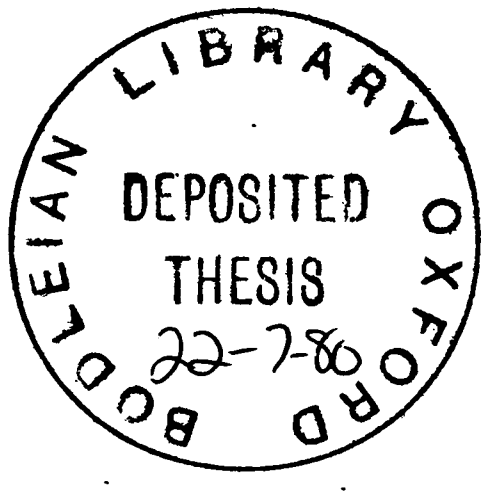
Sparrowhawk with ringed juvenile Blue Tit. (Photo by A. Allen)

The books say that hawks prefer meat,
But eight hours stuck in this seat,
Have taught me that they,
Take tits as main prey,
For the taste of the rings on their feet!

- found in a hide note book on
30 June 1977. Attributed to
N.B. Davies.

Sparrowhawk (*Accipiter nisus*) predation on tits (*Parus* spp.)



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A thesis submitted for the degree of D. Phil.
University of Oxford
Michaelmas Term 1979

Sparrowhawk (Accipiter nisus) predation on tits (Parus spp.).
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ABSTRACT

The present research was conducted to assess the effect of Sparrowhawk predation on the tit population of Wytham Woods, Oxford.

Chapter 1 describes the history of the Wytham hawk population until this study began and the nesting biology of the hawks during the study. Six to nine pairs of hawks settled in the wood each year, but reproductive success was low due to pesticide contamination.

Chapter 2 shows that tit nesting success was reduced when they nested near hawk nests. Circumstantial evidence is presented for reduced tit nesting success throughout the wood since the return of the hawks.

Chapter 3 examines rates of hawk predation during the nesting period. Findings indicate that hunting rates and the percentage of the diet formed by tits are regulated by prey availability or vulnerability, with highest predation rates occurring at the time that tits fledge.

In Chapter 4 the selection of tits by hawks is analysed. Results indicate that on the basis of brood and physical characteristics adult tits were selected on the basis of availability and juvenile tits were selected primarily by date of fledging. The ratio of adult to juveniles taken differed between years and was thought to be related to the number of tits available per hawk each year.

Chapter 5 presents estimates showing that 22-42% of each segment of the tit population was killed by hawks each year. The effects of these losses are discussed, concentrating on the shift in the structure of the tit breeding population which has occurred since the hawks returned to the wood.

In Chapter 6 the findings of the study are compared to the findings of previous predator-prey research and the attributes of Wytham as an area for studying predation discussed.

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Many people contributed time and energy to this project, which would have failed without their co-operation as it was beyond the scope of a single person's efforts.

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Z.A.W. Martin typed the manuscript with speed and accuracy and was able to read my handwriting.

Special thanks are given to Solon and Eve Geer, my grandparents, and Peter and Genevieve Geer, my parents, for their long standing encouragement of my interest in wildlife, as well as for the financial assistance for my studies.

Not forgotten are all the people who have studied the tits of Wytham Woods. Without them a study of this sort would not have been possible. Thank you for laying the ground work.

Lastly, my greatest thanks are to my wife, Julia Geer, who gave abundantly of time, help, understanding and worry to this study. I hope that I may someday achieve the acumen to train hawks with the love, respect and kindness with which she trained a husband, a far more difficult and dangerous species.

CONTENTS

Chapter 3. continued.

Aims of the study.

The population biology of Great and Blue Tits has been under study in Wytham Woods, Oxford, since 1947 (Lack 1966, Krebs and Perrins 1978, Perrins 1979). However, investigations of the effects of predators on the tit population have been limited until recent years. While Southern (1970), during his study of the Tawny Owl Strix aluco, found that tits formed a small percentage of the owls' diet, and checks of tit nests during the nesting season revealed that some losses were incurred by predation from Great-spotted Woodpecker Dendrocopus major, Grey Squirrel Sciurus carolinensis, and weasel Mustela nivalis, it was not until the collation of the data on Weasel predation by Dunn (1977) that interest in the effects of predators on the tit population intensified.

Although Sparrowhawks were known to prey almost exclusively on small avians and to take tits, sometimes in large numbers (Owen 1932, Tinbergen 1946, Gibb 1960), information on hawk predation on tits in Wytham in the past was limited to the recovery of some tit rings from one hawk nest in 1949 by J.A. Gibb (unpubl. data), and the sightings of hawks attacking family parties of tits (Hinde 1952). In addition, at the time that tit research in Wytham became well established, the number of Sparrowhawks in Wytham and throughout Britain was declining (see Chapter 1), so that the awareness of possible influences on the tit population by these predators was reduced. However, with the interest sparked by Dunn on the effects of predators, and the re-establishment of Sparrowhawks as a breeding species, it was decided in 1976 to begin an intensive study of the relationship between the hawks and tits in Wytham.

The main aims of the present study were to: 1) assess the size of the Wytham hawk population, 2) investigate the ecology of hawk predation, especially the rates of predation and the utilisation of tits as prey, 3) determine the manner in which hawks selected tits, and 4) calculate the number of tits taken each year to establish the impact of hawk predation on the tit population.

Chapter 1. The nesting biology of Sparrowhawks.

I. Introduction.

The population of Sparrowhawks breeding in Wytham has generally reflected the trends of the British Sparrowhawk population since the wood was established as a research area in 1947 (see Newton and Blewitt 1973, Newton 1974). Although one Sparrowhawk nest was observed cursorily by J.A. Gibb in 1949 and various researchers recorded sighting of individuals or breeding pairs, no intensive study of the population was conducted until the present study began in 1976.

The history of Sparrowhawks in Wytham from 1947 may be summarised as follows. H.N. Southern (pers.comm.) found during his study of the Tawny Owl in the 1940's and 1950's that about six pairs of Sparrowhawks nested in the wood each year. According to C.M. Perrins (pers.comm.), 1959 was the last year during which the hawks were known to have nested in the wood; this period was followed by the probable extinction of Sparrowhawks as a breeding species in Wytham and it was only a casual, indeed even rare, visitor to the wood in the mid-1960's. This decline is presumed to have been the result of contamination of the population with organochlorine pesticides, the cause attributed to similar declines of Sparrowhawks and other British raptors at the same time (Ratcliffe 1970, Newton 1974). I. Newton (pers.comm.) did not sight any Sparrowhawks in Wytham from 1963 until September 1967, when a juvenile female was seen soaring over Bean Wood, although he was constantly looking for them. It was not until about 1973

that Sparrowhawks were again thought to be breeding successfully in Wytham (C.M. Perrins, pers.comm.). The hawks now appear to have re-established a relatively stable breeding population of about six to nine pairs.

II. Methods.

When this study began in 1976 the number of Sparrowhawk pairs breeding each year in Wytham was unknown. Systematic searching of the 260 ha area of woodland was therefore begun in the spring of 1976.

The following characteristics were used to identify nesting areas: 1) plucking posts, e.g., branches and stumps (usually within 25-50m of the nest used by the hawks when plucking and dismembering prey; 2) whitewash, i.e. hawk excreta which is diagnostic by its similarity in appearance to chalky white emulsion paint and which builds up under roosts near the nest; 3) old hawk nests (new nests are usually built within 50-100m of the previous year's nest); 4) primary feathers moulted by the female during incubation; 5) new nests rimmed with down moulted by the female during incubation; 6) defence of the nest area against human intruders by the adults. Most nests were found in May and early June prior to laying or during incubation.

After a hawk nest was found, regular checks were made to determine the size of the clutch and the hatching date. In 1976 some nests were not found until after the young had hatched; at these nests hatching dates were estimated from the size and development of the young at the first visit after hatching.

In 1977 and 1978 all nests were found before the young hatched. Checks were then made until the eggs were pipping, there were newly hatched young, or the nest was found to have failed. When eggs were found to be at the final stage of pipping the next day was counted as day one of life; if some of the young were already hatched the day of the check was counted as day one of life.

III. Results.

A. Types of trees used for nesting.

Deciduous broadleaf trees were used for nesting in thirteen instances, and coniferous trees in five cases. Of broadleaved trees, Oak Quercus robur was used eight times and Field Maple Acer campestre five times. Of the conifers, both Larch Larix spp. and Norway Spruce Picea abies were used twice and Sitka Spruce Picea sitchensis once.

When both broadleaf and coniferous trees were available in the same area the hawks exhibited no clear preference for either type but appeared to choose the tree that offered the best cover combined with easy access to the nest.

Nests were constructed of conifer twigs when available, but twigs from broadleaves were used when no conifers were nearby. Nests in broadleaf trees were built on top of pre-existing structures such as Woodpigeon Columba palumbus nests and Grey Squirrel Sciurus carolinensis dreys in more than half the cases. In conifers only one nest was built on a pre-existing structure (a Woodpigeon nest).

Most hawk nests were built between 10 and 14m above the ground, but the lowest was about 8m and the highest was more than 20m up.

B. The number of territories occupied in each year.

1976 - Four nests were found; in a fifth area adults were seen performing courtship displays in the spring and young were heard screaming and seen flying late in the summer; in a sixth area there were signs of activity (whitewash and pluckings) but no nest was found and activity ceased about the time other pairs began to incubate.

1977 - Six nests were found. All but one nest was found within 100m of a 1976 nest or occupied area (one 1976 area was inactive and one new area was found).

1978 - Eight nests were found. A ninth area showed signs of activity (calling adults and prey pluckings) which ceased at about the time other pairs of hawks began to lay. Five of the nesting areas were within 100m of 1976 or 1977 nesting areas; three areas were not known to have been occupied before during the study.

C. Spacing of nesting territories.

Analysis of spacing was based on Newton, Marquiss, Weir and Moss's (1977) definition of a nesting territory as an area "...occupied by only one pair which, in the breeding season, drove away other Sparrowhawks and other predators." Recent findings by Newton (in prep.) suggest that even if a pair of Sparrowhawks fails to nest successfully the home range may be maintained through the breeding season, especially by the male. Therefore, all areas in Wytham that showed signs of settling were included in the analysis.

The minimum spacing between two areas occupied in the same year

was approximately 300m (Table 1-1). The greatest distance between two nearest neighbour sites in the same year in habitat offering a continuity of trees suitable for nesting was about 1600m. The greatest distance between two nearest neighbours within the wood regardless of habitat continuity was about 1700m. The mean distance between nearest neighbours in continuous suitable habitat was 791.66 ± 98.83(1 S.E.). The mean distance between nearest neighbours regardless of habitat was 982.35 ± 109.89.

Newton et. al. (1977) found that spacing of Sparrowhawk nesting sites was related to both altitude and a land productivity index. The hawks in Wytham were found to nest most frequently on the flanks of Wytham hill, averaging an altitude of very close to 100m above sea level. The land productivity index, as used by Newton et. al. is about seven for the farmlands surrounding Wytham and about five for Wytham hill giving an average index of about six. Wytham nest site spacing was related to altitude and land productivity in a manner similar to that found by Newton et. al. (Figure 1-1).

D. Nesting success.

The location and name given to each Wytham nesting site in 1976, 1977 and 1978 is shown in Figure 1-2. The use and nesting success of each area in each year is summarised in Table 1-2.

Sometimes eggs were laid but the nest was abandoned almost immediately thereafter for unknown reasons. Two of the many possible causes are: 1) pesticide contamination causing eggshell thinning or breakage; 2) predation of eggs or excessive disturbance

Table 1-1. The distance between nearest neighbour Sparrowhawk nests in each year in Wytham.

Distance (x 100m)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19
Year																			
1976*								0	0	0							X		
1977				0						0	X					0	X		
1978			0	0		0	0	0	0	X							X		

0 = continuous suitable nesting habitat

X = not continuous suitable nesting habitat

* No data included for nest that was presumed to be successful but not found in the Thorny Croft area.

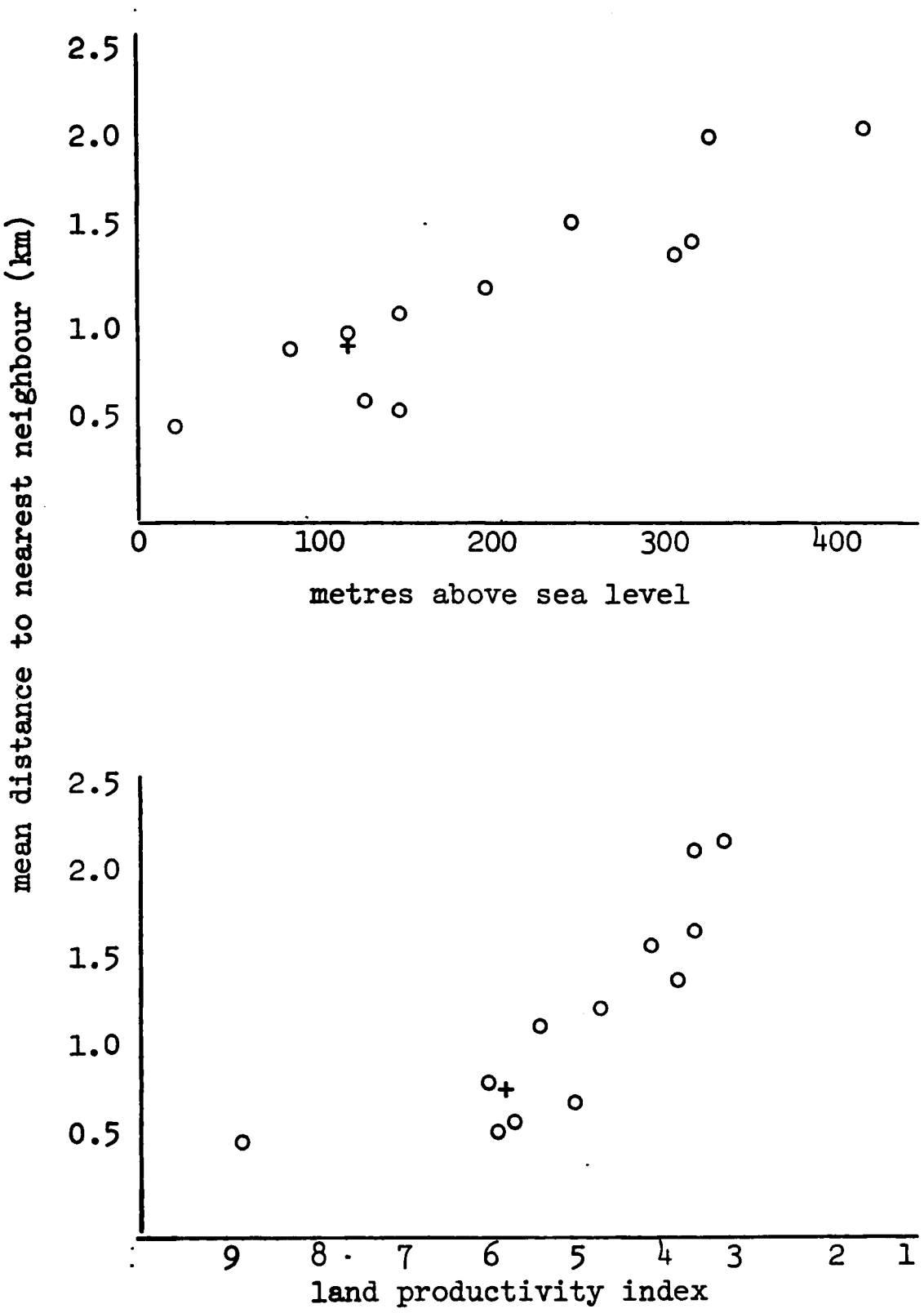

Figure 1-1. The relationship between altitude above sea level and land productivity and the mean distance between nearest neighbour Sparrowhawk territories. The original findings from Newton et. al. (1977) = o ; findings from Wytham = +.

of the incubating female caused by large flocks of Rook Corvus frugilegus and/or Carrion Crow Corvus c. corone roosting close to the hawk nest (this occurred at Bean and Lord's Copse in 1977). The possibility that my activities may have caused nesting failure was considered minimal since: 1) after a nest was found, visits to determine whether incubation had started were made from the ground and were limited to less than five minutes; 2) climbing of the nest tree was not carried out until at least one week after the female was seen to be lying on the nest, presumably incubating; and 3) all failures after the presumed beginning of incubation occurred before the first time the tree was climbed and always coincided with broken or addled eggs being found.

Hatch dates for nests which failed after the female was seen lying on the nest were estimated to be 35 days (the average incubation period) after the female was first seen on the nest. In some cases (e.g., Marley 1978 and Bean 1978) nests were not completed.

The breeding success based on the number of young fledged/nest from which young fledged was calculated for each year; also shown in Table 1-2. Included in Table 1-2 are data on brood manipulations carried out (under N.C.C. licence during 1977 and 1978. Broods were manipulated to maximise the number of pellets used for analysis of predation on tits (see Chapter 3) obtained, as the intent of the study was the effect of hawks on tits and not hawk breeding success. In 1976, at the Radbrook site where eggs were incubated beyond full term without hatching, no pellets were found, in contrast to nests where young were raised, indicating that virtually all the pellets

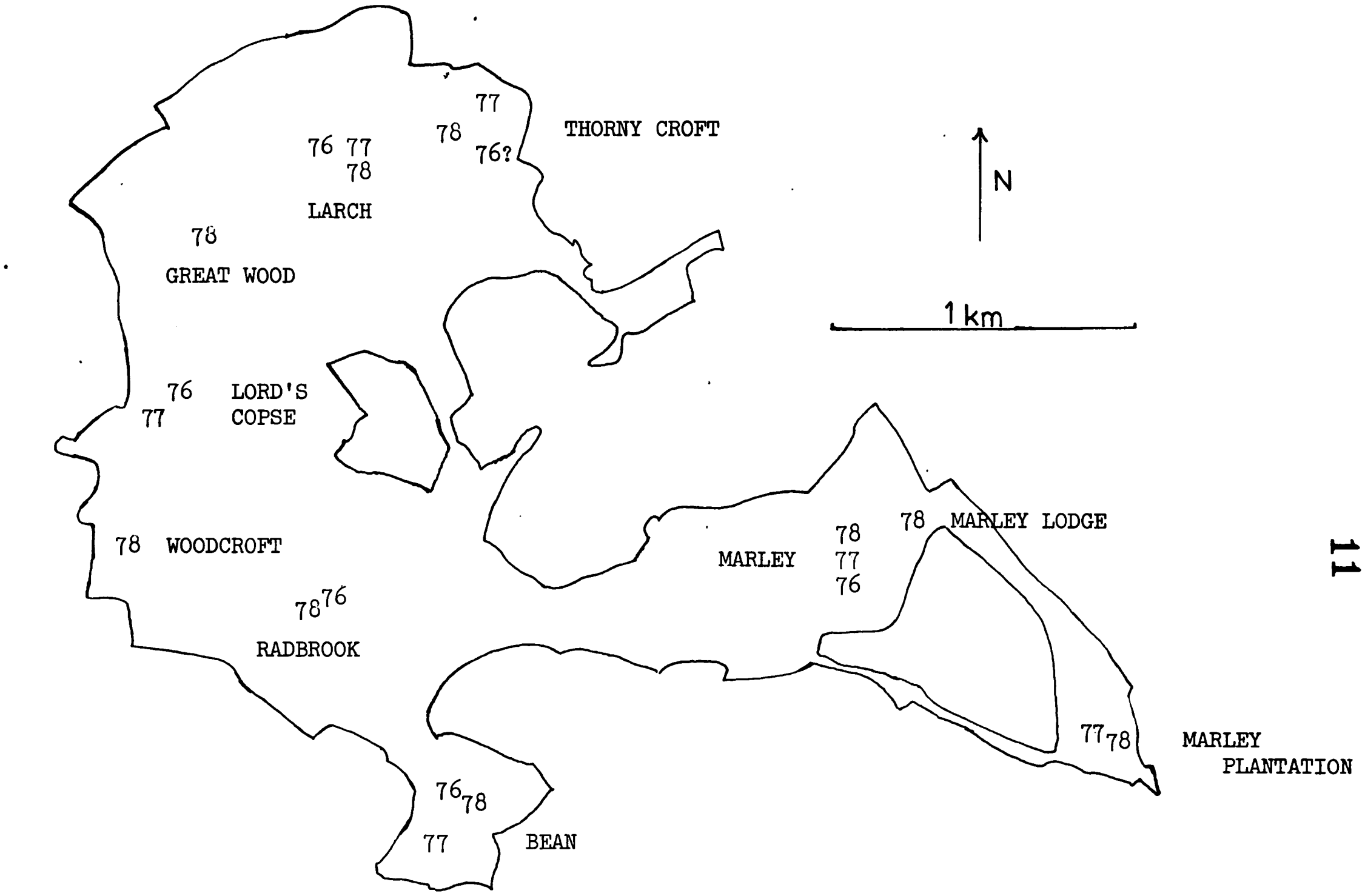

Figure 1-2. Map of Wytham showing nesting areas and the names assigned to them, with years in which they were used.

Table 1-2a. Summary of nest site use and nesting success of Sparrowhawks. Year - 1976

Area	Occupied	Number of eggs	Hatch date	Number young hatched	Number young added	Number young removed	Number young died	Number young fledged
Marley Plantation	No	--	--	--	--	--	--	--
Marley	Yes	?	13/6 [1]	1	0	0	0	1
Marley Lodge	No	--	--	--	--	--	--	--
Bean	Yes	4	22/6 [1]	4	0	0	0	4
Radbrook	Yes	2	(24/6) [2]	0	0	0	0	0
Woodcroft	No	--	--	--	--	--	--	--
Lord's Coppice	Yes	5	13/6	4	0	0	0	4
Great Wood	No	--	--	--	--	--	--	--
Larch	Yes	0	--	--	--	--	--	--
Thorny Croft	Yes	?	?	?	0	0	?	?

$\bar{x}$ number of young fledged/successful nest from natural broods = 3.00

$\bar{x}$ number of young fledged / successful nest including manipulations = 3.00

1) estimated from approximate age of young on first visit after hatching.
2) expected hatch date of eggs which did not hatch estimated from when female first seen incubating.

Table 1-2b Summary of nest site use and nesting success of Sparrowhawks. Year - 1977

Area	Occupied	Number of eggs	Hatch date	Number young hatched	Number young added	Number young removed	Number young died	Number young fledged
Marley Plantation	Yes	3+	23/6	1	1	0	0	2
Marley	Yes	4	9/6	2	2	0	4 disappr'd	0
Marley Lodge	No	--	--	--	--	--	--	--
Bean	Yes	1+	(21/6)[2]	0	0	0	0	0
Radbrook	No	--	--	--	--	--	--	--
Woodcroft	No	--	--	--	--	--	--	--
Lord's Copse	Yes	?	(14/6)[2]	0	0	0	0	0
Great Wood	No	--	--	--	--	--	--	--
Larch	Yes	5	(16/6)[2]	0	3	0	1	2
Thorny Croft	Yes	6	13/6	4	2	2	0	4

$\bar{x}$ number of young fledged/successful nest from natural broods = 2.50

$\bar{x}$ number of young fledged / successful nest including manipulations = 2.66

1) estimated from approximate age of young on first visit after hatching.
2) expected hatch date of eggs which did not hatch estimated from when female first seen incubating.

Table 1-2c. Summary of nest site use and nesting success of Sparrowhawks. Year - 1978

Area	Occupied	Number of eggs	Hatch date	Number young hatched	Number young added	Number young removed	Number young died	Number young fledged
Marley Plantation	Yes	5	21/6	4	0	0	1	3
Marley	Yes	0	?	0	0	0	0	0
Marley Lodge	Yes	2	15/6	2	2	1	0	3
Bean	Yes	0	?	0	0	0	0	0
Radbrook	Yes	4	27/6	3	0	0	0	3
Woodcroft	Yes	4	21/6	3	1	1	0	3
Lord's Copse	No	--	--	--	--	--	--	--
Great Wood	Yes	0	?	0	0	0	0	0
Larch	Yes	4	27/6	1	2	0	1 at hatch	2
Thorny Croft	Yes	1+	$(25/6)^2$	0	0	0	0	0

$\bar{x}$ number of young fledged/successful nest from natural broods = 2.75

$\bar{x}$ number of young fledged / successful nest including manipulations = 2.80

1) estimated from approximate age of young on first visit after hatching.
2) expected hatch date of eggs which did not hatch estimated from when female first seen incubating.

recovered were produced by young. To increase the data collected, young obtained elsewhere were introduced into nests that would otherwise have failed and into nests with small natural broods; these fostering techniques had already been used successfully for Sparrowhawks by Newton (pers.comm.) (and for other raptors, see Martin and Ruos 1976, Fyfe 1987, Meyburg 1978).

In 1977 broods were manipulated at four nests. The Marley pair received two young, three to four days younger than their own chicks, from the Thorny Croft pair. Three young were then obtained from northern Berkshire; two of these young were placed in the Thorny Croft nest to return it to its natural size (the foster young were about the same age as the natural young) and one young was placed in the Marley Plantation nest (this bird being a few days older than the natural chick) to increase the number of young to two. Since the Larch female was sitting after at least 51 days of incubation, three young ranging in age from five to ten days old were acquired from near Windsor, Berkshire, and introduced into the nest. In all cases the foster young were accepted by the adults without hesitation and were treated as natural offspring.

During 1978 three young were again obtained from outside Wytham and placed in Wytham nests. Two were put into the Marley Lodge nest where the young were about the same age and one placed in the Woodcroft nest where the young were just hatching. The approximately six day age difference between the foster and natural Woodcroft young did not appear to cause neglect of either the foster or natural young, and there were no signs of aggression between the chicks. At the Larch nest the only chick to hatch died

immediately, so the foster chick from Woodcroft and one chick from Marley Lodge were transferred to the Larch nest; the foster young at this nest were then about twelve days old. As in 1977 all foster young were accepted without incident.

