DEAD WOOD IN MANAGED FORESTS: HOW MUCH AND HOW MUCH IS ENOUGH?

Development of a Snag Quantification Method by Remote Sensing & GIS and Snag Targets Based on Three-toed Woodpeckers' Habitat Requirements

THÈSE N^{O} 2761 (2003)

PRÉSENTÉE À LA FACULTÉ ENVIRONNEMENT NATUREL, ARCHITECTURAL ET CONSTRUIT
Institut des sciences et technologies de l'environnement
SECTION DES SCIENCES ET DE L'INGÉNIERIE DE L'ENVIRONNEMENT

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

POUR L'OBTENTION DU GRADE DE DOCTEUR ÈS SCIENCES

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Lausanne, EPFL
2003

Another point of view on PhD research….

Number of field days	**104**
Number of measured dead trees	**1812**
Fully inventoried forest area (each tree)	**61 ha**
Number of photo-interpreted and digitised dead trees	**8’222**
Distance walked in order to reach sampling points for measurements	**478 km**
Working files	**2’569 Mo**

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Preface

"…When it comes to counting, evaluating, and explaining the distribution of dead wood in our forests, it is, to put it mildly, incredibly complicated."

Ohmann, J.L. and Waddell, K.L.
two scientists at the Pacific Northwest Research Station

The field data for this research were collected over four years, between 1998 and 2001. As emphasised by the above quotation, dead wood quantification by fieldwork is "incredibly complicated", and time-consuming. I had the chance to supervise several Master diploma theses in Environmental Sciences during my time as Assistant in the EPFL's Laboratory of Ecosystem Management. Field data from two of these have considerably enlarged the data-set of the present research. In addition, Prof. Per Angelstam at the Centre for Landscape Ecology, Örebro University, Sweden kindly accepted to suggest one of my research topics to his diploma students. Peter Ekelund became interested in the dead wood problem. He placed all the data collected in Sweden for his diploma thesis at my disposal for this research.

This thesis is divided into two parts. Part A summarises all the doctoral research. It answers the two main questions: i) How much dead wood ***is*** there in managed forests? and ii) How much dead wood ***is enough*** in managed forests? Part B comprises four research papers, each addressing one specific objective. The 2nd and 4th papers are currently in press, whereas the 1st and 3rd are reproduced here in their current state as submitted to the relevant journals.

Abstract

The aims of this research were twofold: to develop an efficient method for the quantification of large spruce snags (standing dying and dead trees), and to establish snag target values for sustainable forest management. We answer the two basic questions: how much dead wood is currently available in managed forests? And how much dead wood is enough for biodiversity conservation?

It is widely accepted that modern forest management has to be sustainable. One generally recognised criterion of sustainability is the maintenance of biodiversity. Since this concept encompasses a large range of scales and features (landscapes, ecosystems, species and genes; components, processes, functions, etc.), biodiversity indicators have been identified for measurement and monitoring purposes. 'Dead wood' has been recognised as a key indicator for biodiversity in forest ecosystems. Verifying and assessing progress towards biodiversity maintenance or restoration hence requires the measurement of different kinds of dead wood. Yet cost-efficient and rapid methods are still lacking. That is why **we developed in this thesis an efficient method for the quantification of large spruce snags**. Being based on infrared **A**erial **P**hotos and a **G**eographic **I**nformation **S**ystem (GIS), it is called the AP-GIS-method. It enables mapping of snags and calculation of the spatial snag-density, i.e. the number of snags per hectare, and can be used to answer the question: How much dead wood is in managed forests?

Beside techniques to assess dead-wood quantities, forest managers need quantitative target values, i.e. guidelines in order to know how much dead wood should be maintained in managed forests for biodiversity conservation. Natural forests may be used as reference systems to define such targets. However, since dead-wood amounts in natural forests may be extremely high, up to 30% of dead trunks, the retention of such amounts in managed forests would hardly be compatible with economic objectives. Another possibility for defining guidelines is the translation of the habitat requirements of dead-wood-dependent species into management targets. The Three-toed woodpecker *Picoides tridactylus* has previously been recognised as a potential indicator species of features characteristic for forests with natural dynamics (especially old-growth). Although ecological studies had demonstrated its need of dying and dead trees for foraging, nesting and drumming, the required density of such trees has never been quantified. In this thesis, **we analysed the dependence on dead wood for both European subspecies, the Alpine *Picoides tridactylus alpinus* and the northern *P. tr. tridactylus***. The study was conducted in sub-Alpine spruce forests in Switzerland and boreal forests in central Sweden. In both countries, we found a significant non-linear response of the probability of woodpecker presence to different amounts of dead trees, and identified critical ecological thresholds for the local presence of this species. Clearly, the Three-toed woodpecker depends on relatively high amounts of dying and dead trees. In Switzerland, the road network density negatively affected the presence of this woodpecker species, since a high road density facilitates forest management intensification and the removal of diseased and dead trees. Based on our results, and since several other links with biodiversity have previously been demonstrated, we suggest that Three-toed woodpeckers be considered indicators of dead wood and habitat quality. This species has therefore been used in this thesis to find an answer to the question: How much dead wood is enough in managed forests?

