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FACTORS AFFECTING NESTING SUCCESS IN RIPARIAN BIRD COMMUNITIES

LOUIS B. BEST
AND
DEAN F. STAUFFER

ABSTRACT.—Nest and egg successes are documented for open-nesting bird species in a variety of riparian habitats in central Iowa. In most species, nest success was higher during the nestling period than during the incubation period. Causes of nest failure in order of decreasing importance were: predation by birds, snakes, or small mammals; predation by large mammals; desertion; cowbird parasitism; natural disasters.

Relationships between nesting outcome and the following variables are analyzed statistically: adult weight, date, nest height, nest concealment, vegetation form supporting the nest (support life-form), and habitat type. Nest failure resulting from predation by large mammals and parasitism by cowbirds was greater among smaller-sized birds. The percentage of nests successfully fledging young increased with nest height. Losses from natural disasters differed among the support life-forms.

Relationships among the factors that may affect nesting outcome are compared statistically to determine possible interactions. Mean body weight, which differed according to nest support life-forms, decreased as the season advanced. Body weight also was inversely related to nest concealment. Concealment differed among nest supports and was greater later in the breeding season. Concealment also was inversely related to nest height. The distribution of nests in the support life-forms changed during the season.

Species more generalized in selecting nest substrates had lower nest success.

Nesting success probably has been documented more extensively than any other facet of avian breeding ecology (for reviews see Nice 1957, Ricklefs 1969), but few workers (Kendeigh 1942, Young 1949, Nolan 1963, Gates and Gysel 1978) have considered nesting success at the community level. Detailed analyses of factors affecting nesting outcome also are scarce, although several variables are known to contribute to nesting failure. Because the sites selected for nest placement vary in probability for success, mortality during nesting is an important force in the evolution of avian reproductive behavior.

The objectives of this study were to document nesting success among open-nesting species in avian communities occupying riparian habitats, and then to evaluate factors affecting nesting outcome. We attempted to determine if certain nest-site characteristics were associated with certain mortality factors, irrespective of differences in the breeding behavior of the individual bird species. Hence, we focussed on the avian community, rather than any single species or a few closely related species. This approach is reasonable because nests of all members of the community represent potential prey for predators as well as hosts for the generalist brood parasite, the Brown-headed Cowbird (*Molothrus ater*). Also, all nests are subject to the rigors of weather and to other natural catastrophes.

METHODS

Chosen for study were 28 sites along Brushy Creek, Beaver Creek, and the Middle and South Raccoon rivers in Guthrie County, Iowa. These represented a range of riparian habitats from open hayfields to closed-canopy woodland. Procedures for establishing the study sites and the floristic composition of the various habitats are described in Stauffer and Best (1980).

We found most nests by watching the behavior of breeding birds and by searching suitable vegetation. Additional nests were found while censuses were conducted. Nests were harder to find in treeless hayfields and dense forests than in areas with a semi-open woodland canopy. The field season extended from mid-April to mid-July during 1976 and 1977.

We checked the status of active nests every four or five days before June, and every two or three days thereafter. We tried to avoid trampling or disturbing vegetation near the nest site. A mirror on a pole was used to view contents of high nests; data were restricted to nests within 8 m of the ground. At each visit, we recorded the number of eggs and(or) young, as well as any evidence of predation or cowbird parasitism. Nest predation where the nest bowl was torn apart and(or) the nest partly or entirely pulled from its original po-

TABLE 1. Success of nests and eggs (nestlings) according to stage of the nesting cycle.