IV. Discussion

In Wytham the majority of Sparrowhawk nests were built in deciduous trees, as in other parts of Britain where deciduous woodland is predominant (Owen 1916d, Mavrogordato 1973). However, when both conifers and broadleaves of suitable characteristics were available in the same area there did not appear to be a preference for nesting in either type; this is in contrast to the suggestions of certain authors (Brown and Amadon 1968, Brown 1976) who state that Sparrowhawks exhibit a preference for conifers. The selection of trees for nesting is apparently made on the basis of finding a tree offering the best conditions dependent on local vegetation characteristics, as suggested by Tinbergen (1946). The suggestion that Sparrowhawks prefer conifers is probably a misinterpretation of information based on the fact that most Sparrowhawk nesting studies have been carried out in areas of conifer plantations (e.g., those studies by Tinbergen 1946, Hald-Mortensen 1974, and Newton 1976). The manner in which nests were constructed and the height above the ground at which they were built in Wytham resembled the findings of previous observers (Owen 1916d, Tinbergen 1946, Sulkava 1964, Hald-Mortensen 1974).

The Wytham Sparrowhawk nests showed regular nest spacing consistent with land productivity and altitude relationships

indicated by Newton et. al. (1977), and the nearest neighbour distance in continuous suitable habitat was also comparable to some of the lowest distances found in other parts of Britain. The use of the same nesting area in a succession of years supports the findings of pronounced nest site fidelity described by Tinbergen (1946), Hald-Mortensen (1974), Newton (1976), and others.

The Sparrowhawks in Wytham exhibited a lower nesting success than those in Dumfriesshire which were studied slightly earlier (Newton 1976). The Wytham birds had both a lower mean clutch size (4.08 versus 4.78) and a lower mean number of young fledged/successful nest (2.69 versus 3.18) than the hawks in Dumfriesshire, although the rate of nest failures (percent of nests built which failed to produce natural young that fledged) was similar in both areas (44.4% in Wytham, 43.3% in Dumfriesshire).

The lower nesting success in Wytham may have been due to the fact that the area around Wytham is more extensively agricultural than the Dumfriesshire study area so that the use of pesticides was curtailed later, and to a lesser extent, than in Dumfriesshire. This theory is supported by the findings of Newton (1974) that Sparrowhawk nesting success was lowest near farm land, i.e. the areas of heaviest pesticide use. That pesticide contamination of the Wytham Sparrowhawks was still high during the course of the study is shown by the levels of pesticides in unhatched eggs collected under N.C.C. licence in Wytham during the study (Appendix 1).

Without fostering there would have been no young fledged from the Larch 1977 and 1978 nests, although eggs were laid and incubated full term. It might be argued that this fostering created an

artificially high number of nests fledging young, but it is felt that fostering probably only served to bring the number of successful nests to the minimum expected had there been no pesticide contamination. Prior to the advent of pesticide use in 1947, it was usual for Sparrowhawks that incubated a full clutch of eggs to fledge at least one young if undisturbed by Man; since pesticide use began the incidence of non-breeding pairs has increased dramatically (Newton 1974).

The fostering of young to nests that were already successful served most likely to bolster the Wytham population in the following years and to offset reductions in reproduction rates due to pesticide contamination.

Summary

1) The Wytham population of breeding Sparrowhawks appears to have reflected the trends of the British population, with a crash, due presumably to pesticide contamination, in the mid-1960's followed by re-establishment to its pre-pesticide era level of about six pairs in the mid-1970's.

2) Nests were most often built in deciduous broadleaf trees, often on pre-existing structures, and were usually 10 to 14m above the ground.

3) Areas occupied by breeding hawks averaged about 800m apart in continuous suitable habitat, with spacing corresponding to land productivity and altitude relationships found in other parts of Britain.

4) The percent of nests which failed was similar to the findings

of Newton (1976) for another part of Britain at a slightly earlier time. The nesting success of Wytham hawks was lower than that of the hawks in Newton's study area; this is thought to be the result of the continuing high level of pesticide contamination of the Wytham population.

Chapter 2. The effects of nesting Sparrowhawks on nesting tits.

Introduction.

This chapter, detailing the depression in nest box use and nesting success in tits due to Sparrowhawks, is presented in the form of a paper published in Condor in 1978 (80: 419-22). The material in the paper was based on the results of the analyses of 1976 and 1977 records. Tabulations of the data for 1978 were made at a later date and are included in Appendix 2; they serve to confirm the findings from the previous years, which may be summarised as follows.

1) Tits nesting within 60m of Sparrowhawk nests in the main body of Wytham showed reduced nest box use and nesting success if the nearby hawk pair incubated at least full term, while no reduction in nest box use and nesting success was found for tits when nearby hawk pairs failed at about the time of laying.

2) Reduction of tit breeding was linked to the presence of hawks and was not due to habitat, or other apparent factors. The mechanism for the depression of breeding is thought to be predation of breeding tits by the hawks and not avoidance of the vicinity of hawk nests by tits.

3) The analysis of tit breeding records from years when hawks were absent from the wood and years when hawks were breeding in the wood indicate that since the return of the hawks there has been an increase in the rate of tit breeding failure. As no other

factors were known to have affected tit breeding since the return of the hawks, it is felt that the hawks were the cause. These breeding failures since the return of the hawks encompass an area wider than the 60m from successful hawk nests, suggesting that the hawks have a widespread influence on the breeding tit population, reducing the number of tit pairs raising young by about 5%.

Condor, 80:419–422

EFFECTS OF NESTING SPARROWHAWKS ON NESTING TITS

TIMOTHY A. GEER

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.

Nest and year	Annulus I (0–60 m) U	S	N	II (61–120 m) U	S	N	III (121–180 m) U	S	N	IV (181–240 m) 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).

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

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.

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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Chapter 3. The feeding biology of Sparrowhawks during the nestling period.

I. Introduction.

Eight Sparrowhawk nests in which young were raised were watched from hides during the nestling period to assess the number and type of prey brought to the broods, with special attention paid to the utilisation of tits as prey by the hawks.

The nestling period, from hatching until the first flight away from the nest by female young, lasts about 30 days (Owen 1916c, Tinbergen 1946, Sulkava 1964, Newton 1978). This portion of the breeding cycle was selected for the most intensive study as the majority of prey taken during this period is brought to the nest, at which detailed observations can be made.

II. Methods.

A. Watches of nests from hides.

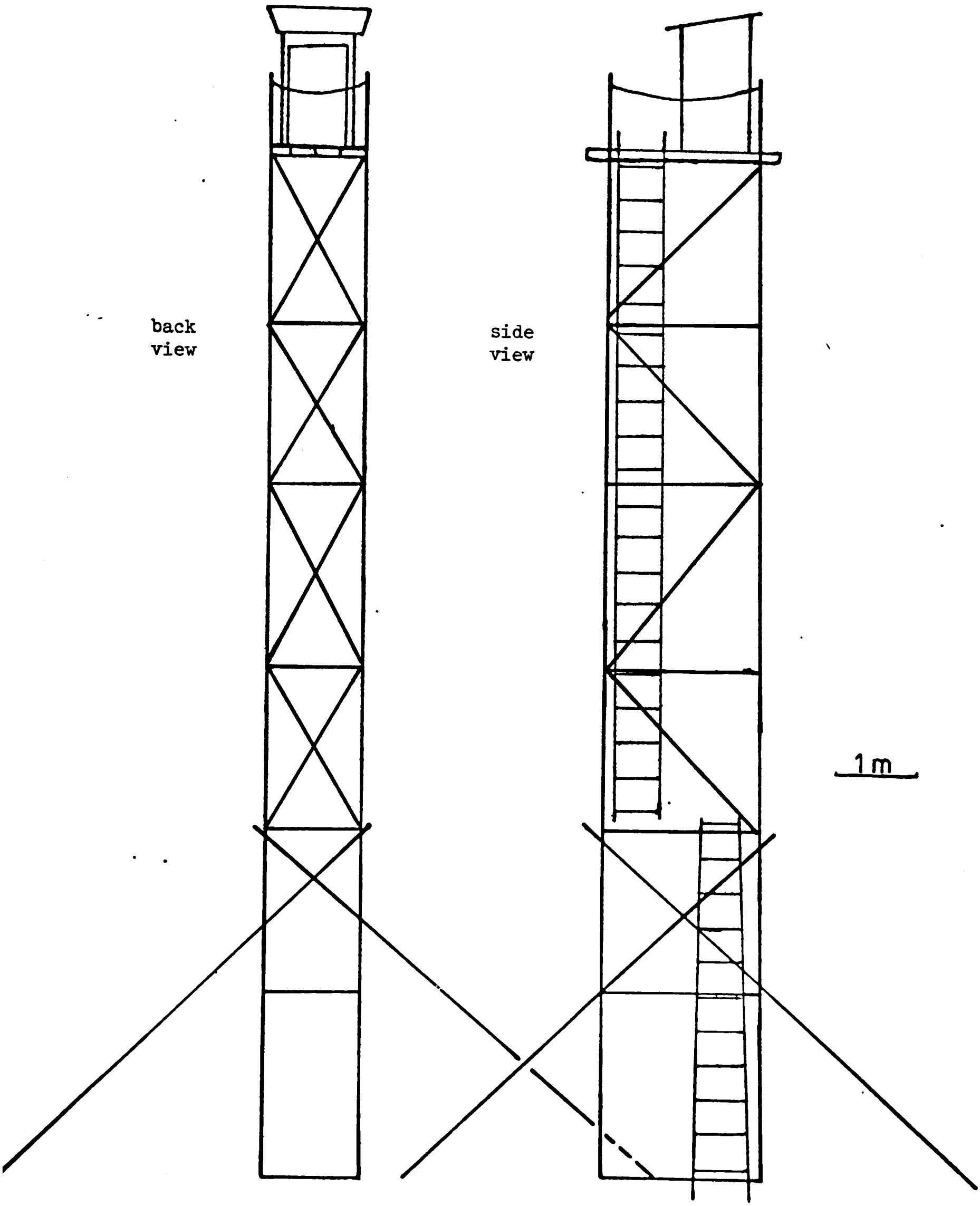
Eight hides were constructed at Sparrowhawk nests to observe the type and number of prey brought to the nests during the nestling period.

In 1976 the first hide was built at the Lord's Copse nest, in a tree about 6m from the nest tree, by suspending a pre-constructed canvas hide over a platform of angle-iron and wood which was constructed in a fork level with the hawks' nest. To minimise disturbance of the adult birds, work did not start until two days after hatching and was carried out in five one-hour periods over four days. Although the female parent flew past the nest "kek-ing" while work was in progress, she remained in the area of the nest;

once the hide was occupied the adults accepted it readily and showed no signs of shyness. Observations were carried out from the eighth day after hatching (day nine of life) for about three hours/day using a 35mm SLR camera with a 300mm lens to identify and photograph the prey items brought to the nest. These observations were generally unsatisfactory because the three hour watches were too short and, moreover, the distance between the hide and the nest made it difficult to identify prey both at the time and from photographs. A second method of observation was therefore tried at the Bean nest. A hide was placed on the ground at about 4m from the point where the female collected prey brought by the male. The prey exchange occurred rapidly, with its location shifting up to 3m on the branch each time, making observations fruitless.

To improve on the 1976 observations, the hides in 1977 were built closer to the nests. Newton (1978) had successfully placed hides as close as 2m from Sparrowhawk nests. Hides were built on free-standing towers of tubular scaffolding with independent clamps because suitable trees were seldom available. Wooden planks were lashed to horizontal poles of the tower at the height of the nest to make a platform on top of which a hardboard hide was placed (Figure 3-1). The first tower was built at Marley, the first nest to have young hatch. Construction began on day three of life and was done in four one-hour sessions over four days to minimise disturbance. The 13m high structure was completed on the seventh day of life at which time observations began. The front of the hide was 1.5m from the centre of the nest cup with the wooden platform touching the bottom of the

Figure 3-1. Diagram of a scaffolding tower with a hardboard hide.



nest. Even though the hide was so close, the female was back brooding and feeding the young within 15 minutes of completion and first occupation of the hide. Observations at this nest were made through a 35mm SLR camera with a 135mm lens; prey was readily identifiable, usually to species, both at the time and from photographs. Eight hour watches were carried out from dawn to dusk, 0500 to 2100 hours BST, or as close to this as manpower would permit, until the young disappeared on day 24 of life.

Due to its success at Marley, scaffolding was also used at Marley Plantation in 1977. A 14m high tower was built in four days beginning 15 days after hatching, once again in short work periods, and observations began at the end of construction on day 18 after hatching. This late start was due to a lack of manpower to both build towers and run watches at the Marley nest, which had been given preference so as to get as complete an idea as possible of the events at one nest. The hide at Marley Plantation was about 2m from the centre of the nest cup, so that a 35mm SLR camera with a 135mm lens could again be used for observations. As at Marley, watches were run when possible for 16 hours from dawn to dusk each day. On day 26 of life the climbing of the tower to the hide caused the young to fledge prematurely; they were subsequently recovered and replaced in the nest. Observations were discontinued until day 30 of life, but nearly all food was then brought to the young away from the nest; after two days, watches were terminated. The adults at this nest showed no signs of shyness.

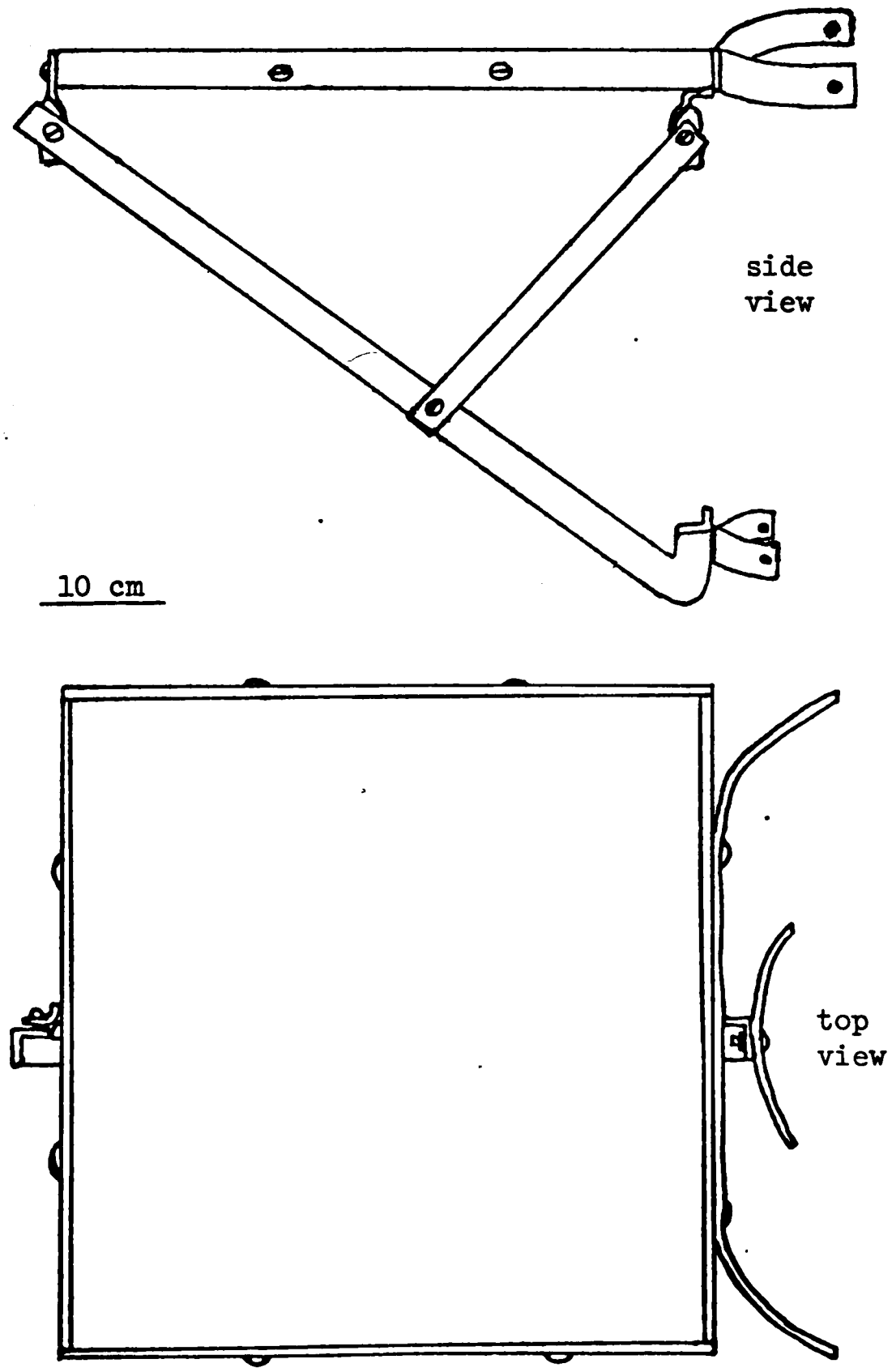
At the Larch nest in 1977 the eggs failed to hatch and three

foster young were introduced and readily accepted by the adults (see Chapter 1). Originally there was no intention of building a tower at this nest, located 18m above the ground, because the tree was growing off the perpendicular and the ground was soft and sloping. However, after the loss of the Marley brood, it was decided to observe the Larch nest for a short period to obtain as many and as varied data as possible. Since a tower could not be built to the nest, it was decided to lower the nest. First, a 6.5m high tower was built 3m from the trunk of the nest tree. The young and nest were then lowered to a platform of wood and angle-iron (Figure 3-2), which was lashed to the tree about 4m below the original position of the nest, and left for the night to see how they fared. The following day the young had been fed and were in good condition; they were therefore lowered along with the nest platform to a point another 4m down the tree. On the third day the platform and young were lowered another 4m to the level of the hide, a total of about 12m, and watches begun; at this time the young were due to fledge in about six days. The parents appeared somewhat nervous with this arrangement but continued to bring food and to feed the young regularly. The nest was observed for 3.5 days for a total of 43 hours, after which the young were attached to a tether platform (see below).

The only other successful hawk nest in 1977, Thorny Croft, was not observed because it was too high above the ground (over 21m) to use scaffolding safely.

The use of free-standing scaffolding towers was continued in 1978. The first 1978 tower was built at Marley Plantation primarily

Figure 3-2. Diagram of nest platform used at Larch 1977.



for cinematographic filming of the nest life of Sparrowhawks. So as to film the female during incubation, building was begun about one week before the eggs were due to hatch. The female continued to incubate while construction was underway below her. When work reached the level of the nest she flew off, only to return less than ten minutes later; she continued incubation while watching us work less than 2m from the nest. This hide was used intermittently for observations totalling 29 hours when filming was not in progress.

The second hide built in 1978 was at Marley Lodge. Work was begun on the second day after hatching and was completed, with watches started, on day three after hatching. The tower was 9m high with the hide 1.25m from the centre of the nest cup. No camera was used as it was too close for any telephoto lens to focus. Watches of five and six hours duration were carried out for as close to 16 hours/day as possible, but were suspended from the end of day 24 of life until day 30 of life to avoid having the young fledge prematurely. The adults at this nest were not shy of the hide.

At Radbrook a third tower was built in four days, with watches begun eight days after hatching. The hide was 2.5m from the centre of the nest cup such that a 35mm SLR camera with 135mm lens was used for observation. Watches at this nest were also carried out for as close to 16 hours/day as possible. The female spent little time at the nest except to feed the young and to brood them in heavy rain.

The Larch and Woodcroft nests in 1978 were not watched because time and other resources could not be spared.

B. Tethering young.

To investigate the type and frequency of prey delivered during the post-fledging period, tether platforms of the type described by Petersen and Keir (1976) were tried in 1977. The purpose of these platforms was to prevent the young from leaving the nest area, so that prey brought to them could be analysed and the number of prey brought/day calculated.

The first attempt to use a platform, at Thorny Croft, failed because the young left the nest and moved into adjacent branches when the tree was climbed; pursuit was discontinued to avoid forcing the young from the tree before they could fly properly. In the second attempt, the two surviving young from Larch were tethered to a platform on the scaffolding where the hide had been, three to four days before they were due to fledge. Food had to be supplied for two days because the parents brought none. On the third day after tethering the female began to supply food at what was thought to be a reduced rate (about two prey/day) and prey from the male (judged by size of prey) did not begin to appear until five days after tethering; additional food was supplied to the young during this period also. The young were released from tether after twelve days, after which they remained in the area for more than two weeks, being fed by the parents away from the platform. Since the results obtained from tethering were probably inaccurate, they were not included in the analyses. The use of tethering was discontinued due to the poor results and the amount of time required for the care of the young.

C. Collection of pellets and rings.

Hawk pellets (regurgitated indigestible matter) were collected from successful hawk nests in order to recover any rings eaten by hawks. Records of the number of pellets and rings during each collection at each nest were made. While most rings were contained within the pellets, some were found loose in the nest; it is thought that these had come out of pellets cast into the nest and subsequently trampled by the young.

During 1976 and 1977 successful nests were checked as often as possible (usually every other day, but sometimes every three to four days) during the nestling and post-fledging periods; nests were checked daily while under observation from hides. During 1978 all successful nests were checked daily from the day after hatching until one week after the young had fledged, except at Radbrook, where nest checks started the day observations began, and at Marley Plantation where access to the nest was impossible.

In 1976 pellets began to appear on the ground around the nest after the beginning of the second week of the nestling period. Watches from hides revealed that at this time the young had begun to shake their heads sufficiently forcefully during regurgitation to send pellets over the side of the nest. Beginning in 1977, small mesh nylon nets of up to 5.5m square ($30.25m^2$) were placed under all nests, either in the tree or on the ground, to catch pellets. The nets were checked for pellets whenever pellet collections were made at the nest.

Roosts and plucking posts frequented by the adults in each territory were checked for pellets in all three years. During

this time only one pellet was found. This was due, most likely, to the fact that the adults' roosts and plucking posts were usually tree limbs more than 3m above the ground, so that head shaking during regurgitation probably caused the pellets to fall a good distance from the perch into heavy growths of brambles (Rubus spp.) and stinging nettles (Urtica dioica), which characterised the ground cover. An attempt was made during 1976 to locate pellets containing rings in these areas using a metal detector, but the metal content of the rings was too low to obtain satisfactory results.

Near the end of the post-fledging period, the nests from all successful pairs, with the exception of Marley Plantation 1978, were removed for dissection to recover pellets and loose rings in the structure.

During the course of the study a total of 329 pellets were recovered, containing 218 rings from tits and 15 from other species.

III. Results.

A. Roles of the parents during the nestling period.

At both Marley 1977 and Marley Lodge 1978, observed from early in the nestling period, the male parents provided all of the food during the first third of the nestling period. The males continued to supply food for the young throughout all watched periods after day ten of life at all nests under observation.

At all watched nests the females did all the brooding of, and food distribution for, the young. At Marley 1977 and Marley Lodge 1978 the females began to hunt when the young were 11 and nine days old, respectively; at Radbrook 1978, the female was hunting on the first full day of observations, when her young were ten days old.

B. The rate of prey delivery through the nestling period.

After females began to hunt, it was possible to distinguish with reasonable reliability which adult had supplied each item brought to the nest during watches. The following criteria from Newton (1978) were used for prey supplied by the male: prey brought to the nest by the male; prey brought to the nest by the female after she had been called from the nest by the male; and prey brought by the female after she had been out of sight for only a very short time (c. five minutes). All other prey were attributed to the female. Prey were categorised in this way at Marley 1977, Marley Lodge 1978, and Radbrook 1978, but not at Lord's Copse 1976, Bean 1976, Marley Plantation 1977 and Larch 1977. The number of prey delivered/hour watched was calculated for three day periods, to obtain adequate sample sizes.

i. Prey deliveries by males.

Figure 3-3 shows the prey delivery rate at Marley 1977, Marley Lodge 1978, and Radbrook 1978 plotted against day of life of the young at each nest during the period watched. The data for days 23 and 24 of life at Marley Lodge were excluded because of insufficient observations. These males showed a decrease in the number of prey brought/hour watched as the nestling period progressed. At Radbrook, the decrease (averaging 0.13 less prey/day assuming hunting for 16 hours/day) was less marked than for the other two males (0.32 and 0.24 less prey/day for Marley and Marley Lodge, respectively).

ii. Prey deliveries by females.

Figure 3-4 shows the rate of prey deliveries by females from

Figure 3-3. The number of prey brought/hour watched by male Sparrowhawks plotted against day of life of their young.

