Umbrella Species as a Conservation Planning Tool

An Assessment Using Resident Birds in Hemiboreal and Boreal Forests

Jean-Michel Roberge
Faculty of Natural Resources and Agricultural Sciences
Department of Conservation Biology
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2006

Acta Universitatis Agriculturae Sueciae
2006: 84

ISSN 1652-6880
ISBN 91-576-7133-8

Tryck: SLU Service/Repro, Uppsala 2006

Abstract

Roberge, J.-M. 2006. *Umbrella species as a conservation planning tool: an assessment using resident birds in hemiboreal and boreal forests*. Doctor's dissertation.
ISSN 1652-6880, ISBN 91-576-7133-8.

In northern Europe, a long history of anthropogenic land use has led to profound changes within forest ecosystems. One of the proposed approaches for conservation and restoration of forest biodiversity is the use of umbrella species, whose conservation would confer protection to large numbers of naturally co-occurring species. This thesis aims to evaluate some of the prerequisites to the umbrella species concept, focusing on resident birds in hemiboreal and boreal forests. The study was performed in four areas belonging to the southern Baltic Sea region: central and southern Sweden, south-central Lithuania and northeastern Poland. A review of empirical evaluations of the umbrella species concept performed in various systems suggested that multispecies approaches addressing the requirements of both the umbrellas and the beneficiary species have better potential than approaches based coarsely on the area needs of single species. An analysis of co-occurrence patterns among resident forest birds in landscape units of 100 ha showed that some species reliably indicated high species richness through their presence. For birds of deciduous forests, there was high cross-regional consistency in the identity of the best indicators. Specialised woodpeckers (Picidae) were prominent among the species that performed well as indicators. Their presence in the landscape units was generally linked positively to the degree of naturalness of the forest and to the amounts of resources that have become scarce in intensively managed forests, such as dead wood and large trees. In Sweden, occurrence of the white-backed woodpecker (*Dendrocopos leucotos*) in bird atlas squares was positively related to species richness among forest birds of conservation concern, as well as to the area of deciduous and mixed forests of high value for conservation. Moreover, the number of red-listed cryptogam species linked to deciduous trees and dead wood was higher where the woodpecker bred. Those results for birds of northern forests suggest that the umbrella species concept may constitute a useful component of conservation planning, especially in the work towards the derivation of quantitative targets. However, umbrella species are not a panacea and should therefore be seen as part of a complementary suite of approaches.

Keywords: biodiversity, conservation planning, cross-regional assessment, forest naturalness, hemiboreal forests, indicator species, management targets, resident birds, umbrella species, woodpeckers.

Author's address: Jean-Michel Roberge, Grimsö Wildlife Research Station, Department of Conservation Biology, Swedish University of Agricultural Sciences (SLU), S-730 91 Riddarhyttan, Sweden. E-mail: Jean-Michel.Roberge@nvb.slu.se

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Roberge, J.-M. & Angelstam, P. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology 18*, 76-85.

II. Roberge, J.-M. & Angelstam, P. 2006. Indicator species among resident forest birds – a cross-regional evaluation in northern Europe. *Biological Conservation 130,* 134-147.

III. Roberge, J.-M., Angelstam, P. & Villard, M.-A. Specialised woodpeckers and naturalness in hemiboreal forests – deriving quantitative targets for conservation planning. *Manuscript*.

IV. Roberge, J.-M., Mikusiński, G. & Svensson, S. The white-backed woodpecker: umbrella species for forest conservation planning? *Manuscript*.

Introduction

Background

North European forests have been subject to extensive anthropogenic influence, including forest clearance for agriculture and various activities that have affected the internal characteristics of the forests (McNeely, 1994; Östlund, Zackrisson & Axelsson, 1997; Lindbladh & Bradshaw, 1998). As a consequence of those changes, the populations of many species dependent on properties found in naturally dynamic forests have declined or even gone extinct (Ingelög, Andersson & Tjernberg, 1993; de Jong, 2002; Gärdenfors, 2005). A number of international initiatives have been undertaken that promote sustainable forest management and the halting of forest biodiversity loss, such as the Montréal Process and the Ministerial Conference on the Protection of Forests in Europe (Rametsteiner & Mayer, 2004). The conservation of forest biodiversity has also been integrated into legislation at the national level. In the Swedish Forestry Act, for example, sustained forest production and the maintenance of viable populations of all naturally occurring forest species are stated to be two goals of equal importance (Anon., 1994).

The maintenance of forest biodiversity requires sound ecological knowledge about its elements (composition, structure and function; *cf.* Noss, 1990). Moreover, it requires an understanding of the effects of different management regimes on biodiversity, as well as the development of tools for the conservation and restoration of forest ecosystems. This thesis presents results from applied ecological research that will contribute to the knowledge base for conservation planning and management in forested landscapes.

Approaches to conserving forest biodiversity

Following the emergence of the concept of biological diversity in the 1970s-1980s (Kaennel, 1998), conservation biologists showed growing interest in developing shortcuts for the conservation of whole biota. In the face of limited funding, knowledge, and time for action, two main types of approaches were proposed: species-oriented approaches (Landres, Verner & Thomas, 1988; Tracy & Brussard, 1994) and ecosystem approaches (Franklin, 1993; Walker, 1995; Hansson & Larsson, 1997).

In species-oriented approaches, the focus is generally on one or a limited set of species instead of whole ecosystems. In many cases, the efforts are directed towards species of special conservation concern. In Europe, for example, the EU Birds Directive (Anon., 1979) and the Habitats Directive (Anon., 1992) list species whose habitats should be the subject of special conservation measures in order for their populations to attain a "favourable conservation status". Special recovery plans for endangered species constitute another common type of species-based conservation strategies. Species-oriented approaches may also focus on: (1) species which can be used as indicators for different attributes of the environment (‘indicator species’; Landres, Verner & Thomas, 1988; Noss, 1990; Carignan & Villard, 2002); (2) species which play a crucial role in maintaining the organisation and diversity within communities (‘keystone species’; Paine, 1969; Mills, Soulé & Doak, 1993); (3) charismatic species that can be used as a symbol for raising conservation awareness and action (‘flagship species’; Simberloff, 1998); or (4) very demanding or sensitive species whose conservation is expected to benefit the populations of several co-occurring species (‘umbrella species’; Caro & O’Doherty, 1999; Fleishman, Murphy & Brussard, 2000).

Given the limitations posed by the huge numbers of (known and unknown) species in the earth’s biota and by our relatively low level of knowledge of their requirements, ecosystem approaches have been proposed as an alternative to species-based management (Franklin, 1993). Such approaches typically focus on conserving the essential structures and processes in the ecosystem (Walker, 1995; Hansson & Larsson 1997). Key elements include the establishment of protected areas to secure native habitats, an adapted management of the landscape matrix and a range of restoration measures based on general ecological principles (Franklin, 1993; Lindenmayer & Franklin, 2002).

Following a long-standing debate, the proponents of the species-based and ecosystem approaches now seem to have come close to a consensus through the observation that the distinction between the two approaches may be a ‘false dichotomy’ (Wilcove, 1994a). Indeed, both of these approaches should be considered as part of a continuum of necessary steps for biodiversity conservation (Wilcove, 1994b; Thompson & Angelstam, 1999). Although ecosystem approaches could provide an effective ‘coarse filter’ for biodiversity conservation, species of conservation concern not captured by the filter may still require special management. Some species, *e.g.* indicator species, may also prove useful for monitoring the effects of ecosystem management. Moreover, while general knowledge on ecosystem processes and structures is essential, referring to the requirements of the species is crucial in order to establish concrete and quantitative landscape design criteria at multiple spatial and temporal scales (Hansen *et al.*, 1993; Lambeck, 1997, 1999). Finally, species may constitute effective tools for communicating the needs for conservation and restoration to the different actors (Thompson & Angelstam, 1999; Freudenberger & Brooker, 2004). Therefore, there is a need to integrate the species-based and ecosystem approaches in conservation planning and management (Carignan & Villard, 2002).

The umbrella species concept

An umbrella species can be defined as a species whose conservation confers protection to a large number of naturally co-occurring species (Fleishman, Murphy & Brussard, 2000). The umbrella species concept has been proposed as a way to use species requirements to guide ecosystem management. Its main premise is that directing management efforts toward the requirements of the most exigent (*i.e.*, umbrella) species is likely to address those of many co-occurring species that use the same habitat or resource.

The concept of umbrella species is related to that of indicator species, but the two concepts emphasise different uses of species in conservation planning. Landres, Verner & Thomas (1988) defined an indicator species as "an organism whose characteristics (*e.g.*, presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest". Thus, indicator species are used to provide a surrogate measure for some ecological attribute, for example species richness within a given taxonomic group. The umbrella species concept goes further by stating that management or conservation efforts directed at the most demanding species for some properties will also benefit other species dependent on the same properties (Lambeck, 1997). While the focus of the indicator species concept is on using the status of a given species to 'indicate' something about the environment, the umbrella species concept emphasises the effects of conservation actions directed at the umbrella species on the populations of other species. Therefore, the umbrella species concept generally makes explicit reference to the types and size of habitats to be protected or restored (Caro & O'Doherty, 1999), with consideration to the requirements of the species or to their sensitivity to anthropogenic land uses. The indicator and umbrella species concepts are not mutually exclusive. Indeed, it is necessary for an umbrella species to be a reliable indicator of the presence of a large number of naturally co-occurring species (Fleishman, Murphy & Brussard, 2000), as this provides some assurance of a wide umbrella coverage.

