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The Control of Sparrowhawk *Accipiter nisus* Nesting Densities

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ABSTRACT

1. In continuously suitable woodland, Sparrowhawk nesting places were regularly spaced, but at different distances apart in different districts. Comparing districts, the spacing of nesting places within suitable woodland varied according to prey density, with hawks nesting at higher densities in districts where their prey were more numerous. Nest spacing also varied with elevation above sea level and local land fertility, presumably because these factors in turn influenced prey numbers.
2. In Eskdale, south Scotland, nest numbers remained fairly stable during 1972-84, fluctuating around a mean of 35. This stability was achieved by competition for a relatively fixed number of prime home ranges, which meant that entry to the breeding population was largely dependent on gaps created by the deaths of previous occupants. The proximate mechanism was a density-dependent recruitment of new breeders. The weather in early spring intervened to prevent a perfect density-dependent system; cold, wet conditions in March-April led to greater decline, or less marked increase, than expected from nest numbers the previous year. Annual losses of established breeders were not density-dependent, nor was production of young.
3. At least among females, non-breeders in the population were almost as numerous as breeders. Their total numbers were probably limited by competition for living space (= food supply), in the same way as those of breeders.

INTRODUCTION

A central problem in ecology is to understand why the density of a given species varies from one district to another and why, in any one district, numbers vary in a particular manner from year to year. With these questions in mind, I studied the Sparrowhawk *Accipiter nisus* for some years in different parts of Britain. This species is not the easiest for work of this type; like most other raptors, it lives at relatively low density, and its nests are hard to find and reach. More particularly, the bird is secretive and practically impossible to observe for any length of time, except with a hide at the nest. In consequence, many crucial facts can be obtained only indirectly, or collected by radio-tracking and trapping programmes.

The Sparrowhawk breeds in woodland, but also hunts in open country, feeding primarily on other birds, especially songbirds. Like some other raptors, it tends to breed in the same restricted localities in different years, building a new nest each time. These regular nesting places can be recognised at any time of year from the groups of nests of varying ages. Individual hawks are not especially long-lived; some 30-40% of adults die each year, and few reach more than 9 years old. They have a high reproductive rate, however, with up to 6 young in the annual brood. This paper summarises work which has been published in greater detail elsewhere (Newton 1986; Newton & Marquiss 1986; Newton *et al.* 1986), and proposes a model to suggest how breeding populations are regulated in relation to habitat.

REGIONAL VARIATIONS IN BREEDING DENSITY

From surveys in suitable woodland, Sparrowhawk nesting places were found to be regularly spaced, but at different distances apart in different districts. Average nearest neighbour distances varied from as little as 0.5km in certain districts to more than 2km in others. Breeding density was broadly related to landscape, as mean nest spacing became greater with increase in elevation above sea level, or with decrease in land productivity. These environmental features were themselves correlated with one another, for as elevation rose, land fertility declined. The relationships were useful, however, because they enabled Sparrowhawk nest spacing to be predicted from maps.

Sparrowhawks presumably did not respond to soil or elevation as such, but rather to food supply, which itself varied with soil and elevation. Songbird populations were assessed in the woodlands of 14 different districts, using the method of "point counts" (Dawson 1981; Fuller & Langslow 1984), and for each district an index of songbird densities in woodland was calculated (Newton *et al.* 1985). The spacing of Sparrowhawk nesting places was broadly related to the songbird indices, whether these were expressed as prey biomass, or as prey numbers (Fig. 1). In other words, maximum Sparrowhawk breeding densities in woodland varied from one district to another, in line with the food supply.

This relationship held within woodland, but the overall density of nesting places in any landscape also depended on the proportion of woodland in the district concerned. In general, sparsely wooded districts held fewer nesting places than did well wooded ones, with recorded densities of 14-96 per 100km^2. These figures were maxima for breeding densities, however, because in each year in all districts a proportion of nesting places remained unused (see later).

COMPOSITION OF THE POPULATION IN SPRING

In spring, at the start of breeding, the Sparrowhawk population in any one district consisted of several components. Some individuals remained unpaired, occupying large home ranges and showing no attachment to a nesting place. Others showed temporary attachment to a nesting place, and may have become paired for a few days or weeks, but did not build a nest. Yet other birds proceeded to nest-building, but did not produce eggs. A fourth category of birds produced eggs, and some of these birds went on to raise young.

Only the nest builders could be counted accurately, because only they left a visible and unequivocal sign of their presence (the nest), which remained for long after the place had been abandoned. Hence, knowledge of the distribution and fluctuation of Sparrowhawk populations was based primarily on nests.

