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Influence of prey availability on re-establishment of Goshawk *Accipiter gentilis* nesting territories

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Despite many years of protection, nesting Goshawks (*Accipiter gentilis*) are still killed by man in Norway to save small game, especially grouse, from predation. In a 650-km^2 area in southern Norway, the re-establishment of Goshawk nesting territories was studied during four, 4-year periods 1972–75, 1980–83, 1984–87 and 1988–91. After a reduction in the Red Fox (*Vulpes vulpes*) population because of an infestation of sarcoptic mange, the grouse population increased during 1984–87, and then remained high for the rest of the study period. The number of Goshawk nesting territories per 100 km^2 was three/year in 1972–75 and in 1980–83, and four/year in 1988–91. During these periods, the nesting territories were regularly spaced, and their number and distribution were unaffected by the removal of breeding birds. During 1984–87, five nesting territories, in which one or both of the breeding hawks had been removed by man, were replaced by eleven new ones. The study results indicate that removal of breeding pairs of goshawks may lead to an increase in the breeding density during periods of increasing food availability.

1. Introduction

The breeding density of many bird species within any given area is often limited by the territorial behaviour of the birds present (Newton 1992). The existence of territorial behaviour as well as of surplus nonbreeding birds has been demonstrated by several removal experiments, where newcomers in the same breeding season have settled in a similar density as the birds removed (Newton 1992). The density of breeding pairs may however differ from year to year, or between different areas, presumably because the birds adjust the size of their territories to correspond with the local food supplies (Newton 1980, 1994).

Some of the most extreme examples of population stability among birds are known from long-lived raptor species feeding on prey having relatively stable population densities (Newton 1979). Nest sites of such raptors are usually regularly spaced, and used by the same individuals for many years (Newton 1979). This may make it difficult for newcomers to establish a territory between the existing pairs, despite some fluctuations in prey availability, so that fluctuations in the number of breeding pairs are inhibited. Actually, in some passerine birds, individuals have held smaller territories, giving higher population densities, when they have settled simultaneously than when they have settled sequentially over longer periods (Knapton & Krebs 1974, Stenseth et al. 1979, Drent 1984). This suggests that although the supply of food may be insufficient to allow new settlements between existing pairs, there may be sufficient food available to allow a higher number of breeding pairs to settle if the established territorial birds are removed.

Because of their low mortality, territorial individuals of medium-sized and large raptors are usually replaced one by one over long periods. Thus, under natural conditions, an increase in density resulting from smaller territories because of newly settled birds is not likely to occur. However, during this century, several European raptor species have been subject to intensive human persecution. This persecution has provided evidence for the existence of surplus nonbreeding birds (Newton 1979), but to my knowledge, no cases of increased breeding density after removal of territorial birds have been reported.

Perhaps the most persecuted raptor species in Europe is the Goshawk (*Accipiter gentilis*), primarily because of its predation on forest grouse (*cf.* Höglund 1964a, Wikman & Tarsa 1980, Widén 1987). In Fennoscandia, grouse abundance usually influences both breeding density and reproduction of the Goshawk (Sulkava 1964, Sollien 1979, Lindén & Wikman 1980, Wikman & Lindén 1981, Tornberg & Sulkava 1990). In a continuous forest habitat, active nest sites of Goshawks are regularly spaced (Widén 1985) and these nests or nest sites are typically used by the same individuals for several years (Höglund 1964b, Selås unpubl. data).

Beginning in the late 1970s, an epizootic of sarcoptic mange (*Sarcoptes scabiei*) among Red Foxes (*Vulpes vulpes*) was followed by an increase in the population of Black Grouse (*Tetrao tetrix*) and Capercaillie (*T. urogallus*) in Sweden and Norway (Small et al. 1993, Lindström et al. 1994, Selås et al. 1995). In southern Norway, I recorded Goshawk breeding density before, during, and after the infestation of mange in 1984. Throughout this study, breeding Goshawks were illegally shot at more than 10% of the known nest sites each year. This made it possible to compare the effect of the removal of territorial Goshawks on the settlement pattern, during a period with increasing prey number, with that during periods of more stable prey densities.

