The Auk 110(4):921–923, 1993

Nest Defense in Relation to Nesting Stage and Response of Parents to Repeated Model Presentations in the Eastern Kingbird (*Tyrannus tyrannus*)

JOANNE A. SIDERIUS
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

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

Methods.—The study was conducted in the Creston Valley Wildlife Management Area in south-eastern British Columbia, Canada, from 3 June to 16 July 1987. A taxidermic mount of an American Crow (*Corvus americanus*) 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. American Crows are predators of Eastern Kingbird eggs and young in Creston, and frequently are pursued, hit, and mobbed by kingbirds. 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 one to six days old; 1 brood with nine-day-old chicks). In group B, the model was presented twice: once when there were eggs (one to six days old) in nest and once when there were young (one to six 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 (one to six days old) in nest; and once when there were young (one to six 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 three 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. The Kruskal-Wallis (K-W) test was used to determine whether three or more ranked values belonged to the same population. The Mann-Whitney (M-W) U-test was used to determine whether two ranked values were significantly different (Sokal and Rohlf 1981).

Results.—The average scores for each of the presentations in groups A, B, and C are given in Table 1. For nests with young (group and presentation A1, B2, and C3; see Table 1), scores for parents differed according to the number of model presentations (K-W $U = 8$, $P < 0.02$). 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 1; 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 1; 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 nest structure without eggs (C1) than they did when defending eggs (B1, M-W $U = 14$, $P < 0.02$) or young (A1, M-W $U = 80$, $P < 0.01$).

TABLE 1. Mean response scores of three experimental groups of parent Eastern Kingbirds when presented with a crow model.

Presentation	*n*	Test conditions	Score[a]
		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 ($\bar{x}$ ± SD with range in parentheses) followed Blancher and Robertson (1982), with higher values representing more intense responses.

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). 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). Other studies have used investigators (e.g. Barash 1975, Searcy 1979, Greig-Smith 1980, East 1981, Andersson 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 defense increases as nest contents advance in age. However, few studies (Knight and Temple 1986) have been designed to account for the potential change in nest-defense response by parents due to repeated exposure to the model predator. Knight and Temple (1986) 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 (1986). 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 defense, increases with the age of the nest contents. Eastern Kingbird parents did not defend young more vigorously than they did eggs (A1 vs. B1, ns; and C2 vs. B2, ns), contrary to the results of Blancher and Robertson (1982) who used Eastern Kingbird reactions to repeated visits by an investigator to measure nest-defense response. Why does nest defense 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 color banded, several of the pairs remained on their territory, but did not renest. This fact, along with my regular visits to pairs and various behavioral cues, suggests 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, since 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 effectively forage, as well as 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 since young can fly, scatter and use vegetative cover in various ways.

Parents would be expected to show differential in-

vestment if nest defense 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. Since 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 parents responding to presentations (i.e. A1, B1, C1) in my study were responding to an apparent danger presented in proximity to their nest, 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 also may have resulted in: (1) different predators being present; (2) different predation pressures; and (3) different experiences with predators. Perhaps these factors influenced parental responses to some degree.

In summary, Eastern Kingbird parents in Creston responded less vigorously 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 defense, must be great enough to warrant differentiation of effort.

Acknowledgments.—I thank B. Beasley, A. Harfenist, W. Rendell, D. Wiggins, S. Wilson, N. A. M. Verbeek, and R. Ydenberg for reading earlier drafts of this manuscript and making useful comments; M. Machmer for her assistance with statistical logistics; and L. W. Schalla for technical assistance. I am also grateful to editor G. D. Schnell, and reviewers R. J. Robertson and W. A. Searcy for comments which improved the manuscript. This work was funded by a grant from the Natural Sciences and Engineering Research Council of Canada to N. A. M. Verbeek.

Literature Cited

Andersson, M., G. Wiklund, and H. Rundgren. 1980. Parental defence of offspring—A model and an example. Anim. Behav. 28:536-542.

Barash, D. P. 1975. Evolutionary aspects of parental behavior: Distraction behavior of the Alpine Accentor. Wilson Bull. 87:367-373.

Blancher, P., and R. J. Robertson. 1982. Kingbird aggression: Does it deter predation? Anim. Behav. 30:929-945.

Coleman, R. M. 1987. Does experience with predators affect parental investment? Auk 104:791-792.

Curio, E. 1978. The adaptive significance of avian mobbing. 1. Teleonomic hypotheses and predictions. Z. Tierpsychol. 48:175-183.

Dawkins, R., and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131-133.

East, M. 1981. Alarm calling and parental investment in the Robin *Erithacus rubecula*. Ibis 123:223-230.

Greig-Smith, P. W. 1980. Parental investment in nest defence by Stone-chats (*Saxicola torquata*). Anim. Behav. 28:604-619.

Knight, R. L., and S. A. Temple. 1986. Why does intensity of avian defense increase during the nesting cycle? Auk 103:318-327.

Maynard Smith, J. 1977. Parental investment: A prospective analysis. Anim. Behav. 25:1-9.

McLean, I., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behaviour, nest exposure, and breeding success in the American Robin. Behaviour 96: 171-186.

Montgomerie, R. D., and P. J. Weatherhead. 1988. Risks and rewards of nest defence by parents. Q. Rev. Biol. 63:167-187.

Robertson, R. J., and G. Bierman. 1979. Parental investment strategies determined by expected benefits. Z. Tierpsychol. 49:124-128.

Robertson, R. J., and G. Bierman. 1981. Residual reproductive value and parental investment. Anim. Behav. 31:311-312.

Searcy, W. A. 1979. Female choice of mates: A general model for birds and its application to Red-winged Blackbirds (*Agelaius phoeniceus*). Am. Nat. 114:77-110.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Co., San Francisco.

Sordahl, T. A. 1990. The risks of avian mobbing and distraction behavior: An anectdotal review. Wilson Bull. 102:349-352.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 137-179 *in* Sexual selection and the descent of man, 1871-1971 (B. G. Campbell, Ed.). Heinemann, London.

Weatherhead, P. J. 1989. Nest defense by Song Sparrows: Methodological and life history considerations. Behav. Ecol. Sociobiol. 25:129-136.

Wilkinson, L. 1986. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.

Received 18 June 1992, accepted 29 March 1993.