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NEST-SITE SELECTION BY FOUR SYMPATRIC FOREST RAPTORS IN SOUTHERN NORWAY

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ABSTRACT.—Differences between 0.1 ha nest-site plots of Honey Buzzards (*Pernis apivorus*), European Sparrowhawks (*Accipiter nisus*), Northern Goshawks (*A. gentilis*) and Common Buzzards (*Buteo buteo*) were compared to randomly sampled 0.1 ha control plots within a 400 km^2 area with 80% forest and <2% agricultural land in southern Norway. At Honey Buzzard nest sites, forests were more productive than in control plots and there was a higher proportion of spruce, older trees and a higher tree density at Northern Goshawk nest sites than in control plots. Nests of European Sparrowhawks were also in sites with higher tree density than expected. Common Buzzard nest sites were situated in steeper terrain than control plots and more often had a southern aspect. For sparrowhawks, nesting in forests with high tree density may be an adaptation to avoid goshawks and pine martens (*Martes martes*) which are their main nest predators. For the larger species, nest-site selection may be a response both to nest predation risk, microclimate, foraging habitat and food supply.

KEY WORDS: *Honey Buzzard*; *European Sparrowhawk*; *Common Buzzard*; *Northern Goshawk*; Accipiter nisus; Accipiter gentilis; Buteo buteo; Pernis apivorus; *forest*; *nest-site selection*; *Norway*.

Selección del nido de cuatro rapaces de bosque sin que no aparean en el sur de Norway.

RESUMEN.—Diferencias entre 0.1 ha parcela de sitio de nido de *Pernis apivorus, Accipter nisus, A. gentilis* y *Buteo buteo* fueron comparados con muestras alazar 0.1 ha parcelas manejadas dentro de una área de 400 km2 con 80% bosque y <2% tierra agricola en el sur de Norway. En nidos de *Pernis apivorus,* los bosques fueron mas productivo en las parcelas manejadas y había una proporción alta de *Picea,* árboles maduros y densidad alto de árboles en nidos de *A. nisus* también estaban en sitios con densidad alta de árboles mas de lo que esperábamos. Nidos de *B. buteo* estaban situados mas en terreno abrupto que en parcelas manejadas y con frecuencia tenía aspecto del sur. Para *A. nisus* , nidos en el bosque con densidad alta de árboles puede ser un adaptación para evitar *A. gentilis* y *Martes martes* que son su principal depredador de nido. Para la especie mas grande, la selección del nido puede ser reacción a riesgo de depredador al nido, microclima, hábitat de forraje y suministro de comida.

[Traducción de Raúl De La Garza, Jr.]

Breeding pairs of raptors use relatively large areas, and thus have a good opportunity to select nesting places that maximize the probability of successful breeding and lifetime reproduction (Newton 1979). Interspecific differences in nest-site selection may be due to differences in body size and flight performance of different species, but it can also be due to interspecific differences in nest predation risk, climatic conditions during breeding and feeding habits (Newton 1979, Janes 1985), or to interspecific competition for nest sites and territories (Newton 1979).

For several bird species, dense foliage close to the nest both reduces the rate of detection, and impedes the ability of predators to hunt in the vicinity of the nest (Martin 1993). On the other hand, dense foliage may decrease the possibility for breeding birds to detect and escape from predators (Götmark et al. 1995). Thus, selection of nest site may be a trade-off between concealment and opportunities to escape or attack predators, which also depend on flight ability, body size or other characteristics of the species. Selection may also be affected by a trade-off between current and future reproduction, since short-lived species with large brood sizes have more to lose when nesting attempts fail than long-lived species with smaller brood sizes.

Cover may also be an important factor since it can shield nests from wind or rain and limit excessive nocturnal radiation loss or excessive diurnal heat-gain from solar radiation (Walsberg 1985).

Protection from thermal extremes may be the most important factor in nest-site selection by medium- and large-sized raptors where nest predation is low (Newton 1979, Janes 1985). At higher latitudes, the timing of breeding in these birds should be important, since early breeders are faced with more severe climatic conditions than those species which begin nesting later in spring.