2. Methods

The study area was situated in the south-eastern part of Aust-Agder county in southern Norway (lat. 58°43´N, long. 8°44´E). It covers about 650 km^2 and is located 2–30 km inland from the coast in the boreo–nemoral zone (Abrahamsen et al. 1977). Elevation ranges from 100 to 400 m. The area is dominated by forest (80%), and has scattered lakes (10%), bogs (5%), and agricultural land (< 2%). The climate is suboceanic, and snow usually covers the ground from December through April.

From 1984 to 1991, I monitored the study area each year to determine the breeding density of Goshawks and other birds of prey, following the methods described by Forsman and Solonen (1984). Although monitoring was carried out throughout the year, it was most intensive during the breeding season (April–July). Goshawk breeding density was also carefully investigated in 1972–75 (Lørdahl 1975) and 1980–83 (K. Vehusheia pers. comm.). For the period between (1976–79), observations of nests were too infrequent to give reliable results on the breeding density. Over the course of several years, Goshawks frequently moved between alternative nest sites within their territories and also built new nests. As a consequence, it was usually not possible to find all active nests in a single year. Therefore, I used 4-year periods when presenting the results; 1972–75, 1980–83, 1984–87, and 1988–91. From all periods, additional information was given by some of the hawk hunters.

For periods with a stable breeding population, the mean neighbour distance was measured by the minimum spanning tree method (Gower & Ross 1969), using the most used nest site in each nesting territory. When n nests are plotted on a map, a line is drawn from one of the nests to the closest neighbour nest. Then a line is drawn from the nearest nest to one of those already connected, until all nests are connected to the tree, giving n – 1 lines or neighbour distances. To get a measure of the regularity of nest spacing in each period (Brown 1975), I measured the distance to the nearest neighbour for each nest, giving n neighbour distances. Then, a G-value, ranging from 0 (complete randomness) to 1 (complete regularity), was calculated by the formula:

$$\frac{(\prod v_i)^{\frac{1}{n}}}{\frac{1}{n}\sum v_i}, \qquad (1)$$

where $v_1, \ldots, v_n$ denotes the squared nearest neighbour distances (Brown 1975).

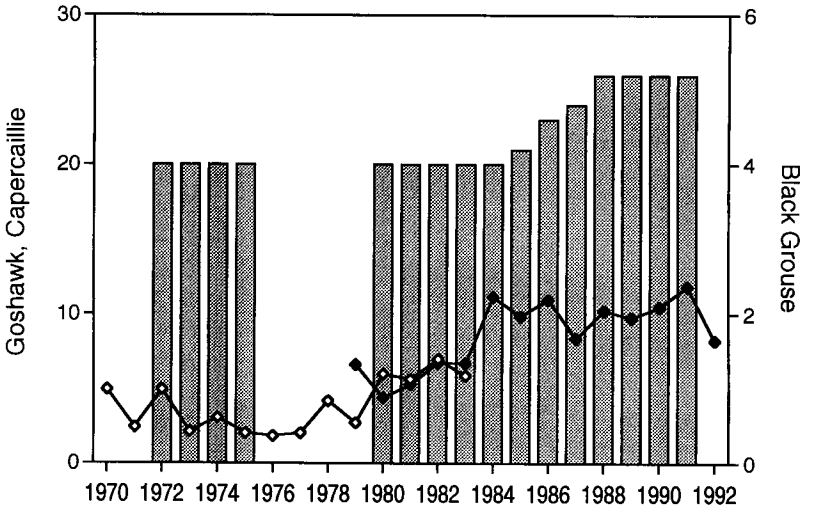

Fig. 1. Number of Goshawk pairs (bars) in a 650-km² area in southern Norway compared with the autumn population of the Capercaillie, given as the estimated number of birds per km² (line, open squares) and the annual number of Black Grouse shot (total n = 1952) per 10 hunter days (line, filled squares) during 1972–1991.