These four categories of birds were not discrete, but formed a continuum from one extreme to another. Thus the temporary residents varied from birds which spent only a few days on a nesting place to others which stayed for several weeks, leaving many droppings, pluckings and other remains of their presence; the nest builders varied between individuals which made only the flimsiest structure, barely recognisable as a nest, to others which built bulky structures, almost ready for eggs; the egg-layers varied between those which laid only one or two eggs and then deserted them to others which laid 6 or 7 eggs and ultimately produced a large brood of young.

From birds that were trapped on nesting places in early spring, I found that the different components of the population differed in age composition. In particular, first-year birds were in greatest proportion in the sector which occupied nesting places without building a nest, in intermediate proportion in the sector which built without laying, and in smallest proportion in the egg-lay

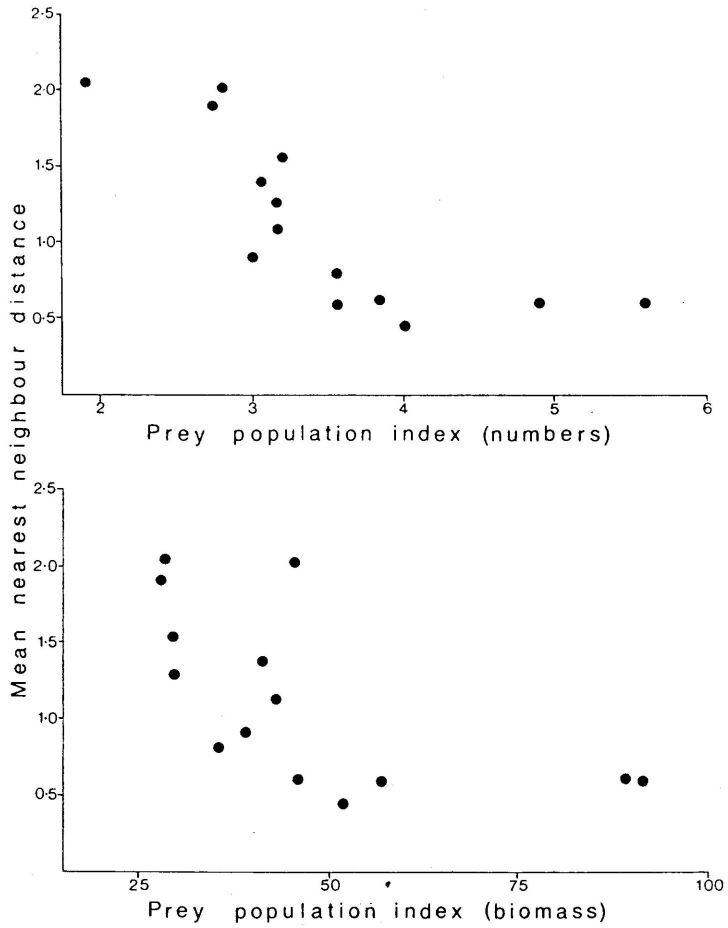

Figure 1. **Spacing of Sparrowhawk nesting places in the woodland of 14 districts shown in relation to food supply. Mean nearest neighbour distances decrease (so densities increase) with rise in prey number and biomass. Relationship between spacing and prey numbers: r = -0.77, P ‹ 0.01; betweeen spacing and prey biomass, r = -0.61, P ‹ 0.05.**

ing sector (Fig. 2). Thus the age of a bird influenced the stage of breeding reached, and generally older birds progressed further than young ones. Nonetheless, birds of 3 years and older were still represented among the non-layers.