If prey are not evenly dispersed throughout the landscape, raptors should select nest sites closest to the best hunting areas in order to reduce time and energy connected with foraging. Thus, local variation in the availability of food may influence the nest-site selection (Janes 1985), and explain interspecific differences in nesting habitat.

In Fennoscandia, four raptor species hunt and nest in forest-dominated landscapes. The European Sparrowhawk (*Accipiter nisus*; mean body mass male 150 g, female 260 g) is the main predator on small birds (Sulkava 1964a, Selås 1993), while the Northern Goshawk (*A. gentilis*; mean body mass male 870 g, female 1330 g) primarily feeds upon larger bird species and mammals (Höglund 1964, Sulkava 1964b, Widén 1987, Selås 1989). The Common Buzzard (*Buteo buteo*; mean body mass male 740 g, female 1100 g) is a generalist predator that responds functionally to changes in populations of its vole (*Microtus* spp.) prey (Suomus 1952, Spidsø and Selås 1988), while the Honey Buzzard (*Pernis apivorus*; mean body mass male 750 g, female 910 g) mainly feeds on the larvae and pupae of social hymenoptera species (Holstein 1944, Hagen and Bakke 1958, Itämies and Mikkola 1972).

Several authors have described nest sites used by sparrowhawks (Tinbergen 1946, Holstein 1950, Hald-Mortensen 1974), goshawks (Holstein 1942, Dietzen 1978, Link 1986), Common Buzzards (Holstein 1956, Knüwer and Loske 1980, Solonen 1982, Jedrzejewski et al. 1988, Hubert 1993) and Honey Buzzards (Holstein 1944, Amcoff et al. 1994) in Europe. However, no one has compared nest-site selection of sympatric populations of these species in a continuous forest habitat. My aim was to study the importance of different habitat variables on nest-site selection of these species by comparing habitat variables from plots at nest sites with those from plots placed randomly in the study area.

STUDY AREA AND METHODS

The study was conducted from 1985–93 in southern Norway (58° 43'N, 8°44'E). The study area covers about 400 km^2 and is situated 50–300 m a.s.l. and 10–30 km inland from the coast, in the boreo-nemoral zone (Abrahamsen et al. 1977). The climate is suboceanic, and snow usually covers the ground from December–April. The study area is hilly and sharply undulating. It is dominated by forests (80%), with scattered lakes (10%), bogs (5%) and less than 2% agricultural land. Forests are characterized by a fine-grained mosaic of young-, medium- and old-aged coniferous, mixed and deciduous stands, with Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), oak (*Quercus* spp.), aspen (*Populus tremula*) and birch (*Betula* spp.) the dominant tree species.

Forestry based on clear cutting, replanting and thinning of the regrowth was introduced to the area in the 1950s. At the time of my study, approximately 30% of the area had been clear-cut, with most regeneration <20 yr. The area is divided into numerous small ownerships with management of forests controlled by each of the land owners. Most of the properties are managed to provide a mosaic of forest types. Thus, there is a heterogeneous environment on a small scale, but a homogeneous, fragmented environment on a large scale.

The study area was searched for nest sites each year (cf. Forsman and Solonen 1984), and habitat variables were described at one nest site in each nesting territory located. If possible, the nest site used in 1988 was selected. In territories where the 1988 nest was not found, I usually described the nest site used in 1989. Alternatively, the nest site used closest in time to 1988 or 1989 was described. The breeding density of goshawks increased during the time of the study. To get a larger number of nest sites of this species, I first selected one nest site from each of the nesting territories used since 1985. Then, I selected one nest site in each of the 11 new nesting territories established during 1986–88, even though these territories substituted five of the existing ones. Since the goshawks in the five old territories had all been illegally shot by game keepers, I regarded the data to be independent. Thus, I described a total of 48 nest site plots of the sparrowhawk, 30 of the goshawk, 50 of the Common Buzzard, and 21 of the Honey Buzzard.

