

Are forest birds categorised as “edge species” strictly associated with edges?

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Imbeau, L., Drapeau, P. and Mönkkönen, M. 2003. Are forest birds categorised as “edge species” strictly associated with edges? – *Ecography* 26: 514–520.

In recent years, studies of bird-habitat relationships undertaken in the context of habitat fragmentation have led to the widespread use of species categorisation according to their response to edge alongside mature forest patches (edge species, interior species, interior-edge generalist species). In other research contexts, especially in less fragmented landscapes dominated by a forested land base in various age classes, bird-habitat relationships are often described in relation to their use of various successional stages (early-successional species, mature forest species, generalist species). A simple comparison of these two commonly-used classifications schemes in a close geographical range for 60 species in eastern North America as well as for 36 species in north-western Europe clearly reveals that in these two particular biomes the two classifications are not independent. We believe that this association is not only a semantic issue and has important ecological consequences. For example, almost all edge species are associated with early-successional habitats when a wide range of forest age-classes are found in a given area. Accordingly, we suggest that most species considered to prefer edge habitats in agricultural landscapes are in fact only early-successional species that could not find shrubland conditions apart from the exposed edges of mature forest fragments. To be considered a true edge species, a given species should require the simultaneous availability of more than one habitat type and consequently should be classified as a habitat generalist in its use of successional stages. However, 28 out of 30 recognised edge species were considered habitat specialists in terms of successional status. Based on these results, we conclude that “real edge species” are probably quite rare and that we should make a difference between true edge species and species which in some landscapes, happen to find their habitat requirements on edges.

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During the last two decades, research on bird-habitat relationships has been undertaken largely within the perspective of habitat fragmentation. Ecologists have devoted considerable efforts to identify potential patch size and isolation effects on the composition of bird assemblages and species' abundance patterns in forest fragments (e.g. Ambuel and Temple 1983, Opdam et al. 1985, Freemark and Merriam 1986, Blake and Karr

1987, Freemark and Collins 1992). To identify such fragmentation effects, a common practice in avian ecology has consisted of classifying birds according to their response to habitat edge (e.g. Whitcomb et al. 1981, Freemark and Merriam 1986, Askins et al. 1987). Bender et al. (1998) provide a good example of a typical classification scheme. They categorised individual species' responses according to three possible types of

Accepted 30 December 2002

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ISSN 0906-7590

habitat use within patches: 1) edge species, which are associated primarily with the perimeter of a habitat patch and not the core; 2) interior species, which are associated with the centre of patches, thereby avoiding edge habitat; and 3) interior-edge generalist species, which utilise both edge and interior habitats. In such a framework, edge species are believed to be associated to the greater vegetative complexity usually found at forest boundaries or to require the simultaneous availability of more than one type of habitat (Yahner 1988, Hunter 1990, Matlack and Litvaitis 1999). Bender et al. (1998) found that this categorisation of species according to their forest habitat use was a major determinant of species response to habitat loss and fragmentation. For instance, they found that edge species experienced a decline in population size that was less than predicted by pure habitat loss of patches alone. Most of the studies that have used such ecological categories were conducted in landscapes where the forest land base was converted into other land uses (agriculture, urban development). Such highly fragmented landscapes can be defined as contrasted divided environments (*sensu* Addicott et al. 1987) of simple forest and non-forest habitats.

In contrast to studies conducted in converted landscapes with remnant mature forest fragments, in forested ecosystems natural disturbances or timber harvesting generate mosaics of forest cover types at different stages of development. In such landscapes, researchers usually have a better opportunity to document distribution patterns of birds across habitats and provide essential information regarding the basic habitat associations of forest-associated species than in highly converted fragmented landscapes such as those in agricultural areas. When forest fragmentation is not the key-issue studied, a common classification scheme in such cases is to categorise each species according to their use of various successional stages (e.g. Hagan et al. 1997, Imbeau et al. 1999, Drapeau et al. 2000, see also Helle and Fuller 1988 as well as Helle and Mönkkönen 1990 for a review of more than 25 earlier studies): 1) early-successional species are associated with regenerating shrublands or young forests; 2) mature forest species are associated only with older forest stands; and 3) generalist species occur in all successional stages.