Species	Number of nests	Percent successful					
		Incubation period		Nestling period		Incubation and nestling periods combined	
		nests	eggs	nests	nestlings	nests	eggs (nestlings)
Mourning Dove (*Zenaida macroura*)	42	16	21	84	78	13	16 (15)[a]
Yellow-billed Cuckoo (*Coccyzus americanus*)	5	68	61	54	45	36	27
Black-billed Cuckoo (*C. erythropthalmus*)	5	12	9	—[b]	—	—	—
Eastern Wood Pewee (*Contopus virens*)	6	100	100	74	80	74	80
Blue Jay (*Cyanocitta cristata*)	12	72	69	75	76	54	53 (47)
Gray Catbird (*Dumetella carolinensis*)	56	57	56	78	63	44	36 (34)
Brown Thrasher (*Toxostoma rufum*)	18	64	66	75	57	48	38 (38)
American Robin (*Turdus migratorius*)	9	82	83	100	100	82	83 (69)
Red-winged Blackbird (*Agelaius phoeniceus*)	17	37	46	57	36	21	16 (16)
Cardinal (*Cardinalis cardinalis*)	46	32	23	49	33	16	8 (6)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	18	45	41	73	44	33	18 (18)
Indigo Bunting (*Passerina cyanea*)	26	18	23	7	2	1	<1 (<1)
Dickcissel (*Spiza americana*)	5	31	31	—[b]	—	—	—
Field Sparrow (*Spizella pusilla*)	8	29	31	33	16	10	5
Song Sparrow (*Melospiza melodia*)	10	16	13	39	45	6	6

[a] This computation includes hatching success (see Mayfield 1975), where it was determined for at least five clutches.

[b] Percent success was not calculated because fewer than five nests were sampled during the nestling period.

sition was attributed to larger mammals. Also, the surrounding vegetation sometimes was matted down. Nests showing no sign of disturbance but from which the contents had been removed were considered to have been lost to birds, snakes, or small mammals. Robertson (1972), Thompson and Nolan (1973), Beaver (1975), Best (1978), and Nolan (1978:413–416) used similar criteria for distinguishing these categories of nest predation.

We calculated nesting success using Mayfield's (1975) exposure method, based upon the number of days nests were under observation. This method assumes a constant mortality rate within each stage of the nesting cycle, an assumption that may not have been met in all instances (see Woolfenden and Rohwer's [1969:38] discussion of Mourning Dove nest losses during incubation). Nest losses involved only whole-brood losses, whereas egg or nestling losses included both whole-brood and within-brood losses. When calculating "nest-days" and "egg-days," losses were assumed to have occurred midway through the interval between nest visits. Nests were considered successful if the young were scheduled to fledge (herein "fledge" refers to leaving the nest) during an interval between nest visits and if, on the later visit, the nest was found empty with no evidence of disturbance. Some predation during the final days of the nestling period (particularly by snakes, birds, and small mammals) may have occurred unnoticed, resulting in overestimates of nesting success in some instances. Incubation and nestling periods were obtained from the species accounts in Bent et al. (1932–1968).

Hatching success was determined for nests found before hatching that remained active and undisturbed through this phase of the nesting cycle. Egg losses before hatching should not have biased the results, assuming that predators and cowbirds did not preferentially select or avoid infertile or addled eggs.

We evaluated six variables considered possible influences on nesting outcome: adult body weight; date; nest height; nest concealment; vegetation form supporting the nest; and habitat type. Weights of adult birds of the species studied were obtained from the literature (see Table 3). Date of nest initiation either was determined by direct observation of nest building or was estimated by back-dating from known stages in the nesting cycle. Height was measured directly for lower nests and by use of a range-height finder for the higher nests. Cover, both above and below nests, was visually estimated as poor, fair, good, or excellent, yielding concealment-index values of 1 through 4, respectively. Overall concealment was determined by summing values above and below the nest. These visual estimates correlated closely with measurements of relative light intensity taken immediately above and below nests. Visual estimates were used because they were more easily obtained than light intensity measurements, particularly for less accessible nests. The life-forms of plants providing nest support were categorized as grasses (or grass-like plants), forbs, shrubs, deciduous saplings (< 3 m tall), deciduous trees (> 3 m), and evergreen trees. Ground nests were assigned the life-form of the principal plant affording cover, and nests in vines ($n = 12$) were assigned the life-form most similar to the structure of the vine. General habitat was classified as upland woodland, floodplain woodland, scrub, or open herbaceous cover. Statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

POTENTIAL NEST PREDATORS

Avian predators, including Common Crows (*Corvus brachyrhynchos*), Blue Jays, House Wrens (*Troglodytes aedon*), and Starlings (*Sturnus vulgaris*), bred on most study areas. Bull snakes (*Pituophis melanoleucus*) and garter snakes (*Thamnophis* spp.) were occasionally seen. Eastern chipmunks (*Tamias striatus*), fox squirrels (*Sciurus niger*), white-footed mice (*Peromyscus leucopus*), least weasels (*Mustela rixosa*), and mink (*M. vison*) were among the small mammals present that are known to destroy nests. Racoons (*Procyon lotor*) were the most abundant large-mammal predators, and striped skunks (*Mephitis mephitis*), opossums (*Didelphus virginianus*), and coyotes (*Canis latrans*) also were present. Domestic dogs frequented some sites.

