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The Role of the Individual Bird and the Individual Territory in the Population Biology of Sparrowhawks *Accipiter nisus*

Ian Newton

ABSTRACT

1. From a long-term study of Sparrowhawks *Accipiter nisus*, involving marked individuals, it was possible to measure lifetime reproductive success (LRS); that is, the total numbers of young raised by individuals during their entire lives. In the population studied, 72% of fledgling females died before they could breed at 1-3 years of age, another 5% laid eggs but failed to produce young, while 23% produced young, but in greatly varying numbers (1-24). It was calculated from this skewed distribution that 5% of females in one generation produced half the young in the next generation. Similar patterns have been found in other birds. LRS values are useful because they combine two key measures of performance (annual survival and annual breeding success) into a single overall measure, which could give a close approximation to Darwinian fitness.

2. Annual reproduction and survival varied during the course of the Sparrowhawk lifespan, first rising year-by-year to mid life, as individuals gained in experience and status, and then declining year-by-year as senescence took hold.

3. In the study area, Sparrowhawks did not use the available territories at random for nesting, but preferred those where nest success was highest. They occupied conifer plantations for nesting after trees had been thinned for the first time, at around 20 years of age. Occupancy and nest success was then high for the next ten years or so, but declined thereafter, as plantations matured. Owing to rotational management, in which a proportion of plantations was felled and replanted each year, the age structure of available plantations remained fairly stable through time. Sparrowhawk breeding numbers were also fairly stable, but each year some old plantations were abandoned and young ones occupied.

4. The most striking finding from these studies was the great variation,over a ten-year period, in the productions of individual birds and of individual territories in the same 200 km² area.

INTRODUCTION

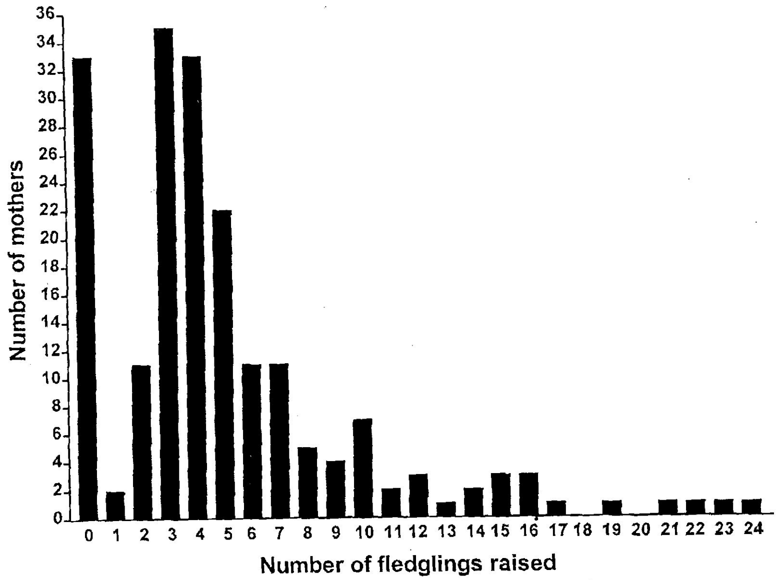
It is only in the last 30 years that research on raptors has begun to contribute substantially to the mainstream of ecological understanding, the work on pesticide impacts being an obvious example (Ratcliffe 1970, Newton 1979, Cade *et al.* 1988). In this paper, I discuss three other aspects of raptor biology that are of more general relevance. They have all emerged from long-term population studies involving marked (ringed) individuals, namely (1) lifetime reproductive success, (2) changes in annual reproductive and survival rates that occur as birds age, and (3) effects of habitat quality on reproductive success and population limitation. I shall illustrate these issues mainly from my own work on the Eurasian Sparrowhawk *Accipiter nisus*, but will also draw comparisons with other raptors and other birds. Several of the aspects discussed here have been described in greater detail elsewhere (Newton 1986, 1988, 1989, 1991).