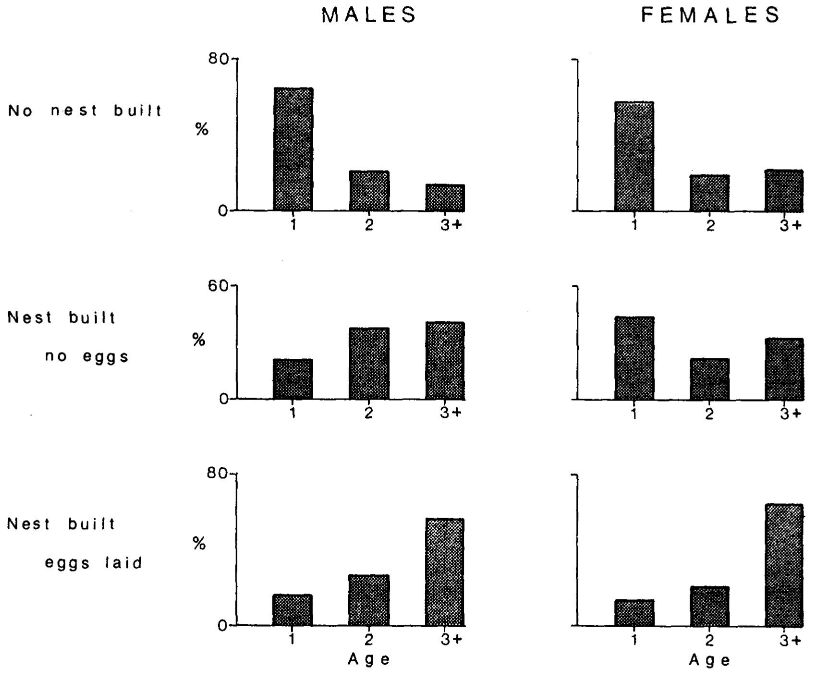

Figure 2. Age composition of different components of a Sparrowhawk population in spring; based on trapping records from south Scotland, 1971-84.

ANNUAL VARIATIONS IN BREEDING DENSITY

Sparrowhawk nesting populations have traditionally been regarded as remaining stable through time. This idea came from early naturalists and egg collectors who could usually rely on finding nests in the same localities year after year. Stability has prevailed in all the British populations which have been studied in recent years, providing that: (1) numbers had recovered from the low level imposed by organochlorine pesticide use in the 1950s and 1960s; and (2) the land use (= habitat) remained stable during the investigation. In some areas, the proportion of woodland changed greatly during the study, so not surprisingly the numbers of breeding Sparrowhawks changed in the same direction.

Figure 3 shows the trends in nest numbers during 1972-84 in the Esk Valley in south Scotland, where the habitat hardly changed over the 13-year period. Sparrowhawk nest numbers also remained fairly constant over this time, varying between 29 and 39, around a mean of 35. All fluctuations were within about 16% on either side of the mean. Compared to the changes which were theoretically possible, this represented a remarkable degree of stability. As explained above, not all nests subsequently contained eggs, but over the years the numbers of clutches produced each year also remained fairly stable (Fig. 3).

Such constancy in numbers implied the action of density-dependent regulating factors, which had a stronger reducing effect at high population levels than at low ones. Density-dependent regulation could have involved competition for food or territories, or avoidance of disease or predation. Such factors contrasted with density-independent factors, which would have acted regardless of population level. The most obvious factor which might have acted in a density-independent manner was the weather. I therefore attempted to assess the relative importance of density-dependent and density-independent factors in the year-to-year changes in Eskdale nest numbers.

The importance of density-dependent factors was apparent from the pattern of fluctuations. In general, years of lowest population were followed by the greatest increases, whereas years of highest population were followed by the greatest declines. In other words, the extent and direction of change each year were correlated with nest numbers in the preceding year (Fig. 4). This meant that numbers tended to return each year close to the mean level. Now if density-independent factors had prevailed, the direction of change in any one year should have been independent of population level; and this was clearly not the case.

Density-dependence in the annual nest counts was tested formally using the randomisation procedure of Pollard *et al.* (1987). This entailed comparing the observed sequence of annual changes with a large number (1,000) of sequences that might have been observed if the same changes had occurred in random order (i.e. independently of density). This procedure showed that, if the fluctuations were density-independent, then the probability of obtaining the observed sequence of changes was only 0.025. Hence, the null hypothesis of density independence in the annual nest counts could be firmly rejected.

The overall stability of the Eskdale population could thus be attributed to the action of density-dependent factors. However, some of the fluctuations about the mean may have been due to density-independent factors, such as weather. Figure 4 shows a considerable scatter of points about the line. In fact, most of the points below the line, which refer to years when the population was lower than expected from nest numbers the previous year, came from relatively cold, wet springs. Conversely, most of the points above the line, which referred to years when the population was higher than expected, came from relatively mild, dry springs. To put it another way, when the months March-April were unusually cold and wet, declines in population were more marked, or increases less marked, than expected from nest numbers the previous year. But when March-April were warm and dry, declines were less marked or increases more marked, than expected. On a statistical analysis, some 58% of the variance in nest numbers between years could be explained in terms of nest numbers the previous year, whereas 84% could be explained in terms of previous nest numbers plus the number of rain days in March-April.