Seral stage associations vs edge avoidance classifications

Because large tracts of forestlands under natural or anthropogenic disturbance regimes and converted landscapes with remnant forest fragments are rarely located in the same region, only one of these two forest bird classifications is generally used in published scientific

studies. For example, Freemark and Collins (1992) classified responses to edge for 102 bird species occurring in deciduous forest fragments embedded in agricultural matrices located in Ontario, Missouri, and Illinois. On the other hand, Drapeau et al. (2000) classified 84 species occurring in Québec's mixed-wood forested landscapes in relation to their preferred successional status. A total of 57 species are classified in both studies. Three additional species reported in Drapeau et al. (2000) have also been classified by Freemark and Merriam (1986). To our present knowledge, these studies represent the best case in North America of a simultaneous availability of both classifications for a large number of species in a relatively close geographical range. A simple comparison of these two classifications clearly reveals that most forest-interior species in small fragments are also associated with mature forests in a forested landscape (Fig. 1). But more importantly,

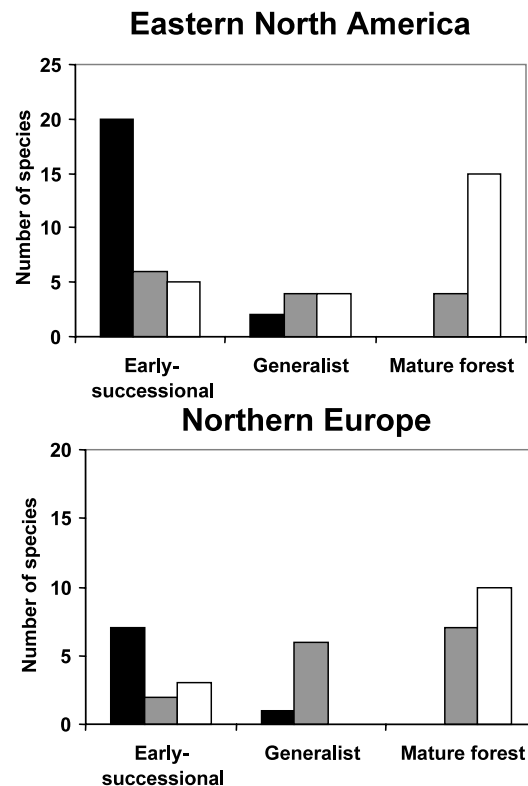


Fig. 1. Comparison between successional status of 96 breeding birds species in forested landscapes and their corresponding habitat use in forest fragments in agricultural landscapes. Edge species (black bars) are mostly categorised as early-successional, interior species (white bars) as mature forest species, while edge-interior generalists (grey bars) are found in all categories. Classifications for successional status were obtained in Drapeau et al. (2000) for eastern North America and in Haapanen (1965), Mönkkönen (1984) or Helle (1985) in northern Europe. Classification for patch use were obtained in Freemark and Collins (1992) or Freemark and Merriam (1986) for eastern North America and in Kurlavicius (1995) or Cieślak (1992) in northern Europe.

almost all edge species are associated with early-successional habitats or young forests when a wide range of forest age-classes are found in a given area. This pattern is strong enough to reject a null hypothesis of total independence between these two classifications (G-test, $p < 0.005$; data in Appendix 1). A similar pattern was found in European bird classifications. Data on preferred successional stages in natural or industrial forests were obtained in Haapanen (1965), Helle (1985), and Mönkkönen (1984) in northern Europe (Finland). Response to edges in a close geographical range were available in Kurlavicius (1995; Lithuania) for 28 species, and in Cieślak (1992; Poland) for an additional 8 species. Again, the same pattern was found between these two classifications, which was strong enough to reject a null hypothesis of total independence between them (G-test, $p < 0.005$; details in Appendix 1). Both G-tests are uncorrected to account for phylogenetic relationships because we are not attempting to make any evolutionary statement in which we would have to make assumptions about the possible changes along evolution in successional and edge-related traits. Our point here is that it seems that in these two particular biomes the two classifications are not independent.