This paper is based mainly on data collected over a 20 year period (1972-91) from a 200 km² study area centred on Eskdale (55° 16'N 3° 5'W), a farmland area with conifer plantations, in south Scotland. Within this area, I searched all suitable plantations every year to find Sparrowhawk nests and count the numbers of young raised. I also ringed the young, and as many of the breeders each year as I could catch.As in the rest of Britain, Sparrowhawks were resident in Eskdale throughout the year, feeding on other birds, especially song-birds. Within their plantation nesting habitat, the hawks tended to nest in the same restricted localities year after year. Individuals could live up to ten years (though hardly any did so), and could breed every year after the year of birth, each time raising up to six young. Among nesting birds, females proved much easier to catch than males, giving larger samples, so the analyses in this paper are based entirely on data for females.

LIFETIME REPRODUCTIVE SUCCESS

For more than half a century, detailed field studies have been made of the breeding ecology of birds, but most have been concerned with the numbers of young raised in individual nesting attempts or in individual years. Such studies can be described as "cross-sectional", in that they involve the collection of data at specific points in time, mostly from different and unknown individuals. It is only in the last ten years, as a result of local long-term studies of marked individuals, that it has become possible to track the breeding performance of particular birds year after year (Clutton-Brock 1988, Newton 1989). For several species, this has enabled the measurement of lifetime reproductive success (LRS); that is, the total numbers of young raised by individuals during their entire lives. Interest in such longitudinal studies has grown rapidly with the realisation that lifetime reproductive

Figure 1. Lifetime fledgling productions of 194 female Sparrowhawks that made one or more breeding attempts. Mean per breeding female = 5.03 young. From Newton 1989.

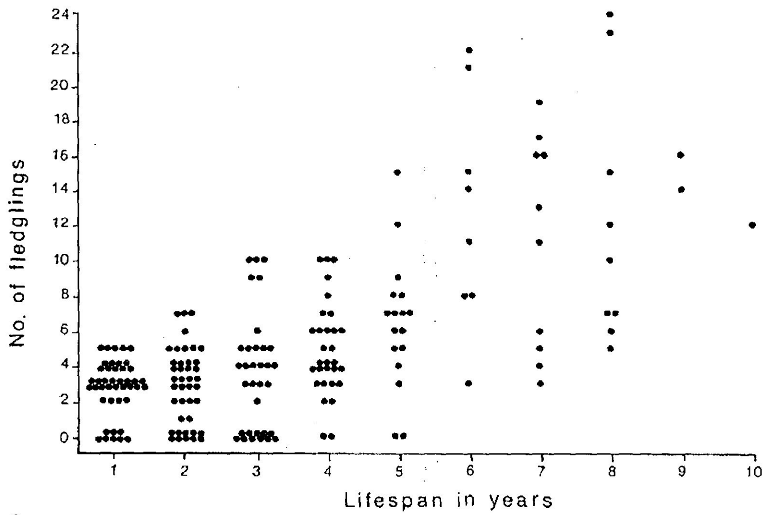


rates could provide good approximations of Darwinian fitness: that is, of the contributions that particular types of individuals make to future gene pools. Despite the great theoretical importance of fitness, which is discussed in almost every recent textbook on evolution, it has remained one of the most elusive measures in biology.

Over the 20-year period, I recorded lifetime reproductive success for 194 different breeding females (Figure 1). These birds were representative, in their respective lifetimes, of the female population as a whole (Newton 1986). They spent 1-8 years (mean 2.3 years) as breeders, and raised from 0 to 24 young (mean 5.0 young) during their lives. They thus showed enormous variation in their lifetime productions. The peak at 3-5 young in Figure 1 was because most birds raised only one brood per lifetime, and most broods contained 3-5 young. About 17% of females which laid eggs failed to produce any young, even though they laid in up to four different years.

Much of the variation in lifetime fledgling production among these breeding females could be attributed to individual variation in longevity (1-10 years) and to variation in age of first breeding (1-3 years), which together determined the length of breeding life (1-8 years). On linear regression analyses, some 43% of the variance in individual lifetime productions could be explained in terms of

Figure 2. Lifetime fledgling production in relation to lifespan in 194 female Sparrowhawks that made one or more breeding attempts. From Newton 1989.