In order to ascertain dead-tree targets, **we developed a bioenergetic model for Three-toed woodpeckers, enabling estimation of snag amounts required by this species to satisfy its energy needs**. By comparing modelling results with the previously identified critical dead-wood thresholds, we were able to derive reliable targets, since both approaches resulted in similar critical values.

We recommend, for both boreal and sub-Alpine spruce forests, aiming for 5% of the standing tree basal area, or volume to be dead. Such snag-retention levels, to be applied over an area of about 100 ha, correspond in sub-Alpine forests to a basal area of ≥ 1.6 m^2 ha^{-1}, or a volume of ≥ 18 m^3 ha^{-1}, or a minimum of 14 snags with a diameter ≥ 21 cm per hectare.

Considered as a pragmatic way to stimulate forest managers’ interest in dead wood maintenance or restoration, **we analysed the potential usefulness of Three-toed woodpeckers as natural agents against bark beetles**. By defining three scenarios for different levels of woodpecker effectiveness, we compared the numbers of bark beetles consumed with those caught in pheromone traps used in forestry. We demonstrate that woodpeckers catch 2-19 times more bark beetles than traps do. This result is true for both cases, when one woodpecker is compared with one trap, and when the whole Swiss woodpecker population is compared to all traps installed in Swiss forests.

Version abrégée

Cette recherche poursuit deux buts: d'une part de développer une méthode efficace pour quantifier des arbres morts sur pied, et d'autre part, d'élaborer des valeurs de références pour une gestion forestière durable en ce qui concerne la quantité de tels arbres nécessaires pour le maintien de la diversité biologique. Nous traitons les deux questions suivantes: Combien de bois mort se trouve-t-il actuellement dans les forêts gérées ? Et quelle est la quantité nécessaire, afin de garantir une biodiversité élevée ?

A l'heure actuelle, le principe d'une gestion forestière moderne dite durable est largement accepté. Parmi les critères de durabilité figure la conservation de la diversité biologique. Ce concept complexe englobe cependant de multiples échelles (paysages, écosystèmes, espèces et gènes), ainsi que de nombreuses caractéristiques (composantes, processus, fonctions etc.), ce qui rend sa mesure et surveillance fort compliquées. C'est la raison pour laquelle des indicateurs de biodiversité ont été identifiées. Le « bois mort » figure parmi les indicateurs clé pour la diversité biologique dans l'écosystème forestier. Cela signifie que pour vérifier les progrès effectués en vue de maintenir ou de restaurer la biodiversité, le bois mort dans ses différents états doit être quantifié. Néanmoins, il n'existe pas encore de méthodes efficaces et rapides. Afin de combler cette lacune **nous avons développé une méthode efficace permettant de quantifier des épicéas morts de gros diamètre**. Cette méthode, appelée AP-GIS-méthode, s'appuie sur la photo aérienne infra-rouge (**A**erial **P**hoto) et un Système d'information géographique (**G**eographic **I**nformation **S**ystem). Grâce à elle, il est possible de créer des cartes de répartition spatiale d'arbres secs, ainsi que de calculer leur nombre par surface (p.ex. par hectare). Cette méthode permet de répondre à la question de savoir combien de bois mort se trouve actuellement dans les forêts gérées.

Outre des techniques fiables de mesure de bois mort, les gestionnaires des forêts ont également besoin de valeurs quantitatives de référence, c'est-à-dire des recommandations précisant la quantité de bois mort nécessaire au maintien de la diversité biologique. Une possibilité de définir de telles valeurs est de se fonder sur des systèmes de référence, telles les forêts naturelles. Néanmoins, les quantités de bois mort dans ces forêts peuvent s'avérer extrêmement grandes, allant jusqu'à 30% du volume total sur pied. Appliquer des valeurs de référence si élevées serait incompatible avec les objectifs économiques de forêts exploitées. Une autre possibilité de définir des recommandations

de gestion est de se baser sur les besoins d'habitats de certaines espèces dépendant du bois mort. Le Pic tridactyle *Picoides tridactylus* a déjà été identifié comme indicateur potentiel de caractéristiques typiques de forêts avec une dynamique naturelle (en particulier de vieux peuplements). Même si des études écologiques concernant ce pic ont démontré son besoin en arbres sénescents et morts pour se nourrir, creuser sa cavité et tambouriner, la quantité nécessaire en termes absolus n'a jamais été évaluée. Dans cette recherche **nous avons analysé la dépendance des deux sous-espèces européennes alpine et nordique, le *Picoides tridactylus alpinus* et le *P. tr. tridactylus* du bois mort**. L'étude a été menée dans des forêts subalpines en Suisse, ainsi que dans des forêts boréales en Suède. Dans les deux pays nous avons pu mettre en évidence une relation non-linéaire entre la probabilité qu'un territoire de pic soit effectivement occupé par cet oiseau et la quantité d'arbres morts présents. Il a été possible de déterminer des valeurs seuil de bois mort nécessaire, afin d'assurer la présence locale du Pic tridactyle. Très clairement, ce pic dépend d'une quantité d'arbres sénescents et mort relativement élevée. Nous avons également constaté que la densité élevée du réseau routier forestier en Suisse exerce une influence négative sur la présence de cet oiseau. La raison est qu'une densité de route élevée facilite l'accès à la forêt et ainsi l'intensification de la gestion, souvent allant de pair avec l'abattage d'arbres malades ou morts. En nous basant sur nos résultats, et en nous référant à d'autres études ayant démontré des liens entre le Pic tridactyle et la biodiversité, nous suggérons de considérer cette espèce comme indicatrice de bois mort et d'un habitat de qualité. Dans la suite de notre recherche nous avons donc utilisé ce pic pour répondre à la question suivante : Combien de bois mort devrait-on maintenir dans une forêt gérée, afin de garantir une biodiversité élevée?

