Ornis Fennica 74:121–129. 1997

Breeding density of Sparrowhawk *Accipiter nisus* in relation to nest site availability, hatching success and winter weather

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Received 31 December 1996, accepted 11 March 1997

A 360-km^2 study area in southern Norway was searched for Sparrowhawk (*Accipiter nisus*) nests each year during 1985–96. The number of nests found increased from 21 in 1987 to 42 in 1992, and then decreased to 23 in 1996. Nest site spacing became more regular throughout the study period, with a higher frequency of the preferred young forest. The percentage of one-year-old breeding birds increased with greater snow depth during December–March, possibly because of the higher mortality of older winter-resident individuals. Both the proportion of hatched clutches and the number of breeding pairs were negatively correlated with snow depth and positively correlated with mean temperature in March. When snow depth was controlled for, there was also a positive correlation between the number of pairs and the proportion of hatched clutches in the previous year. The study confirms that the breeding density of the Sparrowhawk is sensitive to environmental conditions that influence the body condition, survival or breeding performance of the birds. It could, however, not be concluded that surplus non-breeding birds were absent in years of low breeding density.

1. Introduction

The breeding density of territorial raptor species is usually limited either by food supply or by nest site availability (Newton 1979), unless species encounter human persecution, disturbance or pesticides. In a homogenous habitat where nest sites are in surplus, active nests are usually regularly spaced, though more densely in an area rich in prey than in a poor one (Newton 1979). For several raptor species, removal experiments have provided evidence not only for territorial behaviour, but also for the presence of surplus non-breeding birds able to breed only when nesting territories are made available to them (Newton 1979, 1992). Annual fluctuations in the reproductive success are usually not important to the breeding density of raptors because of their low adult mortality.

Some small and r-selected raptor species may, however, deviate from the general trends mentioned above. One of the best studied raptor species is the European Sparrowhawk (*Accipiter nisus*), which because of a relatively high mortality (Newton et al. 1983a, 1993, Ryttman 1994) would be expected to show population fluctuations corresponding to annual variations in survival or breeding success. Actually, in Finland, Sparrowhawk nesting territories seemed to be less permanent than those of sympatric, larger-sized raptor species, like the Goshawk (*A. gentilis*) and the Common Buzzard (*Buteo buteo*) (Forsman & Solonen 1984).

In Scotland, Newton and Marquiss (1986) found that cold and wet conditions in winter led to a smaller breeding population of Sparrowhawks than expected based on the number of nests from the previous year. A decline in breeding populations has also been observed in Scandinavia after cold winters (Jørgensen 1987, Rasmussen & Storgård 1989, Jansson 1990). Such declines may be explained by a higher mortality in cold winters (see Newton et al. 1993), but also by the poorer body conditions of the hawks present in spring, because only high quality birds appear to be able to nest in low-quality nesting territories (see Newton 1991, Newton & Marquiss 1991). Therefore, it cannot be concluded whether the breeding density of this species is determined by winter survival, or by the relationship between the body condition of the birds and the quality of the available nesting territories.

The relatively high proportion of one-year-old birds among breeding Sparrowhawks (e.g. Newton et al. 1981, Bomholt 1983, Wyllie & Newton 1991) indicates that there are usually too few older birds to occupy all nesting territories. Hence, if the total number of Sparrowhawks present in spring is critical for the breeding density of this species, then the breeding success in the previous year might also influence the number of breeding pairs. However, there seems to be no evidence of a relationship between the number of young fledged and the breeding density the following year (e.g. Newton 1988), even though marked annual variations in breeding success have been observed (Newton & Marquiss 1986, Wyllie & Newton 1991).

Additionally, the availability of high quality nest sites may be important for the breeding density of a raptor, especially if the risk of nest predation is high. For instance, on islands where mammalian predators are absent, raptors which usually require cliffs for their nest may nest on level ground (Newton 1979). In mixed-age forest, Sparrowhawks prefer to nest in dense, young forest stands (Ortlieb 1979, Newton 1986, Selås 1996), presumably because the risk of Goshawk predation is lower in this habitat than in older and more open forest stands (Selås 1996). Hence, a lack of suitable nest sites may limit the breeding density of Sparrowhawks, as has been found for the similar-sized Kestrel (*Falco tinnunculus*) (Village 1983).