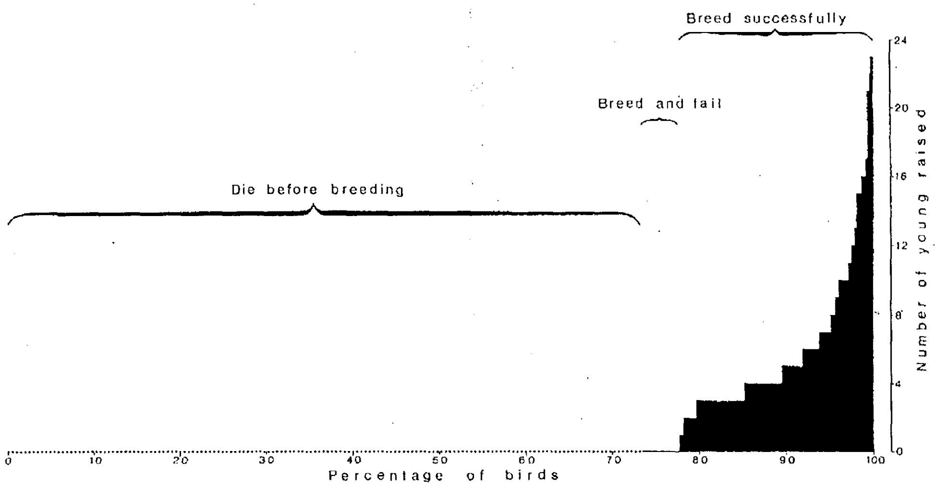


variation in lifespan (Figure 2), 10% in terms of variation in age of first breeding, and 48% in terms of the two factors together (length of breeding life).

Within each age group, individuals varied greatly in the number of young they had produced up to that age. Some individuals lived for five years and still produced no young; others lived eight years and raised only five young (no more than some one-year birds); and the longest lived bird, which died at 10 years, produced only 12 young. With up to six young in a brood, and a lifespan up to 10 years, an individual could theoretically produce 60 young in its lifetime. But as none produced more than 24, none produced anywhere near this maximum.

From knowledge of mortality at different ages, it was possible to calculate the lifetime productions of a whole generation of female fledglings from the time they left the nest, including those which died before breeding (Newton 1988). About 72% of female young died in their 1st-3rd year of life without having bred, another 5% produced eggs but no young, and only 23% produced young, but in greatly varying numbers (Figure 3). So overall, less than one fourth of individuals in one generation of fledglings contributed to the next generation. These birds produced enough young to replace themselves and all other non-contributing individuals. On the pattern observed, less than 5% of fledglings (or 20% of breeders) produced half the next generation, and 7% of fledglings (or 30% of breeders)

Figure 3. Lifetime fledgling productions for a whole generation of female Sparrowhawks including birds that died before they could breed. Birds are arranged in order of their lifetime productions. From Newton 1988.



produced 90% of the next generation. The pattern of gene flow from one generation to the next was therefore enormously skewed. One could expect that the same pattern would be repeated in each successive generation.

AGE-RELATED TRENDS IN PERFORMANCE

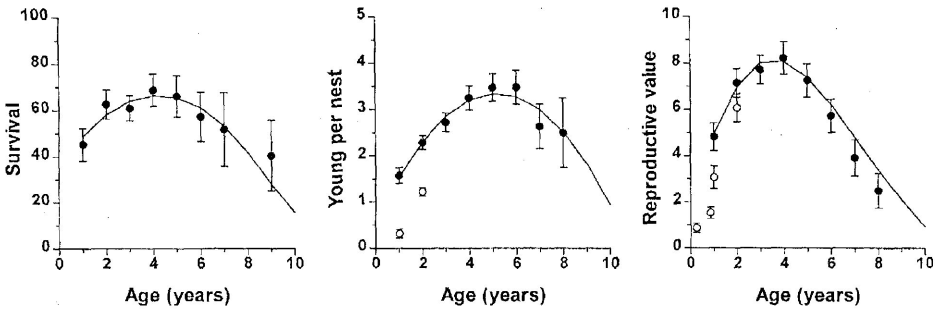
By following the same individuals year after year, the changes in survival and breeding success that occur during the course of the average lifespan can be assessed. In the Sparrowhawk, as in some other birds, both reproduction and survival increase year by year to mid life, and then decline as the bird ages (Figure 4). Both annual reproductive and survival rates are lower in 9-year-olds (near the end of their lives) than in one-year-olds.