COMPARISON OF NESTING SUCCESS AMONG SPECIES

Table 1 shows nest and egg or nestling successes for species with five or more nests sampled. Causes of nest failure in the individual species are given in the Appendix. Losses during egg laying were excluded from the computations because samples were inadequate. Including this period would reduce the estimates of nesting success for some species. Indigo Buntings had the lowest nesting success. Losses were especially high during the nesting period, mainly because cowbird nestlings displaced host young from the nest.

For 10 of 13 species where comparisons could be made, nest success was higher during the nestling period than during the incubation period (Table 1). This was particularly evident in the Mourning Dove (see also McClure 1942, Harris et al. 1963). McClure (1942) attributed higher nest mortality during the egg stage to the facts that: adult Mourning Doves are more protective of young than of eggs, young cling to the nest, and the additional weight of the young adds to the stability of the nest. In his study, winds and heavy storms were the greatest decimating factors. The large, white eggs of Mourning Doves are much more conspicuous to predators than are the cryptically-colored nestlings, which also may account for some difference in egg and nestling loss rates. Greater nest success during the nestling period than the incubation period is consistent with other studies (Howell 1942, Kendeigh 1942, Hudde 1959, Goddard and Board 1967, Roseberry and Klimstra 1970, Thompson and Nolan 1973, Harmeson 1974, Knupp et al. 1977), although exceptions have been reported for the Red-winged Blackbird (Young 1963, Robertson 1972, Caccamise 1976). Certain mortality factors, such as infertility and embryonic death, affect only the egg stage, and nest desertion occurs much more frequently before hatching. Nests most vulnerable to predation are very likely to be found and destroyed by predators early in the nesting cycle; consequently, those that survive this period are more likely to remain undetected (e.g., Nolan 1978:404). Finally, the development of the young may progressively restrict the variety of animals that prey upon them (Ricklefs 1969), although predation may be more likely when activity at the nest increases after hatching (Skutch 1949, Mayfield 1975).

TABLE 2. Egg hatching success of selected species.[a]

Species	Number of clutches	Number of eggs	Percent of eggs hatching
Mourning Dove	11	22	91
Blue Jay	9	36	89
Gray Catbird	31	110	94
Brown Thrasher	11	36	100
American Robin	7	23	83
Red-winged Blackbird	8	31	100
Cardinal	19	43	86
Rose-breasted Grosbeak	11	36	100
Indigo Bunting	8	14	100

[a] Determined for nests found before hatching that remained active and undisturbed through this phase of the nesting cycle. Includes only species where hatching success was determined for at least five clutches.

Percentages of nest success and egg or nestling success differed much more during the nestling period than during incubation (Table 1). This was particularly evident in Rose-breasted Grosbeaks, Red-winged Blackbirds, Brown Thrashers, Field Sparrows, Cardinals, and Gray Catbirds. In these species, nestling success was lower than nest success during the nestling period, largely the result of within-brood losses.

The percentage of eggs hatching in 139 nests was 93% of those present at hatching time and ranged from 83% to 100% for individual species (Table 2).

FACTORS POTENTIALLY AFFECTING NESTING OUTCOME

The 302 nesting attempts were divided into six categories of outcomes: 124 successfully fledged at least one young, 104 presumably were disrupted by avian, snake, or small-mammal depredation, 36 probably were destroyed by large mammals, 15 were deserted for unknown causes, 14 failed as a result of cowbird parasitism (desertion, removal of all host eggs, or loss of all host young), and 9 were lost from natural disasters (dislodged by growth of nest-support vegetation, wind, or branch falling on nest). Predators were the major cause of nest failure (79% of all nest losses; see also Lack 1954:77, Nolan 1963, Ricklefs 1969). The relationships among the six factors thought to influence nesting success and the nesting outcomes were tested statistically by chi-square contingency analyses. Analyses were run for classes of each factor comparing all nesting outcomes simultaneously (n × 6) and also comparing nests of each individual outcome with all other nests combined (n × 2). Some nesting outcomes are combined in Tables

TABLE 3. Nesting outcome in relation to adult body weight. Values represent percentages of the total number of nests.

