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Spacing of birds of prey in southern Finland

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Birds of prey were studied in central Uusimaa, southern Finland, during 1972–90. Eight diurnal species and six owl species bred regularly in the study area (of up to 4800 km^2). As their food supply was relatively stable, most long-term territorial (site-tenacious) species demonstrated even spacing of nesting places, while irregular patterns characterized the widely fluctuating short-term territorial (nomadic) vole specialists. Dispersion of traditional nesting places had a major effect on spacing of occupied locations. Irregularities in spacing of nesting places were largely due to the uneven distribution of suitable habitats. Avoidance of predation might have affected the spatial structure of the bird assemblage studied, while interspecific competitive effects were less evident.

1. Introduction

Food and nest sites are generally the main factors affecting habitat selection in birds (see, e.g., Hildén 1965, Cody 1985). Home ranges of wide-ranging species such as birds of prey often include separate habitats for foraging and nesting (e.g., Newton 1979, Janes 1985). Territories are so situated that both main aspects of habitat requirements are at least potentially fulfilled. In many territorial birds of prey the dispersion of territories in suitable habitat seems to be more or less regular due to intraspecific territoriality (e.g., Newton 1979, 1986, Nilsson et al. 1982). The uneven supply of resources is evidently the major reason for deviations from a regular pattern, but interspecific interactions might also have some effects. In birds of prey, many species occupy traditional, long-term nesting territories, while others occupy annual, short-term territories (e.g., Cramp & Simmons 1980, Cramp 1985). The long-term territorial species commonly occupy the same general areas (traditional nesting territories) during several successive breeding seasons, though nest sites or other activity centres may vary from year to year within the area. In short-term territorial species, the areas occupied (annual nesting territories) usually vary considerably between years.

In this paper, I examine the intra- and interspecific distribution patterns of nesting territories and nesting places of birds of prey on the basis of data gathered over 19 years in Uusimaa, southern Finland, in order to elucidate the factors affecting the spacing of birds. Nesting territories refer here to locations occupied by birds in a given breeding season, whereas nesting places refer to all the sites known to have been occupied in the study period (Newton 1991, cf. Newton et al. 1977, Newton 1986). The null hypothesis, designed to detect regularity of spacing, is that positions of territories are independently and randomly distributed within the study area (Brown & Rothery 1978). To explore how the temporal

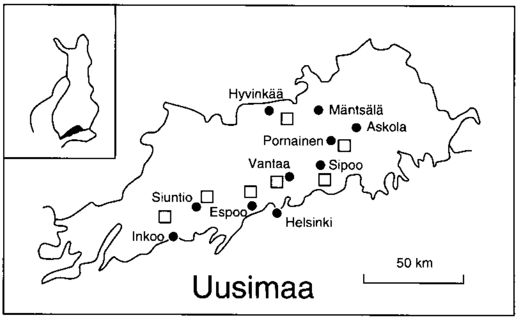

Fig. 1. The locations of the study areas in Uusimaa, southern Finland (cf. the names of localities in Tables). The areas studied most intensively are indicated by squares.

aspect of the territorial system (annual vs. traditional) explains the dispersion of territories and how the spatial structure of local assemblages of birds of prey is affected by various factors, I tested the following predictions:

1) The regular spacing of traditional nesting places over long periods suggests that long-term distribution patterns are maintained by intraspecific territoriality. This suggestion is reinforced if the regularity of spacing of traditional nesting places is as high or higher than that of the annually occupied territories of the population.
2) Shifts from a regular territorial pattern are due to spatial and/or temporal variations in the resources of the local environment (uneven supply of suitable habitats, nest sites, or food), or to interspecific interactions (competition, predation/avoidance of predation). If interspecific interactions are important, it is expected that the interspecific distribution patterns in a given area are at least as regular as the intraspecific ones.

2. Material and methods

Spacing of birds of prey was mapped in Uusimaa, southern Finland (60°N, 25°E) in 1972–90, in five main study areas: Sipoo (260 km^2), Askola (120 km^2), Hyvinkää (230 km^2), Espoo (200 km^2) and Vantaa (250 km^2) (see Fig. 1). In addition, other data from various sources were included. The data on some sparse species were gathered over larger regions which included the smaller main study areas. Eight diurnal species and six owl species bred regularly in the study area. Long-term territorial species, commonly occupying traditional nesting territories, included Honey Buzzard *Pernis apivorus*, Marsh Harrier *Circus aeruginosus*, Goshawk *Accipiter gentilis*, Sparrowhawk *A. nisus*, Common Buzzard *Buteo buteo*, Osprey *Pandion haliaetus*, Hobby *Falco subbuteo*, Eagle Owl *Bubo bubo*, Pygmy Owl *Glaucidium passerinum*, Tawny Owl *Strix aluco* and Ural Owl *S. uralensis*, while Kestrel *Falco tinnunculus*, Long-eared Owl *Asio otus* and Tengmalm's Owl *Aegolius funereus* occupied mainly short-term, annual territories. Most species occurred in suitable habitats throughout the area, but the distribution of the Eagle Owl was somewhat western and that of the Ural Owl northeastern (Solonen 1984, Solonen et al. 1990).

In the field work, the primary aim was to establish the numbers of breeding pairs by finding as many active nests as possible, and to locate other occupied territories. When no nest was found, other observations indicating breeding or occupancy of a territory were accepted (see Forsman & Solonen 1984). Unoccupied nesting places (recognized by the presence of old nests) were recorded as well. For different species and at different stages of the breeding cycle, different methods were used to locate territories and nests (see Lammin-Soila & Uusivuori 1975, Fuller & Mosher 1981, Forsman & Solonen 1984). None the less, species-differences in detectability still affected the data (see also Forsman & Solonen 1984, Saurola 1985). Intensity of field work also varied between areas and years; for instance, not all nesting places were checked annually. In most of the study areas, all species of birds of prey were included, but not all were studied equally well. So, only those with the best coverage were used in the analyses (Table 1). Depending on suitability, I used different data sets for different aspects of the study (see below).

