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Clear-cut areas and breeding success of Tengmalm's owls *Aegolius funereus*

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The effect of mature forest fragmentation on breeding success of vole-eating Tengmalm's owls *Aegolius funereus* was studied in western Finland during 1981-1995. The owl pairs produced more fledglings in territories with high (>30%) proportions of clear-cut and plantation areas than in territories with low (<30%) proportions of such areas. Territory occupancy, clutch size, laying date, and parental characteristics such as wing length, body mass and age were not associated with the proportion of clear-cut areas within territories. Snap-trapping data from the 'increase' vole year 1994 revealed that the *Microtus* vole density tended to be higher in large clear-cuttings than in small ones. The increasing amount of sapling and clear-cut areas in coniferous forests during the last three decades has created suitable grass habitats for *Microtus* voles, and simultaneously new hunting habitats for Tengmalm's owls. Therefore, forest fragmentation due to clear-cuttings may benefit Tengmalm's owls at the present scale. However, nest-boxes should be erected and old groves should be protected, because forest harvesting apparently reduces the number of suitable natural cavities for owls in the long run.

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During the last decades modern forestry has had a large-scale impact on boreal forest ecosystems, both in Palearctic and Nearctic regions. Especially, at landscape level, there is a lack of large pristine forests (e.g. Ohmann et al. 1988), while remaining patches of mature forests have become internally more homogeneous and more isolated from larger forest complexes (Hansson 1992). This human disturbance evidently causes harmful effects on organisms that are strictly dependent on mature forest habitats and that have restricted ability to disperse between suitable habitat patches (Hansson 1992). The direct costs of loggings for such species are caused by the decrease in the amount and the fragmented spacing of resources required by these individuals. In addition to that, organisms may be incapable of moving between vitally important habitat patches, and the energy expenditure of food and mate searchings along with failures in social behaviour may increase substantially in strongly fragmented land-

scapes (e.g. Rolstad & Wegge 1989). Furthermore, the change in landscape composition may modify community structure and therefore affect inter-specific interactions (Addicott et al. 1987, Angelstam 1992). One of the most studied examples is the increased predation pressure in fragmented forest landscapes (Kuitunen & Helle 1988, Small & Hunter 1988, Andrén 1992, Kurki & Lindén 1995, Huhta 1995). Therefore, we need to evaluate how clear-cut areas affect reproduction and survival of species subsisting on forest resources, as the density decline of many forest species is suggested to be connected with forest fragmentation (e.g. Haila et al. 1979).

Birds of prey living in forest habitats are generally considered to be sensitive to forest management and habitat change (e.g. Newton 1979). One example of such detrimental effects is the spotted owl *Strix occidentalis*, which primarily uses old forests for foraging and roosting (Forsman et al. 1984, Carey et al. 1992). Birds of prey inhabit

large territories (Newton 1979), where, as top carnivores, they consume prey, which is scarce and difficult to catch (e.g. Temeles 1985). Therefore, they may lose much energy in each feeding event, especially, if prey is sparsely and patchily distributed within a territory. Forest harvesting may also induce a lack of nesting places, such as natural cavities and large nesting trees for many owl, hawk and eagle species. Loggings also reduce habitat quality of many birds of prey by decreasing the amount of suitable hunting perches (Widen 1994). On the other hand, vole-eating predators may benefit from large clear-cut and plantation areas, as these may sustain a large number of field voles (Henttonen 1989).

Tengmalm's owl *Aegolius funereus* is a small nocturnal hole-nesting bird of prey, which commonly breeds in coniferous forests in northern Europe (e.g. Mikkola 1983). In Finland, *Microtus* voles (the field vole *Microtus agrestis* and the sibling vole *M. rossiaemerdionalis*) and the bank vole *Clethrionomys glareolus* form the main prey of Tengmalm's owl (e.g. Korpimäki 1981, 1988a, Koivunen et al. 1996). *Microtus* voles inhabit field areas as well as clear-cut and plantation areas, whereas bank voles mainly live in forest habitats (e.g. Hansson 1978). Based on Henttonen's hypothesis (1989) that predators may benefit from expanding populations of field voles in logged and planted areas, we examined whether such areas enhance the breeding frequency and reproductive success of Tengmalm's owls. We also evaluated whether density and occurrence of the main prey of Tengmalm's owls increase along with the size of clear-cut areas.