Control plots were described during 1989. Aerial photographs of the study area taken in spring 1989 (scale 1: 15000) were covered by a grid with 100 numbered intersections of which two were randomly selected as control plots. Out of 122 selected points, 80 (65.6%) were located in forests >20 yr old and 25 (20.5%) were in forests <20 yr old (clear-cuts and regrowth), while 9 (7.4%) were on lakes, 4 (3.3%) on bogs, and 4 (3.3%) on agricultural land or developed areas. Measurements were made only in control plots in habitats apparently suitable for raptors (i.e., forests >20 yr old, $N = 80$).

Each of the nest site plots and the control plots covered 0.1 ha within a circle with a radius of 17.8 m. In nest site plots, the nest was in the center of the circle. The following habitat variables were used:

1) Site type, determined from the plant community (Kielland-Lund 1981, 1994). Plots dominated by *Barbilophozio-Pinetum* or *Vaccinio-Pinetum* were classified as sites with poor productivity, plots dominated by *Leucobryo-Pinetum, Eu-Piceetum myrtilletosum,* or *Populo-Quercetum* were classified as sites with intermediate productivity, and plots dominated by *Melico-Piceetum typi-*

Table 1. Test results (upper, right) and P-values (lower, left) of correlation analyses of habitat variables from randomly-sampled control plots ($N = 80$). Categorical variables were tested against each other by use of contingency table analysis (χ^2 value given) and against continuous variables by use of Mann-Whitney U-test (two categories, U-value given) or Kruskal-Wallis test (more than two categories, H-value given), while continuous variables were tested against each other by use of Spearman rank correlation (correlation coefficient given).

	SITE TYPE	FOREST TYPE	FOREST AGE	TREE DENSITY	SLOPE	ASPECT	ALTITUDE CATEGORY
Site type (3 categories)		40.60	5.78	28.51	9.70	4.97	5.52
Forest type (5 categories)	<0.01*		1.79	18.12	22.17	11.25	17.30
Forest age (continuous)	0.06	0.77		−0.26	0.01	770.5	2.79
Tree density (continuous)	<0.01*	<0.01*	0.02*		0.13	775.5	7.67
Slope (continuous)	<0.01*	<0.01*	0.91	0.25		778.0	4.00
Aspect (2 categories)	0.08	0.02*	0.81	0.85	0.87		1.30
Altitude category (3 categories)	0.24	0.03*	0.25	0.02*	0.14	0.52	

* Statistically significant.

cum, Melico-Quercetum, Alno incanae-Prunetum padi or *Ulmo glabrae-Tilietum cordatae* were classified as sites with the highest productivity.

2) Forest type, defined according to % pine and spruce trees with diameters >7 cm at breast height (DBH, 1.3 m above ground). Pine forest was >50% pine and spruce with pine >67%. Mixed coniferous forest was >50% pine and spruce with pine and spruce ≤67%. Spruce forest was >50% pine and spruce with spruce >67%. Mixed forest was 25–50% pine and spruce. Deciduous forest was <25% pine and spruce.
3) Forest age, defined as the mean age of four trees judged to represent the age of all trees with DBH >7 cm. Ages were measured using an increment borer at breast height.
4) Number of trees, regardless of species with DBH >7 cm.
5) Slope, measured from 0–100°.
6) Aspect, defined as one of two categories: north (1–100°, 301–400°) or south (101–300°). Nest-site plots and control plots with slopes <5° were omitted.
7) Altitude, defined as three altitude possible categories in relation to the altitude variation within a radius of 1 km from the plot. Plots were assigned to the lower altitude zone if situated in the lower third of the altitude difference between the lowest and highest point within this area. Middle and upper altitude zones were assigned correspondingly.

Table 2. Results (P-values) from Likelihood-Ratio tests in a logistic regression model with nest-site plots and randomly-sampled control plots ($N = 80$) as responses, and all habitat variables as explanatory variables. R^2 is the proportion of variation that is explained by the logistic regression model.