Besides the annual censuses, which attempted to locate all nesting places, I also applied an additive survey method (see Forsman & Solonen 1984, and below). If there were gaps obviously due to insufficient field work in long-term territorial species, the pattern of territories revealed in a single year was supplemented with data from later years to fill in the gaps. To increase the geographical coverage, data from adjacent areas surveyed in different years were pooled. In this way, it was possible to reconstruct the general spatial structure of several populations in fairly large areas, though the quality of the data used varied between species and areas (Table 1). Some heterogeneity in the accuracy of the data is almost inevitable in attempts to assess the distribution patterns of several rare species simultaneously.

As a measure of spacing behaviour and territory size, I used the nearest neighbour distances of nests or other activity centres, e. g., locations of hooting owls (accuracy of the measurements 0.1 km). The regularity of spatial patterns of territories and nesting places was studied with the aid of the following indices based on the nearest neighbour distances (d):

1) z (standard normal deviate) = the difference between the mean of d:s observed and the mean of random d:s per the standard error of the random d:s (Ripley 1981, Upton &

Table 1. The data used (for localities, see Fig. 1).

Species	Locality	Year(s)	N of nesting places Total	Nest found	Source
Pernis apivorus	Sipoo	1974–85	17	7	1
Pernis apivorus	Sipoo	1989	10	4	1
Circus aeruginosus	Uusimaa	1974–80	18	18	1, 2
Accipiter gentilis	Inkoo	1975	25	25	3
Accipiter gentilis	Sipoo	1974	16	16	4
Accipiter gentilis	Sipoo	1974–85	23	18	1, 4
Accipiter gentilis	Hyvinkää	1977	17	14	1
Accipiter gentilis	Hyvinkää-Askola	1974–88	34	26	1
Accipiter gentilis	Espoo	1974–85	20	16	1
Accipiter gentilis	Espoo-Vantaa	1988	12	12	1
Accipiter nisus	Sipoo	1974	10	10	4
Accipiter nisus	Sipoo	1974–85	35	27	1, 4
Accipiter nisus	Sipoo	1988	10	7	1
Accipiter nisus	Espoo	1974–85	21	12	1
Accipiter nisus	Askola	1974–85	11	9	1
Buteo buteo	Sipoo	1974–85	24	15	1
Buteo buteo	Askola	1974–85	21	10	1
Pandion haliaetus	Uusimaa	1974–85	50	50	5
Falco tinnunculus	Sipoo-Pornainen	1974–77	10	10	6
Falco subbuteo	Central Uusimaa	1974–85	11	2	1
Bubo bubo	Central Uusimaa	1974–85	40	20	1
Bubo bubo	Central Uusimaa	1989	48	16	7
Glaucidium passerinum	Central Uusimaa	1974–85	12	2	1
Strix aluco	Sipoo-Mäntsälä	1972–74	146	*	8
Strix aluco	Sipoo-Pornainen	1986–90	19	15	9
Strix aluco	Espoo-Vantaa	1974–85	32	23	1
Strix aluco	Siuntio	1985	33	28	10
Strix uralensis	Central Uusimaa	1974–85	40	26	1
Strix uralensis	Central Uusimaa	1989	57	35	7
Asio otus	Central Uusimaa	1974–85	22	**	1
Aegolius funereus	Sipoo-Pornainen	1972–74	38	*	8
Aegolius funereus	Sipoo-Pornainen	1986–90	40	27	9

Sources: 1. This study, 2. Ekstam 1981, 3. Lindén & Wikman 1975, 4. A. Leinonen, unpubl., 5. Mus. Zool., Helsinki, 6. S. Kuusela, unpubl., 7. Solonen et al. 1990, 8. R. Lammin-Soila & P. Uusivuori, unpubl., 9. T. Solonen & K. af Ursin, unpubl., 10. Ahola & Karstinen 1985. Notes: * Mainly hooting males; ** Mainly fledged broods.

Fingleton 1985). z = 0 indicates a random distribution, while z > 0 suggests an even distribution and z < 0 a clumped distribution. Nearest neighbour tests were done using an edge correction, by the method of Upton & Fingleton (1985).

2) R = the square root of population density multiplied by two means of d (Clark & Evans 1954; see also Ripley 1981, Upton & Fingleton 1985). R-value one indicates randomness, increasing values above one indicate an increasing degree of regularity, and decreasing values below one indicate progressively clumped distributions.

3) G = the geometric mean of d_i^2 per arithmetic mean of d_i^2 (Brown 1975, Brown & Rothery 1978). G-values from zero to about 0.65 indicate randomness and above that, up to one, an increasing degree of regularity (e.g., Newton et al. 1977, Nilsson et al. 1982; for suitability of this index for testing local regularity and for approximation of the critical point, see Brown & Rothery 1978, Ripley 1987).

In homogeneous environments, shifts from a regular pattern might have been due to interactions between species. The most probable interspecific interactions in the species studied are shown in Table 2. Interspecific distribution patterns more regular than the respective intraspecific ones alone were thought to support the predictions of interactions.

3. Results

3.1. Annual occupancy of nesting places

Distribution patterns of nesting territories occupied in any one year were studied in habitats that were more or less "homogeneous" with respect to the species considered. In general this means that at least the distribution (or mixture) of forests and fields was relatively constant throughout the study area (see below). When all (or the largest number of) known nesting places were simultaneously occupied, the spacing of territories was more or less even (Table 3, Figs. 2–4). However, in small samples of less than ten territories after edge correction the patterns often were not quite significant (P < 0.10). In general, a larger proportion of nesting places seemed to be unoccupied and the spacing of occupied territories was more irregular than that of all known nesting places of a population (see below).

3.2. Long-term and general distribution patterns

Long-term and general distribution patterns of birds of prey were studied on the basis of the combined data of all the known nesting places of the species and areas considered. Spacing of nesting places in most of the long-term territorial

Table 2. The most probable interactions between the species studied (based on general handbook data and own observations): A = avoidance of predation, C = competition (f = food, n = nest sites), P = predation (left symbols in combinations of A and P refer to the species mentioned at left, symbols of the especially vulnerable prey species are in italics).