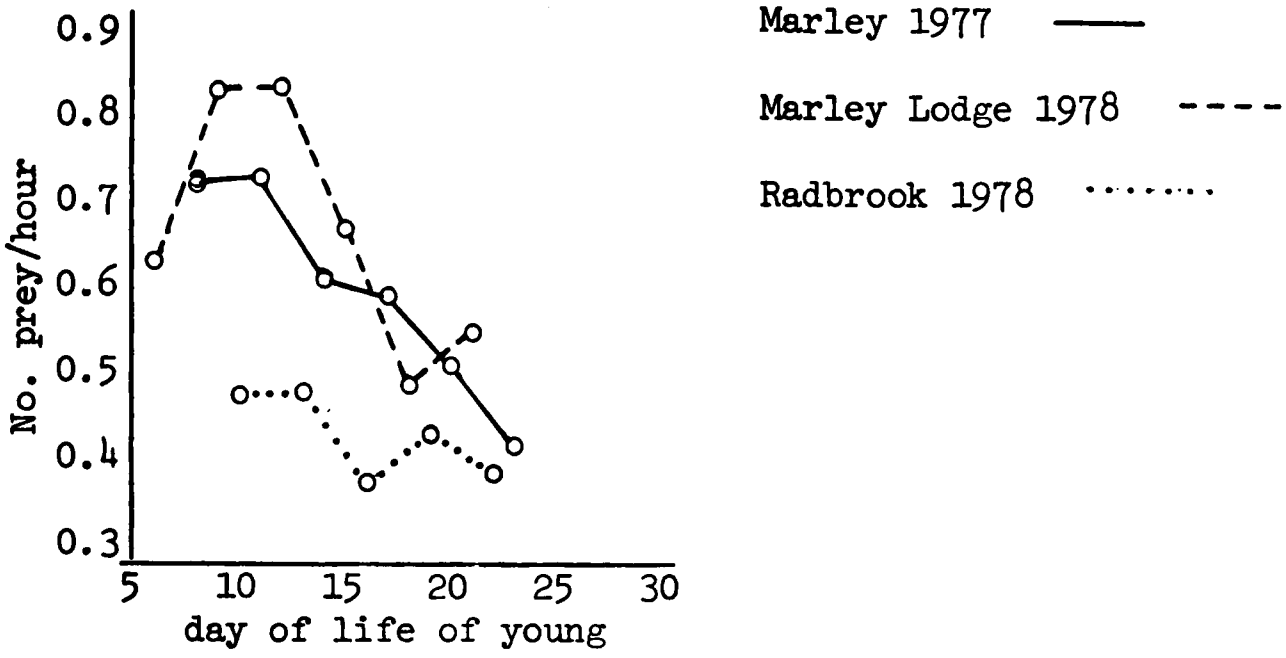


Figure 3-4. The number of prey brought/hour watched by female Sparrowhawks plotted against day of life of their young.

Key as for Figure 3-3.

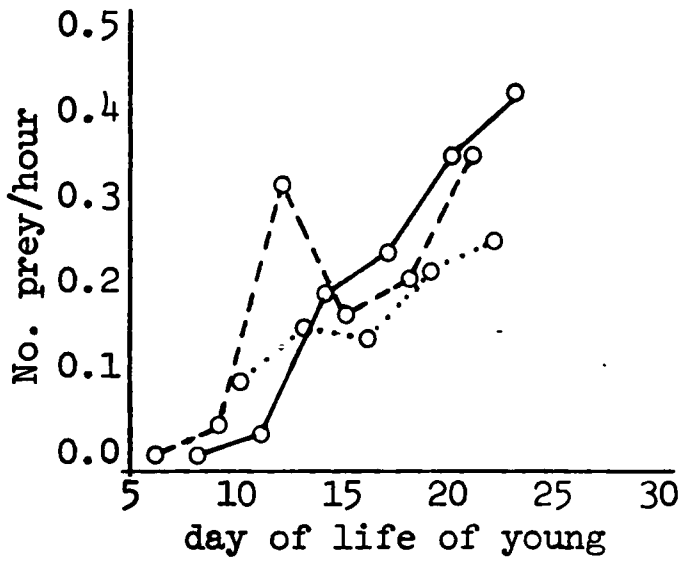
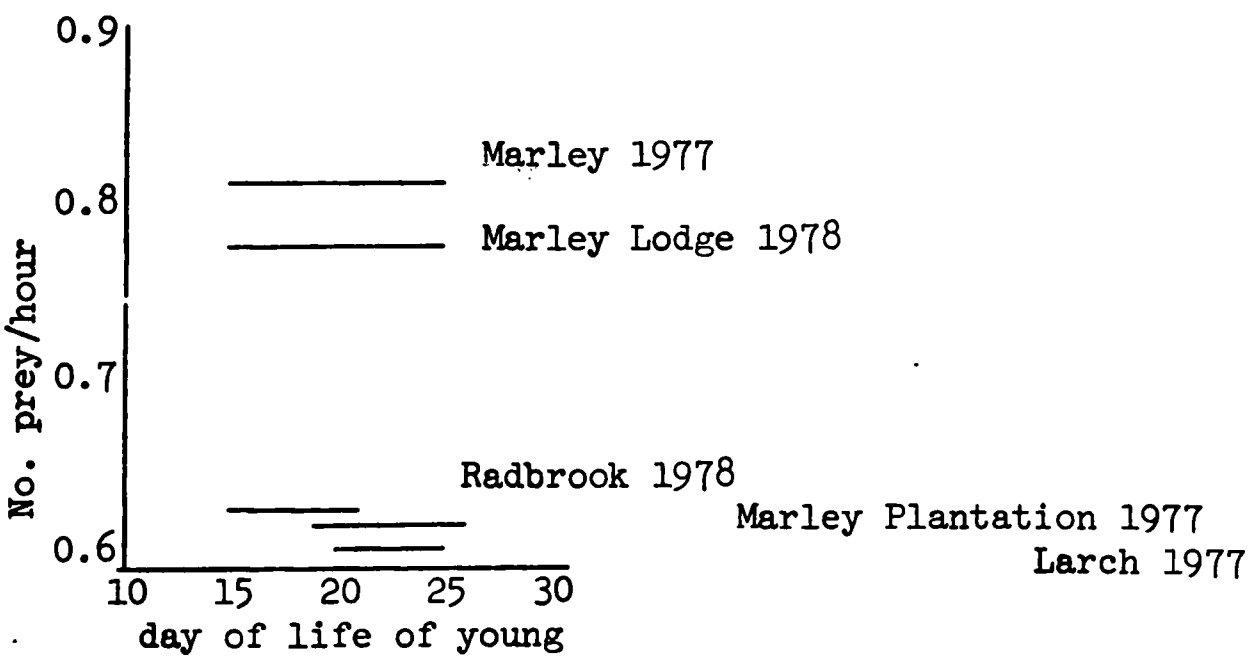


Figure 3-5. The mean of the total number of prey brought/hour watched by both parents after day 15 of life of their young plotted against the days of life of young after day 15 until the end of watching.



the above nests. Their number of prey brought/hour watched increased from about day ten of life of their young, reaching about 67% and 100% of the males' delivery rates between day 20 and 25. Mirroring the patterns of the males, delivery rate increases were greatest for the females at Marley and Marley Lodge (averaging 0.48 and 0.32 prey/day, respectively) and least for the female from Radbrook (0.19 prey/day, average).

iii. Total prey delivery from both parents.

Watches at Marley Plantation 1977 and Larch 1977 were conducted when both parents were hunting, but contributions from each parent were not distinguished. The mean prey delivery rates for Marley Plantation and Larch are compared to the mean delivery rates for Marley, Marley Lodge, and Radbrook for the period when both parents were hunting regularly (from day 15 of life to the end of watches). Mean rates from both parents were not calculated for Lord's Copse 1976, Bean 1976, and Marley Plantation 1978 due to possible bias from the small number of hours watched/day at these nests. The hawks at Marley and Marley Lodge showed higher combined prey delivery rates (0.82 and 0.77 prey/hour, respectively) than those at Marley Plantation, Larch, and Radbrook (0.63, 0.61, and 0.63 prey/hour, respectively). (Figure 3-5).

C. The pattern of prey deliveries through the hours of the day.

Information on the total rate of prey delivery in each hour of the day during watches is given in Table 3-1 for the five nests. (There were too few samples from females to test for sex differences in the within-day pattern of deliveries.) Calculations of diurnal

Table 3-1. The pattern of prey deliveries through the hours of the day at watched Sparrowhawk nests. Hr.obs. = number of hours watched; Del.obs. = number of deliveries observed; x^2 = chi-square value for the hour.

	Marley 1977			Marley Lodge 1978			Marley Plantation 1977			Radbrook 1978			Larch 1977		
Hour of day	Hr. obs.	Del. obs.	x^2	Hr. obs.	Del. obs.	x^2	Hr. obs.	Del. obs.	x^2	Hr. obs.	Del. obs.	x^2	Hr. obs.	Del. obs.	x^2
0400-0500	0	-	-	1	0	0.8	0	-	-	0	-	-	0	-	-
0500-0600	14	13	3.4	14	5	3.4	8	7	2.3	6.5	8	2.5	2.5	1	-
0600-0700	17	10	0.8	15	14	0.3	8	8		8	5		3	4	-
0700-0800	17	9	1.4	16	13	0.0	8	7	0.8	8.5	8	0.1	3	1	-
0800-0900	17	17	1.0	17	13	0.0	8	6		9	3		3	0	-
0900-1000	17	8	2.1	17	11	0.5	8	5	0.1	8	3	0.0	3	1	-
1000-1100	17	12	0.1	16	11	0.3	8	4		10	8		3	3	-
1100-1200	17	11	0.4	16	11	0.3	8	5	0.0	11	8	0.1	3	2	-
1200-1300	17	21	4.5	16	15	0.4	8	5		11	4		3	2	-
1300-1400	16.5	11	0.3	16	10	0.6	5.25	4	1.5	11	2	0.1	2	2	-
1400-1500	17	20	3.4	16	14	0.1	5.5	6		10	11		2.5	2	-
1500-1600	18	18	1.1	17	17	0.9	6	1	1.7	10	6	0.0	3	1	-
1600-1700	18	11	0.7	16	17	1.4	6	3		8	4		3	1	-
1700-1800	18	14	0.0	16	20	4.1	6	3	0.2	8.75	3	0.3	2.5	2	-
1800-1900	18	17	0.6	15	17	2.1	6	5		10	6		2	1	-
1900-2000	18	17	0.6	15	9	0.8	6	1	5.4	8.75	4	1.4	2	1	-
2000-2100	17	5	5.2	12.5	4	3.6	5.5	0		8	2		2	2	-
Total	273.5	214	25.6	251.5	201	19.6	110.5	70	12.0	146.5	85	4.5	42.5	26	-

All x^2 totals not significant.

patterns were not made for the Lord's Copse 1976, Bean 1976, and Marley Plantation 1978 because of possible bias from the lack of spread in the hours of watches.

The rate of prey delivery through the day did not differ significantly between hours at Marley and Marley Lodge, or the two hour periods (to permit analysis, as hourly samples were too small) at Marley Plantation 1977 and Radbrook (x^2 goodness-of-fit tests). There were too few observations at Larch to permit analysis even with data pooling, but the pattern of deliveries at that nest appeared similar to those at the other nests.

D. The effect of brood size changes on prey delivery rates.

To investigate any effect of brood size manipulations (Chapter 1), the rate of prey delivery was calculated for watches during the 32 hours of daylight before and after the size changes. The delivery rates showed no significant change (Table 3-2) after any manipulation.

E. Size composition of prey.

Appendix 3 lists the species of prey which were taken by Sparrowhawks in Wytham during the breeding season, as determined from hides, ring recoveries, and the identification of prey remains.

Prey brought to five of the watched nests were classified into the following approximate weight categories (adults and juveniles of the same species were put into the same category):

1. Tit size (15g) - e.g., Parus spp., Phylloscopus spp. Prunella modularis, Erithacus rubecula.

Table 3-2. The effect of brood-size changes on prey delivery rates at watched nests during the 32 daylight hours before and after the manipulation.

Marley 1977 (2 young added to existing brood of 2 on day 9 of life)

No. prey brought		23	24	
	2 young			4 young
No. hours watched		32	32	x^2 = 0.004 with Yate's correction, N.S.

Marley Lodge 1978 (2 young added to brood of 2 on day 7 of life; 1 young removed on day 13 of life)

No. prey brought		21	23	
	2 young			4 young
No. hours watched		32	29.5	x^2 = 0.056 with Yate's correction, N.S.

No. prey brought		38	14	
	4 young			3 young
No. hours watched		31	18	x^2 = 0.72 with Yate's correction, N.S.

2. Finch size (30g) - e.g., Passer domesticus, Fringilla coelebs, Pyrrhula pyrhulla.
3. Thrush size (85g) - e.g., Turdus merula, Sturnus vulgaris.
4. Jay size (275g) - e.g., Garrulus glandarius.
5. Pigeon size (500g) - e.g., Columba spp.
6. Unknown avian - all of which were brought to the nest partially eaten or were obscured from view during the feed and could not be identified but which would have fallen into the first three categories; assigned an approximate mean weight of 30g.
7. Mammals - both of these were Bank Voles Clethrionomys glareolus brought to the Radbrook nest; assigned an approximate mean weight of 25g.

Table 3-3 shows the number of prey in each category, subdivided by sex of parent providing each item where appropriate. At all nests where the contribution of each parent was known, significant differences were found between the size of prey brought by the male (a greater proportion of classes 1 and 2) and the female (larger classes). However, no significant differences were found between the size of prey brought by members of the same sex at different nests.

F. The proportion of the diet composed of ringed tits during watches.

During watches at Marley 1977, Marley Plantation 1977, Larch 1977, Marley Lodge 1978, Radbrook 1978, and Marley Plantation 1978 all prey were classified as to whether or not a tit, and, if a tit, whether or

Table 3-3. Size categories of prey brought to nests during watches.

Nest and year.	Marley 1977		Marley Lodge 1978		Radbrook 1978		Marley Plantation 1977	Larch 1977
Sex of parent.	male	female	male	female	male	female	both	both
1. Tit size.	139	28	118	32	41	10	31	15
2. Finch size.	14	5	13	12	11	6	27	3
3. Thrush size.	2	19	7	13	1	9	11	7
4. Jay size.	0	2	0	1	0	0	0	1
5. Pigeon size.	0	0	0	0	0	2	0	0
6. Unknown avian.	3	2	2	2	1	2	1	0
7. Mammal.	0	0	0	0	2	0	0	0

x^2 between sexes (categories 3,4, and 5 pooled) - Marley, 58.52, $P < 0.001$; Marley Lodge, 22.80, $P < 0.001$; Radbrook, 22.66, $P < 0.001$.

x^2 between males at Marley, Marley Lodge, and Radbrook (categories 2,3,4, and 5 pooled) - 5.09, not significant.

x^2 between females at Marley, Marley Lodge, and Radbrook (categories 3,4, and 5 pooled) - 6.53, not significant.

N.B. Categories 6 and 7 excluded from all analyses.

Table 3-4. The percent of prey composed of tits and ringed tits at watched nests.

Nest and year	Marley 1977		Marley Lodge 1978		Radbrook 1978		Marley Plantation 1977	Larch 1977	Marley Plantation 1978
Sex of parent	male	female	male	female	male	female	both	both	both
No. tits known to be ringed	59	6	51	7	8	2	1	4	2
No. tits known to be unringed	34	5	38	5	11	3	19	2	12
% of tits ringed	63.44	54.55	57.30	58.33	42.11	40.00	5.00	66.67	16.67
No. other tits	25	7	11	2	12	3	3	4	2
Total prey in this analysis	153	53	136	57	53	27	65	25	29
% prey tits	77.12	33.96	73.53	24.56	58.49	29.63	30.78	40.00	48.28
% prey ringed tits	49.02	18.87	41.91	33.68	24.53	11.11	1.54	28.00	6.90
	41.26		33.68		20.00		1.54	28.00	6.90

not they were ringed. Table 3-4 shows the breakdown of prey into these classes for each nest, and by parent where appropriate.

Tit prey whose legs could not be seen (because they were brought to the nest missing one or both legs, or because they were obscured during the feed) were assumed to have been ringed in the same proportion as those tits whose legs were seen. This treatment was justified by the stability throughout the period of hide watches in the proportion of ringed birds among tits brought by the male hawks at Marley and Marley Lodge (Figure 3-6). Samples from the male at Radbrook and the females from Marley, Marley Lodge, and Radbrook were too small for analysis, but again the percentage of tits which were ringed did not appear to vary greatly with time at each nest.

G. Production of pellets.

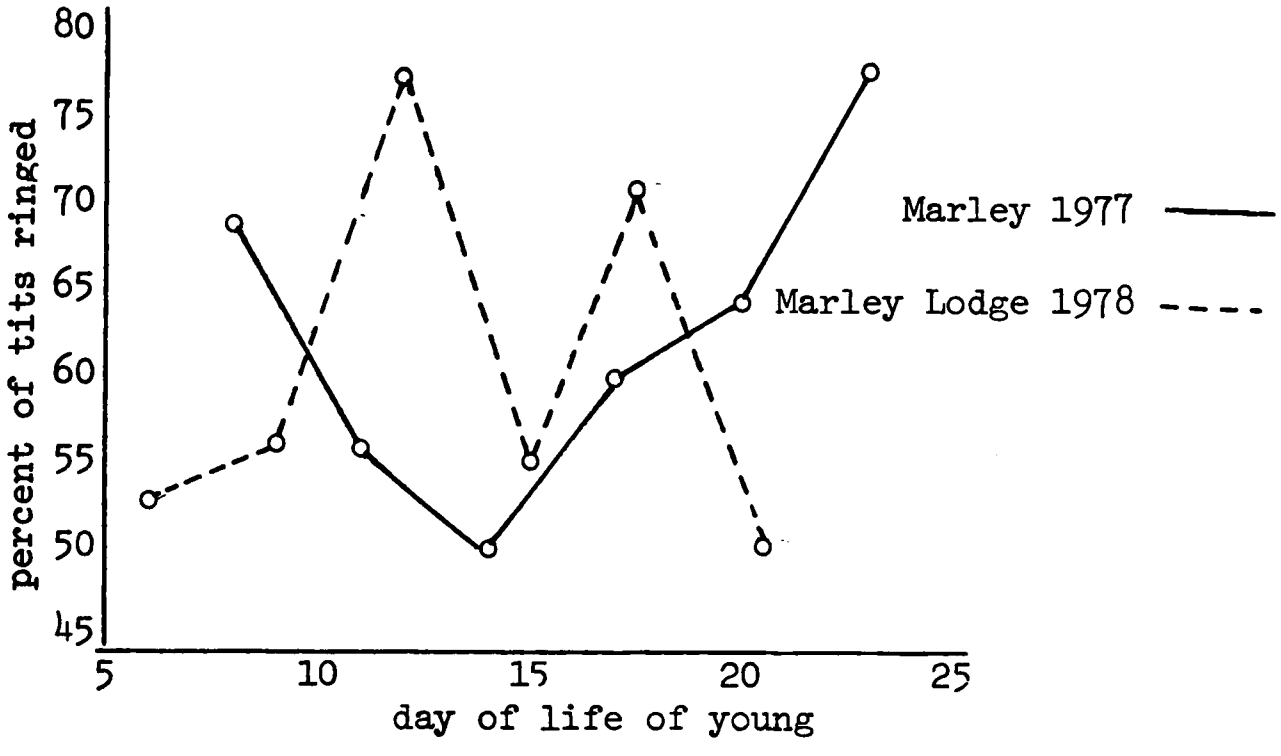
i. By the young.

Pellet recoveries and early morning hide watches showed that each young produced on average one pellet/day. Records also indicated that the young did not begin to produce pellets until about day four of life and that the pellets did not contain rings or bones until about day seven of life.

ii. By the females.

No pellets were found in either nests or nets erected to catch pellets during regular checks in the incubation period. Moreover, females were never seen to cast pellets at the nest. However, one pellet recovered at Marley 1977 during the nestling period contained ten rings, a number greater than the number of rings

Figure 3-6. The percent of the tits brought by the male during watches which were ringed.



seen consumed by the young in the two previous days combined. This pellet probably came from the female, with the large number of rings due, perhaps, to prey consumed away from the nest and pellets produced by the young that she had eaten (see below). As no other pellets containing more than four rings were found, and because females were not seen to cast at the nest, all other pellets were assumed to have been produced by the young.

H. Feeding and pellet removal behaviour of the females.

The recovery of pellets and rings was affected by two aspects of female behaviour: the swallowing of hard parts of the prey before feeding the young; and her removal from the nest of pellets produced by the young.

Until about day seven of life the females were seen during feeds to consume all hard parts of the prey, including ringed legs. Where recorded, the percentage of rings consumed by young at each nest is given in Table 3-5.

After about day ten of life the number of pellets recovered/day/young declined at all nests. At this point, the females were seen to be eating or removing pellets recovered in relation to the estimated number produced (based on one pellet/day/young) is also given in Table 3-5.

I. The ring/pellet and ring/nest ratios.

Table 3-6 shows the number of rings from tits from each nest collected after day seven of life (excluding the rings from the ten Marley 1977 pellet and pellets from dissected nests). Marley 1976

Table 3-5. The percent of rings which were fed to the young (%FY), and the estimated percent of the pellets produced by the young (%P) which were recovered at watched Sparrowhawk nests.

Nest and year	%FY	N	%P	N
Marley 1977	70.37	54	37.50	64
Marley Plantation 1977	?	1	50.00	20
Larch 1977	80.00	5	81.82	11
Marley Lodge 1978	77.14	35	50.82	61
Radbrook 1978	83.33	6	45.83	48

is omitted because only three pellets were collected prior to the removal of the nest. The data are divided into two parts, collections made through day 20 and after day 20 of life, for two reasons: to separate the periods when the male was doing the majority of the hunting and when both parents were hunting regularly, and because the proportion of the pellets produced in the two periods recovered at each nest were not equal.. Day 20 was chosen because a shorter period did not provide large enough samples.

The ring/pellet ratio shown in Table 3-6 for each period at each nest is independent of the total complement of young, i.e. a nest containing two young fed a total of x rings would have 50% of the rings in each pellet, while a nest with four young would have 25% of x rings in each pellet, assuming equal distribution of items among the young as suggested by Newton (1978). Therefore, the ring/pellet ratio for each nest in each period was multiplied by the number of young in the nest in the same period to obtain the ring/nest ratio. For nests where young were introduced, removed, or died, the mean number of young in the nest over each period was used.

J. <u>The relationship between the percent of the prey which was ringed tits and the ring/nest ratio at watched nests</u>.

A significant correlation was found between the percent of prey which was ringed tits and the ring/nest ratio (Figure 3-7). The percent of the prey which was ringed tits accounted for 93.33% of the variance (r^2) of the ring/nest ratio. The percent of prey which was ringed tits in each period was estimated for each nest

Table 3-6. The number of rings from tits (R) and pellets (P), the ring/pellet ratio (r/p), the number of young (Y), the ring/nest ratio (r/n), and the estimated percent of prey which was ringed tits (%RT) at nests where pellets were collected (excluding Marley 1976 due to small sample size).

	Through day 20						After day 20					
Nest and year	R	P	r/p	Y	r/n	%RT	R	P	r/p	Y	r/n	%RT
Lord's Copse 1976	9	11	0.818	4	3.272	36.64	4	10	0.400	4	1.600	20.19
Bean 1976	9	12	0.750	4	3.000	33.96	6	28	0.214	4	0.857	12.88
Marley 1977	23	20	1.150	3.714	4.271	46.47	3	4	0.750	4	3.000	33.96
Larch 1977	14	27	0.519	3	1.556	19.75	3	7	0.429	2	0.858	12.89
Marley Plantation 1977	0	7	0.000	2	0.000	4.44	0	6	0.000	2	0.000	4.44
Thorny Croft 1977	0	0	-----	---	-----	-----	8	34	0.235	4	0.940	13.69
Marley Lodge 1978	22	23	0.957	3.267	3.127	35.21	10	17	0.588	3	1.764	21.80
Larch 1978	11	8	1.375	2	2.750	31.50	2	7	0.286	2	0.572	10.07
Woodcroft 1978	14	18	0.778	3	2.333	27.40	12	26	0.462	3	1.386	18.08
Radbrook 1978	9	14	0.643	3	1.923	23.36	10	18	0.555	3	1.667	20.85
Watched nests during period of observation												
Marley 1977	26	24	1.083	3.778	4.092							
Marley Plantation 1977	0	10	0.000	2	0.000							
Larch 1977	6	9	0.667	2.750	1.834							
Marley Lodge 1978	26	31	0.839	3.211	2.694							
Radbrook 1978	13	22	0.591	3	1.773							

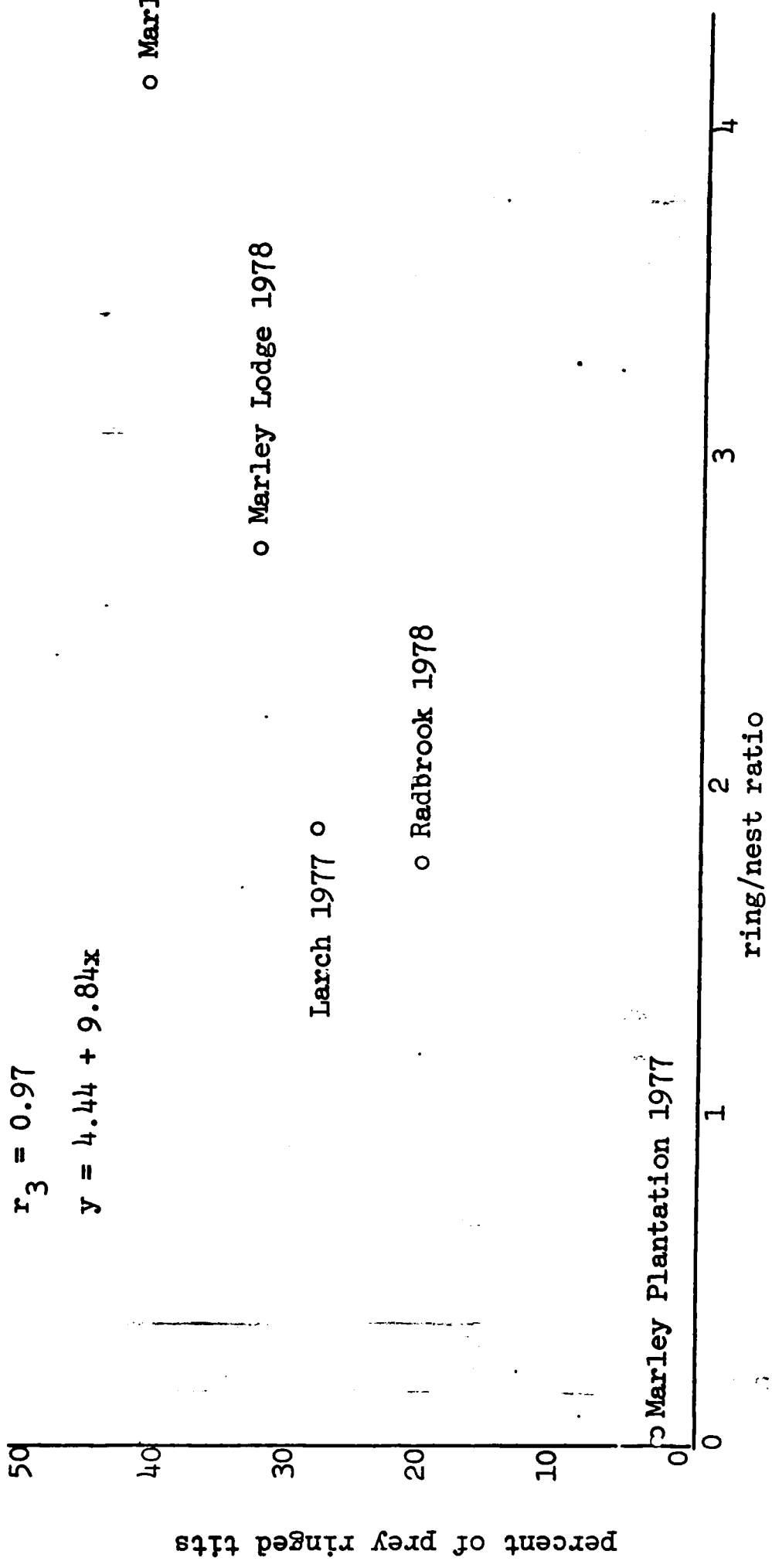


Figure 3-7. The relationship between the ring/nest ratio and the percent of the prey which was ringed tits during watches.

where pellets were collected, excepting Marley 1976 due to the small sample size, using the formula:

% of prey ringed tits = ring/nest x 9.84 + 4.44 (Figure 3-7). The results for each nest, shown in Table 3-6, indicate that, as expected based on type of prey selected by each sex, a higher percentage of the diet was ringed tits when the majority of hunting was done by the male. Also, with the exception of Marley Plantation 1977, the figures for different nests in the same period were quite similar.