We believe that this simple correlation between edge species and early-successional species, although apparently trivial, is not only a semantic issue and has at least two important ecological consequences. First, most species considered to prefer edge habitats in agricultural landscapes are in fact only early-successional species that could not find shrubland conditions apart from the exposed edges of mature forest fragments. The high land use activity in agricultural fields probably "push" early-successional species to live in edges but they apparently not require to do so in other conditions. Thus, it seems that in a strict sense, these edge species are not attracted to the greater vegetative complexity occurring at forest boundaries per se. The presence of a shrub layer in itself is probably sufficient to explain the occurrence of early-successional species along these edges.

Secondly, forest-interior species are likely to avoid the edge of a patch simply because characteristics at forest edges, especially vegetation structure, differ from those found in mature forests. We believe that the variability in the pattern of edge-avoidance of several species considered to be forest-interior birds, as shown by Villard (1998), might in fact simply reflect the variability in the extent of edge-induced modifications in various forest patches across studies (detailed edge characteristics are usually never reported in such studies). This could be verified by studying the distribution of late-successional forest species, considered forest-interior specialists, near and away from abrupt edges created by forestry, which probably show a simpler vegetation structure than fragments located in agricultural areas. In such cases, we expect that edge-avoid-

ance patterns should not be predominant among late-successional forest species. Indeed, Hansson (1994) found that many boreal forest birds preferring mature forest showed no avoidance of edges, and even that some species were more abundant at edges than in the forest interior (see also Helle 1983). Another example is given by Lambert and Hannon (2000), where ovenbird *Seiurus aurocapillus* territories included forest edges near a clear-cut border in 100-m buffer strips. If edge-avoidance patterns are found (see Brand and George 2001), detailed vegetation sampling should be conducted to ensure that they are not tied to specific habitat characteristics that may differ alongside edges.

In the case of studies using nest site placement as a measure of edge-avoidance, we have to point out another important consideration that should not be neglected. During the breeding period, all forest birds are central place foragers, i.e. they do not consume their prey where they are captured but return with them to the nest to feed dependent offspring (Orians and Pearson 1979). In such cases, it is generally recognised that if the habitat is plane and uniform, the optimal foraging area will be bounded by a circle around the central place, in this case, nest site (Andersson 1981). For a "forest-interior" bird, placing its nest along an agricultural edge (or along any habitat which is not optimal for foraging) seems to be a very bad strategy (Huhta et al. 1999). In fact, according to central place foraging theory, we should be expecting edge-avoidance proportional to home range size for nest site placement in such breeding birds.

Thirdly, the use of a classification scheme based on species' response to edges of fragmented habitats is landscape-dependent. It is thus tied to the structure of the entire landscape mosaic not only the size or shape of habitat fragments. It does not stem strictly from the life-history characteristics of a given species. For instance, an edge-associated species occupying patches located in an agricultural landscape is likely to be found on the edge as well as in the interior of its preferred habitat in a forested landscape: regenerating stands in early-successional stages. Therefore, there is possibly no absolute classification relating to edge preference or edge avoidance; a fact which is often neglected in meta-analyses of fragmentation studies (e.g. Bender et al. 1998). In the case of so-called interior-edge generalists, their roughly equal distribution among early-successional specialists, generalists, and mature forest specialists may explain why some behave as area-sensitive species while others could be more easily classified as edge species (Austen et al. 2001). On the other hand, we must point out that classifications based on successional status might also be affected by the latitude and the ecoregion where a study is conducted; some species do show some startling changes in habitat use in different regions. This is why we have attempted to compare bird classifications in studies conducted in a

close geographical range. Still, early-successional habitats in Drapeau et al. (2000) were dominated by deciduous tree species while mature forests were largely coniferous. Several early-successional species in this boreal region (e.g. blue jay, broad-winged hawk, downy woodpecker, eastern wood-pewee, rose-breasted grosbeak, veery; scientific names given in Appendix 1) are probably more associated with mature forests in temperate regions studied by Freemark and Collins (1992). However, if these species were categorised as mature forest species, the pattern we have found (a strong association between early-successional and edge species) would only be stronger than what we have documented here.