Body weight (g)[b]	Nesting outcome[a]					
	Successful fledging	Large-mammal predation	Avian, snake or small-mammal predation	Cowbird parasitism	Other[c]	Total nests
1–20	29	25	21	15	10	52
21–40	49	14	27	0	10	73
41–60	35	9	42	6	8	78
61–80	59	7	27	2	5	56
>80[d]	30	5	58	0	7	43

[a] Individual nesting outcomes differing significantly among the bird body weight classes were: successful fledging (χ^2 = 16.07, df = 4); large-mammal predation (χ^2 = 12.72); avian, snake or small-mammal predation (χ^2 = 19.96); and cowbird parasitism (χ^2 = 20.81). (Although percentage values are presented in the table, statistical analyses were run on the actual counts.)

[b] Bird body weights were obtained from Gross (1921), Stewart (1937), Baldwin and Kendeigh (1938), Hartman (1946), Norris and Johnston (1958), and Lanyon (1957).

[c] Includes nest losses from desertion and natural disasters.

[d] All but one nest belonged to Mourning Doves.

3 and 4, but the analyses were run using all six of the original outcomes.

Body weight. Adult body weights were categorized into 20-g classes (Table 3). The contingency analysis comparing all nesting outcomes with the weight classes was highly significant (χ^2 = 61.16, df = 20). No pattern was evident between body weight and either the number of nests successfully fledging young or the number lost to avian, snake, or small-mammal predators, although both comparisons were significant. The influence of adult size on nest susceptibility very likely differs among these three sources of predation and could account for the lack of a consistent trend. Perhaps size does not directly affect this nesting outcome. Montevecchi (1976), however, reported that smaller eggs (associated with smaller birds) were more vulnerable to Common Crow predation than were larger eggs.

Incidence of large-mammal predation decreased consistently as body weight increased. This suggests that larger birds are better able to defend their nests against large mammals and (or) that nests of larger birds are less vulnerable to these predators.

Nest failure resulting from cowbird parasitism was greatest in species weighing less than 20 g. Small birds may be more prone to desert their nests when parasitized, and their nestlings suffer more in competition with cowbird young for food (Friedmann 1963:1,2) or space in the nest (Mayfield 1965). Larger birds may not be suitable hosts, either because their larger eggs would prevent successful incubation of the cowbird eggs (Friedmann 1929:190), or because they are more likely to be predatory (e.g., corvids) or strongly aggressive toward other birds (Payne 1973). King (1979) reported that under experimental conditions, female cowbirds preferred to parasitize nests which contained host eggs smaller than their own.

Ricklefs (1969, 1972:372) reported that daily nest mortality rates decreased as the size of altricial land birds increased, presumably because large species can better defend their nests against predators and because their larger young can better withstand inclement weather. Smaller prey species also are within the food-size range of a wider variety of predators.

Date. Nesting outcome was determined for 34 nests initiated in April, 133 in May, 108 in June, and 27 in July. There were no statistically significant relationships between the month in which nests were built and nesting outcomes, although the percentage of nests successfully fledging young tended to decrease (47%, 45%, 36%, and 33% for the respective months), and nests lost to large mammals tended to increase (3%, 11%, 14%, and 19%) as the breeding season progressed. Other workers have reported nesting success either increasing or decreasing with the advance of the season, although in most instances it increased. Several explanations have been proposed

TABLE 4. Nesting outcome in relation to nest height. Values represent percentages of the total number of nests.

Nest height (m)	Nesting outcome				
	Successful[a] fledging	Large-mammal predation	Avian, snake or small-mammal predation	Other[b]	Total nests
0–1	32	16	35	18	133
1–2	48	10	34	9	103
>2	50	8	35	8	66

[a] Nests successfully fledging young differed significantly among the height classes (χ^2 = 8.92, df = 2).