The exact origin of the umbrella species concept is unclear. Frankel & Soulé (1981) used the term 'umbrella' to suggest that conservation measures directed at the largest species could confer protection to "denser species". A few years later, Wilcox (1984) proposed that management should focus on those species whose habitat requirements are "at least as comprehensive as that of the rest of the community", thus providing a "protective umbrella" for other species. Other authors had put forward the same basic idea before that, although without using the term 'umbrella' (*e.g.*, Eisenberg, 1980; East, 1981; Mealy & Horn, 1981).

To assess trends in the use of the umbrella species concept in biological research, I surveyed the last 17 years of all journals included in the BIOSIS database (the accessed version of the database did not include papers published before 1989). I searched all fields for the term 'umbrella(s)' and then examined the abstracts to eliminate papers that did not refer to the umbrella species concept. The yearly numbers of records were divided by the total number of papers in the database for each year, so as to correct for a general increase in the amount of biological literature. The observed pattern is one of a clear positive trend in the number of citations throughout the 1990s and well into the 2000s, with the highest number of papers for the last year (Fig. 1). Thus, the umbrella species concept is more popular than ever, at least as a theoretical notion. However, most references to the umbrella species concept do not include any empirical evaluation (*cf.*, Paper I). This stresses the need to assess critically the validity of that potential conservation tool in various systems.

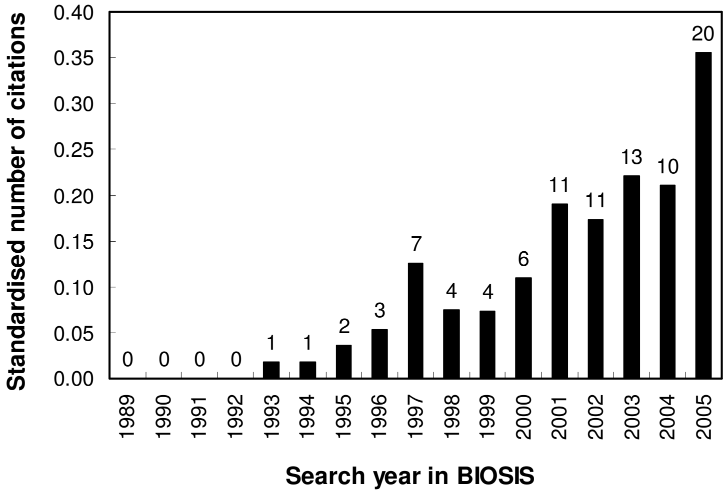

Fig. 1. Yearly numbers of references to the umbrella species concept in the BIOSIS database for the period 1989-2005, standardised by the total number of papers in the database for each year. The figures above the bars give the actual (unstandardised) numbers of references.

Resident birds of north European forests as a model group

Among the various taxonomic groups that have been proposed as conservation planning tools, birds present many advantages: (1) They are well-studied; knowledge on their taxonomy, habitat requirements and life histories is good relative to other taxonomic groups. (2) Birds are easily surveyed; their detection and identification is facilitated by the fact that many species advertise their presence through vocalisations. Indeed, data on tens of species can be collected simultaneously using a single survey method. As a consequence, birds present relatively low inventory costs compared to other taxonomic groups (Juutinen & Mönkkönen, 2004). (3) Their occurrence, abundance and reproductive success has been shown to be influenced by habitat composition and configuration at multiple scales, from that of the individual substrates for nest placement (*e.g.*, Stenberg, 1996) through the forest stand scale (*e.g.*, Harrison, Schmiegelow & Naidoo, 2005) and to the landscape and regional scales (Drapeau *et al.*, 2000; Pakkala, Hanski & Tomppo, 2002; Huhta *et al.*, 2004). (4) They represent a wide range of ecological guild types (Glennon & Porter, 2005). (5) Many bird species occupy high trophic levels and may thereby respond to functional changes in the food web on which they rely (O'Connell, Jackson & Brooks, 2000; Carignan & Villard, 2004). (6) Many birds have large distribution ranges, yielding large potential geographical domains for their use as conservation planning tools. (7) Due to their charisma, many birds are useful tools for communicating the needs for habitat conservation and restoration to the stakeholders and may function as flagship species (Uliczka, Angelstam & Roberge, 2004; Liedholm, 2006).

Among north European forest birds, resident species are a particularly interesting group from a conservation point of view. Their ecology is relatively well known due to a long history of research (Wiens, 1989). Many resident species have life-history traits that make them vulnerable to intensive forest management (Imbeau, Mönkkönen & Desrochers, 2001). Consequently, residents are prominent among forest species that have declined following the advance of industrial forestry in boreal Europe (Väisänen, Järvinen & Rauhala, 1986). While aspects of the ecology of migrants are affected by events occurring on their wintering grounds or along migratory routes (Marra, Hobson & Holmes, 1998), resident species usually spend their whole life cycle within a restricted area, which facilitates the identification of the factors behind population changes (Landres, Verner & Thomas, 1988; Hannon & McCallum, 2004). Moreover, in northern forests most resident bird species can be surveyed efficiently during a relatively short period in early spring.

There are, however, a number of limitations to the usefulness of birds as tools for conservation planning. One is that birds are highly mobile organisms. Thus, landscapes that are suitable for birds may not necessarily have high enough connectivity for species from other taxonomic groups that disperse less easily (Lindenmayer & Fischer, 2003; Freudenberger & Brooker, 2004). Moreover, birds may not always indicate habitat quality for taxa dependent on fine-scale microhabitats or on properties that are not directly relevant to avian habitat selection (Rubinoff, 2001; Lindenmayer & Fischer, 2003). Therefore, birds alone would not be sufficient as biodiversity indicators or umbrella species. There is a need for a greater taxonomic variety in any indicator system or species-based conservation planning tool. Still, due to the numerous advantages offered by birds – and particularly resident species – they offer a good starting point for evaluating some of the prerequisites to the umbrella species concept.

Rationale for the thesis

This thesis builds on four papers dealing with different aspects of the use of species as tools in conservation planning. The overarching rationale for the thesis can be summarised as follows:

To begin with, the conceptual framework for the umbrella species concept is presented in Paper I, where the empirical evidence for the usefulness of this concept is reviewed. The following three papers aim to evaluate some of the prerequisites to the umbrella species concept, focusing on resident birds in European hemiboreal and boreal forests. As stated above, an effective umbrella species should be a reliable indicator of species-rich communities. Moreover, it should ideally indicate the presence or abundance of many species of special conservation concern. Paper II focuses on identifying such indicator species among resident forest birds. A second requirement for a species to function as an umbrella species is that it should have large requirements regarding some resources or a high degree of sensitivity to human disturbance (Lambeck, 1997). Moreover, those requirements should be both quantifiable and manageable. Paper III focuses on four species of specialised woodpeckers (Aves: Picidae) that were shown to have a high indicator value in Paper II and that have high requirements for resources which are scarce in today's managed forests. In that paper, the relationship between the occurrence of those woodpeckers and the characteristics of the forest ecosystem is assessed with the aim to derive targets for conservation management. One of those species, the white-backed woodpecker (*Dendrocopos leucotos*), is a *de facto* umbrella species for forest conservation in Fennoscandia. Paper IV evaluates the potential of this woodpecker as an umbrella species for conservation of the biodiversity associated with deciduous and mixed forests containing large amounts of dead wood.

Objectives and methods

The umbrella species concept as a conservation tool (Paper I)

The aims of Paper I were to (1) review the history of the umbrella species concept and distinguish its different uses, (2) evaluate the extent to which the concept has been validated empirically, and (3) suggest directions regarding the use of umbrella species in conservation planning.

This paper covers the literature published on the umbrella species concept, without geographical or taxonomic constraints. The literature was obtained through examining biological database information and reference lists from relevant papers. Only papers published in English were considered. In total, 110 published peer-reviewed articles, book chapters, governmental research papers and technical reports, as well as papers from conference proceedings that discussed the umbrella species concept were included in this review.

Indicator species among resident forest birds and requirements of specialised woodpeckers (Papers II and III)

Focusing on resident forest birds, Paper II aimed to (1) explore whether the occurrence of some species could be used to indicate high species richness and abundance of other bird species, and (2) compare the results among four regions characterised by a common species pool, but different forest management intensities and varying proportions of deciduous and coniferous trees. Then, for four species of woodpeckers that were shown to have a high indicator value, Paper III proceeds by (1) assessing the relationship between the occurrence of the woodpeckers and the degree of naturalness of the forest, and (2) quantifying the requirements of those species regarding critical resources in the different regions.