K. The effect of date of mean tit fledging on predation rates.

Various factors were examined for effect on between nest variation in rates of prey delivery and percent of prey which was ringed tits.

The most important factor found was the date of data gathering after mean tit fledging date. Mean fledging dates were obtained from date of laying of first egg and clutch size of Great and Blue Tit pairs nesting in Wytham nest boxes as both Great and Blue Tits: lay one egg/day (allowing accurate backdating to obtain first egg date); begin incubation with the penultimate egg; incubate fourteen days; with Great Tits fledging on day 19 of life (all from Gibb 1950) and Blue Tits fledging on day 18 of life (C.M. Perrins, pers.comm.). Mean tit fledging date ($\pm$ 1 S.D.) was June 7.13 $\pm$ 6.16 days (corrected for leap year), June 10.46 $\pm$ 6.45, and June 14.94 $\pm$ 9.80, in 1976, 1977, and 1978, respectively.

i. Prey delivery rates.

Prey delivery rates for male hawks showed better agreement between individuals when re-adjusted for days after mean tit fledge

(Figure 3-8). Although a highly significant inverse relationship was found for male delivery rates and day of life of young (r_{15} = -0.65, $p < 0.01$), replotting of these delivery rates against days after mean tit fledge showed a higher level of correlation (r_{15} = -0.85, $P < 0.001$) and explained over 29% more of the variance (r^2) in the number of prey brought/hour watched.

Replotting of the females' delivery rates (Figure 3-9) showed that the Radbrook female's poor increase in prey delivery rate was associated with hunting done longer after an increase in prey availability (especially as tit fledging date may correspond closely to fledging of the young of other species) than by the females at Marley and Marley Lodge, and occurred when male prey delivery rates were ebbing.

Replotting of mean prey delivery from both parents against days watched after mean tit fledging showed that nests watched earliest had the highest delivery rates while those watched latest after tit fledging had lower, and quite similar, delivery rates (Figure 3-10).

ii. <u>The percent of prey that was ringed tits</u>.

In Figure 3-11 the estimated percent of prey that was ringed tits obtained from ring/nest estimates was plotted against mean pellet collection date minus mean tit fledging date for each nest and period (excluding Marley Plantation 1977 as habitat structure is thought to have caused these hawks to take different prey; cf. discussion in Chapter 2). Arranged in this manner, the percent of prey that was ringed tits shows a strong inverse relationship with the number of days after mean tit fledge. Of the two constituent

Figure 3-8. The relationship between male prey delivery rates (prey brought/ hour watched) and the timing of hunting in days after mean tit fledging.

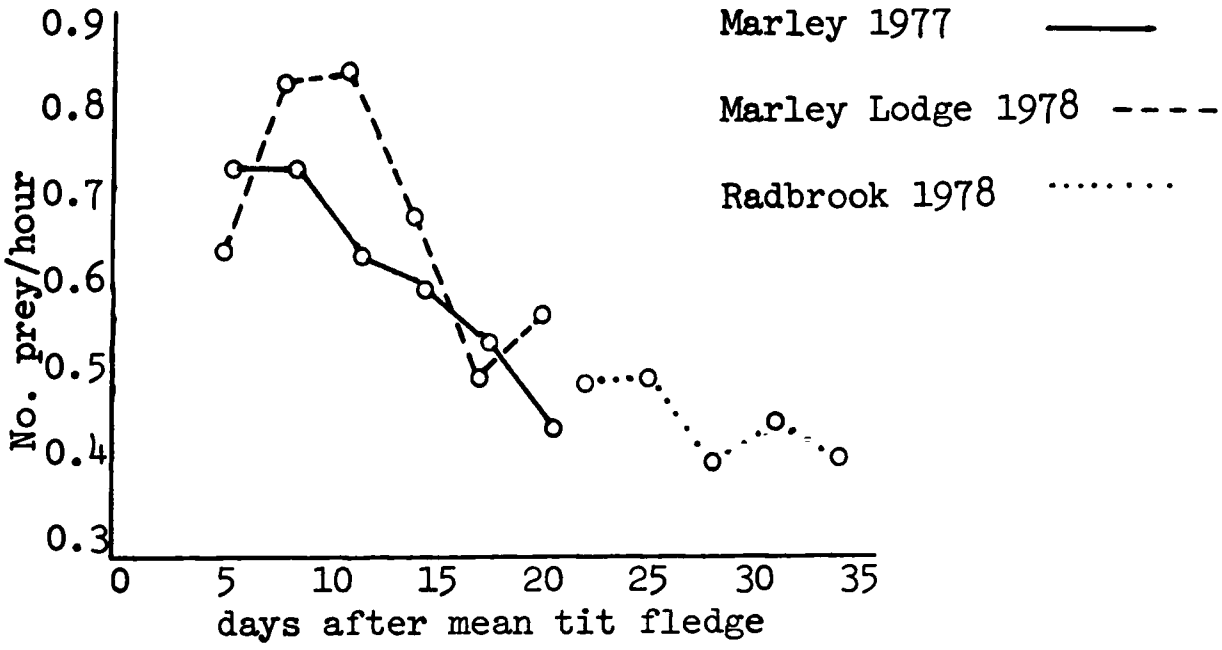


Figure 3-9. The relationship between female prey delivery rates (prey brought/hour watched) and the timing of hunting in days after mean tit fledging.

Key as for Figure 3-8.

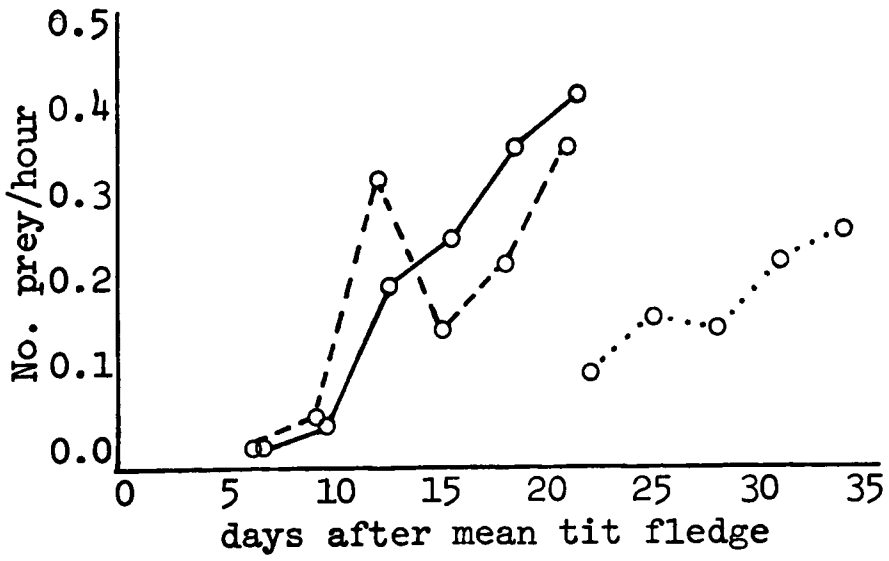


Figure 3-10. The relationship between total prey deliveries (prey brought/ hour watched) from both parents after day 15 of life (mean value) and the timing of hunting in days after mean tit fledging.

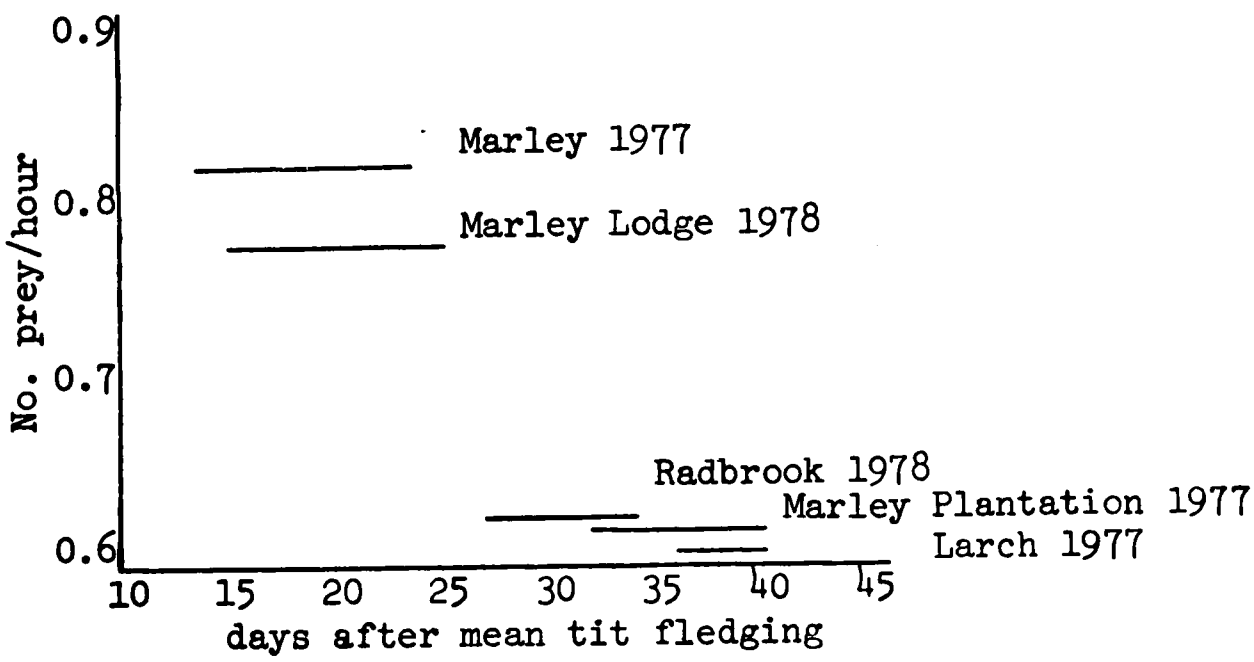
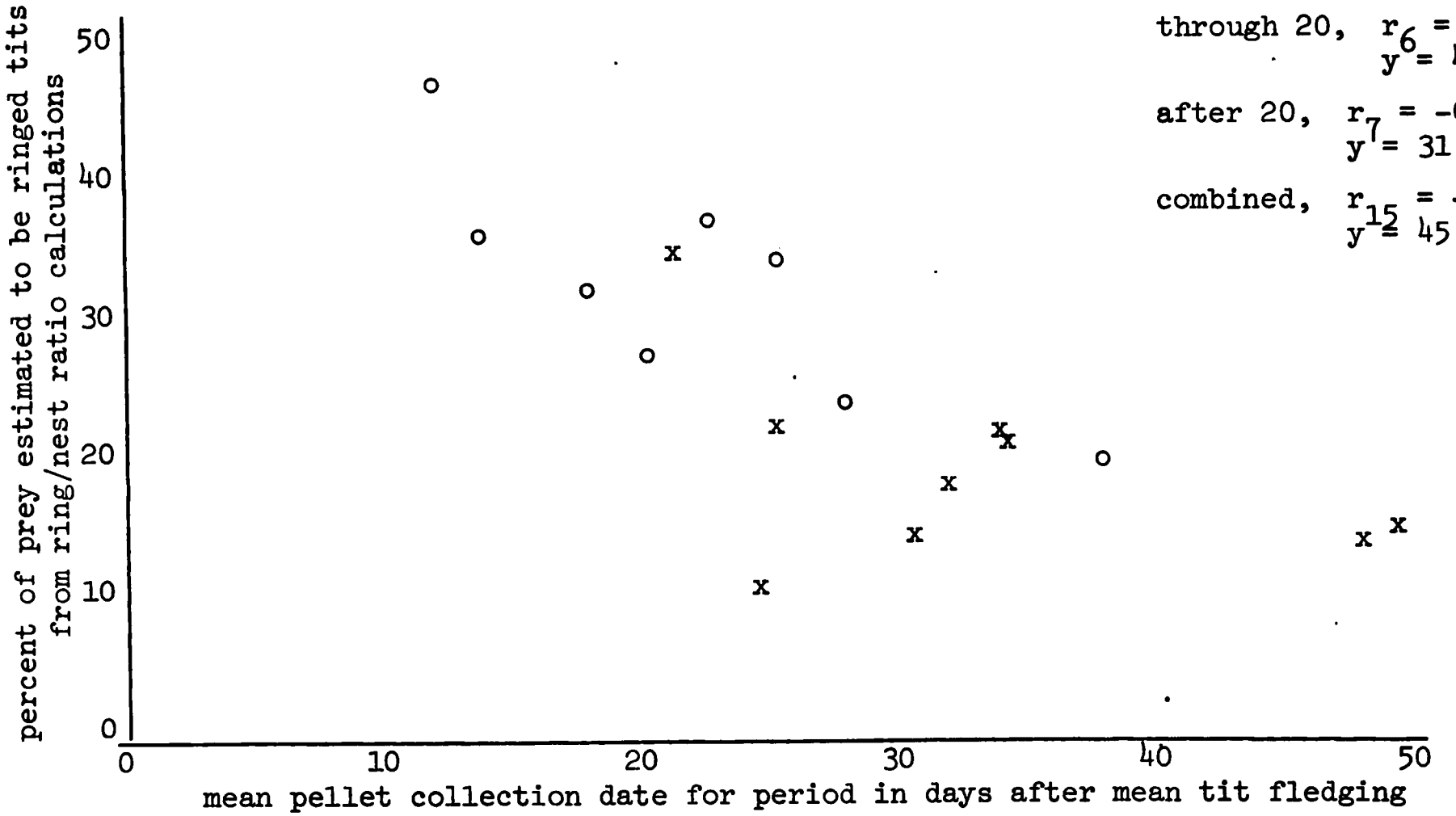


Figure 3-11. The relationship between the percent of the diet composed of ringed tits and the timing of hunting in days after mean tit fledging.



through 20, $r_6 = -0.81$, $P < 0.02$
$y = 49.82 - 0.81x$

after 20, $r_7 = -0.54$, n.s.
$y = 31.67 - 0.40x$

combined, $r_{15} = -0.78$, $P < 0.001$
$y = 45.89 - 0.75x$

o = period through day 20 of life of young

x = period after day 20 of life of young

periods, through day 20 showed a significant negative correlation with days after mean tit fledge, while the period after day 20 did not. However, no significant difference was found between the slopes of the regression equations of the two periods ($t_{13} = 1.27$).

IV. Discussion.

A. The use of hides.

The use of hides close to Sparrowhawk nests provided a high degree of accuracy in the identification of prey brought to the nest and the parent supplying each item. In contrast to the findings of Owen (1916b) and Newton (1978), in the majority of instances the hawks in Wytham brought prey to the nest only partially plucked and with the head still on. This usually allowed easy identification of species (and if the prey was a tit, whether or not it was ringed). Since the prey were intact in most instances, especially those brought early in the nestling period, it was indicated that the male hawks in Wytham were obtaining food from prey other than those brought for the young. The minority of prey which was brought to the nest entirely plucked could usually be identified to species on the basis of the head, foot structure, or coverts which were often left on. Since it was almost impossible to miss a feed and watches were carried out for a large number of hours/day, the estimates of the number of prey brought to the nest during the nestling period were very reliable.

B. The roles and type of prey selected by each sex.

The role of each parent in providing food during the nestling period, especially the change in the role of the female from total care of the young to an increasing participation in hunting after the first one-third of the nestling period, was as noted by Owen (1916 a,b,c); Tinbergen (1946); Sulkava (1964); and Newton (1978). The females at Lord's Copse 1976, Marley 1977, and Marley Lodge 1978 remained in the vicinity of the nest during the early stages of their hunting cycle, as found by Newton (1978). The females at Larch 1977, Marley Plantation 1977, and Radbrook 1978 spent very little time in the vicinity of the nest except to feed during watches. At all of the watched nests the males brought prey throughout the period watched.

As suggested by Amadon (1975) and Newton (1978), the change in the role of the female may be beneficial to the young as she can utilise a greater prey spectrum (cf. Table 3-3) while restricted to hunting near the nest or for a short period away from the nest. She makes up, not only in number but also in prey weight, for the decreasing male contribution at a time when the young need increasing amounts of food.

C. The rate of prey delivery.

In agreement with Newton's (1978) findings, 1) the different sexes at each nest provided fairly similar numbers of prey/hour watched towards the end of the nestling period, 2) brood size did not affect delivery rates (also found by Snyder and Snyder (1973 for The Cooper's Hawk Accipiter cooperii), 3) there was no diurnal

rhythm to predation, and 4) total prey deliveries/hour remained fairly stable at each nest during the period of watches. The last contrasted with the findings of Tinbergen (1946) that the total number of prey brought/hour increased as the nestling period progressed. At nests watched early in the season total prey deliveries/hour were higher than those found by Newton (1978), while nests watched later in the season showed rates comparable to those found by Newton (1978) but higher than those found by Tinbergen (1946).

The decrease in the number of prey brought/hour by Wytham males was more strongly correlated with days after mean tit fledge than with the age of young in the nest. Moreover, the rate of predation by females watched later in the season increased less rapidly than for females watched earlier (and hunting may have begun earlier in the nestling stage for females nesting later, as at Radbrook). Total prey deliveries when both parents were hunting were higher earlier in the season, as would be expected.

The findings that brood size did not affect delivery rates and that there was no diurnal rhythm to predation suggested that the parents, and especially the males, were hunting to their maximum capacity throughout the watched period, as discussed by Newton (1978). This being the case, Newton postulated that the causes for his finding a decrease in the male delivery rates with age of young might have been: 1) decrease in prey availability, 2) fatigue, 3) wing moult, or 4) a realisation that the female was becoming increasingly free to hunt. It is felt that fatigue, wing moult, and realisation of female freedom may be discounted as

major factors for the male hawks in Wytham for the following reasons. Fatigue should be regulated by the number of days spent hunting at full capacity, hence, age of young and not date after maximum prey availability. Wing moult in male Sparrowhawks begins at the time young fledge (Heinroth cited by Welty 1975). Although there may be some increase in the food requirements of the males about to undergo moult causing them to increase the proportion of prey caught that they eat for themselves, the decrease in rate of deliveries was not similar between males as would be expected if all were eating the same proportion of the prey they caught. Additionally, should moult begin earlier than indicated, it should not be aerodynamically detrimental as male Sparrowhawks moult only one feather at a time, with the replacement growing in before the next feather is moulted. Realisation of increased female freedom to hunt should once again be regulated by the age of young and not by date; if the male knew the amount of time spent by the female away from the nest and adjusted his hunting rate accordingly, the male at Radbrook, where the female spent the longest periods away from the nest, should have decreased his hunting rate more rapidly than the other males, but the opposite occurred. The major factor affecting male delivery rates in Wytham was probably prey availability. In rich deciduous woodland there is a flush of prey early in the hawk nestling period due to recently fledged young of prey species, e.g., 2,800 to 3,800 tits fledged. While these potential prey are readily available when first fledged, high juvenile mortality depletes the stocks rapidly and, at least in the case of tits, the surviving young begin to forage in denser cover after independence

from their parents (Goodbody 1952, Perrins 1965, Webber 1975), thus reducing their vulnerability and, probably, the hunting success of the predator. Additionally, while no significant difference was found between the type of prey taken by males at different nests, the Radbrook male brought more prey larger than tit size (22.64%) than the males at Marley (10.32%) and Marley Lodge (14.49%). This suggests that different prey were available at different times (the habitat was similar around all of these nests so this was discounted as a factor) or that the later males, having lower prey encounter rates, spent greater time selecting for more profitable (heavier) prey.

The above suggestion that the male prey delivery rates were regulated to a great extent by prey availability appears to be borne out by the findings that females hunting later in the season showed less rapid increases in delivery rates and lower ultimate delivery rates. Like the males, females hunting later in the season took more larger than tit size prey (48.15%, 44.83%, and 62.96% at Marley 1977, Marley Lodge 1978, and Radbrook 1978, respectively). As a result of these effects, total prey deliveries decreased as the season progressed. It is supposed, as suggested by Newton (1978), that the participation of the female in hunting was to make good the deficit from the male, due, apparently, to reduction in hunting success because of reduced encounter rates with prey and/or reduced prey vulnerability.

Lastly, based on the prey delivery rates of males and both parent combined, it is suggested that the number of prey brought to each nest each day, assuming 16 hours of hunting, was close to

13/day at about mean tit fledge, declining to about 10/day four to five weeks later, at which point it is thought to have stabilised (Figure 3-10).

D. The percent of prey formed by ringed tits at each nest.

The use of rings and pellets via the ring/nest ratio provided an accurate way to estimate the percent of the diet that was ringed tits at each nest where sufficient pellet samples were collected. It is felt that the important factors leading to obtaining accurate estimates were: 1) dividing the pellet collections into two periods so as to limit bias due to the different proportion of pellets produced that were collected with time, 2) that the females at each nest fed approximately the same proportion of rings from tits to the young, and 3) that although the distribution of rings among the young may not have been equal, the collection of the pellets produced by each young was random.

The most important factor affecting the percent of ringed tits in the prey at each nest appeared to be date after mean tit fledge, although habitat was also influential at Marley Plantation. All hawks in the main part of the wood showed similar percentages of ringed tits in their prey, when adjusted for tit fledge, while those at Marley Plantation took few ringed tits, indicating that the Marley Plantation pair did not have to travel great distances (< 1km) regularly to obtain food, while hawks nesting in the main part of the wood probably did not travel any further and may have restricted themselves to the wood for the most part. This is in contrast to the findings of Tinbergen (1946) and Newton et. al. (1977)

that Sparrowhawks will travel great distances to obtain prey (3+km regularly and over 9km, respectively). It is thought that this was the result of high prey densities within the wood and the surrounding areas; this is further supported by the high prey delivery rates in Wytham compared to the previously mentioned areas indicating that encounter rates were lower in Wytham.

The relationship between days after mean tit fledge and percent of the prey that was ringed tits indicated that all of the hawks nesting in the main body of the wood were utilising tits as prey to the same degree at the same point after tit fledging. Although this is at first quite astonishing, the tits were fairly uniformly distributed over the wood (due to the pattern of nest box location), and were fledging and moving into denser foraging areas at about the same time. As tits formed the main prey of the male hawks in the wood, the decline in the percent of tits in the prey may have been due to decreased stocks and/or vulnerability, and this decline in availability of tits may have been a contributing, if not a major, cause in the decline of the male prey delivery rates.

Summary.

1) Male hawks provided all of the food for consumption at the nest during the first third of the nestling period and continued to supply prey throughout the nestling period. Female hawks did all of the brooding of, and food distribution for the young and began to reduce the time spent at the nest after the first third of the nestling period, at which time they began to hunt.

2) Prey delivery rates from males decreased with the passage of time, with the delivery rates more closely linked to days after mean tit fledging (an indicator of the onset of the period of high prey availability due to the fledging of large numbers of young of prey species) than the age of the hawk young. Female prey delivery rates increased steadily from about day 10 of life of their young until about day 25 of life of the young when rates comparable to those of the males were attained. The rate of increase and ultimate level of female deliveries was also more closely linked to days after mean tit fledging than age of young.

3) No diurnal rhythm of predation was found. Also, changes in brood size did not affect the rate of delivery. Together, these findings were thought to indicate that the parents, and most especially males, were hunting to maximum capacity with delivery rates set by encounter rates.

4) Evidence was found for sexual size dimorphism related selection of prey. Additionally, members of the same sex from different nests selected prey of similar sizes.

5) The percent of the diet that was ringed tits was related to the number of days after mean tit fledging that hunting occurred for birds which nested in the main part of the wood. For hawks not nesting in the main body of Wytham, habitat structure appeared to be the most important factor influencing prey selection.