[b] Includes nest losses from desertion, cowbird parasitism and natural disasters.

TABLE 5. Nesting outcomes in the six life-forms supporting nests. Values represent percentages of the total number of nests in each life-form.

	Nesting outcome						
Vegetation life-form	Successful fledging	Large-mammal predation	Avian, snake or small-mammal predation	Natural[a] disaster	Desertion	Cowbird parasitism	Total nests
Grass	50	6	28	0	11	6	18
Forb	17	21	38	17	0	8	24
Shrub	42	14	28	3	7	6	121
Deciduous sapling	40	15	32	0	5	8	40
Deciduous tree	46	7	41	1	4	1	83
Evergreen tree	38	6	56	0	0	0	16

[a] Nest losses from natural disasters differed significantly among the vegetation life-forms supporting nests ($\chi^2 = 18.77$, df = 5).

for seasonal increases, including an increase in protective cover (Lanyon 1957, Longcore and Jones 1969), reduced predation pressure (Howell 1942, Nice 1957, Nolan 1963, Roseberry and Klimstra 1970, Harmeson 1974, Nolan 1978:414–415), reduced brood parasitism by Brown-headed Cowbirds (Nolan 1963, Best 1978), more predictable weather conditions (Howell 1942), and greater parental care per nestling when clutches are smaller (Longcore and Jones 1969). The most common explanation advanced for seasonal decreases in nesting success is an increase in nest predation (Zimmerman 1971, Beaver 1975, Dolbeer 1976, Caccamise 1978).

Nest height. When compared simultaneously, nesting outcomes did not differ significantly ($P = 0.07$) among the three nest-height classes (Table 4). The percentage of nests successfully fledging young, however, did increase significantly with nest height (see also Meanley and Webb 1963, Holcomb and Twiest 1968, Holcomb 1969, Holm 1973), accompanied by a statistically insignificant but noticeable decrease in nest predation by large mammals. Others have reported no relationship (Nolan 1963, Francis 1973, Harmeson 1974, Krapu 1978) or even an inverse relationship (Goddard and Board 1967, Longcore and Jones 1969, Holcomb 1972, Ortego and Hamilton 1978) between nest height and nesting success. In our study, predation by birds, snakes, or small mammals was uniformly distributed among nests of different heights, probably because these predators range higher in vegetation than larger mammals and have access to smaller branches. Optimum nest height may change as the breeding season advances and could be related to factors such as seasonal changes in concealment afforded by vegetation and in microclimatic conditions (Nolan 1978:127).

Nest concealment. Overall nest concealment was divided into three classes (nest concealment indices <5, 5 or 6, 7 or 8). Sixty-eight nests had cover indices of less than 5, 99 of 5 or 6, and 135 of 7 or 8. Nest concealment was not related significantly to nesting outcome, although the percentage of nests successfully fledging young tended to decrease (49%, 44%, 35%) and nests destroyed by large mammals tended to increase (6%, 10%, 16%) with greater nest cover. Nice (1937:93–94) and Nolan (1978:401) reported higher nest success in well-concealed than poorly concealed nests, although others (Roseberry and Klimstra 1970, Anderson and Storer 1976, Caccamise 1977, Best 1978, Gottfried and Thompson 1978) have found no such relationship.

Nest support vegetation. When analyzed simultaneously, nesting outcomes were significantly different among the various nest support life-forms (Table 5; $\chi^2 = 41.49$, df = 25). When each nesting outcome was compared individually with all other nests, only nest losses from natural disasters differed significantly. Nests in forbs suffered most from this kind of loss, primarily by being dislodged by growth of the support vegetation (see also Holm 1973, Krapu 1978). The contents of nests placed in forbs also may be dumped in high winds (Stokes 1950). In our study, the percentage of successful nests was lowest in forbs, but nest success in the other five life-forms was comparable. Harmeson (1974) reported much lower success of Dickcissel nests placed in forbs compared with those situated in grass litter, and Knupp et al. (1977) found that American Robin nests built in deciduous trees were more successful than those in conifers. Evans (1978) stated that nest success of Field Sparrows was highest in evergreens because of reduced losses to predators, and Best (1978) found that mammalian predation on nests in grass litter was significantly less than on those in forbs, shrubs, or trees.