This relationship between nesting population and spring weather made sense in terms of Sparrowhawk biology. In March-April, Sparrowhawks experienced their greatest food shortage because the numbers of resident prey were at their annual low, most winter visiting prey had left, and most summer migrants had not yet arrived. In these months, more hawks were found dead and reported through the national ringing scheme than in any other months (Newton 1986). They included many birds which starved to death. Moreover, as judged from food deliveries at nests later in the year, Sparrowhawks could not hunt effectively during rain. It was not unexpected, therefore, that nest numbers were related to rainfall in the months when prey were scarcest.

In conclusion, annual changes in the Eskdale breeding population were controlled primarily by density-dependent factors, which tended to stabilise the population. Density-independent factors (early spring weather) intervened to cause fluctuations from year to year greater than expected on a perfect density-dependent system. Any other factors which influenced nest numbers could have had at most a small effect.

A model of density-dependent regulation

As mentioned, density-dependent regulation implied competition for food or living space, or for avoidance of disease and predation. In south Scotland, more than a thousand Sparrowhawks were trapped, but none showed signs of disease, insofar as could be judged from external examination. Nor did more than 30 that were examined internally, post-mortem. This did not of course mean that the population was free of disabling disease and parasite loads, but I would be surprised if these factors had a significant effect on population size. Similarly, in south Scotland Sparrowhawks had no major predators. The main natural enemies elsewhere in the range, namely Goshawks *Accipiter gentilis* and Pine Martens *Martes martes*, were absent from the study area. What little predation occurred was attributable to Tawny Owls *Strix aluco*, which occasionally took chicks from unguarded nests, but again did not seem significant in population control.

On the other hand, breeding depended primarily on food-supply, and Sparrowhawks competed strongly for home ranges containing food and nesting places. Such competition appeared to be the crucial density-dependent factor responsible for regulating breeding numbers. The way in which I believe the system operated is depicted in Figure 5 and described below.

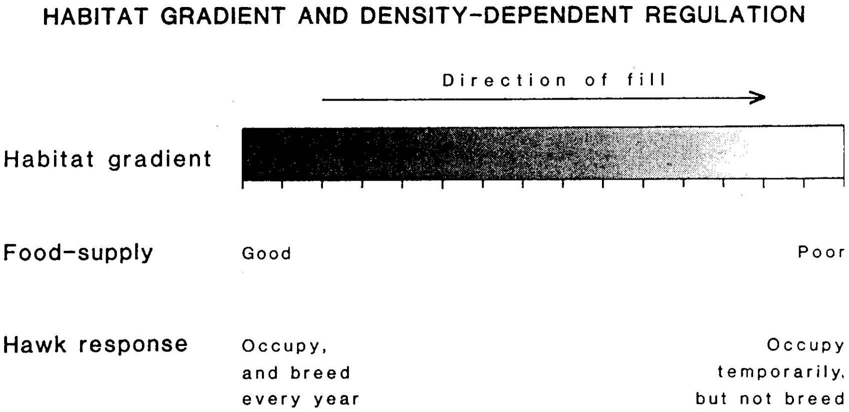

Figure 5. Density-dependent regulation of population in relation to habitat quality. For explanation, see text.

To judge from the survival and nesting success of individuals (Table 1), habitat quality (= food supply) in the study area varied from place to place. In the best patches, birds could survive well and reproduce almost every year; in less good patches, they might attempt to breed in some years but seldom raise young; while in the worst patches, birds could survive - at least for short periods - but not reproduce. Again, there was no clear division between categories, but a continuum of habitat variation between extremes. At low population levels, birds occupied mainly the best patches, and only at higher levels spread to the less good patches. Thus, as the population rose, new settlers encountered progressively poorer habitat, presumably making it increasingly difficult for them to settle or reproduce. This mechanism, I suggest, provided the density-dependent resistance to further population growth; the capacity of the area to support extra breeders fell disproportionately as numbers rose.

Table 1. **Breeding success and persistence of females on nesting places used in different numbers of years. The data came from 54 nesting places which were available throughout a 13-year period in Eskdale. In general, nesting places which were in most frequent use had the highest proportion of successful nests, and the greatest year-to-year persistence of females.**

Nesting places used in	Total number of nests	% of all nests which produced young	% of all occasions when the same female was present in successive years*
10-13 years	114	63	73
7-9 years	178	54	47
4-6 years	64	53	33
1-3 years	16	50	0

Note* Calculated only from nesting places where females were trapped in successive years, and then checking whether it was the same or a different individual in the second year. By definition, no such records were available from places used in only one year.