HABITAT VARIABLES	SPARROWHAWK ($N = 48$)	GOSHAWK ($N = 30$)	COMMON BUZZARD ($N = 50$)	HONEY BUZZARD ($N = 21$)
Site type	0.58	0.80	0.54	0.004*
Forest type	0.38	0.023*	0.23	0.35
Forest age	0.94	0.027*	0.39	0.50
Tree density	<0.001*	0.013*	0.15	0.10
Slope	0.82	0.98	<0.001*	0.31
Aspect	0.92	0.06	0.037*	0.05
Altitude category	0.53	0.47	0.20	0.59
R^2	0.90	0.27	0.34	0.47

* Statistically significant.

When considering the randomly-sampled control plots, several of the habitat variables were highly correlated (Table 1). To control for the effect of these correlations when comparing nest site plots and control plots, I used likelihood-ratio tests (SAS 1994) in a logistic regression model, with nest-site plots and control plots as responses and all habitat variables as explanatory variables (cf. Manly et al. 1993).

RESULTS

Site Type and Forest Type. Of sparrowhawk nest-site plots, none were on sites with poor productivity, 66.7% were on intermediate sites and 33.3% in the highest productivity sites. Corresponding values for goshawk nest-site plots were 16.7%, 73.3% and 10.0%; for Common Buzzard 16.0%, 60.0% and 24.0%, and for Honey Buzzard 0.0%, 57.1% and 42.9% compared to 42.5%, 47.5% and 10% for control plots. When controlling for effects of correlations between all habitat variables, there was a significant difference between Honey Buzzard nest-site plots and control plots, while the other species did not differ from the control plots (Likelihood-ratio tests, Table 2).

The distribution of goshawk nest-site plots in different forest types differed significantly from that