Although nest support vegetation may influence the likelihood that a nest will be parasitized, failure of the entire nest after cowbird parasitism is primarily a function of individual bird-species characteristics and not the vegetation supporting the nest.

General habitat. Nesting outcome was determined for 134 nests located in upland woodland habitat, 120 in floodplain woodland, 19 in scrub, and 29 in open herbaceous cover. Outcomes among the four general habitat types were not significantly different (compare Longcore and Jones 1969). Others, however, have reported differences in nesting success among habitats (Hudde 1959, Case and Hewitt 1963, Robertson 1972, Krapu 1978, Gates and Gysel 1978).

RELATIONSHIPS AMONG FACTORS

Relationships among the six variables potentially affecting nesting outcome were compared statistically (analysis of variance, correlation analysis, chi-square contingency analysis) to determine possible interaction effects. That is, nesting outcomes were ignored, and for each nest, the factors were analyzed to determine the degree to which they varied independently. General habitat was excluded from these comparisons because it showed no observable relationship to nest success. To provide a more extensive sample, data from all located nests were used, including nests for which nesting outcome was not recorded. This additional sample included nests that were inaccessible for monitoring nesting success and those that were identifiable to species but found after active nesting. The former accounts for the substantial increase in the number of nests sampled from deciduous trees. Sample sizes vary slightly from one analysis to another because not all variables were recorded at every nest.

Mean body weights (using midpoints of 10-g classes) of adults of the nesting species decreased significantly from April through July (F = 21.43, df = 3/485); means and standard deviations for the four months were, respectively, 93 ± 88, 58 ± 35, 42 ± 33, and 35 ± 29 g. This suggests that larger species tend to nest earlier in the season or to renest less often than smaller species. Bird weight was not correlated significantly with nest height, but was related inversely to nest concealment ($r = -0.318$, $n = 489$). Larger birds may be better able to defend their nests and are outside the obtainable prey size range of many predators; thus they probably rely less on concealment than smaller birds. Also, herbaceous plants, which afforded the best nest concealment (see below), provided less suitable nest support for larger species than did woody vegetation. Mean body weights differed significantly among the herbaceous, shrub/sapling and tree nest-support life-forms (F = 24.34, df = 2/484). Means and standard deviations for the three life-forms were, respectively, 33 ± 22, 43 ± 25, and 67 ± 57 g.

Nest height did not differ significantly according to month of nest initiation; mean values for the four months studied were, respectively, 2.98, 2.87, 3.00, and 1.93 m. Seasonal increases in nest height have been documented for some of the species studied (Nice 1937:92–93, Taylor 1965, Holcomb and Twiest 1968, Dow 1969, Best 1978), but at the community level increases in some species may be balanced by other species that breed later in the season and place their nests relatively low (e.g., American Goldfinch [*Carduelis tristis*], Dickcissels, and Indigo Buntings). Thus, all strata in the community tend to be used throughout the season.

Degree of nest concealment increased significantly with the advance of the breeding season (F = 8.14, df = 3/485); means and standard deviations for the four months studied were 4.8 ± 2.0, 5.8 ± 1.6, 5.9 ± 1.7, and 6.5 ± 1.3. The most noticeable change occurred from April to May and probably resulted mainly from foliage development. Also, a higher percentage of nests later in the season were placed in plant life-forms that provided better nest cover (see below).

The distribution of nests in the various forms of vegetation differed significantly among the four months of the breeding season ($\chi^2 = 66.0$, df = 18; Fig. 1). Early nests placed in grasses were undersampled because of inexperience in searching for nests at the beginning of the first field season when the open-hayfield plots were studied. For example, Field Sparrows are known to prefer grass substrates early in the season (Best 1978), but no nests were found in grass cover (Stauffer and Best 1980). The seasonal increase in the use of forbs for nest sites paralleled an increase in height and foliage coverage of these plants. Some species that nest in herbaceous substrates have been reported to shift from grass to forb nest sites as the breeding season progresses (Zimmerman 1966, Best 1978).