Avec le but d'élaborer des valeurs de référence de bois mort, **nous avons développé un modèle bioénergétique pour le Pic tridactyle**. Ce modèle permet de prédire la quantité d'arbres morts nécessaire, pour que cet oiseau puisse satisfaire ses besoins énergétiques. Par la comparaison des résultats de modélisation avec les valeurs seuil de bois mort identifiées auparavant, nous avons pu déterminer des valeurs de référence jugées fiables, car les résultats des deux approches étaient très similaires.

Nous recommandons de laisser un volume (ou une surface terrière) d'arbres morts sur pied correspondant à 5% du volume total (ou de la surface terrière totale) sur pied. Ce pourcentage de bois mort devrait être maintenu sur des surfaces d'environ 100 ha. Dans les forêts subalpines cela représente une surface terrière de ≥ 1.6 m^2 ha^{-1} ou un volume de ≥ 18 m^3 ha^{-1} ou au minimum 14 arbres morts avec un diamètre de ≥ 21 cm par hectare.

En tant que moyen pragmatique pour stimuler l'intérêt des gestionnaires pour le maintien de bois mort dans la forêt, **nous avons analysé l'utilité potentielle du Pic tridactyle comme ennemi naturel des bostryches**. En définissant trois scénarios différents d'efficacité du pic, nous avons comparé le nombre de bostryches capturés par cet oiseau avec celui piégé par des pièges à phéromones utilisés en foresterie. Il s'est avéré que le pic détruit 2-19 fois plus d'insectes que les pièges. Ce résultat est valable si un individu de pic est comparé à un piège, mais également si l'on compare toute la population de Pics tridactyles suisses avec tous les pièges installés dans les forêts en Suisse.

Kurzfassung

Diese Studie verfolgt zwei Ziele: erstens die Entwicklung einer rationellen Methode für die Quantifizierung von grossen, stehenden toten Fichten und zweitens die Erarbeitung von ökologischen Totholz-Zielgrössen zur Erhaltung von Biodiversität. Wir beantworten die folgenden zwei grundlegenden Fragen: Wieviel Totholz ist zur Zeit in Wirtschaftswäldern vorhanden? Und wieviel Totholz ist nötig zur Erhaltung der biologischen Vielfalt?

Gemäss der heutigen allgemeinen Auffassung muss moderne Waldbewirtschaftung nachhaltig sein. Ein wichtiges Nachhaltigkeitskriterium ist die Erhaltung der biologischen Vielfalt. Dieses Vorhaben ist jedoch kompliziert und umfasst vielerlei Ebenen (Landschaften, Oekosysteme, Arten, Gene) sowie Merkmale (Komponenten, Abläufe, Funktionen). Deshalb sind für Mess- und Monitorzwecke schon verschiedene Biodiversitäts-Indikatoren bestimmt worden. Ein Schlüsselindikator für biologische Vielfalt im Waldökosystem ist Totholz. Um die Fortschritte in Richtung Erhaltung oder Wiederherstellung der Biodiversität zu überprüfen, müssen darum die verschiedenen Totholzformen gemessen werden. Jedoch fehlen zur Zeit noch kostengünstige, schnelle Methoden. Aus diesem Grund **haben wir in dieser Studie eine rationelle Methode für die mengenmässige Erfassung von Totholz, genauer gesagt von grossen, stehenden toten Fichten entwickelt**. Die Quantifizierung erfolgt mittels Luftbildern (**A**erial **P**hotos) und einem Geografischen Informationssystem (**G**eographic **I**nformation **S**ystem), und wird deshalb AP-GIS-Methode genannt. Mit Hilfe dieser Methode können einerseits Totholz-Karten angefertigt werden, andererseits kann die Totholzdichte pro Flächeneinheit (z.B. Hektare) berechnet werden. Die Methode dient somit zur Beantwortung folgender Frage: Wieviel Totholz ist zur Zeit in Wirtschaftswäldern vorhanden?