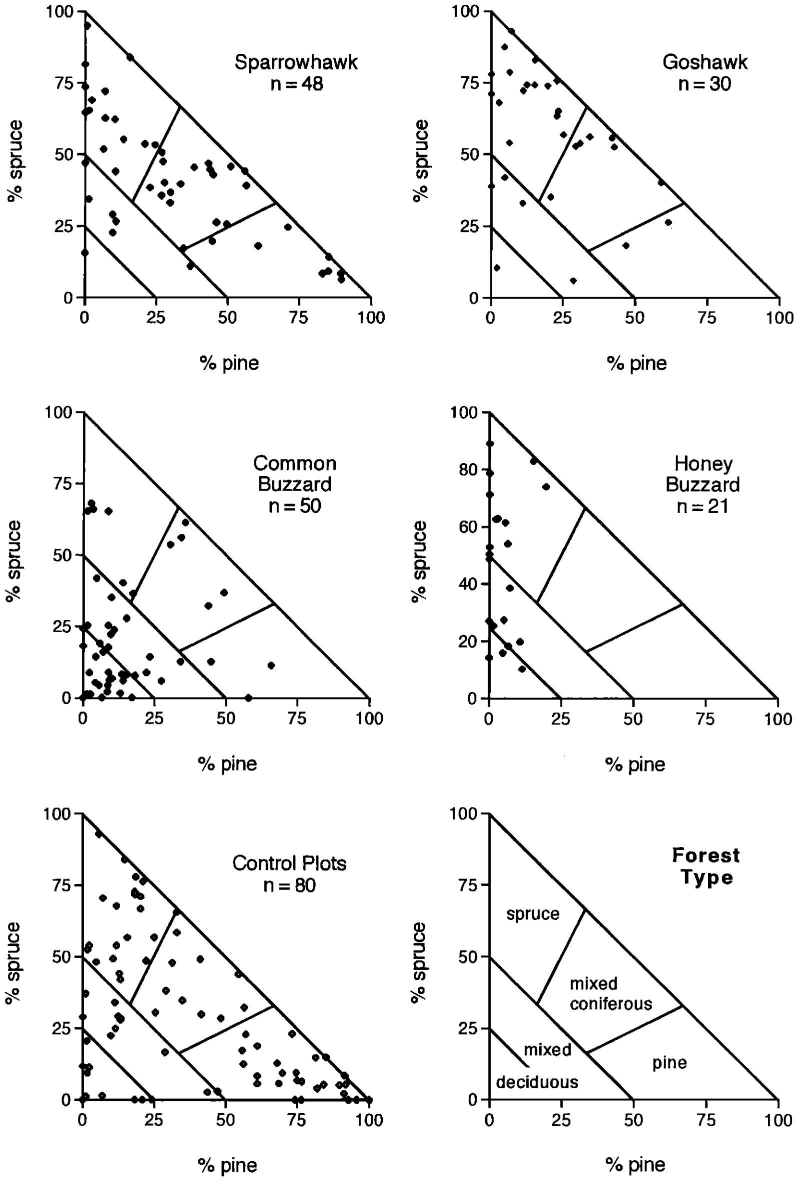

Figure 1. Distribution of nest-site plots of European Sparrowhawks, Northern Goshawks, Common Buzzards and Honey Buzzards, and randomly-selected control plots on different forest types. Forest types were defined according to the frequency of pine and spruce among all trees >7 cm in breast height (1.3 m above ground). The size of each plot is 0.1 ha.

of control plots, with a higher proportion of nest sites in spruce forests (Table 2, Fig. 1). Sparrowhawk, Common Buzzard and Honey Buzzard nest-site plots did not differ from control plots with respect to forest type when effects of correlations between habitat variables were adjusted for (Likelihood-ratio tests, Table 2, Fig. 1).

Forest Age and Tree Density. The mean forest age was 36.8 ± 18.5 (SD) yr in nest-site plots of sparrowhawks, 99.3 ± 19.1 yr in those of goshawks,

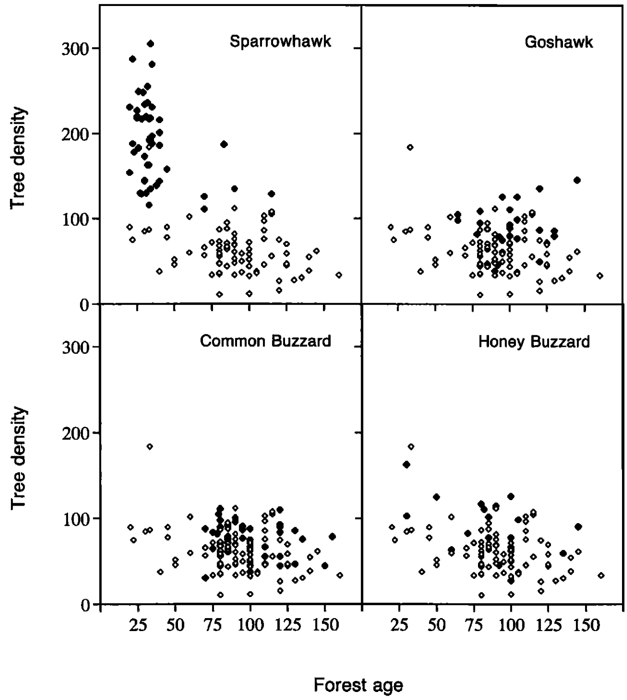

Figure 2. Forest age and number of trees (>7 cm in breast height) in nest-site plots of European Sparrowhawks, Northern Goshawks, Common Buzzards and Honey Buzzards (solid squares), and in randomly-selected control plots (open squares). The size of each plot is 0.1 ha.

98.5 ± 20.4 yr in those of Common Buzzards and 86.7 ± 28.3 yr in those of Honey Buzzards. When using likelihood-ratio tests, only nest sites of goshawks differed significantly from control plots, where the mean forest age was 90.7 ± 29.0 yr (Table 2, Fig. 2).

The mean number of trees was 190.4 ± 47.7 in nest-site plots of sparrowhawks, 84.9 ± 27.7 in those of goshawks, 73.3 ± 19.9 in those of Common Buzzards and 86.4 ± 33.4 in those of Honey Buzzards. The number of trees in nest-site plots of sparrowhawks and goshawks was significantly higher than in control plots, where the mean number of trees was 62.3 ± 26.3 (Likelihood-ratio tests, Table 2, Fig. 2).