Use of shrubs for nest sites fluctuated somewhat over the season; the greater usage in May corresponded to peak nest building by Cardinals and Brown Thrashers. The

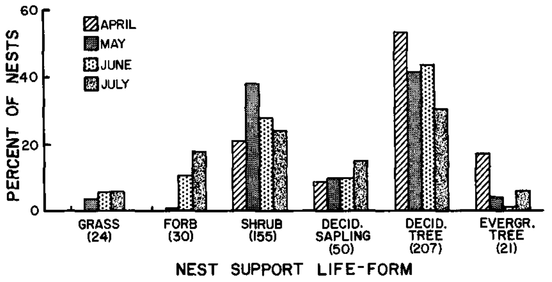

FIGURE 1. Distribution of the nests constructed each month among various nest support life-forms (types of supporting vegetation). Values represent percentages of the total nests for each month. Sample sizes are in parentheses.

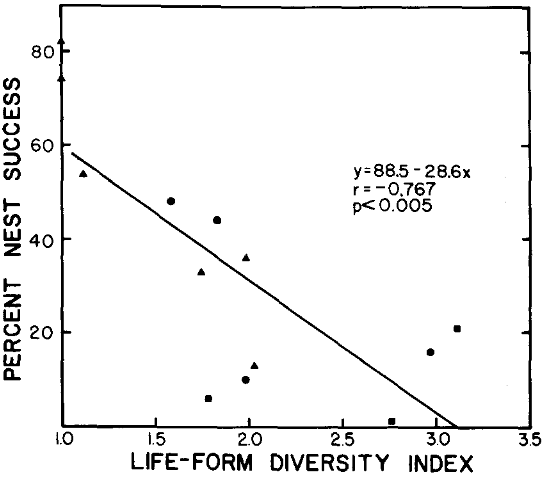

FIGURE 3. Relationship between the diversity of life-forms selected for nest support and nest success. Triangles represent species nesting predominantly in trees; circles, those nesting primarily in shrubs; and squares, those using mainly herbaceous plants.

seemingly greater use of deciduous trees in April reflects, at least in part, the ease with which nests can be found in trees before foliation. Evergreen trees provided better concealment than other woody species in April, which may explain their heavy use that month. American Robins (Howell 1942) and Cardinals (Nolan 1963) have been reported to nest in evergreens early in the breeding season, shifting later to deciduous trees after leaves emerge.

The higher the nest, the less was its overall concealment (r = −0.314, n = 489). Concealment below the nest was more strongly correlated with nest height (r = −0.402, n = 489) than concealment above the nest (r = −0.128), although both were highly significant. Higher nests are less accessible to certain predators (e.g., snakes and larger mammals), possibly causing nest concealment to be less important.

Mean heights of 487 nests according to support life-form were: grasses, 0.3 m; forbs, 0.7 m; shrubs, 1.1 m; deciduous saplings, 1.1 m; evergreen trees, 1.2 m; and deciduous trees, 5.4 m. Concealment both above and below nests differed significantly among the various nest support life-forms (F = 13.35, 63.99; df = 5/481; Fig. 2), but the difference was greater for cover below. Nests in grass had more cover below than above, mainly because they generally were placed at or near the ground. Nests in deciduous trees had much less cover below them than above, and to a lesser degree the same was true for those in shrubs. Nests placed in these plant forms generally have a protective canopy of numerous branches, twigs, and leaves, but the space below the nest may be quite open.

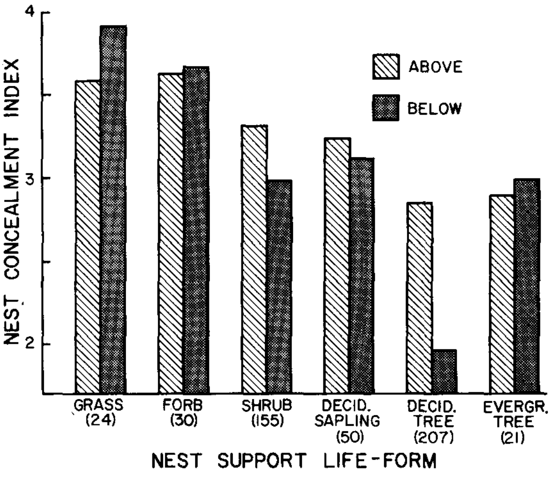

FIGURE 2. Mean concealment above and below nests placed in various support life-forms.