Chapter 4. The selection of tits by Sparrowhawks.

I. Introduction.

The selection of prey by accipiters has been shown to be influenced by factors including physical condition of prey, environmental aspects such as habitat or cover, and the sex of the prey individual (Kenward 1976, 1977, and 1978; Tinbergen 1946). Additionally, other predators have been found to select for age classes (see Mech 1970 for overview).

Selection of tits by Sparrowhawks in Wytham was investigated via rings from tits eaten by hawks and ringing records, which provided information about physical and age characteristics of tits raised or nesting in the wood.

II. Methods.

Tit rings recovered from hawk pellets, nests, and prey were used to analyse the selection of tits. By matching the serial number of each ring to ringing records, the recoveries for each nest were classified by species, whether juvenile or adult, and for juveniles whether resident (raised in Wytham nest box) or immigrant (not raised in Wytham nest box). The breakdown of rings from each nest is shown in Table 4-1.

The accuracy of using recovered rings to determine the characteristics of tits taken by hawks was tested by comparing ring recoveries and data collected during watches (Table 4-2 for selection of species; Table 4-3 for selection of age groups). As no significant differences were found between ring and hide watch samples it was felt that the rings were an accurate sample

Table 4-1. The number of rings (N) recovered from each nest and the percent of these rings from individuals from each of the following age/origin groups; resident (raised in Wytham nest box) juveniles (%RJ) and adults (%A); for each tit species for which rings were recovered - Great Tit (GT), Blue Tit (BT), and Coal Tit (Cl T). Recoveries from Marley 1976 excluded due to recovery of only five rings (40% RJGT, 40% RJBT, 20% AGT).

		GT		BT		Cl T	
Nest and year	N	%RJ	%A	%RJ	%A	%RJ	%A
Lord's Copse 1976	16	18.75	6.25	62.50	12.50	0.00	0.00
Bean 1976	18	22.22	11.11	66.67	0.00	0.00	0.00
Marley 1977	51	31.37	1.96	60.78	3.92	0.00	1.96
Larch 1977	18	50.00	11.11	22.22	16.67	0.00	0.00
Thorny Croft 1977	9	22.22	11.11	66.67	0.00	0.00	0.00
Marley Lodge 1978	40	22.50	5.00	55.00	15.00	0.00	2.50
Larch 1978	13	23.08	0.00	53.85	15.38	7.69	0.00
Woodcroft 1978	27	25.93	3.70	59.26	11.11	0.00	0.00
Radbrook 1978	21	42.86	0.00	42.86	9.52	0.00	0.00

Table 4-2. The ratio of ringed Great to Blue Tits seen brought to nests during watches and in recovered rings.

		seen at nest	in recovered rings
Marley 1977	Great Tits	17	21
	Blue Tits	33	30
			x^2 = 0.29 with Yate's correction, N.S.
Marley Lodge 1978	Great Tits	12	13
	Blue Tits	46	43
			x^2 = 0.01 with Yate's correction, N.S.

Table 4-3. The ratio of ringed adult to juvenile tits seen during watches and in recovered rings at Marley Lodge 1978. Probabilities are from Fisher's exact tests and are two-tailed.

		seen at nest	in recovered rings	
Great Tits	adults	1	2	
	juveniles	6	9	P = 0.94
Blue Tits	adults	3	5	
	juveniles	31	22	P = 0.46

of the type of tits selected by hawks and could be used for more complete analyses of selection. Only recoveries from Great and Blue Tits were used as the number of Coal Tit rings recovered was small, corresponding to the low number of this species in the wood.

III. Results.

A. Selection of juveniles.

i. The ratio of species selected.

Table 4-1 shows that most of the hawk pairs took resident juveniles in the ratio of one Great Tit for every two to three Blue Tits. This ratio was close to the ratio of species availability for the age group in the wood (751 : 2050; 1128 : 2638; 1280 : 2288 resident juvenile Great Tits : Blue Tits fledged in 1976, 1977, and 1978, respectively).

At two nests, Larch 1977 and Radbrook 1978, the ratios of species selected was equal or favoured Great Tits. As the ring samples from these two nests were collected later in the year than at other nests in the same years (while still overlapping with collection dates for other nests), the effect of date on the species ratio of resident juveniles taken was investigated. Figure 4-1 suggests a curvilinear relationship between time after tit fledging and the ratio of species taken. Since ring recoveries from each nest often encompassed a considerable time span, re-examination of ring recoveries was done by placing recoveries into five day periods after mean tit fledging (ten days for final period to allow adequate sample size) for each year (Table 4-4). Using the mean value and and collection date for each period, a significant inverse

Figure 4-1. The ratio of resident juvenile Blue Tits to Great Tits caught by hawks from ring samples at each hawk nest (excluding Marley 1976 due to the small sample size) plotted against mean ring recovery date in days after mean tit fledging. Mean ring recovery dates calculations excluded rings collected immediately after a hiatus in collections and from nest nest dissections. A value of 1 represents selection at the rate of availability; greater than 1 shows favouring of Blue Tits, less than 1 favouring of Great Tits.

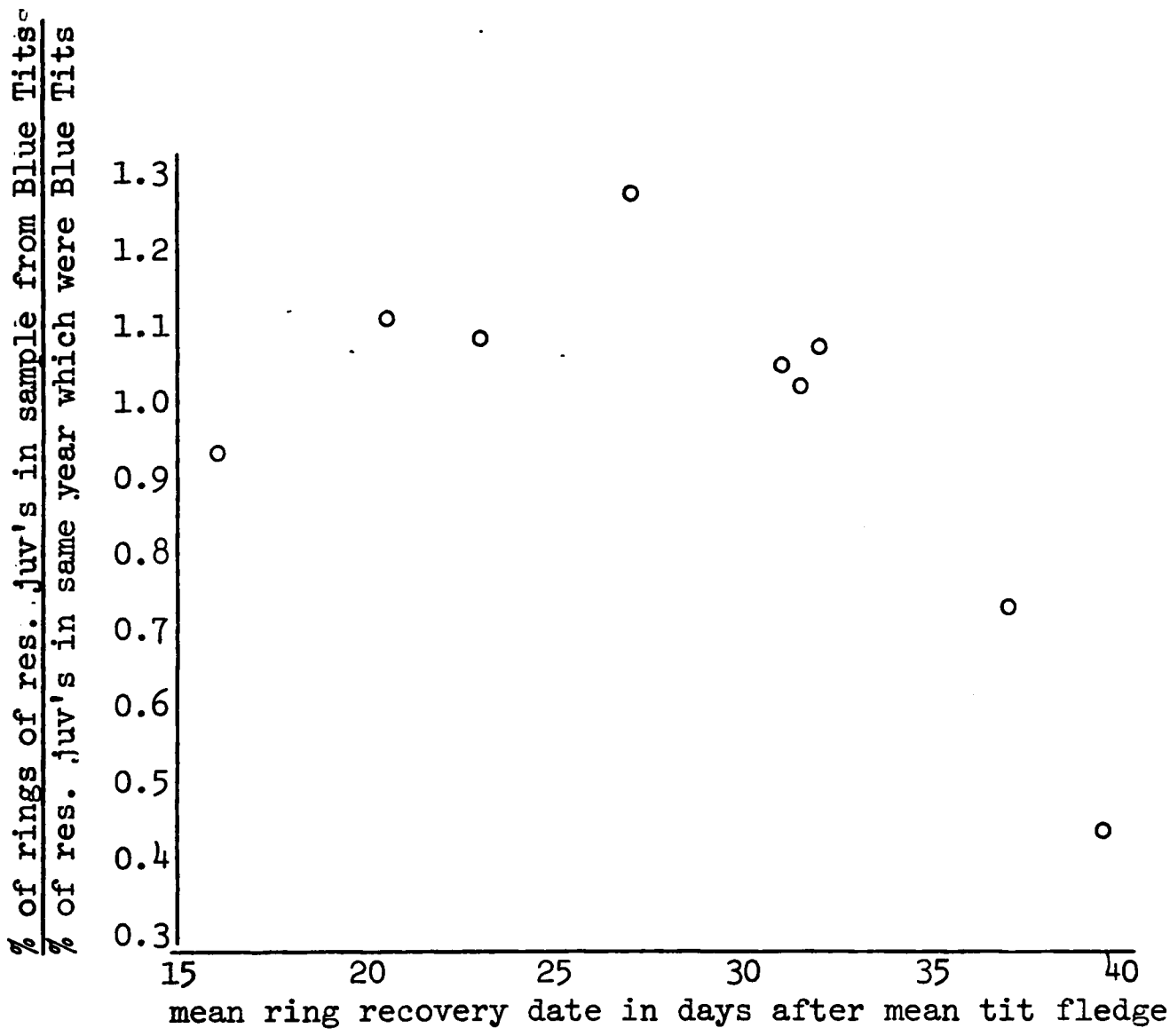


Table 4-4. The ratio of resident juvenile Blue to Great Tits in all rings recovered in each year in five day periods from mean tit fledging. Calculations made in the same way as for Figure 4-1, with variation around a value of 1 interpreted similarly.

Year		% of juvenile tits fledged which were Blue Tits.	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-49
1976		73.19				1.37	0.91	0.68	---	1.37	1.37
	N	(2801)				(4)	(3)	(8)	(0)	(3)	(1)
1977		70.05			1.14	0.80	1.19	1.43	0.95	0.37	0.71
	N	(3766)			(5)	(32)	(6)	(2)	(3)	(8)	(2)
1978		64.13		1.17	1.21	1.08	1.04	0.78	0.72	1.10	0.52
		(3568)		(4)	(9)	(13)	(15)	(10)	(13)	(10)	(3)
Mean		(152)		1.17	1.19	0.92	1.06	0.81	0.77	0.86	0.73

relationship was found to exist between date and the ratio of species selected ($r_6 = -0.87$, $P<0.01$).

ii. In terms of brood and physical characteristics.

Previous research in Wytham has shown that the survival of juvenile tits is affected by factors including brood size (Perrins 1965, Perrins and Moss 1975), hatching date (Perrins 1965), individual weight (Perrins 1965), and age of female parent (Perrins 1965, Perrins and Moss 1974). Additionally, Drent (1977) suggests that, in Holland, juvenile tits from immigrant parents appeared to be more susceptible to mortality, often from predators, than the young of resident parents.

To determine whether Sparrowhawks selected juvenile tits which had lower potential for survival based on the above criteria, the characteristics for individuals for which rings were recovered were obtained from nest records and compared with the characteristics for the whole population of the same species in the same year, as well as juveniles from the same species raised in the same year which were trapped at nest boxes while breeding in the following year (hereafter called survivors). Years were analysed separately because significant heterogeneity in the variance of many characteristics was often found within species between years. Moreover, parametric tests between the general population, killed birds, and survivors within a species within a year were limited to Student's 't' tests between each group as significant heterogeneity of variance was often found between classes.

Data for each species, population class, and year are detailed in Appendix 4. Significance levels from all tests

performed are presented in Table 4-5.

Also presented in Appendix 4 are data regarding the selection of resident juveniles on the basis of being first ringed in their brood, as during compilation of data of Great Tits in 1977 it was found that this group was selected significantly more frequently than birds which had not been first ringed; no similar selection effect was found for other species groups in any year. An analysis of the characteristics of first ringed and non-first ringed Great Tits selected by hawks in 1977 is also presented in the Appendix in an attempt to elucidate the cause for the findings.

iii. Date of capture.

The capture dates of resident juvenile tits were examined in relation to brood and physical characteristics to determine if Sparrowhawks selected prey with higher survival potential later in the season. Capture dates for individual tits were calculated to be one day prior to recovery of the pellet containing the ring or the date of ring recovery for rings removed from corpses. Rings from pellets obtained at the end of a hiatus in collections and from nest dissection were excluded from the analyses as they could not be dated accurately. The analysis by multiple regression used the following characteristics related to survival potential for comparisons:

x_1 - Size of clutch laid by adults raising individual.

x_2 - Number of young fledged from individual's final brood.

x_3 - Number of young fledged from individual's final brood $\pm$ number of young added/subtracted from brood by manipulation.

Table 4-5. Summary of the data from Appendix 4 on the selection of juvenile resident Great and Blue Tits on the basis of brood and physical characteristics; comparisons made between the general population (G), killed by hawk (K), and survivor (S) classes. ! = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; and n.s. = no significant difference. Letters in () indicate trend of significance. N.B. No data on survivors from 1978 were available. n/a indicates data not available for specific test.

Characteristic	Year	Great Tit			Blue Tit		
		G.K	K.S	G.S	G.K	K.S	G.S
No. fledged	1976	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	1977	n.s.	n.s.	n.s.	n.s.	* (K>S)	** (G>S)
	1978	n.s.	n/a	n/a	! (G>K)	n/a	n/a
Hatch date	1976	n.s.	** (K>S)	*** (G>S)	n.s.	* (K>S)	* (G>S)
	1977	n.s.	! (K>S)	! (G>S)	** (K>G)	** (K>S)	n.s.
	1978	n.s.	n/a	n/a	** (K>G)	n/a	n/a
Individual weight	1976	n.s.	n.s.	** (S>G)	n/a	n/a	n/a
	1977	n.s.	! (S>K)	* (S>G)	n/a	n/a	n/a
	1978	! (K>G)	n/a	n/a	* (K>G)	n/a	n/a
Mother's age	1976	n.s.	n.s.	n.s.	n/a	n/a	n/a
	1977	n.s.	n.s.	n.s.	n/a	n/a	n/a
	1978	n.s.	n/a	n/a	n/a	n/a	n/a

Origin of parents - Great Tits only and only between general and killed class. No significant differences found for 1977 or 1978. 1976 sample too small to permit analysis, but data appeared to indicate results similar to 1977 and 1978.

x_4 - Date young from brood fledged.

x_5 - Individual's weight.

x_6 - Mean weight of young in brood.

Analyses of Great and Blue Tits fledged and caught in 1976 were not performed as sample sizes were too small due to frequent interruptions of collections.

In 1977, none of the brood or physical characteristics of either Great Tits ($F_{5,16} = 1.02$, r^2 corrected for inter-correlations = 0.00) or Blue Tits (excluding x_5 and x_6 as no weights were taken - $F_{3,29} = 1.56$, r^2 corrected = 0.05) affected the date of capture significantly.

In 1978, none of the parameters affected Great Tits significantly ($F_{5,21} = 1.37$, r^2 corrected = 0.08). The capture date of Blue Tits, once again excluding weight factors, was affected significantly by the number of young fledged, the number of young fledged $\pm$ the number manipulated, and fledging date (Total - $F_{3,42} = 3.18$, $P < 0.05$, r^2 corrected = 0.17; $t_{x_2\ 43} = 2.65$, $P < 0.05$; $t_{x_3\ 43} = 2.65$, $P < 0.05$; $t_{x_4\ 43} = 2.32$, $P < 0.05$; regression equation = $155.5 + 1.65x_2 - 1.36x_3 - 0.60x_4$).

B. Selection of adults.

The number of ringed adult Great and Blue Tits in the wood each year was estimated from the number of pairs of each species occupying nest boxes and the results of trapping done at nest boxes (discussed further in Appendix 5). As estimated 221, 421, and 353 ringed Great Tit adults, and 448, 726, and 601 Blue Tit adults were nesting in 1976, 1977, and 1978, respectively, in Wytham.

i. Selection of species.

The ratio of Great to Blue Tit ringed adults in ring samples from hawks was analysed for each year in relation to estimated availability. In all years hawks appeared to select ringed adults from each species in terms of availability (Table 4-6). While sample sizes were too small to determine if selection of adults changed with increasing time after tit fledging, subjective interpretation of the data suggested that it did not.

ii. Selection by sex of adult tit.

The ratio of male to female adult ringed tits in rings from hawks and in the estimated population was analysed for each year (Table 4-7). The selection did not differ significantly from estimated availability in any instance. However, the composite data for all years for Great Tits suggested that there was an overall trend towards the selection of males.

iii. On basis of origin.

Great Tits trapped at nest boxes were classified as to whether resident or immigrant by birth for each year. Comparison of rings from eaten adults to the number available from each class in each year showed no significant preference by hawks (Table 4-8). In addition no inter-year trend was found for this tit species. No analysis of Blue Tits was carried out as the number of individuals in the ring samples for whom origin could be determined was too small due to the low proportion of the breeding population trapped each year.

Table 4-6. Selection of ringed adult tits on the basis of species. Probabilities are from Fisher's exact test and are two-tailed.

Year		Great Tit	Blue Tit	
1976	No. rings from hawks	4	2	
	Est. no. available	221	448	P = 0.19
1977	No. rings from hawks	4	5	
	Est. no. available	421	726	P = 0.90
1978	No. rings from hawks	3	13	
	Est. no. available	353	601	P = 0.22

Table 4-7. Selection of ringed adult tits of each species on the basis of sex. Blue Tits in 1976 and 1977 were not analysed as records of sex of individuals not available in most cases for ring sample. Probabilities are from Fisher's exact test and are two-tailed.

Year	Species		Male	Female	
1976	Great Tit	No. rings from hawks	2	1	
		Est. no. available	111	110	P = 0.98
1977	Great Tit	No. rings from hawks	3	1	
		Est. no. available	214	207	P = 0.65
1978	Great Tit	No. rings from hawks	3	0	
		Est. no. available	177	176	P = 0.26
all	Great Tit	No. rings from hawks	8	2	
		Est. no. available	502	493	P = 0.12
1978	Blue Tit	No. rings from hawks	1	5	
		Est. no. available	268	333	P = 0.33

Table 4-8. Selection of adult Great Tits on the basis of origin. Probabilities are from Fisher's exact test and are two-tailed.

Year		Resident	Immigrant	
1976	No. rings from hawks	1	3	
	Number available	66	105	P = 0.98
1977	No. rings from hawks	4	1	
	Number available	144	184	P = 0.25
1978	No. rings from hawks	0	3	
	Number available	139	152	P = 0.36

Table 4-9. The selection between age classes by hawks: the number of rings from juveniles and adults recovered from hawks and the number of each age class available (both species combined). All x^2 values are with Yate's correction.

Year		Adults	Juveniles	
1976	No. rings from hawk	5	29	
	Est. number available	669	2801	x^2 = 0.21, N.S.
1977	No. rings from hawks	9	68	
	Est. no. available	1147	3766	x^2 = 5.16, P 0.05
1978	No. rings from hawks	16	83	
	Est. no. available	954	3568	x^2 = 1.14, N.S.

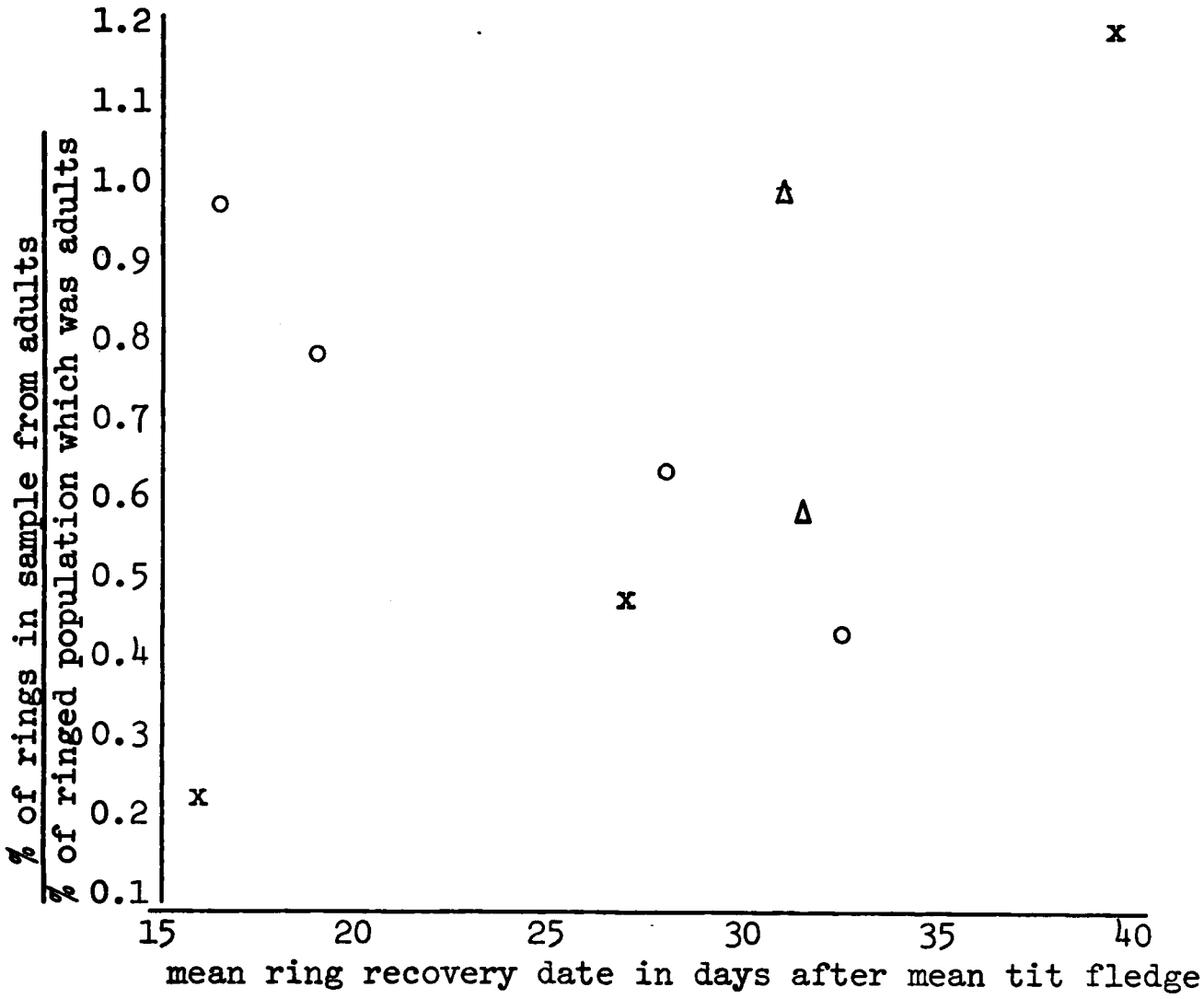
C. Selection for age - adults vs. juveniles.

Rings from hawks and the estimated number of ringed individuals in the adult and juvenile segments of the combined Great Tit and Blue Tit populations were used to determine if hawks selected for age.

Table 4-9 shows that according to total ring samples for each year hawks showed no preference for either age group in 1976 and 1978, while they selected juveniles significantly more frequently than adults in 1977.

An index of the selection of adults versus juveniles was calculated by taking the percentage of Great and Blue Tits which were from adults and dividing that by the percentage of the ringed tit population that were adults. Values less than one suggest selection favouring juveniles and values greater than one suggest selection of adults. These values were then plotted against the mean ring recovery date in days after mean tit fledging for each nest (Figure 4-2). In 1977 the hawks took very few adults at first but took increasingly more in their prey as the season progressed. In 1978 the hawks took adults at about the same rate as available soon after the fledging of the young tits, the time when adults were still associated with their broods, and fewer later in the season when the young became independent and the adults became increasingly solitary in habit. The difference in the slopes of the regression equations for 1977 and 1978 was significant (1977 - $y = -0.54 + 0.04x$; 1978 - $y = 1.37 - 0.03x$; $t_3 = 7.45$, $P < 0.01$). The data for 1976 show no clear pattern. This may be the result of the limited number of nests sampled and the fact that there were

Figure 4-2. The ratio of ringed adult to juvenile tits selected by hawks from ring samples at each hawk nest (excluding Marley 1976 due to small sample size) plotted against mean ring recovery date at the same nest in days after mean tit fledging. A value of 1 represents selection at rate of availability; greater than 1 shows favouring of adults, less than 1 favouring juveniles.



1976 = Δ

1977 = x

1978 = o

many interruptions in pellet and ring collections in that year which affected the mean ring recovery dates. The majority of collections at Lord's Copse were made earlier than at Bean, and the percent of adults at the former nests was higher than at the latter nest, from which it is felt that the pattern in 1976 probably resembled that found for 1978.

IV. Discussion.

A. Selection of juveniles.

Soon after tit fledging the Wytham hawks selected Blue Tit juveniles slightly more frequently than Great Tit juveniles, relative to the total numbers fledged. The earlier fledging of Blue Tits possibly provided a slightly higher ratio of Blue Tits to Great Tits soon after their fledging than suggested by the total numbers fledged. Later in the season, the situation reversed itself and Great Tits were taken more frequently than would have been expected on the basis of availability. This shift could result from the passage of large numbers of unringed Blue Tit juveniles through the wood. Goodbody (1952) and Gibb(1954) both found evidence of an influx of unringed birds and an exodus of ringed birds from Wytham around the beginning of July. Other research has shown that the percent of juvenile Great Tits bearing rings decreases to about 70% at the time of this passage and remains at about the same level throughout the summer (Webber 1975), while percent of Blue Tits ringed decreases to about 40% by the end of the summer (C.M. Perrins, V.E. Wood, N.J. Phillips, unpubl. data). Therefore, the results obtained

from species ring ratios for late summer are thought to represent the shift in the percent of birds from each species ringed and not changes in the pattern of selection by hawks. The decrease in the percentage of Blue Tits, and to a lesser degree Great Tits, ringed should mean that the percent of the hawks diet that was formed of all tits should have decreased less steadily, possibly the cause for the levelling off of hawk predation rates (Chapter 3) during the middle of July.

In terms of brood size and individual weight, the juvenile tits caught by hawks were generally intermediate between the birds in the general population and those that survived to breed. Previous work (Gibb 1957, Perrins 1965) suggests a high level of non-predator related mortality of juvenile tits very soon after leaving the nest, which may be related to weight and brood size. Hawks probably took tits of intermediate weight and from intermediate sized broods because these birds survived out of the nest long enough to be exposed to the hawks. It is not known whether hawks selected randomly from the group that survived long enough to be susceptible to predation, or if they selected the weakest birds from those still available.