Species	Pa	Ag	An	Bt	Ph	Ft	Fs	Bb	Gp	Sa	Su	Ao	Af
Pernis apivorus	C	Cn		Cn				*AP*			Cn		
Accipiter gentilis		C	*PA*	Cn		PA		AP	PA	PA	Cn	PA	PA
Accipiter nisus			C				Cf	AP	Cf	AP	AP		Cf
Buteo buteo				C		Cf		*AP*	Cf	Cf	C	Cf	Cf
Pandion haliaetus					C			*AP*					
Falco tinnunculus						C		*AP*		CP	Cf	C	C
Falco subbuteo							C	AP				Cn	
Bubo bubo								C	PA	*PA*	PA	*PA*	PA
Glaucidium passerinum									C	Cf	CP	Cf	Cf
Strix aluco										C	C	Cf	PC
Strix uralensis											C	Cf	PC
Asio otus												C	Cf
Aegolius funereus													C

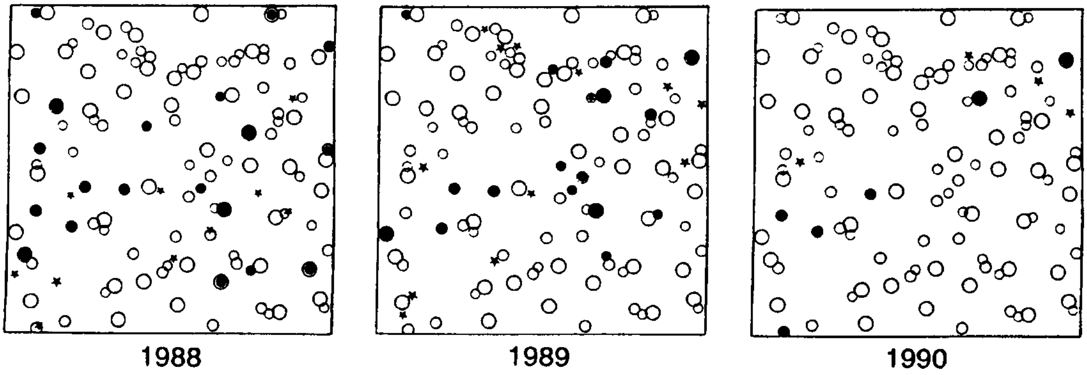

Fig. 2. Spacing of occupied nests (filled dots) and other territories (stars) of hole-nesting owls in an area of 100 km² saturated with nest boxes (open dots that also indicate their three size classes) in 1988–90 (T. Solonen & K. af Ursin, unpubl.). Only the largest holes (largest symbols) were available for *Strix uralensis* while nearly all the boxes were suitable for *Aegolius funereus*. *Strix aluco* used boxes of the two largest size classes (cf. Table 6). The southwestern half of the area is a relatively homogeneous mixture of medium-sized forests and fields, the northeastern one is a larger forest area split by minor fields.

species was even, while irregular patterns characterized the short-term territorial species (Tables 4 and 5). A significant correlation between the statistics (R, G) used to measure distribution patterns ($r_S = 0.71$, $n = 20$, $P < 0.01$) showed that the indices generally gave comparable results though some discrepancies occurred in single cases (cf. also Tables 4 and 5). A nonsignificant or negative correlation was found between the mean nearest neighbour distances of the species and the spatial statistics (i. e., the regularity of spacing) (R: $r_S = 0.10$, $P > 0.10$; G: $r_S = -0.46$, $P < 0.05$), but the degree of regularity in the spacing of nesting places tended to increase with density (R: $r_S = 0.34$, $P > 0.10$; but G: $r_S = 0.76$, $P < 0.001$). The same probably occurred also among populations of the same species, but there were too few data to test the trend statistically. A similar trend was not convincingly indicated on the basis of annual samples either, due to their small size (Table 3). In similar areas, the regularity of the spacing (z) of all known nesting places

Table 3. Annual distribution patterns of some intensively studied populations of birds of prey in southern Finland. Nnd = mean nearest neighbour distance, z = standard normal deviate with edge correction; positive values suggest regular distribution, P = significance of z (for further details, see Methods and Upton & Fingleton 1985).

Species	Locality	Year	Area (km²)	Pairs	Pairs/ 100 km²	Nnd (km)	z	P <
Pernis apivorus	Sipoo	1989	60	7	11.7	2.5	1.84	0.10
Accipiter gentilis	Sipoo	1974	65	6	9.2	2.9	1.70	0.10
Accipiter gentilis	Inkoo	1975	500	25	5.0	3.3	2.87	0.01
Accipiter gentilis	Hyvinkää	1977	122	8	6.6	3.3	1.74	0.10
Accipiter gentilis	Espoo	1988	277	11	4.0	4.8	3.58	0.001
Accipiter nisus	Sipoo	1974	61	10	16.4	2.2	2.79	0.01
Accipiter nisus	Vantaa	1988	35	9	25.7	1.5	1.50	ns
Bubo bubo	Uusimaa	1989	400	13	3.3	4.4	2.42	0.05
Strix aluco	Siuntio	1985	250	33	13.2	2.0	3.41	0.001
Strix aluco	Pornainen	1988	21	9	42.1	1.3	2.18	0.05
Strix uralensis	Uusimaa	1989	300	15	5.0	3.3	2.03	0.05
Aegolius funereus	Pornainen	1988	70	13	18.6	2.0	3.08	0.01