Nebst Techniken für Totholzquantifizierung brauchen Forstpraktiker auch Zielgrössen, d.h. Richtlinien, um zu wissen, wieviel Totholz für die Erhaltung der biologischen Vielfalt nötig ist. Für die Festlegung solcher Zielgrössen kann man sich z.B. an Totholzmengen in Naturwäldern orientieren. Jedoch sind diese manchmal extrem hoch, bis zu 30% des stehenden Vorrats, weshalb solche Richtwerte in Wirtschaftswäldern mit vorwiegend ökonomischer Funktion kaum anwendbar wären. Eine andere Möglichkeit besteht darin, Zielgrössen aus Habitatsansprüchen totholzabhängiger Tierarten abzuleiten. Der Dreizehenspecht *Picoides tridactylus* ist in früheren ökologischen Untersuchungen als potentielle Indikatorart für Merkmale natürlicher Wälder (insbesondere Altholzbestände) erkannt worden. Obwohl seine Abhängigkeit von sterbenden und toten Bäumen für Nahrungssuche, Höhlenbau und Trommeln bekannt ist, wurde nie untersucht, wieviel Totholz für diese Spechtart effektiv nötig ist. Deshalb **haben wir in unserer Studie die quantitative Totholzabhängigkeit der beiden europäischen Unterarten, d.h. der Alpinform *Picoides tridactylus alpinus* und der Nominatform *P. tr. tridactylus*, untersucht**. Diese Untersuchung ist in subalpinen Fichtenwäldern der Schweiz sowie in borealen Nadelwäldern Schwedens durchgeführt worden. In beiden Fällen fanden wir eine signifikante nichtlineare Korrelation zwischen zunehmender Totholzmenge und der Wahrscheinlichkeit, dass ein Spechtterritorium besetzt ist. Wir konnten daraus ökologische Totholz-Schwellenwerte für das lokale Vorkommen dieser Art ableiten. Es zeigt sich eindeutig, dass der Dreizehenspecht relativ grosse Totholzmengen braucht. In der Schweiz stellten wir zudem fest, dass die Wahrscheinlichkeit, ein besetztes Spechtterritorium anzutreffen, durch ein dichtes Waldstrassennetz negativ beeinflusst wird. Dies liegt daran, dass eine hohe Strassendichte eine Intensivierung der Bewirtschaftung und somit das Entfernen geschwächter und toter Bäume erleichtert. Aufgrund unserer Resultate sowie anderer Hinweise aus der Wissenschaft auf Beziehungen zwischen Dreizehenspecht und Biodiversität schlagen wir vor, diese Vogelart als Indikator für Totholz und Habitatsqualität zu qualifizieren. Aus dieser Ueberlegung haben wir diese Spechtart auch benützt zur Beantwortung der folgenden Frage: Wieviel Totholz braucht es in Wirtschaftswäldern?

Wir haben ein bioenergetisches Modell für den Dreizehenspecht erarbeitet mit dem Zweck, Totholz-Zielgrössen festzulegen. Dieses Modell sagt voraus, wie viele stehend-tote Bäume nötig sind, damit dieser Specht seinen Energiebedarf decken kann. Die Aussagen des Modells sind anschliessend mit den schon besprochenen Totholz-Schwellenwerten verglichen worden. Da beide Ansätze zu ähnlichen Resultaten führten, konnten wir verlässliche Zielgrössen formulieren.

Wir empfehlen sowohl für subalpine als auch für boreale Nadelwälder einen Anteil von 5% toten Bäumen (Basalfläche oder Volumen) anzustreben. Dieser prozentuale Totholzanteil sollte auf etwa 100 ha grossen Flächen als Mittelwert vorliegen. Für subalpine Nadelwälder entspricht dies einer Basalfläche von $\geq 1.6\ m^2\ ha^{-1}$ oder einem Volumen von $\geq 18\ m^3\ ha^{-1}$ oder 14 toten Stämmen mit einem Durchmesser von mindestens 21 cm pro Hektare.

Wir haben überdies den potentiellen Nutzen des Dreizehenspechts als natürlicher Borkenkäferfeind analysiert, sozusagen als pragmatischen Weg, um unter Forstleuten das Interesse für das Belassen von Totholz im Wald zu fördern. Wir haben die Anzahl vertilgter Borkenkäfer verglichen mit der Anzahl Käfer, die in herkömmlichen Borkenkäfer-Pheromonfallen gefangen werden. Dafür wurden drei Szenarien mit unterschiedlicher Effizienz des Spechtes definiert. Gemäss unseren Resultaten vertilgen Dreizehenspechte 2-19 mal mehr Käfer als Fallen. Dies gilt sowohl für den Vergleich eines Spechtes mit einer Falle als auch für die Gegenüberstellung der ganzen Schweizer Spechtpopulation und sämtlicher Borkenkäferfallen in Schweizer Wäldern.

Chapter

1

Study background

1.1. Sustainable management, biodiversity, criteria and indicators

Global concern for the loss of biodiversity made its first appearance in the political arena in the early 1990s and constituted a main theme of the United Nations Conference on Environment and Development held in Rio de Janeiro in 1992. “Forestry” and “biodiversity” issues were considered a priority at the conference. As a result, a large number of European countries i) signed a framework agreement, the “Convention on Biological Diversity”, ii) agreed on a set of “Forest Principles” and finally, iii) contributed to a component of “Agenda 21”, outlining a non-legally binding authoritative statement of principles for a global consensus on the management, conservation and sustainable development of all types of forest.

Since the Rio Conference, various national and international initiatives, dealing with criteria and indicators including the maintenance of biological diversity in forests, have been implemented world-wide. Among the most notable were the “Intergovernmental Seminar on Criteria and Indicators for Sustainable Forest Management” (the Helsinki Process, 1994), the meetings of the “Intergovernmental Working Group on Global Forests” (the Montreal Process, 1995), and the “Tarapoto Proposal of Criteria and Indicators for Sustainability of Amazon Forest” (1995).

Throughout Europe, many pan-European activities to implement the Convention on Biological Diversity are currently under way (cf. Table 1). Regional and national initiatives have also been drafted and in most cases implemented, or are being researched.

