THE RELATIONSHIP BETWEEN NEST DEFENCE, NEST VISIBILITY, HABITAT AND NEST SUCCESS IN THE EASTERN KINGBIRD (TYRANNUS TYRANNUS)

by

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The relationship between nest defence, nest visibility, habitat and nest success in the Eastern Kingbird (*Tyrannus tyrannus*)

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Abstract

This 5-year study (1987-1991) was conducted in south-eastern British Columbia, Canada, and is an investigation of nest defence behaviour in the Eastern Kingbird (Tyrannus tyrannus) with respect to nest visibility, behaviour at the nest, nest site and habitat characteristics and nest success. The study stresses the different choices that parents defending eggs make as opposed to parents defending nestlings and how these choices affect nesting success.

Kingbird nest contents survived better than comparable pseudonest contents but, while contents of visible pseudonests were preyed upon more than contents of hidden pseudonests, kingbird nests which were more visible from overhead were not preyed upon as heavily as kingbird nests which were less visible from overhead. Noisy behaviour influenced nesting success and was beneficial when it occurred close to the nest. Kingbirds chased predators when the predators were most dangerous and the defence effort of parents increased with the amount of danger posed by the predator at the time of the chase. Predators responded to kingbird attacks in ways that may have impaired their hunting efficiency, but kingbirds which approached closest to a crow model were the most likely to lose nest contents to predators. Pseudonests near kingbird nests were preyed upon significantly more often than control pseudonests which were not located near kingbird activity. Kingbird parents destroyed the eggs in pseudonests near their own nests.

The percentage of water in the vicinity of the nest influenced nest success when there were nestlings and incubating females spent more time on the nest and incubating pairs visited the nest more often when nests were near water. Kingbirds also responded less to subsequent exposures to a model predator and they did not defend nestlings more vigorously than eggs.

A multivariate logistic regression showed that percentage water, noise at the nest and nest height influenced fledging success. All of these variables can be related to vigilance behaviour in Eastern Kingbirds.

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Chapter 1: General introduction

Eastern Kingbird (Tyrannus tyrannus) parents are notorious for their vigorous nest defence (Davis 1941, this study), but often their nests are not well-hidden from predators. How effective is nest defence, and how effective is nest cover in preventing predation of eggs or nestlings? This 5-year study (1987-1991) is an investigation of the nest defence behaviour of the Eastern Kingbird with respect to: nest visibility, behaviour at the nest, nest site characteristics, and habitat characteristics. Habituation of nest defence behaviour to repeated presentations of a model predator and the relationship between nest defence behaviour and age of nest contents were also examined.

Current nest defence investigations have focussed on costs and benefits of nest defence (Montgomerie and Weatherhead 1988). This study investigates the costs and benefits of choices (nest visibility, nest location and defence behaviour) made by kingbird parents with regards to predation and reproductive success.

Effective nest defence depends upon a variety of interacting factors, yet most studies have approached the problem from single factor considerations. A unique aspect of this study is the combining of various measures of the 3 factors under investigation into a logistic regression model (Banneheka 1991).

This study also differs from similar studies because it investigates how nest defence and nest predation differed with respect to eggs and nestlings; how defence of eggs and nestlings differed with respect to nest visibility, nest site and habitat characteristics and parental behaviour at the nest. Parents may chose alternate strategies, at different ages of nest contents and in different habitats. Parents may also use alternate strategies with different predators, depending upon the danger of the predator to the present age of the nest contents. Habitat choices that facilitate survival of eggs with respect to predation may be costly to nestling survival, or vise versa.

Finally, this study also considers how habituation to repeated presentations of a model predator affects parental nest defence behaviour and also whether nest defence behaviour intensifies as nest contents age. Both questions are currently under debate (see Chapter 5).

The natural history of the Eastern Kingbird at Creston

The mean arrival date of the first kingbird seen in the study area (1987-1991) was 15 May (range 4-20 May), and the mean date of the last brood fledged was 18 July (range 10 July-3 August). Most kingbirds were gone from the nest vicinity by mid-August.

The mean clutch size ($\pm$ S. D.) was 3.5 $\pm$ 0.7 eggs per pair (range 2-5 eggs) and the mean number of young fledged per successful nest was 2.5 $\pm$ 1.2 (range 1-4 fledglings).

Incubation lasts about 14 days after the first egg is laid, and fledging occurs from 14-21 days after the first young hatches. Parents feed fledglings for up to 24 days after fledging. Nestlings are quiet while in the nest, but are quite noisy after fledging, and may then be found in visible as well as hidden situations. Fledglings stay together near the nest for about 5 days after fledging; after that families may stay near the nest or travel far from the nest.

Kingbird adults catch large flying insects (i.e. Odonata: blue darner dragonflies, smaller dragonflies, damselflies; Coleoptera: large beetles; Hymenoptera: honey bees, bumblebees, and other large hymenopterans; Lepidoptera: butterflies and moths), glean smaller insects from vegetation (especially on cool rainy days) and they also eat berries, especially those of red-osier dogwood (*Cornus stolonifera*). Kingbirds will also eat Pacific tree frogs (*Hyla regilla*). Both parents feed the young and they deliver items singly to the nest (with the exception of berries) and increase the size of these items as the young grow. Fledglings begin picking at and exploring leaves quite early and eat quite a few red-osier dogwood berries; I have seen fledglings make short (unsuccessful) flycatching sallies at about 7 days after fledging. Parents have been observed chasing a fledgling from the vicinity around the nest at about 30 days after fledging. Although 62 nestlings (from 20 broods) were banded, only two returned to the study area, and only one of these (a male) nested there.

Some kingbirds arrive alone, others appear to arrive already paired; different "waves" of kingbirds appear until early June. Kingbirds are comparatively quiet until pairs are established in the study area. Established pairs of kingbirds, however may be quite noisy at their nest sites.

Kingbirds usually nest near water, over water or in open fields; in snags (either in the crotch of a dead tree or in a shallow hollow created at the tops of broken boles); and in unconventional places, e.g. under benches or at the end of catwalks. A variety of species of trees were used for nesting, including black cottonwood (Populus trichocarpa), willow (Salix spp.), black hawthorn (Crataegus douglassii), sitka alder (Alnus sinuata) and infrequently pine (Pinus spp.); height of nests used in the study ranged from 0.25 m to 15 m ($\bar{x}$=2.3 $\pm$ 1.9 m). A few nests, not used in the study, were located at the top of cottonwoods, approximately 20 m from the ground.

The study area

The Creston Valley Wildlife Management Area (49^{o}N, 117^{o} S) is located along the Kootenay River, and approximately 12 km west of Creston, in south-eastern British Columbia, Canada. The Management Area consists of about 100 ha of marsh, flooded fields, woodlots, and oldfield habitats. Both the Kootenay River and Summit Creek run through the area as do several canals, and ditched dikes. The area is managed on a seven-year draw down cycle for the marsh areas;

new dikes and canals were built and fields flooded during the 5 years of this study.

Eastern Kingbirds nest in the alders and willows overhanging the rivers and canals, in the shrubs and trees in the oldfield habitats (usually within 100 m of water), and in snags or live trees in the flooded areas. As a result, kingbirds can be found in most areas of the Management Area, with the exception of the upper slopes; woodlots and marshes (although they hunt in the margins and sometimes the interior of the woodlots and marshes, especially after vacating the nest site for the season).

Chapter 2: Nest visibility and nest success

Introduction

Some Eastern Kingbirds build nests that are quite visible, while others build well-hidden nests. How effective is nest cover in hiding nests from predators? Experiments with pseudonests (artificial nests) suggest that hidden nests are less likely to be found by predators than are open nests (Jones and Hungerford 1972, Gottfried and Thompson 1978, Gotmark and Ahlund 1984, Angelstam 1986, Storaas 1988). Other studies of nesting birds have found no difference in nest visibility between successful and preyed upon nests (Erikstad et al. 1982, Storaas and Wegge 1987, and Storaas 1988). Most studies, however, have found that hidden nests are less likely to be discovered by visual predators than are exposed nests (Dwernychuk and Boag 1972, Ehrhart and Connor 1986, McLean et al. 1986, Martin and Roper 1988, Marzluff 1988, Vacca and Handel 1988, Ludvig et al. 1991). As might be expected then, many birds choose to nest in situations where nests are hidden (Reese and Kadlec 1985, Ehrhart and Connor 1986, Marzloff 1988) but a few choose to nest in open situations (Belles-Isles and Picman 1986, Marzluff 1988).

Is nest cover equally effective in preventing predation of nestlings as it is in preventing predation of eggs? Eastern Kingbirds are noisy at the nest and are quite conspicuous in nest defence activities such as patrolling and vigilance behaviours. The conspicuous activity of the parents may attract predators or nest parasites to the nest (Gramza 1967, Robertson and Norman 1977, Biermann and Robertson 1983, Smith et al. 1984, Gottfried et al. 1985, McLean et al. 1986) and, once there are young in the nest, the feeding visits of the parents and the behaviour of the young may attract predator attention (Perrins 1965, Redondo and DeReyna 1988). Nest cover alone will not protect a nest from a predator that is capable of detecting the presence of parents and nestlings. Corvids, the major predators of Eastern Kingbirds in Creston, often find nests by watching behaviour at the nest (Erikstad et al. 1982, Sonerud and Fjeld 1985, Quinn 1989). Nest defence behaviour also enhances nest survival (Andersson and Wiklund 1978, Andersson et al. 1980, Greig-Smith 1980, Slagsvold 1980, Blancher and Robertson 1982, Roell and Bossema 1982, Elliot 1984, Gotmark and Andersson 1984, Knight and Temple 1986b, Breitswish 1988) and may vary with nest visibility (McLean et al. 1986, Montgomerie and Weatherhead 1988).

In this chapter, I investigate the effect of nest visibility on predation of kingbird nest contents and of contents in pseudonests that resemble kingbird nests. I studied the effectiveness of nest concealment in preventing predation of nests with eggs and parents (kingbird nests during incubation); nests with young and parents (kingbird nests with nestlings); and nests with eggs but no parents (pseudonests).

Methods

Kingbird nest visibility

Kingbird nest visibility was measured during 1988-1991, resulting in twelve measures of lateral visibility and one measure of overhead visibility for each nest. I measured all visibilities from mid-July to mid-August each year, after the kingbirds had left their nests and before leaf fall to avoid causing nest desertion. Lateral visibility of each nest was determined from a distance of 15 m and four directions (north, south, east and west) in three ways. 1) I estimated percentage visibility from each of four directions by visually judging how much of the nest was exposed. The other two methods of measurement involved a square (5 x 10 cm) of plastic, with four white and three black stripes per side, that was placed directly on top of each nest. Two lateral visibility measures for each of four directions were obtained: 2) the number of black and 3) the number of white stripes visible from 15 m away. The overhead visibility of each nest was obtained by estimating the percentage of sky visible in a 1 m diameter circle above each nest.

In this thesis, the term lateral visibility refers to the mean of the four percentage visibility measures (from the four directions) of kingbird nests. The term overhead visibility refers only to the visibility of either a kingbird nest or pseudonest from above.

Pseudonests were placed so that overall visibility (based on the four lateral percentage visibility measures and overhead visibility) fitted into one of three categories: open (75-100% overall visibility), medium (40-60%) or hidden (overall visibility 0-25%).

Nesting success

Kingbird nests were usually visited every third day until fledging or until the nest contents disappeared. Nest contents were checked using a mirror on an extendable pole or by looking directly into nests. Nest checks enabled me to determine the date of the first egg laid, clutch size, date of predation and fate of nest contents. If the above information could be obtained without approaching the nest (i.e. if the female was on the nest and clutch size was known, or if older young in the nest were visible from a distance) then the nest was not approached. Nests containing older young were checked daily from a distance using a spotting scope to determine fledging date and the number of young fledged. Young in accessible nests were banded with aluminum US Fish and Wildlife Service bands and plastic coloured bands at about 9 days of age to facilitate identification of broods after fledging.

Predation resulted in the loss of all eggs or young in a nest, and so, a successful kingbird pair was defined as one that raised at least one young to fledging. Young were judged to have fledged if they were seen alive outside the nest. Nest contents were defined as preyed upon, when eggshells or evidence of dead kingbird young were found in or around the nest or when the nest contents had disappeared since my last visit.

Nest site availability and overhead visibility

The overhead visibility of 400 randomly chosen sites was measured in kingbird nesting habitat along dikes, rivers and canals from 15 July to 5 August 1991. At each 10 m stop along the dike road, I took from 1 to 20 paces into the vegetation on each side of the dike road (i.e. 1 pace in, then return to the road, walk a further 10 m take 2 paces into the vegetation, return to the road and take 3 paces into the vegetation etc. up to 20 paces into the vegetation then descending again from 19 paces to one and increasing to 20 paces, etc.). A 3 m pole (the approximate mean height of kingbird nests in the study area) was placed on the selected spot and the nearest appropriate nesting site (i.e. tree branch) within a 0.5 m radius of the tip of the pole was selected as the spot where overhead visibility was measured. I then estimated the percentage of sky visible in a circle with a 1 m diameter around the pole tip. The same procedure was used to sample the overhead visibility along rivers and canals by canoe. I entered the vegetation on either bank at every 20 canoe strokes. I took one to 10 paces into the vegetation as follows: I took 1 pace into the vegetation, then returned to the canoe and paddled for 20 strokes, entered the vegetation for 2 paces, then paddled the canoe 20 strokes, then entered 3 paces etc. to 10 paces, then repeated the procedure by descending from 9 paces, to one pace then ascending again, etc. Overhead visibility was measured as described above.

Survival rates of pseudonests

Thirty-five pseudonests (made of grass and sewn together with thread), each containing three Japanese Painted Quail (Turnix varia) eggs, were placed in appropriate kingbird nesting sites within kingbird habitat from 27-29 April 1988 and 35 more from 5-7 May 1991. Pseudonests were placed in trios before the kingbirds had returned for the season. Pseudonests within each trio were placed at least 100 m and no further than 200 m from each other to allow for differences in predator abundance between different areas and were matched for placement height and situation (i.e. all three pseudonnests in each trio were set in alder bushes, or cottonwood trees). Pseudonests within each trio were hidden in a tree or a bush in each of three visibility categories: open (overall visibility - 75-100% visible overhead and on four sides; medium (40-60% visible); hidden (0-25% visible).

Pseudonests within a trio were set out at the same time, 5 different trios a day for 3 consecutive days, for a total of 15 trios. Pseudonests were left in place for 15 days to simulate the length of kingbird incubation which is usually about 14 days. I checked pseudonest contents every 3 days with a mirror on the end of an extendable pole.

Pseudonests were considered preyed upon if all or some of the quail eggs disappeared. Data were log transformed and a regression was used to determine whether there was a significant relationship between visibility of pseudonests and the rate of predation of pseudonests. Analysis of covariance was used to determine whether there was a difference in slopes of the rate of predation between pseudonests of the three visibility types.

Survival rates of kingbird nest and pseudonest contents

Survival rates of kingbird eggs and nestlings in kingbird nests (1988 to 1991) and of eggs in pseudonests (1988 and 1991 combined) were calculated for a 15-day period. Survival rates of kingbird nest and pseudonest contents were log transformed and a regression analysis was used to determine 1) the relationship between survival rate and overhead visibility and 2) the survival rate and the age of the nest contents. Analysis of covariance was used to determine whether there was a difference between the slopes of survival rates being compared.

Predators and pseudonests

I set out two sets of 14 pseudonests containing 3 quail eggs per nest from 8-10 May 1988 to distinguish between nocturnal and diurnal predation upon nests. Both groups of pseudonests were set out on the same day and paired for type of placement (i.e. shrub type, and height) and for medium overall visibility and were located about 150 m from each other. I placed quail eggs in one set of 14 pseudonests each morning just before dawn and removed them at dusk, when I noted any disappearance of eggs. I placed eggs in a second group of 14 pseudonests at dusk and removed them at dawn, noting any losses of eggs.

In a second experiment, I set out 23 pseudonests with two quail eggs and one plasticine egg (tied to the nest) in each nest, from 8-10 May 1990 before the kingbirds returned for the season. Plasticine eggs were painted with acrylic paint to resemble the quail eggs in the nest. Pseudonests were checked every 3 days for 15 days to determine the survival rate. Plasticine eggs retained the impressions of the beak or teeth of the nest predator and allowed me to determine the type of predator that was taking eggs from pseudonests in kingbird habitat.

Statistical analyses

The following discussion of statistical analysis techniques applies to the entire thesis, including this chapter. Alpha for all analyses was 0.05, so that a result was considered to be statistically significant when $P \leq 0.05$; power was measured and a beta value (B value) given for each analysis that was not statistically significant (Cohen 1988). The Mann-Whitney U test (M.W.U.) was used to compare the mean ranks of two variables, and the Kruskal-Wallis test (K-W.H.) was used to compare the mean ranks of three or more variables (Sokal and Rohlf 1981). Values of means are reported with standard deviations (±). Spearman rank correlations were used to determine correlations between two variables. A principal components analysis was used (after variables were transformed) to reduce 12 lateral visibility measures to six variables, and a MANOVA was used to analyse the influence of the principal components (lateral visibility) upon nest predation.

A cubic spline is a curve-fitting tecnique which describes the survival function (an estimate of the fitness function) of a variable; in this study, it describes the probability of nest predation with respect to an independant variable. Accuracy of splines was assessed by 100 bootstraps of the spline procedure, resulting in measures of standard errors. I considered a curve or slope given by the cubic spline technique to be an accurate representation of the fitness function if the standard errors allowed for no other curve or slope to be fitted. Figures of splines show the survival function described by the program and the standard errors, which allow subjective determination of how often the function is duplicated by the program (Schluter 1988). Although the survival functions described by cubic splines are sufficient to comment upon the relationship between a variable and survival of nest contents, cubic splines can also be used to indicate further possibilities for analysis. If a cubic spline analysis indicated there was a linear relationship between the survival function and the variable involved, I performed a logistic regression of the original data. If a cubic spline indicated a non-linear relationship, subsequent analysis involved the use of contingency tables. A log-linear model (Chapter 6) was used to describe the multivariate relationship between the probability of nest predation (a categorical variable) and several variables pertaining to nest defence behaviour, nest visibility, nesting habitat and other aspects of nest site choice.

Results

Kingbird nest visibility and nesting success

During 1988-1991, 76 of 160 kingbird nests (47.5%) were preyed upon (Table 1). In 33 of 62 preyed upon nests (53%) (it was not possible to determine whether 14 of the 76 nests of Table 1 were preyed upon as eggs or young), predation occurred in the egg stage and 47% in the nestling stage. Thirty-four percent (55 of 160 nests) survived to fledging and 19% (29 of 160 nests) of kingbird nests were lost to other causes. Successful parents fledged a mean of 2.5 $\pm$ 1.2 young (n=48, 1988-1991).

Visibility distributions (Fig. 1) were similar for all four directions: most kingbird nests were well hidden from all sides. A cubic spline performed on the mean percentage lateral visibility of the four directions combined shows that the survival function is linear and negative (Fig. 2). However, the standard errors are so large, and the slope so slight that the relationship shown may be inaccurate. Logistic regression shows that the relationship between survival and lateral visiblility is not significant (logit p(success)=-1.01 + 0.004x; X^2=0.58, n=105, P=0.4, B<0.1). A comparison of means shows that the visibilities of successful nests and preyed upon nests did not differ (successful: n=52, $\bar{x}$=19.2$\pm$20.4; preyed upon: n=63, $\bar{x}$=20.3$\pm$22.5, M.W.U.=1632.5, P=1.0, B=.08). A principal components analysis performed on the 12 lateral visibility measures (percentage visibility (N,S,E,W), black stripes

Table 1. The fate of Eastern Kingbird nests, 1988 to 1991.

Fate of kingbird nests	Number of kingbird nests
Successful	55
Preyed upon	76
Other:	30
Deserted with eggs	10
Young dead in nest	4
Eggs did not hatch	3
Eggs flooded	2
Ants invaded nest	2
Nest tree destroyed	5
Nest fell apart	2
Eggs broken	1
Eggs taken by people	1
Unknown [1]	21

[1] Unknown refers to additional nests that may have been deserted and subsequently preyed upon or that were initially preyed upon, but due to an extended time between visits, (greater than 6 days), the exact fate of the nest could not be determined.

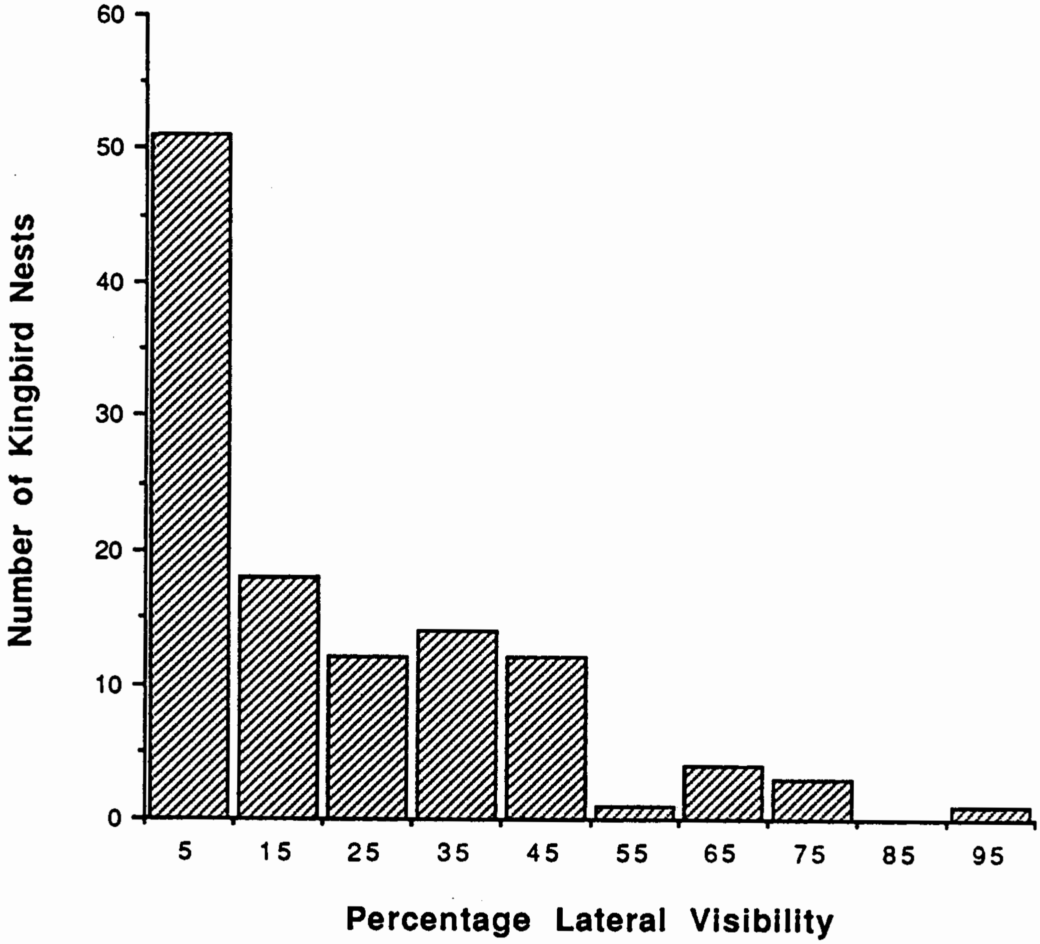

Figure 1. Distribution of mean percentage lateral visibility for 4 directions (combined) of Eastern Kingbird nest (north, south, east, and west), 1988 to 1991.

