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EFFECTS OF NESTING SPARROWHAWKS ON NESTING TITS

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Since 1976 I have been examining Sparrowhawk (*Accipiter nisus*) predation upon Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) in Wytham Woods, Oxford, England. The Wytham tit population has been studied since 1947 (Perrins 1965) and virtually 100% of the Great Tits and over 75% of the Blue Tits nest in nest boxes which are regularly checked and in which all of the young are banded. The extensive banding program has allowed me to recover bands of eaten individuals from the hawk nests and thus to analyze the predator's effect on the prey population. The Sparrowhawks are major predators of the tits, taking 20–25% of the population during the breeding season. The number of breeding tits in the woods has not decreased since Sparrowhawks returned to breed in 1973 after their disappearance in the mid-1960's, which was due presumably to pesticides. There has, however, been a significant decrease in the number of breeding tits that were born in the woods, with a corresponding increase in the number of breeding tits that are immigrants (unpubl. data).

Only one instance of nesting depression caused by a predator has been documented—in Ruffed Grouse (*Bonasa umbellus*) preyed upon by Goshawks (*Accipiter gentilis*) in Minnesota (Eng and Gullion 1962). Brown and Amadon (1968) stated for Sparrowhawks that "Since the male does not normally kill near the nest this results in a population of undisturbed birds near it." I shall demonstrate here that a population of a prey species that lives near a Sparrowhawk nest is disturbed by the predator.

STUDY AREA AND METHODS

Wytham Woods is a 260-ha area of mixed deciduous woodland 6.5 km northwest of the city of Oxford in south-central England. In 1976, 966 nest boxes were available for use by tits with 249 successfully used (broods fledged) by Blue Tits and 104 by Great Tits. In 1977, of 990 boxes in the wood, 358 were used successfully by Blue Tits and 173 by Great Tits. Nest boxes are distributed so as to exceed the number used by tits with the highest densities per nesting pair in Marley (about 5.5:1) and Bean (about 2.75:1) woods.

Ten Sparrowhawk nests were located, four in 1976 and six in 1977. In 1976, four pairs incubated to full term and three of these pairs fledged young. In 1977, four pairs incubated to full term and fledged young. I assume that all nests were found in 1977; one or more hawk nests were not found in 1976. In areas of continuous suitable habitat Sparrowhawk nests are most commonly 800 m apart, a figure similar to that given by Newton et al. (1977) for other areas of Britain. The minimum spacing between two nests was 400 m (1977) and the maximum about 1,800 m (both years). Nests were most frequently in deciduous trees even though conifer stands were available in some areas and were usually 10.5 to 14 m above the ground.

The method of collecting information about tit nesting is described by Dunn (1977). I determined the proportion of nest boxes occupied in four consecutive annuli, each 60 m wide, centered on each hawk nest. In the analysis of tit nest box use, the following parameters were used to describe occupation: (1) Real availability—the number of nest boxes occupied by tits minus those nest boxes occupied by tits that were unsuccessful for reasons not attributable to Sparrowhawks, i.e., predation by weasels (*Mustela nivalis*), Great Spotted Woodpeckers (*Picoides major*), and squirrels (*Sciurus carolinensis*) (Dunn 1977). The proportion of nest boxes in this category is the same for each annulus so it does not bias the findings. (2) Used—nest boxes in which tits laid one or more eggs. (3) Successful—nest boxes from which a pair of tits fledged young. (4) Unsuccessful—at least one egg laid but no young fledged; as there was no apparent cause for desertion of eggs or young, I considered that the parent(s) may have been killed by hawks. (5) Percent use/success—use/success in an annulus divided by real availability in that annulus multiplied by 100.

RESULTS

Table 1 shows the percent successful occupancy and use by tits of the nest boxes in each annulus around successful and unsuccessful hawk nests. These data indicate: 1) a depression in annulus I (0–60 m) around all successful hawk nests except in Marley Plantation, 2) a depression in annulus I for the Radbrook nest, which the hawks incubated full term and beyond, 3) no depression in the same annulus for those hawk nests which were abandoned soon after the eggs were laid.