In Norway, the Goshawk has been protected by law since 1971. Therefore much of the persecution in my study area was done secretively. Even though I knew most of the hawk hunters, it was not possible to record the total number of hawks shot at their nests each year. To my knowledge, however, when robbing a Goshawk nest all hunters first tried to shoot the adult hawks. Therefore, I assume that the frequency of unsuccessful breeding attempts in a period also reflects the degree of hunting pressure on breeding Goshawks. For individual identification of the breeding hawks, I used moulted feathers collected at the nest sites (see Opdam & Muskens 1976).

In the study area, hunting statistics and autumn counts indicated that the populations of the Black Grouse and the Capercaillie fluctuated synchronously (Grasaas 1960, 1961, Wegge 1979, Krafft 1980, 1981, 1982, 1983, 1984), as was also found elsewhere in Norway (Moksnes 1972, Myrberget 1976, Hjeljord 1980) and in Finland (Ranta et al. 1995). Adjusted for weight, these two species made up equal parts of the Goshawk diet during the breeding season in my study area, both in 1972–75 (Lørdahl 1975) and 1988–91 (Selås unpubl. data).

In the central part of the study area, autumn counts of the Capercaillie were conducted until 1983 (Wegge & Grasaas 1977, Wegge 1979, 1980, Krafft 1980, 1981, 1982, 1983, 1984). As an index of the grouse population from 1979 to 1992, I have used the mean annual hunter harvest of the Black Grouse (total n = 1952) from a 100-km² area located 5–15 km north-east of my study area (the Capercaillie was not hunted). To correct for a potential functional and numeric response by the hunters to the Black Grouse density (*cf.* Lindén 1981), the hunting harvest is expressed as the number of birds shot per 10 hunter days. The hunting yield prior to 1979 was too low to give reliable estimates of the population level.

3. Results

Sarcoptic mange infestation of red foxes occurred in the study area in 1984 (Holt & Berg 1990), and a marked increase in the number of Black Grouse was subsequently observed (Fig. 1). From 1984 to 1991, the grouse population was continuously high (Fig. 1). Thus, I obtained three, 4-year periods with consistent food supply (1972–75, 1980–83 and 1988–91), and one period where the food supply increased from the previous period (1984–87).

In 1972–75 the breeding density of Goshawks was approximately three pairs per 100 km². In 1980–83, the distribution of breeding pairs, and thus the breeding density, was equal to the period 1972–75. The breeding density of the Goshawk increased during 1984–88, and reached four pairs per 100 km² in 1988 (Fig. 1). The mean neighbour distance decreased from 5.4 km (n = 19) in 1980–83 to 4.5 km (n = 25) in 1988–91 (Mann Whitney U-test, $Z = 2.47$, $P = 0.01$).

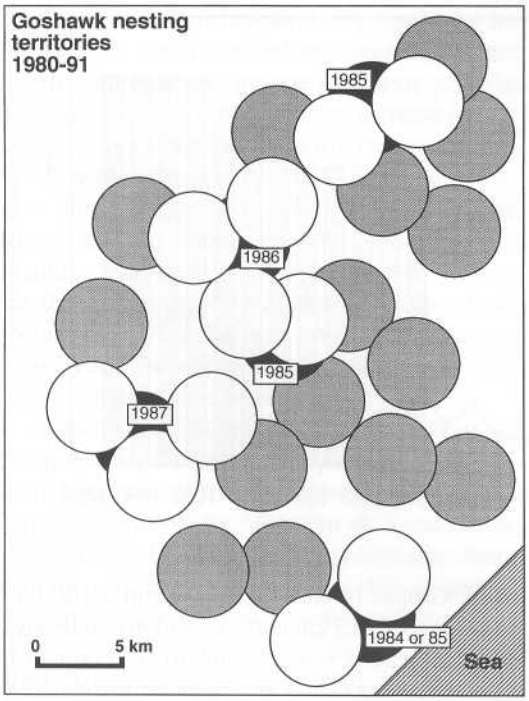

Fig. 2. Nesting territories of the Goshawk (circles with nest in centre) before and after removal of territorial hawks by man during a period with greater food supplies (1984–87). Open circles denote new nesting territories, established in 1986–88. Black circles denote old territories, used until 1985–87. The year of removal of breeding hawks (= last year of breeding) is given for each of the old nesting territories. Grey circles denote territories used during the whole period 1980–91.