Favoured localities, with high occupancy and breeding success, were in woods of varying composition, size and setting. But all nesting woods were fairly thick, with a good supply of songbird prey nearby.

In addition to the spatial variation, the habitat may have varied somewhat from year to year, depending on prey numbers and weather (which influenced prey availability). Weather pattern affected the whole study area, but changes in prey numbers may have been general or confined to particular localities. Either way, the effect was to upgrade some marginal localities in certain years, but not in others. In any one year, breeding numbers may also have depended to some extent on the particular hawks present, which almost certainly varied in their hunting skills. An unusually competent individual may have bred successfully in a marginal locality, where a less competent one could not even attempt to breed. The essence of the model, however, was the spatial variation in habitat (food supply), and the priority occupation of the good patches first. Although the model has not been formally tested, all the data collected on territory occupation, adult survival and breeding success were consistent with it (Table 1; see also Newton 1986).

Proximate mechanism of population change

My concern so far has been with the ultimate factor of food supply (modified by weather), which influenced population change. It remains to investigate the proximate causes of change; that is, the births, deaths, movements or other events that occurred within the population to promote the fluctuations in nest numbers.

Changes in nest numbers between years might have resulted from: (1) changes in the numbers of breeders remaining from the previous year; (2) changes in the numbers of new breeders added to the population each year; or (3) a combination of both. These possibilities could be examined only for females in 1977-84, when enough were caught and identified. Most females which were lost from the nesting population each year had probably died, but some had moved out of the area (known from ring recoveries) or had reverted to a non-breeding existence. Most birds which were added to the nesting population each year were probably breeding for the first time, but some may have bred previously outside the area or were breeding again after a break.

The number of previous breeders and of new breeders in the Eskdale population varied from year to year, but independently of one another (Table 2).

Table 2. Numbers of established females and new females in the Eskdale breeding population each year.

	1977	1978	1979	1980	1981	1982	1983	1984
(a) % population change from previous year	-15	+24	-11	+19	+3	-18	+6	0
(b) % survival of established breeders from previous year*	52.6	65.2	55.6	60.9	58.3	60.9	47.8	58.1
(c) Number of established breeders**	18	19	20	19	22	24	15	20
(d) Number of new breeders**	11	17	12	19	17	8	19	14

Notes

* Calculated from the proportion of breeders in any one year which was retrapped alive in subsequent years. This gave a measure of persistence in the area from one year to the next, from which the annual losses could be calculated.

** These numbers were estimated from the ratio of established breeders to new breeders among the sample trapped each year. In most years, this sample exceeded 80% of all breeders. The total breeding female population in the area each year is given by the sum of c and d.

Relationship between a and b, $r_s = 0.14$, NS; between a and c, $r_s = -0.42$, NS; between a and d, $r = 0.89$, $P < 0.1$; and between c and d, $r = -0.45$, NS - not significant.

Population changes were related more to the numbers of new breeders added each year than to the numbers of previous breeders remaining from the year before. In fact, the number of new breeders recruited each year was density-dependent, as it varied inversely with nest numbers in the preceding year (Fig. 6). Many new birds were added following years of low nest numbers, leading to increases in breeding population, and few new birds were added following years of high nest numbers, leading (with losses of previous breeders) to declines in population. The recruitment of new breeders thus emerged as crucial to the annual changes in nest numbers. The percentage of previous breeders which disappeared from the population each year did not vary with density, but with the number of rain days in March-April, being greater after cold, wet springs than after warm dry ones (b=0.62, r=0.72, $P < 0.05$).

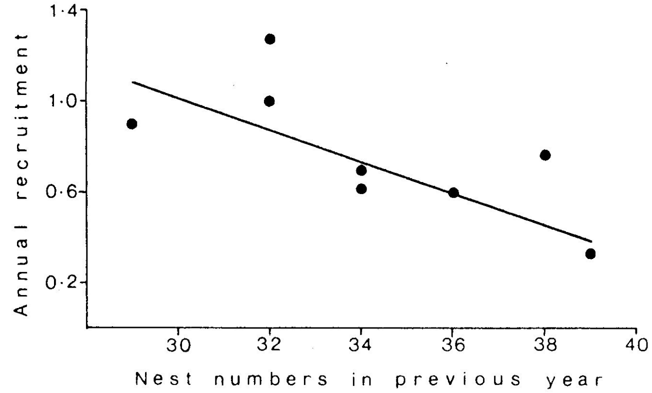

Figure 6. Annual recruitment of new females to the nesting population in Eskdale, in relation to nest numbers the previous year. Recruitment was density-dependent, in that more new females were found breeding after years of low population. Annual recruitment was measured as the ratio of new breeders/previous breeders. Spearman rank correlation: $r_s = -0.75$, $P < 0.05$.