Hatching date analysis indicates that the hawks consistently chose the most recently fledged young. Two possible explanations for this are: 1) because the time of heaviest predation by hawks occurs after mean tit fledging, many of the early hatched young had already died from non-hawk causes and only later hatched young were still available to them; and 2) that the hawks were selecting the most vulnerable prey, such as recently fledged young (i.e. late

broods) still in family parties, rather than more experienced (i.e. early broods) young (which were independent and had begun to forage in the forest canopy which provides good cover). The earlier mean hatching date of survivors favours the second suggestion.

The age of female parent and origin of both parents do not appear to have influenced the selection of juveniles significantly. However, the young killed by hawks had the youngest mothers, while survivors had the oldest. This may be a hidden factor affecting selection as older parents have young with higher survival potential since they breed earlier (Perrins and Moss 1974), and young hatched earlier in the season are generally heavier than later young (Perrins 1965).

The reason for the selection of first ringed Great Tits in 1977 cannot be clearly determined. The higher weights of these birds may indicate that they have survived better initially than their sibs and were thus exposed to hawk predation.

B. Selection of adults.

Hawks appeared to take adults on the basis of availability when considered in relation to species and origin. Within years there was no selection by sex, but male Great Tits appeared to be favoured slightly when all years were considered. Bulmer and Perrins (1973) suggested that there may be an excess of first year males in the wood which do not obtain nesting territories and were therefore not included in the calculations of the numbers of each sex of ringed birds available. However, Bulmer and Perrins based

their work on data from years when hawks were absent from Wytham; the return of the hawks appears to have shifted the breeding structure of the Wytham tit population by creating more openings for first year breeders (Chapter 5), so that an excess of males may no longer be found. Should this be the case, the differential selection of sexes may result from differences in the foraging areas of the sexes of tits (as found for Parus atricapillus in winter, Glase 1973) or from greater risk of exposure to hawks for males during territorial behaviours.

C. Selection of adults vs. juveniles.

In 1977, the hawks selected juveniles preferentially. Gibb (cited by Lack 1954) found a similar situation based on tit rings recovered from a single hawk nest in 1949. In 1978 the hawks did not appear to select juveniles preferentially during the time that adults were associated with their young, although adults were taken less frequently once the young began to forage in flocks and the adults became more solitary. The lack of marked age group preference in 1978 (and 1976 based on total ring samples) agrees with the findings of Tinbergen (1946) for Sparrowhawk predation on Passer domesticus and Hamerstom and Hamerstom (1951) for Cooper's Hawks preying on a variety of woodland birds.

The cause for the differential selection of age classes in 1977, but not in 1976 or 1978 is thought to be the result of one of two factors. Firstly, the number of ringed tits available per hawk (excluding Marley Plantation hawk pairs) was 578.33, 982.60, and 565.25, with 4.17, 3.28, and 3.74 ringed juveniles per ringed adult

in 1976, 1977, and 1978, respectively. Because the number of juveniles per adult did not differ greatly between years, it is thought that in years when large numbers of tits were available per hawk (e.g., 1977) hawks took the most vulnerable (juvenile) prey preferentially. Relatively low numbers of tits per hawk (e.g., 1976 and 1978) may have caused non-selective hunting, in regards to age, since the time spent searching for easier prey (juveniles) may have posed a greater loss than the energy expended trying to catch more experienced prey. Alternatively, there may have been differences between years in the behaviours such as flocking or the rate of mortality of juveniles which caused the different patterns of adult versus juvenile selection.

Summary.

1) The selection of ringed juvenile tits by hawks shifted from favouring Blue Tits soon after tit fledging to favouring Great Tits about 30 days after tit fledging. It is proposed that this was the result of a shift in the percentage of juveniles of each species which were ringed due to the passage of unringed juvenile Blue Tits through Wytham during July, and not the result of changes in prey choice.

2) Juvenile tits caught by hawks were intermediate in terms of individual pre-fledging weight and brood size when compared to the general population of juvenile tits and those that survived to breed the following year. They were, however, always from broods hatched later than birds in the general population and survivor classes. The age of female parent and the origin of the parents did

not appear to affect selection by hawks.

3) Sparrowhawks selected adult tits on the basis of species at rates that did not differ significantly from availability. Selection for sex did not differ significantly from availability in any year, but there was an indication that male Great Tits tended to be selected more than females when years were considered together.

4) In 1976 and 1978, when total ring samples were analysed, there appeared to be no preferential selection for either juvenile or adult tits; in 1977 juvenile tits were selected significantly more often than adults. This may have been due to relatively low tit per hawk ratios in 1976 and 1978, making it beneficial for the hawks to catch the more experienced adults, and to a relatively high tit per hawk ratio in 1977, allowing the hawks to preferentially select the more vulnerable juveniles while still abundant.

Chapter 5. The impact of Sparrowhawk predation on the Wytham tit population.

I. Introduction.

In previous chapters it has been shown: 1) that Sparrowhawks in Wytham rely heavily on tits for prey (Chapter 3), and 2) how the hawks select the tits they prey on (Chapter 4).

In Part 1 of this chapter, estimates of the losses to hawks from the tit population during different parts of the year are made. For these estimates data on tit brood failures due to hawks (Chapter 2), hawk prey delivery rates and percents of prey which were ringed tits (Chapter 3) and selection of tits by hawks (Chapter 4) found in Wytham were used, along with other data obtained from the Sparrowhawk literature.

Part 2 of this chapter examines the effect that these losses have had on the tit population. Comparisons of: 1) the structure of the population of breeding tits, and 2) the numbers of pairs of tits breeding were made for the periods when hawks were absent and present in Wytham. Findings indicate that hawk predation has caused shifts in the structure of the breeding population, but no marked changes in the size of the breeding population.

II. Part 1. The percent of the Wytham population of ringed tits killed by hawks each year.

A. Methods.

i. Spring (1 April until mean tit fledge).

The number of tits killed by hawks during the spring period was estimated from data on the number of pairs of tits breeding

each year during this study and the rate of brood failure in the periods defined as non-hawk and hawk present presented in Chapter 2 and Appendix 2.

For the period when tits had young in the nest estimates were made for Great Tits by subtracting the mean brood failure rate in the non-hawk period from the brood failure rate in the appropriate year of the study (hawk present year), and multiplying the difference by the number of adjusted broods failed due to hawk predation. On the assumption that loss of only one parent from a pair would cause the brood to fail the number of broods failed was taken to be the number of adults killed by hawks. As no data were available on the rate of brood failure for Blue Tits, it was supposed that the rates would equal those for Great Tits in the same year. The rest of calculations for Blue Tits were performed in the same manner as for Great Tits. The number of ringed adult tits of each species killed in each year was estimated by multiplying the estimated number killed by the estimated percent of adults ringed (Appendix 5) for the appropriate species year.

The number of adult tits lost to hawks during the period from 1st April until young tits were in the nest was estimated as follows. It was assumed that: 1) only the male would catch tits, even though females may also have been hunting for themselves since incubation by hawks does not occur until about the time tits hatch. 2) Only 40% as many prey would be taken by the male during this period as during the time that young tits were in the nest, since he was only hunting for himself and his food requirement is about 40% of the total needed by both parents (see below). 3) The male

would have the same percentage of his diet as tits as during the time that the young were in the nest. 4) The length of the period was calculated as being equal to 1st April until mean hatch minus 1 S.D. for each species in each year (Appendix 4). The number of adult tits taken was obtained by multiplying the number of adults taken during the time that young tits were in the nest by 40% (the correction for the number of prey taken by the male) and then multiplying this result by the number of days in the period divided by the number of days the young tits were in the nest (18 days for Blue Tits and 19 days for Great Tits; C.M. Perrins pers.comm., Gibb 1950) to adjust for the differences in the lengths of the periods. The number of birds which were ringed was estimated by multiplying the estimated number killed by the estimated percentage of these birds that were ringed.

The greatest source of potential error in these estimates is the accuracy of the rate of brood failure used for each year. The yearly levels should be accurate as losses for known causes had been eliminated (Chapter 2), but by using the mean level from the non-hawk years as the base for losses not attributable to hawks, the fluctuations in yearly levels of losses for non-predator causes in each year that hawks were present were not allowed to vary. This may mean that estimates of brood failure due to hawks were low for years when non-predator related brood losses were low, or high for years when these levels were high. However, other estimates and assumptions used in the calculations probably produce conservative results. While it was considered that a brood would fail if one parent was lost, the loss of a male tit does not always

result in the loss of a brood since a female can raise young single-handed (C.M. Perrins pers.comm.). Also, no allowance was made for losses of tits to female hawks during the time that she was hunting for herself. It is considered unlikely that the female hawks did not take any tits at this time. Therefore, although error may be present, estimates derived in the above manner are considered reasonable.

ii. Summer (mean tit fledge through 31 August).

a. The number of prey taken by pairs raising young.

The number of prey brought to the nest and to young after fledging was estimated for each nest from hawk hatching dates (Table 1-2) and hawk prey delivery rates adjusted for date after tit fledging. All calculations assumed hunting of 16 hours/day by the hawks. The number of prey brought each day by males was estimated from the regression equation $y = 0.85 - 0.015x$ prey/hour (Figure 3-8) through day 36 after mean tit fledge, after which time stabilisation of deliveries at 0.3 prey/hour was assumed from findings in Chapter 3. The number of prey supplied by the female was calculated on the basis that they: 1) brought the same number of prey/hour from the 20th day of life of their young as the male, with equal delivery rates for each sex thereafter; and 2) began hunting on day 11 of life of their young and increased deliveries by 10% of the day 20 value each day until day 20. Deliveries from females at Larch 1977 and 1978 were assumed to have equalled the males after only four days of hunting, since large young were introduced into these nests neccessitating the female to hunt sooner. These treatments include delivery of prey by parents to

young for a period of up to two weeks after the young from some nests had become independent; this should not, however, have biased the results greatly as the independent young would have been taking a fairly similar number of prey during this time for themselves. Also, prey delivery during the post-fledging period was assumed to have been equal from each parent, as both sexes were seen to have delivered prey to fledged young in Wytham. This is not thought to have introduced unacceptable bias; no definitive information on the role of prey delivery by each sex of adult Sparrowhawks during the post-fledging period was found in the literature (Brown (1976) suggested from a review of the literature that females deliver more prey than males, while Owen (1916 b and c) observed that the majority was supplied by the male).

The number of prey consumed by the adults at each nest was estimated from daily food requirements of Sparrowhawks given by Newton and Blewitt (1973). These figures of two to three sparrow-sized birds for males (55-85g) and three to four sparrow-sized birds for females (85-110g) each day, including wastage, are only slightly higher than the requirements for the needs of captive, trained Sparrowhawks (pers.obs.), as might be expected since captive birds are less active than free-living birds. The number of prey taken by the male between mean tit fledging and the hatching of the hawk young to feed himself and his mate (all hunting is done by the male while the female does all of the incubating (Owen 1916 a and b, Tinbergen 1946, Sulkava 1964, Newton and Blewitt 1973) was estimated as follows. A combined food requirement of 150g/day was used (60g for male, 90g for female). This was considered to

equal ten birds/day at mean tit fledging since tit size prey were found to predominate at this point in the season for males (Table 3-3). The number of prey required/day was then estimated to have decreased at the same rate as the number of prey supplied/day to the nest by the male in relation to date after tit fledging. After hatch of the young hawks, males were thought to have obtained all their food from prey not brought to the nest, since observations from hides showed that prey supplied by the male was usually intact. Therefore, an estimate of four tit-size birds/day for each male at mean tit fledging, decreasingly proportionately to the rate for deliveries to the nest by the male, until reaching 1.38 prey/day 36 days after mean tit fledge, and stabilising thereafter, was used. The rate of decrease used may have served to underestimate the number of prey taken by males if prey capture rates were not solely linked to prey abundance or vulnerability, especially if males have increased food requirements to prepare for moult.

Watches at nests indicated that females obtained the majority during the nestling period from prey brought by themselves or the males for the young. There were, however, times when females returned from hunting forays with blood and feathers on their feet and beak and some distension of the crop. It was considered, therefore, that females obtained all of their food from prey brought to the nest until the young had fledged, after which time each female was estimated to have eaten one prey item/day separate from prey caught for the young.

b. The number of prey taken by pairs not raising young.

The number of prey taken by pairs which incubated beyond mean tit fledging but which did not raise young was calculated in the same manner used for successful pairs, with termination of male supplying prey to the female when incubation ceased.

For pairs which failed before mean tit fledge, it was assumed that both members of the pair remained in the wood but hunted independently of each other. The male's prey consumption was calculated as for males from successful pairs. The female from an unsuccessful pair was estimated to have taken two prey/day based on food requirements and prey size preferences, without a decrease occurring in the number of prey taken with increasing date.

c. The number of ringed tits taken each day.

The percent of the diet that was ringed tits was estimated for each day from the regression equation $y = 45.89 - 0.75x$ (Figure 3-11) until 44 days after mean fledge, when the percent of the diet that was ringed tits was thought to have stabilised at 13.00%. This stabilisation was thought to have occurred on the basis of stabilisation of delivery rates and the continued equal contribution of prey by each sex. The number of ringed tits taken each day was obtained by multiplying the total number of prey taken each day in each year by the percent of prey which was ringed tits for the same day.

d. The percent of ringed tits which were adults.

The percent of the population of ringed tits in each year which were adults was multiplied by each day's value from the regression equation $y = 1.37 - 0.03x$ for 1976 and 1978, and $y = -0.54 + 0.04x$

for 1977 (see Chapter 4 for regression equation values) to obtain the percent of the ringed tits which were adults for each day. The number of ringed adults of each species killed each year was obtained by multiplying the number of ringed tits killed each day by the percent of these which were adults, and dividing the result according to the estimated number of adults of each species available in the appropriate year since no selection for species was found for this age class. As data were not available for the period before 15 days, or after 40 days, following mean tit fledge it was assumed that the pattern of selection was sigmoidal over time, with stability through 15 days, and after 40 days, after tit fledging. Although these treatments are from information based on small samples with incomplete coverage of the time under consideration, the results produced did not differ greatly from those obtained using total ring samples for each year without adjusting for the effect of date.

e. <u>The percent of juveniles killed which were Blue Tits</u>.

Using the regression equation $y = 1.23 - 0.012x$ from Table 4-4 and the percent of ringed juvenile tits which were Blue Tits in each year, the percent of all juvenile ringed tits killed each day which were Blue Tits was calculated. Multiplying the percent of juveniles which were Blue Tits by the difference between the number of ringed tits taken and the number of these which were adults provided the number of ringed juvenile Great and Blue Tits killed each day.

Table 5-1 shows samples of calculated data for the summer period for one year.

iii. Autumn and Winter (1 September to 31 March).

During the winter of 1976-77 trained Sparrowhawks were released with radio-telemetry equipment in an attempt to determine their prey and predation rates, as had been done by Kenward (1976) with Goshawks Accipiter gentilis. All tracking attempts failed due to the difficulty of following and sighting the hawks in the wood. While it was known the Sparrowhawks attacked tit flocks frequently during the winter (Morse 1973), no extensive data on the attack success rate were available. Therefore, estimates of the percent of the Wytham tit population killed by Sparrowhawks outside of the breeding season were made from information obtained during the breeding season and from the literature.

Data used.

a. The number of hawks in the wood.

The number of male hawks in the wood during autumn and winter was considered to be equal to the number forming pairs in the preceding breeding season. It was assumed that the immigration of young from outside the wood and settling by young born in the wood was only at a level sufficient to sustain losses from mortality or emigration. All male hawks were treated as hunting entirely within the wood. Opdam (1975) found that male Sparrowhawks do not appear to leave the vicinity of woodland during winter and Goshawks have been shown to spend the greatest amount of time in the areas of highest prey abundance in their winter territories.

Table 5-1. An example of of calculated data for estimating the number of ringed tits in each class taken by hawks each day. Shown are calculations for a nest where young hatched six days after mean tit fledging.

Days after mean tit fledging	No. prey to nest from male	No. prey to nest from female	No. prey eaten by male	No. prey eaten by female	% prey ringed tits	No. ringed tits eaten	% tits adults	% juv Blue Tits
0	0	0	4.00	6.00	45.89	4.59	20.20	79.17
5	0	0	3.64	5.28	42.12	3.76	20.20	75.37
10	11.08	0	3.27	0	38.34	5.50	20.20	71.57
15	9.85	0	2.91	0	34.56	4.41	20.20	67.77
20	8.62	2.86	2.55	0	30.79	4.32	17.28	63.97
25	7.40	6.44	2.19	0	27.01	4.33	14.36	60.17
30	6.17	6.17	1.82	0	23.24	3.29	11.44	56.37
35	4.94	4.94	1.46	0	19.46	2.21	8.52	52.75
40	4.80	4.80	1.38	1.00	15.68	1.88	5.61	48.77
45	4.80	4.80	1.38	1.00	13.00	1.56	5.61	44.97

(Wytham supports large flocks of tits and finches during winter.) Female hawks were thought to have hunted primarily outside of woodland, as suggested by the findings of Opdam (1975) for winter and Newton (in prep.) for late summer. This is as might be expected from prey size preference and thefact that the fields around Wytham support flocks of House Sparrows and thrushes. These assumptions are partially supported by over 150 hours of observation in the fields around Wytham during the winter, during which numerous hunting females, but only one hunting male, were sighted. Any overestimates made of the amount of time spent by males hunting in the wood should be balanced by the exclusion of females from hunting in the wood, where they are sometimes seen or mist-netted while hunting during winter (pers.obs. and N.J. Phillips, V.E. Wood, A Klessling, B. Cockrell, pers.comm.). The estimates of the numbers of males in the wood are also likely to be low for at least part of the period.

b. <u>The number of prey taken/day by male Sparrowhawks</u>.

The figure of 1.38 prey/day/male Sparrowhawk from the estimates for the end of the summer period were used for the autumn and winter period. This estimate is considered to be somewhat conservative because the food requirements for winter should be higher due to the colder weather.

c. <u>The percent of prey which was ringed tits</u>.

The passage of unringed juvenile tits through the wood during the late summer and early autumn ends in October (Webber 1975) and the percent of juvenile Blue and Great Tits which are ringed during winter increases to about 60% and 70%, respectively

(V.E. Wood, N.J. Phillips, unpubl. data). Therefore, the percent of tits caught by hawks which are ringed should be higher during autumn and winter than late in the summer. With all other factors being equal, the estimate from the end of the summer of 13% of prey being ringed tits should be low for winter due to the difference in the ratio of ringed to unringed birds, as well as the fact that the summer estimates were derived from prey from both parents while only males are considered here. On the basis of the above, it was estimated that 20% of the prey of male Sparrowhawks during the winter is ringed tits.

d. Division of ringed tits killed into species and age groups.

Morse (1978) found that the ratio of Blue Tits to Great Tits during the winter was about 2.7:1 in Wytham. This corresponds closely to the ratio in summer. Since the findings for hawk selection during summer showed species choice approximating availability, tabulations of the number of each species killed were made on the approximate relative abundance obtained from summer records.

The age group selection was assumed to follow availability as Perrins (1965) showed that the ratio of adult to first year Great Tits found breeding in the wood in a given year was the same as the ratio in the wood the preceding autumn, suggesting that both groups by autumn are equally susceptible to predation. Therefore, the adult : juvenile ratios of 1: 1.73 and 1: 0.91 for Great Tits and 1: 2.30 and 1: 0.90 for Blue Tits in the winters of 1976 - 77 and 1977 - 78, respectively, were used to determine the ratio of age groups of each species taken. No data on adult : juvenile ratios were available for the winter of 1978 - 1979. Estimates which were obtained from the above adult to juvenile ratios

may be somewhat biased in favour of adults, as work on Great and Marsh Tits (Webber 1975, Morley 1953) suggests that adults may only join foraging flocks in winter as the flock passes through their territory, so that if hawks attack flocks preferentially to solitary individuals, more juveniles should have been taken than were estimated.

B. Results.

i. The percent of the population of ringed tits killed each year.

Table 5-2 shows the percent of each segment of the ringed tit population estimated to have been killed by hawks during each period in each year.

These estimates are thought to be generally conservative for the spring and autumn/winter period for reasons discussed previously. The summer estimates are thought to be the most accurate, although use of information derived from the data of the three years combined for individual years may have introduced small, but not unacceptable, biases. This is reflected by the estimates of the number of prey taken during the summer by a hawk pair raising and fledging young, which averaged 800-900 items, agreeing closely with the figure given by Newton and Blewitt(1973).

ii. The percent of the average annual mortality of tits caused by Sparrowhawk predation.

Bulmer and Perrins (1973) estimated the average annual mortality of Great Tits in Wytham to be 78% for juveniles, 52% for adult females, and 44% for adult males. However, about 33% of all young and 5% of all females were lost to predation while in the nest during the years from which they obtained their data.

Table 5-2. The percent of the population (N) of ringed Great Tit juveniles (GTJ), Great Tit adults (GTA), Blue Tit juveniles (BTJ), and Blue Tit adults (BTA) estimated to have been killed by Sparrowhawks during the spring (1st April to mean tit fledge)(SPR), summer (mean tit fledge to 31st August)(S), and autumn and winter (1st September to 31st March)(AW) pericds in each year.

Year		GTJ	GTA	BTJ	BTA
1976	N	751	221	2050	448
	SPR	--	0.90	--	1.12
	S	33.82	17.49	26.88	17.49
	AW	8.26	16.29	8.59	17.19
	TOTAL	42.08	34.68	35.47	35.80
1977	N	1128	421	2638	726
	SPR	--	4.51	--	4.82
	S	18.00	7.67	17.74	7.67
	AW	4.70	13.78	5.56	17.36
	TOTAL	22.70	25.96	23.30	29.85
1978	N	1280	353	2288	601
	SPR	--	2.83	--	3.49
	S	33.05	18.24	27.23	18.24
	AW [1]	----------Not available----------			
	TOTAL	33.05	21.07	27.23	21.73

1) No figures available for the ratio of adults:juveniles in the wood in winter. However, a estimated 190 Great Tits and 337 Blue Tits were taken in the autumn-winter period 1978-79.

Changes in the type of nestboxes used have reduced these losses to about 5% and less than 1%, respectively, for the years of the present study. Readjustment of Bulmer and Perrins calculations for the lower nest predation losses in recent years provided estimates of average annual mortality of 44% for both sexes of adult Great Tits and 85% for juvenile Blue Tits, assuming that 1.05 young still survived from each pair.

No estimates have been made for Blue Tit mortality in Wytham, but Snow (1956) established an average annual mortality of 70% for adults in Britain. An estimate of juvenile mortality for this species was made in the manner used by Bulmer and Perrins assuming similarities in all factors between Blue and Great tit biology, except a larger clutch size (11 eggs on average in Wytham) for Blue Tits and 1.59 young surviving from each pair to compensate for the higher adult mortality of Blue Tits. From this an average annual mortality for Blue Tit juveniles of 82% was established.

Using the above annual mortality estimates and the estimates of the percent of the Wytham tit population killed by hawks in each year, the percent of the annual mortality of tits in each species/age group caused by hawks was estimated, shown in Table 5-3.

Without more accurate figures on the mortality of tits than are available it is not possible to quantify the differences in the rates of mortality between periods when hawks were and were nct present. However, it appears that hawks have caused sufficient increases in adult mortality to decrease their contribution to the breeding population. This does not appear to have been the case for juveniles where, although the annual mortality may have

Table 5-3. The percent of the average annual mortality of the Wytham population of ringed tits caused by Sparrowhawks each year.

Year	Great Tit		Blue Tit	
	juvenile	adult	juvenile	adult
1976	49.51	78.82	43.26	51.14
1977	26.71	59.00	28.41	42.64
1978[1]	38.88	47.89	32.04	31.04

[1]excluding losses over the autumn/winter period.

increased beyond the level of non-hawk years, the number of young surviving has been sufficient to replace adults from the breeding population lost to hawks (see below).

III. Part 2. The effect of Sparrowhawk predation on the Wytham tit population.

As substantial losses from the Wytham tit population were incurred in each year of this study due to hawk predation, examinations were made to determine if these losses had a measurable impact on the tit population.

A. Changes in the structure of the Great Tit breeding population.

Great Tits trapped each year during the breeding season at nestboxes were classified by sex into the following age/origin classes: 1) first year resident (Wytham born); 2) first year immigrant; 3) older than one year resident; and older than one year immigrant; for three periods of hawk presence: 1) hawks absent from Wytham (1964-67); hawks present but not breeding successfully (1968-72); and hawks breeding successfully (1973-78). Years prior to 1964 were not included in the analysis as the status of hawks was not accurately known for this period and because tit trapping records prior to this were incomplete. Table 5-4 shows the number of individuals of each sex trapped in each period and the percent of these birds in each age/origin class.

For both sexes it was found that the structure of the breeding population differed significantly between periods (males, $x^2_4 = 34.34$, $P < 0.001$; females, $x^2_6 = 22.08$, $P < 0.001$). Subdivision of the contingency tables indicated that residents older than one year were the class which differed from the rest as no significant

Table 5-4. The percent of Great Tits trapped (N) from the breeding population in resident first year (Rly), resident older than one year (R1+), immigrant first year (Ily), and immigrant older than one year (Il+) classes for each sex in the hawk absent (1964-67), hawk present but not breeding successfully (1968-72), and hawk breeding successfully (1973-78) periods.