A chi-square analysis was performed on the combined 1976 and 1977 data for successful hawk areas (excluding Marley Plantation but including Radbrook; see below) and unsuccessful hawk areas in each of the four annuli to determine if the same ratio of occupied to unoccupied nest boxes occurred in each annulus. Significant heterogeneity was found for the number of nest boxes occupied in the four annuli for both use ($P < 0.05$, $\chi^2 = 9.74$, 3 df) and successful occupancy ($P < 0.01$, $\chi^2 = 14.35$, 3 df) around the successful hawk nests. I subdivided the contingency tables and found homogeneity for annuli II, III, and IV

TABLE 1. Percent nest box use (U), percent successful nest occupancy (S) by its tits, and number of nest boxes available (N) in each annulus.

	Annulus											
	I (0–60 m)			II (61–120 m)			III (121–180 m)			IV (181–240 m)		
Nest and year	U	S	N	U	S	N	U	S	N	U	S	N
SPARROWHAWK NESTS INCUBATED FULL TERM OR FLEDGING YOUNG												
Marley 1976	0	0	9	29	26	35	18	16	38	28	19	32
Bean 1976	0	0	7	46	38	26	43	40	30	44	39	36
Lord's Copse 1976	33	33	3	80	80	5	40	20	5	50	50	10
Radbrook 1976	0	0	3	56	56	9	40	40	10	45	27	11
Marley 1977	50	0	6	33	29	24	59	41	41	43	27	51
Larch 1977	100	0	1	100	100	1	100	71	7	89	78	9
Thorny Croft 1977	0	0	1	88	88	8	100	100	2	92	58	12
Marley Plantation 1977	100	100	5	92	88	13	90	80	10	89	67	9
Total (excluding Marley Plantation)	17	3	30	44	40	108	44	35	133	47	35	161
SPARROWHAWK NESTS FAILED SOON AFTER EGGS LAID												
Bean 1977	75	50	8	63	50	16	72	59	32	67	56	27
Lord's Copse 1977	100	100	2	90	80	10	75	44	16	57	43	7
Total	80	60	10	73	62	26	73	64	42	65	58	36

for use ($P > 0.50$, $\chi^2 = 0.41$, 2 df) and successful occupancy ($P > 0.50$, $\chi^2 = 0.78$, 2 df). Annulus I was tested for the same null hypothesis against pooled data for annuli II, III, and IV and a significant difference was found for both use ($P < 0.005$, $\chi^2 = 8.19$ with Yates' correction) and successful occupancy ($P < 0.001$, $\chi^2 = 12.10$ with Yates' correction) indicating that both use and success were reduced in the first annulus.

I also tested for heterogeneity of the occupied to unoccupied ratio for the annuli around unsuccessful hawk nests. No significant difference was found for either use ($P > 0.50$, $\chi^2 = 1.18$, 3 df) or success ($P > 0.50$, $\chi^2 = 0.31$, 3 df).

Marley Plantation is anomalous in that it has the only successful hawk nest with a higher successful occupancy of nest boxes in annulus I than in II. It differs from other successful hawk areas in that during 106 h of observing this hawk nest, 62 prey items were brought into the nest. Of these, 15 were tits, a lower percentage of the diet than at other nests observed the same year. Only one of the tits was banded, a very much lower proportion of banded to unbanded tits than at other hawk nests I watched in Wytham (unpubl. data). This information combined with the composition of the remaining 47 prey items (mostly House Sparrow [*Passer domesticus*], Starling [*Sturnus vulgaris*], Dunnock [*Prunella modularis*], and a variety of open country fringillids) suggests that these hawks were hunting outside the woodland, unlike the other hawks.

I considered whether the tits in the first annulus around hawk nests might be unsuccessful for reasons other than the hawks' presence. Since Sparrowhawks shift the location of their nest by about 50–100 m each year, nest boxes located in annulus I in one year might have been situated in annulus II, III, or IV the following year. Therefore, the first annuli around hawk nests successful in 1976 were examined for successful nest box occupancy by tits in 1977 (Table 2).