Biogeographically, the study system for Papers II and III was located in the European hemiboreal vegetation zone, situated between the boreal and lowland temperate forest ecoregions (Mayer, 1984; Laasimer *et al.*, 1993). Hemiboreal forests are characterised by the dominance of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with varying proportions of birch (*Betula* spp.) and aspen (*Populus tremula*), which are particularly abundant in early successional and unmanaged mid-successional phases. The proportion of broadleaved deciduous trees (*e.g.*, pedunculate oak *Quercus robur*, lime *Tilia cordata*, and ash *Fraxinus excelsior*) increases towards the south within the hemiboreal zone (Mayer, 1984), but has declined strongly over time due to anthropogenic land use (Björse & Bradshaw, 1998).

To address issues such as habitat loss, there is a need for landscape-scale research across regions (Angelstam *et al*., 2004). Northern Europe is characterised by strong gradients in land-use history yielding much geographical variation in the status of forest biodiversity (Angelstam *et al*., 1997). In landscapes of central and southern Sweden, for example, a long history of intensive management has modified the properties of the forests (*e.g.*, Linder & Östlund, 1992; Östlund, Zackrisson & Axelsson, 1997). Today, only small remnants of forests with a natural character can be found dispersed in a matrix of production forests. In the southeastern part of the Baltic Sea region, by contrast, relatively large areas of forest have been subject to much less intensive anthropogenic use. Here, reference landscapes can still be found where species composition and forest structures are similar to those of naturally dynamic forests (Faliński, 1986). These forests offer unique opportunities for research, because they allow the study of viable populations of species that have declined or become extirpated in the West, as well as of the characteristics of forest ecosystems that still are in a near-natural state (Angelstam *et al*., 2004). Moreover, performing studies in multiple regions may help answering the question as to whether the species identified as potential indicator or umbrella species in one area also can serve the task in other parts of their distribution range (Verner, 1984; Betrus, Fleishman & Blair, 2005; Sætersdal, Gjerde & Blom, 2005), and exploring the extent to which the requirements of the species are consistent in different parts of their distribution range (Fuller, 2002).

The study system included four areas belonging to the southern Baltic Sea drainage basin: Bergslagen (south-central Sweden), Småland (southern Sweden), south-central Lithuania and northeastern Poland (Fig. 2). These study areas were selected with two principal aims: (1) to cover a wide span of anthropogenic impact on forests, from near-natural benchmarks to altered systems, and (2) to account for the variation in the relative proportions of different tree species across the hemiboreal forest zone. Bergslagen lies in the transition zone between the south boreal and hemiboreal forest zones (Mayer, 1984). It is the study area with the longest history of intensive forest management. As a consequence, it is characterised by little forest in a near-natural state and a high dominance of coniferous stands (Angelstam, 1997). Småland also has a long history of land and forest management (Nordström *et al*., 1989), but still contains some larger tracts of near-natural forests characterised by a large deciduous component in the managed coniferous matrix (Andersson & Löfgren, 2000). In the south-central Lithuanian study area, the forests show considerable variation in tree species composition and vegetation structure, owing to a relatively low intensity of past forest management compared to Sweden (Kurlavičius *et al*., 2004). The study area in NE Poland is located in the transition zone between the hemiboreal and the temperate forest zones (Mayer, 1984). Forests in this area show much variation in their degree of naturalness, from the old-growth mixed forests of Białowieża to intensively managed plantations (Angelstam *et al*., 2002; Angelstam & Dönz-Breuss, 2004).

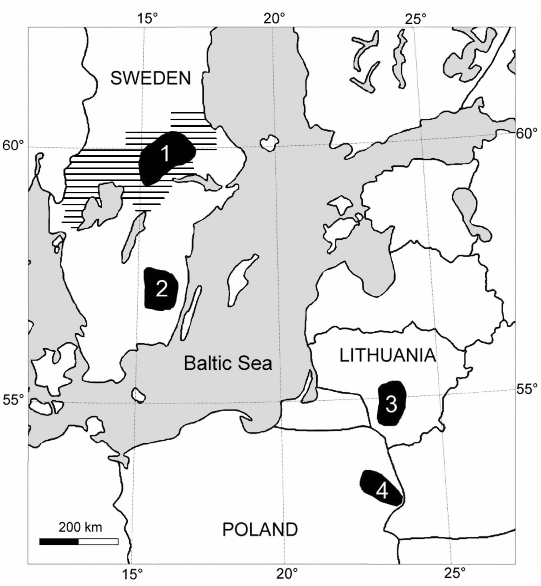

Fig. 2. The Baltic Sea region with the study areas for Papers II and III (in black; 1- Bergslagen, Sweden; 2- Småland, Sweden; 3- south-central Lithuania; 4- NE Poland) and Paper IV (hatched area).

The data were collected in a total of 112 landscape units of 1×1 km, each covered by ≥ 80% forest land. This spatial scale (1 km^2) has been shown to be relevant to habitat selection among forest birds. Many authors have reported significant landscape effects on forest birds for spatial scales of ~0.8–1 km^2 (*e.g.*, Drolet, Desrochers, & Fortin, 1999; Jansson & Angelstam, 1999; O'Connell, Jackson, & Brooks, 2000; Lichstein, Simons, & Franzreb, 2002; Gjerde, Sætersdal & Nilsen, 2005). Moreover, Angelstam *et al*. (2002) observed stronger relationships between forest structure and the occurrence of woodpeckers at the scale of 1 km^2 than for quadrants of 0.25 km^2 in Poland. Given the typical fine-grained mosaics of managed forest in the southern Baltic Sea region, each landscape unit was composed of a large number of forest stands with various tree species admixtures and successional stages.

For the selection of the landscape units, a totally random sampling design would have been inappropriate because large tracts of forest in a near-natural state with a full complement of species are so rare in most study areas that they would probably not have been represented at all in the sample. Therefore, data collection was stratified with the aim to cover a gradient of forest naturalness within each of the four study areas (*cf*. Papers II and III). The numbers of landscape units were 30 in Bergslagen, 30 in Småland, 26 in south-central Lithuania, and 26 in NE Poland. (Due to logistic constraints, data on forest structure could not be collected in one of the units in NE Poland, yielding a sample size of 25 in that area for the analyses based on forest characteristics in Paper III.)

Paper II deals with a guild of 22 species of resident forest birds. Under the time of this project, the Taxonomic Sub-Committee of the British Ornithologists' Union Records Committee adopted a new classification of the tits (Aves: Paridae) (Sangster *et al.*, 2005). In this thesis, tit species names follow the older classifications. To avoid possible confusion, the former and current scientific names of the tit species included in this study are listed in Appendix A. As to Paper III, it focuses on four species of resident woodpeckers with specialised requirements: the three-toed (*Picoides tridactylus*), middle spotted (*Dendrocopos medius*), white-backed and lesser spotted (*D. minor*) woodpeckers.

In each landscape unit, birds were surveyed using a combination of four 16-minute point counts enhanced by the use of playbacks of woodpecker drummings, as well as silent surveys along four line transects joining the point count stations. Surveys were conducted during the period of highest singing and drumming activity for resident birds in early spring, on mornings with favourable weather. In each unit, bird counts were performed once a year on two different years.

As to forest characteristics, they were assessed through measurements performed in 16 survey plots distributed systematically within each square landscape unit (Angelstam & Dönz-Breuss, 2004). To assess the degree of naturalness of the forest, a total of 9 variables were used to represent composition (tree species diversity within stands, importance of deciduous component in the landscape units, diversity of coarse woody debris types), structure (age structure, abundance of large trees, presence of special trees providing important micro-habitats) and function (uprooting, flooding, harvesting intensity) in forest ecosystems.

Patterns of co-occurrence among species (Paper II) were explored using nestedness analysis (Patterson & Atmar, 1986). An index of relative indicator value was calculated for each species by combining its species-specific contribution to nestedness and its frequency of occurrence. The best-scoring indicators were also evaluated as to whether their presence was related to high abundances of the co-occurring species. Because different forest bird species have different requirements regarding forest composition, the analyses were performed separately for birds of deciduous forest and those of coniferous forest. The relationships between the occurrence of specialised woodpeckers on the one hand, and forest naturalness as well as the amounts of critical habitat features on the other (Paper III), were assessed using logistic regression.

The white-backed woodpecker as an umbrella species (Paper IV)

In Fennoscandia, the white-backed woodpecker has become a flagship for the conservation, management and restoration of deciduous and mixed forests (Liedholm, 2006). Its role in the forest conservation debate can be compared to that of the northern spotted owl (*Strix occidentalis caurina*) in western North America. Paper IV aimed to evaluate the potential of this woodpecker as an umbrella species for conservation of the biodiversity associated with forests rich in deciduous trees and dead wood.

The study area for Paper IV spreads across central Sweden and encompasses the provinces of Dalsland, southern Värmland, Närke, Västmanland, southeastern Dalarna, northwestern Uppland and southern Gästrikland (Fig. 2). Data from the Swedish Bird Atlas for grid cells of 5×5 km (Svensson, Svensson & Tjernberg, 1999) were used to identify landscapes with recent occurrences of the white-backed woodpecker (period 1974-1994 [1974-1992 in Värmland]). The analyses were restricted to atlas squares that had been surveyed well in terms of spatial coverage and survey time. To minimise the risk of the same individual woodpecker being recorded in two adjacent squares, only squares separated from each other by at least 5 km were included.