Sex	Period	N	Rly	R1+	Ily	Il+
M	64-67	290	16.55	35.52	16.21	31.73
	68-72	412	21.84	31.55	19.66	26.94
	73-78	727	26.13	20.91	20.50	32.46
F	64-67	663	23.23	22.47	25.64	28.66
	68-72	670	24.33	15.68	33.43	26.57
	73-78	795	24.90	15.22	29.43	30.44

differences were found between periods for the other class together for either sex (males, $x^2_4 = 6.09$; females, $x^2_4 = 6.48$).

From Table 5-4 it can be seen that the female residents older than one year showed less of a decline than the males of the same class, with the difference being significant ($x^2_2 = 14.44$, $P < 0.001$). The difference in the rate of decrease is the most marked for the last period. The cause of this is thought to be the change in the type of nest box used in Wytham (with the change begun in the early 1970's) to ones more impervious to weasels. This caused reductions in the numbers of females lost at the time that hawk predation was intensifying, resulting in stabilisation of losses to the group. This did not occur for males as negligable numbers of males suffered from weasel predation since they do not incubate or spend substantial periods of time in the nest caring for the young.

The decline in the percent of breeders which were older residents coinciding with increases or maintenance of the contributions from the other groups suggests that the population was expanding or that older residents were dying faster than they could be replaced. Figure 5-1 shows that the breeding population was not expanding in the years under consideration, suggesting that mortality had caused the decrease in the contribution by older residents. As no other factors are known to have affected the breeding population during these years, it is believed that predation by Sparrowhawks caused the change in the structure, relative to the time of their absence.

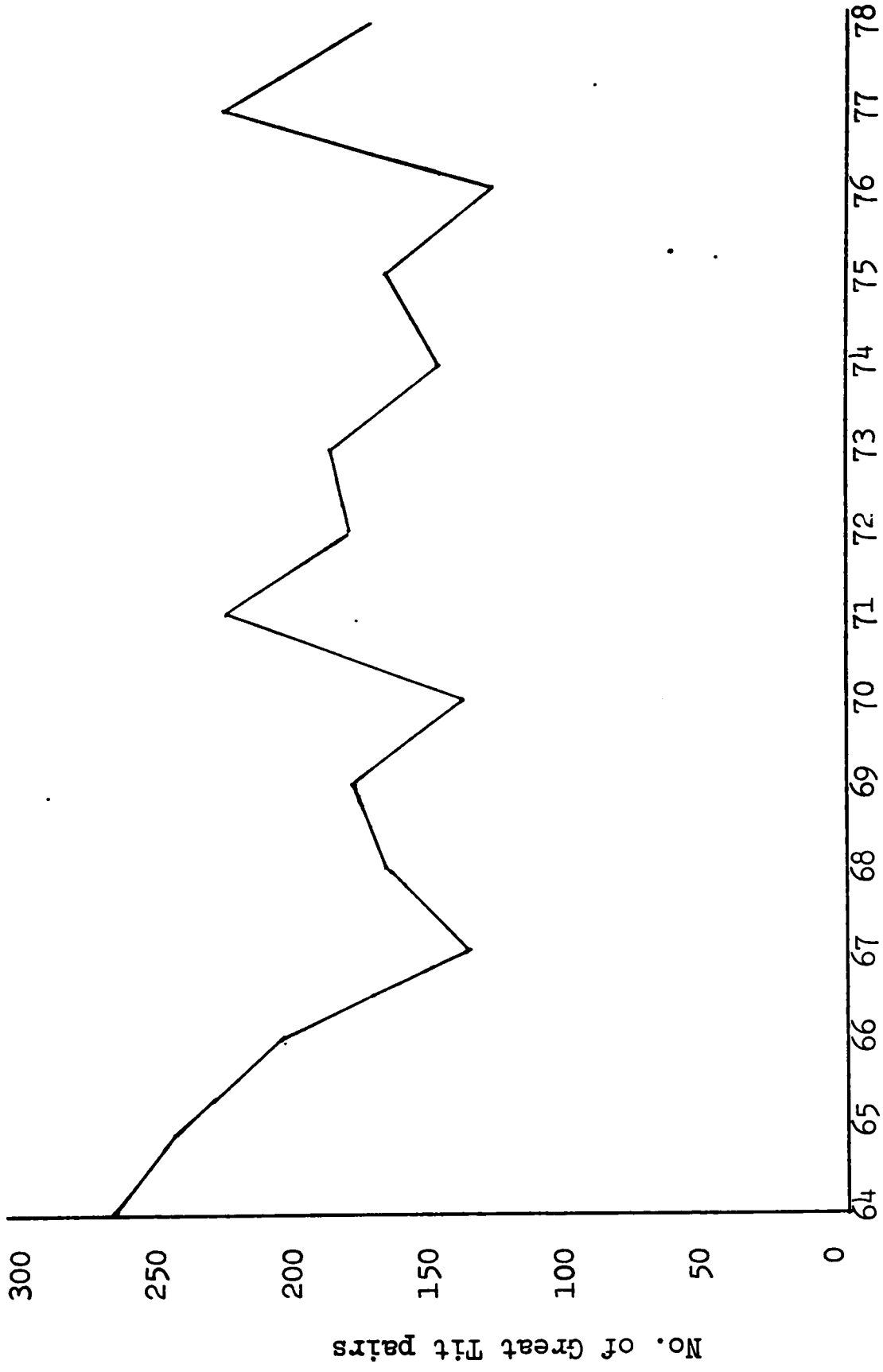


Figure 5-1. The number of Great Tit pairs using Wytham nestboxes from 1964-78.

B. Changes in the number of tit pairs.

As previously discussed (Chapter 1), the Wytham hawk population underwent a serious decline in the 1950's and 1960's, followed by an expansion in the 1970's. In addition, Newton (1972) showed that the British Sparrowhawk population reached extremely high levels during the years of the Second World War due, presumably, to severe curtailment of gamekeepering. Comparisons of hawk population levels were made with tit numbers to see if reduction in the prey population had occurred when predator levels were highest, or increased when they were lowest.

For this examination, data on the number of tits in Wytham was drawn from the number of pairs breeding in Marley Wood in each year from 1947. The numbers of pairs of tits breeding in the whole wood were not accurate for years prior to 1964 as nest boxes had not been placed throughout the wood until that year. The number of Great Tit pairs in Marley reached its highest level in the 1960's, and its lowest levels in the 1940's-50's and 1970's (Figure 5-2). The number of pairs of Blue Tits increased steadily over the years, but the increase from the early 1970's has been attributed to the new type of nest box used which appears to be favoured by this species over the type used formerly (C.M. Perrins, pers.comm.) so that the species appear to have paralleled each other in numbers for the most part. While the high and low points in tit numbers seem to be inversely related to hawk population levels, other factors may have caused these changes. The mid-1960's showed extremely good crops of beechmast, an important winter food for tits, the level of which can affect tit survival and hence,

Figure 5-2. The number of pairs of tits breeding in Marley wood each year.

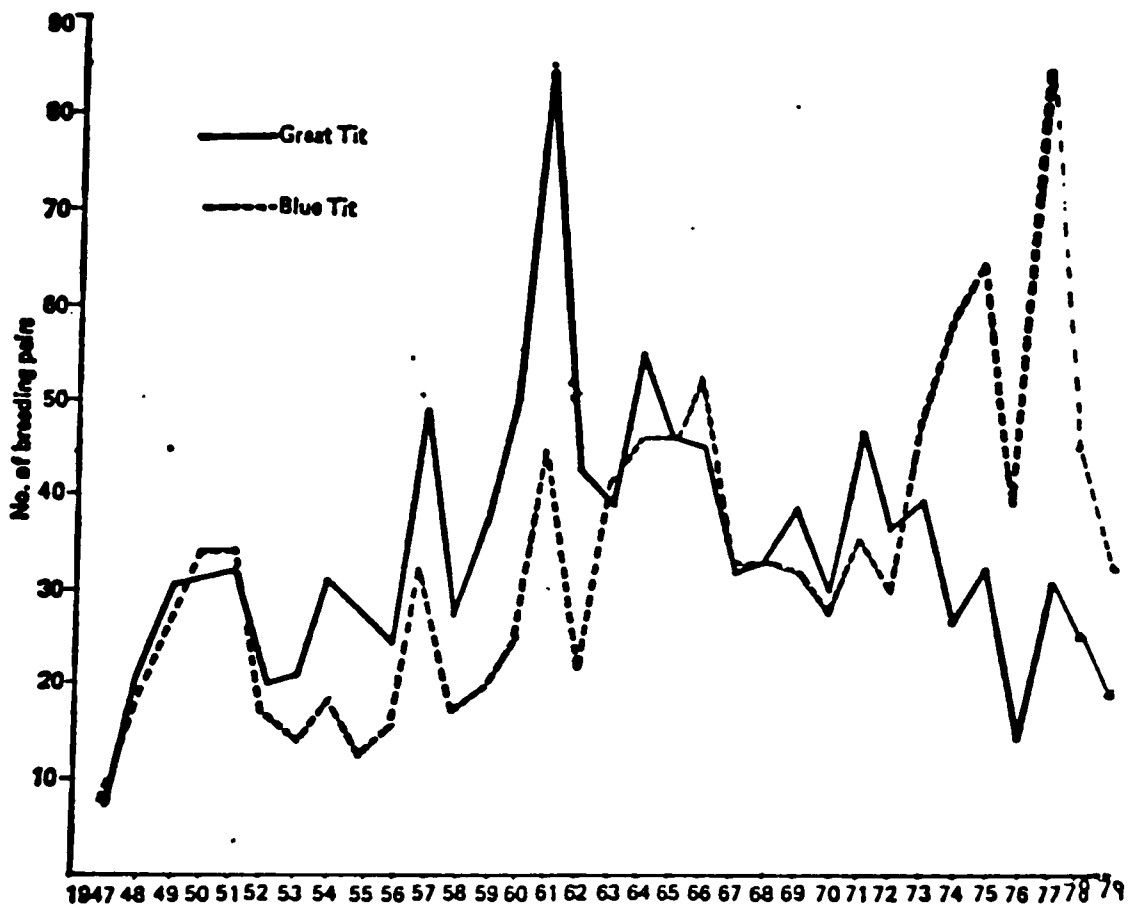
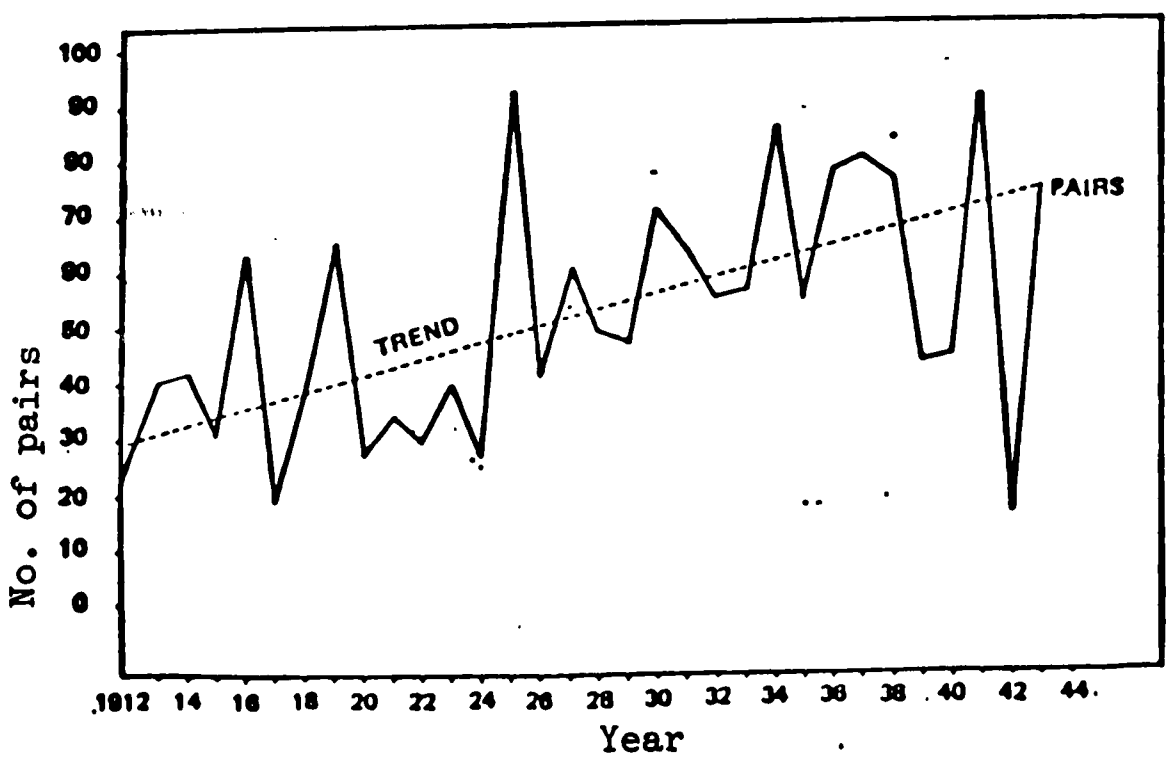


Figure 5-3. The number of pairs of Great Tits breeding in Kluijver's (1951) study area in each year.



tit numbers (Perrins 1965). The late 1940's - early 1950's and the 1970's did not show such high levels of this important crop. Further, the winters of the 1960's were very mild, with the exception of 1962-63 which was severe but had a good beechmast crop, also serving to increase tit survival.

As no other comprehensive data for a number of years were available for British tit population levels, Kluijver's (1951) data for Great Tit numbers in Holland were examined to determine whether changes had occurred in tit numbers with changes in hawk population levels. It is thought that the population of Sparrowhawks in Holland underwent similar changes to the British population, with the following exception. N. Tinbergen (pers.comm.) states that the Goshawk population of Holland underwent a dramatic increase in the early 1940's which coincided with a decrease in the Sparrowhawk population, due presumably to the loss of the latter to nesting Goshawks. Prior to this time Sparrowhawks had been relarively common and Goshawks very scarce. While Kluijver's data (Figure 5-3) shows that tit numbers increased in his study area during the time that Sparrowhawk levels were presumably decreasing, the relationship between hawks and tits for this area is not clearly cause and effect; Kluijver attributed the increase in tit numbers to maturing of the woodland in which the study was conducted, allowing a higher carrying capacity for the wood.

IV. Discussion.

An estimated 23%-42% of juvenile and 22%-36% of adult tits from the Wytham population were lost to direct Sparrowhawk

predation during each year of this study. The estimates for the summer period were considered to be the most accurate as they were based on the most complete data, but the results obtained for the other periods show close agreement with the findings of other studies. Tinbergen (1946) estimated that 5.7% of the Great Tit population in his study area in Holland were lost to Sparrowhawks during May, compared to 2.7% of the Great Tits in Wytham estimated to have been lost during the Spring period. Additionally, Craighead and Craighead (1956) estimated that between 4% and 11% of the small in their Wisconsin study area were lost during the winter to raptor predation, mostly from Cooper's hawks. This agrees well with the average estimated loss of 16.2% of the years adult population and 13.6% of the juveniles surviving until autumn (based on an estimated 50% of the juveniles having died since fledging from Figure 81 in Perrins 1979) each year to Sparrowhawks in Wytham.

While these figures indicate substantial losses to the Wytham Tit population, they are probably conservative in conveying the full consequences of the hawk predation. Firstly, as seen in Chapter 4, the juveniles killed by hawks during the summer appeared to be ones that had survived the initial period of post-fledging mortality. In such a case the number of juveniles killed should be divided by the number of juveniles surviving these initial losses (for which no figures are available) to obtain the percent of the potential survivors killed. Such a figure would be higher than the percent of the entire fledged population killed. Secondly, while the figures on the percent of the population killed detail the number of birds eaten by hawks, they do not include indirect losses

still attributable to hawks. An example of this type of loss was found in 1979 (C.M. Perrins pers.comm.). A male Great Tit was recorded as having been killed by a Sparrowhawk during the late incubation or early nestling period: on the day the young of this male fledged the female parent was also killed, leaving the young, it is presumed, to die due to lack of care. Other similar incidents most likely occurred, once again contributing to conservative estimates of losses due to hawks. The major apparent effect of the hawk predation on tits in Wytham is the shift in the structure of the breeding population since the return of the hawks. The losses of the older resident breeders at a rate greater than the recruitment rate has caused them to be replaced mainly by first year resident and immigrant birds, which are rather less successful breeders (Perrins and Moss, 1975). Also, the first year birds which breed now may be less fit than first year birds that bred in the past, as the increasing number of openings in the breeding population may allow in birds which otherwise would have lost out in competition with older breeders or fitter first year birds. The overall effect of this shift may be the lowering, albeit probably to a slight degree, of the reproductive output of the breeding population commensurate with the lower nesting success of younger breeders.

The size of the breeding population does not appear to have changed markedly as a result of hawk predation. The evidence from the shift in the breeding structure suggests that the number of juveniles raised in Wytham surviving to the following year is sufficient to maintain numbers, although increasing participation

from immigrants may help. While comparisons between the levels of tits and hawks may hint at lowered numbers of tits when hawks are high, the other factors which regulate the tit population, such as food and other environmental parameters, are as likely to have produced the minor fluctuations found as the changes in hawk numbers.

The Wytham Sparrowhawk-tit relationship poses an interesting point for consideration. The hawks take large percentages of the tit population, especially in years when there are not extremely high numbers of tits. However, the hawks have not begun to take tits in numbers sufficient to reduce, per se, the number of tits that can breed and produce the food required by the hawks. They have only created a situation where a prey population must draw on the least fit home produced breeders and immigrants to maintain the population. In the past, the habitat in Wytham was considered optimal for tits, with abundances of food and nest sites. At the present time the hawks may have changed this, making previously less good habitat safer for producing progeny which will survive to reproduce, as well as safer for adults to live in so that they may breed for as long as possible. In Chapter 2 it was shown that the tits do not appear to recognise areas where they are likely to suffer from hawk predation while breeding. Presumably, this is why immigrants continue to choose Wytham as an apparently desireable area in which to nest. If hawk predation in Wytham has reached a level where it would be safer for the tits to nest in a less good habitat, it provides an interesting example of the prey not being able to recognise the best habitat, a reversal of Kluijver and Tinbergen's buffer effect (1953). If such is the case, the prey

serve the predator's needs better than their own.

Summary.

1) Data on hawk predation rates and tit selection were used to determine the percent of the population of each age class of Great and Blue Tits killed by hawks during each year. Between 23% and 42% of juveniles, and 21% and 36% of adults were killed by hawks, with the majority of losses incurred during the time that hawks had dependent young. These losses accounted for about 27% to 50% of juvenile mortality, and about 31% to 79% of adult mortality of tits each year.

2) The high numbers of tits lost appears to have affected the structure of the population of breeding tits in Wytham by decreasing the contribution made by older birds which were born in Wytham, and increasing the contribution made by first year Wytham and immigrant birds. There does not, however, appear to have been a decrease in the number of tits breeding each year, suggesting that the tits were maintaining numbers through recruitment of younger or immigrant individuals into the breeding population.

Chapter 6. Final discussion.

I. Wytham as an area for the study of predator-prey relationships.

Wytham Woods offers an excellent opportunity to study the relationship bewteen avian predators and prey. It is a relatively small area of uniform habitat supporting high densities of both predators and prey. The isolation of the wood from other wooded areas means that research is limited to a contained area and that incursion into the wood by non-resident predators is probably minimal. Most importantly, the extensive studies and ringing of the tit population make available information about the population size, the rate at which theseprey are taken, and the manner in which they are selected. Generally, Wytham is one of the few areas which can fulfil the criteria set out by Brown (1974) for the effective study of raptor predation.

The findings of the present study are important in that they present a variety of information on the nature of predation derived from studying a single population of predators and prey in the wild. They do not, however, present the total knowledge which can be drawn from Wytham, but only lay the groundwork from which more intensive and specific studies can develop.

II. The percent of the prey which was tits.

A. Summer.

The percentage of the prey of Wytham Sparrowhawks which was ringed tits during the summer showed striking agreement between pairs when related to date after mean tit fledging. This was most

likely the result of two factors, the uniformity of the habitat over which the majority of hawks hunted and the preferential selection of temporarily abundant prey.

As discussed previously (Chapter 3) Sparrowhawks hunt over wide areas. In Wytham this distance is not known with certainty and can only be confirmed by tracking via radio-telemetry. (Originally, the distance from the nest of the capturing hawk to the nest box from which the captured individual fledged was going to be used for determinations, but the dispersal of tits could produce erroneous results). However, if the distance is only 1-2km, each bird would still cover much of the wood. Since Sparrowhawks do not have mutually exclusive hunting areas (Newton and Blewitt 1973, and I. Newton, pers.comm.), different birds should hunt the same parts of Wytham and catch the same type of prey. (This contrasts with predators which hunt in exclusive territories and for which prey type reflects territory habitat - e.g., the findings of Southern and Lowe 1968 for the Tawny Owls).

Much work (e.g., Tinbergen 1960, Holling 1965) has shown that predators will switch to predation of a single species at a rate higher than expected on the basis of relative prey abundances when the population of that species reaches moderate levels. The high rate of tit utilisation by hawks soon after tit fledging is most probably an example of this "switching". The rapid decrease in the proportion of tits in the diet is assumed to represent a decrease from exploitation at a rate higher than expected to the expected rate, resulting from decreased availability/vulnerability of the tits. This switching to tits soon after they fledged is also

thought to have accounted for the elevated prey delivery rates at hawk nests found during the time tits were most abundant (see below).

B. Other seasons.

The percent of Wytham Sparrowhawks' prey which is tits during the autumn, winter and spring periods can only be determined through the direct observation of the hawks or by the collection of prey remains (in the manner used by Tinbergen 1946, van Beusekom 1972 and Opdam 1975.

The estimates of the percent of male Sparrowhawk prey which was tits during the autumn and winter periods used to calculate the number of tits taken are considered to be fairly accurate. Morse (1978) found that Great and Blue Tits formed 29.5% of the winter avifauna in a 10 ha area of Wytham. If prey were evenly distributed in the wood during this time of year, it would be unlikely that less than 30% of Sparrowhawk prey taken would be tits, since some of the species included in Morse's data would be too large for these hawks to take. However, it is not likely that prey would be distributed evenly in the environment and tits, because of their size and flocking habits, might actually serve as prey patches inviting preferential exploitation by the predator (see Royama 1970, Hassell and May 1974).

III. The feeding rates of hawks.

The most important finding as regards feeding rates in this study is the relationship between changes in prey abundance and the rate with which adult predators supply thier young with food.

For Sparrowhawks, Newton (1978) postulated that female hawks began to hunt because male hawks were having increasing difficulty supplying prey due to descreases in prey availability. He did not, however, inter-relate differences in prey delivery rates for members of the same sex with prey availability/vulnerability. This was most likely due to the fact that the observed hawks were hunting in different habitsts with, presumably, different prey densities. Tinbergen (1946) found that total prey deliveries increased with age of young. This may have been the result of: 1) initial low prey densities so that males could not afford to reduce delivery rates even when females began to hunt; or 2) continued high prey availability in his study area throughout the hawk nestling period due, possibly, to fledging of second broods of prey species (Great Tits in Holland produce second broods much more frequently than in Wytham - Perrins 1979), so that males maintained high delivery rates and were supplemented by the female.

For other avian species only one example of the relationship between prey availability and feeding rate was found in the literature. Royama (1966) found for Great Tits that late broods were fed less frequently than early ones and he presumed that this was due to changes in the abundance of prey. Additionally, he found that prey were larger later in the season, which parallels the findings for hawks in Wytham. This was due to shifts in prey availability; a higher proportion of prey available later in the season were larger caterpillars. Whether changes in hawk prey size occur with season because of changes in prey types available or because hawks bring larger prey later in the season to maximise food intake of

their young can only be determined by censusing the Wytham avifauna late in the season.

The higher prey delivery rates of hawks nesting earlier in the season in Wytham suggests that hawks should nest so that their young hatch at the same time as tits fledge to ensure maximum growth rates. Other birds have been shown to have higher nesting success and survival of young when they nest so that young hatch as close as possible to periods of food abundance (Perrins 1970). As high growth rates of young Sparrowhawks are associated with high delivery rates (Moss 1976, Newton 1978), it is assumed that the earliest nesting hawks would produce greater proportions of surviving young. This could easily be confirmed in Wytham with growth rate studies combined with a ringing programme. Further, as older hawks are more exoerienced hunters than first year breeders, they may also produce a greater proportion of surviving young. This could also easily be studied in Wytham.

Of great importance is the need to study feeding rates of adult hawks in Wytham. Radio-telemetry should be able to provide the means for studying both sexes during all periods of the year. Such work could provide the answer to questions such as whether male hawks reduce their food consumption as they decrease their delivery rates, and the proportion of prey provided by each parent for fledged young.

Lastly, the nesting success or numbers of pairs nesting each year has been linked to prey abundance for many raptors; generally these are species for which prey undergo cyclic fluctuations

(Southern 1959, Cavé 1968, Snow 1968, Hagen 1969, White and Cade 1971, McGowan 1975). Prey delivery rates affect the survival of young hawks. Small passerine population size, upon which delivery rates depend, fluctuates considerably from year to year (cf. Figure 5-2), and it might be possible to link the numbers of hawk pairs in Wytham to tit density in future years. The data from the present study suggest that there may be a relationship (a higher number of hawks in 1978 following a high tit population in 1977), but this would have to be studied further for confirmation of cause and effect.

IV. Selection of prey.

During the summer, hawks in Wytham did not exhibit selection for the weakest prey, except in the case of late hatched young in all years and the preference shown for juveniles in 1977.