Table 1: *Framework and ongoing activities for implementing the conservation of biodiversity in forest ecosystems (not exhaustive).*

Framework	**On-going activities**
Global level:	
• Convention on Biological Diversity 1992 • Agenda 21, Chapter 15	• Intergovernmental Working Group on Global Forests (Montreal Process), 1995 • International Tropical Timber Organization ITTO efforts • The Tarapoto Proposal of Criteria and Indicators for Sustainability of the Amazon Forests, 1995 • Forest certification processes (Pan European Forest Certification, Forest Stewardship Council FSC, ISO 14001 Environmental Management System Standard, etc.)
Pan-European level:	
• Pan-European Biological and Landscape Diversity Strategy (PEBLDS), 1996-2000 • A) Resolution H2: General Guidelines for the Conservation of the Biodiversity of European Forests; B) Resolution L2: Pan-European Criteria, Indicators and Operational Level Guidelines for Sustainable Forest Management • Bern Convention 1979: Convention on the Conservation of European Wildlife and Natural Habitats	• The Ministerial Conference “Environment for Europe”, Dobris (1995), Lucerne (1993), Sofia (1995) • The Ministerial Process “Ministerial Conference on the Protection of Forests in Europe” (MCPFE), 1990 in Strasbourg, 1993 in Helsinki and 1998 in Lisbon • The Community Biodiversity Strategy developed by the EU Commission • The implementation of EU Habitats Directive – NATURA 2000 • Pan-European Process on the Protection of forests in Europe • The Community Forestry Strategy for the European Union, developed by the EU Commission
Swiss level:	
• Law on Forests 1993 (Loi fédérale sur les forêts LFo, RS 921.0). Art. 20 al. 4 • Ordonnance sur les forêts 1992 (OFo), RS 921.01. Art. 21 al. 5b, Art. 50 al. 1, 2d • Loi fédérale sur la protection de la nature et du paysage 1966 (LPN), RS 451 • Ordonnance sur la protection de la nature et du paysage 1991 (OPN), RS 451.1. Art. 14 al. 2a, Art. 15 al. 1, Art. 20 al. 3a, Art. 21 c, Art. 27 al. 1	• Biodiversity-Monitoring Switzerland • Swiss National Forest Programme (Waldprogramm Schweiz WAP-CH)

The conservation of biological diversity is one of the goals of sustainable forestry, although the concept encompasses much more. Biodiversity includes diversity at the genetic, species, ecosystem and landscape levels. Given this complexity, it is difficult to judge whether forests are being managed in an ecologically-sustainable way (Lindenmayer et al. 2000). Moreover, it is impossible to measure and monitor the effects of various management practices on all species. To overcome this problem, many indicators – a subset of attributes that could serve as surrogates for total biodiversity – have been identified. Indicators can be used to provide decision-makers with useful information on biodiversity status and trends, and to help determine if broad goals and targets for conservation are being reached. An indicator may be a species, a structural component, a process or some other feature of the biological system, the presence of which insures the maintenance or restoration of the most important aspects of biodiversity for that system (Hansson 2000).

The recently increased interest in dead wood coincides with the world-wide discussion on the role of forests as carbon sink and rich reservoirs of biodiversity (Bobiec 2002). The importance of dead wood in forest ecosystems is becoming more and more evident to conservation biologists, forest and wildlife managers and political circles. This is why "dead wood" has recently been proposed as a key factor of European forest biodiversity (Project BEAR[1]; Larsson, 2001) and a new indicator of forest biodiversity, to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (<http://www.minconf-forests.net> April 29th 2002). It also appears in modern certification standards for best forestry practices, for example those defined by the Forest Stewardship Council (FSC).

1.2. "Dead wood" indicator not yet operational

A major problem affecting the use of biodiversity indicators is that ecological knowledge lags behind policy initiatives (Lindenmayer et al. 2000). It is difficult to determine how the indicators might be identified, measured, interpreted and monitored. Standardised methodology and protocols are still lacking. In particular, for dead wood no agreement

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[1] BEAR : The project " Indicators for monitoring and evaluation of forest biodiversity in Europe BEAR", initiated in 1998, is a pan-European concerted action, bringing together expertise from 27 European research organisations to build a framework for the development of forest biodiversity indicators on various scales.

exists on the kind of dead wood items to be inventoried: e.g. standing or lying dead wood, from small up to large tree diameters, expressed in volume or number of stems per ha? In addition, dead wood inventories for research and monitoring purposes, are generally carried out using labour-intensive and expensive field methods. Taking a long-term view, a system of biodiversity indicators must however be cost-effective and standardised. This thesis intends to contribute to the introduction into operational use of the biodiversity indicator “dead wood”.

The establishment of reference values and critical thresholds for forest biodiversity is among priorities for the further development of biodiversity evaluation tools (Esteban 1999). Scientific knowledge is still lacking on the fundamental question: “How much dying and dead wood is enough in managed forests?” (Angelstam 1997). This lack would appear evident for European forest standards, as illustrated for example by the English national initiative of the FSC: “Due to the lack of scientific evidence it is not possible at present to give precise guidance on the amount, distribution and composition of dead wood that is appropriate to the individual site” (Anonymous 1999). In Switzerland, the non-governmental national organisation Pro Natura and the Swiss Agency for the Environment, Forests and Landscape (Bolliger 2001) both demand for “more dead wood” in managed forests, without any quantitative precision. Quantitative recommendations, however, are essential as operational management goals. Without quantitative targets, neither verification of progress towards sustainable forest management nor sound adaptive management is possible. This thesis will contribute towards defining dead-tree target values, derived from identified dead-wood thresholds important for the Three-toed woodpecker.