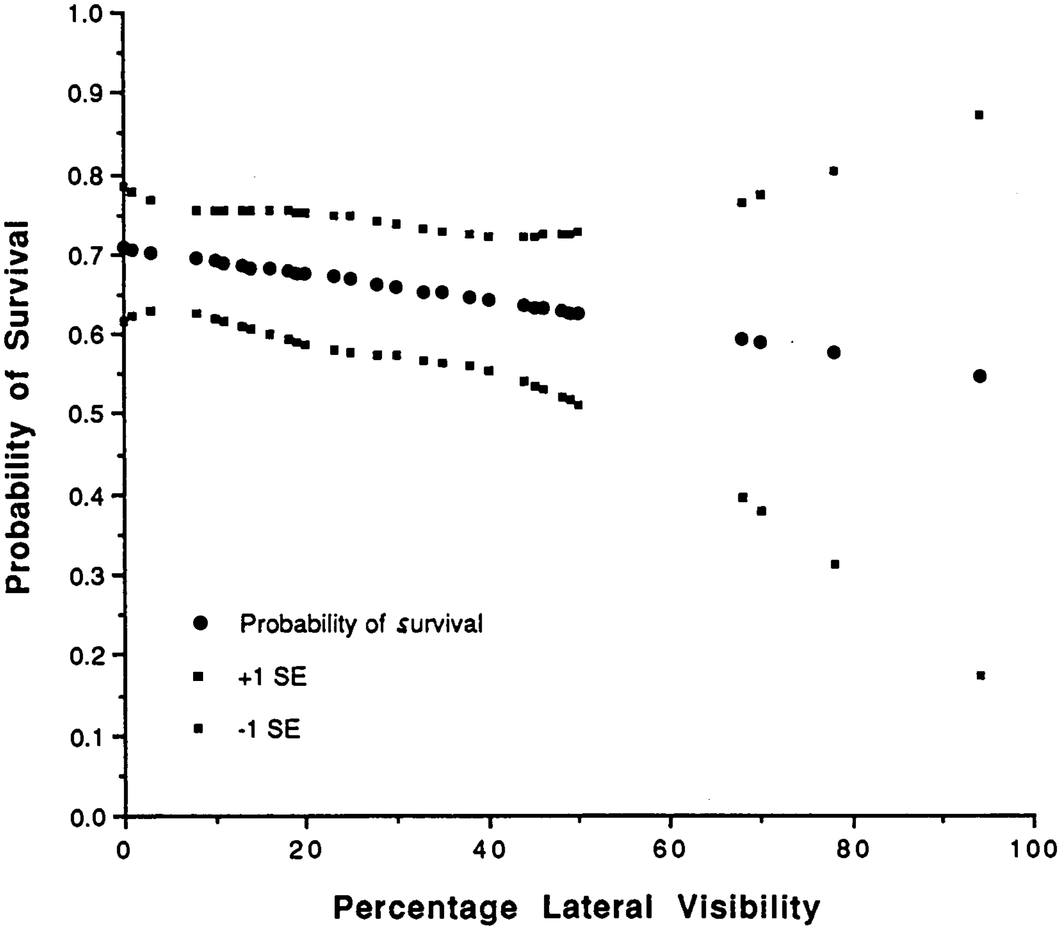

Figure 2. Cubic spline of lateral visibility of Eastern Kingbird nests, 1988 to 1991.

visible (N,S,E,W) and white stripes visible (N,S,E,W)), resulted in 6 components accounting for 88.5% of the variation in lateral visibility (Table 2). A MANOVA performed on all 6 principal components showed no difference between nests of successful and preyed upon pairs, although a non-significant trend was apparent for the most hidden nests (lateral visibility) to be those of successful parents (Table 3).

The distribution of overhead visibility for all kingbird nests (1988-1991) is shown in Fig. 3, and the distributions for successful and preyed upon nests are shown in Fig. 4. The cubic spline of overhead visibility of all kingbird nests is shown in Fig. 5c. The resulting survival function is non-linear, and suggests that nests of open, overhead visibility are more successful than nests of medium or hidden, overhead visibility. A comparison of distributions confirms the results of the cubic spline (Table 4). Nests of open, overhead visibility are more likely to survive than are medium and hidden, overhead visibility nests.

The overhead visibility of nests affects predation of nest contents differently in the egg and in the nestling stages. The survival function described by the cubic spline of eggs is non-linear (Fig. 5a) and suggests that eggs in hidden (0-25% overhead visibility) and open (75-100% overhead visibility) nests survive better than eggs in medium visibility nests (40-60% overhead visibility). The

Table 2. Principal component scores of eighteen lateral visibility measures of Eastern Kingbird nests, 1988-1991.

	Principal component number					
	1	2	3	4	5	6
	Percentage variance					
	43.74	55.73	66.29	75.46	82.30	88.46
Percentage visibility factor scores						
%N[1]	0.22	-0.23	-0.16	-0.24	0.53	-0.46
%S	0.18	0.41	-0.06	-0.21	-0.25	-0.11
%E	0.20	-0.22	-0.14	-0.15	-0.49	0.14
%W	0.20	0.11	0.09	-0.41	0.16	0.32
%$\bar{X}$	0.30	0.01	0.17	-0.36	0.15	-0.08
%SD	0.28	0.02	-0.34	-0.30	-0.00	-0.05
Number of black stripes factor scores						
BN[2]	0.24	-0.29	0.05	0.11	0.26	-0.38
BS	0.18	0.45	0.16	0.20	-0.14	-0.26
BE	0.22	-0.27	0.21	0.23	-0.38	0.15
BW	0.24	0.07	0.35	-0.15	0.24	0.27
B$\bar{X}$	0.23	0.02	-0.02	0.20	-0.02	0.03
BSD	0.19	0.07	-0.45	0.31	0.18	0.24
Number of white stripes factor scores						
WN[3]	0.26	-0.23	0.11	0.10	0.32	-0.26
WS	0.19	0.47	0.14	0.21	-0.10	-0.22
WE	0.23	-0.28	0.19	0.19	-0.35	0.13
WW	0.24	0.02	0.36	-0.16	0.25	0.25
W$\bar{X}$	0.32	0.05	0.02	0.21	0.08	0.05
WSD	0.19	0.07	-0.46	0.25	0.17	0.29

Table 2. Continued

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[1] %N refers to the percentage nest visible seen at 15 m north of the nest. The same measure was taken at the four compass directions: %S refers to south, %E refers to the east, and %W refers to the west; $\%\bar{X}$ refers to the mean of all four direction, and %SD to the standard deviation of the mean.

[2] BN refers to the number of black stripes (of 3 possible stripes) seen 15 m north of the nest. As above N, S, E, and W, refer to the four compass directions; $\bar{X}$ and SD refer to the mean of the four directional measures and the standard deviation of the mean, respectively.

[3] WN refers to the number of white stripes (of 4 possible stripes) seen 15 m north of the nest. As above N, S, E, and W, refer to the four compass directions; $\bar{X}$ and SD refer to the mean of the four directional measures and the standard deviation of the mean, respectively.

Table 3. MANOVA of six principal components of lateral visibility and nest success of Eastern Kingbird nests, 1988-1991.

	Score	
Principal component	Successful	Preyed upon
Prin1	3.16	3.19[1]
Prin2	3.17	3.14
Prin3	3.20	3.12
Prin4	3.19	3.13
Prin5	3.15	3.17
Prin6	3.15	3.17

[1] F=1.47, P=0.20, n=108, B=0.22 (successful n=50; preyed upon n=58)

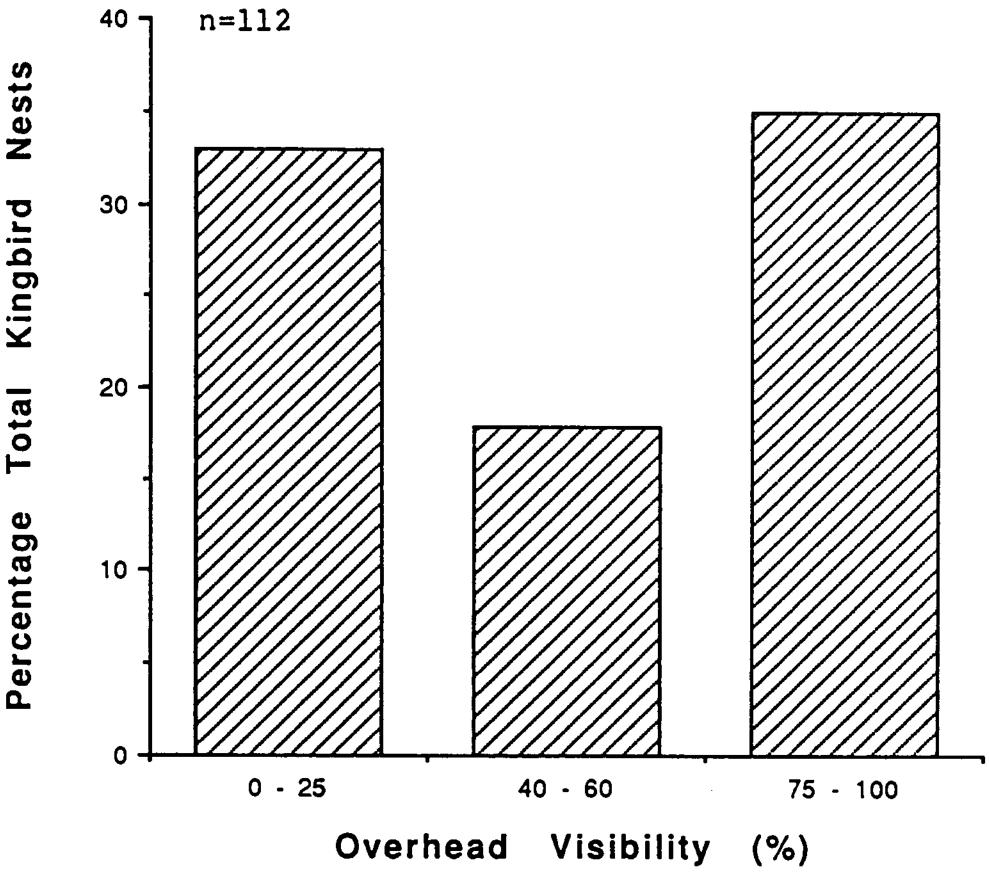


Figure 3. Distribution of overhead visibility (hidden: 0-25%; medium: 40-60%; open: 75-100%) of Eastern Kingbird nests, 1988 to 1991. Nests with overhead visibilities between 26-39% and 61-74% are not included in the three (hidden, medium and open) overhead visibility types.

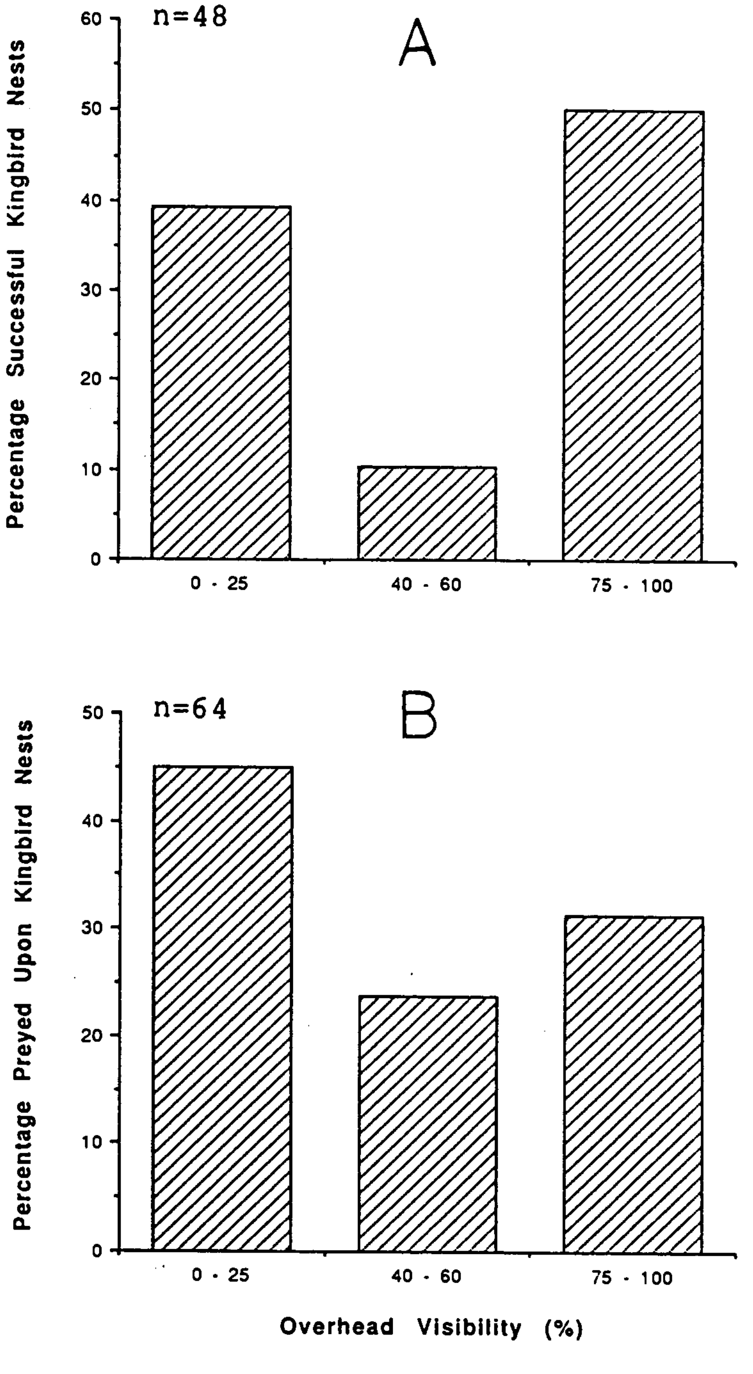


Figure 4. The distribution of overhead visibility of A: nests of successful Eastern Kingbird parents and B: nests of preyed upon Eastern Kingbird parents, 1988 to 1991.

Figure 5. Cubic splines of overhead visibility of Eastern Kingbird nests for nest contents that survived: A) incubation; B) the nestling stage; and C) for all nests combined, 1988 to 1989.

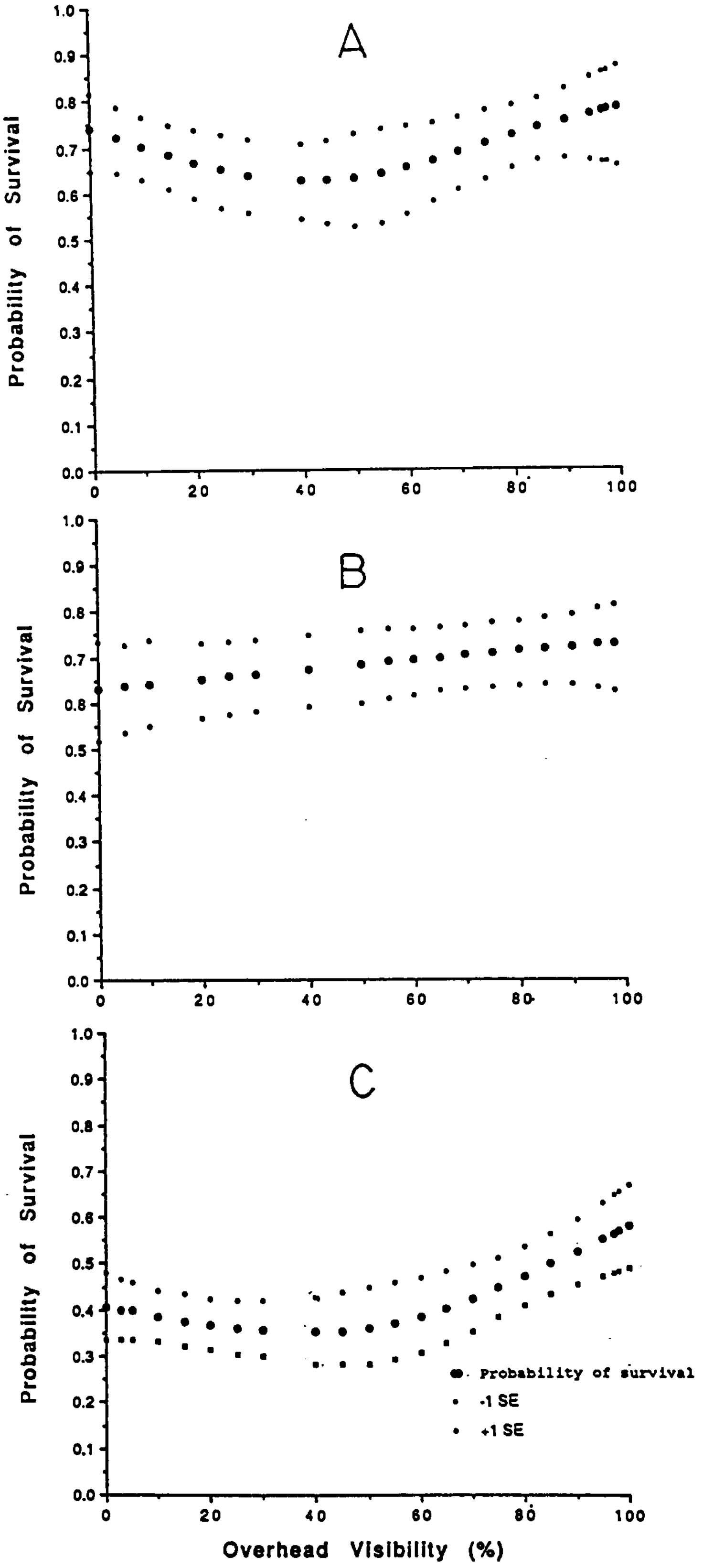

A
B
C
Probability of Survival
Overhead Visibility (%)
Probability of survival
-1 SE
+1 SE

Table 4. Overhead visibility and nest success in the Eastern Kingbird, 1988-1991.

	Overhead visibility	
	0-60%[1]	75-100%[2]
Successful nests	25	24
Preyed upon nests	45	20

[1] this category is comprised of the 0-25% and 40-60% overhead visibility categories, combined.

[2] $X^2=4.0$, $P<0.05$

standard errors are small enough to indicate that the "dip" shown for middle overhead visibility nests is likely to be accurate. Open and hidden nests survive the egg stage better than middle overhead visibility nests (Table 5) although the result is not statistically significant. A cubic spline of overhead visibilities of nestlings suggests that the survival function is linear and slightly positive (Fig. 5b). The standard errors are not small enough, however, to eliminate the possibility of there being no real slope. A logistic regression of survival of nestlings and overhead visibility shows no significant relationship (logit p(success)=0.303+0.004x; X^2=0.94, n=83, P=0.3, B<0.1). There is also no statistical difference in overhead visibility between nestlings that are preyed upon and nestlings that fledge (successful $\bar{x}$=48.6$\pm$39.3, n=53; preyed upon $\bar{x}$=44.8$\pm$39.3, n=30, P>0.05, B=0.08).

Nest site availability and overhead visibility

The distribution of 400 randomly chosen sites, measured with respect to overhead visibility, is shown in Figure 6. Kingbirds chose open, overhead visibility nest sites more frequently than expected, fewer than expected medium, overhead visibility sites and chose an expected number of hidden nest sites (Table 6). There is also a weak negative correlation, which approaches significance, between the date the first egg is laid and percentage overhead visibility (r_s=-0.22, n=53, P=0.07, B=0.31). If it is assumed that

Table 5. Overhead visibility and survival of eggs in the Eastern Kingbird, 1988-1991.

	Overhead visibility		
	0-25%	40-60%	75-100%[1]
Successful nests	34	9	34
Preyed upon nests	11	8	9

[1] $X^2=4.5$, $P<0.1$

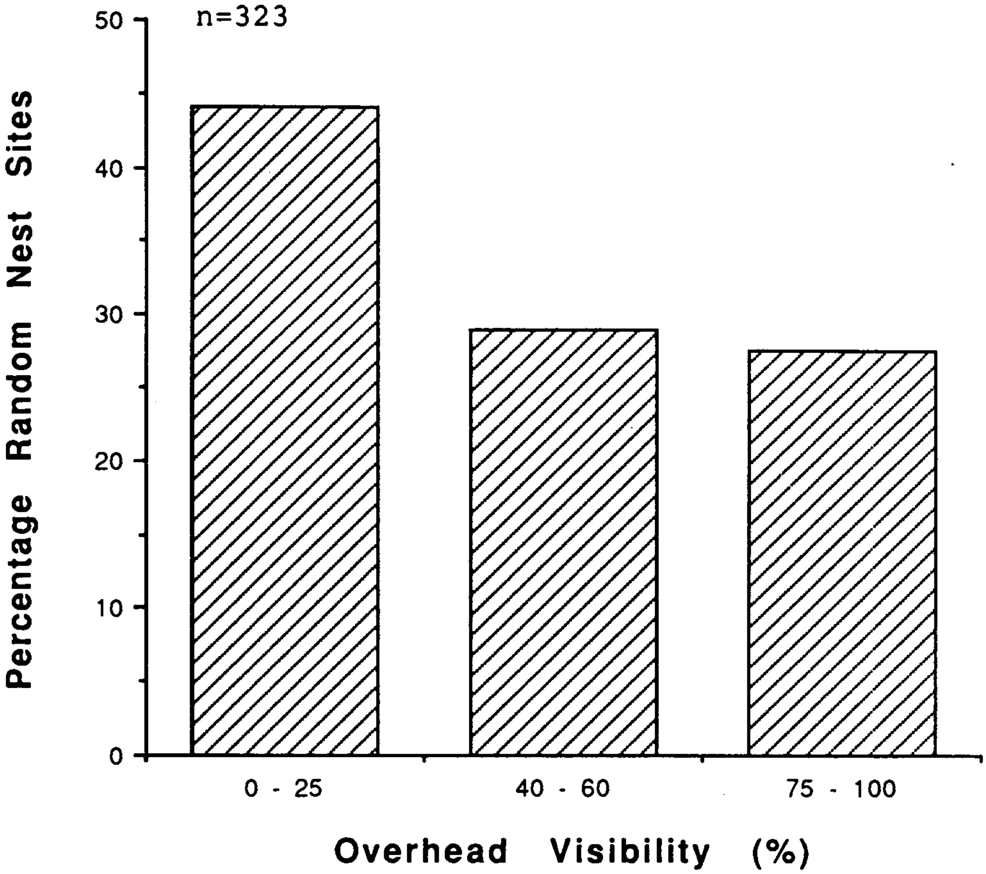


Figure 6. Distribution of overhead visibility of 400 randomly chosen potential nest sites in Eastern Kingbird habitat, 1991. The nest sites available do not add up to 400 as there were more sites sampled than those defined by the three visibility categories.

Table 6. The availability of randomly chosen nesting sites and those actually chosen by Eastern Kingbirds with respect to overhead visibility.

Overhead visibility	Kingbird nest sites (1988-1991)	Nest sites available (1991)
Hidden (0-25%)	46	142[1] [2]
Medium (40-60%)	20	93
Open (75-100%)	44	89

[1] $X^2=7.8$, $P<0.025$

[2] Nest sites available do not add up to 400 because more sites were sampled than those defined by the 3 visibility categories.

kingbirds which settle earlier also begin their clutches earlier, then it appears that territories with nest sites with higher overhead visibilities may be chosen first.

Survival rates of kingbird nest and pseudonest contents

Survival rates of eggs in pseudonests

The greater the overall visibility of a pseudonest, the greater the likelihood of its predation (Fig. 7). Analysis of covariance shows a significant difference in survival rate of eggs in pseudonests with different visibilities (Table 7). Nest visibility, then, affects the likelihood of nest predation when there are no parents in attendance.

Predation rates on kingbird nests (with eggs and nestlings) and pseudonests

The survival of pseudonest and kingbird nest contents with respect to open, medium and hidden visibility categories were compared to determine the influence of the parents' behaviour upon survival of the nest contents. In most cases kingbird eggs and nestlings survived better than the eggs in pseudonests of the corresponding visibility type (Fig. 8a, b, and c, Table 8).