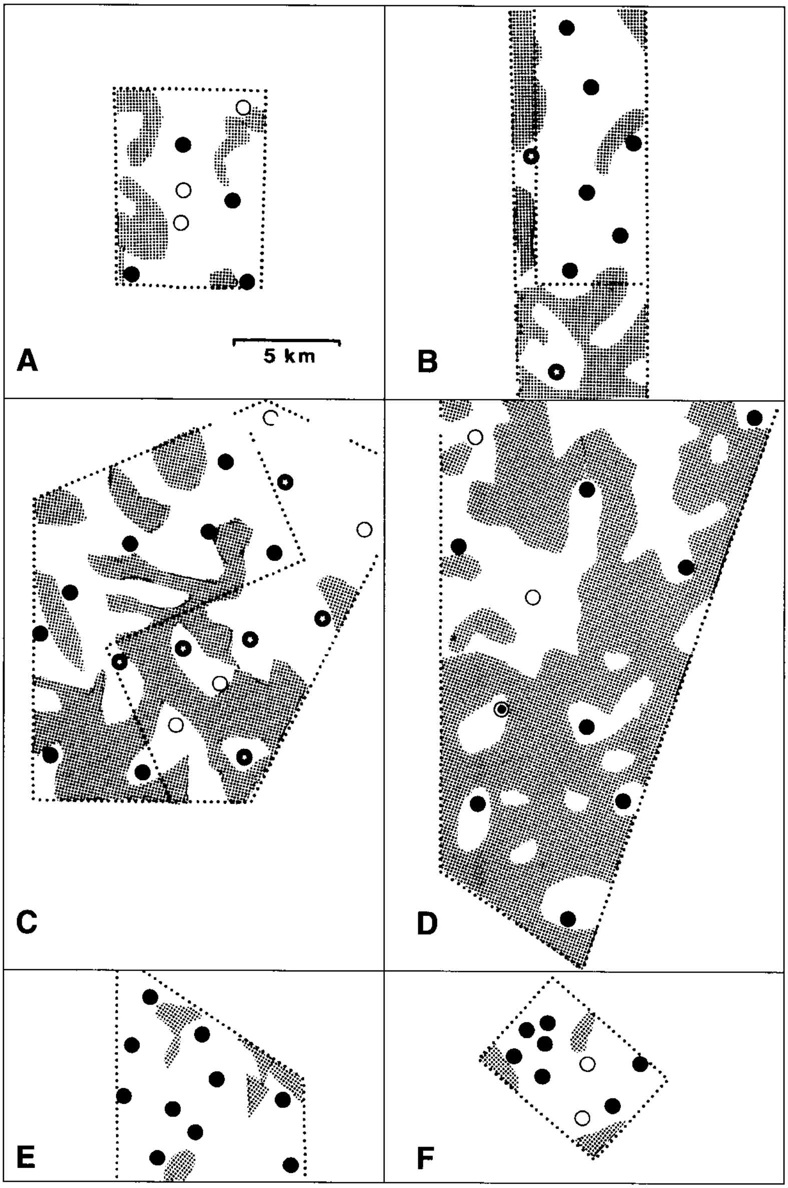

Fig. 3. Distribution patterns of occupied nesting places of some birds of prey in some intensively studied areas (marked with dotted line). Nests found are marked with filled dots, other territories with open dots. Nests found in later years when the study area was widened are marked with dots filled with a star. A. *Pernis apivorus*, Sipoo 1989. B. *Accipiter gentilis*, Sipoo 1974. C. *Accipiter gentilis*, Hyvinkää 1977 (and thereafter). D. *Accipiter gentilis*, Espoo-Vantaa 1988. E. *Accipiter nisus*, Sipoo 1974. F. *Accipiter nisus*, Sipoo 1988. Shaded areas indicate unsuitable habitats.

was in general similar or higher than that of simultaneously occupied territories of the species (Tables 4 and 3, respectively) supporting the idea that intraspecific territoriality had a dominant role in the spacing of both their annual territories and traditional nesting locations.

The density estimates for different species varied from <1–42 pairs/100 km^2 (Tables 3–5). The range of the mean intraspecific nearest neighbour distances of nesting places was from about 1.5 km (Sparrowhawk and Tawny Owl) to about 14 km (Marsh Harrier). In long-term territorial species, the results based on temporally or spatially combined samples (i.e., long-term and general distribution patterns, respectively; see Methods) in general corresponded reasonably well with those of scantier annual samples (cf. Tables 3 and 4). Densities were, however, highest and nearest neighbour distances shortest in smaller areas of the most uniform habitat for the species considered. Thus local densities might be much higher than the general ones (e.g., Sparrowhawk and Tawny Owl in this study).

3.3. Effects of variations in the resource environment

The nesting place requirements of birds of prey vary from species to species from a single nest site (e. g., hole or tree) to patches of some hectares of certain types of habitat that provides at

Table 4. Spacing of nesting places in some populations of birds of prey in southern Finland: long-term and general distribution patterns as indicated by standard normal deviate with edge correction (z) (based on combined data, see Methods, cf. Table 3).

Species	Locality	Years	Area (km^2)	n	Density/ 100 km^2	Nnd (km)	z	P <
Pernis apivorus	Sipoo	1974–85	260	17	6.5	2.9	2.28	0.05
Accipiter gentilis	Sipoo	1974–85	260	21	8.1	2.5	2.25	0.05
Accipiter gentilis	Hyvinkää	1974–85	560	31	5.5	3.4	4.31	0.001
Accipiter nisus	Sipoo	1974–85	260	27	10.4	2.1	2.14	0.05
Buteo buteo	Sipoo	1974–85	260	21	8.1	2.7	3.05	0.01
Bubo bubo	Uusimaa	1974–85	4800	40	0.8	5.9	0.03	ns
Strix aluco	Uusimaa	1972–74	1500	146	9.7	1.8	1.78	ns

Table 5. Spacing of birds of prey nesting places in southern Finland: general distribution patterns as indicated by R- and G-indices (spatially combined data; see Table 1). R-value one indicates randomness, increasing values above one indicate an increasing degree of regularity, and decreasing values below one indicate increasingly clumped distributions. G-values from zero to about 0.65 indicate randomness, and above that, up to one, an increasing degree of regularity (for further details, see Methods).

