during predator-presentation experiments at Plain-fronted Thornbird nests with active nesting attempts (top graph). Number of species recorded within 3 m of nest during predator-presentation experiments at thornbird nests with active nesting attempts (bottom graph). Means with different letters are significantly different from each other ($P < 0.05$; Newman-Keuls multiple range tests).

Mechanisms of associate effects on thornbird reproductive success.—Some associate species, including Troupials and Cattle Tyrants, guarded the nest when they had nestlings. One of the adults often perched within a few meters of the nest while the other foraged. Thornbirds did not engage in this guarding behavior to the same extent as associates. During thornbird nesting attempts with no associates in the nest, an adult bird was within 5 m of the nest significantly less often ($\bar{x}$ = 6.5 ± 2.5 min/h, n = 7) than when one of the associate species was nesting in a thornbird nest ($\bar{x}$ = 32.6 ± 12.7 min/h, $n = 3$; $Z = -2.39$, $P = 0.02$). For two nest watches conducted when two species were simultaneously feeding nestlings in a nest, an adult was within 5 m of the nest 29.5 min/h, on average.

The number of individual-minutes and species recorded within 3 m of active thornbird nests during the presentation of a pygmy-owl were significantly greater than during the prepresentation and postpresentation periods (repeated-measures ANOVA on square root-transformed values; individual-minutes, $F = 43.64$, df = 2 and 28, $P < 0.001$; species, $F = 38.63$, df = 2 and 28, $P < 0.001$; Fig. 4). I recorded significantly more individual-minutes during the presentation of a pygmy-owl at nests with simultaneous thornbird and Troupial nesting attempts than at nests with only thornbirds nesting ($F = 6.11$, df = 1 and 14, $P < 0.05$; Fig. 4). The interaction between the repeated measure (number of individual-minutes recorded during the prepresentation, presentation, and postpresentation periods) and the nesting species (thornbirds alone or thornbirds and troupials together) was not significant ($F = 2.21$, df = 2 and 28, $P > 0.1$). The difference in the number of species at nests with simultaneous thornbird and Troupial nesting attempts compared with the number of species at nests where only thornbirds nested approached significance ($F = 3.47$, df = 1 and 14, $P < 0.1$). There was a significant interaction between the repeated measure and whether thornbirds nested alone or with Troupials ($F = 3.36$, df = 2 and 28, $P < 0.05$). This result indicates that more species arrived to mob the predator when the two species were nesting simultaneously than would be expected, given the effects of pygmy-owl presentation and simultaneous nesting as separate influences on species number.

In 1992, we recorded the number of attacks by any species on the pygmy-owl during the presentation. The mean number of attacks per presentation was much lower at nests with only thornbirds ($\bar{x} = 7.9 \pm 11.8$, $n = 8$) than at nests with only Troupials ($\bar{x} = 50.7 \pm 21.6$, $n = 3$), or with thornbirds and Troupials nesting simultaneously ($\bar{x} = 61.0 \pm 17.0$, $n = 2$). I did not conduct statistical analyses because of the small sample sizes.

DISCUSSION

Biologists have long recognized that certain nest sites are more valuable than others. Birds that nest in cavities, for example, generally have greater reproductive success than open-cup nesters (Nice 1957, Ricklefs 1969), particularly cavity nesters that excavate their own nests (Martin and Li 1992). One also would expect enclosed nests, such as those built by thornbirds, to provide valuable nest sites, presumably because they are safer from predators than are open nests (Lack 1948). Nice (1957) presented evidence indicating that species with enclosed nests experience greater reproductive success than those with open-cup nests. If enclosed nests are preferred by many species and are costly to build, such nests might become the focus of interspecific interactions. Indeed, this was supported by my results, in which Plain-fronted Thornbird nests served as potential nest sites for at least 11 other species. Four of these species used thornbird nests regularly as nesting sites. Because species association at thornbird nests was common (more than 90% of territories observed for at least two nesting seasons had associate nesting attempts at least once), associates and thornbirds have the potential to act as significant selective pressures on one another.

Interactions between thornbirds and nest associates may be particularly important in the context of nest predation. Predation by birds such as Crane Hawks (*Geranospiza caerulescens*), Yellow-headed Caracaras (*Milvago chimachima*), and Troupials was the most common cause of thornbird nest failures for those instances in which evidence was available (Table 3). Predation by predators or associates caused at least 27% of all thornbird nest failures. Thornbird nest structure (enclosed), composition (sticks, many of them with thorns), and placement (near the ends of branches) probably are responses to nest predation. Although thornbird nests are visible from a substantial distance (sometimes hundreds of meters), predators such as raptors spend much more time extracting chicks from a thornbird nest (sometimes without success) than they do from an open-cup nest (pers. obs.). Ironically, the features that make thornbird nests more secure against predators also probably attract other species. Nilsson (1986), in contrast to other investigators, found similar rates of nesting success for cavity and open-cup nesters in a temperate forest. He suggested that high rates of interspecific competition for cavities was a major cost of using that type of nest site.