Survival of kingbird eggs and nestlings with respect to overhead visibility

Kingbird eggs survived equally well in all three overhead visibility categories (Fig. 9a, Table 9). Kingbird nestlings show a non-significant trend for open visiblility

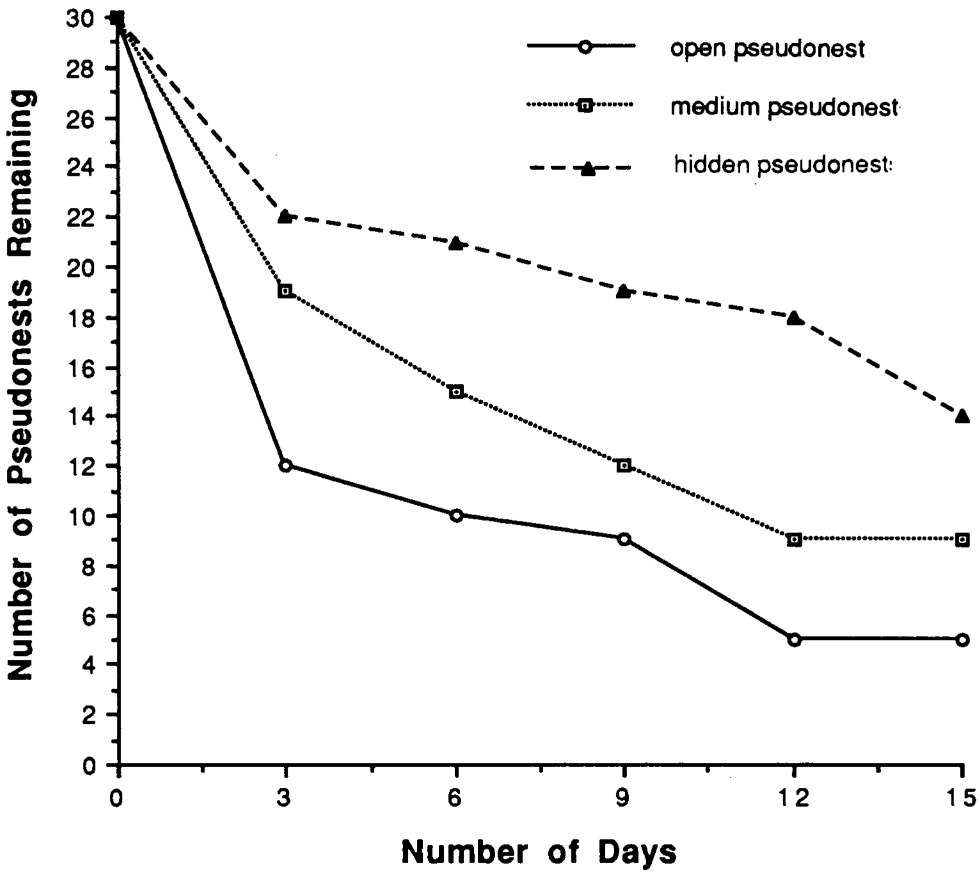
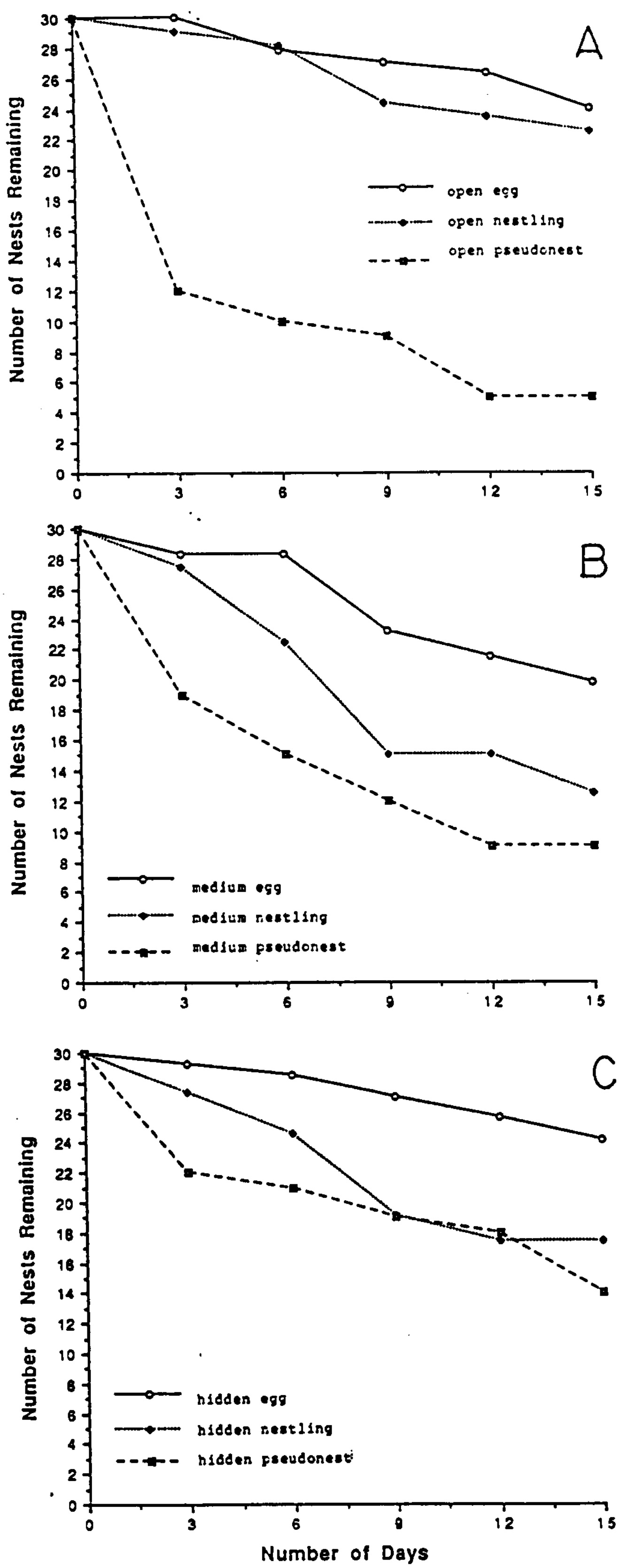


Figure 7. Survival rate of eggs in pseudonests of open (75-100%), medium (40-60%) and hidden (0-25%) overall visibility for 1988 and 1991, combined.

Table 7. The analyses of covariance results for comparison of survival rate of eggs in pseudonests of hidden, medium and open overall visibility (1989 and 1991) (Fig. 7).

Null hypothesis: equal slopes	F value	P value
Open, medium, and hidden	13.6	0.0009
Open and medium	4.7	0.0600
Hidden and open	23.6	0.0010
Medium and hidden	12.5	0.0080

Figure 8. Survival rate of: A) open overall visibility pseudonests, open overhead visibility kingbird eggs, and open overhead visibility kingbird nestlings; B) medium overall visibility pseudonests, medium overhead visibility kingbird eggs and medium overhead visibility kingbird nestlings; and C) hidden overall visibility pseudonest, hidden overhead visibility kingbird eggs and hidden overhead visibility kingbird nestlings.



A
open egg
open nestling
open pseudonest
B
medium egg
medium nestling
medium pseudonest
C
hidden egg
hidden nestling
hidden pseudonest
Number of Nests Remaining
Number of Days
0 3 6 9 12 15
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30

Table 8. Analyses of covariance comparing the predation rates of eggs and nestlings in kingbird nests and eggs in pseudonests, and kingbird nestlings, for the visibility classes.

Null hypothesis: equal slopes	F value	P value
Open visibility (Fig. 8A):		
Pseudonest, kingbird eggs, and kingbird nestlings	45.4	0.0000
Pseudonest and kingbird eggs	55.2	0.0001
Pseudnest and kingbird nestlings	46.0	0.0001
Medium visibility (Fig. 8B):		
Pseudonest, kingbird eggs, and kingbird nestlings	6.8	0.0100
Pseudonest and kingbird eggs	22.9	0.0010
Pseudonest and kingbird nestlings	2.0	0.2000
Hidden visibility (Fig. 8C):		
Pseudonest, kingbird eggs and kingbird nestlings	5.5	0.2000
Pseudonest and kingbird eggs	13.4	0.0060
Pseudonest and kingbird nestlings	0.1	0.7000

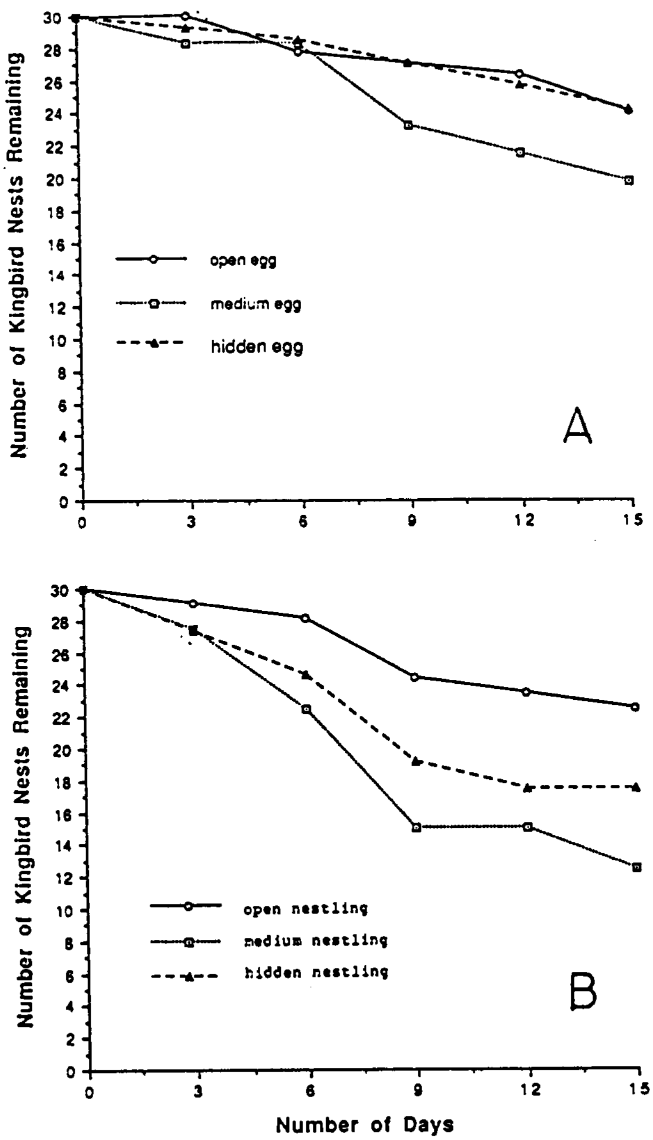


Figure 9. Survival rate of Eastern Kingbird A) eggs and B) nestlings (1-6 days old) in open (0-75%), medium (40-60%) and hidden (0-25%) overhead visibility nests.

Table 9. Analysis of covariance comparing survival rates of kingbird eggs and nestlings in nests with open, medium and hidden, overhead visibilities.

Null hypothesis: equal slopes	F value	P value
Kingbird eggs (Fig. 9A):		
Open medium and hidden	1.9	0.20
Kingbird nestlings (Fig. 9B):		
Open, medium and hidden	3.3	0.07
Open and hidden	2.6	0.10
Open and medium	5.5	0.05
Hidden and medium	1.6	0.20

nestlings to survive better than either hidden nestlings or medium visibility nestlings (Fig. 9b, Table 9).

Fledging date and overhead visibility

Mean fledging date was 33.1 ± 2.0 days (n=37) after the first egg of the clutch was laid. Fledging date of nestlings did not differ with overhead visibility (r=0.11, n=37, F=0.43, P=0.50, B=0.09).

Survival of kingbird nestlings and eggs

The survival of kingbird eggs and nestlings (Fig. 8a, b, and c) was compared. In all cases eggs survived better than nestlings but only the comparison between kingbird eggs and nestlings in hidden overhead visibility nests was statistically significant (Table 10).

Advantage of parental attendance to nest contents

Both eggs and nestlings in open visibility situations show the greatest advantage over open pseudonests, but medium, and hidden kingbird nests also show differences from the pseudonests (Fig. 10, Table 11). The results for nestlings show that the advantage of parental attendance is greatest for open visibility nestlings and least for hidden and medium overhead visibility nestlings. These results show that the behaviour of kingbird parents enhances the survival of both eggs and nestlings when compared to similar, untended pseudonests regardless of overhead visibility except for medium and hidden visibility

Table 10. Analyses of covariance comparing predation rates between kingbird eggs and kingbird nestlings for similar overhead visibilities.

Null hypothesis: equal slopes	F value	P value
Open visibility (Fig. 8A)	0.9	0.40
Medium visibility (Fig. 8B)	3.8	0.09
Hidden visibility (Fig. 8C)	7.4	0.03

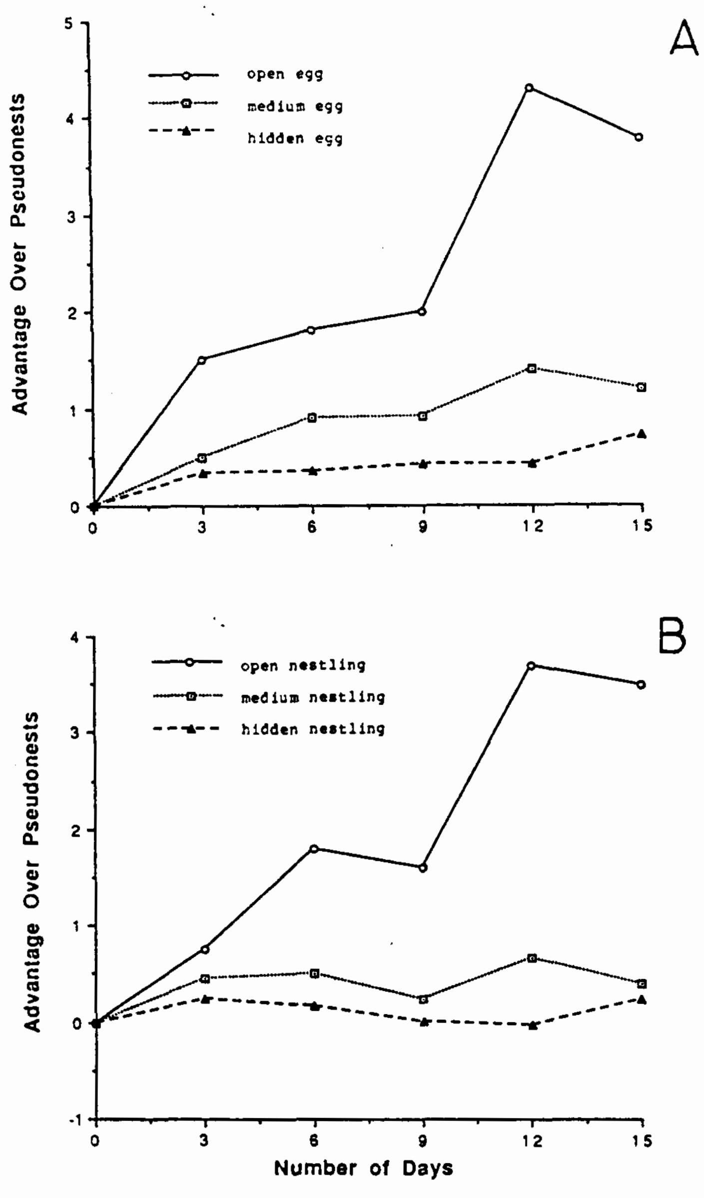


Figure 10. Advantage ((kingbird nests remaining - pseudonests remaining)/pseudonests remaining)) of kingbird A) eggs and B) nestlings (1-6 days old) in nests of open, medium, and hidden overhead visibilities, in comparison with pseudonests of the same visibility.

Table 11. Analyses of covariance comparing advantage of kingbird nests ((kingbird nests remaining - pseudonests remaining)/pseudonests remaining), with eggs and with nestlings, over pseudonests between open, medium and hidden overhead visibilities.

Null hypothesis: equal slopes	F value	P value
Advantage of kingbird eggs over pseudonests (Fig. 10A)		
Open, medium and hidden	13.5	0.0008
Open and medium	9.1	0.0200
Open and hidden	18.2	0.0030
Medium and hidden	12.4	0.0080
Advantage of kingbird of nestlings over pseudonests (Fig. 10B)		
Open, medium and hidden	16.0	0.0004
Open and medium	14.6	0.0050
Open and hidden	21.1	0.0020
Medium and hidden	2.0	0.2000

nestlings. Survival curves show that eggs survive better than nestlings for all overhead visibility types, implying that parental attendance is an advantage to nest contents, but that something changes when there are nestlings.

Predators and pseudonests

None of 14 pseudonests, that were set out only during the night for 15 days, were preyed upon. In contrast, 8 of 14 pseudonests, set out during the day for 15 days, were preyed upon (X^2=18.1, n=28, P<0.001) indicating that the primary nest predators are diurnal. Marks on 14 plasticine eggs tied to 23 pseudonests in a second experiment showed that: 5 plasticine eggs were not touched, 6 had large bill marks - probably American Crow (Corvus brachyrhynchos) or Northern Raven (Corvus corax), 2 were pulled entirely out of the pseudonest - likely by ravens, and 1 was pock-marked, probably by a Marsh Wren (Cistothorus palustris).

Predators and kingbird nests

Most predation of kingbird nest contents was by avian predators. Crows and ravens often did not disrupt the nest cup but sometimes left yolk or eggshells in the nest. Corvids removed eggs one at a time, often pecking a hole in the egg before carrying it off to eat it; shells with holes pecked in them were often found near preyed upon nests. Few remains of young were found. Mammals often distorted the nest shape and pulled nests down, leaving bits of nest and nest content strewn about. Snakes usually removed nest contents one at a time, often leaving days between eating subsequent eggs or young in the same nest. Most indications were, however, that avian predators were responsible for kingbird nest content predation, but there were a few instances where mammalian predation was a possibility. I also found adult kingbird feathers near some preyed upon nests and subsequently, only one, or neither of the pair was seen.

In summary: 1) open pseudonests disappear at a greater rate than medium than hidden pseudonests; 2) in most cases, kingbird nests survive better than pseudonests of a comparable visibility; 3) kingbird nests which are laterally hidden survive better than nests which were laterally visible; 4) kingbird nests with greater overhead visibility, however, are preyed upon at a lesser rate than kingbird nests of more hidden overhead visibility; 5) eggs which stand the best chance of surviving are more visible overhead; eggs which don't survive are in nests of medium overhead visiblility and there is no difference in overhead visibility between kingbird nestlings which survive and those which do not; 6) overall, kingbirds that fledge are usually in nests which are most visible from overhead, and the influence of overhead visibility is shown most during incubation; 7) nestlings of hidden and medium visibility nests gained no advantage from parental presence compared with eggs in pseudonests of a similar visibility. Open overhead visibility kingbird nests containing both eggs and nestlings show the greatest advantage from having parents present; 8) the earliest nesting kingbirds chose nests with open overhead visibility; and 9) birds are the major predators of both kingbird nests and pseudonests.

Discussion

Predation is the major source of nest loss for Eastern Kingbirds in Creston, so I would predict that they, like some other birds (e.g. Page et al. 1985, Reese and Kadlec 1985, Belles-Isles and Picman 1986, Ehrhart and Connor 1986, Bekoff et al. 1987, Marzluff 1988, Rands 1988) should choose nesting sites that minimize nest predation. Because my experiments showed that the predation rate of hidden pseudonests was less than that of more visible pseudonests and as several studies of both pseudonests (Dwernychuk and Boag 1972, Jones and Hungerford 1972, Picozzi 1975, Gottfried and Thompson 1978, Gotmark and Ahlund 1984, Westmoreland and Best 1985, Angelstam 1986, Sugden and Beyersbergen 1986, Marzluff 1988, Storaas 1988, Vacca and Handel 1988) and nesting birds (Dwernychuk and Boag 1972, Ehrhart and Conner 1986, Martin and Roper 1988, McLean et al. 1986, Marzluff 1988, Vacca and Handel 1988, Bekoff et al. 1989, Ludvig et al. 1991) indicate that greater nest cover provides protection from predation, I would predict that if hiding a nest is effective against predators, nests of successful kingbirds should be more hidden than nests of kingbird parents with preyed upon eggs or nestlings. In fact, most kingbird nests in this study were laterally hidden, but nests from which nestlings fledged were not more hidden than nests with preyed upon contents. Kingbird nests which were the most visible from overhead, however, were the most successful nests and kingbirds also chose to nest in sites that were more visible from overhead than that expected on nest site availability.

A kingbird nest which is more visible overhead may afford a greater view of approaching predators, both to the female kingbird incubating on the nest, and to either kingbird parent elsewhere on the territory. Fieldfares (Turdus pilaris) also defend their nests quite vigorously and nest more conspicuously than most other species (Andersson and Wiklund 1978, Slagsvold 1980) and Lapwings (Vanellus vanellus), who defend actively, select nest sites which afford better detection of approaching predators, rather than concealment (Elliot 1984). Corvids, the major kingbird predators in Creston, often find nests by chance while they are flying by (Erikstad et al. 1982, Quinn 1989, Sonerud and Fjeld 1985). A nest hidden from the side is less likely to be found by a corvid from a distance and a pair of kingbirds which can see the approach of a hunting predator may be able to drive it away before the predator flies directly over the nest. I would like to caution the reader that I did no spectral analysis of the colours or the contrast involved in nest visibility, and I that I judged nest visibility with my eyes, and as a result my indices of nest visibility may not reflect what a kingbird or a crow may see. My observations of both kingbirds and crows, however make me confident that the visibility indices which

I used are the best option available and an acceptable estimate of what a bird sees when approaching a nest.

Parents defending a nest with a sparse canopy over it will be more likely to see the approach of a predator from all sides and be able to chase the predator before it flies over the nest. As I measured overhead visibility by looking upward from the nest, a nest of greater overhead visibility also has a sparse overhead canopy. Nests that are only partially hidden from overhead may not be hidden well enough from predators flying overhead or nearby. Partial cover, as opposed to sparse or total cover, may only serve to obscure the arrival of approaching predators from the defending parents.

Kingbird nests had the same or lower predation rates than pseudonests of corresponding visibility, indicating that kingbird behaviour leads to greater nest survival; improved survival, however, varies with overhead nest visibility. The behavioural changes in parents which accompany the appearance of nestlings may also depend upon the visibility of the nest. In general, kingbird nests with eggs had lower predation rates than those containing young. When there are nestlings, kingbirds make more visits to the nest (Chapter 3), and since parents are noisy at the nest, they may attract predators. The parents must make more feeding visits as the nestlings grow, and the young themselves may attract attention as they begin to move about. The survival curves of kingbird nestlings for all overhead visibility classes show that the survival rate decreases between 6 and 9 days when feeding rates are high, and the nestlings begin to move about. At this time the female begins to contribute more to feeding and will start to spend less time incubating. The incubating female may add some camouflage to the nest and her increased absence may leave the young exposed to predators. Overhead cover may provide some protection for eggs, but it may also obscure the approach of predators from defending parents. Once the nestlings require more feeding and begin to move about in the nest, they may attract more predators. Kingbird young are quiet in the nest until near fledging time (Davis 1941, this study) but they do move about: flapping their wings, etc. In contrast, a more visible nest may enhance the effectiveness of kingbird nest defence. Parents may be able to see approaching predators more readily, intercept them, and prevent them from spending time in the vicinity of the nest. As fewer predators are allowed to spend time in the vicinity of the nest, there is less opportunity for predators to cue in on activity around the nest.

In summary, nest visibility does affect suceptibility of a nest to predation, but its effectiveness varies with the age of the nest contents and behaviour of adult kingbirds at the nest site.

Chapter 3: Kingbird nest defence behaviour and nest success

Introduction

Eastern Kingbirds are quite vigorous in defending their nests (Davis 1941, Bent 1963, Smith 1966, McFie 1981, Blancher and Robertson 1982, this study) but can be so noisy on the nest and active in chasing other birds from its vicinity that they may actually attract predators to the nest. How effective is Eastern Kingbird nest defence? While some studies have shown that birds which defend their nests most vigorously are successful in preventing nest predation (Robertson and Norman 1977, Andersson et al. 1980, Greig-Smith 1980, Blancher and Robertson 1982, Elliot 1984, Knight and Temple 1986b, Breitwisch 1988), other studies have shown that activity at the nest can also attract predators (Gramza 1967, Robertson and Norman 1977, Biermann and Robertson 1983, Smith et al. 1984, Gottfried et al. 1985, McLean et al. 1986, Yasukawa 1989).

As the risk of predation differs for eggs and nestlings of birds in general (Holcomb 1972, Willis 1973, Best 1978, Wiershkul 1979, Tiainen 1983) and for Eastern Kingbirds in particular (Chapter 2), defence strategies and behaviour of parents at the nest may differ for eggs or nestlings (Montgomerie and Weatherhead 1988). I observed kingbirds at the nest during incubation, when there were newly hatched nestlings and when they had older nestlings, to determine differences in nest defence strategies.

Montgomerie and Weatherhead (1988) predicted that parents nesting in exposed nests will defend more vigorously than parents nesting in hidden nests. A study of American Robins (<u>Turdus</u> <u>migratorius</u>) (McLean et al. 1986) confirmed this prediction. Nest defence strategies of Eastern Kingbirds may also differ with respect to overhead nest visibility as nest predation of Eastern Kingbirds is influenced by nest visibility (Chapter 2). I used kingbird responses to an American Crow model and observations of kingbird behaviour at the nest to determine whether kingbird nest defence behaviour differed with overhead nest visibility.

Nest defence may be costly in terms of both effort and danger. If kingbirds are minimizing costs, the effort of defence should differ depending upon the danger posed by the predator (Montgomerie and Weatherhead 1988). Birds defend most vigorously against predators when the predators are most dangerous to the parents or to the nest (Elliot 1984, Walters 1990) and defence tactics differ for different predators (Hinde 1952, Kruuk 1964, Verbeek 1973, Curio 1975, Veen 1977, Gottfried 1979, Greig-Smith 1980, East 1981, Buitron 1983, Stephens 1984, Gottfried et al. 1985, Ficken 1990). Few studies (but see Buitron 1983) have quantified non-experimental encounters between predators and defending parents to demonstrate that parents expend effort where it is most effective and that defence tactics differ depending on the predator species that is confronted.

Evidence suggests that some predators avoid confrontation with mobbing birds (Bildstein 1982, Stephens 1984) and that birds can repel attacks by predators larger than themselves (Elliot 1984), but the evidence from actual observations is scarce (but see Buitron 1983). Predators may avoid mobbing defenders, or could use the behaviour of parents to locate nests. How do predators respond to harrassment by kingbirds? To determine how predators responded to kingbird behaviour and how kingbirds responded to predators, I quantified interactions between predators and nesting kingbirds for four breeding seasons (1998 - 1992).

This chapter thus documents the behaviour of Eastern Kingbird parents at the nest, how they defended their nests, the response of predators to this defence, and some of the costs and benefits of defence behaviour at the nest.