In this paper, I present a 12-year data set on the breeding density of the Sparrowhawk in southern Norway. The fluctuation in the number of breeding pairs is analysed in relation to the availability of suitable nesting habitats, hatching success and winter weather. The null hypotheses tested were: 1) The distribution of nests is independent of the availability of young forest. 2) The age distribution of breeding birds is independent of the winter weather. 3) The breeding success is independent of the winter weather. 4) The number of breeding pairs is independent of the winter weather. 5) The number of breeding pairs is independent of the breeding success in the previous year.

2. Methods

The sparrowhawk's breeding density was investigated from 1985 to 1996 in a 360-km^2 area in Aust–Agder county, in southern Norway (58°43'N, 8°44'E). The study area is situated at 50–300 m a.s.l. and 10–30 km inland from the coast in the boreonemoral zone (Abrahamsen et al. 1977). The climate is sub-oceanic, and snow usually covers the ground from December through April. Data on snow depth, precipitation and temperature from the study period were provided by the Norwegian Meteorological Institute.

The study area is hilly and sharply undulating, and dominated by forests (80%), with scattered lakes (10%), bogs (5%) and less than 2% agricultural land. The forests are characterised by a fine-grained mosaic of young, medium and old-aged coniferous, mixed and deciduous stands. Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*), oak (*Quercus* spp.), aspen (*Populus tremula*) and birch (*Betula* spp.) are the dominant tree species. Forestry based on clear-cutting, replanting and thinning of the regrowth was introduced in the mid-1950s. In Aust–Agder county, the proportion of forests aged 20–40 years, which is the habitat most likely to be used by Sparrowhawks for nesting (cf. Selås 1996), increased from 6% in 1974 to 11% in 1988 (Table 1).

I estimated the frequency of forests of different age classes within the study area in 1989 and 1996. In both years, a total of 61 aerial photographs (taken in spring 1989; scale 1:15 000) were covered by a grid with 100 numbered intersections, and then two intersections were randomly selected in each photograph. Of these 122 plots, 105 were situated in forests in 1989 and 100 in 1996. The age of the forest stand in each plot was measured in the field (cf. Selås 1996). These results, together with the values for Aust–Agder county, indicate that the frequency of forests 20–40 years old was at least doubled during the period of my study, from less than 10% in the mid 1980s to approximately 20% in 1996 in my study area (Table 1).

I and two field assistants searched for nests of Sparrowhawks and other birds of prey in the study area each year, following the methods described by Forsman and Solonen (1984) and Newton (1986). Even though all field workers were residents in the study area, the search may have been less efficient in the first years, especially in 1985, than later on, when the field workers became more familiar with the study area. Hence, when testing for correlations between the annual number of breeding pairs and other variables, the data from 1985 and 1986 were excluded. Some pairs were probably also overlooked during 1987–96, but for this period, this source of error is not likely to differ between the years.

When measuring neighbour distances for the test of nest distribution, all Sparrowhawk nesting attempts were assigned to one of four periods; 1985–87, 1988–90, 1991–93 and 1994–96. This was done mainly because I suspected that some active nests were missed each year, but also because I wanted to include seven nesting territories where the breeding attempt could only be assigned to one of these periods, and not to a specific year. For each period, a G-value (see Brown 1975), ranging from 0 (complete randomness) to 1 (complete regularity), was calculated by the formula $((\prod v_i)^{1/n})/(1/n\sum v_i)$, where $v_1, \ldots, v_n$ denotes the squared nearest neighbour distances.

From 1988 and onwards, the breeding hawks were classified as one year or older based on the moulted feathers found at the nest sites, or in a few cases by observing the birds from a hide placed near the nest or the plucking posts. The annual variation in the proportion of old birds among breeding hawks was assumed to reflect the annual variation in winter survival of this age category; more older birds tend to remain in the study area in winter than juveniles (cf. Kjellén 1994).

From 1989 and onwards, I also tried to determine the proportion of breeding attempts that failed before hatching because I assumed nesting failures prior to hatching to depend more on the body condition of the birds, and less on predation, compared with nesting failures later in the breeding season (e.g. Newton 1976, 1986). Since 85% of the unsuccessful breeding attempts in my study area failed before hatching, the proportion of hatched clutches was also used as an index of the breeding success. The total number of birds with known age and of nests with known breeding result is given in Table 2. To increase the sample size, I have also included data on bird age and breeding success from nests located up to 15 km from the main study area.