Methods

The owl population

The study was conducted during 1981-1995 in the Kauhava region (ca 63°N, 23°E), western Finland, in an area covering 1,300 km² and containing 500 nest-boxes and approximately 30 natural cavities suitable for Tengmalm's owls. Spruce forest, pine forest and clear-cut areas cover 46% of the study area, while the rest of the habitats consist of agricultural land (27%), peatlands (23%), and urban and water areas (4%), respectively (e.g. Korpimäki 1981). All territories and nest-boxes were checked annually at least twice per breeding season. On the basis of map observations (scale 1:20,000), all nest sites situated within extensive forest areas (only forest within 1.5 km from the nest-box), were chosen for this study (N = 30). The 1.5 km radius from the nest-box covers the mean territory size (2-5 km²) of Tengmalm's owls (Sonerud 1986a, Korpimäki 1992, our own unpubl. radio-tracking data). All territories that included some agricultural fields were excluded, because the proportion of ag-

Table 1. Habitat composition expressed as mean proportion of clear-cut areas (SD) within 1.5 km from the nest-boxes of Tengmalm's owls in sparsely (low) and widely (high) clear-cut territories. All habitat types outside clear-cut areas are included.

	Proportion (%) of clear-cut areas within territory		Mann-Whitney U-test	
	Low	High	U	P
Number of territories	17	13		
Habitat type				
Pine forest	38 (9)	40 (16)	121.0	0.65
Spruce forest	33 (10)	31 (10)	102.0	0.72
Deciduous forest	2 (6)	2 (5)	102.0	0.61
Peatland bog	27 (15)	27 (11)	110.5	1.00

ricultural fields within Tengmalm's owl territories is positively related to the breeding frequency and reproductive success of Tengmalm's owls (Korpimäki 1988b). Therefore, even small agricultural fields would have led to increased vole numbers in the territory, and, thus would have confounded our analyses on the effects of clear-cut areas within owl territories. Based on map evaluations and our own field observations, the 30 territories were divided into two groups with respect to the frequency of clear-cuttings. In the whole study area, about one third of total forest areas was clear-cut, and therefore, 30% clear-cutting was chosen as the limit value between the two groups. Based on this criterion, we had two groups: 1) territories, in which <30% of total forest area was clear-cut within 1.5 km from the nest-boxes (on average 18%, SD = 7%, range 10-30%, N = 17), and 2) territories, in which >30% of total forest area was clear-cut (on average 49%, SD = 11%, range 35-70%, N = 13). In our classification, the term 'clear-cut area' also included some areas with up to 2 m high saplings, but 0.2 - 1 m high saplings were prevailing. Clear-cut features, such as mean age of clear-cuts and saplings were similar in the two territory groups. The habitat composition outside clear-cuttings did not differ between the two territory groups, indicating that there were no obvious differences in soil productivity between the sparsely and widely clear-cut territory groups (Table 1). Accurate estimates for clear-cut areas, however, are difficult to calculate because of continuous temporal and

Table 2. Number of Tengmalm's owl nests in sparsely (low) and widely (high) clear-cut territories in the three phases of the vole cycle.

Phase of vole cycle	Proportion of clear-cut areas within territory	
	Low	High
Low	1	2
Increase	7	4
Peak	13	12

Table 3. Mean annual breeding percentage in nest-boxes (SD), mean laying date (SD; 1 = 1 April), mean clutch size (SD) and mean fledgling production (SD) in sparsely (low) and widely (high) clear-cut territories of Tengmalm's owls. Statistical tests were performed by Student's T-test and Mann-Whitney U-test (two-tailed). N = number of territories.