Methods

Behaviour of kingbirds at the nest

The behaviour of kingbird pairs at nests was observed during 1990 and 1991. Watches were conducted during incubation (1-3 days after clutch completion) in 1991, and chick-rearing (1-6 and 7-9 days after the first egg hatched) in 1990 and 1991. Observers were located about 50 m or more away from the nest and watches usually lasted 90 min. Watches which were terminated at 60 min or longer were also used in the analysis, but data from these watches were adjusted to 90 min. Pairs were observed with binoculars and spotting scopes and behaviours were timed using digital watches. Noisy behaviour and other behaviours, such as nest visits, that might attract predators to the nest, were quantified, as was parental attendance at the nest.

Descriptions of the behaviours observed follows:

1) **Presence of the parents near the nest**: the relative time that both, one or neither of the parents were within sight of the nest while there were nestlings. Parents were under continuous surveilance during the watch, and during the nestling period, it was possible to locate both parents. The male was not always present during incubation, and not always evident when he was present; therefore, the female's presence on the nest was used as a measure of attendance. Males do not incubate and so were never recorded on the nest during incubation.

2) **The number of visits to the nest**: the presence of either parent within a 2 m radius of the nest was considered to be a visit. Feeding a nestling was also counted as a visit.

3) **The number of noisy visits to the nest**: a call or series of calls delivered from a perch within 2 m of the nest was considered to be a noisy visit. A change of perches, within a 2 m radius of the nest, accompanied by a call or a series of calls, was considered to be a second noisy visit.

4) **The number of noisy perches**: any perch where either parent gave a call or a series of calls. A change of perch, accompanied by a call or series of calls was considered to be a second noisy perch.

5) **The distance of noisy activity from the nest**: all distances were estimated (in meters) by observers during the watch and resulted in three measures of distance of noisy activity from the nest: mean distance, standard deviation and range of all noisy perches.

Behaviour of kingbirds towards predators

The behaviour of kingbird parents towards predators was recorded in 1990 and 1991, during the 90 min watches described above, and the recorded behaviours are described below.

1) **The number of chases**: any encounter, by either parent, with an intruder of the same or another species was recorded. A chase involved the parent leaving a perch and

pursuing that other individual. Chases included pursuits of predators, kingbirds and others (usually passerines).

2) **The number of corvids seen**: the number of crows and ravens seen near the nest during each watch was noted. The distance of the crow or raven from the nest (estimated in meters) was recorded and reported under observations of kingbird-predator encounters. Sightings of other avian predators were also recorded during watches.

Crow model presentations

A model American Crow on a 1-m stick was placed 5 m from each active nest to determine how vigorously kingbirds attacked a predator that was close to the nest, and whether the intensity of attack varied with nest visibility and nest success. I approached each nest slowly, on foot or by canoe (in the case of the canoe, an assistant was present), placed the crow model and speaker in position and retreated to a hiding place. Each trial lasted 12 min: 6 min of crow calls followed by 6 min of silence. I then removed the crow model and speaker, checked the nest contents and left. The most aggressive response of either parent was given a score following Blancher and Robertson (1982). The score increases with the risk taken by the bird, as follows: 1) the bird perches; 2) perches and calls; 3) hovers over the model; 4) dives at the model; 5) and hits the model. The visibility of each nest and the nesting success of each pair were measured as described in Chapter 2.

Distance of the observer from the nest when the female leaves the nest (flight distance)

During 1988, 1989, and 1991, I estimated (in meters) how far I was from the nest when the incubating female flushed from the nest (flight distance). Observations were taken within 3 days of clutch completion. Visibility of the nest was measured as in Chapter 2. I also determined how many of four sides (north, south, east and west) gave a view of ≤100 m or ≤300 m from the nest. Each nest was scored from zero (unable to see in any direction) to four (able to see in all four directions from the nest) for both 100 m and 300 m categories.

Effectiveness of nest defence

Pseudonests placed near kingbird nests

Three pseudonests, each containing two Painted Quail eggs and one plasticine egg tied to the pseudonest, were placed 5-15 m, 40-60 m, and 90-110 m from an active kingbird nest during 1990. Controls were placed at least 200 m from and out of sight of an active kingbird nest. Plasticine eggs were painted with acrylic paints to resemble the Painted Quail eggs. All pseudonests were placed in a medium overall visibility situation where four sides (directions: N,S,E,W) were 40-60% visible and overhead visibility was 40-60%. All three pseudonests near a kingbird nest and the control nest were set out on the same day (within 1-3 days of clutch completion by the kingbird pair), and were matched for shrub or tree species, height, and habitat type. Pseudonests were checked every 3 days for a period of 15 days.

The experiment was modified in 1991, to reduce kingbird destruction of pseudonests. Pseudonests containing two large Japanese Quail eggs and one plasticine egg (tied to the nest, and painted with acrylic paint to resemble a quail egg) were placed 5-15 m from the nest of an active kingbird pair within 3 days of clutch completion. Cellophane tape was placed on the upper half of each quail egg to deter kingbirds from breaking and removing the egg. Control pseudonests were set out on the same day, and were at least 200 m from and out of sight of any kingbird nest. Pseudonests near kingbird nests and control pseudonests were matched for medium overall visibility, height, and habitat type. Pseudonests were checked every 3 days for 6 days. Predators were identified by the impressions left in the plasticine eggs and by method of predation.

Kingbird-predator encounters

Observations of kingbird-predator encounters were made during 1988-1991, to determine what kingbirds do when a predator is in the nest vicinity and what the predator does when near a kingbird nest and confronted by a defending kingbird. Whenever an encounter was observed, the following information was recorded, where possible: 1) the species being pursued by the kingbirds; 2) the distance of the encounter from the kingbird nest; 3) the stage of development of the kingbird nest contents; 4) the duration (sec) and distance (m) of the chase; 5) whether the kingbird dove at or hit the predator; 6) how close (m) the kingbird came to the predator during the encounter; 7) how far from the nest the kingbird was before it called and began the chase and 8) whether the predator changed direction or altitude as a result of the kingbird pursuit. The presence of American Crows (Corvus brachyrhynchos), Northern Ravens (C. corax), American Kestrels (Falco sparverius), Merlins (F. columbarius), Great Horned Owls (Bubo virginianus), Sharp-shinned Hawks (Accipiter striatus), Cooper's Hawks (A. cooperii), Black-billed Magpies (Pica pica), and Brown-headed Cowbirds (Molothrus ater) was noted whenever they were seen. An index of kingbird pursuits with respect to kingbird predator occurrence was computed for each day as follows: e.g. number of kingbird-kestrel chases / number of kestrels seen in the study area on the same day.

Results

Behaviour of kingbirds at the nest

Presence of the parents near the nest

Kingbird parents with young (1-6 days old) and older nestlings (7-9 days old) spent about 80% of the time within sight of the nest (n=30; $\bar{x}$=0.79±0.18). Incubating females (within 3 days of clutch completion) spent 40% of the time on the nest (n=24; $\bar{x}$=0.40±0.08). Males perched by nestlings when females left the nest but were often not visible in the vicinity of the nest during incubation. Some males were often not seen within 150 m of the nest during incubation, a situation which was not recorded (with the exception of predator chases) when there were nestlings. Chases of predators accounted for all incidents when neither parent was within sight of the nest. A cubic spline of the proportion of time that incubating females spent on the nest suggests that the more time a female spent on the nest, the greater the probability of nest success (Fig. 11). Standard errors are large, however, and the possibility of other relationships cannot be excluded. Logistic regression on the original data shows a positive, but non-significant linear relationship between successful and failed nesting attempts and proportion of time spent upon the nest (logit p(success)=-3.96+0.0006x, n=23, X^2=0.95, P=0.33, B<0.1). Neither was there a difference in the proportion of time that successful and unsuccessful females spent upon the nest during incubation (Table 12). A cubic spline of the proportion of time that both parents spent

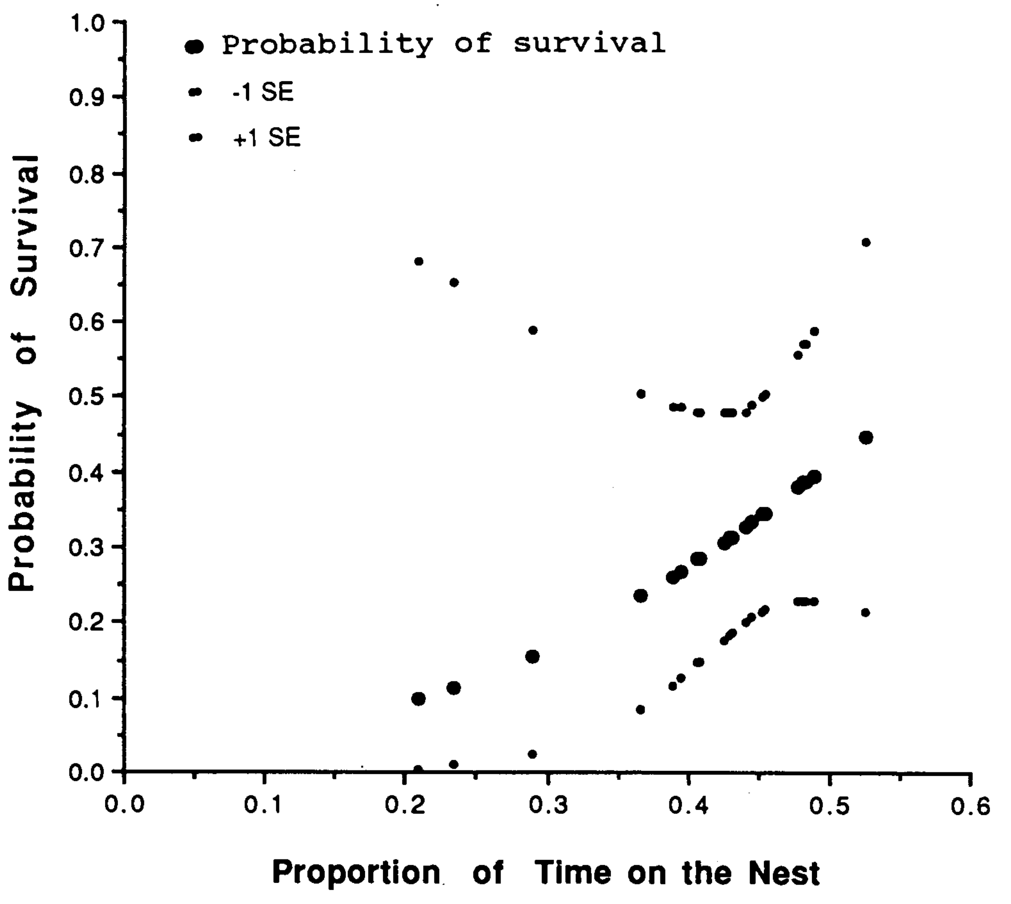


Figure 11. Cubic spline (giving the probability of survival of nest contents until fledging) of the proportion of time that incubating Eastern Kingbird females spent on the nest, 1991.

Table 12. The proportion of time (for 90 min) that both, one, or neither of the kingbird parents spent within sight of the nest.

Age (days)	Successful N	Successful $\bar{x} \pm$ S.D.	Preyed upon N	Preyed upon $\bar{x} \pm$ S.D.
Female on the nest				
Incubation	5	0.44±0.05	15	0.40±0.10
	M.W.U.=32.0	P=0.50	B<0.1	
Both parents within sight of the nest				
1-6 d	17	0.80±0.20	13	0.80±0.20
	M.W.U.=98.5	P=0.60	B<0.1	
7-9 d	12	0.70±0.30	6	0.80±0.20
	M.W.U.=35.0	P=0.69	B<0.1	
One parent within sight of the nest				
1-6 d	17	0.20±0.20	13	0.20±0.20
	M.W.U.=97.0	P=0.60	B<0.1	
7-9 d	12	0.30±0.30	6	0.20±0.20
	M.W.U.=36.0	P=0.70	B=0.3	
Neither parent within sight of the nest				
1-6 d	17	0.01±0.02	13	0.01±0.03
	M.W.U.=108.5	P=0.80	B<0.1	
7-9 d	13	0.00±0.00	6	0.01±0.02
	M.W.U.=24.0	P=1.00	B<0.1	

within sight of the nest when the nestlings were 1-6 days of age also suggests that the more time both parents are present within sight of the nest, the greater the probability of nest success (Fig. 12). Standard errors appear small enough to confirm a positive slope. Logistic regression also indicates there is a positive linear relationship between success and nest failure and the proportion of time that both parents are present, however this relationship was not significant (logit p(success)=-0.34+0.00008x, n=30, X^2=0.14, P=0.70, B<0.1)). Successful parents did not differ from parents of preyed upon nestlings, with respect to the proportion of time that both, one, or neither parent spent within sight of the nest when there were nestlings (Table 12).

Number of visits to the nest

Parents visited the nest more often as nest contents aged (Table 13). Cubic splines on the number of nest visits during incubation (Fig. 13a), young nestlings (Fig. 13b) and combined visits (Fig. 13c) suggest that an increased number of visits to the nest increases the probability of nest survival. Logistic regression confirmed these positive relationships (incubation: logit p(success)=-1.45+0.11x, n=22, X^2=1.77, P=0.20, B=0.1; 1-6 day old nestlings: logit p(success)=-0.02+0.026x, n=30, X^2=0.09, P=0.77, B=0.3; All visits: logit p(success)=2.9+0.25x, n=52, X^2=12.4, P=0.0009) but only the regression for combined visits was significant. There was no difference between successful and preyed upon nests with

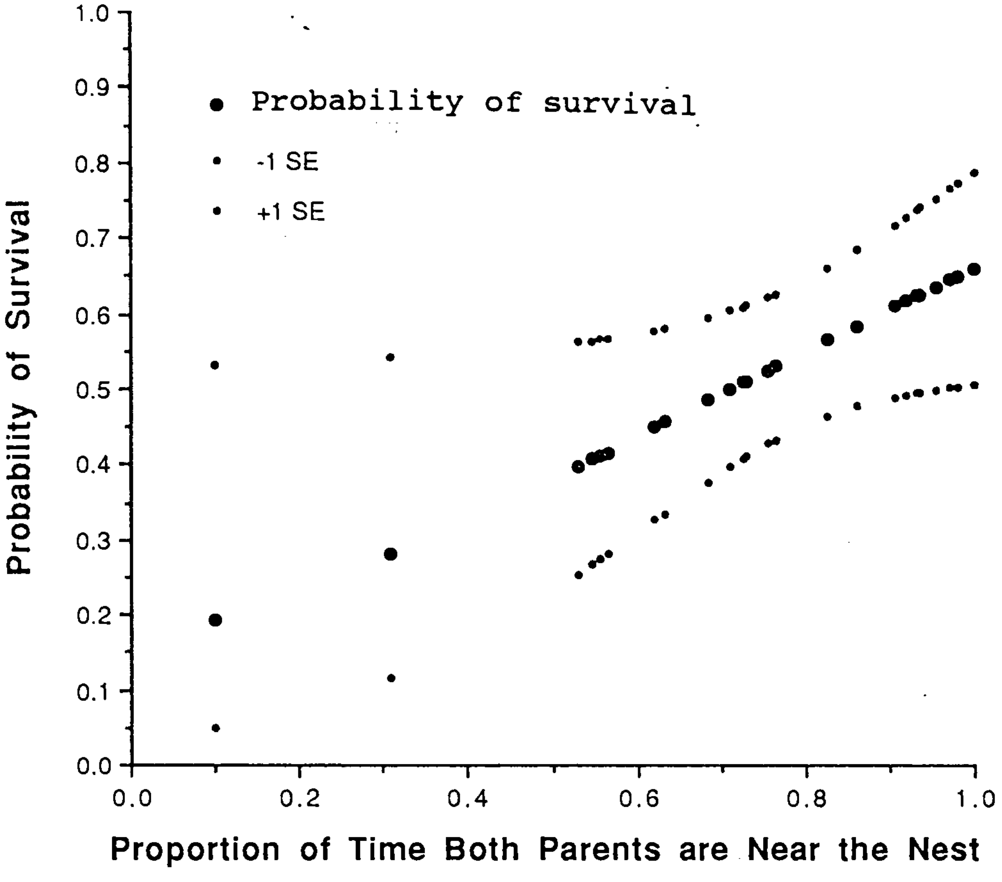


Figure 12. Cubic spline (giving the probability of survival of nest contents until fledging) of the proportion of time that both Eastern Kingbird parents spend within sight of the nest with nestlings, 1990 and 1991.

Table 13. The number of visits, noisy visits, and noisy perches during 90 min watches, 1989 and 1990.

Age (days)	Successful		Preyed upon[1]		All nests[2]	
	N	x ± S.D.	N	x ± S.D.	N	x ± S.D.
Visits[3]						
Incubation	7	4.5 ± 2.0	16	4.0 ± 2.3	27	4.1 ± 2.2
	M.W.U.=39.5	P=0.60	B=0.2			
Nestlings						
1-6 d	17	11.2 ± 4.7	13	10.8 ± 3.9	30	11.0 ± 4.3
	M.W.U.=88.5	P=0.40	B=0.2			
7-9 d	12	16.0 ± 7.6	6	18.0 ± 7.5	18	16.7 ± 7.4
	M.W.U.=28.5	P=0.30	B=0.1			
Noisy visits[4]						
Incubation	7	3.6 ± 2.7	16	3.6 ± 2.0	22	3.5 ± 2.2
	M.W.U.=54.0	P=0.40	B=0.1			
Nestlings						
1-6 d	17	4.2 ± 4.7	13	2.6 ± 4.0	30	3.8 ± 4.4
	M.W.U.=76.0	P=0.14	B=0.2			
7-9 d	12	6.5 ± 9.7	6	2.0 ± 2.4	18	5.0 ± 8.2
	M.W.U.=24.0	P=0.30	B=0.1			
Noisy perches[5]						
Incubation	7	11.7 ± 7.9	16	12.6 ± 4.6	22	12.5 ± 5.7
	M.W.U.=45.0	P=0.30	B=0.1			
Nestlings						
1-6 d	17	18.9 ±17.7	13	12.2 ± 4.7	30	16.0 ±10.5
	M.W.U.=73.0	P=0.12	B=0.4			

Table 13 continued.

7-9 d	12	19.6 $\pm$10.6	6	10.5 $\pm$ 2.1	18	16.6 $\pm$ 9.4
	M.W.U.=10.0	P=0.005	B=0.6			

[1]Mann-Whitney U values compare preyed upon and successful nests.

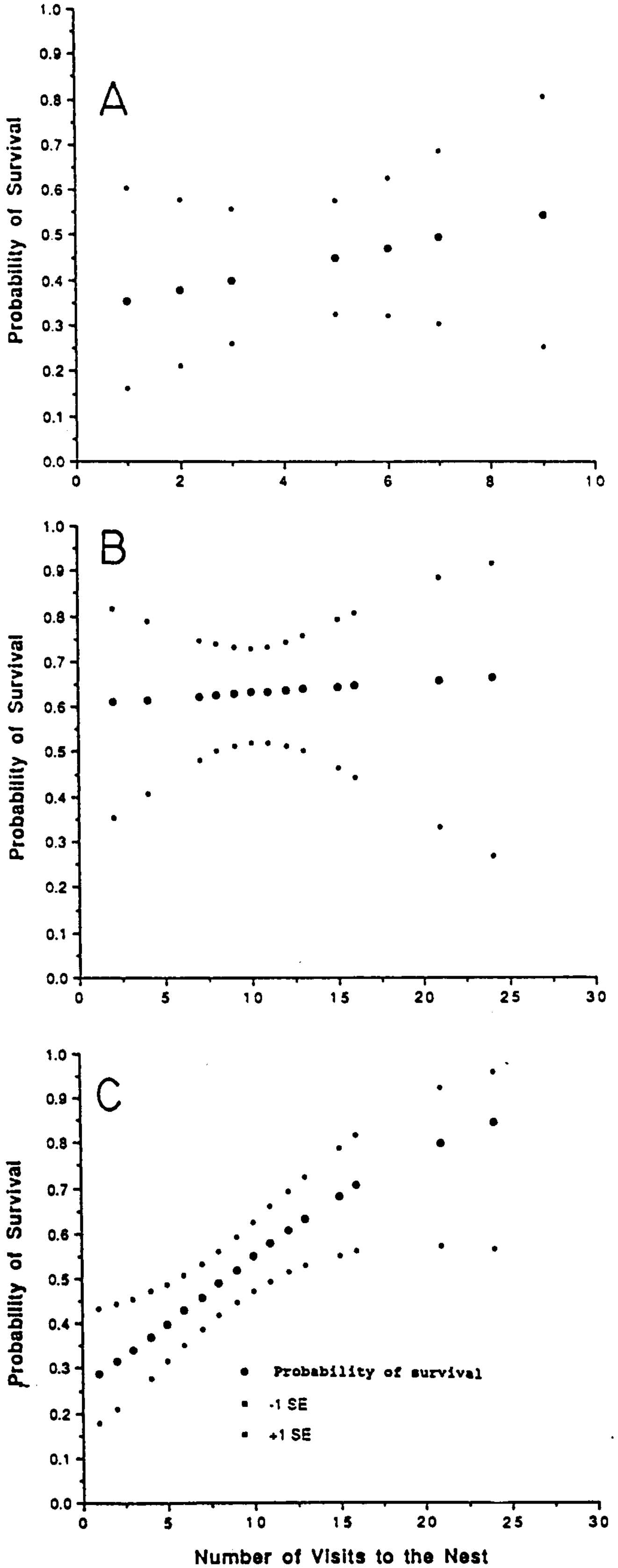
[2]All nests includes kingbird nests which were not preyed upon, but were later deserted due to flooding which occurred after the information was collected.

[3]K.W.U.=45 P=0 for comparison between visits during incubation, 1-3 d and 7-9 d nestlings.

[4]K.W.U.=0.2 P=0.9 for comparison between noisy visits during incubation, 1-3 d and 7-9 d nestlings.

[5]K.W.U.=2.5 P=0.3 for comparison between noisy perches during incubation, 1-3 d and 7-9 d nestlings.

Figure 13. Cubic splines (giving the probability of survival of nest contents until fledging) of the number of visits to the nest made by Eastern Kingbird parents for nest contents that survived: A) incubation, 1991; B) the nestling stage (1-6 days old), 1990 and 1991 and C) of all nests combined.


A
B
C
Probability of Survival
Number of Visits to the Nest
Probability of survival
-1 SE
+1 SE

respect to numbers of visits to the nest for either eggs or nestlings (Table 13).

The number of noisy visits to the nest

While visits to the nest increased with the age of the nest contents, the number of noisy visits did not. The number of noisy visits to the nest was not significantly different at any age of nest contents, and although successful parents were noisier, the difference was significant only for nestlings 7-9 days old (Table 13).

A cubic spline of noisy visits to nests with eggs and with young nestlings, combined, shows that the fitness function is not linear and that parents which are either quiet or noisy fledge young (Table 14, Fig. 14). Noisy visits and the amount of time that both parents (r_s=0.34, P=0.02, n=75) and one parent (r_s=-0.16, P=0.02, n=75) spend near the nest are correlated. Noisy visits and the following measures of habitat (Chapter 4) were also correlated: number of perches available near the nest (r_s=-0.34, P=0.003, n=75); number of stems near the nest (r_s=-0.23, P=0.05, n=75) and percentage field surrounding the nest (r_s=-0.34, P=0.003, n=75).

The number of noisy perches

The mean number of noisy perches used by successful parents and parents that lost nest contents to predation did not differ during incubation or when there were nestlings (Table 13). A cubic spline of the number of noisy perches during incubation and when there were young nestlings,

Table 14. Nest success and the number of noisy visits for Eastern Kingbird parents to nests with eggs and nestlings (1-6 days old), combined.