The ratio of nest boxes successfully occupied to unoccupied was significantly different between annulus I and annuli II, III, and IV combined ($P < 0.05$, $\chi^2 = 4.46$ with Yates' correction) in 1976. The ratio of successfully occupied to unoccupied nest boxes was not significantly different between the 1976 first annuli in 1977, and the 1977 annuli II, III, and IV minus the boxes from 1976 that fell within them ($P > 0.50$, $\chi^2 = 0.02$ with Yates' correction). This shows that the areas in the first annuli are not avoided for reasons other than hawk presence.

TABLE 2. Reoccupation of 1976 first-annuli nest boxes in 1977.

	Marley	Bean	Lord's Copse
No. of nest boxes in first annulus 1976	9	7	4
No. successfully occupied	0	0	1
No. of 1976 first-annulus nest boxes available outside 1977 first annulus	9	7	4
No. successfully occupied	2	3	3

DISCUSSION

INFLUENCE OF SPARROWHAWKS ON TITS NESTING NEARBY

The significant depression in both nest box use and breeding success in tits within 60 m of successful Sparrowhawk nests can be attributed solely to the influence of the hawks. The results suggest that about 1.8% of the area of Wytham is unsuitable for nesting tits on account of successful nesting by Sparrowhawks.

The reduction of the nesting tit population could be due to either avoidance of the first annulus by tits, or the predation in a greater degree of the tits nesting in the first annulus than in other areas. The reason may be found by comparing the successful and unsuccessful hawk nesting areas as well as comparing Marley Plantation to other successful hawk nesting areas.

Sparrowhawks begin to occupy nesting areas in February and to build nests in March (Owen 1916). The tits are in the area of their future territories in February and have clearly defined territories by late March (Hinde 1952). Thus, they should be well aware of the presence of hawks nesting nearby and, if fewer nest boxes are used because tits avoid the area, the area would be clear early in the season. The fact that both the unsuccessful hawk areas and Marley Plantation show no reduction of use or nesting success in the first annulus suggests that the tits do not avoid the area because hawks are present. If tits waited to nest in the first annulus until it was clear whether or not the hawks would nest successfully, those which moved in would be expected to hatch their broods later than those in other annuli. This is not the case in areas where hawks leave soon after laying.

If nest box use and nesting success are lowered because of predation by Sparrowhawks, the proportion of occupied and unoccupied nest boxes around incubated and non-incubated nests would be expected to differ. The hawk nests that failed (except for the one in Radbrook) did so as soon as the eggs were laid, the time when a male Sparrowhawk begins to hunt for himself and his mate. I found that the male preys much more heavily upon tits than does the female. As a result, heavy predation of tits begins at about the time when some of the hawk nests fail, leaving the nesting tits around the unsuccessful hawk nests relatively undisturbed.

The tits nesting in Marley Plantation were undisturbed, similar to those around hawk nests that failed soon after laying, but for a different reason. Marley Plantation is a peninsula of woodland over 1 km long, surrounded by fields and hedgerows; it is the part of Wytham closest to Oxford, as well as being the closest wood to the suburbs. The other hawk nesting areas in Wytham are either in the main part of the wood or in more extensive tracts of woodland. Many hedgerow and garden tits probably arrive in the area around Marley Plantation during the breeding season because of its location and structure and attempt to take up territories in the wood. However, about half (a figure which corresponds closely to that of Bulmer and Perrins 1973) of the previous year's breeding adults return to breed, allowing only a few of the immigrants in to breed (Krebs 1971) and leaving the rest in the fields and hedges. The Sparrowhawks hunted outside the small Marley Plantation probably because it was more profitable to do so. The low proportion of remains of banded tits at the hawk nest indicates that the hawks were taking hedgerow and garden birds, and were not disturbing those tits occupying nest boxes. Hence it appears that the reduction in tit nest box use and breeding success is caused by predation on the tits by Sparrowhawks.

TABLE 3. Number of clutches and broods of Great Tits in each year and percent of clutches (%C) and percent of broods (%B) failed due to unknown causes.