	Proportion of clear-cut areas within territory				Test value	P
	Low	N	High	N		
Breeding percentage	15 (9)	17	14 (15)	13	U = 139.0	0.22
Laying date	1.41 (19.44)	14	1.10 (21.98)	10	T = 0.04	0.97
Clutch size	5.43 (0.88)	14	5.20 (1.26)	11	T = 0.54	0.59
Number of fledglings	2.45 (1.26)	14	3.55 (1.39)	11	T = 2.06	0.05

spatial changes in forest landscape caused by loggings. This forced us to use only rough classifications of the proportion of clear-cut areas within owl territories (sparsely vs widely clear-cut territories).

The nests were checked as many times as necessary to determine the final clutch size and fledgling production (for further details see Korpimäki 1981, 1988a,b). The laying date of the first egg was usually back-dated from the known hatching date of the young (Korpimäki 1981, Carlsson & Hörnfeldt 1994). All parent owls were trapped and measured (body mass to the nearest 1 g, and wing length to the nearest 1 mm) at the same stage of the breeding cycle, i.e. 1-2 weeks after hatching, in order to reduce variation in the measurements. Parent owls were aged as 1, 2, 3, 4 and >4 years old by using moult pattern of primary feathers (Glutz von Blotzheim & Bauer 1980).

Based on intensive snap-trappings in the study area (Korpimäki & Norrdahl 1989, E. Korpimäki & K. Norrdahl, unpubl. data), the breeding seasons were divided into three phases. In the low phase (1981, 1984, 1987, 1990, 1993) voles were scarce during the owls' breeding season. Thereafter, voles increased to a moderate level by the beginning of the next breeding season (the increase phase: 1982, 1985, 1988, 1991, 1994). Early in the spring of the following years (the peak phase: 1983, 1986, 1989, 1992, 1995), voles reached the highest abundance, but crashed during late summer and autumn to be followed by the low phase again.

Snap-trappings

The abundance of *Microtus* voles in 27 different clear-cut areas (mean = 4.7 ha, SD = 4.4 ha) was investigated in Ikaalinen (ca 62° N, 23° E) in the 'increase' vole year 1994 in late summer using the small quadrat method (Myllymäki et al. 1971). Three quadrats including 12 snap-traps were located in each clear-cut area for two days. The traps were baited with a piece of dried apple. Trapped animals were identified every morning. We selected only clearly grassed clear-cut areas with similar habitat features (e.g. proportion and height of saplings and grass about the same among clear-cuts) for snap-trappings to minimise the effect of habitat variation in different clear-cuts. Furthermore, within each clear-cut area the trap-quadrats were spaced to the most grassed areas which seemed to be favourable for *Microtus* voles. Bank voles were not included in the analyses because of scanty data.

Results

The number of owl breeding attempts during a 10-year period did not differ between the sparsely and widely clear-cut territory groups (Tables 2 and 3). In addition, territory related means of clutch size and laying date of Tengmalm's owls were similar in the two different clear-cut territory categories (see Table 3). Owl territories with large clear-cut areas, however, produced more fledglings

Table 4. Wing length (mm), body mass (g) and age (years) of breeding male and female Tengmalm's owls in the sparsely (low) and widely (high) clear-cut territories. Figures in parentheses indicate SD and N the number of owls. Statistical tests were performed by Student's T-test and Mann-Whitney U-test.

	Proportion of clear-cut areas within territory				Test value	P
	Low	N	High	N		
Female						
Wing length, mm	179.80 (2.71)	N = 13	180.38 (2.20)	N = 10	T = 0.56	0.58
Body mass, g	164.01 (11.43)	N = 13	163.08 (17.03)	N = 10	T = 0.17	0.87
Age, years	1.91 (0.72)	N = 13	2.55 (1.26)	N = 10	U = 42.50	0.24
Male						
Wing length, mm	172.58 (2.12)	N = 12	173.9 (3.60)	N = 10	T = 1.13	0.27
Body mass, g	109.42 (10.64)	N = 12	110.61 (8.12)	N = 10	T = 0.29	0.77
Age, years	2.50 (1.38)	N = 12	2.84 (1.33)	N = 10	U = 50.50	0.53