Table 3. Calculation of proportion of pre-breeders among females of different age groups. The number of females first found breeding in their first, second, third and fourth years respectively was known (underlined in the table), and all other figures were calculated assuming a 64% annual survival (Newton *et al.* 1983). B = breeder; PB = pre-breeder.

Year of first breeding	Numbers alive (% of which were pre-breeders) in the following years after birth						
	1		2		3		4
1	73 B		46.7 B		29.9 B		19.1 B
2	123.4 PB	(81.7)	79 B		50.6 B		32.4 B
3	134.3 PB		85.9 PB	(50.8)	55 B		35.2 B
4	68.7 PB		43.9 PB		28.1 PB	(17.2)	18 B

Notes From knowledge of the age distribution of the total female population, pre-breeders were calculated to form 43% of this total.

It emerged that about 43% of the total female population at any one time consisted of pre-breeders. This was an average figure, based on merging results from the whole study period. It did not give the total number of non-breeders, because it took no account of those (probably few) individuals among established breeders which occasionally skipped a year. It did, however, indicate that non-breeding female Sparrowhawks formed a substantial part of the total female population. The proportion of non-breeders among males was probably smaller, because the species was primarily monogamous, and males were scarcer than females in the population at large (Newton 1986).

The numbers of non-breeders were probably regulated in the same way as those of breeders, by competition for living space in a variable habitat. Radio-tracking and trapping indicated that non-breeders occupied the poorer parts of the habitat gradient, shifting to better places where they could breed following the deaths or movements of previous occupants. This system held despite the fact that for much of the year the home ranges of different individuals were not mutually exclusive, but overlapped to some extent with those of neighbours. The numbers in any one area were evidently regulated, however, and remarkably consistent from year to year (Marquiss & Newton 1982).

DISCUSSION

Several points to emerge from this study may be relevant to some other raptors, and indeed to other birds. First, it was no more than a practical convenience to subdivide the population into breeders and non-breeders. All gradations existed, as different individuals reached different stages in the process of reproduction each year, depending largely on their individual food supply. This was shown by correlations between the stages of breeding reached on the one hand, and habitat quality, ages and body weights on the other (Newton 1986) and by experiments in which extra food was provided by the observer (Newton & Marquiss 1981). The same point was made years ago by Hagen (1969) in his study of Rough-legged Buzzards *Buteo lagopus* in Norway, and had parallels in the work by Mendelsohn (1981 and this volume) on Black-shouldered Kites *Elanus caeruleus* in South Africa.

Similarly, given enough nesting places, it was unrealistic in Sparrowhawks to separate habitat suitable for breeding from habitat unsuitable for breeding.

The habitat showed continuous gradation from poor to good, influencing both the survival and the breeding success of the birds which occupied it. The model proposed here, of density-dependent population control through competition for living space, and at the same time allowing for limited annual variation in breeding numbers, could well apply to some other raptors, which show similar slight fluctuations around a stable, long-term mean.

Thirdly, the most important proximate process concerned with control of the nesting population was recruitment, which gave special importance to that stage of life between fledging and first breeding. This is the most difficult stage to study, but it may well repay attention, both in the Sparrowhawk and in other raptors. In practice, it would entail a special study of the non-breeders and of the factors affecting their numbers, distribution and recruitment to the breeding sector.

Finally, two responses to a poor food supply were identified. The first entailed larger home ran ges and wider nest spacing, as found by comparing nest distribution in different districts. This was evidently a response to low overall density of prey, so that only by taking a large area could a hawk obtain its daily needs. The annual fluctuations in breeding numbers, which occurred within districts, were mostly too small to affect the overall nest spacing, as reflected in nearest neighbour distances. The second response, which occurred across all levels of breeding density, entailed the failure of individuals in certain localities to obtain enough prey to breed, or even to survive. This probably occurred in situations where it was no help to increase the size of home range: where the chances of prey capture were low, whether the hawk covered a small area repeatedly or a large area less often. It was this type of situation, resulting from poor habitat or poor hunting skill, which prevented some individuals from breeding, whatever the overall nest-spacing in the area concerned.

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