Species	Locality	n	Density/ 100 km^2	Nnd ± SD (km)	R	G
Pernis apivorus	Sipoo	17	10	2.7 ± 0.5	1.7	0.94
Circus aeruginosus	Uusimaa	18	<1	13.9 ± 5.7	1.8	0.74
Accipiter gentilis	Hyvinkää-Askola	31	7	3.4 ± 0.9	1.9	0.88
Accipiter gentilis	Sipoo	23	7	3.2 ± 0.9	1.7	0.85
Accipiter gentilis	Espoo	20	5	4.0 ± 1.4	1.7	0.81
Accipiter nisus	Sipoo	35	9	2.0 ± 0.5	1.2	0.88
Accipiter nisus	Espoo	21	11	2.2 ± 0.7	1.4	0.82
Accipiter nisus	Askola	11	9	2.1 ± 0.6	1.3	0.86
Buteo buteo	Sipoo	24	9	2.7 ± 0.6	1.6	0.91
Buteo buteo	Askola	21	18	2.0 ± 0.4	1.7	0.92
Pandion haliaetus	Uusimaa	50	1	2.9 ± 1.4	0.6	0.66
Falco tinnunculus	Sipoo-Pornainen	10	1	4.7 ± 2.5	0.9	0.63
Falco subbuteo	Central Uusimaa	11	1	7.7 ± 2.1	1.8	0.88
Bubo bubo	Central Uusimaa	40	1	5.9 ± 2.1	1.2	0.79
Glaucidium passerinum	Central Uusimaa	12	<1	8.0 ± 4.0	1.0	0.68
Strix aluco	Sipoo-Mäntsälä	146	9	1.8 ± 0.6	1.1	0.84
Strix aluco	Espoo-Vantaa	32	6	2.4 ± 0.9	1.2	0.77
Strix uralensis	Central Uusimaa	40	1	3.7 ± 2.0	0.7	0.63
Asio otus	Central Uusimaa	22	1	4.0 ± 3.3	0.8	0.32
Aegolius funereus	Sipoo	38	3	2.3 ± 1.1	0.8	0.68

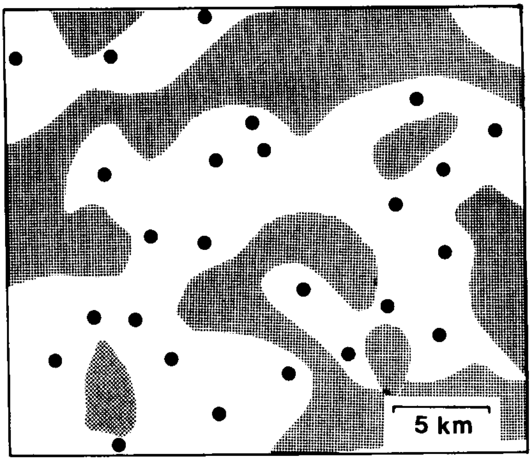

Fig. 4. Distribution of occupied nests of *Accipiter gentilis* in a study area in southern Finland in 1975 (modified after the data presented in Lindén & Wikman 1975). In shaded areas there are no potential nesting habitats for the species.

least one suitable nest site. Especially for hole-nesting species, the homogeneity of habitat largely means an even availability of nest sites in a suitable spatial scale, though there are still species-specific differences in preferred surroundings (e. g., Fig. 2). This was also more or less true for other species, even though not so evidently due to their less specific nest site requirements.

Suitable nesting trees, especially for Ospreys, were scarce and unevenly distributed. Artificial nests were constructed only to compensate for a few natural ones, not to increase the supply of nest sites (cf. Saurola 1986). In contrast, for the hole-nesting owls there was generally a superabundant and relatively even supply of nest boxes (e.g., Fig. 2), of which only 2.9–17.6% was occupied in any one year (Table 6). Hence, it seems improbable that the provision of artificial nest sites had caused marked irregularities in the spacing of the species — rather the opposite.

Irregularities in the spacing of nesting places were largely due to the uneven distribution of habitats (e. g., Figs. 3–4). In a larger spatial scale the heterogeneity of the environment (as well as the chance to miss some nesting places) inevitably increases, causing additional irregularities in the spatial pattern revealed. This was particularly evident in such species as the *Accipiter* hawks, whose habitat requirements are relatively strict. In Goshawk, scarcity of old forests suitable for nesting clearly limited the regular spacing of territories. Due to the very fixed and long-lasting territorial system of the species, however, its distribution changed only slowly in response to changes in the environment.

Local differences in the real fragmentation of forest habitats were not, however, as great as was suggested by their very prominent splitting by bodies of water and cultural habitats (fields, built-up areas etc.) (e.g., Figs. 3–4). Forest land was, of course, additionally split into a mosaic of various habitats including stands of trees of different age classes from clearings to older stands of mainly spruce-dominated forests. Relatively minor differences in distribution of required habitats were also indicated by the quite slight local differences in distribution of nesting places (e. g., Table 5, Figs. 3–4). So, the distribution of birds largely matched that of suitable habitats.

In the long-term territorial species, the mainly avian food supply was relatively stable (CV in general less than 20%), whereas the food of the short-term territorial vole specialists fluctuated greatly in three year cycles (CV nearly 70%) (Fig. 5). Populations of the long-term territorial species were fairly stable during the early years of the study, but in the 1980's major declines occurred in Marsh Harrier, Goshawk and Tawny

Table 6. Occupancy of nesting holes by owls in western and central Uusimaa in 1979–89 (Solonen et al. 1990). Up to 295 holes were available for *Strix uralensis* and 1500 for *Strix aluco*. Most of the holes (about 500–2000 in each year) were suitable for *Aegolius funereus*.

Year	Holes checked	Nests found	Occupancy (%)
1979	498	37	7.4
1980	853	54	6.3
1981	806	29	3.6
1982	818	85	10.4
1983	1170	148	12.6
1984	1000	38	3.8
1985	1143	132	11.5
1986	1661	293	17.6
1987	1448	42	2.9
1988	1871	277	14.8
1989	2077	270	13.0

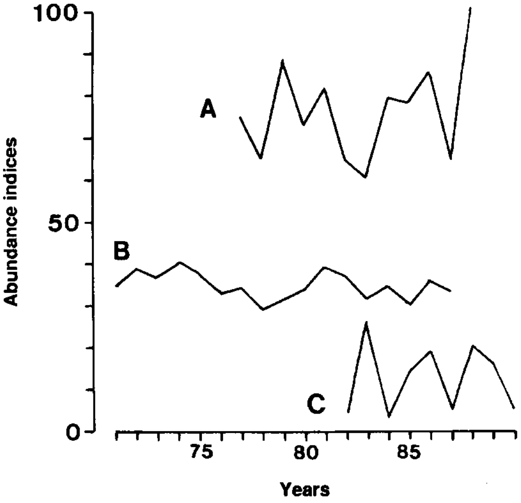

Fig. 5. Examples of general variations in the food supply of birds of prey in southern Finland: A. wintering small passerines (Sammalisto 1977, 1978, 1979, 1980, 1981, 1982, Hildén & Saurola 1985a, 1985b, 1986, Hildén & Haapala 1987, Hildén et al. 1988, Väisänen et al. 1988). B. a breeding passerine community (T. Solonen, unpubl.). C. small mammals (Solonen et al. 1990).