Chapter

2

Aims of the study

2.1. Conceptual and methodological design

A general overview of the relationships addressed in this thesis is presented in Fig. 1.

Ecologists and forest resource managers need measurement techniques to judge the success or failure of management regimes designed to sustain biodiversity. Total biodiversity is an extremely complex concept and cannot be measured using only one indicator (species). Currently, the relationships between potential indicator species and total biodiversity are not well established (Lindenmayer et al. 2000). In addition to taxon-based indicators of biodiversity in forests, there are also *structure-based indicators*. One of them is “dead wood”, more precisely dying and dead trees, a stand-level characteristic of structural complexity. Currently, rapid and cost-effective techniques for dead-wood inventories are not available. Therefore, **we want to develop a new method for the quantification of spruce snags**. Based on infrared **A**erial **P**hotos and a **G**eographic **I**nformation **S**ystem, this method is called the AP-GIS-method. It is presented in § 4.4. and some potential applications are outlined in § 4.5. Paper **I** provides a detailed presentation of the method and its validation.

A next step is to determine the critical thresholds regarding what amounts of the dead wood found in landscapes with a natural dynamic are sufficient for maintaining biodiversity in the managed landscape. Species that are unique to the different habitats and ecological properties of forest landscapes with natural dynamics have to be identified (Angelstam 1998a). Following this author, if it is possible to translate the species’ habitat requirements into criteria based on their environmental demands, these criteria can be used as opposed to the more costly inventories of certain indicator species in the field. The Three-toed woodpecker *Picoides tridactylus* has been identified as a species associated with old-growth forests and indicating properties of naturally dynamic forests (Angelstam & Mikusinski 1994; Derleth et al. 2000; Hess 1983; Imbeau & Desrochers 2002; Mikusinski et al. 2001). We hence use this species as *functional indicator* and want to determine if it is dependent on dead wood.