These figures in turn enable the calculation of reproductive value, the number of young that females of different ages can expect to produce during the rest of their lives (Fisher 1930). Because both survival and breeding rates peak in mid -life, so does reproductive value. In the Sparrowhawk, the average female of one year old could expect to produce 3.1 young during the rest of her life (or 4.8 if she bred in her first year), but a female that lived to 4 years could expect to produce 8.2 young during the rest of her life, while one that reached 9 years could expect to produce only 2.1 further young (Figure 4).

HABITAT VARIATION

Another source of inequality in productivity among wild bird populations arises from variation in habitat quality. In birds-of-prey, it has long been apparent

Figure 4. Annual survival, breeding success and reproductive value for female Sparrowhawks of different ages. Filled circles and solid lines refer to breeders only, and open circles include non-breeders.

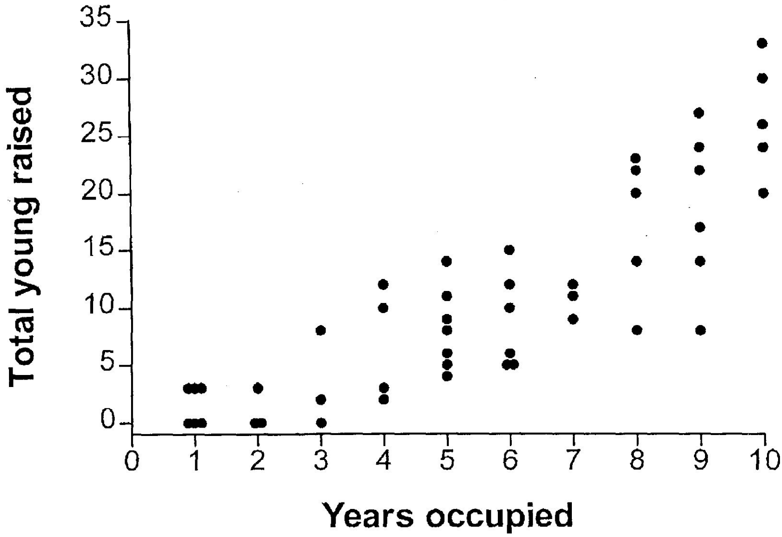


in particular regions, that certain nesting places are occupied every year, or almost every year, and invariably produce young, while other places are occupied irregularly, and seldom or never produce young. In the sections below, I examine spatial variation in habitat quality in the Sparrowhawk, taking as a measure of nesting place quality the number of young produced over a 10-year period (1976-85). I then examine how the quality of particular nesting places changes through time.

Within the Eskdale study area, conifer plantations in which Sparrowhawks nested were managed on a rotation basis. Each year some areas of mature plantation were felled and replanted, so that at any one time the total plantation area consisted of a mosaic of patches of different ages, giving a fairly uniform age-structure over time. The plantations were scattered among farmland and open sheep pasture, and covered a total of about 20 km^2. Despite continual changes to the forest, Sparrowhawk nest numbers remained fairly constant. Over the 20-year period, the average number of nests found per year was 34, and the numbers in particular years varied between 29 and 39; that is, always within 15% of the mean (Newton 1991).

Because in each year a Sparrowhawk pair could raise up to 6 young, in theory each nesting place could have produced 60 young in a 10-year period. In practice, however, the individual nesting places varied greatly in the numbers of young they produced in this time (range 0-33), and none yielded anywhere near the maximum possible. Much of this variation in productivity resulted, as expected, from variation in the number of years a place was used for nesting. Although all patches of plantation habitat considered were available for the whole 10-year period, not all were used every year. Some places were used only once in that time. In general, then, total production of young over ten years increased with the number of years a nesting place was occupied (Figure 5). The variation was considerable,

Figure 5. Relationship between the total number of young produced on particular nesting places over ten years and the number of years those places were occupied. From Newton 1991.



however, and one plantation was occupied in eight of the ten years but still produced no young.

In no year did Sparrowhawks occupy all available plantation nesting places (if available was defined on the basis of age, structure and nest spacing). and nor over a period of years did they occupy the available places at random. Rather they showed marked preferences for certain places, using them more than expected by chance at the population levels found, and avoiding others which they used less than expected by chance (Newton 1991). To examine whether such preferences were related to nest success, I took the data for a 15 year period, and graded all the nesting places used in that time according to the number of years they were occupied. A grade 1 place was used in 1-3 years (not necessarily successive years) in the 15-year period, a grade 2 place in 4-6 years, grade 3 in 7-9 years, grade 4 in 10-12 years and grade 5 in 13-15 years (Table 1). Places available for fewer than 15 years (because of timber felling) were graded according to the proportion of the available years they were occupied.