What is really an edge species?

Considering the ecological requirements of forest bird species found in natural habitats, which is generally described in reference to various successional stages, we can even question the validity of the edge-species concept. A true edge species should not be found only in either one of two separated, distinct habitats. Instead, it should only occur in a limited area located at the boundaries of two different habitats, and require non-substitutable resources found in these two habitats. Consequently, regions of the landscape where both habitats are relatively close will support more individuals than regions where one habitat is relatively rare (Dunning et al. 1992). Early successional species (associated to young forests or shrublands) as well as mature forest species do not seem to be likely candidates for edge species. Indeed, they are habitat specialists found preferentially in a given successional stage, and apparently do not need the complementation of more than one type of habitat to fulfil their nesting activities. On the other hand, species appearing as generalists in terms of habitat structure may, at least potentially, require more than one habitat type within their home range. Unfortunately, the evidence presented here is weak: only 2 out of 10 North American generalist species according to Drapeau et al. (2000) were categorised as edge species in forest fragments (Freemark and Merriam 1986, Freemark and Collins 1992): the American crow and the white-throated sparrow. However, the white-throated sparrow is considered early-successional in other similar successional studies (Crête et al. 1995, Imbeau et al. 1999). Similarly, only one out of seven European generalist species was categorised as an edge species in forest fragments: the yellowhammer. According to data available within studies used in this paper for 96 forest bird species, only the American crow and the yellowhammer could possibly deserve a landscape-independent edge species status. Based on these results, we agree with Hansson (1983) and Hunter (1990) that

“real edge species” are probably quite rare. This statement is especially true in agricultural landscapes in which the contrast between edges is extreme and where row crop fields offer limited usable resources to potential edge species during much of the breeding season. To conclude, we believe that we should make a difference between true edge species and species which in some landscapes, happen to find their habitat requirements on edges.

Acknowledgements – We wish to thank Marc Bélisle, Daniel Brongo, Shelley Hinsley, Marc Mazerolle, Antoine Nappi, and Jean-Michel Roberge for their helpful suggestions on previous drafts of this manuscript. Financial support while writing this commentary was provided by post-doctoral scholarships from the Natural Sciences and Engineering Research Council of Canada (NSERC) and NSERC-UQAT-UQAM industrial Chair in sustainable forest management to LI and by the Academy of Finland to MM.

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Appendix 1. Successional status and patch use classifications for 96 bird species for which both classifications were available in a close geographical range.