Behavioral interactions between thornbirds and nest associates indicate that association poses costs to thornbirds in terms of energy expended interacting with these species. Conversely, my data demonstrate that thornbird reproductive success is enhanced in the presence of associate nesting groups. Although data for 1992 do not demonstrate a significant difference in probability of nest success, this is probably because nesting occurred early that year, and I was not able to use nesting attempts that began before I arrived. Data for later nesting attempts demonstrated high nest mortality and few instances of associate overlap. Average nest mortality rates in both years for both early and late nesting attempts were consistently lower in thornbird nests with associate overlap, compared with those without overlap.

Rainfall in the month before fledging or nest failure explained nearly 50% of the variance in fledgling number in 1991, and none of the variance in 1992, whereas association was positively associated with the number of thornbird fledglings produced in 1992, but not in 1991. These patterns may have resulted because the early wet season in 1991 was very dry, and many successful attempts produced only one fledgling. Only 44.9 mm of rain fell in May 1991, compared with a mean of 211.7 ± 107.8 mm in May from 1978 to 1988. In contrast, 315.3 mm of rain fell in May 1992. In times of low precipitation, food supplies may be the major limiting factor influencing fledgling numbers. When food is abundant, however, predation may have a more important influence on fledgling numbers than does food availability. Thornbirds may raise more young in the presence of associates because associates reduce predation pressure.

Troupials are documented egg and nestling predators (Robinson 1985, K. N. Rabenold pers. comm.) and were likely involved in several cases of thornbird nesting failure (Table 3). After observing thornbirds and Troupials for four months at another site in Venezuela, Skutch (1969b) stated that "it is doubtful whether they [thornbirds] could rear a brood in a structure where Troupials are breeding, as the latter become fiercely aggressive toward the builders of their stolen nest." Troupials weigh two to three times as much as thornbirds and often chased thornbirds from their nests (Table 2). Although results from the predator-presentation experiments indicate thornbirds should benefit by nesting with Troupials, Troupials apparently preyed on several thornbird nests during this study. Because thornbirds nesting with Troupials had about the same success as when nesting alone, it appears that the benefits and costs to thornbirds of nesting with Troupials are approximately equal.

Thornbirds typically roosted and nested in the upper chambers of a nest with 0.5 to 2 m of nest below them. Nests with both thornbirds and associates were significantly longer than nests with only thornbirds. These results concur with Thomas' (1983) hypothesis that differences in thornbird nest length between the llanos ($\bar{x}$ = 82.3 cm, n = 10) and the Venezuelan coast ($\bar{x}$ = 51.5 cm, n = 10) exist because of the greater number of Troupials in the llanos. Thomas' work suggests that nests may vary among thornbird populations because of varying numbers of associates, whereas my data indicate that nest differences exist within populations as well. Ultimately, in areas with many associates, selection may have favored thornbirds that build longer nests. The enhanced reproductive success for thornbird nesting attempts that overlap associate attempts supports this idea. Proximately, perhaps thornbirds use cues such as the number of associate visits to their territory to assess the likelihood of a future associate nesting attempt. If the likelihood is high, thornbirds may build nests of longer than average size. Another potential explanation, not mutually exclusive with those stated above, is that thornbirds actively recruit associates by constructing long nests.

Because nesting with associates has some costs for thornbirds, they should employ strategies to reduce such costs. One such strategy involves the timing of nesting. In 1992, when thornbirds and associates overlapped, associates were significantly more likely to begin nesting first. This pattern was not evident in 1991, which may be a result of associate species delaying nesting because of the sparse May rainfall. If thornbirds can determine when the probability of nest association is high, they may delay their own nesting until the associate attempt has begun. This would reduce the probability of associates destroying thornbird eggs and chicks and would enhance the chances of thornbirds and associates peacefully coexisting in the same nest.

Why do the benefits of thornbirds nesting with associates other than Troupials seemingly outweigh the costs? A likely explanation is the enhanced guarding and mobbing activity of associates. Associate species guarded nests much more vigorously than did thornbirds, perhaps because they were at a later stage in nesting. Hence, they were more likely to detect nest predators and initiate mobbing efforts than were thornbirds.

The presence of a caged pygmy-owl at active thornbird nests elicited mobbing from numerous individuals of different species. The mobbing effect was enhanced (i.e. more species, more individual-minutes, more attacks on the predator) in thornbird territories with associates compared with thornbird territories without associates. If we assume that larger numbers of species and individuals are more successful at driving off predators than are smaller numbers, then territories with thornbird and associate overlap should experience fewer nesting failures as a result of predation. Associate species are likely to be more effective mobbers than thornbirds because they are larger (Troupials and Cattle Tyrants), likely to be in groups (Stripe-backed Wrens), and/or more aggressive (Troupials, Cattle Tyrants, Stripe-backed Wrens, Saffron Finches).