In general, the proportion of nests that produced young increased with grade of nesting place (= frequency of usage) (Table 1). Evidently Sparrowhawks nested most often in those places where their chances of raising young were greatest. Over the five grades, there was a 2-fold variation in the average number of young produced per nest. Hence, it seemed that plantation nesting habitat varied in quality, as measured by the number of young produced over a period of years; certain nesting places were used more often than others, and in these favoured places

Table 1. Frequency of use and nest success among Sparrowhawks in plantation nesting places over a 15-year period, Eskdale, south Scotland.

Grade of nesting place	*Number of years occupied*	*Total number of nests*	*Percentage of nests successful*	*Average number of young per nest*
1	1-3	26	31	1.19
2	4-6	54	48	1.57
3	7-9	161	47	1.60
4	10-12	150	60	2.11
5	13-15	123	71	2.63

Significance of variation among grades of nesting place in the proportion of nests that were successful: $\chi^2_4 = 26.87$, $P<0.001$. Frequencies of different brood-sizes among nests were not normally distributed, so no standard deviations were calculated for the right-hand column.

individual nest success was greatest.

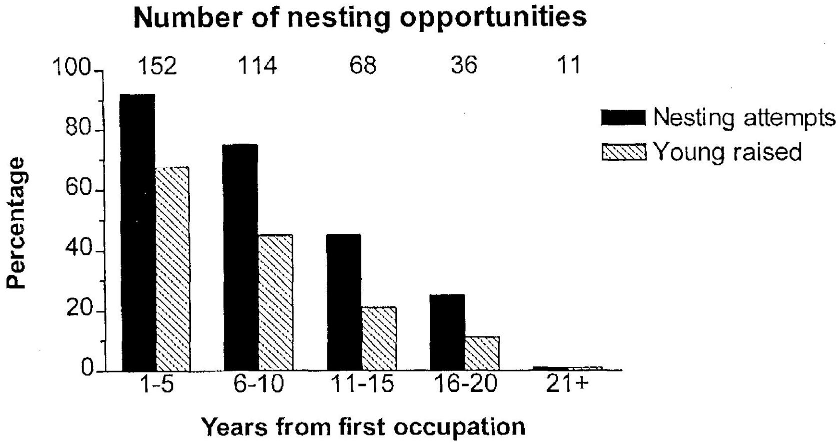
The high productivity of certain plantation nesting places could not be attributed to the same "high quality" birds using these places over long periods. On average, most Sparrowhawks remained on particular nesting places for only one year, although others stayed up to six years (mean 1.5 years) (Newton 1986). This high turnover in occupancy was due partly to mortality and partly to movement, for many individuals used different territories in different years (Newton & Wyllie 1992). Continued occupancy of certain nesting places was therefore due mainly to different Sparrowhawks occupying them in rapid succession but most staying only 1-2 years.

There was, however, a significant tendency for high grade nesting places to be occupied by older (more experienced) birds. In particular, first-year birds, which often have low nest success (Newton 1986), formed a greater proportion of breeders on low grade places than of those on high grade places. However, when first-year and older birds were examined separately, nest success within each age group was still higher on the high-grade places (Newton 1991). Hence, the higher performance recorded on high-grade nesting places was partly a function of place quality and partly of bird quality. Despite high turnover, good places tended to be occupied repeatedly by good birds.

Over a period of 10-20 years, plantations changed greatly in internal structure. When first occupied, at around 20 years of age, the trees had been thinned for the first time, enabling Sparrowhawks to fly below the canopy, among the trunks and branches. The trees were still small (less than 10 m high) at that age and close together (less than 4 m apart). Then, as the trees grew, and with further thinning every 5 years or so, they gradually became larger and farther apart. At 50 years, the trees themselves had reached more than 30 m in height, and through thinning were more than 6 m apart. A similar change would presumably have occurred in natural forest, regrowing after fire (say), but in managed plantations the periodic

Figure 6. Decline in occupancy and nest success, according to years from first occupation of a nesting place (reflecting age of trees).