	Successful nests	Preyed upon nests
0-1 Noisy visits	10	11[1]
2-6 Noisy visits	6	14
9+ Noisy visits	5	2

1 X^2=4.4, P>0.05, B=0.4

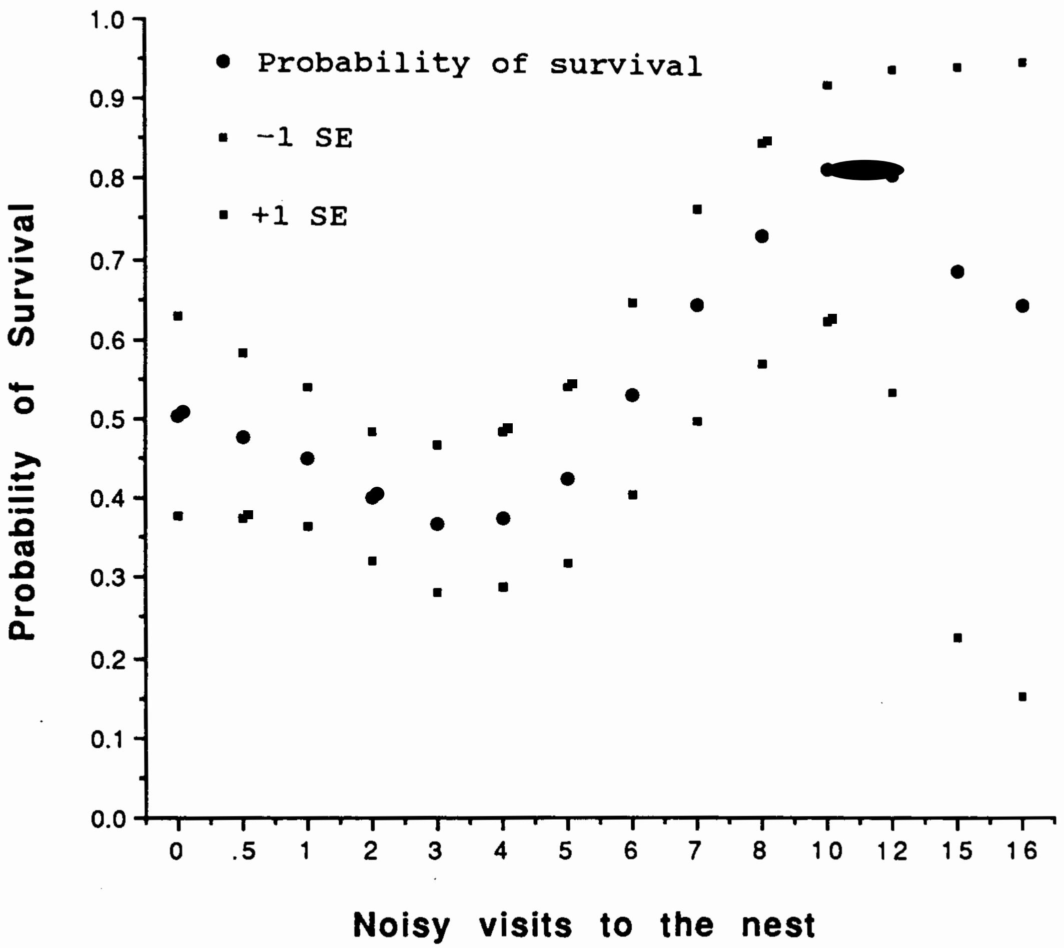


Figure 14. Cubic spline (giving the probability of survival of nest contents until fledging) of the number of noisy visits made by Eastern Kingbird parents during incubation and to nestlings (1-6 days old), combined.

combined, showed that parents which were either quiet or relatively noisy were more likely to raise young to fledging than parents exhibiting an intermediate level of noisy behaviour (Fig. 15). A comparison of parents exhibiting either noisy or quiet behaviour and parents exhibiting an intermediate level of noisy behaviour, confirms that being either noisy or quiet, but not an intermediate strategy, is most successful (Table 15).

There was a negative correlation between the number of noisy perches and original clutch size, shown when there were nestlings, but not during incubation (incubation: r_s=-0.15, n=22, P=0.5, B=0.09; 1-6 days of age: r_s=-0.36, n=30, P=0.08, B=0.52; 7-9 days of age: r_s=-0.57, n=18, P=0.04).

The distance of noisy activity from the nest

The distance from the nest at which calls were made did not differ between successful parents and preyed upon parents (Table 16). A cubic spline of mean distance of noisy behaviour from the nest suggests that during incubation parents which made noise close to the nest and those making noise farther from the nest had the best probability of fledging young (Fig. 16a). Standard errors are small enough to confirm that the "dip" shown in the function is real. A comparison of the success of parents making noise either close to or far from the nest confirms that these parents are more successful than parents concentrating noisy activity at an intermediate distance (Table 17), although the difference was

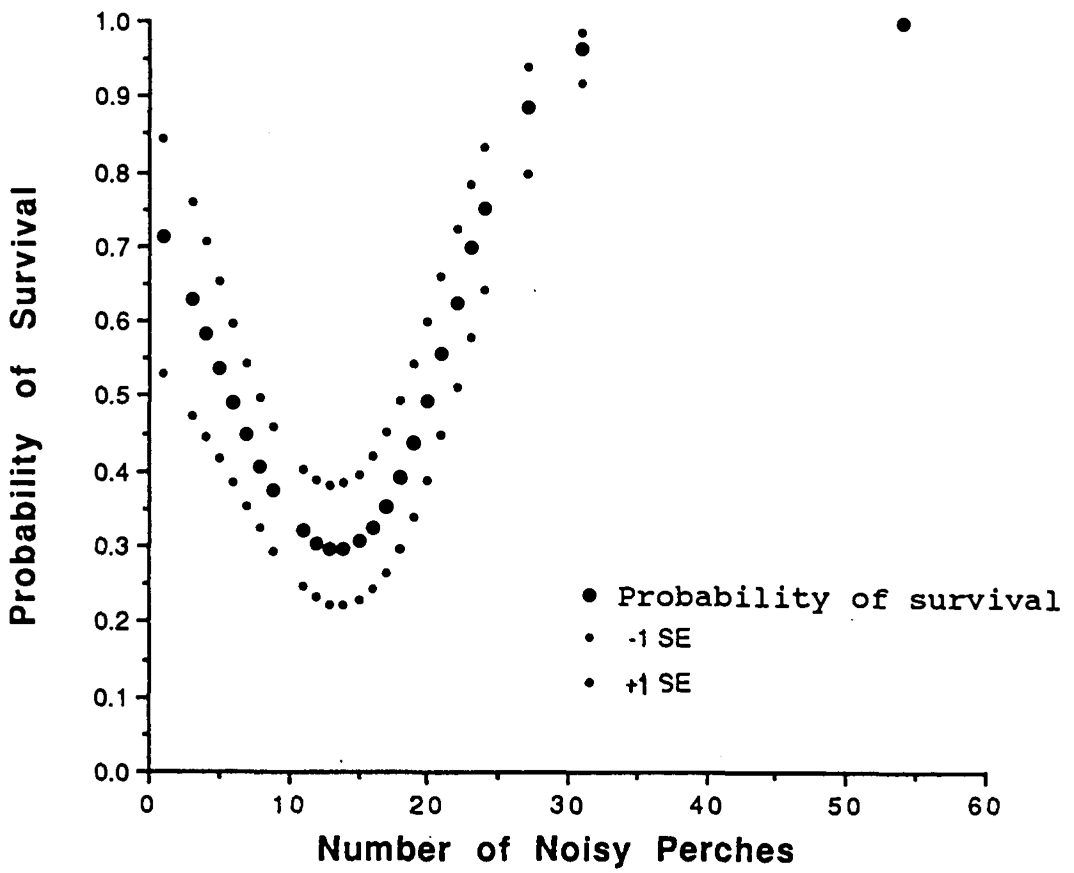


Figure 15. Cubic spline (giving the probability of survival of nest contents until fledging) of noisy behaviour (number of noisy perches) in the vicinity of the nest, by Eastern Kingbird parents during incubation and to nestlings (1-6 days old), combined.

Table 15. Nest success and the number of noisy perches for Eastern Kingbird parents to nests with eggs and nestlings 1-6 days, combined.

	Successful nests	Preyed upon nests
≤ 10 Noisy perches	9	10[1]
12-18 Noisy perches	5	13
≤ 20 Noisy perches	9	2

[1] $X^2=7.9$, $P<0.025$

Table 16. The distance of noisy kingbird activity from the nest during incubation, and when there are nestlings 1-6 and 7-9 days of age.

Age	Successful		Preyed upon[1]		All nests[2]	
(days)	N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.
Mean distance of noisy activity to the nest						
Incubation	7	31.8±38.9	16	38.7±24.9	27	36.2±0.2
	M.W.U=46.0		P=0.44	B=0.1		
1-6 d	17	37.2±68.1	13	36.2±26.2	30	36.7±53.3
	M.W.U=80.0		P=0.20	B=0.1		
7-9 d	12	26.5±15.9	6	22.4±8.6	18	25.1±13.8
	M.W.U=34.0		P=0.70	B=0.1		
Mean distance of noisy activity closest to the nest						
Incubation	7	0.1±0.4	16	0.7±2.5	27	1.0±2.7
	M.W.U=53.0		P=1.00	B=0.1		
1-6 d	17	2.8±5.9	13	3.6±7.4	30	3.1±6.5
	M.W.U=96.0		P=0.50	B=0.1		
7-9 d	12	3.3±6.8	6	4.5±9.6	18	3.7±7.5
	M.W.U=32.0		P=0.70	B=0.1		
Mean distance of noisy activity farthest from the nest						
Incubation	7	95.7±114.5	16	141.7±105.1	27	130.6±108.0
	M.W.U=39.0		P=0.30	B=0.2		
1-6 d	17	113.8±121.5	13	96.9±58.1	30	106.5±98.0
	M.W.U=101.0		P=0.70	B=0.1		
7-9 d	12	99.0±43.1	6	80.8±34.4	18	92.9±40.4

Table 16. continued

M.W.U=29.0 P=0.70 B=0.2

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[1]Mann-Whitney U values compare preyed upon and successful nests.

[2]All nests includes successful, preyed upon and some nests which were not preyed upon, but were later deserted due to flooding, which occurred after the above information was collected.

Figure 16. Cubic splines (giving the probability of survival of nest contents until fledging) of the mean distance of noisy behaviour of Eastern Kingbird parents from nests during: A) incubation, B) the nestling stage (1-6 days old) and C) for incubation and nestling stages combined.

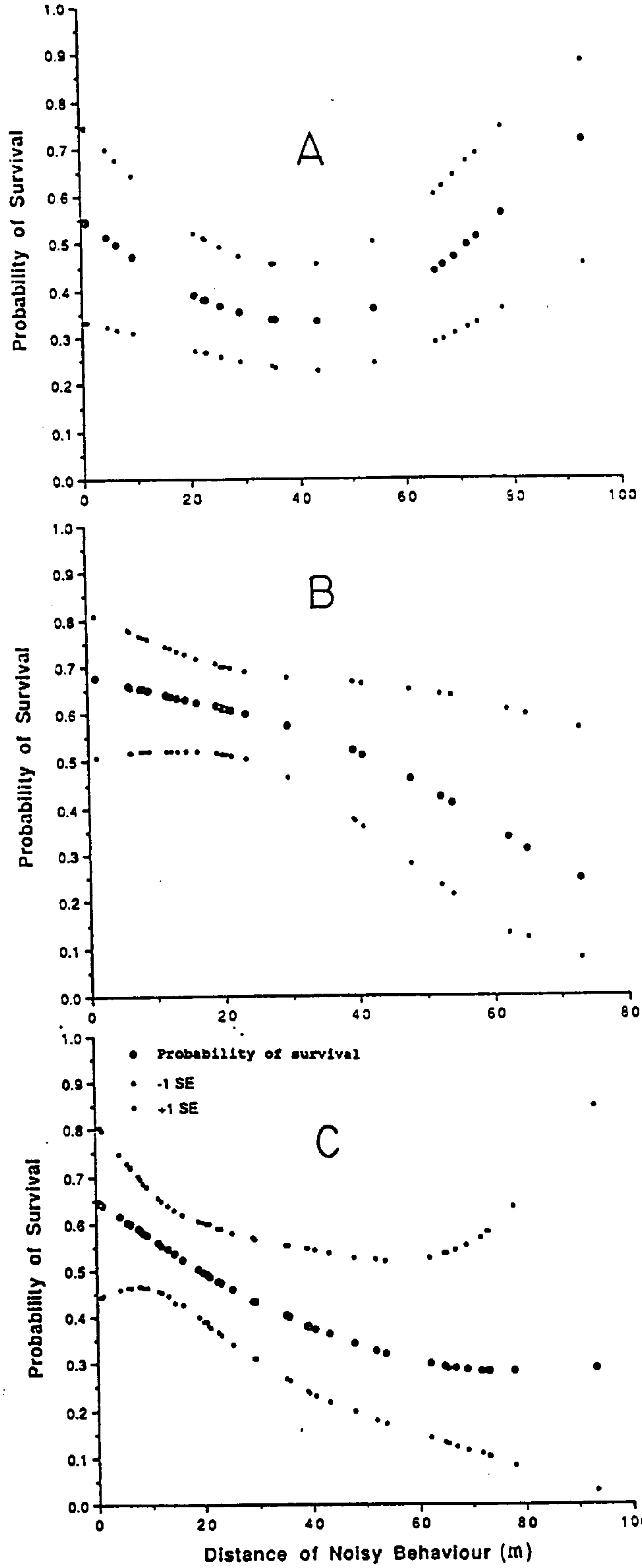

A
B
C
Probability of Survival
Probability of survival
-1 SE
+1 SE
Distance of Noisy Behaviour (m)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
20
40
60
80
100

Table 17. Nest success and distance from the nest of noisy behaviour in Eastern Kingbirds.

	Successful nests	Preyed upon nests
20-60m	2	7[1]
0-10m and >60m	8	5

[1] X^2=3.1, P<0.1, B=0.8

not statistically significant. Parents of young nestlings had the greatest probability of fledging young when noisy behaviour was closest to the nest (Fig. 16b). Logistic regression shows, however, that there is no significant relationship between mean distance of noisy behaviour from the nest and failure or success (logit p(success)=0.26+0.0004x, n=17, X^2=0.003, P=0.96, B<0.1). A cubic spline of the combined mean distance of incubation and young nestlings indicates that noisy behaviour near the nest is of greater benefit than in noisy behaviour further from the nest (Fig. 16c). Logistic regression shows a positive, non-significant relationship (logit p(success)=-0.88+0.0005x, n=57, X^2=0.006, P=0.94, B<0.1).

Behaviour of kingbirds towards predators

The number of chases

The number of chases between kingbird parents and other species of birds did not increase with the age of nest contents nor did the number of chases differ between parents of successful and preyed upon nest contents. In all cases, successful parents chased more, but the difference was not significant (Table 18). A cubic spline of the number of chases (for incubation and young nestlings combined) indicates that the probability of nest survival may increase with the number of chases (Fig. 17). The standard errors are so large, however, that the possibility of a slope of zero or a negative slope cannot be discounted. Logistic regression shows no

Table 18. The number of chases during 90 min periods by Eastern Kingbird parents.

Age	Successful		Preyed upon[1]		All nests[2]	
(days)	N	$\bar{x} \pm$S.D.	N	$\bar{x} \pm$S.D.	N	$\bar{x} \pm$S.D.
Incubation:	7	1.6±1.6	16	1.1±1.3	27	1.1±1.3
	M.W.U.=44.0	P=0.40	B=0.1			
Nestlings:						
1-6 d	17	1.0±1.1	13	0.7±0.9	30	0.9±1.0
	M.W.U.=92.0	P=0.40	B=0.6			
7-9 d	12	1.1±1.2	6	0.6±0.6	18	0.9±1.0
	M.W.U.=29.0	P=0.40	B=0.1			

[1]Mann-Whitney U values compare successful and unsuccessful nests.

[2]All nests includes kingbird nests which were not preyed upon, but were later deserted due to flooding which occurred after the information was collected.

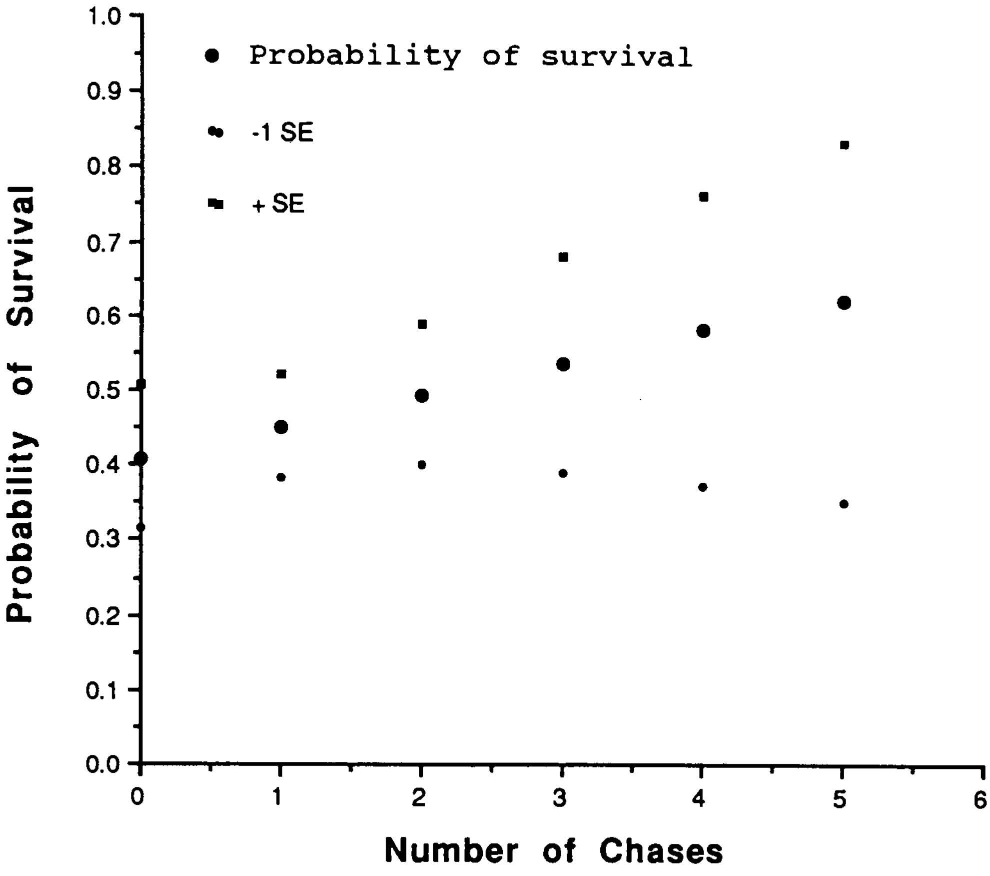


Figure 17. Cubic spline (giving the probability of survival of nest contents until fledging) of the number of chases in the vicinity of the nest by Eastern Kingbird parents during incubation and when they had nestlings, combined.

relationship (logit p(success)=-0.86+0.009x, n=57, X^2=0.001, P=0.97, B<0.1).

The number of corvids seen

A cubic spline of the number of crows and ravens seen near kingbird nests during incubation and nests with young nestlings combined suggests that the fewer crows and ravens were seen in the vicinity of the nest, the greater was the chance of fledging (Fig. 18). Standard errors are large, however, and the possibility of other slopes cannot be discounted. Logistic regression suggests that this is a positive, non-significant relationship between nesting success or failure and number of corvids seen (logit p(success)=0.86+0.009x, n=57, X^2=0.001, P=0.97, B<0.1). The number of crows and ravens seen during the 90 min watches did not differ between successful and preyed upon nests (Table 19).

Crow model presentations

A cubic spline of the nest defence scores of parents during model presentations shows that parents with lower scores had the greatest probability of raising young to fledging (Fig. 19). A Fisher's Exact test (Sokal and Rohlf 1981) also shows that pairs which dove at or hit the model (Scores: 4 or 5) were less likely to raise young than those which perched, perched and called or hovered (Scores: 3, 2 or 1) (Table 20). Logistic regression also confirms the relationship (logit p(success)=0.68-0.43x, n=25, X^2=3.27,

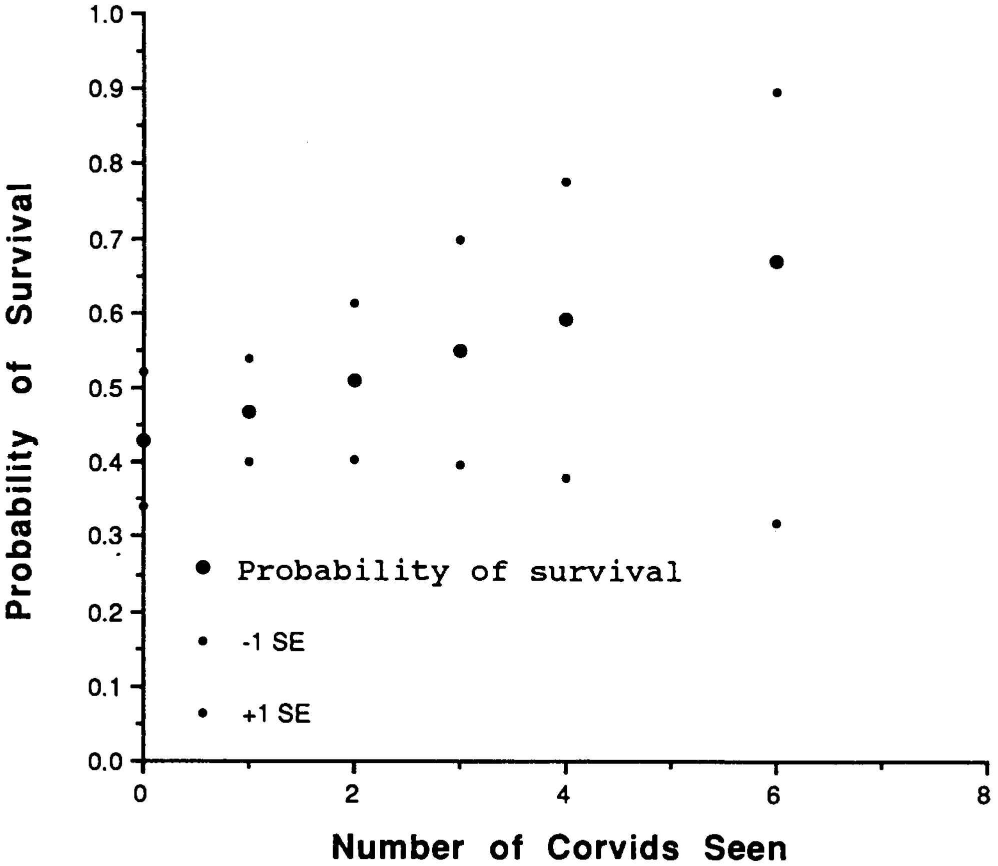


Figure 18. Cubic spline (giving the probability of survival of nest contents until fledging) of the number of crows and ravens seen in the vicinity of Eastern Kingbird nests during incubation and when they had nestlings (1-6 days old), combined.

Table 19. The number of American Crows and Northern Ravens seen during 90 min watches at Eastern Kingbird nests during incubation, and with nestlings 1-6 and 7-9 days of age.

Age	Successful		Preyed upon[1]		All nests[2]	
(days)	N	$\bar{x} \pm$ S.D	N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.
Incubation	7	1.4±2.2	16	0.5±0.8	27	1.1±1.3
	M.W.U.=46.0		P=0.10	B=0.5		
Nestlings:						
1-6 d	17	0.8±1.0	13	0.9±1.2	30	0.9±1.0
	M.W.U.=105.5		P=0.80	B<0.1		
7-9 d	12	0.7±1.2	6	0.7±0.8	18	0.9±1.0
	M.W.U.=32.0		P=1.0	B<0.1		

[1]Mann-Whitney U values compare successful and preyed upon nests.

[2]All nests includes kingbird nests which were not preyed upon, but were later deserted due to flooding which occurred after the information was collected.

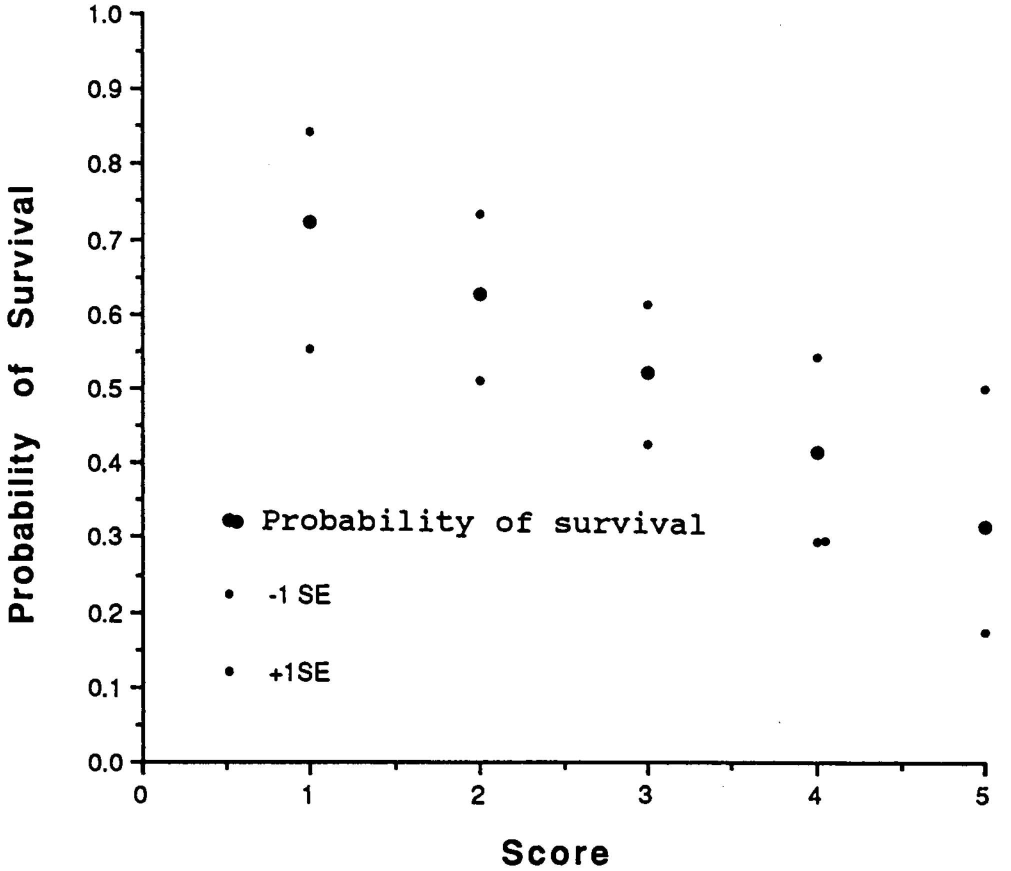


Figure 19. Cubic spline (giving the probability of survival of nest contents until fledging) of the nest defence score of Eastern Kingbird parents when presented with a model crow. An increase in the score is an increase in the risk taken to defend the nest.