Year	No. clutches	%C	No. broods	%B
SPARROWHAWKS ABSENT				
1964	196	9.18	130	3.08
1965	192	13.02	138	0.72
1966	177	8.47	120	5.00
1967	125	14.40	93	3.23
Total	690	$\bar{x} = 11.00$	481	$\bar{x} = 2.91$
SPARROWHAWKS PRESENT				
1973	165	16.97	125	6.40
1974	138	17.39	110	6.36
1975	178	8.43	147	9.52
1976	114	7.89	102	3.92
1977	221	8.60	192	11.46
Total	816	$\bar{x} = 11.64$	676	$\bar{x} = 8.12$

OVERALL INFLUENCE OF SPARROWHAWKS ON TIT BREEDING SUCCESS

Nest records for Great Tits were checked for the years 1964–67, when Sparrowhawks were absent from Wytham, and the period 1973–77, when the hawks had returned and were breeding successfully, to determine whether Sparrowhawks reduced tit breeding success throughout the woods, albeit to a lesser de-

gree than in annulus I. The data for Blue Tits were inadequate for such analysis, yet I feel that the findings described for Great Tits would be true for Blue Tits owing to the similarities between the species. The records were tabulated for non-hawk years (1964–67) and breeding hawk (1973–77) years and losses for known causes (see above) were eliminated. The adjusted number of clutches for each year represents the number of clutches that hatch plus the number of clutches that fail due to unknown causes. The adjusted number of broods for each year represents the number of broods fledged plus the number of broods failed for unknown reasons. The percent failure due to unknown causes for each category was calculated for each year by dividing the number of failures/year by the adjusted number occurring each year in the appropriate breeding cycle stage multiplied by 100.

Table 3 shows the percent clutches and broods that failed for unknown causes per year. The percent failure was ranked for each year in each category and analyzed by a Mann-Whitney U Test. No difference ($P = 0.452$, one-tailed) was found between the two periods for clutch failures, but a significant difference ($P = 0.016$, one-tailed) was found between the two periods for brood failures.

Tits will not abandon their clutches, still less their broods, except under exceptional (and usually identifiable) circumstances. Clutches may be abandoned because of addling or infertility, but this does not occur in more than a few cases each year (Perrins, pers. comm.); it should not mask the yearly level of clutch failures due to unknown causes. The lack of difference in the failure rate for clutches between the periods when hawks were absent and present would lead one to expect a similar finding for the failure rate of broods. However, this is not the case. The 180% increase in the percent of broods that failed during the breeding hawk period appears to be the result of hawk predation. Nothing else is known to have affected the tit breeding during this time.

Failures of broods, but not clutches, increased probably because Sparrowhawk eggs hatch a few days after the mean fledging date of young tits. Consequently, the period of heavy predation on tits, when only male hawks are hunting, largely overlaps the period when tits have nestlings; it overlaps only briefly with the period when tits are incubating.

Most brood failures occurred more than 200 m from successful Sparrowhawk nests in the years for which hawk nests were found. Owing to the extensive area outside the annuli around successful hawk nests, however, the proportion of failures per nest box successfully used is much lower than in the first annuli. This indicates that nesting Sparrowhawks effect a widespread reduction of tit breeding success, most severely within 60 m of successful hawk nests.

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LITERATURE CITED

Brown, L. and D. Amadon. 1968. Eagles, hawks and falcons of the World. Country Life Books, Feltham, Middlesex, United Kingdom.

Bulmer, M. G. and C. M. Perrins. 1973. Mortality in the Great Tit (*Parus major*). Ibis 115: 277–281.

Dunn, E. K. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. J. Anim. Ecol. 46:634–652.

Eng, R. L. and G. W. Gullion. 1962. The predation of Goshawks upon Ruffed Grouse on the Cloquet Forest Research Center, Minnesota. Wilson Bull. 74:227–242.

Hinde, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour, Suppl. 2: 1–201.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52: 2–22.

Newton, I., M. Marquiss, D. N. Weir, and D. Moss. 1977. Spacing of Sparrowhawk nesting territories. J. Anim. Ecol. 46:425–441.

Owen, J. H. 1916. Some breeding-habits of the Sparrow-hawk. (5) General habits. Br. Birds 10:106–115.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34:601–647.

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