For each of the three, 4-year periods with a constant number of breeding pairs, the nesting territories were regularly spaced. The G-value (Brown 1975) was 0.97 in 1972–75 (n = 12), 0.94 in 1980–83 (n = 13) and 0.95 in 1988–91 (n = 21). The location of nesting territories was fairly stable from year to year, with distances between alternative nests (within territories) usually less than 1.5 km.

The frequency of unsuccessful breeding attempts was 27% in 1972–75 (n = 41), 67% in 1980–83 (n = 36), 41% in 1984–87 (n = 27) and 31% in 1988–91 (n = 78), and differed significantly among these periods ($X^2 = 16.45$, 3 df, $P < 0.001$). The low frequency of unsuccessful breeding attempts in 1972–75 was due to the fact that several hawk hunters refrained from nest robbing, hoping that results from the ongoing investigation (Lørdahl 1975) would open legal Goshawk hunting. The results from 1972 to 1975 were published by the local game authorities, with the effect that most of the nesting territories and a large number of the nest sites were known by hawk hunters during the next study period 1980–83 (K. Vehusheia pers. comm.).

In the periods with constant numbers of breeding pairs (1972–75, 1980–83 and 1988–91), nesting territories where breeding Goshawks had been removed were always reoccupied with the same spacing, and no change in the distribution of nesting territories from one year to the next was observed. For instance, during 1988–91, both mates were removed from at least two nesting territories, and both territories were reoccupied the next year.

During the period with more abundant food supplies (1984–87), several new nesting territories were established after removal of breeding hawks in some of the existing territories (Fig. 2). In two territories where the nests had been used for more than five years in a row, no reoccupancy occurred after removal of the breeding pairs in 1985. This also happened in two other nesting territories where the nests were robbed by man in 1984 or 1985 and in 1986, but I do not know whether only one or both of the breeding hawks were shot at these nests. By 1988, two new nesting territories had been recorded in the area of each of the four old territories (Fig. 2). In 1988, I also found three new nesting territories in an area where a single Goshawk pair, which had bred in the old territory for several years, was removed in 1987 (Fig. 2). In all territories where the old pairs were replaced by two or three new pairs during the period of greater food supplies, breeding hawks had also been removed in the previous 4-year period, when no changes in breeding density were observed.

4. Discussion

This study is the first to indicate that removal of breeding pairs of Goshawks may lead to an increase in the Goshawk breeding density in periods with increasing food supplies, but not in periods in which the food supply remains unchanged.

Unfortunately, it was not possible to compare the result from my study area with a control area where Goshawks were not hunted. It could be argued then that the Goshawk would have responded numerically to the greater abundance of food during 1984–87 regardless of the removal of breeding pairs. It should be noted, however, that all new nesting territories were established after removal of old territorial hawks.

If not exposed to human persecution, breeding Goshawks usually show strong fidelity to their nest sites, and the annual replacement of breeding birds is low (Selås unpubl. data). Because the nesting territories are usually defended with the regularly spaced nest sites as centre, I argue that a considerable increase in the amount of food available is necessary to allow surplus Goshawks to establish nesting territories between the existing ones. Similarly, a time lag in the population increase of the Great Horned Owl (*Bubo virginianus*) relative to the marked increase in cyclic populations of the Snowshoe Hare (*Lepus americanus*) has been suggested to be caused by territorial behaviour (Rohner 1995).

In a Finnish study, the population of Goshawks decreased when the population of the Hazel Grouse (*Bonasa bonasia*) decreased, but then remained stable for several years despite some increase in the Hazel Grouse population (Lindén & Wikman 1983). It is possible then that the breeding population in my study area would also have remained stable, perhaps throughout the study period, if breeding Goshawks had not been removed. Because of the removal of territorial birds, however, the Goshawk population may have reached a new stable density in a few years after the increase in the grouse population in 1984. During 1988–91, when the grouse population was still high, there was no further increase in the Goshawk breeding density, even though several pairs were also removed in this period.