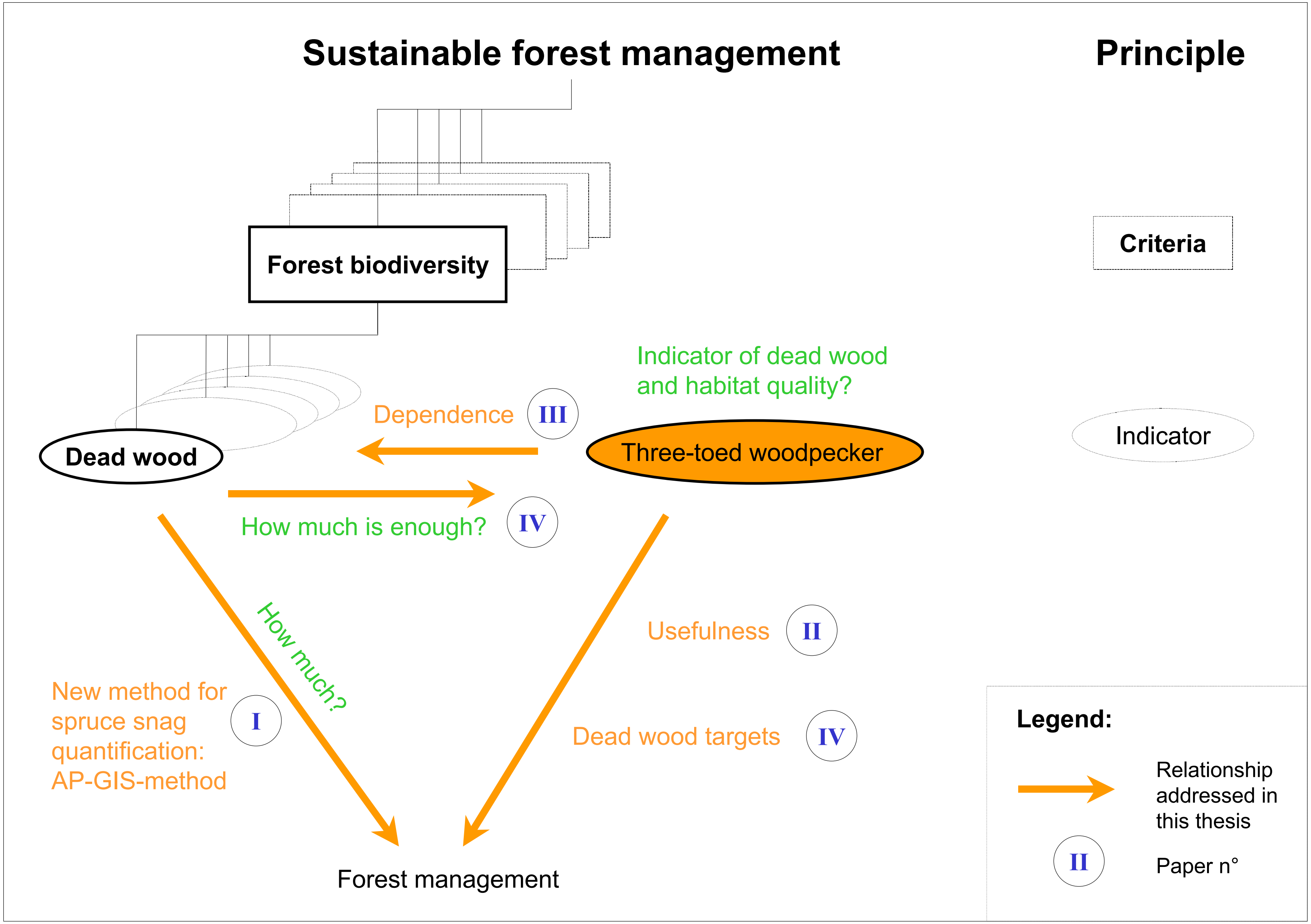

Fig. 1: *Relationships addressed in this thesis and its place within the framework of sustainable forest management.*

This question is addressed in Paper III, and § 5.1. presents the main results. In order to verify this relationship for both European sub-species *P. tr. tridactylus* and *P. tr. alpinus*, we conducted a case study in boreal and sub-Alpine forests.

Since the Three-toed woodpecker shows a significant dependence on dead wood, its requirements can be used to derive dead-wood management targets for the forest types it inhabits. In order to define such targets, two complementary approaches have been adopted. The idea is that, if we obtain similar results using both approaches, we are able to confirm the reliability of the defined snag targets for management purposes. **The first approach involves the development of a theoretical bioenergetic model**, enabling estimation of snag amounts required for the local persistence of Three-toed woodpeckers. For the validation of this model in different study sites, we used the previously developed AP-GIS-method. The model is outlined in the second part of Paper II and § 5.4. A more rigorous presentation is contained in Paper IV. **The second approach is based on the previous case study in boreal and sub-Alpine forests, resulting in an empirical model predicting the snag amounts necessary for the Three-toed woodpecker.** This empirical model is also presented in Paper IV. The proposed dead-tree management targets are given in § 6.4.

A more psychological aspect is the still wide-spread “fear” of harmful insects, such as bark beetles, among (Swiss) foresters. Indeed, forest land owners and forestry managers consider(ed) dead wood as a potential threat to forest sustainability. Depending on the local susceptibility of managed forests to pests or wild fire, management systems have been developed that implicitly include radical reduction of amounts of dead wood. Since biodiversity conservation is not only a scientific, but primarily a management issue, intensive co-operation and mutual understanding between scientists and managers is essential. That is why **we analyse in this thesis the usefulness of Three-toed woodpeckers as natural agents against bark beetles**. This question is addressed in Paper II and § 5.5. Our demonstration of the usefulness of Three-toed woodpeckers is considered a pragmatic way to stimulate managers’ interest in dead-wood maintenance or restoration. Finally, the Three-toed woodpecker’s presence in a landscape indicates that a range of other species depending on the same or similar dead-wood amounts and habitat qualities is also present (cf. § 5.3.).

2.2. Axioms and postulates

Here we present the axioms on which this thesis is based, and the postulates tested. According to Ford (2000) an axiom is a proposition assumed to be true on the basis of previous research, and is used in defining the working part of the foundation of the research. A postulate is a conjecture, a new or unexplored idea. It is untested, or considered sufficiently uncertain to be the subject of further investigation.

Axiom 1: Coarse woody debris, in particular large standing dead trees, are a key element of forest biodiversity.

Axiom 2: Dead-wood amounts in managed forests are in general much smaller than in natural forests, and may cause a lack of habitat and resources for species dependent on dead wood.

Axiom 3: Woodpeckers are considered the most demanding guild among resident bird species, and the presence of the most specialised woodpecker species, in particular the Three-toed woodpecker, is indicative of the properties of forests with natural dynamics.

Postulate 1: Large standing dead spruce trees can be effectively quantified by a method based on remote sensing and GIS techniques. → § 4.4. and Paper I

Postulate 2: The presence of Three-toed woodpeckers shows a non-linear response related to dead-wood quantities in both boreal and Alpine spruce forests. → § 5.1. and Paper III

Postulate 3: The amount of dying/dead trees required for the presence of Three-toed woodpeckers can be predicted by modelling and translated into management recommendations. → § 5.4., 6.3. and Papers IV and II

Postulate 4: Three-toed woodpeckers are an interesting alternative to bark beetle control using pheromone traps in spruce forests. → § 5.5. and Paper II

2.3. Specific objectives

This thesis addresses the following specific objectives:

Paper I: 1) to present a method enabling efficient quantification of large snags (standing dying and dead trees) using a combination of colour infrared aerial photos scaled to 1:10,000 and a Geographic Information System; 2) to validate it by comparing the results obtained with these combined techniques at several study sites with the ground-truth using classical field methods.

Paper II: 1) to compare the effectiveness of Three-toed woodpeckers in bark-beetle control with bark-beetle traps; 2) to determine the number of declining/dead spruce trees per ha required to meet the Three-toed woodpecker's foraging needs.