Topographical Variables. The mean slope was 8.6 ± 5.6° in nest- site plots of sparrowhawks, 15.1 ± 9.1° in those of goshawks, 28.6 ± 13.3° in those of Common Buzzards, 16.3 ± 7.2° in those of Honey Buzzard and 15.0 ± 10.5° in control plots. Only nest sites of Common Buzzards differed significantly from control plots (Likelihood-ratio tests, Table 2, Fig. 3).

Sparrowhawk nest sites were on south-facing slopes 34.1% of the time while 63.3%, 76.0%, 33.3% and 53.8% of goshawk, Common Buzzard, Honey Buzzard, and control plots were on south-facing slopes, respectively. Only nest sites of Common Buzzards were on south-facing significantly more than control plots (Likelihood-ratio tests, Table 2, Fig. 3).

None of the nest sites of the four raptor species differed significantly from control plots in terms of their altitude (Likelihood-ratio tests, Table 2, Fig. 4).

DISCUSSION

Site Type and Forest Type. Only the Honey Buzzard showed a significant preference for nesting in sites with the highest productivity. This finding agreed with that of Amcoff et al. (1994). Unlike other raptor species, Honey Buzzard males do not provision females with food during the egg-laying and incubation period (Holstein 1944), possibly because their prey are too small to be profitably transported to the nest. Because of small size of its prey, short

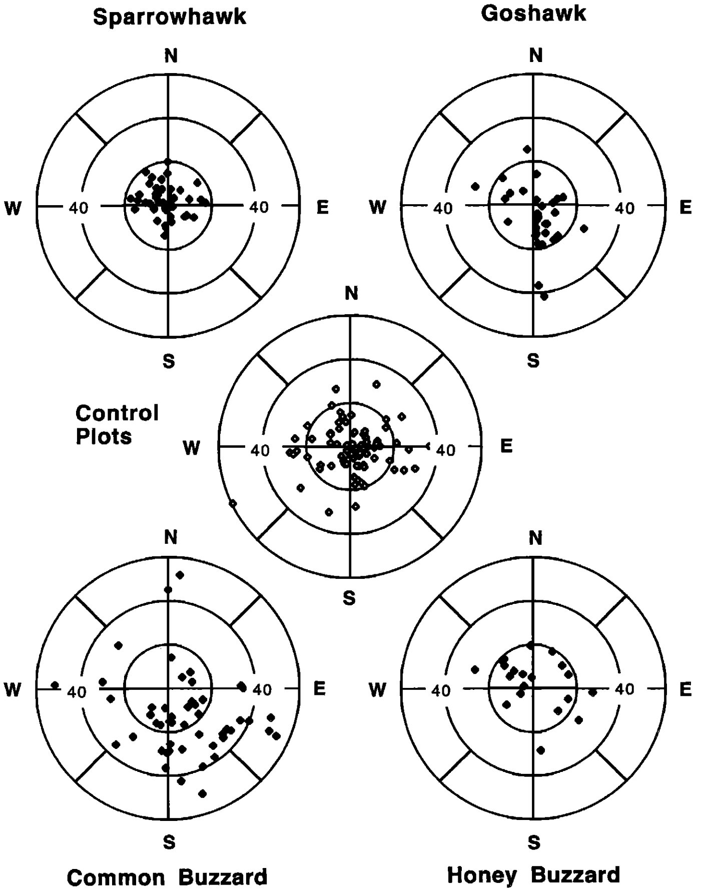

Figure 3. Slope (0–100°) and aspect (NE, SE, SW, NW) of nest-site plots of European Sparrowhawks, Northern Goshawks, Common Buzzards and Honey Buzzards. The distance from the origin reflects the slope while the direction reflects the aspect of the plot. The size of each plot is 0.1 ha.

distances between nesting and foraging areas during incubation may be especially valuable for this species. Highly productive forests may be important for Honey Buzzards because they support high densities of juvenile passerines (Tiainen 1981, Helle 1985, Stokland 1994) which appear to be important prey in early stages of the breeding season (Amcoff et al. 1994). These forests also support high biomass of invertebrates (Birkemoe 1993, Stokland 1994) on which Honey Buzzards may also rely.