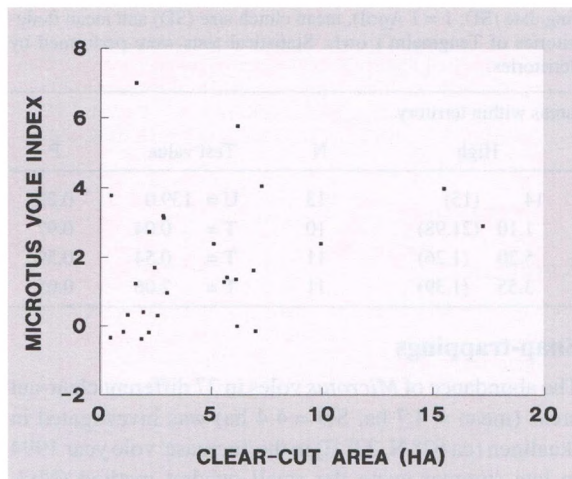


Figure 1. *Microtus* vole density expressed as the number snap-trapped per 100 trap-nights in relation to clear-cut areas (N = 27) in the 'increase' vole year 1994. Jitter-option (Sygraph drawing program) was used to separate overlapping datapoints.

than sparsely clear-cut territories (see Table 3). This result could be ascribed to widely clear-cut territories being occupied only in good vole years, when fledgling production is high, as is the case especially in increase vole years (Korpimäki & Hakkarainen 1991). This possibility, however, did not confound our results, because breedings occurred approximately in the same phase of the vole cycle in the sparsely and widely clear-cut areas (see Table 2). In addition, the proportion of clear-cut areas in the territory was not related to body mass, wing length and age of breeding Tengmalm's owls (Table 4). The proportion of unsuccessful nests (i.e. eggs were laid but no fledglings were produced) did not differ between widely and sparsely clear-cut territories (11.1% vs 9.5%; $\chi^2 = 0.02$, $P = 0.88$).

Microtus voles were snap-trapped in clear-cuttings of different sizes. A nearly significant positive association was found between the rank of clear-cut areas and the density of *Microtus* voles (Spearman rank correlation, $r_s = 0.37$, $N = 27$, $P < 0.10$; Fig. 1). The clear-cut areas in which at least one *Microtus* vole was snap-trapped were larger than those where no *Microtus* voles were trapped (mean = 5.7 ha, SD = 4.8 ha, $N = 18$, and mean = 2.5 ha, SD = 2.4 ha, $N = 9$, respectively; Mann-Whitney U-test, $U = 39.0$, $P = 0.03$).

Discussion

Our results imply that removing the forest by clear-cutting on about half the area of a Tengmalm's owl territory does not harm this species. Instead, breeding Tengmalm's owls seemed to benefit to some extent from the increasing amount of clear-cut areas, as our snap-trapping

results suggest that large clear-cut areas may sustain denser *Microtus* vole populations than small clear-cut areas.

Accordingly, fledgling production of Tengmalm's owls seemed to be high in widely clear-cut territories. In addition, fledgling production in intensively clear-cut territories (mean 3.6; see Table 3) represents exceptionally good values for fledgling production of Tengmalm's owls (see Table 1 in Korpimäki & Hakkarainen 1991), which suggests that loggings may enhance reproductive success of Tengmalm's owls in forested habitats. Furthermore, in Tengmalm's owl, lifetime reproductive success (LRS) is highly linked with the number of fledglings produced in each reproductive event (Korpimäki 1992). At present, LRS is the best known indicator of fitness (Clutton-Brock 1988, Newton 1989). Survival is another important indicator of fitness (Endler 1986). Unfortunately, our data was insufficient to perform survival analyses (Pradel & Lebreton 1993) on males living in sparsely and widely clear-cut territories, respectively. The data we have compiled so far (as calculated for males that have been recruited into the breeding population by 1992; H. Hakkarainen & E. Korpimäki, unpubl. data), however, suggest that in widely clear-cut territories the mean breeding life span of males tend to be higher than in sparsely clear-cut territories (means: 2.0 vs 1.2 years). This implies that large proportions of clear-cut areas within owl territories have no adverse effects on breeding life span and winter survival of male Tengmalm's owls. If anything, even positive effects may be expected. Therefore, males may achieve beneficial fitness when breeding on widely clear-cut territories. In addition, the proportion of nesting failures was not related to the proportion of clear-cut areas within territories, suggesting that nest predation by pine marten *Martes martes* (see Korpimäki 1981) was not affected by the proportion of clear-cuts in our study area.