When testing for the effect of winter weather on the proportion of old birds, hatching success and breeding density, I used the mean snow depth

Table 1. The percentage of forest in different age classes in Aust–Agder county (3 190 km² productive forest land) and in the study area (300 km² productive forest land). The values from Aust–Agder county are taken from Løvseth and Nordby (1980) and Tomter (1994). The values from the study area are based on randomly selected control plots (see text).

	Year	Age class %		
		Regrowth 0–20	Young forest 21–40	Older forest > 40
Aust–Agder county	1955	6	4	90
	1974	21	6	73
	1988	21	11	68
Study area	1989	24	6	70
	1996	28	22	50

(measured each day) from December to March, because this index reflects both temperature and precipitation. To get an index for the late winter, which may be especially important to the hawks because of poor body condition and food availability at this time, I used the mean temperature in March. This was because the snow depth for this month will also reflect the weather of the previous months. For the period 1985–96, the two indices selected, were however highly correlated (Kendall's rank correlation, $T = -0.60$, $p = 0.007$, $n = 12$).

All statistical tests are nonparametric and two-tailed. If more than one test was carried out for a null hypothesis, I adjusted for the increased probability of at least one type I error by use of the sequential Bonferroni method (Rice 1989). When comparing the number of breeding pairs with one of the winter condition variables, I also controlled for the effect of the hatching success of the previous year, by use of partial correlation (Siegel & Castellan 1988). Similarly, when I tested for correlation between breeding density and hatching success, I controlled for the effect of the winter index which was best correlated with the breeding density.

3. Results

The number of occupied nesting territories found increased from the first to the third period, but then decreased from the third to the fourth period. The mean nearest neighbour distance varied in the opposite way; it decreased from 1985–87 to 1991–93, and then increased from 1991–93 to 1994–96 (Table 3).

The shortest distance to the nearest neighbour increased throughout the study, from 0.5 km in 1985–87 to 1.3 km in 1994–96 (Table 3), as did the nest site regularity, from a G-value of 0.78 in 1985–87 to 0.92 in 1994–96 (Table 3). Assuming that the frequency of young forest stands increased between each period (Table 1), there was a significant correlation between the nest site regularity and the frequency of young forest stands (Kendall's rank correlation, $T = 1$, $p = 0.042$, $n = 4$). In the first period, 14.3% of the nest sites found were located in old forests, while less than 2% were found in such habitats during the two next periods (Table 3). During the last period, no nests were found in old forests.

During 1988–96, the proportion of old birds (≥ 2 years) among breeding Sparrowhawks varied from 63% in 1994, which was a very snow-rich winter, to 87% in 1993, the second in a row of two almost snow-free winters. The proportion of old birds was negatively and significantly correlated with snow depth (Fig. 1; $T = -0.67$, $p = 0.012$, $n = 9$), even with the Bonferroni adjustment. There was, however, no significant correlation between the proportion of old birds and the mean temperature in March ($T = 0.37$, $p = 0.17$, $n = 9$).

Table 2. Number of breeding Sparrowhawk individuals which could be aged one year or older and number of nesting attempts with known result during 1988–96.

	1988	1989	1990	1991	1992	1993	1994	1995	1996
Number of individuals	28	31	48	60	60	46	62	42	47
Number of nesting attempts	–	35	41	48	53	46	45	34	33

Table 3. Mean nearest neighbour distances of Sparrowhawk nests, nest site regularity (G-values), and the percentage of nests found in older forests, during four, three-year periods in southern Norway.

Period	n	Nearest neighbour distance Mean (Range)	G-value	In forest > 40 year (%)
1985–87	32	2.2 (0.5–3.3)	0.78	14.3
1988–90	40	1.9 (0.6–3.4)	0.80	1.1
1991–93	57	1.6 (0.8–3.0)	0.83	1.6
1994–96	45	1.8 (1.3–3.0)	0.92	0.0