Region	English name	Scientific name	Successional status		Patch use	
			Classification	Reference	Classification	Reference
North America	Alder flycatcher	<i>Empidonax alnorum</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	American crow	<i>Corvus brachyrhynchos</i>	Generalist	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	American goldfinch	<i>Carduelis tristis</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	American kestrel	<i>Falco sparverius</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	American redstart	<i>Setophaga ruticilla</i>	Generalist	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	American robin	<i>Turdus migratorius</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Black-and-white warbler	<i>Mniotilta varia</i>	Generalist	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Black-capped chickadee	<i>Poecile atricapilla</i>	Generalist	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Black-throated blue warbler	<i>Dendroica caerulescens</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Black-throated green warbler	<i>Dendroica virens</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Blackburnian warbler	<i>Dendroica fusca</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Blackpoll warbler	<i>Dendroica striata</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Merriam 1986
	Blue jay	<i>Cyanocitta cristata</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Broad-winged hawk	<i>Buteo platypterus</i>	Early-successional	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Brown creeper	<i>Certhia americana</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Brown thrasher	<i>Toxostoma rufum</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Canada warbler	<i>Wilsonia canadensis</i>	Early-successional	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Cedar waxwing	<i>Bombycilla cedrorum</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Chestnut-sided warbler	<i>Dendroica pensylvanica</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Chipping sparrow	<i>Spizella passerina</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Common grackle	<i>Quiscalus quiscula</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Common raven	<i>Corvus corax</i>	Generalist	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Common yellowthroat	<i>Geothlypis trichas</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Downy woodpecker	<i>Picoides pubescens</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Eastern kingbird	<i>Tyrannus tyrannus</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Eastern wood-pewee	<i>Contopus virens</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Golden-crowned kinglet	<i>Regulus satrapa</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Hairy woodpecker	<i>Picoides villosus</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Hermit thrush	<i>Catharus guttatus</i>	Early-successional	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Least flycatcher	<i>Empidonax minimus</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Magnolia warbler	<i>Dendroica magnolia</i>	Generalist	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Mourning warbler	<i>Oporornis philadelphia</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Nashville warbler	<i>Vermivora ruficapilla</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Northern flicker	<i>Colaptes auratus</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Northern goshawk	<i>Accipiter gentilis</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Merriam 1986
	Northern parula	<i>Parula americana</i>	Mature forests	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Northern waterthrush	<i>Seiurus noveboracensis</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Olive-sided flycatcher	<i>Contopus cooperi</i>	Early-successional	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Ovenbird	<i>Seiurus aurocapillus</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Pileated woodpecker	<i>Dryocopus pileatus</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Purple finch	<i>Carpodacus purpureus</i>	Mature forests	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Red-breasted nuthatch	<i>Sitta canadensis</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Red-eyed vireo	<i>Vireo olivaceus</i>	Generalist	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Red-tailed hawk	<i>Buteo jamaicensis</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Red-winged blackbird	<i>Agelaius phoeniceus</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	Early-successional	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992
	Ruby-throated hummingbird	<i>Archilochus colubris</i>	Early-successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Ruffed grouse	<i>Bonasa umbellus</i>	Generalist	Drapeau et al. 2000	Interior-edge	Freemark and Collins 1992

Appendix 1. (Continued).