In contrast, Sonerud (1985) showed that nest predation rate of Tengmalm's owl was lower in open forest landscapes than in mature spruce forests due to pine marten preference on closed mature spruce forests in Norway. In accordance with this, Tengmalm's owls preferred to breed in nest-boxes put up in clear-cuts, and avoided those put up in old forests (Sonerud 1985). Therefore, open forest landscapes with clear-cuts may provide safe breeding habitats for Tengmalm's owls.

It seems that the increasing amount of sapling and clear-cut areas during the last three decades (Järvinen et al. 1977) has created new suitable grass habitats for field voles (Henttonen 1989). In sunny clear-cut areas, different grass species grow fast, and grass-eating field voles may colonise them successfully for about 10 years (Hansson 1978). Possibly, loggings also take place in the most productive forest areas and this may further increase the productivity of new clear-cuts. In such areas, the breeding density of field voles may be much higher than the

bank vole density of the same area before logging, because the territory size of field voles is smaller than that of bank voles (Henttonen 1987). In contrast to bank voles, female field voles also allow their female offspring to reproduce within their own territory (Myllymäki 1977), which also increases the population density of field voles compared to that of bank voles. Therefore, large clear-cut areas may sustain high densities of field voles, which are the most preferred prey of Tengmalm's owls (Koivunen et al. 1996). The diversity of prey populations may also be higher at edges of forests and clear-cut areas, as both field voles and bank voles exist in this zone. Therefore, in such areas both main prey species are available to the Tengmalm's owl. However, bank vole densities seem to be low close to forest edges, probably because of high predation risk from hunting Tengmalm's owls (Hansson 1994). Radio-tracking data also imply that Tengmalm's owls mainly hunt at the edges of forests (Sonerud 1986b). Therefore, Tengmalm's owls may benefit from large clear-cut areas, if saplings are high enough (about 2 m) to serve as hunting perches (Bye et al. 1992, our own unpubl. radio-tracking data).

Bird densities are also found to peak at the edges of forests (Hansson 1983, 1994, Helle 1984), and many passerine birds increase in numbers with forest fragmentation (Haila et al. 1989). Therefore, clear-cuttings may increase the amount of alternative prey (small birds) for Tengmalm's owls in poor vole years, when voles are scarce (Korpimäki 1981, 1988a). Especially, the breeding densities of chaffinches *Fringilla coelebs* which form the main avian prey of Tengmalm's owls (Korpimäki 1981), peak at the edges of forests (Hansson 1994).

Although it seems that prey abundance and fledgling production even increased with forest fragmentation, it is sure, however, that increased forest fragmentation also reduces the number of suitable natural cavities for breeding Tengmalm's owls. This is attributable to the fact that large trees with nesting cavities of the black woodpecker *Dryocopus martius* are becoming scarce due to loggings. This creates a need to save natural cavities and to erect nest-boxes for Tengmalm's owls. In the long run, the establishment of snags and patches of old mature forests with large trees, dense enough for hole-nesting black woodpeckers, will provide a natural way of establishing new nesting cavities for Tengmalm's owls.

In accordance with our preliminary expectations, loggings had positive effects on the fledgling production of Tengmalm's owls, while no negative effects were found. This implies that species may also respond positively to forest fragmentation (Rosenberg & Raphael 1986, Hansen et al. 1991). Especially the number of vole-eating generalist and specialist predators may increase in logged forests enhancing predation pressure on vole populations (e.g. Henttonen 1989, Angelstam 1992).