The predator-presentation experiments were time- and labor-intensive, and, sometimes, could not be conducted because of unforeseen difficulties. Hence, because Troupials were one of the most common associate species, and I was likely to obtain adequate sample sizes by concentrating on this species, all experiments were conducted with Troupials as the associate. This may call into question the applicability of these results for situations where the associates are not Troupials. However, part of the reason for the enhanced mobbing effect is likely the guarding behavior and associated fast response to predators described previously. Associates other than Troupials engage in guarding behavior. In addition, all the associates are more colorful and more aggressive than thornbirds, so their presence is more likely to attract other birds to the scene. Hence, I expect that similar results would have been obtained with other associates.

An alternative explanation for the predator-presentation results is that Troupials nest in thornbird territories that maintain more species and more individuals than territories without Troupials. However, Troupials nested in 58% of the territories that were observed for at least two nesting seasons ($n = 33$). Troupial territories generally abut each other and encompass two or three thornbird territories (pers. obs.). There were several incidents of Troupials chasing each other from nests at roost time. Hence, although it is possible Troupials prefer particular territories that happen to have more species and individuals, their high population density makes it unlikely they can avoid many thornbird territories as potential nest sites. Also, of the 12 territories that served as sites for predator-presentation experiments in which only thornbirds were nesting, six had Troupial nesting attempts at some point during the study.

The seasonal change in aggressive interactions between Troupials and Saffron Finches (each species becoming the aggressor during its respective nesting season) suggests that a competitive relationship exists between them. The nesting phenology of Troupials and Saffron Finches (Troupials nested from April through August, whereas Saffron Finches nested from September through November, and probably through the dry season) may function in part to reduce competition for thornbird nesting sites. Unlike Troupials, Saffron Finches also nest in sites other than thornbird nests. If they nest in other sites from May through August, this suggests that they are being excluded from thornbird nests by Troupials during these months. In 1992, I actively searched for Saffron Finch nesting activity but did not find any nests before September. B. T. Thomas (pers. comm.), however, found one nest in a nest box in July 1977 at Hato Masaguaral, and Cherrie (1916) described four Saffron Finch nests (one in May, two in June, one in July) near the village of Caicara, less than 200 km from Hato Masaguaral. (Three of the four nests were found in old nests of other species, and the fourth was in a cavity.) P. Schwartz (cited in Hilty and Brown [1986]) found a Saffron Finch nest in Venezuela in June. Hence, Saffron Finches are capable of nesting before September but appear to do so uncommonly, suggesting that their nesting phenology in thornbird nests is related to factors other than the presence of Troupials.

Nest-site interactions.—Competitive interactions for access to enclosed nests may have been overlooked in the past because of the low number of this type of nest in the Temperate Zone, where most research has been conducted. Ricklefs (1969), in an analysis of oscine nest types, found that 6% of the species in a temperate area, and 25% of the species in a tropical area, built domed or enclosed nests. Domed nests may be attractive to other species for nesting because they are safer than open nests and costly to build. Hence, when a valuable resource such as an enclosed nest is available, species may converge rather than diverge in resource use, leading to interspecific interactions that will further influence the behavior and ecology of the interacting species.

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LITERATURE CITED

BIJLSMA, R. G. 1984. On the breeding association between Woodpigeons *Columba palumbus* and Hobbies *Falco subbuteo*. Limosa 57:133–139.

BURGER, J. 1984. Grebes nesting in gull colonies: Protective associations and early warning. American Naturalist 123:327–337.

BURGER, J., AND M. GOCHFELD. 1988. Nest-site selection and temporal patterns in habitat use of Roseate and Common terns. Auk 105:433–438.

CHERRIE, G. K. 1916. A contribution to the ornithology of the Orinoco region. Museum of the

Brooklyn Institute of Arts and Sciences Science Bulletin 2:133–374.

CLARK, K. L., AND R. J. ROBERTSON. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator defenses. Behavioral Ecology and Sociobiology 5:359–371.

DURANGO, S. 1949. The nesting associations of birds with social insects and with birds of different species. Ibis 91:140–143.

FAVALORO, N. 1942. The usurpation of nests, nesting sites and materials. Emu 41:268–276.

FOGDEN, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:307–343.

GASTON, A. J., G. CHAPDELAINE, AND D. G. NOBLE. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: Inter- and intra-colony variation. Canadian Journal of Zoology 61:2465–2475.

GORANSSON, G., J. KARLSSON, S. G. NILSSON, AND S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: An experimental study. Oikos 26:117–120.

HARRISON, C. J. O. 1973. Observations on the behaviour and breeding of the Saffron Finch (*Sicalis flaveola*). Avicultural Magazine 79:207–213.