First, the bird atlas data were used to assess the relationship between the occurrence of the white-backed woodpecker and species richness of forest birds. Then, the occurrence of the woodpecker was related to the number of red-listed species of birds, beetles and cryptogams expected to benefit considerably from the habitat-based conservation actions directed at the woodpecker (*cf.*, Mild & Stighäll, 2005). Data on the occurrence of those species were obtained from the Swedish Species Information Centre database. Finally, the relationship between the occurrence of the white-backed woodpecker and the current area of deciduous and mixed forests with high conservation value was assessed. Spatial data for such forests (with or without automatic protection status) were obtained from the Swedish Forest Agency and Sweden's County Administrations.

Results and discussion

The umbrella species concept as a conservation tool (Paper I)

This study yielded insight regarding the applications of the umbrella species concept and its potential for being used as a conservation planning tool. Three main variants of the umbrella species concept were identified: the area-demanding umbrella, the site-selection umbrella and the extended umbrella species concept. In its classic form, the umbrella species concept usually considers the requirements of area-demanding species (Wilcox, 1984). Here, the assumption is that providing enough space for species with large habitat requirements will also protect a suite of species with smaller spatial needs. The umbrella species concept has also been suggested as a tool for selecting sites to be included in conservation networks (*e.g.*, Fleishman, Murphy & Brussard, 2000). Typically, the occurrence of single- or multispecies umbrellas is used as a basis for choosing the units to be included in the network. Finally, an 'extended version' of the umbrella species concept has been proposed. It broadens the area-based idea to also include other landscape attributes such as habitat connectivity, ecosystem processes, or the distribution of scarce resources (*e.g.*, the 'focal-species' approach; Lambeck, 1997, 1999).

The review showed that most species suggested as umbrella species were large mammals and birds, but that invertebrates were increasingly being considered. Among the reviewed studies, a total of 18 evaluated empirically the performance of umbrella species. However, several additional articles presenting such empirical evaluations have been published since the date of acceptance of Paper I for publication (April 2003). To provide an updated assessment, those recent studies are summarised in Table 1. Considering the studies reviewed in Paper I and the more recent articles presented here, it seems that different evaluations of the umbrella species concept have yielded very varied results, even within each of the three variants of the concept. Contrary to most earlier assessments, a number of recent studies have found that umbrella species selected mostly on the basis of their large area requirements may constitute effective tools for conservation planning (Suter, Graf & Hess, 2002; Pakkala, Pellikka & Lindén, 2003; Berglind, 2004; Dunk, Zielinski & Welsh, 2006). Some recent accounts have also shown that single species can be effective umbrella species (Wood *et al.*, 2004; Dunk, Zielinski & Welsh, 2006). There is evidence that umbrella species from a given higher taxon may not necessarily confer protection to assemblages from other taxonomic groups (Rubinoff, 2001). Yet, in some cases, cross-taxon applications of umbrella species have proven useful (Berglind, 2004; Sergio, Newton & Marchesi, 2005; Dunk, Zielinski & Welsh, 2006). A number of evaluations of the extended umbrella species concept have been performed recently. Some of those studies have shown that using the requirements of one or a few specialised bird species for guiding forest conservation planning and management can prove useful for the conservation of bird communities (Jones, McLeish & Robertson, 2004; Wood *et al.*, 2004; Bani *et al.*, 2006), while others found only limited support for such approaches (Rubino & Hess, 2003; Hess *et al.*, 2006).

Thus, current knowledge suggests that umbrella species may constitute effective conservation tools in some – but by no means all – situations. Single-species umbrellas probably cannot ensure the conservation of absolutely every co-occurring species because some species are inevitably limited by ecological factors that are not relevant to the umbrella species. Thus, a more realistic approach would be to stratify the ecosystems into different landscape types or to identify the main threats (Lambeck, 1997) and test whether umbrella species-based management can be useful for the conservation of species that are dependent on similar habitats or sensitive to the same threats. Indeed, a common characteristic for many of the studies that found umbrella species useful is that they considered explicitly the match between the habitat requirements of both the umbrella species and the expected beneficiary species (*e.g.*, Suter, Graf, & Hess, 2002; Bani *et al.*, 2006). In general, it seems that a suite of focal species covering the main ecosystem or landscape types could constitute a useful tool for designing explicit and quantitative guidelines in conservation management, with the restriction that it should be used in combination with additional complementary approaches.

Table 1. *Evaluations of the usefulness of different types of umbrella species for conservation planning. This table is an addendum to Paper I's Table 2 and covers papers published from 2003 to 2006*

Umbrella species category and citation	**Ecosystem type**	**Investigated umbrella taxon/taxa**[a]	**Targeted beneficiary taxa**	**Protection conferred**[b]
Area-demanding umbrella				
Pakkala, Pellikka & Lindén (2003)	Boreal forest, Finland	Capercaillie, *Tetrao urogallus* (S)	Birds and mammals	Effective
Berglind (2004)	Pine heath forest, Sweden	Sand lizard, *Lacerta agilis* (S)	Spider wasps	Effective
Hitt & Frissell (2004)	Freshwater habitats, northwestern USA	Bull trout, *Salvelinus confluentus* (S)	Westslope cutthroat trout, *Oncorhynchus clarki lewisi*	Ineffective
Bifolchi & Lodé (2005)	Freshwater/riparian habitats, western France	European otter, *Lutra lutra* (S)	Birds, amphibians, molluscs	Ineffective
Dunk, Zielinski & Welsh (2006)	Forest, western USA	Northern spotted owl, *Strix occidentalis caurina* (S)	Terrestrial molluscs and salamanders	Effective
Rowland *et al.* (2006)	Sagebrush, western USA	Greater sage-grouse, *Centrocercus urophasianus* (S)	Sagebrush-associated vertebrate species of concern	Limited in general; effective for sagebrush obligates
Thorne, Cameron & Quinn (2006)	Diverse ecosystems, southwestern USA	Mountain lion, *Puma concolor* (S)	Vertebrates and plants	Limited
Ozaki *et al*. (in press)	Forest and agricultural land, Japan	Northern goshawk, *Accipiter gentilis* (S)	Birds, butterflies, beetles and plants	Ineffective
Site-selection umbrella				
Pavlik (2003)	Diverse ecosystems, southwestern USA	Plants of concern (M)	Plants and animals of concern	Effective to ineffective, depending on the taxa and ecosystem types

Table 1. *(Cont.)*

Caro *et al.* (2004)	Rainforest, Belize	Jaguar *Panthera onca* and Baird's tapir *Tapirus bairdii* (S)	Frogs, bats, mammals and birds	Ineffective
Betrus, Fleishman & Blair (2005)	Mountain canyons, western USA	Birds and butterflies (M)	Birds and butterflies	Limited
Sergio, Newton & Marchesi (2005)	Various ecosystem types, Italian Alps	Raptors (S)	Birds, trees and butterflies	Effective
Rondinini & Boitani (2006)	Mainland Africa	Mammals and amphibians (M)	Mammals and amphibians	Effective
Extended umbrella species concept				
Rubino & Hess (2003)	Forest, eastern USA	Barred owl, *Strix varia* (S)	Species from various taxonomic groups and natural communities of concern	Limited
Jones, McLeish & Robertson (2004)	Forest, eastern Canada	Cerulean warbler, *Dendroica cerulea* (S)	Birds	Effective for species of the same broad habitat
Wood *et al.* (2004)	Pine-grassland, southeastern USA	Red-cockaded woodpecker, *Picoides borealis* (S)	Birds	Effective
Bani *et al.* (2006)	Broadleaved forest, northern Italy	Birds (M)	Birds	Effective to limited, depending on site selection method
Hess *et al.* (2006)	Forest, eastern USA	Birds, mammal, reptile (M)	Species from various higher taxa and natural communities of concern	Ineffective to limited, depending on the measure of effectiveness used

[a] Abbreviations: S, single-species umbrella; M, multispecies umbrella.
[b] Interpretation (by the author of the present paper) of the original authors' conclusions. The protection conferred by the umbrella scheme was summarised in three classes: effective, limited, and ineffective.

Indicator species among resident forest birds (Paper II)

The analyses of co-occurrence patterns among resident forest birds shed light on the potential for identifying indicator species within that group. Assemblages of deciduous forest birds were generally nested, indicating that rare species were over-represented in species-rich units. This suggests that species richness may be predicted based on the presence of a few indicator species. For species of coniferous forest, conformity to nestedness was high in Lithuania and NE Poland, but poorer in Bergslagen and Småland.

Species-specific analyses yielded results in accordance with the general patterns of nestedness. In every study area and for both groups of species, several species were significantly over-represented in species-rich sites. For birds of deciduous forest, specialised woodpecker and tit species dominated among the species with the highest relative indicator value. For birds of coniferous forests, the best-scoring indicators belonged to a wider variety of families.