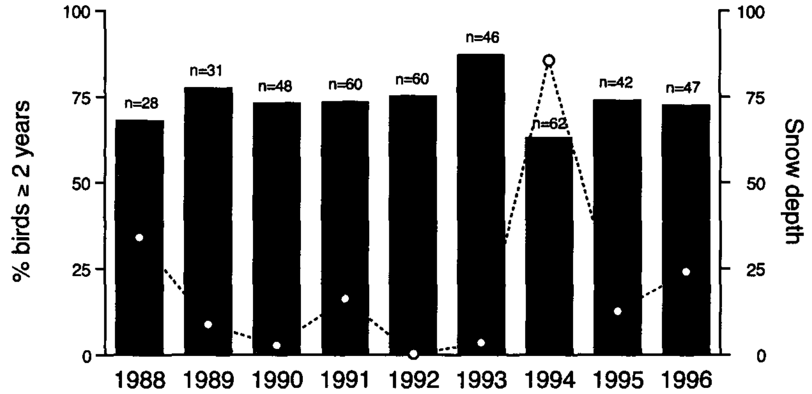

Fig. 1. Mean snow depth in December–March (broken line) and the annual percentage of individuals (males and females pooled) older than one year (bars) in a breeding population of Sparrowhawks in southern Norway.

For the period 1989–96, the proportion of hatched clutches varied from 65% in 1995 to 85% in 1990. The number of hatched clutches was less when snow depth in winter was greater (Fig. 2; T = – 0.64, p = 0.026, n = 8) and temperatures in March were colder (T = 0.64, p = 0.026, n = 8). With the sequential Bonferroni adjustment, which sets the critical confidence limit for the best test result to 0.025 when two tests are carried out, these correlations must be regarded as nearly significant.

In 1995, hatching success was especially low, despite apparently favourable winter conditions (Fig. 2). One reason for this may be that the amount of precipitation in May and June was unusually high, leading to the worst spring flood in southeastern Norway for several decades. Heavy rain in spring is known to lower the breeding success of Sparrowhawks and other raptors (see Newton 1986, Kostrzewa 1987, Kostrzewa & Kostrzewa 1990). When controlling for the effect of rain, the correlations between hatching success and snow depth and March temperature became significant (Kendall's partial rank correlation, T = – 0.60, $p < 0.025$ and T = 0.60, $p < 0.025$, respectively).

The number of nests found increased steadily from 21 in 1987 to 42 in 1992, and then decreased to 23 in 1996 (Fig. 3). The number of nests found was negatively correlated with snow depth (T = – 0.42, p = 0.089, n = 10), and positively correlated with temperature in March (T = 0.54, p = 0.030, n = 10). When the hatching success of the previous year was controlled for, both correlations became significant even with the Bonferroni adjustment (Kendall's partial rank correlations, T = – 0.53, p < 0.025 and T = 0.43, p < 0.05, respectively).

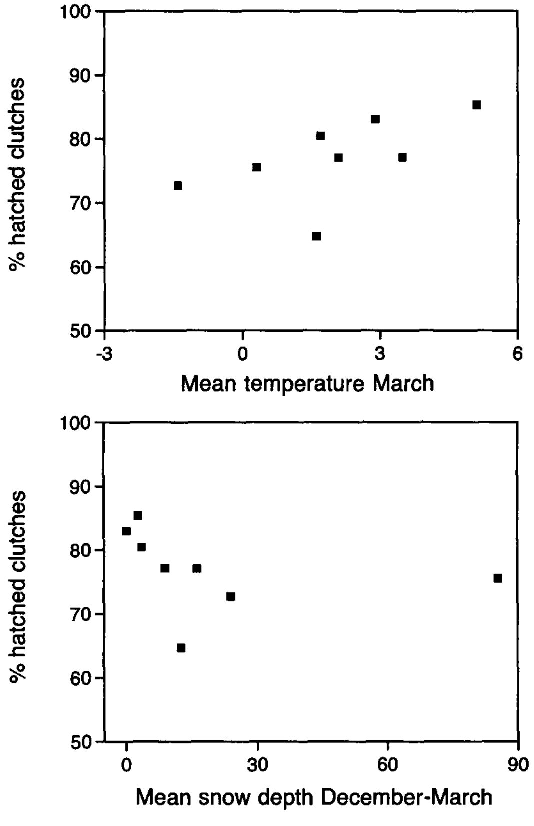

Fig. 2. Percentage hatched Sparrowhawk clutches in relation to mean snow depth in December–March and mean temperature in March.