HILTY, S. L., AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey.

HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecological Monographs 46:33–58.

HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York.

KONRAD, P. M., AND D. S. GILMER. 1982. Nesting associations between passerines and birds of prey in central North Dakota. Condor 84:343.

LACK, D. 1948. The significance of clutch-size. Part III. Ibis 90:25–45.

LINDELL, C. A. 1994. Nest placement among coexisting bird species: An investigation of interspecific usurpation of *Phacellodomus rufifrons* nests in a tropical savanna. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.

LINDELL, C. A. 1996. Patterns of nest usurpation: When should species converge on nest niches? Condor 98: in press.

MARTIN, T. E. 1988a. On the advantage of being different: Nest predation and the coexistence of bird species. Proceedings of the National Academy of Sciences USA 85:2196–2199.

MARTIN, T. E. 1988b. Habitat and area effects on forest bird assemblages: Is nest predation an influence? Ecology 69:74–84.

MARTIN, T. E. 1988c. Processes organizing open-nesting bird assemblages: Competition or nest predation? Evolutionary Ecology 2:37–50.

MARTIN, T. E. 1993. Nest predation and nest sites. BioScience 43:523–532.

MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

NILSSON, S. G. 1986. Evolution of hole-nesting in birds: On balancing selection pressures. Auk 103: 432–435.

PARKER, J. W. 1981. Nest associates of the Mississippi Kite. Journal of Field Ornithology 52:144–145.

PETTINGILL, O. S. 1942. The birds of a bull's horn acacia. Wilson Bulletin 54:89–96.

POST, W., AND C. A. SEALS. 1993. Nesting associations of Least Bitterns and Boat-tailed Grackles. Condor 95:139–144.

POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295–2309.

RABENOLD, K. N. 1990. *Campylorhynchus* wrens: The ecology of delayed dispersal and cooperation in the Venezuelan savanna. Pages 159–196 *in* Cooperative breeding in birds: Long-term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

ROBINSON, S. K. 1985. The Yellow-rumped Cacique and its associated nest pirates. Pages 898–907 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithological Monographs No. 36.

SHIELDS, M. A., AND J. F. PARNELL. 1986. Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. Auk 103:531–539.

SKUTCH, A. F. 1966. A breeding bird census and nesting success in Central America. Ibis 108: 1–16.

SKUTCH, A. F. 1969a. A study of the Rufous-fronted Thornbird and associated birds, part I: Life history of the Rufous-fronted Thornbird. Wilson Bulletin 81:5–43.

SKUTCH, A. F. 1969b. A study of the Rufous-fronted Thornbird and associated birds, part II: Birds which breed in thornbirds' nests. Wilson Bulletin 81:123–139.

SKUTCH, A. F. 1989. Life of the tanager. Cornell University Press, Ithaca, New York.

SLACK, R. D. 1976. Nest guarding behavior by male Gray Catbirds. Auk 93:292–300.

SLAGSVOLD, T. 1980. Habitat selection in birds: On the presence of other bird species with special regard to *Turdus pilaris.* Journal of Animal Ecology 49:523–536.

SNOW, B. K., AND D. W. SNOW. 1979. The Ochre-bellied Flycatcher and the evolution of lek behavior. Condor 81:286-292.

SNOW, D. W., AND B. K. SNOW. 1963. Breeding and the annual cycle in three Trinidad thrushes. Wilson Bulletin 75:27–41.

SNOW, D. W., AND B. K. SNOW. 1973. The breeding of the Hairy Hermit *Glaucis hirsuta* in Trinidad. Ardea 61:106–122.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W.H. Freeman and Company, New York.

THOMAS, B. T. 1979. The birds of a ranch in the Venezuelan llanos. Pages 213–232 *in* Vertebrate ecology in the northern Neotropics (J. F. Eisenberg, Ed.). Smithsonian Institution Press, Washington, D.C.

THOMAS, B. T. 1983. The Plain-fronted Thornbird: Nest construction, material choice and nest defense behavior. Wilson Bulletin 95:106–117.

TROTH, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Pages 17–30 *in* Vertebrate ecology in the northern Neotropics (J. F. Eisenberg, Ed.). Smithsonian Institution Press, Washington, D.C.

WELTY, J. C., AND L. BAPTISTA. 1988. The life of birds. Saunders College Publishing, New York.

WIKLUND, C. G. 1979. Increased breeding success for Merlins *Falco columbarius* nesting among colonies of Fieldfares *Turdus pilaris.* Ibis 121:109–111.

WIKLUND, C. G. 1982. Fieldfare (*Turdus pilaris*) breeding success in relation to colony size, nest position and association with Merlins (*Falco columbarius*). Behavioral Ecology and Sociobiology 11: 165–172.

WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* Avian Biology, vol. 3 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.