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References

- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. 1987: Ecological neighbourhoods: scaling environmental patterns. - *Oikos* 49: 340-346.
- Andrén, H. 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. - *Ecology* 73: 794-804.
- Angelstam, P. 1992: Conservation of communities: the importance of edges, surroundings and landscape mosaic structure. - In: Hansson, L. (Ed.); *Ecological Principles of Nature Conservation: Applications in Temperate and Boreal Environments*. Elsevier, Barking, pp. 9-70.
- Bye, F.N., Jacobsen, B.V. & Sonerud, G.A. 1992: Auditory prey location in a pause-travel predator: search height, search time, and attack range of Tengmalm's owls (*Aegolius funereus*). - *Behavioral Ecology* 3: 266-276.
- Carey, A.B., Horton, S.P. & Biswell, B.L. 1992: Northern spotted owl: influence of prey base and landscape character. - *Ecological Monographs* 62: 223-250.
- Carlsson, B.G. & Hörnfeldt, B. 1994: Determination of nestling age and laying date in Tengmalm's Owl: use of wing length and body mass. - *Condor* 96: 555-559.
- Clutton-Brock, T.H. (Ed.) 1988: *Reproductive success*. - University of Chicago Press, Chicago, 352 pp.
- Endler, J.A. 1986: *Natural selection in the wild*. - Princeton University Press, Princeton, 336 pp.
- Forsman, E.D., Meslow, E.C. & Wight, H.M. 1984: Distribution and Biology of the spotted owl in Oregon. - *Wildlife Monographs* 87: 1-64.
- Glutz von Blotzheim, U.N. & Bauer, K.M. 1980: *Handbuch der Vögel Mitteleuropas*, Vol. 9. - Akademische Verlagsgesellschaft, Wiesbaden, 1148 pp.
- Haila, Y., Järvinen, R. & Väisänen R.A. 1979: Effects of mainland population changes on the terrestrial bird fauna. - *Ornis Scandinavica* 10: 48-55.
- Haila Y., Hanski, I.K. & Raivio, S. 1989: Effect of mainland population changes on the terrestrial bird fauna of a northern island. - *Annales Zoologici Fennici* 26: 173-180.
- Hansen A.J., Spies T.A., Swanson F.J. & Ohmann, J.L. 1991: Conserving biodiversity in managed forests. - *BioScience* 41: 382-392.
- Hansson, L. 1978: Small mammal abundance in relation to environmental variables in three Swedish forest phases. - *Studia Forestalia Suecica* 147: 1-39.
- Hansson, L. 1983: Bird numbers across edges between mature conifer forests and clearcuts in Central Sweden. - *Ornis Scandinavica* 14: 97-104.
- Hansson, L. 1992: Landscape ecology of boreal forests. - *Trends in Evolutionary Ecology* 7: 299-302.
- Hansson, L. 1994: Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. - *Landscape Ecology* 9: 105-115.

