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*The Condor* 96:812-816  
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## EFFECTS OF HEIGHT OF NEIGHBORING NESTS ON NEST PREDATION IN THE RUFIOUS TURTLE-DOVE (*STREPTOPELIA ORIENTALIS*)

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*Key words:* Rufous Turtle-Dove; nest predation; area-restricted searching; breeding density; nest height.

In many bird species, nest predation is one of the most significant causes of breeding failure (Ricklefs 1969).

Breeding density is often considered to affect nest predation. Higher breeding density often results in lower predation pressure for species which will mob nest predators (Berg et al. 1992, Westneat 1992). Alternatively, in species which build cryptic nests and do not attack nest predators, nest predation tends to be higher when nesting density is high (Murton 1958, Krebs 1970, Fretwell 1972, Dunn 1977, Weller 1979, Page et al. 1983, Hill 1984). In some experimental studies using

<sup>1</sup> Received 15 December 1993. Accepted 17 March 1994.

artificial nests, a positive correlation between predation pressure and nest density is also reported (Göransson et al. 1975, Andersson and Wiklund 1978, Nilsson et al. 1985, Sugden and Beyersbergen 1986, Martin 1988, Esler and Grand 1993).

The positive correlation between breeding density and predation pressure for species with cryptic nests may be explained by the searching behavior of nest predators. If nest predators with a search image for previously preyed-upon nests employ area-restricted searching or repeated visits to places they were formerly successful, a density-dependent pattern of nest predation can result (Tinbergen et al. 1967, Croze 1970). In this case, if certain nest sites are more detectable by nest predators than others, nests located near the more detectable nests may also suffer higher predation pressure, because their presence may induce area-restricted searching by predators. Thus, not only the existence of surrounding nests (i.e., breeding density), but also the characteristics of the surrounding nests may affect the fate of a nest.

In this paper, the effect of neighboring nests on the vulnerability of focal nests to predation was examined in the Rufous Turtle-Dove (*Streptopelia orientalis*), a species which does not attack nest predators. Wada (1991) showed that nests placed higher in trees were depredated more frequently than were lower-placed nests. Based on this finding, I hypothesized that the existence of a nest more easily detectable by predators (i.e., higher nests) would increase the vulnerability of the surrounding nests to predation.

#### STUDY AREA AND METHODS

The study was conducted in a 6.1 ha area of the campus of Kyoto University, Kyoto, Japan, from April 1986 to January 1989. The Rufous Turtle-Dove is a common year-round resident in Kyoto, and breeds in pairs that cooperate in nest building, brooding and feeding of nestlings (Haneda and Nozawa 1969). The species builds an open-cup nest with twigs, mainly in trees and rarely on buildings.

The study area was censused more than twice per week during the breeding season from February to November, and at least once a week in December and January. For each census, all nests detected in the study area were checked, and activities related to breeding, such as nest building and nest site choice, were recorded.

Nest height was measured in intervals of 0.5 m at each site. Mean nest height was 4.1 m (range 1.5 m–10.0 m). Height of preyed-upon nests ( $n = 116$ , mean = 4.29 m, SD = 1.75) was significantly higher than that of nests not preyed-upon ( $n = 76$ , mean = 3.70 m, SD = 1.39, Mann-Whitney  $U$ -test,  $z = 2.21$ ,  $P < 0.05$ ) (Wada 1991). In this paper, nest sites were divided into two types according to nest height: higher nests ( $>4.0$  m), and lower nests ( $\leq 4.0$  m).

#### CLASSIFICATION OF BREEDING OUTCOME

In the process of nest site choice, a dove often built several nests before laying eggs. In this paper, nest building and behaviors solely involving site choice were not included in the analyses. Only if egg-laying was

confirmed or assumed the event regarded as a breeding attempt and included in the analyses. Since nests were observed at a distance in order to avoid nest desertion due to disturbance, and breeding pairs seldom left their nests once they started incubating eggs, egg-laying was not confirmed in 41.2% of 192 breedings. However, egg-laying was assumed even in these cases if doves sat continuously on the nest.