Table 20. The relationship between the score of Eastern Kingbirds to a model crow located 5 m from the nest, and nest predation, 1989.

	Score	
	1,2,3[1]	4,5[2]
Successful	11	4[3]
Preyed upon	3	7

[1] The highest score of either parent: perching quietly; perching and calling; or hovering over the model.

[2] The highest score of either parent: diving at the model or hitting the model.

[3] X^2=3.7, P=0.07, B=0.5

P=0.07, B=0.6). There was no relationship, however, between the score of the parents and the overhead visibility of the nest (r_s=0.05, n=34, P=0.8, B<0.1).

Distance of the observer from the nest when the female leaves the nest (flight distance)

A cubic spline of the flight distance of incubating females shows that flight distance does not influence nest success (Fig. 20). There was no significant difference in flight distance between successful females and those with preyed upon nest contents (successful x=4.5±5.3 m n=24; preyed upon x=4.3±4.3 m, n=19, M.W.U=211.5, P=0.7, B<0.1). There was however, a positive, but weak relationship between flight distance and both the number of sides from which the female can see 100 m (r=0.24, F=4.2, n=54, P=0.05) and overhead visibility (regression: r=0.31, F=5.02, n=54, P=0.03).

Effectiveness of nest defence

Pseudonests placed near kingbird nests

Observations at nests in 1990 confirmed that kingbirds were destroying and removing quail eggs from pseudonests placed at and closer than 50 m from the nest and as far away as 100 m from the kingbird nest. One or both members of a pair would perch at the pseudonest and peck at the quail eggs until a hole was made. The quail egg was then carried as far as 150 m or more and dropped. The kingbirds also tried to remove the plasticine egg tied in each pseudonest. Beak marks left on plasticine eggs allowed me to identify other

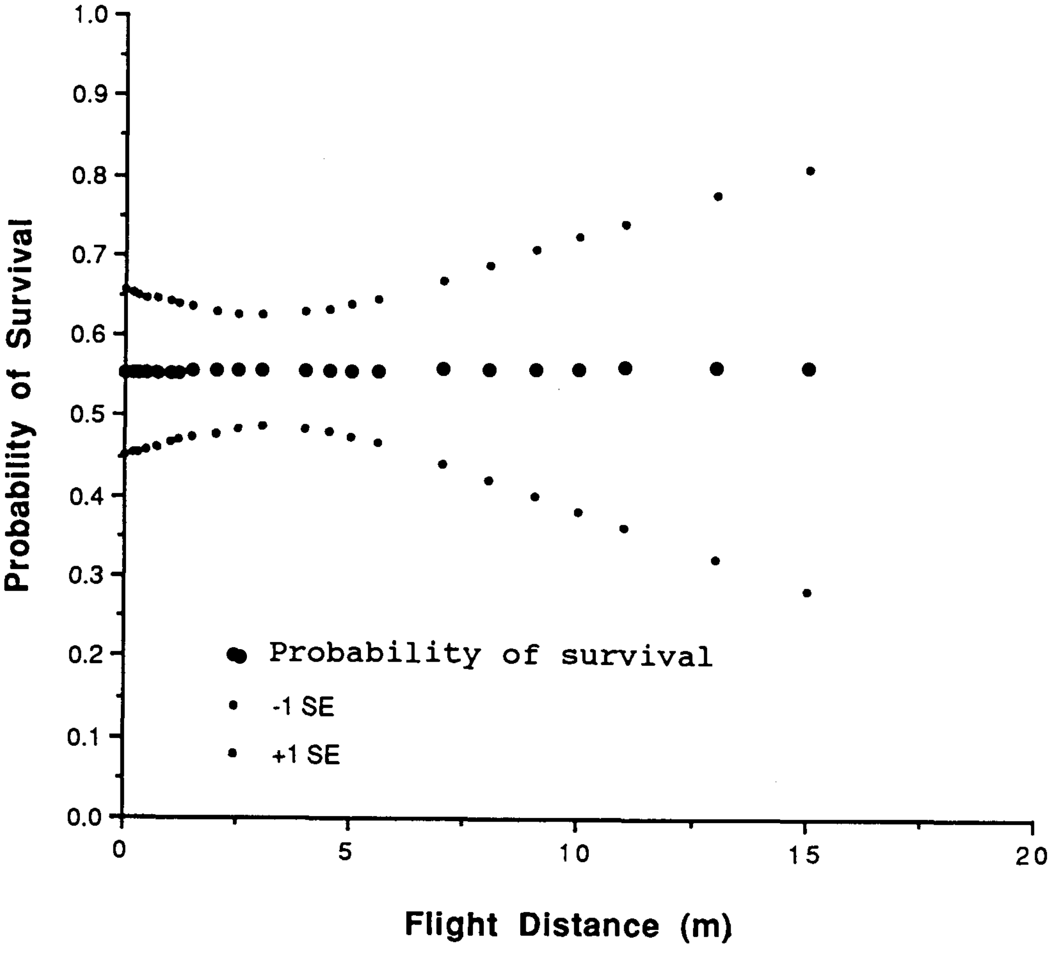


Figure 20. Cubic spline (giving the probability of survival of nest contents until fledging) of the distance from a nest that an approaching observer reached when an incubating Eastern Kingbird female flushed from the nest (flight distance).

plasticine eggs in pseudonests that kingbirds had disrupted. Forty-two pseudonests containing plasticine eggs were placed 5 m, 50 m or 100 m from kingbird nests: 23 of the plasticine eggs tied into the pseudonests showed signs of having been pecked by kingbirds. In 1991 the experiment was modified to deter kingbird destruction of pseudonests. None of the 23 pseudonests placed near kingbird nests were lost to predators after 6 days when the experiment was terminated, but 8 of 18 control nests were lost to predation (X^2=12.5, P<0.001) during the same period.

Kingbird-predator encounters

The daily incidents of predator sightings, observed kingbird-predator encounters, and the number of kingbird-predator encounters divided by the number of predator observations for 1991 are shown in Fig. 21 (a, b, and c, respectively) for corvids (American Crow and Northern Raven), accipiters (Sharp-shinned Hawk and Cooper's Hawk) and falcons (American Kestrel and Merlin). Fig. 22 shows a comparison between kingbird-predator chases / predator observations for the above three groups of predators during 1991.

Corvids prey mainly on eggs and nestlings, kestrels mainly on fledglings and accipiters on adult kingbirds and on fledglings. If kingbirds are maximizing utility of effort, I would predict that the greatest number of chases after corvids should occur when there are eggs and small nestlings (Table 21); after falcons when there are fledglings and older

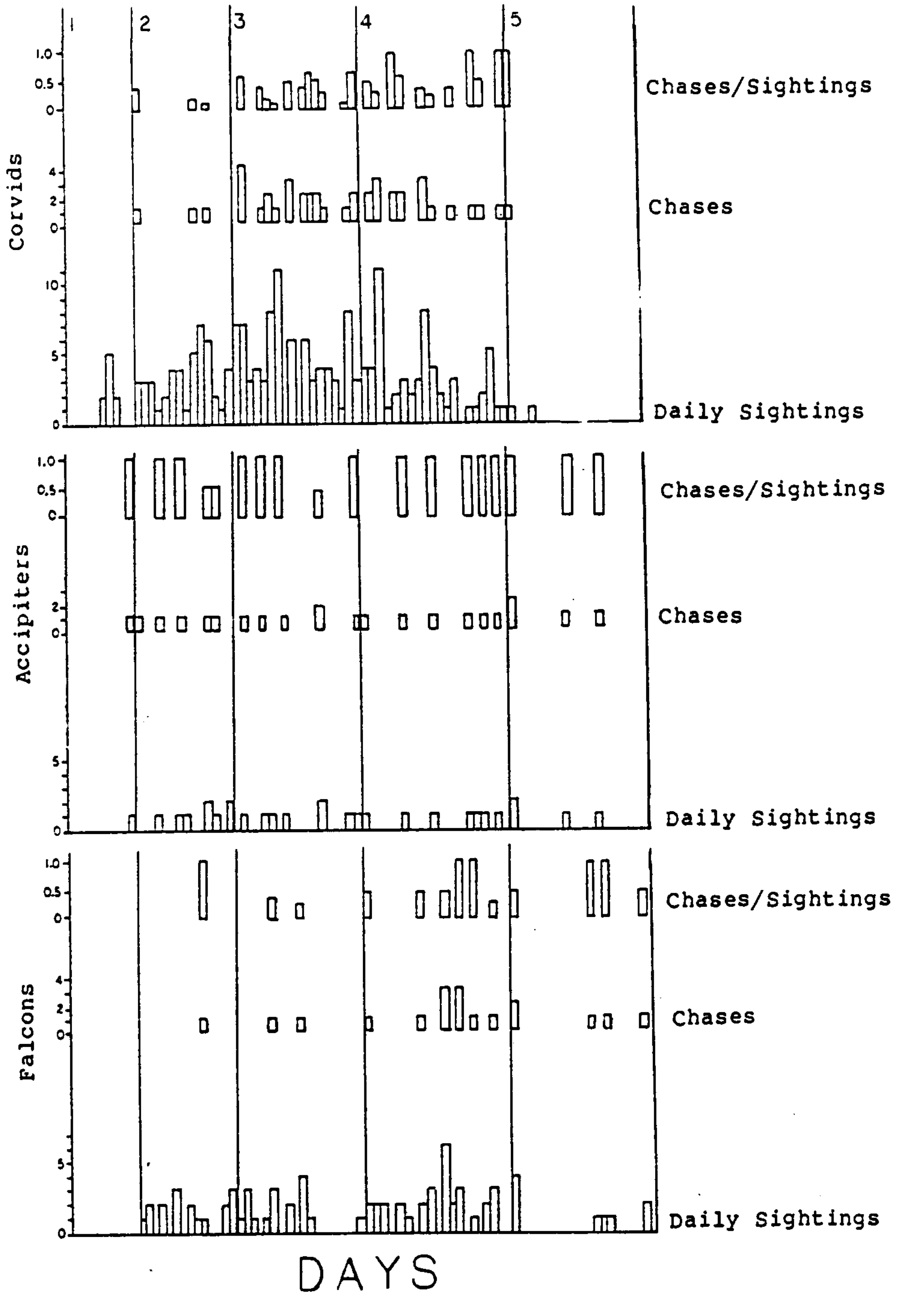


Figure 21. Daily sightings, chases by Eastern Kingbirds and chases/sightings of: corvids (American Crows and Northern Ravens); Accipiters and falcons (American Kestrels and Merlins). 1: Date of first Eastern Kingbird arrival; 2: first Eastern Kingbird nest found; 3: first Eastern Kingbird egg laid; 4: first Eastern Kingbird nestling hatched; and 5: first Eastern Kingbird fledgling.

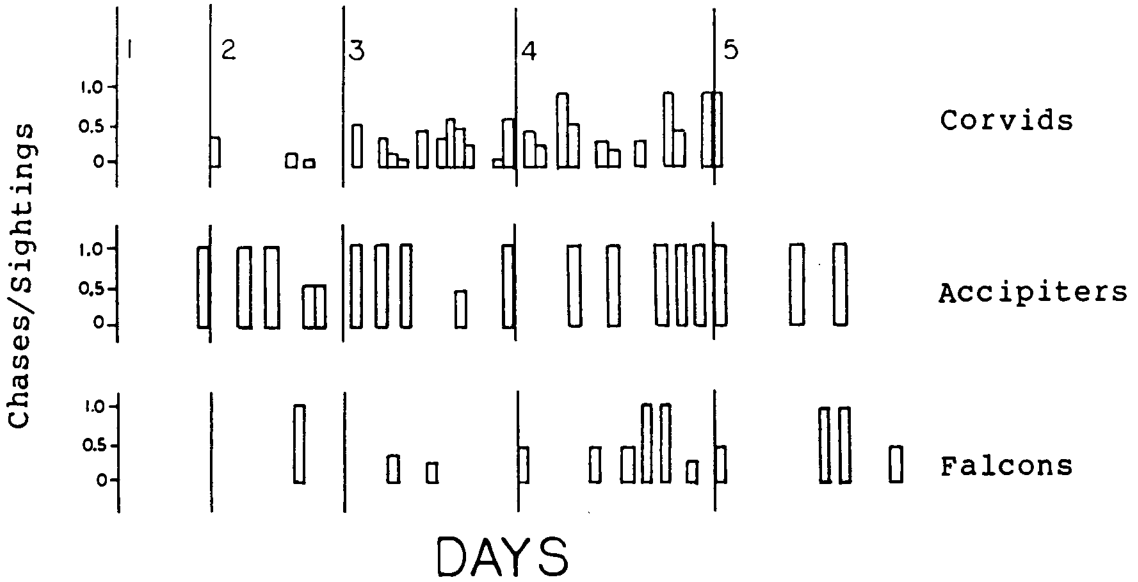


Figure 22. Chases/sightings per day for Eastern Kingbird encounters with corvids (American Crows and Ravens), Accipiters, and falcons (American Kestrels and Merlins). 1: Date of first Eastern Kingbird arrival; 2: first Eastern Kingbird nest found; 3: first Eastern Kingbird egg laid; 4: first Eastern Kingbird nestling hatches; and 5: first Eastern Kingbird fledgling.

Table 21. The number of American Crows and Northern Ravens seen and the number of chases by Eastern Kingbirds (Fig. 21A).

	First kingbird seen and nest building	Egg-Laying and nestlings
The number of crows and ravens seen but not chased	52	108[1]
The number of kingbird chases of crows and ravens	3	37

[1] X^2=91.0, $P<0.01$

nestlings about to fledge (Table 22); and accipiters should always be chased because they are always dangerous to the adults (Table 23). These predictions are confirmed by comparing the number of chases to the number of predator occurrences for the predicted times. Eastern Kingbirds chase specific predators when it is most beneficial.

Table 24 shows the effort in time and chase distance that kingbirds invest in pursuing predators. Measures are estimates, in some cases of small sample sizes, and so no statistics were performed on these data. Measures of initiation distance of chases show that most chases began when intruders were somewhere between 100 and 150 m away. "Others", such as sparrows, warblers, woodpeckers and meadowlarks, were chased when they were much closer (about 3 m) to the nest. I have seen chickadees, however, come as close as 0.5 m to a kingbird nest before being chased.

Kingbirds usually chased crows and ravens for about 200 m and frequently hit them (36 of 42 observed incidents). Chase distances were shorter for kingbird-accipiter chases, but chases were more intense, going from bush to bush with kingbirds calling and frequently diving at the predator. Mobbing by many species (usually Red-winged Blackbirds (Agelaius phoeniciusu) and Tree Swallows (Tachycineta bicolor) as well as kingbirds) occurred more frequently (4 of 7 chases) when accipiters were being chased and less frequently for other types of predator chases. Both kingbird parents left the nest to chase a crow or raven only if the predator was

Table 22. The number of American Kestrels and Merlins seen and the number of chases by Eastern Kingbirds according to nesting stage (Fig. 21C).

	Nest building and incubation	Nestlings and fledglings
Kestrels and Merlins seen but not chased	31	25[1]
Kingbird chases of kestrels and Merlins	3	15

[1] X^2=37.0, P<0.01

Table 23. The number of Sharp-shinned and Cooper's Hawks seen and the number of chases by Eastern Kingbirds according to nesting stage (Fig. 21B).

Kingbird nesting stage	Accipiters seen but not chased	Kingbird chases of accipiters
Nest building	3	4[1]
Incubation	3	5
Nestlings	1	6
Fledglings	0	4

[1] $X^2=0.4$, $P=1.0$, $B=0.8$

quite close to the nest, but often both parents left the vicinity of the nest to chase accipiters. Kingbird-kestrel chases were also shorter in duration than kingbird-crow chases, but were quite fast and the kingbird often could not catch up with the kestrel to hit it. Kingbird-magpie chases were not seen very often despite the presence of magpies in the study area and the fact that magpies preyed upon pseudonests. One pair of kingbirds nested within 200 m of a magpie nest with nestlings.

Predators will change direction or altitude when hit by a kingbird (Table 24). I have recorded three instances where crows and ravens were looking for a kingbird nest within 20-50 m of the nest and were repeatedly being hit by the kingbird parents. These pursuits and encounters lasted up to 20 min. In one instance (an eventually successful nest) four crows flew by within 10 m of the nest and worked in unison to draw the kingbird parents away from the nest. Of the three pairs involved in these encounters, one kingbird pair raised young to fledging.

Data in Table 25 are also estimates from small sample sizes, but document kingbird nest defense effort directed at specific predators over the nesting season. Crows and ravens appear to be intercepted farther from the nest and pursued for a greater distance when there are eggs and are allowed closer to the nest than when there are young in the nest. Kingbirds usually chase Accipiters for a consistant distance and chases are initiated the same distance from the nest regardless of

Table 24. Characteristics ($\bar{x} \pm$ S.D.) of Eastern Kingbird chases, 1989 to 1991. Distances (m) are estimates. (Sample size).

Initiation distance	Chase distance	Chase time	Hits [Mob][1]	Pursuit alters direction
Crows and Ravens				
146±133 (26)	192±138 (35)	53±47 (4)	36 [5] (42)	8 (19)
Accipiters				
157±140 (17)	155±106 (12)	125±116 (4)	2 [4] (7)	NA
Falcons				
115±96 (19)	87±58 (19)	-	2 (2) (19)	2 (4)
Magpies				
50 (1)	200 (1)	-	-	1 (1)
"Hawk-like"[2]				
400±141 (2)	197±87 (5)	23±23 (4)	6 (8)	keep flying
Others[3]				
3±4 (9)	12±16 (8)	<30 (16)	0 (16)	usually

[1] Mobbing by other kingbird pairs or other species.

[2] Northern Harrier (Circus cyaneus), Osprey (Pandion haliaetus), Red-tailed Hawk (Buteo jamaicensis) and Great Horned Owl (Bubo virginianus).

[3] Includes passerines such as Yellow-headed Blackbird (Xanthocephalus xanthocephalus), Black-capped Chickadee (Parus atricapillus), Song Sparrow (Melospiza melodia) and various warblers, etc.

Table 25. Initiation distance from the nest, distance of chase, and number of hits by kingbirds during nest defence. (Sample size).

	Initiation distance from the nest		Chase distance		Hits	
Corvids						
Nest building	-	(0)	73±68	(3)	-	(0)
Incubation	170±173	(11)	244±196	(11)	7	(11)
Nestlings	94±61	(11)	174±103	(14)	11	(14)
Fledglings	-	(0)	-	(0)	-	(0)
Accipiters						
Nest building	-	(0)	-	(0)	-	(0)
Incubation	117±122	(3)	125±106	(2)	1	(3)
Nestlings	111±99	(9)	160±42	(5)	0	(9)
Fledglings	50	(1)	150	(1)	0	(1)
Kestrels						
Nest building	-	(0)	-	(0)	-	(0)
Incubation	70±42	(2)	150	(1)	-	(0)
Nestlings	124±97	(17)	79±58	(16)	2	(16)
Fledglings	-	(0)	-	(0)	-	(0)

the age of nest contents. Kingbird chases of kestrels appear to begin farther from the nest when there are nestlings.

In summary: 1) At least one parent was in attendance at the nest, and usually both parents; 2) Noisy behaviour influences nest success-with both eggs and nestlings, parents should be quiet or relatively noisy at and in the vicinity of the nest; 3) Noisy behaviour is more successful in preventing predation near rather than far from the nest; 4) Noisy behaviour is correlated with habitat around the nest; 5) Predators were chased at a time and in a way which minimizes effort; 6) Flight distance of females varied with overhead visibility and how far the female could see from the nest; 7) Kingbirds approaching a crow model were more likely to lose nest contents to predation than kingbirds which did not approach the model; 8) Pseudonests near kingbird nests were preyed upon less often than control nests; 9) Kingbirds chased most intruding species; 10) Kingbirds destroyed eggs in pseudonests located near their nests; 11) Predators responded to kingbird nest defence in ways that reduced their hunting efficiency.

Discussion

Eastern Kingbird nest defence is effective. Kingbird nests survive better than do pseudonests in the same habitat (Chapter 2) and pseudonests near kingbird nests survive better than control nests but defence strategies differ with nest visibility, habitat, the predator confronted and depending upon whether there are eggs or nestlings in the nest.

During incubation, kingbird females spend most of their time feeding or on the nest, and males are often absent. When the female is incubating, she covers the light-coloured eggs. Hidden and open nests survive best during incubation and when approached, females flush earlier from visible nests than from hidden nests. Both strategies appear to be successful as there was no difference in fledging success between females which flush early and those that flush later as a predator approaches the nest. Females which stay on hidden nests do not give the location of their nests away to approaching predators: they rely on cover to hide them and their nests. Females flushing early from open nests also do not give away nest location as they flush too early for predators to find the nest, and they may be able to drive the predator away or at least redirect its search.

When there are nestlings, however, kingbirds with open nests have a greater survival of nestlings. Parents at this stage visit the nest but are not on the nest for long periods. They do not rely as much on hiding nestlings, but rather rely more on preventing predators from approaching the nest. An open nest has a sparse canopy overhead thereby allowing parents to see both the nest and predators approaching the nest from any direction.

I suggest that co-operative vigilance of parents is an important feature of kingbird nest defence and that kingbird nest defence is very effective in preventing predators from approaching and spending time in the vicinity of the nest. Co-operation between parents is vital to nest defence, and noisy behaviour is the communication which allows co-operative vigilance. There is always, with the exception of chases of dangerous predators, one parent near the nest, and usually both parents. Whenever an incubating female leaves the nest, she calls and often leaves only when the male responds. During conflicts, a female often calls from the nest, presumably giving the male information on the safety of the nest. The parents work as a team to distract and harass predators, calling the entire time. Parents often patrol the vicinity of the nest, changing prominent perches frequently and calling, the other parent responding with a call. This calling may be an "all is well" call, which alerts the other parent to the situation at the nest and the location of the calling parent.

The noisy behaviour which I observed at and in the vicinity of the nest helps in preventing nest predation and is most effective when it occurs close to the nest. There are two successful strategies for noisy behaviour: being either noisy or quiet at and around the nest. Noisy behaviour at the nest is negatively correlated to the percentage of field and shrubs in the nest vicinity. The more perches there are available, the quiter the parents are at the nest, suggesting that parents are calling to determine location of the other parent, and that location can be determined without calling in either an open area, or an area where there are several observation perches. Parents which exhibit intermediate behaviour may be those who call, but receive no response from the partner, perhaps indicating poor co-operation between the pair, which could result in the eventual predation of the nest.

Kingbirds direct some noisy and conspicuous behaviours towards competitors and predators. Kingbirds fly high above the area around the nest, tumbling and calling in a tumble-flight (Bent 1942, Smith 1966); a very conspicuous behaviour. The tumble-flight is often performed after a successful chase, perhaps to advertise the presence of a pair of kingbirds ready and able to harass. Unmated males also perform tumble-flights frequently, perhaps to attract the attention of females and male competitors.

Noise at the nest may attract of the attention of predators, but if kingbirds are effective in keeping predators from the nest, the latter may not have enough time to find the kingbird nest. The noise may also be a warning to predators that there are kingbirds present. Some predators may avoid being hit and harassed by kingbirds: the reward of a clutch of eggs or some nestlings may be too small for a potential loss of feathers and at least a great deal of harassment.

Nest defence can be expensive in terms of energy and risk. Kingbirds, however, defend selectively against predators, doing so when it is most beneficial. They chase nest predators only when nesting, egg predators mostly when they have eggs, predators of young mostly when they have nestlings or fledglings, and always chase predators that are dangerous to adults. The distance and duration of the chase also varies with the type of predator pursued. Predators respond by leaving the area, changing direction or altitude, flying faster, or in some cases by intensifying the search for the nest. Kingbird nest defence is also dangerous. I have seen a Merlin almost catch a mobbing kingbird, and I suspect that some parents were lost to predators that ate the defended nest contents.