Some species had a consistently high indicator value across study areas. Among birds of deciduous forest, the middle spotted and lesser spotted woodpeckers generally figured among the best indicators. In coniferous forest, the three-toed woodpecker and the bullfinch (*Pyrrhula pyrrhula*) generally scored well. Interestingly, the species that have gone extinct in some study areas figured among the best indicators in the areas where they still have breeding populations today. This suggests that the best indicator species would be the ones that are most sensitive to habitat alteration affecting the degree of naturalness of the forests (*cf.* Paper III).

To further assess the generality of the potential indicator species across areas, all species that were absent from any of the areas were excluded from the analyses and the relative indicator values of the remaining species were recalculated. For birds of deciduous forest, the number of species figuring among the best-scoring indicators in many (3-4) or none of the study areas was higher than expected from exact probabilities, whereas the number of species figuring among the best indicators in only 1-2 study areas was lower than expected (Fig. 3, 'V'-shaped pattern). In other words, the identity of the best-scoring species was more consistent across areas than expected by chance. The pattern was statistically significant when considering the top-3 best ranking indicators and a similar but non-significant trend was observed for the top-2 and top-1 indicators. For birds of coniferous forest, however, the differences between the observed and expected distributions were not statistically significant, although there was a trend for a pattern similar to that observed in deciduous forest (Fig. 3).

The relationship between the presence of the best species-richness indicators and the relative abundance of the co-occurring species differed between deciduous and coniferous forests. For deciduous forest birds, the indicators selected on the basis of presence-absence patterns were helpful for identifying sites with high relative abundances of the co-occurring species, including species of conservation concern at the European level. For birds of coniferous forests, however, there was no such general pattern when considering the total species pool. Here, the only apparent pattern was one of higher abundance for coniferous forest specialists in the presence of the indicator in NE Poland.

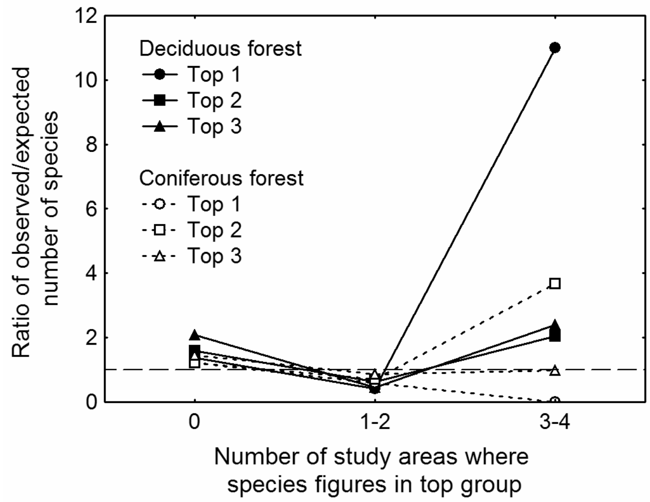

Fig. 3. Ratio of the observed/expected number of bird species figuring among the top-1 (circles), top-2 (squares) and top-3 (triangles) best-scoring indicator species in 0, 1-2 and 3-4 study areas, based on their relative indicator value. Plain lines and filled symbols depict birds of deciduous forest; dashed lines and open symbols represent birds of coniferous forests. Points above the horizontal line (1:1 ratio) denote observed numbers larger than those expected from exact probabilities and vice versa. Only the species found in all 4 study areas were included (*cf.* Paper II).

To sum up, the results suggest that for resident birds of hemiboreal forests in Europe, some species can be used as indicators of high species richness within the same broad habitat. Further studies of the habitat requirements of the best indicators are needed to cast light on the factors influencing their occurrence patterns.

Specialised woodpeckers, naturalness, and amounts of critical resources (Paper III)

The study presented in Paper III focused on linking the occurrence of specialised woodpeckers to the characteristics of the forest ecosystem. A principal components analysis (PCA) based on the variables representing composition, structure and function allowed the identification of a gradient in forest naturalness for the southern Baltic Sea region. The four study areas differed in the range of naturalness of the surveyed forests: the landscape units in NE Poland covered the widest span of naturalness, while those in Lithuania were restricted to a narrow range of high naturalness and the units in Sweden showed intermediate to low values (Fig. 4).

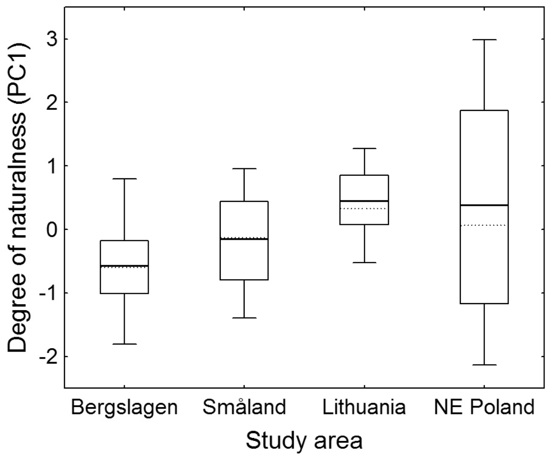

Fig. 4. Degree of naturalness of the forests in the surveyed landscape units of the four study areas as measured by scores on the first axis of a PCA (n = 30 in Bergslagen, n = 30 in Småland, n = 26 in south-central Lithuania, n = 25 in northeastern Poland). The box-plots present the mean (plain line), median (dotted line), 25 and 75 percentiles (box), and range (whiskers).

The three-toed woodpecker was positively linked to the level of naturalness of the forest in all three study areas where it has breeding populations today (Bergslagen, south-central Lithuania and NE Poland). For the middle, white-backed and lesser spotted woodpeckers, the effect of forest naturalness was positive everywhere, although not statistically significant in Lithuania. In the latter region, the limited range of naturalness values may have precluded the detection of patterns that would become apparent at lower or higher degrees of naturalness. The number of woodpecker species observed per landscape unit was positively related to forest naturalness in Lithuania and NE Poland, *i.e.* the two regions with complete woodpecker species pools (Fig. 5).

The occurrence of specialised woodpecker species was then related to the amounts of specific forest resources considered critical to the quality of their respective habitats. The models linking the occurrence of the middle spotted and white-backed woodpeckers to, respectively, large deciduous trees and deciduous snags were fairly consistent for the two study areas where those species are still found today. This allowed the identification of tentative targets for minimum resource amounts for those two species. For the middle spotted woodpecker, a basal area ≥ 1.0 m^2/ha of large (diameter at breast height [DBH] ≥ 40 cm) deciduous trees ensured a very high probability of presence (≥ 0.9). Regarding the white-backed woodpecker, the results suggest that a basal area < 0.4 m^2/ha of deciduous snags (DBH ≥ 10 cm) generally is not suitable, whereas a basal area ≥ 1.4 m^2/ha over an area of 100 ha corresponds to resource levels highly suitable for the species (probability of presence ≥ 0.9). The latter value is much larger than current amounts of standing dead wood in most managed forests. Following the precautionary principle, however, these targets should be seen as working hypotheses for active adaptive management rather than strict guidelines.

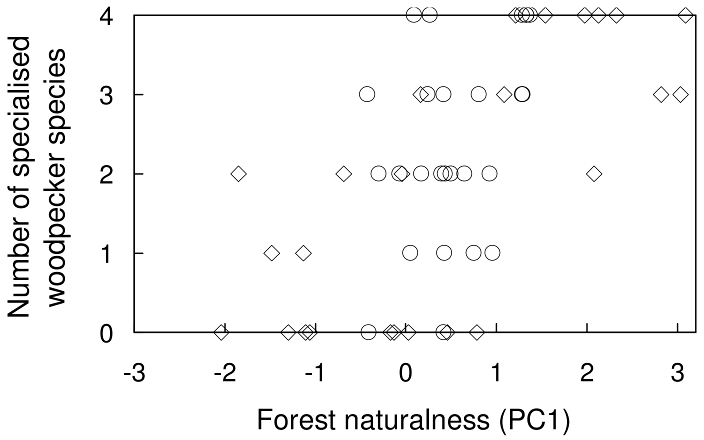

Fig. 5. Relationship between the degree of naturalness of the forest and the number of specialised forest-insectivorous woodpecker species for landscape units of 100 ha in Lithuania (n = 26; circles) and NE Poland (n = 25; diamonds) (*cf.* Paper III).

For the lesser spotted and three-toed woodpeckers, the varied results, including increasing functions with diverging slopes and non-significant relationships, did not allow the definition of general management targets. The results point to the fact that studies performed using the same methodology may lead to different quantitative estimates of the species' requirements in different regions. Such variation can be due, among other things, to differences in the local population dynamics of the species or in the characteristics of vegetation and other structures contributing to the species' habitat.