Preference for forest type was significant only for the goshawk, which selected spruce forest for nesting. This preference may be related to the larger number of important winter and spring prey species such as squirrels (*Sciurus vulgaris*, Andrén and Delin 1994), Hazel Grouse (*Bonasa bonasia*, Swenson and Angelstam 1993), and Capercaillie (*Tetrao urogallus*, Swenson and Angelstam 1993) in spruce forest. However, preference for spruce may simply be related to the fact that it gives the best cover and thus the best protection against the main predator of the goshawk, the Eagle Owl (*Bubo bubo*, Uttendörfer 1952, Mikkola 1983).

Forest Age and Tree Density. Goshawk nest sites were situated in older forests than control plots. Old forest is an important hunting habitat for the goshawk (Widén 1989) and it provides large trees for nest building (Dietzen 1978, Anonymous 1989, Siders and Kennedy 1996, Squires and Ruggiero 1996). Goshawk nests were also found in forests with a higher tree density than control plots. Goshawks may reduce the risk of predation by nesting in dense forests, since Eagle Owls prefer to hunt in open or semi-open landscapes (Mikkola 1983).

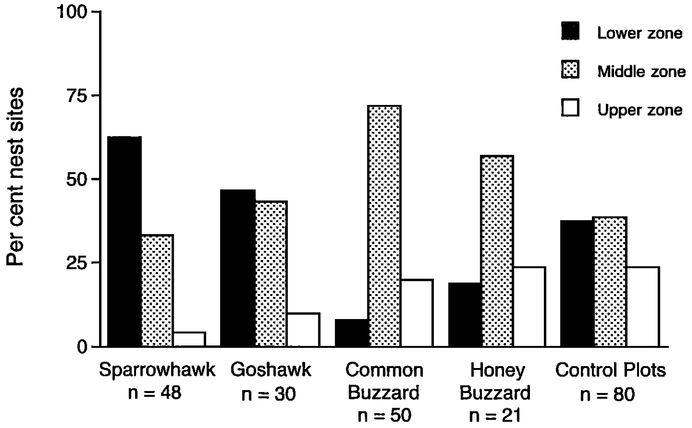

Figure 4. The distribution of nest-site plots of European Sparrowhawks, Northern Goshawks, Common Buzzards and Honey Buzzards, and of randomly-selected control plots by altitude categories. A plot was assigned to the lower altitude zone if situated in the lower third of the altitude difference between the lowest and highest point within 1 km from the plot, to the middle zone if situated in the middle third of this altitude difference, and to the upper zone if situated in the higher third.

For the smallest species investigated, the sparrowhawk, the only variable that discriminated between nest-site plots and control plots was tree density. I obtained similar results after a thinning experiment, where the reuse of nest stands in thinned young forests was lower than of nest stands in young forests not thinned (Selås 1996). Placement of nests in dense forest could hardly be profitable with respect to food of sparrowhawks, because the density of passerines is usually low here (Haapanen 1965, Ødegaard 1982, Glowacinski and Weiner 1983, Helle 1985). Probably, predation is the most important aspect in the nest-site selection of sparrowhawks (Selås 1996), since its main predators, goshawks and pine martens (*Martes martes*), both prefer mature forest rather than young, dense forest when hunting (Pulliainen 1984, Widén 1989, Storch et al. 1990). Actually, dense forest seems to be less important as nesting habitat for the sparrowhawk when the goshawk is absent (Bomholt 1983, Newton 1986, Tømmeraas 1994). Pine martens will probably find raptor nests easy, because of the smell from pellets and prey remains. Since the pine marten is also known to remember different sites of food resources (Sonerud 1985), it is likely to be familiar with most of the old raptor nests within its home range. This may be one reason for why sparrowhawks rarely use nests for two successive years, unlike goshawks and Common Buzzards which are probably less vulnerable to pine marten predation due to their large size.