Region	English name	Scientific name	Successional status		Patch use	
			Classification	Reference	Classification	Reference
Europe	Sharp-shinned hawk	<i>Accipiter striatus</i>	Mature forests	Drapeau et al. 2000	Interior–edge	Freemark and Collins 1992
	Song sparrow	<i>Melospiza melodia</i>	Early–successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Swainson's thrush	<i>Catharus ustulatus</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Swamp sparrow	<i>Melospiza georgiana</i>	Early–successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Tennessee warbler	<i>Vermivora perigrina</i>	Generalist	Drapeau et al. 2000	Interior–edge	Freemark and Merriam 1986
	Tree swallow	<i>Tachycineta bicolor</i>	Early–successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Veery	<i>Catharus fuscescens</i>	Early–successional	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	White-throated sparrow	<i>Zonotrichia albicollis</i>	Generalist	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Winter wren	<i>Troglodytes troglodytes</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	Mature forests	Drapeau et al. 2000	Interior–edge	Freemark and Collins 1992
	Yellow-rumped warbler	<i>Dendroica coronata</i>	Mature forests	Drapeau et al. 2000	Interior	Freemark and Collins 1992
	Yellow warbler	<i>Dendroica petechia</i>	Early–successional	Drapeau et al. 2000	Edge	Freemark and Collins 1992
	Black woodpecker	<i>Dryocopus martius</i>	Mature forest	Helle 1985	Interior	Kurlavicius 1995
	Blackbird	<i>Turdus merula</i>	Early–successional	Haapanen 1965	Interior	Kurlavicius 1995
	Bullfinch	<i>Pyrrhula pyrrhula</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Chaffinch	<i>Fringilla coelebs</i>	Generalist	Mönkkönen 1984	Interior–edge	Cieślak 1992
	Chiffchaff	<i>Phylloscopus collybita</i>	Mature forest	Haapanen 1965	Interior–edge	Kurlavicius 1995
	Coal tit	<i>Parus ater</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Crested tit	<i>Parus cristatus</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Dunnock	<i>Prunella modularis</i>	Early–successional	Mönkkönen 1984	Interior–edge	Kurlavicius 1995
	Garden warbler	<i>Sylvia borin</i>	Early–successional	Haapanen 1965	Interior–edge	Kurlavicius 1995
	Goldcrest	<i>Regulus regulus</i>	Mature forest	Haapanen 1965	Interior–edge	Kurlavicius 1995
	Great spotted woodpecker	<i>Dendrocopos major</i>	Generalist	Mönkkönen 1984	Interior–edge	Cieślak 1992
	Great tit	<i>Parus major</i>	Generalist	Mönkkönen 1984	Interior–edge	Kurlavicius 1995
	Hazel grouse	<i>Bonasa bonasia</i>	Mature forest	Helle 1985	Interior	Kurlavicius 1995
	Icterine warbler	<i>Hippolais icterina</i>	Early–successional	Haapanen 1965	Edge	Kurlavicius 1995
	Jay	<i>Garrulus glandarius</i>	Early–successional	Mönkkönen 1984	Interior	Kurlavicius 1995
	Lesser whitethroat	<i>Sylvia curruca</i>	Early–successional	Mönkkönen 1984	Edge	Kurlavicius 1995
	Mistle thrush	<i>Turdus viscivorus</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Ortolan bunting	<i>Emberiza hortulana</i>	Early–successional	Helle 1985	Edge	Cieślak 1992
	Pied flycatcher	<i>Ficedula hypoleuca</i>	Mature forest	Haapanen 1965	Interior–edge	Kurlavicius 1995
	Pied wagtail	<i>Motacilla alba</i>	Early–successional	Helle 1985	Edge	Cieślak 1992
	Red-backed shrike	<i>Lanius collurio</i>	Early–successional	Mönkkönen 1984	Edge	Cieślak 1992
	Redstart	<i>Phoenicurus phoenicurus</i>	Mature forest	Helle 1985	Interior–edge	Kurlavicius 1995
	Redwing	<i>Turdus iliacus</i>	Early–successional	Helle 1985	Edge	Kurlavicius 1995
	Robin	<i>Erithacus rubecula</i>	Generalist	Mönkkönen 1984	Interior–edge	Kurlavicius 1995
	Siskin	<i>Carduelis spinus</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Song thrush	<i>Turdus philomelos</i>	Mature forest	Helle 1985	Interior–edge	Kurlavicius 1995
	Spotted flycatcher	<i>Muscicapa striata</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Tree pipit	<i>Anthus trivialis</i>	Generalist	Helle 1985	Interior–edge	Cieślak 1992
	Treecreeper	<i>Certhia familiaris</i>	Mature forest	Haapanen 1965	Interior	Kurlavicius 1995
	Whitethroat	<i>Sylvia communis</i>	Early–successional	Haapanen 1965	Edge	Cieślak 1992
	Willow tit	<i>Parus montanus</i>	Mature forest	Haapanen 1965	Interior–edge	Kurlavicius 1995
	Willow warbler	<i>Phylloscopus trochilus</i>	Generalist	Helle 1985	Interior–edge	Kurlavicius 1995
	Wood warbler	<i>Phylloscopus sibilatrix</i>	Mature forest	Mönkkönen 1984	Interior–edge	Kurlavicius 1995
	Wren	<i>Troglodytes troglodytes</i>	Mature forest	Helle 1985	Interior	Kurlavicius 1995
	Wryneck	<i>Jynx torquilla</i>	Early–successional	Helle 1985	Interior	Kurlavicius 1995
Yellowhammer	<i>Emberiza citrinella</i>	Generalist	Haapanen 1965	Edge	Cieślak 1992	