Despite the heavy hunting pressure of Goshawks during 1980–83, no change in the breeding density was observed until the increase in the grouse populations from 1984 onwards. Thus, prey availability, and not the settlement pattern, seemed to determine the distribution and size of breeding territories after removal of breeding hawks. It may, however, have been important that only a part of the population was removed each year throughout my study. If, for instance, the whole breeding population had been removed at the same time, an increase in the breeding density resulting from a synchronous territorial establishment may have also occurred even when the amount of food available was unchanged (*cf.* Stenseth et al. 1979).

In contrast to the apparently positive effect of the present level of human persecution on the Goshawk's breeding density in my study area, hunting may theoretically negatively influence the breeding population in periods with decreasing prey availability. For the Sparrowhawk (*Accipiter nisus*), Newton and Marquiss (1991) found that the breeding success of replacement birds was lower than that of the remaining population. Usually, nonbreeders attempted to nest only when high-quality nesting habitat was made available to them (Newton 1991). Thus, persecution may hasten a decline in a Goshawk breeding population if the prey level is sufficient for the old breeding pairs but not for a similar number of young and less experienced birds. However, in the Finnish study cited earlier several breeding Goshawks apparently left the study area during the years when the prey population decreased (Lindén & Wikman 1983).

Several studies have reported that despite legal protection the Goshawk is still hunted by man in Scandinavia (Storgård & Birkholm-Clausen 1983, Nielsen 1986, Jørgensen 1987, Ryttman 1993). Nevertheless, all nesting territories in my study area were occupied by breeding pairs each spring, even in the 1950s (Selås unpubl. data) when the persecution of birds of prey was especially intense in Norway. This has also been found in other parts of Norway (Sollien 1979, Steen 1989), Sweden (Höglund 1964b, Nilsson 1981), and Finland (Haukioja & Haukioja 1970, Wikman 1977, Huhtala & Sulkava 1981).

The lack of second-year birds among breeding Goshawks in Fennoscandia (Höglund 1964b, Haukioja & Haukioja 1970, Marcström et al. 1990, Selås unpubl. data) indicates that the breeding population is saturated. In central Europe, where the number of Goshawk hunters per Goshawk pair has been much higher than in Fennoscandia, and Goshawk nests are easily found in patches of forest in agricultural landscapes, 10–35% of the breeding females have been second-year birds in

periods of or areas with intensive human persecution (Fischer 1980, Link 1986, Nielsen 1986).

Apparently, the Goshawk breeding density is difficult to regulate by hunting in the continuous forest habitats of Fennoscandia. Because of the Goshawk's high capability of dispersal (Höglund 1964b, Sollien 1978, Marcström & Kenward 1981), nesting territories from which Goshawks are removed are probably rapidly reoccupied. It seems unlikely then that the hunting of breeding Goshawks will have any significant long-term influences on the population evolution of grouse species, which are more vulnerable to Goshawk predation in winter and early spring than during late spring and summer (Angelstam 1984, Wegge et al. 1987), when territorial Goshawks are usually removed.

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Sammanfattning: **Effekt av näringstillgång på återetablering av häckningsrevir hos duvhök**

Duvhöken har varit helt fridlyst i Norge i många år. Trots detta fälls den under häckningstiden på grund av att den beskattar hönsfågelbestånden. Duvhökens återetablering av häckningsrevir efter fällning studerades i ett 650 km^2 stort område i södra Norge under fyra-års perioderna 1972–75, 1980–83, 1984–87 och 1988–91. Bestånden av skogshöns ökade mellan 1984–87 som en följd av att bestånden av rödräv minskade genom skabb. Bestånden av skogshöns höll sig kvar på en hög nivå under hela perioden 1988–91. Tätheten av häckande duvhök per 100 km^2 var 3 par mellan 1972–75 samt 1980–83, och 4 par mellan 1988–91. I var och en av dessa tidsperioder var bebodda revir regelbundet fördelade i terrängen. Såväl antal som fördelning av revir påverkades ej genom fällning av häckande hökar. Under tiden 1984–87 erstattes fem häckningsrevir, där den ena eller båda hökarna skjutits, av elva nya. Studien antyder att ett avlägsnande av häckande duvhökar under perioder med god födotillgång kan medföra att antalet häckande par ökar snabbare än vad det skulle ha gjort utan avlägsnande.

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