The values along the top show the numbers of opportunities for nesting in plantations at each stage, dependent in turn on the number of plantations and the numbers of years they remained available. First occupation is defined by the first nest recorded during the growth of a plantation. From Newton 1991.



removal of a proportion of trees by foresters speeded the process.

The question of interest was whether plantations in which Sparrowhawks performed well over short periods of 5-10 years remained good over longer periods of 10-30 years? The answer to this question was no, because for Sparrowhawks, plantation habitat deteriorated over time. For the first 5-10 years after first occupation at around 20 years, plantation nesting places were occupied frequently and nest success was high (Figure 6). Then, as the plantation aged, places were occupied less frequently and nest success declined. In consequence, most nesting occurred in plantations of 20-30 years of age, less in plantations of 30-40 years, and hardly any in older plantations.

DISCUSSION

The main findings to have emerged from this long-term study concern the inequalities in production between individual birds and between individual territories. The figures on the lifetime reproductive rates of breeders were not too dissimilar from those found in another study of Sparrowhawks on the Dutch-German border (Zollinger & Müskens 1994). However, the females in this increasing population produced an average of 20% more offspring than in the stable Scottish population. The highest production recorded was 31 young, compared with my 24. The difference arose mainly because a larger proportion of nests was successful in the Dutch-German area, and the mean brood-size was slightly larger.

The importance of lifetime reproductive success as a measure of individual performance is two-fold. First, it combines two key measures of performance, namely survival and success at individual breeding attempts, into a single overall measure of performance; and secondly it reveals more than any other measure the full extent of individual variation in reproductive success. Barely perceptible differences in the annual success of individuals can become substantial when repeated over whole lifespans of variable duration. Lifetime studies also provide a comparison on equal terms between the sexes of species which have polygamous mating systems, and in which reproduction may be confined to a smaller part of the lifespan in one sex than in the other. Hitherto, most studies of recognisable individuals have either lasted less than the lifetimes of the individuals concerned, or have fused their individual breeding rates into population averages.

Measures of lifetime reproductive success are now available for more than 20 bird species, and for several mammal species (Clutton-Brock 1988, Newton 1989), all of which show the same points: (a) a large proportion of young that are raised to independence die before they can breed; (b) not all the individuals which survive to attempt breeding subsequently produce offspring; and (c) successful individuals vary greatly in productivity. It is a familiar idea, in fish or other animals which produce large numbers of eggs, that only a tiny fraction of the eggs that are laid survive to produce mature adults. But this recent bird research reveals an additional point, namely that only a proportion of adults in any one generation produce any mature young. In a stable population of Blue Tits *Parus caeruleus*, a species with high annual reproductive and mortality rates, only 3% of fledglings in one generation produce half of the young in the next generation. In species with lower reproductive rates, some 6-9% of individuals produce half the next generation (details in Newton 1989).

Such studies raise two questions: (a) what determines the overall pattern of LRS values in a population, as depicted in Figure 3; and (b) what determines where, within the overall pattern, particular individuals lie. The general pattern could to a large extent be imposed upon the population by prevailing mortality and reproductive rates; that is, by the life history features of the species concerned. In at least three species in which this question has been addressed (including Sparrowhawk), the expected LRS values for a population, calculated from knowledge of mean annual mortality and reproductive rates, do not differ significantly from observed patterns (Newton 1989). So the overall pattern in a population might arise simply from the normal stochastic processes of birth and death which inevitably lead some individuals to live longer and produce more young than others. If this is true, however, it does not exclude the possibility that other factors operate to influence where, within the overall pattern, particular individuals lie. Why does one individual die before it can reproduce, while another lives on to produce large numbers of young? The performance of individuals is likely to be influenced by four types of factor: (a) genetic, predisposing certain individuals to perform badly or well in the conditions prevailing; (b) non-genetic inherited features, an advantage or disadvantage that individuals might gain from their parents, called the "silver-spoon effect" by Grafen (1988); (c) accidents of birth, which lead some individuals to live in circumstances in which they have a high chance of performing well (eg good years or areas), while other similar individuals live in less favourable conditions; (d) other chance factors, such as accidental death. Only when the relative importance of these four types of influence is known, can the contribution of LRS values to Darwinian fitness be more fully evaluated.