Incubating kingbirds which approached closest to a model crow (hitting or diving at it) were most likely to lose their nests to predators. Blancher and Robertson (1982) found that Eastern Kingbirds, which approached researchers closest in repeated trials, were most likely to be successful at fledging young. McLean et al. (1986), however, found that American Robins that showed the strongest responses to predators were also those which subsequently lost nests to predation. Kingbirds in this study were responding to the single exposure of a crow model as a potential predator which they had not encountered before. Kingbirds often dive at and hit a live crow only when it flies, and will usually call from a distance and mob with other birds when the crow is perched. The kingbirds which attacked the model often did so for most of the trial period. If they behaved in the same way towards the predator which eventually found and preyed upon their nest, they may have worn themselves out, or given the location of the nest away to accompanying crows. As corvids usually hunted in groups, kingbirds which observed and called, rather than hitting the closest perched crow, may have been able to detect the presence of other crows in the vicinity and counter the movements of these other crows more effectively.

Predation is the single most common cause of nest loss for kingbirds in Creston, but kingbirds can drive predators away from nests only in co-operation with a mate. Kingbirds which responded most vigorously may also have been inexperienced birds. Kingbirds may learn which predators to chase, and how to defend effectively against predators. I have seen an immature kingbird (out of the nest for about 3 weeks) joining its parents in chasing a kestrel. I have also seen kingbirds repeatedly chasing Ospreys and Belted Kingfishers (Ceryle alcyon), which pose no known threat to kingbird nests, and I suspect these were inexperienced birds.

Kingbird nest defence behaviour involves not only chasing seemingly inoccuous birds from the vicinity of the nest (as described above) but may also involve destruction of other bird's nests. These behaviours are also effective in defending the nest. I have seen Yellow Warblers (Dendroica petechia) and Cedar Waxwings (Bombycilla cedrorum) steal nesting material from kingbird nests under construction and I have seen kingbirds chasing a Northern Oriole (Icterus galbula), which had been pecking at eggs in a pseudonest 5 m from a kingbird nest; a potential danger to the kingbird eggs. Kingbirds chase Western Meadowlarks (Sturnella neglecta). Meadowlarks can destroy eggs (Schaeff and Picman 1988), but they may be pose little danger to kingbird nests. If predators search more in areas where birds and nests are concentrated (e.g. Tinbergen 1953, Weatherhead and Norman 1977, Page et al. 1983), it is probably beneficial for kingbirds to destroy nests and chase other birds from the vicinity of their nest. Some birds may choose to nest in close proximity to kingbird nests to benefit from kingbird nest defence. I have seen two instances where Cedar Waxwings have nested within 5 m of a kingbird nest, succeeding in building a nest only when the kingbird female was too busy incubating to continue chasing them away. Two nests in close proximity may attract more predator attention than one kingbird nest.

Kingbirds that nest in close proximity to each other may benefit from mutual vigilance and nest defence. However kingbirds chase other kingbirds vigorously. When neighbouring kingbirds both chase the same predator, they often chase each other on the return flight, then give tumble-flights. McKitrick (1990) found that both Eastern Kingbird males and females raised young that were not genetically their own, which suggests that it is beneficial for each parent to keep other kingbirds (especially of the same gender) from the vicinity of the nest.

The noisy, conspicuous behaviour of kingbirds is effective in preventing predators from approaching a nest, in driving some predators from the nest and in making nest searching inefficient for predators in the vicinity of a pair of kingbirds. Some predators may learn to cue in on kingbird behaviour to find nests, however. Behaviour at the nest is influenced by nest visibility, habitat (Chapter 4), age of nest contents, and perhaps by the experience of the parents. Chases of seemingly innocuous species may be an efficient means of preventing interference at the nest by these species or reducing attraction of predators to concentrations of nests or individuals.

Chapter 4: Habitat and nest defence

Introduction

Several studies have shown that birds do not nest randomly: they choose nesting sites and nesting habitat (MacKenzie and Sealy 1981, Page et al. 1985, Reese and Kadlec 1985, Ehrhart et al. 1986, Bekoff et al. 1987, 1989, Leonard and Picman 1987, Marzluff 1988, McCallum and Gehlback 1988, Rands 1988, Warkenten and James 1988). While some habitat choices reduce the probability of nest predation (Blancher and Robertson 1985, Belles-Isles and Picman 1986, Marzluff 1988, Rands 1988, Ludvig et al. 1991), others do not (Storaas and Wegge 1987).

As Eastern Kingbirds avoid nest predation, at least in part, by chasing predators from the vicinity of their nests (Chapter 3), they may choose to nest in habitats where it is easier to spot approaching predators, as has been noted in other species (Balda and Bateman 1972, Clark et al. 1983, Burger and Gochfield 1985, Finch 1983, Page et al. 1985, Marks 1986, Santana et al. 1986) or to chase intruders from the nest in other habitat types (Belles-Isles and Picman 1986).

Nest predation, however, is only one factor that affects nesting success. Parents may have to choose a nest site based on several considerations and there may be conflicts between considerations of nest defence (e.g. hiding a nest, detecting and chasing predators) and other concerns such as locating adequate food for nestlings, assuring safety of fledged young, and thermoregulation of nest contents.

Eastern Kingbirds are insectivores, and parents which choose to nest where insects are abundant may spend less time foraging and more time in vigilance about the nest than do parents which nest in an area where insects are less abundant or are located farther from the nest. Open terrain, in which it is easier to spot and chase nest predators, may also be a habitat with reduced insect abundance as compared to wetter, shrubbier and less open habitats where it is more difficult to see and chase predators. The time spent by the parents on or in the vicinity of the nest will influence vigilance at the nest and may influence predation at the nest (Chapter 3).

Thermoregulation of the nestlings is also an important factor in nesting success (Ricklefs and Hainsworth 1969, Balda and Bateman 1972, Clark et al. 1983, Burger and Gochfield 1985, Finch 1983, Walsberg 1985, Bekoff et al. 1987) and some nest site choices may accomodate temperature moderation at the nest better than others. Females may compensate for poor nest sites by brooding on the nest longer, but the amount of time parents spend on the nest may increase nest predation (Chapter 3). Eastern Kingbird females in this study brooded young at least until 6 days after hatching and longer if the weather was wet and cold. Kingbird parents also spent time at the nest shading young from direct sun during hot weather at nests where no shade was available. Additional time spent by parents in some habitats incubating and brooding young could attract predators, increase vigilance, or add to the camouflage of the nest (Chapter 3). A nest which is situated where predators can be readily spotted or a nest which is quite hidden may not be an adequate nest for the thermoregulatory needs of the nest contents.

I chose to examine nest predation in Eastern Kingbirds with respect to characteristics of their nest sites and the habitat surrounding those nests. The relationships between kingbird parental behaviour and nest visibility and nest site and nest habitat were also studied.

Methods

Habitat characteristics

The percentage of water, field, shrubs, marsh and trees within a 100 m radius of each Eastern Kingbird nest was estimated between mid-July and August 1988-1991, after the kingbirds had migrated. The distance to water and whether the nest was located directly over water or directly over land were also recorded. Nest visibility (overhead and lateral) and fledging success were measured as described in Chapter 2, and behaviour at the nest was measured as described in Chapter 3.

Nest site characteristics

During 1988-1991, several nest site characteristics were measured as follows: 1) **nest height** and 2) **tree height**: nest height was measured in 1988 to 1991, and tree height in 1988, 1990 and 1991; 3) **nearest tree**: the nearest tree to the kingbird nest was measured in 1988, 1990 and 1991. A plant had to be taller than 10 m to qualify as a tree; 4) **nearest perch**: the nearest plant greater than 2 cm in diameter, that was taller than the kingbird nest height; 5) **number of stems**: the number of stems within a 1 m radius of the nest was counted as a measure of plant density. A stem was defined as a shrub or tree that was as tall or taller than the nest height and with a diameter greater than 1 cm.

Results

Habitat characteristics

Successful kingbird parents nested in areas with less percentage field surrounding the nest than parents which lost either eggs or nestlings to predators although the comparison was not significantly different (successful parents nested in 31% field; unsuccessful parents in 41% field, Table 26). Other habitat characteristics did not differ between successful parents and parents which lost nest contents to predators although kingbirds that successfully fledged young tended to nest in areas with about 23% water (as opposed to unsuccessful parents that nested in areas of only 19% water). The cubic spline of percentage water shows that the probability of survival increases from 0 to 20% and then decreases. Past 50% water, standard errors are too wide to determine the accuracy of the function (Fig. 23c). The cubic spline of percentage field indicates that the probability of survival decreases with an increase in percentage field surrounding the nest (Fig. 24c).

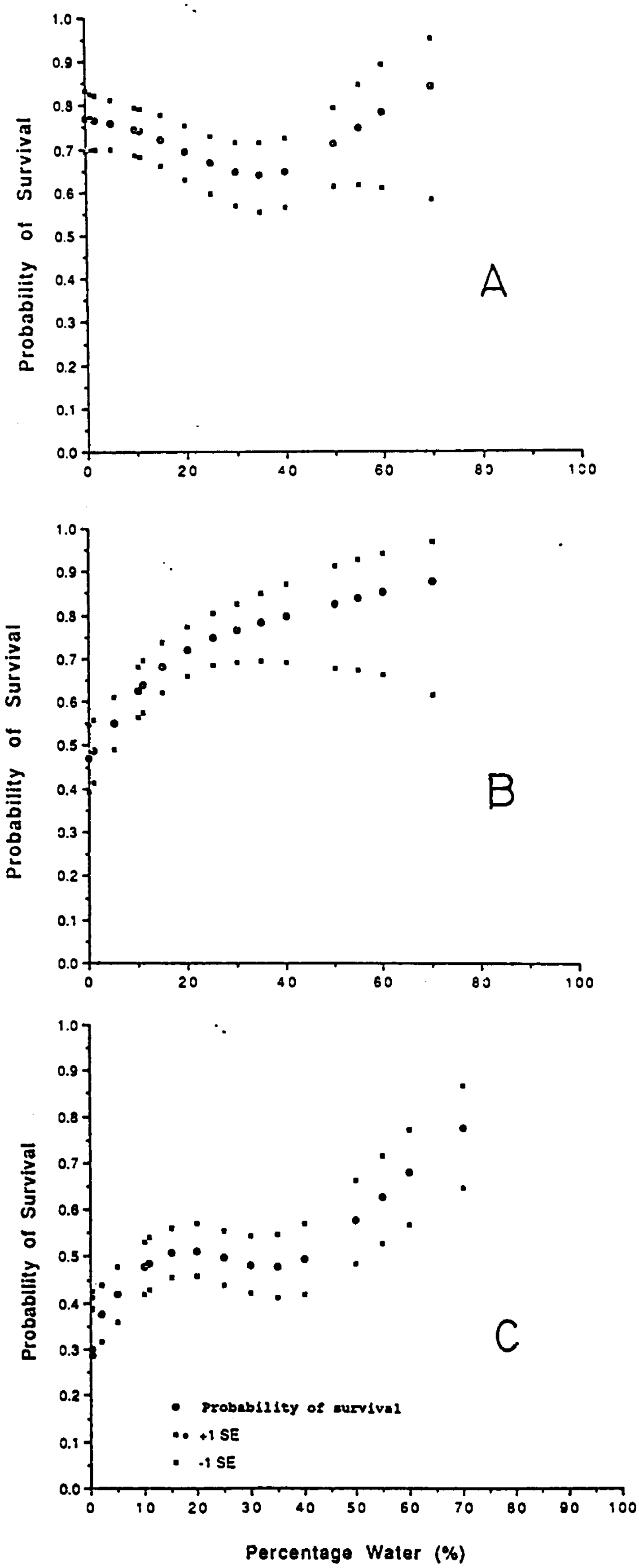
The influence of habitat upon nest predation, however, differs depending upon whether there are eggs or nestlings in the nest. A comparison of means shows that kingbirds that lost nestlings to predators were those nesting in drier areas (higher percentage field (47% versus 31-37%) and lower percentage water (12% versus 21-23%)) than either

Table 26. Habitat characteristics and nest success in Eastern Kingbirds.

	Successful			Preyed Upon	
	N	$\bar{x} \pm$ S.D.		N	$\bar{x} \pm$ S.D.
Percentage water[1]	54	23.1 ± 19.4		74	18.8 ± 19.1
		M.W.U.=2.2	P=0.14		B=0.1
Percentage field	54	31.0 ± 28.3		74	40.8 ± 31.5
		M.W.U.=3.3	P=0.07		B=0.2
Percentage shrub	54	22.5 ± 18.5		74	23.0 ± 18.5
		M.W.U.=0.0	P=0.80		B<0.1
Percentage marsh	54	8.2 ± 20.8		74	7.8 ± 19.1
		M.W.U.=0.0	P=1.00		B<0.1
Percentage trees	54	12.9 ± 17.1		74	8.7 ± 15.0
		M.W.U.=1.8	P=0.20		B=0.2
Distance to water (m)	41	28.1 ± 52.8		60	37.2 ± 63.1
		M.W.U.=1.8	P=0.20		B<0.1

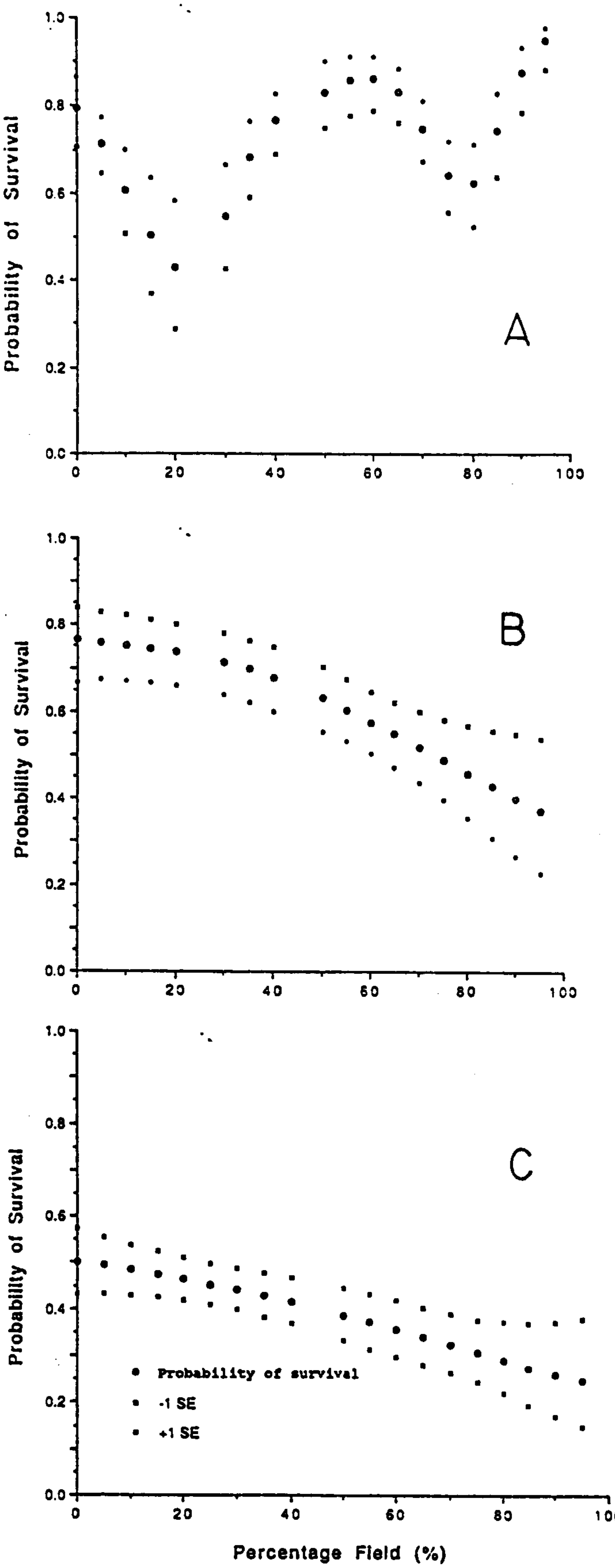
[1]Percentages are estimates of habitat within a 100 m radius circle around Eastern Kingbird nests.

Figure 23. Cubic splines (giving the probability of survival of nest contents until fledging) of percentage water within 100m of the Eastern Kingbird nest for nest contents that survive A) incubation; B) the nestling stage and C) for all nests combined.



Probability of Survival
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
20
40
60
80
100
A
Probability of Survival
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
20
40
60
80
100
B
Probability of Survival
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
C
Probability of survival
+1 SE
-1 SE
Percentage Water (%)

Figure 24. Cubic splines (giving the probability of survival of nest contents until fledging) of percentage field within 100 m of an Eastern Kingbird nest for nest contents during: A) incubation; B) the nestling stage (1-6 days old) and C) for incubation and the nestling stage combined.


Probability of Survival
A
B
C
Probability of survival
-1 SE
+1 SE
Percentage Field (%)

parents that lost eggs or parents that fledged young (Table 27). Cubic splines confirm that there is a different relationship between survival of eggs and nestlings with respect to percentage of water and open field that is present near the nest. The cubic spline of percentage water in the vicinity of the nest during incubation shows a negative relationship until about 50% water and a possible increase in survivorship with a greater percentage of water (Fig. 23a). The standard errors, however, could allow for a zero slope, showing no relationship. The cubic spline for kingbird nestlings and percentage water shows that from 0 to 25% water, there is an increase in survival which then levels out, as the percentage water near the nest increases (Fig. 23b). Standard errors allow only for a positive relationship until about 25% water on the territory when the relationship is no longer well defined. Apparently, to avoid nest predation it is beneficial to have some water in the nest vicinity, especially when there are nestlings. The cubic spline for percentage field in the vicinity of the nest during incubation shows a complex relationship which, although a positive relationship overall, is more difficult to interpret (Fig. 24a). It appears that incubating parents nesting in all field, about 60% field and no field, avoid nest predation equally as well. The standard errors allow for no other relationship. The cubic spline for percentage field shows a negative relationship when there are nestlings; the more field surrounds the

Table 27. Nest habitat characteristics of Eastern Kingbirds preyed upon as eggs, nestlings and for those which fledged.

Eggs		Nestlings		Fledged	
N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.
Percentage water[1]					
32	21.8 ± 18.9	29	12.3 ± 16.9	54	23.1 ± 19.4
		K.W.H.=8.1 P=0.02			
Percentage field					
32	37.0 ± 29.3	29	47.6 ± 31.9	54	31.0 ± 28.3
		K.W.H.=5.5 P=0.06 B=0.5			
Percentage shrub					
32	21.9 ± 18.8	29	22.6 ± 17.9	54	22.5 ± 14.5
		K.W.H.=0.05 P=1.0 B=.01			
Percentage marsh					
32	7.5 ± 19.0	29	9.7 ± 21.5	54	8.2 ± 20.8
		K.W.H.=0.3 P=0.9 B=0.1			
Percentage tree					
32	8.2 ± 15.2	29	9.2 ± 15.4	54	12.9 ± 17.1
		K.W.H.=2.4 P=0.3 B=0.2			
Distance of nest to water (m)					
26	20.3 ± 38.4	25	48.4 ± 46.1	41	28.1 ± 52.8
		K.W.H.=0.8 P=0.02			

[1]Percentages are estimates of habitat within a 100 m radius circle surrounding Eastern Kingbird nests.

nest, the more likely the nest will be preyed upon (Fig. 24b).

There is a negative correlation, which approaches significance, between the number of crows seen during 90 min watches (see Chapter 3) and the percentage of water around the nest (incubation: r_s=-0.34, n=22, P=0.1, B=0.38; young nestlings; r_s=-0.37, n=18, P=0.09, B=0.32). Incubating females nesting in wetter areas spend more time on the nest (r_s=0.45, n=22, P=0.03) and the closer the nest is to water, the more visits incubating parents make to the nest (r_s=-0.37, n=22, P=0.09, B=0.38). The more open field there is around the nest, the quieter the parents are: the number of noisy visits to the nest (Chapter 2) and the percentage field around the nest are negatively correlated when nestlings are young (1-6 days old) (r_s=-0.40, n=18, P=0.07, B=0.39) and number of noisy perches and percentage field are also negatively correlated (r_s=-0.40, n=22, P=0.06, B=0.47).

Nest site characteristics

Nest height did not significantly differ between nests which were preyed upon and nests from which nestlings fledged (Table 29), nor between nests of parents losing eggs, nestlings or those fledging young, although nest height was least in those losing eggs to predators (Table 28). The cubic spline of nest height indicates that there may be a positive relationship between nest height and the

Table 28. Nest site characteristics and nest success in Eastern Kingbirds.

	Successful			Preyed Upon	
	N	$\bar{x} \pm$ S.D.		N	$\bar{x} \pm$ S.D.
Nest height (m)	52	2.67 ± 2.28		69	2.26 ± 1.36
		M.W.U.=0.9	P=0.3	B=0.2	
Nest tree height (m)	33	4.59 ± 2.05		50	4.32 ± 2.44
		M.W.U.=1.3	P=0.3	B=0.1	
Nearest tree (m)	47	2.82 ± 4.15		63	4.28 ± 8.56
		M.W.U.=1.7	P=0.2	B=0.2	
Nearest perch (m)	34	0.56 ± 1.00		52	0.46 ± 1.14
		M.W.U.=2.9	P=0.09	B<0.1	
Number of stems	36	21.5 ± 33.7		53	23.9 ± 31.3
		M.W.U.=0.2	P=0.7	B=0.1	

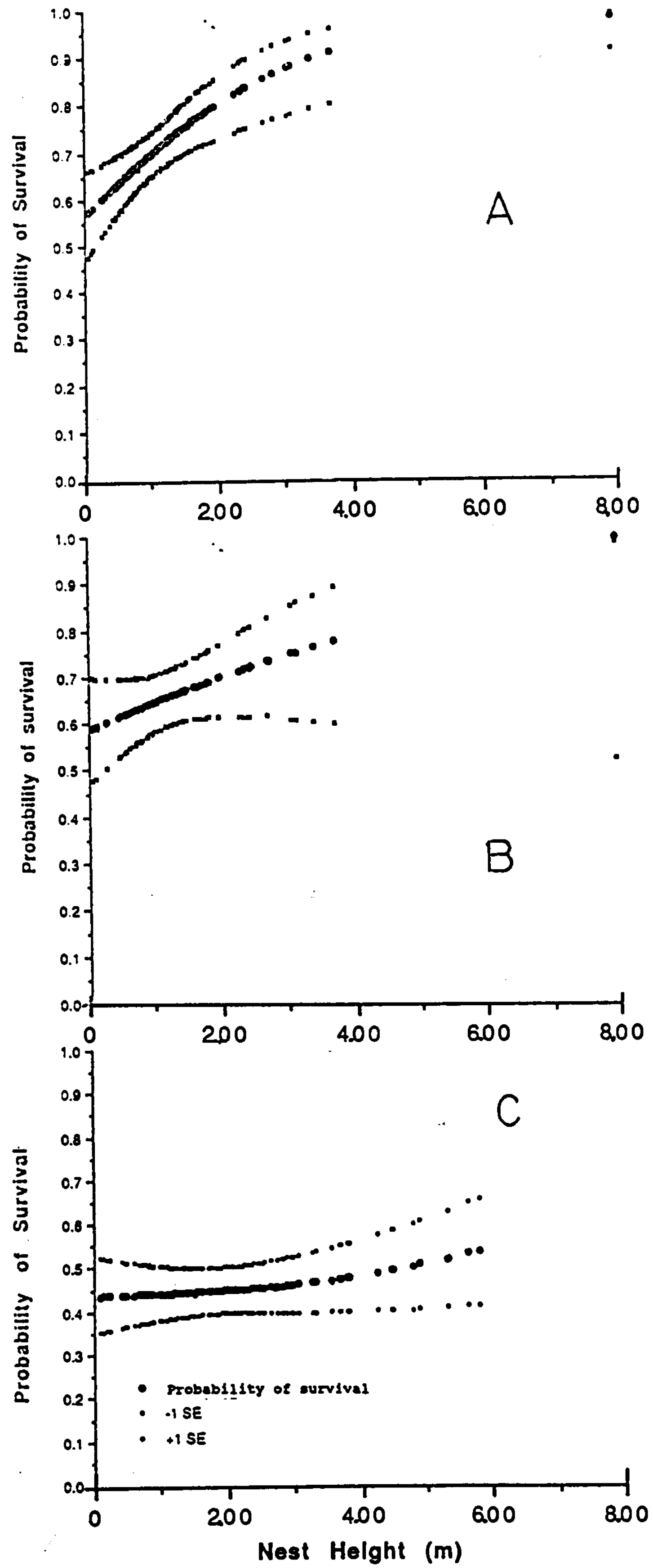
Table 29. Nest site characteristics of Eastern Kingbirds preyed upon as eggs, nestlings and those which fledged.