EFFECTS OF SPECIFICITY IN NEST-SITE SELECTION

Specificity in the substrates selected for nesting differs greatly among bird species. Some birds restrict themselves primarily to a single type of substrate, while others are less choosy. Species which are not very selective have a wider range of suitable substrates and less likelihood that nest-site availability would limit distribution and abundance of breeding populations. Natural selection has not favored such a generalist habit in all species, however, presumably because of disadvantages associated with broadening nest-site selection. One such disadvantage may be an increase in the rate of nest failure as a wider variety of substrates is selected, since specialization in nest placement reduces vulnerability of nests to mortality factors. For example, nesting in more forms of vegetation may expose a bird species to a greater variety of predators, thus lessening the likelihood of evolving efficient antipredator nesting behavior.

We calculated diversity indices for each species on the basis of the vegetation life-form(s) chosen for nest placement, using the reciprocal of Simpson's index $1/\Sigma P_i^2$, where P_i = the proportion of the total nests in the i^{th} vegetation life-form (Whittaker and Levin 1975:169). The life-form diversity index was then regressed on nest success, including only species where at least five nests were sampled. Species that selected a wider variety of nesting substrates experienced significantly lower nest success. This pattern was evident not only when all species were considered together (Fig. 3), but also when the analysis was restricted to species nesting predominantly in trees ($y = 122.0 - 49.6x$, $r = -0.929$) or mainly in shrubs ($y = 73.0 - 20.8x$, $r = -0.649$). Species using herbaceous plants as their predominant nest support did not follow the general pattern.

CONCLUSIONS

Nests placed in the open are more susceptible to predators, inclement weather, and other environmental factors than are those in more protected locations (Nice 1957, Lack 1968, Ricklefs 1969). Thus, it is informative to evaluate those nest-site characteristics that may influence the probability of nesting success. In our study, adult body weight was related significantly to the greatest number of nesting outcomes; general habitat type presumably was unimportant. Considering statistically significant relationships and (or) consistent trends, incidence of large-mammal predation was influenced by bird body size, date of nest initiation, nest height, and nest concealment. Frequency of predation by birds, snakes, or small mammals was affected by bird size, as was nest loss from cowbird parasitism. Vegetation form supporting the nest influenced the number of losses resulting from natural disasters. We considered any area adjoining a stream as riparian, whether it was restricted to the floodplain proper or included adjacent upland habitat; consequently, our results are applicable to both lowland and upland situations. However, we did not exhaust the list of possible factors that could affect nesting outcome (e.g., Anderson and Storer 1976). More research in different habitats and other geographical areas will be required to define all constraints on the nesting success of open-nesting altricial species.

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Department of Animal Ecology, Iowa State University, Ames, Iowa 50011. Present address of second author: Department of Wildlife Resources, University of Idaho, Moscow, Idaho 83843. Accepted for publication 8 August 1979.

APPENDIX. Causes of nest failure among the various species. Values represent percentages of all nest failures for each species.

Species	Large-mammal predation	Avian, snake or small-mammal predation	Natural disaster	Desertion	Cowbird parasitism	Total nests lost
Mourning Dove	7	86	0	7	0	29
Yellow-billed Cuckoo	0	100	0	0	0	3
Black-billed Cuckoo	0	67	0	33	0	3
Eastern Wood Pewee	0	100	0	0	0	1
Blue Jay	25	75	0	0	0	4
Gray Catbird	30	48	7	15	0	27
Brown Thrasher	0	71	14	14	0	7
American Robin	0	0	0	100	0	1
Red-winged Blackbird	27	64	0	0	9	11
Cardinal	18	56	6	9	12	34
Rose-breasted Grosbeak	0	100	0	0	0	9
Indigo Bunting	21	33	17	4	25	24
Dickcissel	0	100	0	0	0	3
Field Sparrow	40	40	0	0	20	5
Song Sparrow	33	50	0	17	0	6