The findings for Sparrowhawks and other bird-species provide evidence, not only for a gradual improvement in performance during the early years of life, attributed mainly to improved status and experience, but also for a deterioration in performance with advancing years, attributed to senility. Senescence has proved extremely difficult to demonstrate in wild birds, as in most other animals, first because most species can be aged only when young, so a prolonged study is needed to give individuals of known old age, and secondly because in most wild populations so few individuals reach old age that a very large sample of young individuals is needed to provide enough old ones. However, declines in annual reproductive and survival rates have recently emerged from long term studies of several bird species (Newton 1989), so perhaps these manifestations of senility will prove to be widespread, as expected.

Variation in habitat quality is a widespread phenomenon, affecting many organisms, and not only birds. Among Sparrowhawks in Eskdale, temporal stability of both population and mean nest success was associated with a system of rotational plantation management, which ensured a continuing availability of stands in the favoured age classes. The numbers of breeding pairs remained approximately constant over the years, but their distribution within the area changed continually, as birds gave up using older plantations and occupied younger ones. Some ringed individuals made the switch during their lifetimes. So both spatial and temporal variations in the physical structure of plantation nesting habitat was reflected in the breeding distribution and nest success of the hawks themselves.

While Sparrowhawk reproduction could be measured on individual territories, mortality could be measured only as an average value for the population as a whole. On high grade territories, annual production exceeded the mean annual mortality, so such territories could have acted as "sources", producing surplus young able to colonise other areas (Newton 1991). But on low grade territories, reproduction was insufficient to offset mean annual mortality, so such territories could have acted as "sinks", whose occupancy could be maintained only with the help of immigration. Variation in habitat quality was thus important in the regulation of breeding numbers in the study area. As explained above, numbers remained fairly stable in the long-term because management ensured that the forest as a whole maintained a fairly constant age-structure. If the forest were left alone, so that it grew steadily older, the findings would predict a progressive decline in Sparrowhawk breeding numbers.

It was not obvious why Sparrowhawks bred better in younger woods than in old ones, but study of the causes of breeding failures offered clues. The main causes of failure were non-laying (having built a nest), egg desertion and chick starvation. All these proximate causes could be attributed to a single underlying problem, namely food-shortage. Moreover, because all these types of failure occurred more frequently in old woods than in young ones, Sparrowhawks may have had more difficulty in catching their prey in mature, open stands than in young, dense ones. Males fitted with radio-transmitters did most of their hunting within 0.5 km of their nests, especially early in the breeding cycle. Within these areas, they showed a strong preference for hunting in young woods, spending much more time there per unit area than they spent in older woods or in other, more open habitats. In continental Europe, Sparrowhawks were also less likely to be killed by Goshawks in young stands than in old ones, but Goshawk predation was not important in Eskdale. The general conclusion was that Sparrowhawks thrived best at a particular stage in forest succession, and in Eskdale benefited from the prevailing forest management, which ensured a continuing availability of young woods.

The findings on spatial variation in habitat may be applicable to any bird species in any habitat, while those on temporal trends would apply most strongly to species (like the Sparrowhawk) which occupy successional habitats. Some other species of raptors that have been studied - including both forest and open country species - show some similar features to the Eskdale Sparrowhawks, namely (a) only a proportion of available nesting places occupied in any one year; (b) some places favoured over others during a period of years; (c) better nest success on the favoured (most frequently occupied) places. All three features have been shown for the Peregrine Falcon *Falco peregrinus* (Hickey 1942, Hagar 1969, Ratcliffe 1980), Kestrel *Falco tinnunculus* (Kostrzewa & Kostrzewa 1994) and Buzzard *Buteo buteo* (Kostrzewa & Kostrzewa 1994), while features (a) and (b) have been shown for the Gyr Falcon *F. rusticolus* (Nielsen & Cade 1990), Merlin *F. columbarius* (Newton *et al.* 1986) and Rough-legged Buzzard *Buteo lagopus* (White & Cade 1971), among others.

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I. Newton
Institute of Terrestrial Ecology,
Monks Wood, Abbots Ripton, Huntingdon,
Cambs PE17 2LS, United Kingdom.