Eggs		Nestlings		Fledged	
N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.	N	$\bar{x} \pm$ S.D.
Nest height (m)					
31	1.9 ± 1.1	27	2.3 ± 1.3	52	2.7 ± 2.3
		K.W.H.=3.2	P=0.2	B=0.3	
Nest tree height (m)					
22	4.3 ± 2.5	22	3.9 ± 2.1	33	4.6 ± 2.1
		K.W.H.=2.4	P=0.3	B=0.1	
Nearest tree (m)					
29	2.7 ± 3.1	27	4.4 ± 5.0	47	2.8 ± 4.1
		K.W.H.=3.4	P=0.2	B=0.2	
Nearest perch (m)					
23	0.6 ± 1.4	23	0.1 ± 0.2	34	0.6 ± 1.0
		K.W.H.=5.7	P=0.06	B=0.5	
Number of stems					
22	22.5 ± 29.4	24	23.1 ± 31.4	36	21.5 ± 33.7
		K.W.H.=0.3	P=0.9	B<0.1	

probability of fledging (Fig. 25c). Logistic regression shows no relationship between nest height and fledging success or failure (logit p(success)=-0.58+0.003x; X^2=1.46, n=121, P=0.22, B<0.1). Cubic splines of nest height during incubation and when there were nestlings indicate that there is a positive relationship between nest height and probability of fledging (Fig. 25b). Logistic regression shows that there is a non-significant, positive relationship between nest height and nesting success and nesting failure (equations are the same for incubation and nestlings: logit p(success)=0.30+0.008x; X^2=2.6, P=0.10, B<0.1). These results indicate that there may be a weak positive relationship between nest height and fledging success, but this relationship was not significant.

Other nest site measures (nearest tree, nearest perch and number of stems) did not differ significantly between successful and preyed upon parents (Table 28). There was also no difference in the above measures among parents that lost eggs, lost nestlings or fledged young (Table 29). The nearest perch to the nest (nearest stem taller than the nest: see Methods), however, was closer in the case of preyed upon parents than in the case of successful parents (Table 28) and appeared to be greater in nest sites where nestlings were lost to predation. This probably indicates that the nest sites of preyed upon parents were located nearer to trees and shrubs than those of successful parents.

Figure 25. Cubic splines (giving the probability of survival of nest contents until fledging) of nest height of Eastern Kingbird nest contents during: A) incubation B) the nestling stage (1-6 days old) and C) for incubation and the nestling stage combined.



A
B
C
Probability of Survival
Probability of survival
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2.00
4.00
6.00
8.00
Probability of survival
-1 SE
+1 SE
Nest Height (m)

Nests that are located over land are more visible overhead than are nests located directly over water and nests located over water are lower than are nests located over land, despite the fact that there is no difference in height of nest trees over water and over land (Table 30). The distance that the female can see from the nest (either farther than 100 m or farther than 300 m from the nest) is greater from nests located directly over land than for nests located over water (>100 m; water: $\bar{x}$=10.76±0.92, n=25; land: $\bar{x}$=1.8±1.0, n=52; M.W.U.=292.0; P=0.0001)(>300 m; water: $\bar{x}$=0.68±0.85, n=25; land: $\bar{x}$=21.4±0.9, n=52; M.W.U.=377.5; P=0.0019).

Table 30. Characteristics of Eastern Kingbird nests located over water and those located over land.

	Over water		Over land	
	N	$\bar{x}$ ± S.D.	N	$\bar{x}$ ± S.D.
Nest height (m)	40	2.03 ± 1.22	58	2.87 ± 2.23
		M.W.U.=850	P=0.03	
Nest tree height (m)	25	4.84 ± 2.69	55	4.32 ± 2.12
		M.W.U.=609	P=0.4	B=0.2
Nearest tree (m)	37	2.68 ± 0.30	57	3.35 ± 4.08
		M.W.U.=996	P=0.6	B=0.3
Nearest perch (m)	27	0.28 ± 0.35	55	0.55 ± 1.17
		M.W.U.=731	P=0.9	B=0.3
Number of stems	28	20.6 ± 32.0	58	22.2 ± 32.0
		M.W.U.=767	P=0.7	B<0.1
Percentage shrub	43	26.6 ± 17.3	59	20.3 ± 18.9
		M.W.U.=971	P=0.05	
Percentage trees	43	8.1 ± 11.9	59	11.9 ± 18.3
		M.W.U.=1184	P=0.5	B=0.2
Clutch size	39	3.4 ± 0.8	47	3.6 ± 0.6
		M.W.U.= 806	P=0.3	B=0.3
Number of fledglings per nest	41	1.0 ± 1.3	56	0.9 ± 1.5
		M.W.U.= 1038	P=0.3	B<0.1
Overhead visibility (%)	40	37.7 ± 35.9	56	54.1 ± 37.8
		M.W.U.= 851	P=0.04	

Discussion

Nesting habitat and nest site characteristics influence the probability of nest predation in Eastern Kingbirds. This influence differs depending on whether there are eggs or nestlings.

The relationship between the presence of water (20% water appears to be ideal) in the vicinity of the nest and nest predation is most marked when there are nestlings, whereas the presence of open field is most influential during incubation (no open field or greater than 60% field is most desirable). Starvation of nestlings in drier areas is not responsible for this difference as there is no relationship between the number of young fledged per successful nest and the amount of water in the area. A relationship would be expected if starvation were responsible for the difference noted (as kingbirds are insectivores and insects are often more abundant near open water).

There may be a conflict between providing food for nestlings and being vigilant at the nest; a parent that can forage close to the nest may be able to spend more time defending the nest or being vigilant (e.g. Martindale 1982). Blancher and Robertson (1987) also found that Western Kingbirds (Tyrannus verticalis) nesting in areas with a high biomass of insects, spent a shorter time between foraging flights and a shorter time between nestling feeds. In fact, the amount of time kingbird parents spent at the nest or in the vicinity of the nest in my study was partly determined by the amount of water in the vicinity of the nest: incubating kingbird females spent longer on the nest (i.e. made fewer trips from the nest) and parents spent more time closer to the nest in wet areas than in dry areas. This may explain why parents with nests located in relatively wet areas were more likely to fledge young than were parents nesting in drier areas: they may have spent more time being vigilant. In the my study, there were fewer corvids in wet areas and nests were more hidden there than in dry areas. If fewer predators fly over a nest, then the chances of the nest being discovered are reduced.

Habitat around the nest influences nest visibility and this in turn influences nest predation (Chapter 2). Open field around a nest, however, can be advantageous in preventing nest predation during incubation because predators can be spotted more readily. In contrast to parents with nestlings, incubating parents make fewer visits to the nest and the incubating female adds camouflage to nest and eggs. Nests in open areas were also more likely to have greater overhead visibility, which probably allows females on the nest to spot approaching predators. When there are nestlings, however, activity at the nest is more obvious and it may attract predators (Chapter 3). The greater number of predators sighted in drier areas (areas with comparatively more open field) may explain why nest predation is greater in these areas when there are nestlings. Nests in drier areas were also more visible from the side; this may result in greater nest predation during the nestling stage (Chapter 1).

Moderation of air temperature around the nest may also influence nest predation. Blancher and Robertson (1985) found that Eastern Kingbird nests over water were lower in height than nests over dry ground and that air temperature was moderated in nests located directly over water. Nest height of kingbirds in this study was also lower over water than over land despite the fact that there was no difference in nest tree height over water and over land. Blancher and Robertson (1985) also found that kingbird parents with nests low over water were more efficient foragers. Kingbird parents may be able to spend less time incubating, brooding or hunting and more in vigilance if their nests are over water. I have watched kingbird parents (probably females) shading young from direct sunlight on days when the temperature was in excess of 30°C in nests with little cover located in open fields. I have also seen the parent that was shading the nest intercept food brought by the other parent that was meant for the young, (I have never seen courtship feeding in Eastern Kingbirds). The interception of food and the subsequent struggle (although brief) between the parents at the nest suggests that there may be an energetic cost involved in shading the young. The costs may be immediate in terms of acquiring food, and in terms of decreased vigilance by either of the parents. The presence of the parent shading the nestlings may attract predators, especially since these nests are more likely to be open. Parents call less in open areas, however, implying that cooperative vigilance may be easier and require less effort in open areas. Parents with an exposed nest in an open field not only encountered more predators (although they were able to spot incoming predators more readily) but may have been forced to moderate temperature changes by their behaviour rather than relying on cover or temperature moderation over water. If they are not located near an abundant source of food, these parents may pay an energetic cost which may be paid at the expense of vigilance at the nest.

Fledglings may have habitat requirements which differ from those of eggs and nestlings. Kingbird nestlings are quiet, but fledglings become quite vocal within a day of leaving the nest. Fledglings did not appear to rely on cover to hide, and often stayed together for the first few days. Some groups of fledglings often left the vicinity of the nest altogether, implying that nest site choice may not be a strategy for avoiding predation of fledglings. Habitat requirements with respect to visibility and food sources may change when young fledge. If parental vigilance and defence vigour remain high, then it may be a priority for fledglings to be near readily available food sources rather than near concealing cover. Fledglings often eat fruit, and their moving away from the nest site may be an attempt to locate red-osier dogwood, blue elderberry (Sambucus cerulea) and other shrubs which may not play a role earlier in the breeding season. I have seen independent young being chased from the home area by parents, which may imply that resources are limited, although other explanations are equally plausible.

Nest height may influence nest defense. Parents with nests located lower over water probably benefitted from moderation of air temperature extremes, but there was also a suggestion that greater nest height could also be a benefit. It appears that kingbirds nesting in open situations may locate their nests just above the surrounding vegetation. Mayfield (1952) found that Eastern Kingbirds that were offered a variety of nest platforms tended to nest just high enough to be above the surrounding vegetation. Although mammals were not major predators in this study, nests that are higher off the ground may discourage mammalian predators from reaching them. Such nests allow a greater view of the surrounding area and thus better interception of predators. In general, however, kingbirds in open habitat tend to nest just above the surrounding vegetation.

The benefits of having shrubs around the nest are difficult to assess because they play such a variety of roles in the overall kingbird nesting strategy. They obscure the nest (and the visibility from the nest), they provide perches for greater vigilance (and hide parents from each other), and are a source of fruit for parents and young, especially when fledglings are beginning to feed themselves. Although there is a correlation between the amount of water in an area and the amount of shrubs, none of the ways in which I chose to assess shrub importance revealed a significant relationship, but I suspect there is an important, but complex relationship.

There appears to be a conflict between choosing a nest site which on the one hand allows both early detection of approaching predators and on the other hand protection from the elements over the entire time that kingbirds are tending eggs, nestlings and fledglings. There may be no ideal kingbird nest sites: several combinations of factors may facilitate efficient vigilance behaviour, temperature moderation, and foraging requirements. Parents may compensate for a lack of temperature moderation, or a lack of visibility, or may fly further to find food, but they may pay a cost for these compensations. While nest site choice is complex and more than one strategy may be successful, kingbird parents which choose nest sites where vigilance at the nest can be maintained during the entire nesting effort, have the greatest chance of preventing nest predation.

Chapter 5: Nest defence in relation to nesting stage and response of Eastern Kingbird parents to repeated model presentations.[1]

Introduction

Should parent birds risk more to defend young than they risk to defend eggs? Nest defence should increase with the age of the young as older young are more valuable (Trivers 1972, Dawkins and Carlisle 1976, Maynard Smith 1977). Some studies show this effect, but Knight and Temple (1986a) suggested that the increase in nest defence shown by parents in these studies could be explained by the experimental situation positively reinforcing nest defence behavior of the parents. Montgomerie and Weatherhead (1988) reviewed the nest defence literature and suggested that nest defence increases with the age of the young despite the effects of positive reinforcement. My study was designed to determine, for Eastern Kingbirds, whether: (1) parents habituate in the manner suggested by Knight and Temple (1986a); and (2) nest defence is greater for young than for eggs.

[1]This chapter has been published in the Auk vol.111

Methods

The study was conducted from 3 June to 16 July 1987. A taxidermic mount of an American Crow perched on a 1-m-high perch was placed 5 m from an active kingbird nest. A speaker used to broadcast crow calls was placed 20 cm below the model crow. I hid in a blind located at least 10 m from the model, and I pulled on a nylon string attached to the model to simulate movement of a live crow. Each observation period consisted of 6 min of calls followed by 4 min of silence. Scoring of the kingbirds' response to the presentation of the crow model followed Blancher and Robertson (1982): (1) silent on a perch; (2) on perch and called; (3) hovered over model; (4) dove at model; and (5) hit model. The most aggressive response during the observation period from each pair of kingbirds was scored.

The model was presented to three groups of parents. In group A, the model was presented only once when there were young in nest (11 broods with chicks 1-6 days old; 1 brood with 9-day-old chicks). In group B, the model was presented twice: once when there were eggs (1-6 days old) in nest and once when there were young (1-6 days old) in nest. In group C, the model was presented three times: once when the nest was complete but did not contain eggs; once when there were eggs (1-6 days old) in nest; and once when there were young (1-6 days old) in nest.

When a kingbird nest was located, the nesting pair was assigned randomly to an experimental group. Only nests less than 6 m above the ground were used. Not all nests were found at the same stage of the nesting cycle, but nest searches as well as nest checks were conducted every 3 days to ensure that all pairs were exposed equally to my presence. Clutch and brood size were checked using a mirror on an extendable pole. Eggs and young were not handled during the course of the experiment. The Systat (Wilkinson 1986) statistical package was used to compute Kruskal-Wallis H values and Mann-Whitney U values.

Results

The average scores for each of the presentations in groups A, B, and C are given in Table 31. For nests with young (group and presentation A1, B2, and C3; see Table 31), scores for parents differed according to the number of model presentations (K.W.H.=8, P<0.02). Further, pairwise comparisons show that scores of parents with young decreased with the number of model presentations: scores for parents seeing the model for the third (C3) time were significantly lower than scores for parents seeing the model for the second (B2) time (M.W.U.=13, P<0.05); and parents seeing the model for the third (C3) time, scored significantly lower than parents seeing the model for the first (A1) time (M.W.U.=13, P<0.02). Parents with young seeing the model for the first (A1) time did not differ significantly in score from parents seeing the model for the second (B2) time (M.W.U.=45, P>0.05). The scores of parents with eggs also decreased with repeated model presentations (Table 31; group and presentation B1 vs. C2; M.W.U.=65, P=0.05).

Eastern Kingbirds defended their eggs as vigorously as they defended their young (Table 31; group and presentation A1 vs. B1: M.W.U.=61, P>0.05; B2 vs. C2: M.W.U.=45, P>0.05). Parents did, however, score lower when defending a completed

Table 31. Mean response scores of three experimental groups of parent Eastern Kingbirds when presented with a model crow.

Presentation	n	Test Conditions	Score[a] $\bar{X} \pm SD$ (range)
		Group A	
1	12	1- to 6-day-old young	3.3±1.3 (2-5)
		Group B	
1	11	1- to 6-day-old eggs	3.4±1.4 (1-5)
2	9	1- to 6-day-old young	2.9±1.3 (2-5)
		Group C	
1	8	Completed nest, no eggs	1.8±0.7 (1-3)
2	8	1- to 6-day-old eggs	2.3±1.2 (1-5)
3	7	1- to 6-day-old young	1.7±0.5 (1-2)

[a]Scoring followed Blancher and Robertson (1982), with higher values representing more intense responses.

nest structure without eggs (C1) than they did when defending eggs (B1; M.W.U.=14, $P<0.02$) or young (A1; M.W.U.=80 $P<0.01$).

These experiments show that Eastern Kingbirds respond less vigorously upon successive exposure to the same model predator (A1 vs. C3; B2 vs. C3) and (B1 vs. C2) and, they do not defend young more vigorously than eggs (A1 vs. B1) and (B2 vs. C2).

Discussion

My results show that repeated exposure to a taxidermic model results in a decrease in the response of Eastern Kingbirds to that model (A1, B2, C3) and (B1, C2). Many other studies have used investigators (e.g. Barash 1975, Searcy 1979, Greig-Smith 1980, East 1981, Anderson et al. 1980, Blancher and Robertson 1982, Weatherhead 1989), taxidermic models (e.g. Robertson and Bierman 1979, 1981) or both (McLean et al. 1986) to test whether nest defence increases as nest contents advance in age. However, few studies (Knight and Temple 1986a) have been designed to account for the potential change in nest defence response by parents due to repeated exposure to the model predator. Knight and Temple (1986a) argued that parents may respond more intensely to a model predator or observer after having learned from previous trials that the "predator" can be successfully driven away. The parents may perceive that the danger to themselves and to the nest contents is not very great and, thus, respond more vigorously in defending that nest. The direction of the response observed in my study is opposite to that predicted by Knight and Temple (1986a). The crow model, which may have been viewed as a novel threat by the parents during the first trial, may not have been perceived as a threat during subsequent trials. Parents would be expected to risk less in confronting a situation they had learned was not dangerous than in confronting a dangerous situation (Coleman 1987). Eastern Kingbird parents may have learned that the crow model was not dangerous and their response during subsequent trials was less vigorous as a result.

The results of my study do not support the prediction that parental investment, measured as nest defence, increases with the age of the nest contents. Eastern Kingbirds parents did not defend young more vigorously than eggs (A1, B1, and C2, B2), contrary to the results of Blancher and Robertson (1982), who used Eastern Kingbird response to repeated visits by an investigator to measure nest-defense response. Why does nest defence in Eastern Kingbirds not increase with the age of the nest contents? It may be nearly as costly for kingbirds to replace eggs as it is for them to replace young. Eastern Kingbirds in Creston did not readily renest if they lost a clutch: of 36 pairs that lost eggs or young in 1987, only 7 built a new nest and laid eggs (this includes pairs not used in this experiment). Although none of the parents were colour-banded, several of the pairs remained on their territory, but did not renest. This fact, along with my regular visits to pairs and various behavioural cues, lead me to think that the seven replacement nests represent most, if not all of the renesting attempts. If eggs and young are equally valuable, parents should not invest more in protecting young.

In contrast, Andersson et al. (1980) suggested that even in altricial birds that do not readily renest, such as the Eastern Kingbird, an increase in nest-defense with the age of the young would be expected, because the ratio of the survival expectancy of the young to the survival expectancy of the parents would increase. Eastern Kingbird young, however, are still fed and defended by their parents after fledging. Parents in my study were seen to feed young for as long as 24 days after fledging. The survival expectancy of Eastern Kingbird young probably approaches that of their parents only when they have sufficient flying skills to hunt and avoid predators on their own. Eastern Kingbird parents probably no longer defend young by the time the young are independent. Tactics used by Eastern Kingbirds to defend fledged young are different from those used to defend nest contents, and the costs involved in the two activities may not be comparable as young can fly, scatter and use vegetative cover in various ways.

Parents would be expected to show differential investment if nest defence is costly. Incidents of damage or death to mobbing and defending parents have been recorded (Curio 1978, Sordahl 1990), but the danger to an adept flier like the Eastern Kingbird while confronting the American Crow may be minimal. If there is little or no risk for the parent, and if the behavior is effective in preventing nest predation, then comparable investment would be expected in defending eggs and young.

Why did the results of my study differ from those of Blancher and Robertson (1982)? They handled nest contents during repeated visits to assess nest-defense response, and I did not. As I did not handle nest contents, kingbird parents may not have perceived me as a threat during trials. The model crow, however, may have been perceived as a novel and potentially dangerous predator. The responses of the parents to the presentations (i.e. A1, B1, C1) in my study were made by parents meeting a particular danger to their nest and/or eggs or young for the first time; parents in the Blancher and Robertson study may have been responding to a potentially dangerous, but familiar predator that had previously been driven away.

The geographic differences between the two studies may also have resulted in different: (1) predators being present; (2) predation pressures; and (3) experiences with predators. Perhaps these factors influenced parental responses to some degree.

In summary, Eastern Kingbird parents in Creston responded less vigourously to a model predator during repeat trials than they did during initial trials, and did not defend young more vigorously than they defended eggs. These results are consistent with predictions made by parental investment-theory, but indicate that: the natural history of the study species must be considered in assessing how valuable nest contents are to the parents; and the costs of the investment, in this case nest defence, must be great enough to warrant differentiation of effort.

Chapter 6: General Discussion

The previous chapters have shown that greater overhead visibility benefits avoidance of nest predation, especially in the egg stage, that noisy parental behaviour at the nest influences the probability of nest predation and that the amount of water in the vicinity of the nest, especially in the nestling phase, also affects nest predation of kingbirds. However, many of these factors were shown to interact, for example, female incubation behaviour differed depending on habitat and nest visibility; and parental noise at the nest differed with habitat. While it is of interest to note that univariately these factors influence nest defense behaviour, it is informative and more realistic to analyse these factors in a multivariate way.

To this end, a stepwise logistic model (logistic procedure of SAS (1987)) was used to study the multivariate effects of nest visibility, the nest site and surrounding habitat characteristics and parental behaviour at the nest. Eight variables were chosen because of their univariate statistical influence ($P<0.2$), biological significance, and importance as suggested by cubic spline analysis: the number of noisy incidents (noisy perches) accompanied by a perch change during 90 min watches; the number of chases of other individuals of any species during a 90 min watch; the number of corvids seen in the vicinity of the nest during a 90 min watch; the percentage of water, field and trees (respectively) within 100m of the nest site; the nest height; and percentage overhead visibility for each nest.

There were 68 observation periods for 40 pairs of birds. Observations during incubation, for young nestlings (1-6 days old) or for older nestlings (7-9 days old) for each nest were counted as a separate observation as there were no statistical differences for any of the eight factors considered for incubation, young nestlings or older nestlings. Therefore a nest with three observations (each for a different age of nest contents) was entered three times and a nest where one observation was made was entered once. The procedures for collecting data are described in previous chapters as follows: noisy incidents, chases, and the number of corvids seen during a watch (Chapter 2); percentage water, field and trees and nest height (Chapter 3) and overhead nest visibility (Chapter 1).

The results of the analysis show that noisy incidents, percentage water, and nest height were chosen by stepwise logistic procedure and retained (X^2=8.3 P=0.004). The resultant model was: Logit p(success)=0.13 N + 0.008 H + 0.06 W - 4.02 when N=noisy incidents, H=nest height and W=percentage water around the nest.

Of the variables I chose to study, behaviour, habitat and nest site characteristics interacted to influence the probability of predation of Eastern Kingbird nest contents. The noise that parents make around the nest (being either quiet or very noisy), the amount of water (about 20% being the most successful percentage) and the nest height (in general being taller than the surrounding vegetation), all make it less likely that eggs or nestlings will be preyed upon. All of the variables chosen by the analysis can be related to vigilance behaviour, as previously discussed.

I feel that the noisy behaviour at the nest is an index to pair recognition, communication and co-operation at the nest, and this communication allows co-ordinated nest defence by parents and greater nest vigilance. The percentage water available influences the amount of time spent on feeding (kingbirds are insectivores) and thus the amount of time available to spend on nest vigilance. A nest located above the surrounding vegetation allows better visibility of approaching predators, although a nest located low over the water offers thermoregulative advantages (see Chapter 3). I feel that kingbird nest defense is effective because it keeps predators from approaching nests, and from spending time searching in the vicinity of kingbird nests and all of the factors chosen by the multivariate analysis augment kingbird vigilance.

Kingbird nest defense is based upon vigilance at the nest by both parents, and it is effective. Their behaviour is successful because it keeps predators from spending enough time near a nest to find it, but when a nest is found, kingbirds can occasionally keep the predators at bay. Just as predators such as corvids work as a team to distract parents from the nest, kingbird parents work as a team to concentrate efforts on the predators in the group actually endangering the nest.

Kingbird nest defence often appears indiscriminate (especially when they are reported to chase aircraft etc.) but in fact, this study shows that kingbirds can be very discriminating in how nest defence effort is expended. Nest defence differs with the age of the nest contents and with the type of predator posing a threat. When there are eggs, defence depends upon vigilance by both parents and camouflage provided by the incubating female. Females nesting in hidden situations allowed investigators to approach closer than females nesting in more open situations. It also appears that greater overhead visibility is of benefit to parents defending eggs and that females nesting near water (and presumably more food) spent more time incubating. Greater nest height would allow incubating females a better view of approaching egg predators. Parents defending nestlings appear to rely much more on preventing predators from approaching the nest. It is at this stage that the availability of water influences nest predation: probably due to the greater time spent in vigilance by parents that can feed adequately and close to the nest, and by parents that do not have to shade exposed nestlings. Parents respond less vigorously to nestling predators (i.e. American Kestrels) when there are eggs in the nest than when there are nestlings, and always respond vigorously to a predator that is always dangerous (i.e.

Sharp-shinned Hawk). This discriminatory response not only saves effort, but keeps the parent from revealing the location of the nest to a predator that may be dangerous at a later date or to other predators in the surrounding area.

Kingbird nest defence is also effective because it keeps the predator from hunting efficiently. A predator may find it difficult to fly, let alone search for nests systematically when diving, weaving, changing altitude or speed to avoid being hit by a kingbird, or when a kingbird is clinging to its back.

Finally, this study has shown that kingbird parents respond less vigorously to repeated presentations of a crow model: risking less in a situation that they have learned is not dangerous; and that they do not defend nestlings more than they defend eggs. Kingbirds that responded most to a crow model were more also more likely to lose nest contents to predators indicating that learning plays an important role in efficient nest defence and that an inappropriately vigorous response could be costly. Kingbirds probably do not defend nestlings significantly more than eggs because eggs are as valuable as young when renesting may not be possible.

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