The correlation between the number of nests and the proportion of hatched clutches in the previous year was nearly significant (Fig. 3; T = 0.52, p = 0.099, n = 7). When snow depth was controlled for, the correlation was significant (Kendall's partial rank correlation, T = 0.60, p < 0.05).

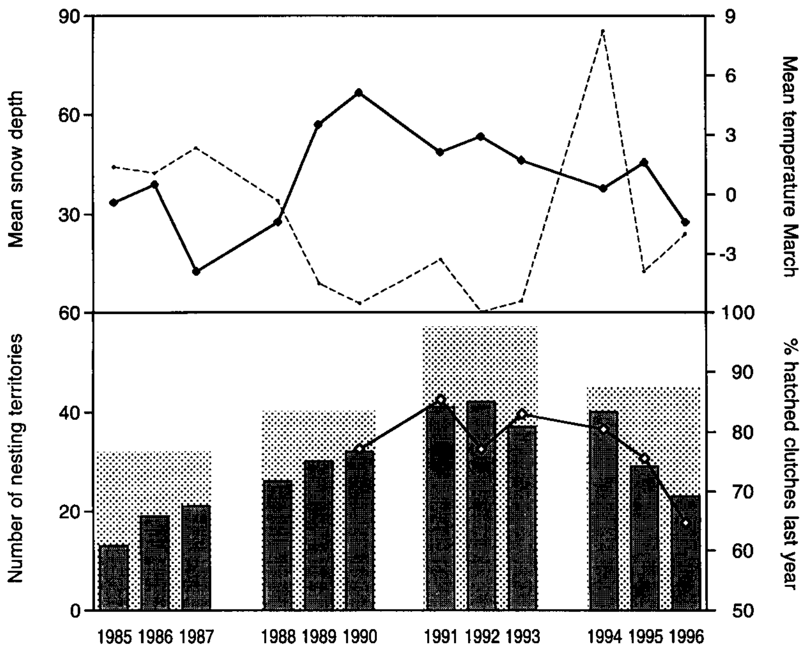

Fig. 3. The annual number of Sparrowhawk nests found (bars), percent hatched clutches previous year (open squares, solid line), mean snow depth in December–March (broken line) and mean temperature in March (filled squares, solid line). The total number of nesting territories found in each three-year period is shown as dotted bars.

4. Discussion

Sparrowhawk nest spacing became steadily more regular throughout this study, as could be expected from the greater frequency of young forest in the study area. During the first three-year period, the low regularity of spacing and the relatively high frequency of nests located in old forests indicated a low availability of high-quality nest sites. Hence, even in continuous forests, nest sites may limit the breeding density of Sparrowhawks if dense, young forests are not available and the risk of nest predation is high. For some small passerines, breeding density has been lowest near raptor nests, indicating that a predation risk influences the distribution of nests of these species (Geer 1978, Suhonen et al. 1994).

In Great Britain, Sparrowhawk nesting places have been very regularly spaced within areas of continuous woodland (Newton et al. 1977, 1986). One reason may be that the Sparrowhawks are less restricted with regard to nest site quality in Great Britain than in my study area, since in Great Britain, its main enemies, the Goshawk and the Pine Marten (*Martes martes*), have been eliminated (Newton 1986). Especially the Goshawk is an important predator on Sparrowhawk nestlings and fledglings (Selås 1996). Traditional nest sites may be abandoned if Goshawks begin to nest in the vicinity (Fischer 1980, Selås unpubl.), while young forests seem to be less important as nesting habitat when the Goshawk is absent (Bomholt 1983, Newton 1986, Tømmeraas 1994). However, even in the absence of Goshawks, Newton (1991) found that nesting places in young dense woods had the highest occupancy and the greatest nest success.

Even though the total number of breeding pairs was probably not regulated by nest site availability during my study, this may have been the case some decades ago, when large parts of my study area consisted of old forest, and there also was a much higher breeding population of Goshawks (Selås unpubl.). Several observers have claimed that the Goshawk was more common than the Sparrowhawk in my study area in the 1950s. In contrast, today, distances between neighbours are less than 2 km for Sparrowhawks and more than 4 km for Goshawks (Selås 1997). Unfortunately, we do not know to what extent the Norwegian Sparrowhawk population has been influenced by pesticides. In another study area in southern Norway, however, there apparently was a normal breeding density in the late 1950s, with some distances between neighbours as low as 1 km (Steen 1989), at a time when the population had started to decline elsewhere in Europe (Benington 1974, Ortlieb 1979, Newton 1986).