Owl, at least in some areas, probably following drastic changes in the food supply (see also Lindén & Wikman 1983, Solonen 1984, Forsman & Ehrnsten 1985). In short-term territorial species, distribution, numbers and breeding frequency clearly followed the fluctuations of small rodents (Table 7). However, Kestrels sharply declined and disappeared almost totally during the study period (see also Solonen 1984).

Table 7. Correlation (r_S) between the number of territories of *Asio otus* and *Aegolius funereus* located in western and central Uusimaa, southern Finland, in 1982–89, and an index of abundance of small mammals in the preceding autumn and in the same spring (data from Solonen et al. 1990).

	Autumn index	Spring index
Asio otus	$r_S = 0.881$, $P < 0.05$	$r_S = 0.310$, ns
Aegolius funereus	$r_S = 0.786$, $P < 0.05$	$r_S = 0.524$, ns

3.4. Effects of interspecific relations

To find whether interspecific interactions might affect the spacing of birds of prey, nearest neighbour distances were measured between all the nesting places located in one of the most intensively studied parts of the area (Sipoo, about 260 km^2), and G-values were calculated for all intra- and interspecific combinations (Appendix). While intraspecific nearest neighbour distances were usually higher than interspecific ones, there were four exceptions. Interspecific distribution patterns were at least as regular as intraspecific ones in 69 (44.2%) out of the 156 comparisons. Predictions of possible interspecific interactions (Table 2) were more or less supported in 27 (54.0%) out of the 50 cases expected (Appendix). With stricter *a priori* criteria of a highly regular interspecific pattern (higher than both intraspecific ones alone), predictions were supported in 12 cases (24.0%). Depending on the criteria used, in diurnal birds of prey a half or 25%, but in owls 73% or 33% of the expectations were supported by the data. In particular, there were many expected high interspecific G-values in combinations with Eagle Owl and Long-eared Owl. From these results it seems that avoidance of predation might affect the spatial structure of the bird assemblage studied, while interspecific competitive effects were less evident. In many cases, however, observations could be explained by differences in the habitat requirements and densities of the species.

4. Discussion

4.1. Representativeness of the data

The number of active nests and territories located in a given year gives a minimum estimate of density for that year, while the reconstruction method used here gives some kind of maximum density for regularly spaced long-term territorial species during a given time period, but only if all potential nesting places are located (cf. Newton et al. 1977, Newton 1991). Short-term territorial species can be censused reliably only by annual counts, but for general densities counts that reveal the population fluctuations in years of different levels of food supply are needed. Accurate population censuses on birds of prey are generally realistic only in relatively small study areas, in Finnish conditions about 50–200 km^2, depending on the habitats and species considered, or if all or most of the potential nest sites of the species can be checked annually (e.g., Osprey). I suggest that reasonable general regional densities can be obtained by careful spatial and temporal combinations of data.

The local samples were reasonably accurate: evidently all territories were found. Because in small local samples there may be some problems of scale (see, e.g., Fig. 2; see also Wiens 1981), regionally representative samples were required. In many cases, there was quite good agreement between the spacing of all known nesting places and those occupied in any one year, suggesting that the "combined" samples were reasonably representative of one year per area. However, the numbers and distribution patterns of active nests, territories and all the traditional nesting places of a population often differ from each other. If the territories of non-breeding birds are not taken into account, more than three fourths of the active territories may be overlooked (see, e.g., Newton 1979, 1986, Forsman & Solonen 1984, Pietiäinen 1988). Because in some years some traditional nesting places may be unoccupied, the dispersion of occupied territories in any one year does not always reveal completely the spatial structure of a long-term territorial population (see also Newton et al. 1977, Newton 1991), never mind that the important population processes take place in a single year.

The requirement to find all the nests of birds of prey in a study area in any one year (see, e.g., Forsman & Solonen 1984, Saurola 1985), is strict, compared with the accuracy generally accepted in the censusing of terrestrial birds (see, e.g., Ralph & Scott 1981). It is seldom possible to locate all active nests and territories in an area of, say, 100 km^2, which is usually required to yield about 1–20 pairs per species of birds of prey in southern Finland. Because of non-breeding and changing of nest sites, it may also be difficult to be sure that a given nesting place is unoccupied.

4.2. Distribution patterns

Regular spacing has been demonstrated in many birds of prey, and has been explained in several ways (e.g., Newton et al. 1977, 1986, Newton 1979, Nilsson et al. 1982). The main reason why birds of prey space their nests and territories regularly is probably intraspecific competition. The three types of competition (interference, exploitation and resource depression) are all likely to produce spacing out of territories (Charnov et al. 1976, Nilsson et al. 1982). Interference decreases rapidly with the distance from the nest (Newton 1979), and, therefore, it is probably not responsible for the longer nearest neighbour distances observed (see also Nilsson et al. 1982). Food depletion due to exploitation decreases with increasing distance from the central place as well (Andersson 1978), and this probably also applies to the effects of resource depression (Nilsson et al. 1982).

The regular spacing of traditional nesting places suggests distribution patterns largely maintained by intraspecific territoriality (cf. Newton 1986). This is in line with prediction 1, suggesting also that the populations remained fairly stable and thus justifying the combinations of data. If there had been large gaps in the annual occupancy of nesting places, new settlers probably would have produced irregularities in dispersion. Occasional short-term territories occur, even in long-term territorial species such as Goshawk (e.g., Forsman 1979), producing irregularities in distribution (for instance, due to exceptionally short nearest neighbour distances).