A breeding attempt was considered successful if at least one chick fledged. Other attempts were regarded as unsuccessful and their outcomes were divided into three categories: (1) desertion of a nest containing unhatched eggs, (2) falling of unbroken eggs or uninjured chicks, and (3) cases including fallen egg shells, disappearance of eggs or chicks, injured chicks or broken eggs which remained in nests, or cases where neither eggs nor chicks were confirmed. Nest predation was observed six times among 192 breeding attempts: three times by crows (*Corvus corone* or *Corvus macrorhynchos*), twice by feral cats (*Felis catus*), and once by a snake (*Elaphe climacophora*). These cases were included in the last category of breeding failure. In this analysis, the last category of breeding failure is assumed to be nest predation. Other causes of breeding failure, such as death of nestlings due to parasites or starvation, were not observed.

#### ANALYSES

The effects of neighboring nests on focal nests were examined by counting the number of other active nests at the start of breeding at each focal nest (other than the focal nest). The number of nests was counted for the entire study area, and within distances of 30, 50, 70, and 90 m from each focal nest. No other nests existed within 10 m of any nest. If more than 5% of any of the above surveyed areas was out of the study area, the focal nest was excluded from the analyses for the distance.

In the analyses regarding nest height, multiple logistic regression analysis on vulnerability of focal nests to predation was conducted in order to evaluate the relative significance of the height of a focal nest itself, and of the number of higher nests and the number of lower nests. Breeding outcome (nest predation or no nest predation) was used as a dependent variable, and assigned dummy variables of 1 and 0, respectively. All statistical tests were conducted using the statistical computer program HALBAU (Yanai and Takagi 1986). Aspin-Welch's method was used to perform  $t$ -tests when variances of two samples were significantly different. Two-tailed tests were conducted for all statistical comparisons.

#### RESULTS

The number of active nests changed seasonally within the study area. Fewer nests were found from January to May, and more nests occurred from June to December. The number of neighboring nests around focal nests was smaller in January–June than in July–December for the entire study area, but there were no significant seasonal differences within the surveyed areas (Table 1).

More nests existed within 70 m of focal nests which were preyed-upon than within 70 m of nests which

TABLE 1. Seasonal comparisons of the number of breeding nests in the neighborhood of focal nests.

Distance to focal nest	Jan-Mar			Apr-Jun			Jul-Sep			Oct-Dec			Kruskal-Wallis test	
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	$\chi^2$	<i>P</i>
<30 m	15	0.200	0.400	33	0.061	0.239	54	0.241	0.469	27	0.333	0.609	5.044	ns
<50 m	14	0.500	0.824	22	0.273	0.538	35	0.543	0.690	21	0.714	1.030	2.719	ns
<70 m	9	1.111	0.737	17	0.471	0.848	23	1.087	0.880	19	0.842	1.136	6.621	ns
<90 m	3	0.667	0.943	6	0.500	0.764	10	1.500	1.118	5	1.200	1.166	3.512	ns
Entire area	23	1.739	1.358	44	2.205	1.618	80	3.725	1.628	45	4.756	1.934	54.931	<i>P</i> < 0.001

ns: *P* > 0.1, *n*: number of focal nests.

were not (Table 2). No significant differences were detected in comparisons between breeding success and failure for all areas surveyed (*t*-test, *P* > 0.1, in all comparisons).

The effect of the height of neighboring nests was analyzed for nests within 70 m from focal nests. There were significantly more higher nests around focal nests which were preyed-upon than around nests which were not, whereas the number of lower nests around them was not significantly different (Table 3). The result of a multiple logistic regression analysis showed that the number of higher nests had the most significant effect on vulnerability of focal nests to predation (Table 4).

#### DISCUSSION

More nests existed within 70 m from focal nests which were preyed-upon than those which were not (Table 2). Seasonal changes in predation pressure may affect the results, such that breeding density was highest when predation pressure was highest. However, this was not the case because density did not differ seasonally within 70 m of focal nests (Table 1).