Winter weather apparently influenced the proportion of one-year-old breeders, the hatching success, and the breeding density of Sparrowhawks in my study area. The proportion of one-year-old birds was highest after snow-rich winters, presumably because of high mortality of adult birds. However, since there was also a lower hatching success after cold winters, indicating a poorer body condition of the breeding birds (see Newton et al. 1983b), the correlation between winter weather and breeding density may still be related to the body condition of the birds in spring, and not to the number of birds present.

Cold winters may increase the hawks' energy demand and reduce their hunting success, but winter survival and spring body condition may also be affected by the influence of weather on the number of prey available, i.e. small passerines (e.g. Svensson 1981). However, for the similar-sized Kestrel, Kostrzewa and Kostrzewa (1991) concluded that body size rather than food availability influenced winter survival and thus the number of territorial pairs of raptors in spring. This was because there was no correlation between winter temperature and the number of breeding pairs for the sympatric and larger-sized Common Buzzard, which feeds on the same prey species as the Kestrel. In my study area, the large amounts of food provided at bird feeders probably improves the survival of small passerines in cold winters (cf. Krebs 1971, Jansson et al. 1981, Källander 1981), and thus tends to stabilise the prey availability for the Sparrowhawk.

Perhaps the most interesting finding of my study was that, when winter weather was controlled for, there was a correlation between the proportion of hatched clutches and breeding density in the following year. The marked decline of the breeding population after 1994 coincided with a lower hatching success. Especially in 1995 the hatching success was low, as was the number of fledglings produced per successful nesting attempt (Selås unpubl.). Hence, the low breeding density in 1996 was probably a combined result of harsh winter conditions and the unusually low breeding success in 1995, indicating that there actually were too few hawks to occupy the nesting territories available. However, at one nest site, continuously used since 1991, we found several moulted feathers from an old female early in the 1996 breeding season, and later on from a one-year-old female, which apparently had replaced the former. If so, then there still were some surplus birds, able to breed when high quality nesting territories were made available.

The study confirms that the breeding density of small raptor species like the Sparrowhawk is sensitive to variations in environmental conditions that influence the body condition, survival or breeding performance of the birds. Winter weather seemed to affect both the number of breeding pairs and successful nesting attempts. Because of the correlation between the number of breeding pairs and the breeding success of the previous year, some time lag between winter weather and breeding density would be expected. It could not, however, be concluded that surplus non-breeding birds were absent in years of low breeding density. Neither could it be stated that the availability of high-quality nest sites influenced the breeding density, despite the low regularity of nest spacing during the first years of this study, when the frequency of young forest stands in the study area was low.

Acknowledgements. I wish to thank K. O. Selås, I. Selås and C. Steel for assistance with the field work, and G. A. Sonerud, J. Valkama, M. Mönkkönen and an anonymous referee for comments on the manuscript. The study was supported by the Nansen Endowment.

Sammanfattning: **Sparvhökens häckningstäthet i relasjon till förekomst av häckningslokaler, häckningsframgång och väderlek under vintern**

Tätheten av häckande sparvhöker studerades i ett område på 360 km^2 i södra Norge under perioden 1985–96. Antalet registrerade par ökade från 21 till 42 mellan 1987 och 1992, men minskade sedan till 23 par 1996. Andelen ung skog (20–40 år), som häckande sparvhökar föredrar, ökade i området, vilket ledde till mer regelbundet utspridning av boplatser i landskapet. Proportionen häckande hökar som var äldre än ett år var lägst efter vintrar med mycket snö, troligen en följd av högre dödlighet hos gamla övervintrande hökar under

snövintrar. Andelen bon med kläckta ägg liksom antalet häckande par var negativt korrelerat med snödjupet december–mars och positivt korrelerat med temperaturen i mars. Då variabeln snödjup hölls konstant statistiskt fanns en positiv korrelation mellan andelen bon med kläckta ägg och kommande års häckningstäthet. Resultaten visar att sparvhökens häckningstäthet påverkas av klimat och väderlek, som bestämmer kondition, överlevnad ock häckningsframgång hos hökarna. Det är oklart icke-häckande sparvhökar förekom under år med låg häckningsfrekvens.

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