The white-backed woodpecker as an umbrella species (Paper IV)

The Swedish population of white-backed woodpecker has declined dramatically during the last decades, with only a few individuals left in the wild today (Mild & Stighäll, 2005). Yet, that species was still found in a relatively large number of sites during the breeding bird atlas period. Out of 122 mainland atlas squares located at least 5 km from each other and fulfilling the survey intensity criteria, a total of 24 had records of white-backed woodpecker. Occurrence of the woodpecker indicated significantly higher species richness of forest birds, with 7% more species in squares with records of white-backed woodpecker compared to squares without the woodpecker. Forest bird species of special conservation concern included on average 13% more species in squares with occurrence of the woodpecker than where it was absent. The number of red-listed cryptogam species expected to benefit from conservation actions directed at white-backed woodpecker habitats was significantly higher in sites with confirmed or probable breeding of the woodpecker compared to where is was absent. No such pattern was found for red-listed beetles, which, however, were very rare in the material. White-backed woodpecker presence was not related to the total land area or to the present area of forest within atlas squares. However, it was positively associated with the current area of deciduous and mixed forests of high conservation value. Since those forests are expected to support many red-listed species (*e.g.*, woodland key habitats), this provides additional evidence that sites with presence of the woodpecker are of importance for the conservation of forest species of special conservation concern.

Considering its potential as an indicator species, its specialised habitat requirements and its role as a flagship species, using the requirements of the white-backed woodpecker as a guide for habitat management may provide a 'coarse filter' for the conservation of a suite of other deciduous forest species. However, the fact that many species remained undetected at sites with occurrence of the woodpecker suggests that focusing solely on the white-backed woodpecker may not provide for the conservation of all deciduous forest species. Therefore, a suite of complementary approaches will be necessary to conserve the biodiversity associated with forests rich in deciduous trees and dead wood.

Conclusions

The increasing amount of knowledge on the world's ecosystems contributes to the identification of elements which are particularly important for the maintenance of biodiversity. In northern forests, research on species-habitat associations and on the properties of naturally dynamic ecosystems has shown that many components, structures and processes are too rare in today's managed forest landscapes to ensure the long-term persistence of the populations of all naturally occurring species. Accordingly, there is wide agreement that forest management and conservation planning should aim to increase the amounts of critical elements, such as the volumes of coarse woody debris of different qualities and the area of older forest (Anon., 2001). To achieve those biodiversity conservation policy objectives in an effective manner, there is a need to define performance targets for the abundance of such elements. Knowledge of the quantities of different structures with particular qualities that are required to satisfy the needs of the most demanding species can constitute an appropriate starting point for defining such conservation targets (Ranius & Fahrig, 2006). Since the focus of most umbrella species applications is on species requirements, the umbrella species concept may be useful for providing explicit and quantitative guidelines in that respect (*e.g.*, Lambeck, 1997, 1999). Hence, much of the potential of the umbrella species concept lies in the opportunities that it presents for linking species and structures in conservation management.

Contrary to classic scientific hypotheses, the umbrella species concept is not subject to general falsification (Lindenmayer *et al.*, 2002). Evidently, lack of support for the validity of that concept in certain conditions does not constitute a proof of the general invalidity of that tool. In fact, conservation or restoration management of the habitat of virtually any taxon will benefit other taxa. Some species, however, are likely to provide better umbrella coverage than others due to their large requirements regarding some attributes of the ecosystem. In the development of umbrella- or focal-species approaches, the challenges are to identify those species in different systems and to quantify their requirements.

This work focusing on north European resident forest birds as a model group has shown that (1) the occurrence of specialised species may be used as an indicator of species-rich assemblages including many species of conservation concern, (2) the identity of the best indicators within deciduous forest birds was fairly consistent among different regions belonging to the hemiboreal zone, (3) woodpeckers as a group included many such indicator species, (4) specialised woodpeckers have requirements for forests with a high degree of naturalness and specific habitat features that can generally be quantified at the local landscape scale, (5) management for the habitat of specialised woodpeckers may benefit the populations of several species from different taxonomic groups which are dependent on dead wood and other resources that have become scarce in managed forests. Thus, in the context of this assessment, performed in a relatively simple system and restricted to a well-known taxonomic group, many of the prerequisites for the application of an umbrella species approach were fulfilled.

Applied ecologists face an often uncomfortable trade-off between scientific rigour and the need for rapid solutions to conservation problems. In-depth knowledge of the earth's ecosystems improves our understanding and thereby our capacity to conserve them. In parallel, conservation shortcuts are and will be an integral component of real-world management subject to temporal and budgetary constraints. Obviously, no single shortcut can solve all conservation issues (Fleishman, Murphy & Blair, 2001). As stressed by Lindenmayer & Franklin (2002), "management of diversity requires a diversity of management". The umbrella species concept may constitute a useful component of conservation planning but, considering its limitations and adopting a risk-spreading perspective, it should be seen as part of a complementary suite of approaches. Other strategies may include the maintenance of ecosystem processes and emulation of natural disturbance regimes, the maintenance of stand structural complexity and critical microhabitats, the planning for representation of all native land-types and for connectivity at multiple scales, as well as special management for keystone species and threatened species that are not efficiently protected by other measures (Simberloff, 1998; Hunter, 1999; Lindenmayer & Franklin, 2002; Lindenmayer, Franklin & Fischer, 2006). Using a philosophy of active adaptive management, such strategies should be improved continuously as more knowledge becomes available. In that context, long-term monitoring is a priority as it will constitute the ultimate evaluation of the usefulness of those approaches (Lambeck 1997, 1999; Lindenmayer, 1999; Watson *et al*., 2001).

References

Andersson, L. & Löfgren, R. (Eds.) 2000. *Sydsvenska lövskogar och andra lövbärande marker: kriterier för naturvärdering, skydd och skötsel*. Swedish Environmental Protection Agency. Stockholm, Sweden. 173 pp. (In Swedish.)

Angelstam, P. 1997. Landscape analysis as a tool for the scientific management of biodiversity. *Ecological Bulletins 46*, 140-170.

Angelstam, P.K., Anufriev, V.M. Balciauskas, L. Blagovidov, A.K. Borgegård, S.-O. Hodge, S.J., Majewski, P., Ponomarenko, S.V., Shvarts, E.A., Tishkov, A.A., Tomiałojć, L. & Wesołowski, T. 1997. Biodiversity and sustainable forestry in European forests: how East and West can learn from each other. *Wildlife Society Bulletin 25*, 38-48.

Angelstam, P., Breuss, M., Mikusiński, G., Stenström, M., Stighäll, K. & Thorell, D. 2002. Effects of forest structure on the presence of woodpeckers with different specialisation in a landscape history gradient in NE Poland. In: *Avian landscape ecology*. (Eds. D. Chamberlain & A. Wilson). IALE(UK). Garstang, UK. pp. 25-38.

Angelstam P. & Dönz-Breuss, M. 2004. Measuring forest biodiversity at the stand scale – an evaluation of indicators in European forest history gradients. *Ecological Bulletins 51*, 305-332.

Angelstam, P., Boutin, S., Schmiegelow, F., Villard, M.-A., Drapeau, P., Host, G., Innes, J., Isachenko, G., Kuuluvainen, M., Mönkkönen, M., Niemelä, J., Niemi, G., Roberge, J.-M., Spence, J. & Stone, D. 2004. Targets for boreal forest biodiversity conservation - a rationale for macroecological research and adaptive management. *Ecological Bulletins 51*, 487-509.

Anon., 1979. *Council directive 79/409/EEC of 2 April 1979 on the conservation of wild birds*. Council of the European Communities. Luxembourg. 25 pp.

Anon., 1992. *Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*. Council of the European Communities. Brussels, Belgium. 57 pp.

Anon., 1994. *Skogsvårdslagen – handbook*. Swedish National Board of Forestry. Jönköping, Sweden. 66 pp. (In Swedish).

Anon., 2001. *The Swedish environmental objectives – the interim targets and action strategies*. Summary of Government Bill 2000/01: 130. Ministry of Environment. Stockholm, Sweden. 80 pp.

Bani, L., Massimino, D., Bottoni, L. & Massa, R. 2006. A multiscale method for selecting indicator species and priority conservation areas: a case study for broadleaved forests in Lombardy, Italy. *Conservation Biology 20*, 512-526.

Berglind, S.-Å. 2004. Area-sensitivity of the sand lizard and spider wasps in sandy pine heath forests - umbrella species for early successional biodiversity conservation? *Ecological Bulletins 51*, 189-207.

Betrus, C.J., Fleishman, E. & Blair, R.B. 2005. Cross-taxonomic potential and spatial transferability of an umbrella species index. *Journal of Environmental Management 74*, 79-87.

Bifolchi, A. & Lodé, T. 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. *Biological Conservation 126*, 523-527.

Björse, G. & Bradshaw, R. 1998. 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *Forest Ecology and Management 104*, 15-26.

Carignan, V. & Villard, M.-A. 2002. Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment 78*, 45-61.

Carignan, V. & Villard, M.-A. 2004. Biological indicators in environmental monitoring programs: can we increase their effectiveness? In: *Environmental monitoring*. (Ed. G.B. Wiersma). CRC Press. Boca Raton (FL), USA. pp. 567-582.

Caro, T.M. & O'Doherty, G. 1999. On the use of surrogate species in conservation biology. *Conservation Biology 13*, 805-814.