This study showed that the effect of neighboring nests on focal nests was detected only within an area of 70 m from focal nests (Table 2). This suggests the importance of area used to calculate density. If a predator searched for nests around a previously depredated nest, then density calculations based upon too small of an estimated search radius may be inadequate. When too large an area is used, most of the area is not searched by the predator, and most of the other nests within the area do not affect the fate of focal nests. In both cases, density effect is obscured and is hardly detected. In some studies which examined density-dependent nest

predation, area-restricted searching by predators was found but density-dependent nest predation was not (Sonerud 1985, Salonen and Penttinen 1988, O'Reilly and Hannon 1989). The absence of density-dependence in the presence of area-restricted searching may be explained by the radius of search by predators and the area used to calculate density.

In the Rufous Turtle-Dove, higher nests were more vulnerable to nest predation than were lower nests (Wada 1991), probably because higher nests were more easily detected by nest predators such as crows. The number of higher nests was greater around preyed-upon nests, while the number of lower nests was not (Tables 3 and 4). The difference in the total number of nests in the neighborhood of preyed-upon focal nests and those that were not can be attributed to the difference in the number of higher neighboring nests. This result agrees with the hypothesis that the existence of a nest more easily detectable by predators raises the vulnerability of surrounding nests more than does a less detectable one. Few studies have examined how the characteristics of neighboring nests affect the fate of a nest, probably because other studies have only tried to detect density-dependent effects caused by nest predation. This study demonstrates that nests can influence each other's outcome as a result of their vulnerability to nest predation. Thus, not only the number of surrounding nests, but also the characteristics of surrounding nests affect the vulnerability of nests to predation.

I am grateful to Takuya Abe for his continuous encouragement, and to Yasuo Ezaki for his advice in conducting this study. I thank Keiji Iwasaki, Hiroya

TABLE 2. Comparison of the number of nests in the neighborhood of focal nests with respect to breeding outcome.

Distance to focal nest	Nest predation			Others			Total			<i>t</i> -test	
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>t</i> -value	<i>P</i>
<30 m	77	0.234	0.484	52	0.173	0.430	129	0.209	0.462	0.730	ns
<50 m	51	0.647	0.820	41	0.341	0.728	92	0.511	0.791	1.866	0.05 < <i>P</i> < 0.1
<70 m	36	1.167	0.941	32	0.531	0.915	68	0.868	0.976	2.815	<i>P</i> < 0.01
<90 m	12	1.000	1.206	12	1.167	1.115	24	1.083	1.139	0.352	ns
Entire area	116	3.534	1.904	76	3.158	2.092	192	3.385	1.984	1.289	ns

ns: *P* > 0.1, *n*: number of focal nests.

TABLE 3. Comparison of the number of nests within 70 m of focal nests with respect to nest height.

Height of surrounding nests	Nest predation (n = 36)		Others (n = 32)		t-test	
	Mean	SD	Mean	SD	t-value	P
Higher nests	0.500	0.697	0.125	0.336	2.874	P < 0.01
Lower nests	0.667	0.828	0.406	0.875	1.261	ns

\*: Aspin-Welch's method is conducted because of unequivalence of variances.  
ns: P > 0.1.

TABLE 4. Results of multiple logistic regression analysis of effects of height of surrounding nests (&lt;70 m) on nest predation or not (n = 68).

Variables	Regression coefficient	Standard error	t-value	P
Number of higher nests	1.443	0.597	2.416	P < 0.05
Number of lower nests	0.490	0.316	1.549	ns
Nest height	0.141	0.163	0.861	ns
Intercept	-1.110	0.726		

ns: P > 0.1.

Kawanabe, Katsuki Nakai, Kensuke Nakata, Misako Urabe, and two anonymous reviewers for their helpful comments. I also thank Linda Turner for revision of the English. This study was partly supported by the Grant-in-Aid for General Scientific Research (Nos. 61480005, 02454005) and for Priority Research Area (Nos. 03269106, 04264101) from the Japan Ministry of Education, Science and Culture. This paper is the contribution from the Laboratory of Ecology, Department of Zoology, Kyoto University, No. 541.

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