In large mammalian carnivores it has been found that the weakest prey, usually the young, old or those showing physical abnormality, are preferentially selected (Murie 1944, Pimlott, Shannon and Kolenosky 1969; Bruns 1970; Kruuk 1970; Mech and Frenzel 1971; Ogle 1971; Kuyt 1972; Schaller 1972). For raptors, preferential predation is usually exhibited towards individuals which exhibit some oddity or weakness (Dice 1947; Rudebeck 1950; Eutermoser 1961, Mueller 1974). In all of the above cases, however, the hunting method of the predator involved chasing a group in which weak individuals lagged behaind, or choosing a single odd individual from a group of prey presented to the predator. Aside from the capture of late hatched young, discussed below, the findings of relative

non-selectivity by Wytham Sparrowhawks is thought to be best explained by the findings of Kenward (1976, 1978) for Goshawk attacks on pigeon flocks. During arranged attacks, Goshawks released at pigeon flocks from a considerable distance took individuals which were in poor condition, but when released close to the pigeon flock they took prey which did not exhibit weakness. Kenward attributed the first finding to slower escape by unfit individuals when prey began to flee from a predator spotted a good distance away and the second finding to random selection by the predator when it had equally good chances of capturing any individual as a result of the surprise factor. As Sparrowhawks in woodland hunt by lying in wait for prey or by dashing into a group of prey from cover (Tinbergen 1946, Hinde 1952), they initiate attacks by surprise and should not exhibit marked selectivity.

The selection of late fledged young is attributed to the fact that they were still in family parties under the forest canopy while early fledged young had moved up into cover in the canopy (see Chapter 4). Inconclusive but suggestive evidence of preference for attacking these parties by hawks was found during 1979 when, in a number of instances, more than one member of late fledged broods were caught by hawks on the same day (C.M. Perrins, pers. comm.). The apparent preference for young in family parties suggests that they are sought after by the hawks because attacking groups may be more successful than attacking individuals. This cannot be confirmed until the proportion of early fledged young captured can be determined for the period prior to when ring recoveried were made from hawk nests (at least seven days after the young hawks hatched - see Chapter 3).

V. The effect of predation on the prey population.

A. The percent of the population lost to predation.

Comparisons between the findings of this study and other predation studies are difficult as few other studies have been able to quantify the losses of prey due to a single predator species. Therefore, in addition to comparisons of other single predator studies, comparisons with studies involving a group of related predators were made.

The literature on raptors shows the following losses to prey populations due to these predators: Craighead and Craighead (1956) estimated that up to 47% of a prey population (in this case rabbit Sylvilagus floridanus) was lost to raptors over winter; losses to avian populations only ran 4-11%. Tinbergen (1946) found that Sparrowhawks caused an estimated 15-79% of the adult mortality in four passerine species during May. Eng and Gullion (1962) estimated that 30% of all mortality of Ruffed Grouse in their study area was caused by Goshawk predation. Smeenk (1974) estimated that losses to eagles accounted for 36-56% of the Dik-Dik Rhynchotragus kirkii population in Tsavo Park, Kenya.

Non-raptor predators are attributed with the following losses: Gulls Larus spp. removed 100% of the ducklings raised on an island in a lake in Alberta (Vermeer 1968). Northern Pike Esox estor removed almost 10% of all ducklings from river deltas in a Canadian study area (King and Pyle 1966). Lions Panthera leo and Spotted Hyenas Crocuta crocuta each remove about 3-10% of their prey species each year (Schaller 1972, Kruuk 1972). Tinbergen (1960) found that Great Tits took 37% of Pine beauty moth Panolis flammea

larvae in conifer plantations in Holland. Lastly, three species of song birds, Scott's Oriole Icterus parisorum, Black-backed Oriole I. abeillei and Black-headed Grosbeak Pheuticus melanocephalus, caused 60-84% of the mortality of Monarch butterflies Donaus plexippus overwintering in Mexico (Calvert, Hedrick and Brower 1979).

While these figures show that the pressure of predation varies substantially, they also show that the estimates for Wytham are not unreasonable, especially when considered in relation to the reproductive capacities of the prey species.

B. The consequences of predation.

Craighead and Craighead (1956) postulated that the pressure from predation in their study area served to reduce fluctuations in the size of the prey populations. While numerous factors aside from hawk predation affect the number of tits nesting in Wytham each year, it seems likely that hawk predation would serve to limit at least upward increases in population size. This could be shown in Wytham in the future, if the hawk population remains stable, by comparing changes in tit breeding numbers between non-hawk and hawk present years.

Additionally, studies have been conducted in which predators were removed from study areas to determine their effect on prey populations. For Ruffed Grouse, predator removal served to increase nesting success, but did not reduce juvenile or adult mortality (Edminster 1939; Bump, Darrow, Edminster and Crissey 1947). In Wytham, where predators were removed without direct human agency, their return caused shifts in the structure of the tit breeding

population through increased adult mortality. Lack (1954) cited adult mortality as the critical factor affecting small passerine population levels. With the present findings it appears that breeding success for tits may be affected, although population size may not have changed due to increased recruitment of resident and immigrant first year birds. Slobodkin (1974) characterised predators as being "prudent" if they maintained their prey populations in a state of highest reproductive capability so that culling could take place without risking the predators' well being. Given the Wytham situation, some might evaluate the hawks as being imprudent. However, since the tits can maintain their population level through outside recruitment, the Wytham Sparrowhawks, by achieving population sizes above those allowable with a closed prey population, may be not only successful, but the most prudent of predators.

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Appendix 1. Levels of pesticides in Sparrowhawks' eggs from Wytham.

One egg analysed from each nest where eggs were collected.

Values are ppm wet weight and lipid weight ().

Nest and Year	DDE	PCB	Dieldrin
Lord's Copse 1976	17.2(225)	23.5(308)	2.2(28)
Radbrook 1976	6.1(76)	8.6(106)	1.3(17)
Marley Plantation 1977	10.0(128)	10.7(137)	0.7(9)
Larch 1977	21.5(293)	27.3(372)	1.2(16)
Thorny Croft 1977	19.5(212)	11.0(120)	1.4(15)
Larch 1978	15.1(150)	31.2(310)	2.1(17)

Ratcliffe (1970) found the mean DDE and Dieldrin levels to be 29.53 and 4.59 ppm wet wt., respectively, for his samples from southern England. PCB levels were not measured for his southern England samples, but northern England samples, averaging about 67% lower than southern samples, showed a mean of 2.15ppm. These levels of contamination were associated with an approximately 30% decrease in egg shell thickness index compared to eggs gathered prior to the introduction of these pesticides.

Appendix 2. Chapter 2 data recalculated to include data from 1978.

A. In 1978 990 nest boxes were available for tits' use.

B. Table 2-1 data for 1978. Woodcroft not included as no nestboxes were located within 60m of the nest.

Nest and Year	annulus I U	S	N	annulus II U	S	N	annulus III U	S	N	annulus IV U	S	N
SPARROWHAWK NESTS INCUBATED FULL TERM OR FLEDGING YOUNG												
Marley 1976	14	14	7	41	27	22	53	26	19	44	33	18
Larch 1978	0	0	1	100	100	2	63	63	8	89	67	9
Radbrook	50	50	2	78	67	9	71	43	7	44	33	9
Marley Plantation 1978	71	71	7	83	67	12	70	70	10	50	40	10
Total (excluding Marley Plantation 1977 & 1978	18	8	40	46	48	141	47	36	167	49	37	197
SPARROWHAWK NESTS FAILED SOON AFTER EGGS LAID												
Thorny Croft 1978	50	0	2	29	29	7	88	63	8	75	75	12
Marley 1978	50	50	6	32	26	31	41	29	41	32	27	37
Total	67	50	18	48	41	64	61	44	97	52	45	83

Appendix 2 continued.

C. x^2_3 between annuli I, II, III and IV for hawks incubating full term or beyond:

= 13.72, $P < 0.001$ for tit use;
= 15.28, $P < 0.001$ for tit success.

D. x^2_2 between annuli II, III and IV for hawks incubating full term or beyond:

= 0.22, N.S. for tit use;
= 0.85, N.S. for tit success.

E. x^2 with Yates' correction for annulus I vs. annuli II, III and IV pooled:

=12.30, $P < 0.001$ for tit use;
= 13.12, $P < 0.001$ for tit success.

F. x^2_3 between annuli I, II, III and IV for failed hawk nests:

= 3.81, N.S. for tit use;
= 1.00, N.S. for tit success.

Appendix 2 continued.

G. Table 2-2 data for 1978. Woodcroft excluded for reasons given above. Larch 1977 first annulus nest boxes all fell within Larch 1978 first annulus. Marley Plantation was excluded due to lack of predation of tits (see text).

	Marley	Larch	Thorny Croft
No. first annulus nest boxes available in 1977.	6	1	1
No. successfully occupied	0	0	0
No. nest boxes from 1977 first annulus available in 1978 outside annulus I.	6	0	3
No. successfully occupied.	3	- -	2

1977 Marley and Thorny Croft difference between annulus I and annuli II, III, IV pooled: Fisher exact test, P = 0.035.

Difference between 1977 Marley and Thorny Croft annulus I in 1978 and other annuli in 1978; x^2 with Yates' correction = 0.90, N.S.

H. Table 2-3 data for 1978.

	No. clutches	%C	No. broods	%B
1978	188	9.04	171	8.03
Total	1004	11.16	847	8.03

Mann Whitney U tests between non-hawk and hawk present years including 1978:

Clutches failed, P = 0.59;

Broods failed, P = 0.01.

Appendix 3. Species of prey taken by Sparrowhawks in Wytham during the breeding season.

Moorhen *Gallinula chloropus*

Gamebird (not known if Partridge *Perdix perdix* or Pheasant poult *Phasianus colchicus*)

Pigeon (not known if Rock Dove *Columba livia* or Woodpigeon *Columba palumbus*)

Lesser Spotted Woodpecker *Dendrocopus minor*

Pied Wagtail *Motacilla alba*

Tree Pipit *Anthus trivialis*

Starling *Sturnus vulgaris*

Jay *Garrulus glandarius*

Wren *Troglodytes troglodytes*

Dunnock *Prunella modularis*

Grasshopper Warbler *Locustella naevia*

Garden Warbler *Sylvia borin*

Blackcap *Sylvia atricapilla*

Whitethroat *Sylvia communis*

Willow Warbler *Phylloscopus trochilus*

Chiffchaff *Phylloscopus collybita*

Wood Warbler *Phylloscopus sibilatrix*

Goldcrest *Regulus regulus*

Robin *Erithacus rubecula*

Blackbird *Turdus merula*

Song Thrush *Turdus philomelos*

Mistle Thrush *Turdus viscivorus*

Marsh Tit *Parus palustris*

Willow Tit *Parus montanus*

Appendix 3 continued.

Blue Tit Parus caerulus

Coal Tit Parus ater

Great Tit Parus major

Nuthatch Sitta europea

Treecreeper Certhia familiaris

House Sparrow Passer domesticus

Chaffinch Fringilla coelebs

Bullfinch Pyrrhula pyrrrhula

Greenfinch Carduelis chloris

Goldfinch Carduelis carduelis

Yellowhammer Emberiza citrinella

Bank Vole Clethrionomys glareolus

Appendix 4. Data on selection of juvenile resident tits on basis of brood and physical characteristics.

A. Number of young fledged.

Table 1 of this appendix (designated Table A 4-1) shows the mean number of young fledged by successful tit pairs for young in general population, killed, and survivor classes for each year (number of young fledged being highly correlated with brood size).

The number of young fledged/successful pair was affected by brood size manipulations carried out for experimental purposes on Great Tits in all years and Blue Tits in 1978 (C.M. Perrins, E.O. Minot, and N. Nur, pers.comm.). The brood size changes did not appear to affect selection as no significant difference was found between the proportion of young from manipulated and non-manipulated broods which were selected by hawks (Table A 4-2). Great Tits for 1977 were divided into two parts as the proportion of young fledged which were from manipulated broods was significantly lower around the Marley nest, which provided about two-thirds of the year's ring sample, than in the rest of the wood where the Larch and Thorny Croft hawk nests were located - x^2 with Yates' correction = 70.48, $P < 0.001$). This is as might be expected since brood size manipulations were carried out early in the nestling stage so that factors affecting survival due to brood size, e.g., feeding rates, size of food items, and maintenance of body temperature (see Perrins 1979 for overview) should have had their full effect.

B. Hatching date.

Table A 4-3 shows the mean hatching date for each group of tits in each year calculated from first egg date and clutch size of successful pairs using criteria from Gibb (1950). Brood size manipulations should not have affected calculations as young were exchanged between broods with the same hatching dates.

C. Weight of individual.

Virtually all juvenile Great Tits in Wytham nestboxes were weighed on the 15th day of life in all years of the study. Only in 1978 were weights recorded for Blue Tits, with about one-half of the juveniles weighed on the 13th day of life. Table A 4-4 shows the mean weight for birds in each species/class/year.

D. Age of female parent.

During each breeding season an attempt was made to trap all Great Tits at the nest box in which they bred; limited manpower meant that relatively few Blue Tits were trapped each year so that analyses for this species were not performed. For many of the adult female Great Tits, accurate ages were obtained from ringing records; the age of female parent was then calculated for each class of Great Tits in each year (Table A 4-5).

E. Origin of parents.

Trapping of Great Tit adults at nest boxes permitted tabulation of the number of broods, young fledged, and rings from young caught by hawks from broods where both parents were trapped and were from

the following origin classes : both parents born in Wytham, female from Wytham and male immigrant, female immigrant and male from Wytham, and both parents immigrants (Table A 4-6). In each year the number of young fledged/pair by parents from each class showed no significant difference. In 1977 and 1978 the proportion of the young fledged and represented by rings from hawks from parents in each class did not differ significantly; for 1976 the sample of rings was too small to permit analysis, but the data appeared to indicate selection similar to that found in 1977 and 1978.

F. First ringed in brood.

During compilation of data on the selection of resident juvenile Great Tits for 1977 it was noticed that an unusually high proportion of the rings were from individuals which had been the first in their brood to be ringed. As the ratio of first ringed to other juveniles did not differ significantly in availability between the Marley area and the rest of the wood, nor did the rate of the two classes selected differ significantly Marley and the other nests (availability - x^2 with Yates' correction = 0.25, N.S.; caught - Fisher exact, $P = 0.89$ two tailed), the significant difference found in the proportion of first and other ringed birds was believed to reflect actual selection trends for Great Tit resident juveniles in 1977. Examinations of data for selection of first ringed resident juveniles of each species during the study showed that Great Tits in 1977 were the only class where first ringed birds were chosen preferentially by hawks.

To determine why first ringed Great Tits were selected preferentially in 1977, physical and brood characteristics of caught birds were examined for first ringed and non-first ringed individuals. The number of young fledged, hatching date, whether female parent was juvenile or adult, and origin of parents did not differ significantly for first ringed and non-first ringed birds (Table A 4-8). However, the first ringed juveniles were found to be marginally heavier than the other caught young that were not first ringed.

Table A 4-1. Mean number of young fledged by successful pairs of tits for young in the general population (G), killed by hawk class (K), and survivor class (S) for Great and Blue Tits in 1976-78 (± 1S.D).

Species	Year	G	K	S
Great Tit	1976	7.61 ± 1.77	6.83 ± 1.72	7.42 ± 1.76
Great Tit	1977	7.21 ± 1.92	7.04 ± 2.09	7.00 ± 1.75
Great Tit	1978	8.66 ± 1.81	8.24 ± 2.17	----------
Blue Tit	1976	8.83 ± 2.03	9.33 ± 2.18	9.06 ± 1.86
Blue Tit	1977	8.23 ± 2.31	8.39 ± 1.70	7.61 ± 2.23
Blue Tit	1978	10.72 ± 3.44	9.92 ± 3.42	----------

Great Tit 1976 - $t_{G.K\ 638} = 1.07$; $t_{G.S\ 738} = 0.99$; $t_{K.S\ 110} = 0.80$

Great Tit 1977 - $t_{G.K\ 1038} = 0.44$; $t_{G.S\ 1097} = 0.96$; $t_{K.S\ 109} = 0.09$

Great Tit 1978 - $t_{G.K\ 1278} = 1.13$

Blue Tit 1976 - $t_{G.K\ 2067} = 1.21$; $t_{G.S\ 2143} = 1.12$; $t_{K.S\ 122} = 0.62$

Blue Tit 1877 - $t_{G.K\ 42.83} = 0.59$; $t_{G.S\ 2676} = 2.67^{**}$; $t_{K.S\ 95.79} = 2.26^{*}$

Blue Tit 1978 - $t_{G.K\ 2338} = 1.65^{!}$

t's given in absolute value. ! = $P < 0.10$; * = $P < 0.05$;

** = $P < 0.01$; *** = $P < 0.001$.

Probabilities are two tailed.

Table A 4-2. The number of young fledged from broods which were and were not subject to brood size manipulations and the number of rings recovered from young in these classes for each species in 1976-78. All probabilities are from Fisher exact tests and are two tailed.

Species and year		Manipulated	Not manipulated	
GT 1976	fledged	23	728	
	caught	1	6	P = 0.55
GT 1977 Marley area	fledged	65	211	
	caught	1	15	P = 0.19
GT 1977 rest of wood	fledged	510	342	
	caught	5	4	P = 0.43
GT 1978	fledged	368	912	
	caught	5	22	P = 0.34
BT 1978	fledged	1311	952	
	caught	29	25	P = 0.27

Table A 4-3. Mean hatching date (1 = 1 April) for residentjuvenile Great and Blue Tits in the general population (G), killed by hawk class (K), and survivor class in 1976-78 (± 1 S.D.).

Species	Year	G	K	S
Great Tit	1976	50.11 ± 7.49	53.83 ± 6.27	47.39 ± 5.78
Great Tit	1977	52.20 ± 5.86	53.85 ± 7.31	50.99 ± 5.18
Great Tit	1978	57.16 ± 5.41	57.56 ± 5.60	----------
Blue Tit	1976	47.48 ± 5.52	48.83 ± 5.17	46.41 ± 4.21
Blue Tit	1977	52.88 ± 6.70	56.03 ± 6.53	52.52 ± 4.43
Blue Tit	1978	57.22 ± 5.86	59.65 ± 6.66	----------

Great Tit 1976 - $t_{G.K\ 638} = 1.21$; $t_{G.S\ 170.10} = 4.29^{***}$; $t_{K.S\ 110} = 2.65^{**}$

Great Tit 1977 - $t_{G.K\ 1038} = 1.40$; $t_{G.S\ 1097} = 1.85^{!}$; $t_{K.S\ 33.04} = 1.86^{!}$

Great Tit 1978 - $t_{G.K\ 1278} = 1.13$

Blue Tit 1976 - $t_{G.K\ 2064} = 1.19$; $t_{G.S\ 23.62} = 2.42^{*}$; $t_{K.S\ 120} = 2.42^{*}$

Blue Tit 1977 - $t_{G.K\ 2592} = 2.87^{**}$; $t_{G.S\ 121\ 43} = 0.78$; $t_{K.S\ 50.09} = 3.06^{**}$

Blue Tit 1978 - $t_{G.K\ 2306} = 2.95^{**}$

Key as for Table A 4-1.

Table A 4-4. Mean weight (grams) of resident juvenile Great and Blue Tits in the general population (G), killed by hawk class (K), and survivor class (S) in 1976-78 (± 1 S.D.).

Species	Year	G	K	S
Great Tit	1976	18.95 ± 1.63	20.00 ± 0.98	19.35 ± 1.15
Great Tit	1977	18.90 ± 1.55	18.72 ± 1.37	19.29 ± 1.42
Great Tit	1978	18.51 ± 1.53	19.04 ± 1.59	----------
Blue Tit	1978	9.99 ± 3.78	10.38 ± 0.79	----------

Great Tit 1976 - $t_{G.K\ 618} = 1.58$; $t_{G.S\ 181.25} = 3.09^{**}$; $t_{K.S\ 108} = 1.35$

Great Tit 1977 - $t_{G.K\ 1026} = 0.56$; $t_{G.S\ 1085} = 2.21^{*}$; $t_{K.S\ 107} = 1.75^{!}$

Great Tit 1978 - $t_{G.K\ 1277} = 1.70^{!}$

Blue Tit 1978 - $t_{G.K\ 83.45} = 1.95^{*}$

Key as for Table A 4-1.

Table A 4-5. Mean age of female parents of resident juvenile Great Tits in the general population (G), killed by hawk class (K), and survivor class (S) in 1976-78 (± 1 S.D.).

Year	G	K	S
1976	2.10 ± 1.38	1.50 ± 0.71	2.37 ± 1.33
1977	1.49 ± 1.01	1.27 ± 0.65	1.72 ± 1.26
1978	1.56 ± 0.84	1.50 ± 0.76	----------

1976 - $t_{G.K\ 199} = 0.61$; $t_{G.S\ 224} = 0.96$; $t_{K.S\ 27} = 0.90$

1977 - $t_{G.K\ 398} = 0.70$; $t_{G.S\ 48.21} = 1.17$; $t_{K.S\ 31.72} = 1.64$

1978 - $t_{G.K\ 622} = 0.20$

Key as for Table A 4-1.

Table A 4-6. The number of Great Tit adult pairs fledging young, the number of young fledged, and the number of rings from young raised by adult pairs where: both parents were born in Wytham (W/W); female born in Wytham and male was immigrant (W/I); female was immigrant and male was born in Wytham (I/W); and both parents were immigrants (I/I).

Year		W/W	W/I	I/W	I/I
	pairs	9	13	21	30
1976	fledged	61	94	133	215
	rings	1	1	3	1
	pairs	28	27	40	52
1977	fledged	191	175	280	330
	rings	8	2	5	7
	pairs	32	27	28	31
1978	fledged	265	238	195	240
	rings	6	3	6	8

1976 - pairs vs fledged, $x^2_3 = 0.20$, N.S.

1977 - pairs vs fledged, $x^2_3 = 0.22$, N.S.;

fledged vs rings, $x^2_3 = 4.28$, N.S.

1978 - pairs vs fledged, $x^2_3 = 0.76$, N.S.

fledged vs rings, $x^2_3 = 2.43$, N.S.

Table A 4-7. Selection for first ringed and non-first ringed resident juveniles by species in 1976-78. All probabilities are from Fisher exact tests and are two tailed.

Species	Year		First ringed	Not first ringed	
		available	106	645	
Great Tit	1976				
		caught	1	6	P = 0.60
		available	249	1801	
Blue Tit	1976				
		caught	2	22	P = 0.81
		available	172	956	
Great Tit	1977				
		caught	9	18	P = 0.02
		available	358	2280	
Blue Tit	1977				
		caught	6	35	P = 0.98
		available	159	1121	
Great Tit	1978				
		caught	3	25	P = 0.98
		available	252	2011	
Blue Tit	1978				
		caught	3	51	P = 0.28

Table A 4-8. Brood and physical characteristics of first ringed and non-first ringed resident juvenile Great Tits for which rings were recovered in 1977. Means are shown ± 1 S.D.

Characteristic	First ringed	Non-first ringed
Hatching date	$\bar{x}$ = 52.67 ± 5.59	$\bar{x}$ = 54.53 ± 8.17
	t_{24} = 0.61, N.S.	
No. fledged	$\bar{x}$ = 7.22 ± 2.33	$\bar{x}$ = 6.94 ± 2.01
	t_{24} = 0.78, N.S.	
Weight	$\bar{x}$ = 19.29 ± 1.04	$\bar{x}$ = 18.33 ± 1.32
	t_{23} = 1.89, 0.10 > P > P.05	

Mother's age	first year	5	11
	older than one year	3	4

Fisher exact, P = 0.95 two tailed

	W/W	W/I	I/W	I/I
Origin of parents: first ringed	3	0	2	4
Origin of parents: not first ringed	5	2	3	2

Mann-Whitney U, P = 0.59 two tailed

Appendix 5. The estimated number of ringed adult tits in the wood each year.

Table A 5-1 shows the number of male and female Great Tits using Wytham nest boxes (equal to the number of occupied nest boxes), the percent of the birds of each sex trapped at nest boxes, the percent of individuals which bore a ring at the time of trapping for each sex, and the estimated total number of ringed birds of each sex for the years 1976-78.

Also shown are similar values for Blue Tits in the same years, except for males in 1976 and 1977 when virtually none were trapped due to manpower limitaions. In addition, the numbers of male and female Blue Tits in the wood in 1978 were unequal due to removal of many of these birds from their nests in Bean Wood for experimental purposes (E.O. Minot, pers.comm.). Estimates of the number of ringed male Blue Tits in the wood in 1976 and 1977 were made by multiplying the number present by the percent of females bearing rings at the time of trapping + 20%. The 20% adjustment was made as it was thought that Blue Tits would follow a pattern similar to that of Great Tits, where males emigrate from the wood at a lower rate than females, as shown by the percent of each sex bearing rings at the time of trapping and the findings of Harvey, Greenwood and Perrins (1979).

Table A 5-1. The estimated number of ringed adult Great and Blue Tits in Wytham in 1976 - 78.

	Great Tit					
	1976		1977		1978	
	Male	Female	Male	Female	Male	Female
No. in wood	120	120	237	237	186	186
% trapped	64.17	78.33	64.98	73.42	77.42	79.03
% ringed prior to trapping	79.22	60.64	68.18	51.72	79.17	73.47
No. birds not trapped est. to have been ringed	34	16	60	33	33	29
Total for sex	111	110	214	207	177	176
Grand total for year	221		421		353	

	Blue Tit					
	1976		1977		1978	
	Male	Female	Male	Female	Male	Female
No. in wood	322	322	493	493	383	363
% trapped	10	65.22	10	66.13	25.33	81.82
% ringed prior to trapping	60.00[1]	40.00	65.77[1]	45.77	59.79	53.95
No. birds not trapped est. to have been ringed	193[2]	45	324[2]	76	171	36
Total for sex	193	225	324	402	268	333
Grand total for year	448		726		601	

1) estimated from females.
2) all individuals classified as not trapped due to small number actually trapped.