Caro, T., Engilis, A.J., Fitzherbert, E. & Gardner, T. 2004. Preliminary assessment of the flagship species concept at a small scale. *Animal Conservation 7*, 63-70.

de Jong, J. 2002. *Populationsförändringar hos skogslevande arter i relation till landskapets utveckling*. Swedish Biodiversity Centre, CBM Series 7. Uppsala, Sweden. 97 pp. (In Swedish with English summary.)

Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P.L., Bergeron, Y. & Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs 70*, 423-444.

Drolet, B., Desrochers, A. & Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor 101*, 699-704.

Dunk, J.R., Zielinski, W.J. & Welsh, H.H. 2006. Evaluating reserves for species richness and representation in northern California. *Diversity and Distributions 12*, 434-442.

East, R. 1981. Species-area curves and populations of large mammals in African savanna reserves. *Biological Conservation 21*, 111-126.

Eisenberg, J.F. 1980. The density and biomass of tropical mammals. In: *Conservation biology: an evolutionary-ecological perspective*. (Eds. M.E. Soulé & B.A. Wilcox). Sinauer Associates, Sunderland (MA), USA. pp. 35-55.

Faliński, J.B. 1986. *Vegetation dynamics in temperate lowland primeval forests – Ecological studies in Białowieża forest*. W. Junk Publishers. Dordrecht, Netherlands. 537 pp.

Fleishman, E., Murphy, D.D. & Brussard, P.F. 2000. A new method for selection of umbrella species for conservation planning. *Ecological Applications 10*, 569-579.

Fleishman, E., Murphy, D.D. & Blair, R.B. 2001. Selecting effective umbrella species. *Conservation in Practice 2*, 17-25.

Frankel, O.H. & Soulé, M.E. 1981. *Conservation and evolution*. Cambridge University Press. Cambridge, UK. 327 pp.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications 3*, 202-205.

Freudenberger, D. & Brooker, L. 2004. Development of the focal species approach for biodiversity conservation in the temperate agricultural zones of Australia. *Biodiversity and Conservation 13*, 253-274.

Fuller, R.J. 2002. Spatial differences in habitat selection and occupancy by woodland bird species in Europe: a neglected aspect of bird-habitat relationships. In: *Avian landscape ecology*. (Eds. D. Chamberlain & A. Wilson). IALE(UK). Garstang, UK, pp. 101-111.

Gärdenfors, U. (Ed.) 2005. *The 2005 red list of Swedish species*. Swedish Species Information Centre. Uppsala, Sweden. 496 pp.

Gjerde, I., Sætersdal, M. & Nilsen, T. 2005. Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. *Biodiversity and Conservation 14*, 377-393.

Glennon, M.J. & Porter, W.F. 2005. Effects of land use management on biotic integrity: an investigation of bird communities. *Biological Conservation 126*, 499-511.

Hannon, S.J. & McCallum, C. 2004. *Using the focal species approach for conserving biodiversity in landscapes managed for forestry*. Sustainable Forest Management Network Synthesis Paper. Edmonton, Canada. 47 pp.

Hansen, A.J., Garman, S.L., Marks, B. & Urban, D.L. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecological Applications 3*, 481-496.

Hansson, L. & Larsson, T.-B. 1997. Conservation of boreal environments: a completed research program and a new paradigm. *Ecological Bulletins 46*, 9-15.

Harrison, R.B., Schmiegelow, F.K.A. & Naidoo, R. 2005. Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types. *Canadian Journal of Forest Research 35*, 1553-1567.

Hess, G.R., Koch, F.H., Rubino, M.J., Eschelbach, K.A., Drew, C.A. & Favreau, J.M. 2006. Comparing the potential effectiveness of conservation planning approaches in central North Carolina, USA. *Biological Conservation 128*, 358-368.

Hitt, N.P. & Frissell, C.A. 2004. A case study of surrogate species in aquatic conservation planning. *Aquatic Conservation: Marine and Freshwater Ecosystems 14*, 625-633.

Huhta, E., Aho, T., Jäntti, A., Suorsa, P., Kuitunen, M., Nikula, A. & Hakkarainen, H. 2004. Forest fragmentation increases nest predation in the Eurasian treecreeper. *Conservation Biology 18*, 148-155.

Hunter, M.L. (Ed.) 1999. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press. Cambridge, UK. 698 pp.
Imbeau, L., Mönkkönen, M. & Desrochers, A. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. *Conservation Biology 15*, 1151-1162.
Ingelög, T., Andersson, R. & Tjernberg, M. (Eds.) 1993. *Red data book of the Baltic region*. Swedish Threatened Species Unit. Uppsala, Sweden. 95 pp.
Jansson, G. & Angelstam, P. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. *Landscape Ecology 14*, 283-290.
Jones, J., McLeish, W.J. & Robertson, R.J. 2004. Predicting the effects of Cerulean Warbler, *Dendroica cerulea* management on eastern Ontario bird species. *Canadian Field-Naturalist 118*, 229-234.
Juutinen, A. & Mönkkönen, M. 2004. Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. *Ecological Economics 50*, 35-48.
Kaennel, M. 1998. Biodiversity: a diversity in definition. In: *Assessment of biodiversity for improved forest planning*. (Eds. P. Bachmann, M. Köhl & R. Päivinen). European Forest Institute. Kluwer Academic Publishers. Dordrecht, Netherlands. pp. 71-83
Kurlavičius, P., Kuuba, R., Lukins, M., Mozgeris, G., Tolvanen, P., Karjalainen, H., Angelstam, P. & Walsh, M. 2004. Identifying high conservation value forests in the Baltic States from forest databases. *Ecological Bulletins 51*, 351–366.
Laasimer, L., Kuusk, V., Tabaka, L. & Lekavicius, A. (Eds.) 1993. *Flora of the Baltic countries: compendium of vascular plants*. Estonian Academy of Sciences. Tartu, Estonia. 362 pp.
Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology 11*, 849-856.
Lambeck, R.J. 1999. *Landscape planning for biodiversity conservation in agricultural regions: a case study from the Wheatbelt of Western Australia*. Environment Australia, Biodiversity Technical Paper 2. Canberra, Australia. 96 pp.
Landres, P.B., Verner, J. & Thomas, J.W. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology 2*, 316-328.
Lichstein, J.W., Simons, T.R. & Franzreb, K.E. 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications 12*, 836-857.
Liedholm, H. 2006. Myndighet värvar fans till "Lövskogens IK". *SkogsEko 2006/2*, 10-11. (In Swedish.)
Lindbladh, M. & Bradshaw, R. 1998. The origin of present forest composition and pattern in southern Sweden. *Journal of Biogeography 25*, 463-477.
Lindenmayer, D.B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management 115*, 277-287.
Lindenmayer, D.B. & Franklin, J.F. 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island Press. Washington (DC), USA. 351 pp.
Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I. & McCarthy, M.A. 2002. The focal-species approach and landscape restoration: a critique. *Conservation Biology 16*, 338-345.
Lindenmayer, D.B. & Fischer, J. 2003. Sound science or social hook - a response to Brooker's application of the focal species approach. *Landscape and Urban Planning 62*, 149-158.
Lindenmayer, D.B., Franklin, J.F. & Fischer, J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation 131*, 433-445.
Linder, P. & Östlund, L. 1992. Changes in the boreal forests of Sweden 1870-1991. *Svensk Botanisk Tidskrift 86*, 199-215. (In Swedish with English summary.)
Marra, P.P., Hobson, K.A. & Holmes, R.T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science 282*, 1884-1886.