When population density is high, intraspecific territoriality tends to maintain the prevailing territorial system. Gaps in the occupancy of nesting places diminish the effect of territoriality. If there are enough gaps, changes in the traditional dispersion are possible. Considerable changes in density may cause pronounced redistribution of territories (e.g., in Goshawk and Tawny Owl in this study; see also Newton 1986). Due to territoriality, however, a more or less regular pattern is established, at least locally. Within the limits of smaller areas, the annual dispersion of short-term territorial species may also be relatively uniform, even if it is clumped in a larger spatial scale (cf. the data in Table 4 and Appendix; large and small areas, respectively). In heavily depleted populations the regular pattern of spacing disappears (see also Newton 1986).

4.3. Effects of resource supply

Nesting habitat offers a combination of various necessary elements, including nest sites and food resources. In general, fragmentation of habitats increases and regularity of spacing of territories and nesting places decreases with increasing area width. The regular pattern of nesting locations is an indication of the relative homogeneity of habitats. There is, however, always some heterogeneity even in the most homogeneous environments. The relevant scale (patch size) of heterogeneity depends on the requirements of the species considered.

Most of the species prefer forests, while some prefer districts where fields or other open habitats prevail. Fragmentation (heterogeneity) of forest habitats *per se* is not necessarily detrimental to the forest-dwelling species. To the contrary, many of them in fact benefit from the fragmentation due to improved availability of prey. The availability and distribution of suitable nesting places, which may be located even in very small-sized plots of suitable habitat (e. g., Fig. 2D), has a decisive effect on the local spacing of birds, whereas availability of prey governs their regional occurrence.

After logging, territoriality and the scarcity of suitable habitats force Goshawks either to be content with the remnants of their old forests, or with less suitable habitats, or to move elsewhere in search of vacant nesting places. After the death of territory owners, nesting places of birds of prey are often reoccupied immediately (e.g., Newton 1979, Cramp & Simmons 1980). Thus, the responses of long-term territorial birds of prey largely tend to maintain the prevailing distribution pattern.

Particularly for the accipiters, nesting resources may become increasingly limiting in the near future if the destruction of habitats continues. Regular distribution, however, seems to be kept partly by the compensatory effect of food supply and other breeding resources; food supply for the species is in general best where breeding habitats are scarce, i. e., in the vicinity of urban and rural areas (T. Solonen, unpubl.). These kinds of patterns give useful clues for conservation purposes.

Strict habitat requirements or a high preference for certain habitats (e.g., Marsh Harrier) can produce a random or clumped dispersion. In marginal ranges, where population densities are low, irregular distribution patterns are common (e.g., Ural Owl in this study). The Osprey population of Uusimaa is concentrated in eastern and western coastal districts; elsewhere few or no breeding pairs occur (Saurola 1983, Solonen 1984).

My results support earlier findings that the character of food supply (birds vs. voles) is important in the spacing out of territories (Newton 1979, Nilsson et al. 1982); spacing was least regular in the species feeding mainly on small mammals (i. e., in nomadic vole specialists). Especially in the short-term territorial species, redispersal due to reduced food supply seems evident (cf. habitat shifts in wintering birds). Among Scottish Sparrowhawks, densities (nearest neighbour distances) of nesting territories were determined by the general food supply in the area, and in poor years only the best places were occupied (Newton 1986, 1991). Such a pattern seems to fit the Finnish Sparrowhawks too, and also many other long-term territorial birds of prey.

4.4. Interspecific interactions

Birds of prey may not occupy the full range of available localities that they might otherwise use, because of interactions with other species. Both competitors and predators may restrict the habitat range of a given species. Antagonistic behaviour and interspecific territoriality among birds of prey are common (see, e.g., Janes 1985). Differential habitat use among ecologically similar sympatric species has been widely observed and it may indicate the effects of competition. Differential use of habitats may also result from actual or potential predation. If interspecific interactions exist, circumstances may in reality be much more complicated, due to indirect effects, than comparisons between pairs of species might indicate. Other explanations for similar patterns can not, of course, be ruled out. Long nearest neighbour distances between species and regular interspecific spacing indicated either different habitat requirements, avoidance of predation, or competitive exclusion, while low nearest neighbour distances and random (or clumped) spacing between species suggested similar habitat requirements. With few exceptions, no strong interspecific effects on distribution patterns were apparent between the species studied (cf., e.g., Janes 1985, Korpimäki 1987). Active nests of different species were sometimes close to one other, apparently with no serious interspecific interactions (e.g., Solonen 1984). Some larger species (e.g., Goshawk, Eagle Owl and Ural Owl) may, however, oust other species from the immediate vicinity of their nests (e.g., Lack 1971, Mikkola 1983, Solonen 1984, unpubl.; see also Janes 1985), though preying upon other birds of prey is probably incidental and occasional rather than deliberate and regular (however, cf. Mikkola 1983). Due to predation, birds of prey seldom breed successfully close to the nests of species able to kill them (e. g., Fiuczynski 1991).

Habitat, nest site and food requirements of different species of birds of prey often overlap, bringing about competitive situations (e.g., Lack 1971, Newton 1979; see also Jaksić & Braker 1983, Janes 1985). Competition for sparse nesting holes is well known (e.g., v. Haartman 1968), but in my study area it has been lessened by providing artificial nest boxes. So, a shortage of nest sites is no longer limiting for hole-nesting owls in the study area. The best sites may, however, be heavily competed for (cf. Newton 1991). There may also be competition for old stick nests, particularly those of large hawks, especially between Honey Buzzard, Goshawk, Common Buzzard and Ural Owl (Solonen 1984).

The abundance of the species also affects interspecific nearest neighbour distances: the sparser the species, the longer the mean nearest neighbour distance, if the dispersion is not clumped. The fluctuations and changes in the long-term territorial populations considered were generally too small to have any marked effect on the interspecific distribution patterns revealed. Both intra- and interspecific competition can be expected to increase and force some birds to less favourable habitats, when, for instance, human-caused environmental changes diminish the availability of the essential resources (see also Nilsson 1984). Competition with and predation upon other species may increase, if conditions for a species improve and population growth is enhanced. For example, in the present study area, as well as more widely in Finland, Eagle Owl has increased, largely with the increase of open foraging habitats in clear-felled forests and especially with the food supply provided by the rat populations of rubbish dumps (e.g., Solonen 1984, Saurola 1985). This increases the chance that other birds of prey will be killed by Eagle Owls.