Goshawks and pine martens are also important predators of Honey Buzzard nestlings (Kostrzewa 1991). The Honey Buzzard seems to prefer spruce, which gives best cover, as nest trees (Amcoff et al. 1994). In contrast to the other species studied, Honey Buzzards are usually silent when disturbed by humans at the nest site (Holstein 1944, Hagen 1952, Kostrzewa 1985). Rather than selecting nesting habitats to avoid nest predation, Honey Buzzards appear to behave as cryptically as possible at the nest site, possibly because they are less efficient than other raptors in defending their nests against predators. In addition, low annual mortality and low clutch size of the Honey Buzzard (Holstein 1944, Kostrzewa 1985, Tjernberg and Ryttman 1994) may make nest defense less profitable than for Common Buzzards and goshawks.

Topographical Variables. The only species which showed any preference for slope was the Common Buzzard, which usually nested in steep terrain. Similar results have been found for the Red-tailed Hawk (*Buteo jamaicensis,* Titus and Mosher 1981, Speiser and Bosakowski 1988). Flight energetics may be more favorable on steeper slopes for larger soaring raptors like eagles and large Buteos (Speiser and Bosakowski 1988). It may however also be important that these broad-winged species can best escape, or attack, predators in this habitat. Even though the Common Buzzard is able to rob prey from the goshawk (Fischer 1980, Jörgensen 1983), its breeding success has been found to be negatively correlated with the distance to goshawk nests (Kostrzewa 1991). One reason for the difference in nest-site selection between the Common Buzzard and goshawk may be that the goshawk, which is better adapted for flight and foraging in dense forest, is more dangerous to Common Buzzard in dense forest.

Common Buzzards also preferred nest sites with southern aspects. There was also a tendency for a higher percentage of nest-site plots of goshawks to have southern aspects than expected, while those of Honey Buzzards tended to have northern aspects. Common Buzzards and goshawks start their breeding nearly one month earlier than sparrowhawks and more than one month earlier than Honey Buzzards (Forsman and Solonen 1984), at a time of the year when the temperatures may still be far below freezing in southern Norway. Nests of both species were most often found at sites with a southeastern aspect, which are the first heated by the morning sun when nest building occurs (Holstein 1942, 1956). Also in Alaska, goshawks have been found to favor southern slopes (McGowan 1975), while in more temperate areas, southern exposures are avoided (Dietzen 1978, Reynolds et al. 1982, Moore and Henny 1983, Link 1986, Speiser and Bosakowski 1987). A similar pattern has been observed for nest sites of Golden Eagles (*Aquila chrysaetos,* Mosher and White 1976, Pfaff 1993).

In Central Europe, Common Buzzards place their nest near forest edges (Knüwer and Loske 1980, Spitzer 1980, Hubert 1993), probably because they hunt from perches in open areas or from forest edges (Widén 1994). In my study area, open areas were usually covered by snow when Common Buzzards arrived to breed, making the field vole (*Microtus agrestis*), which is the most important prey species in this habitat (Hansson 1978, Spidsø and Selås 1988), nearly unavailable (Hansson 1982, Sonerud 1986). Early snow-free areas available for vole hunting in the spring are found on southfacing slopes and in steep terrain, where Common Buzzard nests are usually found.

Goshawks, Common Buzzards and Honey Buzzards rarely used nest sites with southwestern aspect, possibly because too much sun may be harmful to newly-hatched nestlings (c.f. Holstein 1942, Hald-Mortensen 1974, Reynolds et al. 1982, Link 1986). Unless there is good shelter, as in the dense young forests used by sparrowhawks, nest sites with a southwestern aspect are probably unprofitable regardless of when egg-laying begins.

The observed interspecific differences in nest-site selection between the raptor species investigated may be explained by interspecific differences in body size and flight performance, nest-predation risk, time of breeding and feeding habits. The risk of predation probably affects nest-site selection or breeding habits of all these species, but mostly sparrowhawks and Honey Buzzards which were most vulnerable to nest predation. Common Buzzards, goshawks, and Honey Buzzards also showed nest-site preferences which could be explained as an adaptation to microclimate. For these three species, nest-site selection could also be connected to the availability of food in the early stage of the breeding season. These species may have a broader habitat choice and it is possible that factors other than the habitat variables I selected for study may have been of importance. This may have been especially true for the goshawk, which builds larger nests than the other species and may be influenced by characters directly connected to the nest tree.

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