Mayer, H. 1984. *Wälder Europas*. Gustav Fischer Verlag. Stuttgart, Germany. 691 pp. (In German).
McNeely, J.A. 1994. Lessons from the past: forests and biodiversity. *Biodiversity and Conservation 3*, 3-20.
Mealy, S.P. & Horn, J.R. 1981. Integrating wildlife habitat objectives into the forest plan. *Transactions of the North American Wildlife Conference 46*, 488-500.
Mild, K. & Stighäll, K. 2005. *Action plan for the conservation of the Swedish population of white-backed woodpecker (*Dendrocopos leucotos*).* Swedish Environmental Protection Agency, Report 5486. Stockholm, Sweden. 92 pp. (In Swedish with English summary.)
Mills, L.S., Soulé, M.E. & Doak, D.F. 1993. The keystone-species concept in ecology and conservation. *BioScience 43*, 219-224.
Nordström, O., Larsson, L.J., Käll, J. & Larsson, L-O. 1989. *Skogen och smålänningen – kring skogsmarkens roll i förindustriell tid*. Historiska Föreningen i Kronobergs län. Kalmar, Sweden. 216 pp. (In Swedish.)
Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology 4*, 355-364.
O'Connell, T.J., Jackson, L.E. & Brooks, R.P. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. *Ecological Applications 10*, 1706-1721.
Östlund, L., Zackrisson, O. & Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research 27*, 1198-1206.
Ozaki, K., Isono, M., Kawahara, T., IIda, S., Kudo, T. & Fukuyama, K. A mechanistic approach to evaluation of umbrella species as conservation surrogates. *Conservation Biology*, in press.
Paine, R.T. 1969. A note on trophic complexity and community stability. *American Naturalist 103*, 91-93.
Pakkala, T., Hanski, I. & Tomppo, E. 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. *Silva Fennica 36*, 279-287.
Pakkala, T., Pellikka, J. & Lindén, H. 2003. Capercaillie *Tetrao urogallus* - a good candidate for an umbrella species in taiga forests. *Wildlife Biology 9*, 309-316.
Patterson, B.D. & Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society 28*, 65-82.
Pavlik, B.M. 2003. Plants that protect ecosystems: a survey from California. *Biodiversity and Conservation 12*, 717-729.
Rametsteiner, E. & Mayer, P. 2004. Sustainable forest management and Pan-European forest policy. *Ecological Bulletins 51*, 51-57.
Ranius, T. & Fahrig, L. 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scandinavian Journal of Forest Research 21*, 201-208.
Rondinini, C. & Boitani, L. 2006. Differences in the umbrella effects of African amphibians and mammals based on two estimators of the area of occupancy. *Conservation Biology 20*, 170-179.
Rowland, M.M., Wisdom, M.J., Suring, L.H. & Meinke, C.W. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation 129*, 323-335.
Rubino, M.J. & Hess, G.R. 2003. Planning open spaces for wildlife 2: modeling and verifying focal species habitat. *Landscape and Urban Planning 64*, 89-104.
Rubinoff, D. 2001. Evaluating the California gnatcatcher as an umbrella species for conservation of southern California coastal sage scrub. *Conservation Biology 15*, 1374-1383.
Sætersdal, M., Gjerde, I. & Blom, H.H. 2005. Indicator species and the problem of spatial inconsistency in nestedness patterns. *Biological Conservation 122*, 305-316.
Sangster, G., Collinson, J.M., Helbig, A.J., Knox, A.G. & Parkin, D.T. 2005. Taxonomic recommendations for British birds: third report. *Ibis 147*, 821-826.
Sergio, F., Newton, I. & Marchesi, L. 2005. Top predators and biodiversity. *Nature 436*, 192.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation 83*, 247-257.
Stenberg, I. 1996. Nest site selection in six woodpecker species. *Fauna Norvegica Series C, Cinclus 19*, 21-38.
Suter, W., Graf, R.F. & Hess, R. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology 16*, 778-788.
Svensson, S., Svensson, M. & Tjernberg, M. 1999. *Svensk fågelatlas*. Vår Fågelvärld, Supplement 31. Stockholm, Sweden. 552 pp. (In Swedish.)
Thompson, I.D. & Angelstam, P. 1999. Special species. In: *Maintaining biodiversity in forest ecosystems*. (Ed. M.L. Hunter). Cambridge University Press. Cambridge, UK. pp. 434-459.
Thorne, J.H., Cameron, D. & Quinn, J.F. 2006. A conservation design for the Central Coast of California and the evaluation of mountain lion as an umbrella species. *Natural Areas Journal 26*, 137-148.
Tracy, C.R. & Brussard, P.F. 1994. Preserving biodiversity: species in landscapes. *Ecological Applications 4*, 205-207.
Uliczka, H., Angelstam, P. & Roberge, J.-M. 2004. Indicator species and biodiversity monitoring systems for non-industrial private forest owners - is there a communication problem? *Ecological Bulletins 51*, 379-384.
Väisänen, R.A., Järvinen, O. & Rauhala, P. 1986. How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? *Ornis Scandinavica 17*, 282-292.
Verner, J. 1984. The guild concept applied to management of bird populations. *Environmental Management 8*, 1-14.
Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology 9*, 747-752.
Watson, J., Freudenberger, D. & Paull, D. 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. *Conservation Biology 15*, 1364-1373.
Wiens, J.A. 1989. *The ecology of bird communities*. Cambridge University Press. Cambridge, UK. 539 + 316 pp.
Wilcove, D.S. 1994a. Turning conservation goals into tangible results: the case of the spotted owl and old-growth forests. In: *Large-scale ecology and conservation biology*. (Eds. P.J. Edwards, R.M. May & N.R. Webb). Blackwell. London, UK. pp. 313-329.
Wilcove, D. 1994b. Preserving biodiversity: species in landscapes. Response to Tracy & Brussard, 1994. *Ecological Applications 4*, 207-208.
Wilcox, B.A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. In: *National parks, conservation and development: the role of protected areas in sustaining society*. (Eds. J.A. McNeely & K.R. Miller). Smithsonian Institution Press. Washington (DC), USA. pp. 639-647.
Wood, D.R., Burger, L.W., Bowman, J.L. & Hardy, C.L. 2004. Avian community response to pine-grassland restoration. *Wildlife Society Bulletin 32*, 819-829.

Acknowledgements

Financial support

During my doctoral studies, I have been supported financially through two postgraduate scholarships from the Natural Sciences and Engineering Research Council of Canada (NSERC), a scholarship from the Fonds québécois de recherche sur la nature et les technologies (FQRNT) and two grants from the Helge Ax:son Johnson Foundation. Grants from Formas, Mistra, the Wallenberg Foundation and the World Wildlife Fund (WWF) to Per Angelstam and an NSERC discovery grant to Marc-André Villard made this cross-regional study possible. The Lennart Hjelm Foundation, the Royal Swedish Academy of Agriculture and Forestry (KSLA) and SLU's Research Education Council (FUR) provided grants for some of my travels during the course of my doctoral studies.

Thank you!

First of all, I wish to express my gratitude to Per Angelstam, my main supervisor, who supported me throughout this journey. Per has been extraordinarily good at cheering me up in difficult moments and encouraging me to keep the beat when things were rolling fine. He gave me unique opportunities to learn about forest biodiversity research and management, as well as to see and understand the whole gradient of land-use history in Europe. He got me involved in a number of exciting endeavours outside my own PhD project, which contributed greatly to my broader learning in conservation science and practice. I also thank Marc-André Villard, my assistant supervisor, for his support during the field work and the analyses, for insightful and rapid feedback at various stages when writing the manuscripts, as well as for a fruitful and enjoyable stay in New Brunswick in the spring of 2005.

I enjoyed collaborating with the co-authors of the papers: Grzegorz Mikusiński, Sören Svensson and my supervisors. I am grateful to Lena Gustafsson and Sven G. Nilsson for their constructive comments on the project as a whole and to Henrik Andrén, Håkan Berglund, Martin Carel, Bengt-Gunnar Jonsson, Ulf Olsson, Dietrich von Rosen and Jörgen Wissman for statistical and analytical advice. I am thankful to all colleagues who provided constructive comments on the manuscripts: Henrik Andrén, Virginie-Arielle Angers, Marc Bélisle, Anna Danell, Lena Gustafsson, Louis Imbeau, Gunnar Jansson, Grzegorz Mikusiński, and Karin Perhans. I also thank the reviewers and editors who contributed to improving Papers I and II during the review and publication processes. Christiane Seiler, Andreas Seiler, Johanna Wikland and Peter Jaxgård rescued me at many occasions when I ended up stranded due to computer problems.

This project involved much field work. I thank all collaborators who have spent long days in the field under often difficult conditions: Gediminas Brazaitis, Marcin Dziedzic, Peter Ekelund, Silvija Šaudytė, Tommy Gustafsson, Michael G. Manton, Jarosław Matusiak, Andrea Pirovano, Daniel Thorell, Roland Thuvander, and all field ornithologists who participated in the Swedish Bird Atlas surveys. I am also thankful to all those who helped during the planning of the field work: Annika Bladh, Roger Johansson, Thomas Johansson, Grzegorz Mikusiński, Patryk Rowiński, Kristoffer Stighäll, Tomasz Wesołowski and Thorsten Zaar. Ulf T. Carlsson, Jan Edelsjö, Oskar Kindvall, Artur Larsson, Ella Mohlin, Pär Nyman, Sören Svensson and Ulrika Wahlström kindly helped with obtaining species occurrence and forest data. I have probably forgotten to name some of the many people who have helped me during those years… If so, please forgive me.

I thank all my friends at Grimsö and in Uppsala for the valuable input given during seminars and discussions, the entertaining breaks, dinners and parties, the floorball matches, the great bird/insect/frogwatching and the memorable trips. This department really is no average working place and I enjoyed very much being among you!

As a young undergraduate student, about ten years ago, I had the chance to work for Marc Bélisle and André Desrochers during a few summers. They are the ones who really introduced me to the science of conservation ecology. Thank you for your trust, without which I might never have had the opportunity to discover that field which quickly became a passion.

I am thankful to my mother Jacinthe and father Michel for the values they have taught me and for their encouragement during my studies at home and abroad. Finally, I thank Cornelia for her help, support, and understanding.

Appendix A

Appendix Table. *Former and new scientific names (Sangster* et al.*, 2005) of tit species considered in this thesis*

Common species name	Former scientific name	New scientific name
Blue tit	*Parus caeruleus*	*Cyanistes caeruleus*
Great tit	*Parus major*	*Parus major*
Crested tit	*Parus cristatus*	*Lophophanes cristatus*
Coal tit	*Parus ater*	*Periparus ater*
Willow tit	*Parus montanus*	*Poecile montanus*
Marsh tit	*Parus palustris*	*Poecile palustris*