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Selostus: **Petolintujen tilankäyttö eteläsuomalaisessa ympäristössä**

Petolintujen esiintymistä tutkittiin keskisellä Uudellamaalla vuosina 1972–90. Tutkimusalueella (4800 km^2) pesi säännöllisesti kahdeksan päiväpetolintulajia ja kuusi pöllölajia. Ravintotilanteen mukaan runsaudeltaan rajusti vaihtelevia, myyrien syöntiin erikoistuneita lajeja luonnehti epätasainen ympäristöön jakautuminen, mutta useimpien paikkauskollisten, paljolti vakaata linturavintoa käyttävien lajien pesäpaikat jakautuivat ympäristöön tasaisesti. Perinteisten pesäpaikkojen sijainnilla oli ratkaiseva vaikutus asuttujen pesäpaikkojen sijaintiin. Pesäpaikkojen jakautumisen epäsäännöllisyydet johtuivat enimmäkseen sopivien pesimäympäristöjen epätasaisesta saatavuudesta. Pesäpaikkojen ympäristöön jakautumisen perusteella erityisesti huuhkajan taholta uhkaavan saalistuksen välttely näytti vaikuttavan eräiden muiden petolintulajien pesäpaikkojen sijaintiin, mutta eri lajien välisen kilpailun vaikutukset eivät olleet kovin ilmeisiä.

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Appendix. Intra- and interspecific nearest neighbour distances (km; mean ± SD) and G-values (see Methods) of nesting places (number in parenthesis) of birds of prey in an area in southern Finland (data from Fig. 6 in Solonen 1984). The interspecific G-values that are similar or higher than the intraspecific ones, supporting the predictions of possible interspecific interactions (Table 2), are in italics.

Species	*P api*	*A gen*	*A nis*	*B but*	*P hal*	*F tin*	*F sub*	*B bub*	*G pas*	*S alu*	*S ura*	*A otu*	*A fun*
Pernis apivorus	2.9±0.9 0.86 (17)	1.4±0.6 0.70 (38)	1.3±0.5 0.75 (44)	1.3±0.6 0.68 (38)	2.1±0.6 0.83 (21)	2.3±0.5 0.91 (21)	2.2±0.5 0.89 (21)	1.9±0.6 *0.78* (22)	2.0±0.5 0.85 (20)	1.2±0.4 0.78 (58)	1.8±0.6 0.74 (25)	2.0±0.6 0.82 (21)	1.7±0.4 0.87 (25)
Accipiter gentilis		2.5±0.7 0.88 (21)	1.2±0.4 0.76 (48)	1.1±0.5 0.65 (42)	1.7±0.7 0.68 (25)	2.0±0.4 *0.92* (25)	1.9±0.6 0.75 (25)	1.8±0.6 0.75 (26)	1.8±0.6 0.75 (24)	1.3±0.4 0.84 (62)	1.6±0.7 0.67 (29)	1.9±0.6 *0.75* (25)	1.5±0.7 0.62 (29)
Accipiter nisus			2.1±0.5 0.88 (27)	1.2±0.4 0.74 (48)	1.5±0.5 0.75 (31)	1.8±0.5 0.87 (31)	1.7±0.4 *0.89* (31)	1.4±0.4 *0.86* (32)	1.6±0.5 0.82 (30)	1.1±0.3 0.84 (68)	1.3±0.3 *0.87* (35)	1.8±0.4 0.93 (31)	1.3±0.5 0.70 (35)
Buteo buteo				2.7±0.7 0.87 (21)	1.7±0.4 0.88 (25)	2.0±0.4 *0.91* (25)	2.0±0.6 0.78 (25)	1.8±0.4 *0.93* (26)	1.6±0.5 0.78 (24)	1.1±0.4 0.72 (62)	1.5±0.5 0.78 (29)	2.1±0.5 *0.91* (25)	1.4±0.5 0.75 (29)
Pandion haliaetus					5.9±5.6 0.35 (4)	4.0±1.4 0.82 (8)	2.9±1.0 0.81 (8)	2.2±0.8 *0.78* (9)	1.6±0.9 0.58 (7)	1.5±0.5 0.80 (45)	2.4±0.7 0.81 (12)	3.0±0.7 0.92 (8)	1.1±0.4 0.81 (12)
Falco tinnunculus						5.6±3.3 0.59 (4)	1.9±0.9 *0.61* (8)	2.2±0.8 *0.79* (9)	3.5±0.8 0.91 (7)	1.5±0.4 *0.86* (45)	2.4±0.8 *0.82* (12)	2.5±1.0 *0.75* (8)	2.1±1.1 *0.61* (12)
Falco subbuteo							6.2±1.6 0.90 (4)	2.5±1.3 0.61 (9)	2.9±1.3 0.70 (7)	1.6±0.4 0.85 (45)	2.6±1.3 0.61 (12)	2.4±1.0 *0.69* (8)	1.4±0.5 0.77 (12)
Bubo bubo								5.2±2.1 0.77 (5)	2.1±0.4 *0.93* (8)	1.4±0.3 *0.92* (46)	2.2±0.7 *0.83* (13)	2.7±0.3 *0.98* (9)	1.4±0.7 0.69 (13)
Glaucidium passerinum									6.0±1.2 0.95 (3)	1.4±0.3 *0.91* (44)	1.9±0.5 *0.89* (11)	3.0±0.8 *0.90* (7)	1.1±0.5 0.72 (11)
Strix aluco										1.7±0.4 0.88 (41)	1.3±0.3 *0.90* (49)	1.3±0.4 *0.84* (45)	1.2±0.3 *0.89* (49)
Strix uralensis											3.6±0.9 0.90 (8)	2.2±0.4 *0.94* (12)	1.7±0.7 0.72 (16)
Asio otus												4.5±2.5 0.65 (4)	1.7±0.5 *0.82* (12)
Aegolius funereus													1.5±0.5 0.81 (8)