- Helle, P. 1984: Effects of habitat area on breeding bird communities in Northeastern Finland. - *Annales Zoologici Fennici* 21: 421-425.
- Henttonen, H. 1989: Metsien rakenteen muutoksen vaikutuksesta myyrakantoihin ja sitä kautta pikkupetoihin ja kanalintuihin - hypoteesi. - *Suomen Riista* 35: 83-90. (In Finnish with English summary).
- Huhta, E. 1995: Effects of spatial scale and vegetation cover on predation of artificial ground nests. - *Wildlife Biology* 1: 73-80.
- Järvinen, O., Kuusela, K. & Väisänen, R.A. 1977: Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana (In Finnish with English summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945-1975). - *Silva Fennica* 11: 284-291.
- Koivunen, V., Korpimäki, E., Hakkarainen, H. & Norrdahl, K. 1996: Prey choice of Tengmalm's owl (*Aegolius funereus funereus*): preference of substandard individuals? - *Canadian Journal of Zoology* 74: 816-823.
- Korpimäki, E. 1981: On the ecology and biology of Tengmalm's owl (*Aegolius funereus*) in Southern Ostrobothnia and Suomenselkä western Finland. - *Acta Universitatis Ouluensis Sere-ries A. Scientiae Rerum Naturalium* 118: 1-84.
- Korpimäki, E. 1988a: Diet of breeding Tengmalm's owls *Aegolius funereus*: long-term changes and year to year variation under cyclic food conditions. - *Ornis Fennica* 65: 21-30.
- Korpimäki, E. 1988b: Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. - *Journal of Animal Ecology* 57: 97-108.
- Korpimäki, E. 1992: Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. - *Journal of Animal Ecology* 61: 103-111.
- Korpimäki, E. & Norrdahl, K. 1989: Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics - a hypothesis. - *Oikos* 55: 273-280.
- Korpimäki, E. & Hakkarainen, H. 1991: Fluctuating food supply affects the clutch size of Tengmalm's owls independent of laying date. - *Oecologia* 85: 543-552.
- Kuitunen, M. & Helle, P. 1988: Relationship of the Common Tree-creeper *Certhia familiaris* to edge effect and forest fragmentation. - *Ornis Fennica* 65: 150-155.
- Kurki, S. & Lindén, H. 1995: Forest fragmentation due to agriculture affects the reproductive success of the ground-nesting grouse *Tetrao tetrix*. - *Ecography* 18: 109-113.
- Mikkola, H. 1983: *Owls of Europe*. - Poysers, Calton, 397 pp.
- Myllymäki, A., Paasikallio, A., Pankakoski, E. & Kanervo, V. 1971: Removal experiments on small quadrats as a means of rapid assessment of the abundance of small abundance. - *Annales Zoologici Fennici* 8: 177-185.
- Myllymäki, A. 1977: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. - *Oikos* 29: 553-569.
- Newton, I. 1979: *Population ecology of raptors*. - Poysers, Berkhamsted, 399 pp.
- Newton, I. (Ed.) 1989: *Lifetime reproduction in birds*. - Academic Press, London, 479 pp.
- Ohmann, J.L., Carleson, P.L. & Oakley, A.L. 1988: Status of forest-related wildlife and fish resources in Oregon. - In: Lettman, G.J. (Ed.); *Assessment of Oregon's Forests*. Oregon State Department of Forestry, Salem, pp. 17-32.
- Pradel, R. & Lebreton, J.-D. 1993: AVENIX. User's manual for program surge. Version 4.2. July 1993, 52 pp.
- Rolstad, J. & Wegge, P. 1989: Capercaillie *Tetrao urogallus* populations and modern forestry - a case for landscape ecological studies. - *Finnish Game Research* 46: 43-52.
- Rosenberg, K.V. & Raphael, M.G. 1986: Effects of forest fragmentations on vertebrates in Douglas-fir forests. - In: Verner, J., Morrison, M.L. & Ralph C.J. (Eds.); *Wildlife 2000*. University of Wisconsin Press, Madison, pp. 263-272.
- Small, M.F. & Hunter, M.L. 1988: Forest fragmentation and avian nest predation in forest landscapes. - *Oecologia* 76: 62-64.
- Sonerud, G.A. 1985: Risk of nest predation in three species of hole nesting owls: influence on choice of nesting habitat and incubation behaviour. - *Ornis Scandinavica* 16: 261-269.
- Sonerud, G.A. 1986a: Home-range use and habitat selection during hunting in a male Tengmalm's owl *Aegolius funereus*. - *Fauna Norvegica Series C. Cinculus* 9: 100-106.
- Sonerud, G.A. 1986b: Effects of snow cover on seasonal changes in diet, habitat and regional distribution of raptors that prey on small mammals in the boreal zone of Fennoscandia. - *Holarctic Ecology* 9: 33-47.
- Temeles, E.J. 1985: Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. - *American Naturalist* 125: 485-499.
- Widen, P. 1994: Habitat quality for raptors: a field experiment. - *Journal of Avian Biology* 25: 219-223.