Paper III: 1) to test the dependence of Three-toed woodpeckers on dead wood in a boreal and a sub-Alpine landscape by a field study; 2) to search for possible dead-wood threshold values important for the local continued presence of Three-toed woodpeckers; 3) to derive quantitative targets for management implications.

Paper IV: 1) to predict the spatial densities of declining/dead trees required to meet the Three-toed woodpecker's energy requirements by developing and validating a theoretical model based on the energy budgets of this woodpecker species; 2) to verify these predictions by a subsequent field study; 3) to derive quantitative management recommendations through the definition of dead-tree target values.

Chapter
3

Material and methods

3.1. Study sites

In this thesis we used a total of 50 study sites of a size of 0.6-3.1 km^2 (Table 2), located in Switzerland (30) and central Sweden (20). The sites in Switzerland are situated in the sub-Alpine vegetation zone, between 1300 and 1700 m a.s.l., and were dominated by *Picea* spruce forests, sometimes interspersed with pastures. The main vegetation in the Swedish boreal forests, sometimes including bogs, were Norway spruce and *Pinus* pine. In general, the forests were > 100 years old. Two types of study sites have been selected:

i) with breeding Three-toed woodpeckers, such as defined in the International Ornithological Atlases (Sharrock 1973), and

ii) without Three-toed woodpeckers, i.e. where this species has neither been observed by local birdwatchers before the study, nor by ourselves during the study.

3.2. Gathering of dead-wood data

We used three methods to gather dead-wood data: a) AP-GIS-method, b) complete field inventory in forest stands using a tree calliper, and c) point relascope sampling (cf. Table 3). The AP-GIS-method is a new method developed in this thesis (cf. Paper I and § 4.4.). The other methods are based on fieldwork.

Table 2 gives an overview of methods used for dead-wood data gathering on each study site, and the sites involved in data analyses and presented figures.

Switzerland	Eastern/central Pre-Alps												Western Pre-Alps											Jura mountains						
	Vorder Höhi B. SG	Ibergeregg H. SZ	Fräkmüntegg LU	Glaubenberg H.e. LU	Bödmerenwald SZ	Glaubenberg G. LU	Kriens O.W. LU/NW	Schwägalp AR	Ibergeregg S. SZ	Vorder Höhi L. SG	Glaubenberg H.b. OW	Unteriberg SZ	L'Hongrin Malatraix VD	Rougemont M. VD	Rougemont C. VD	La Pierreuse VD	L'Etivaz VD	Pays-d'Enhaut L.J. VD	Col de la Croix VD	Les Tenasses VD	Montreux La N. VD	La Laitemaire VD	Rougemont L. A. VD	Grand-Petit Cunay VD	Mt. Tendre R. P. VD	Bois de la Baragne VD	Bois de Peney VD	Marchairuz VD	Crêt de la Neuve VD	Mt. Pelé VD
Three-toed woodp.	y	y	y	y	y	n	n	n	n	n	n	n	y	y	y	y	y	n	n	n	n	n	n	y	y	y	n	n	n	n
Size [km^2]	0.9	1.8	1.0	3.1	2.3	1.0	1.0	1.0	1.0	0.6	2.6	2.1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	3.1	3.0	1.0	1.0	1.0	1.0	3.0
AP-GIS-method	x	x		x	x					x	x	x											x	x	x					x
Field inventory	x	x		x						x	x			x	x	x	x													x
Relascope sampling	x	x	x	x		x	x	x	x				x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	
Development AP-GIS m.	o	o								o																				o
Validation bioenerg. m.	o	o		o	o					o	o	o											o		o					o
Empirical log. regr. m.	o	o	o	o		o	o	o	o				o	o	o	o	o	o	o	o	o	o		o	o	o	o	o	o	
Figure 2	o	o																												o
Figure 3	o	o		o						o	o			o	o	o	o													o
Figure 9	o	o	o	o		o	o	o	o				o	o	o	o	o	o	o	o	o	o		o	o	o	o	o	o	

Sweden	Fermansbo	Janolsskogen	Stora Kloten	Hallaren	Dammsjön	Gårtjärnen	Gränsen	Stora Björktjärnen	Ölsta	Grankärret	Karmansbo	Olgots-berget	Spelmossen	Saladamm	Storsjön	Ungen	Pålsbenning	Skärsjön	Broddbo	Svenskmossen
Three-toed woodp.	y	y	y	y	y	y	y	y	y	y	n	n	n	n	n	n	n	n	n	n
Size [km^2]	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Relascope sampling	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Empirical log. regr. m.	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Figure 9	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o

Table 2:
General overview presenting all study sites, the method used to gather dead-wood data (x) *and the analyses and figures the data have been used for* (o).

y = *Three-toed woodpecker present*
n = *Three-toed woodpecker absent*

Table 3: *Methods and material used to gather dead-wood data.*

Method	Material	Type of data
AP-GIS-method	Infrared aerial photo, stereoscope, scanner, digital elevation model, GIS	Number of snags ha^{-1}
Complete field inventory	Tree calliper	Snag diameter [cm] Snag characteristics Stage of decomposition
Relascope point sampling	Relascope	Basal area [m^2 ha^{-1}]

a) AP-GIS-method

Details of the development and validation of this method are given in Paper I. The validated method was used to produce maps of the spatial distribution of snags (with a breast-height diameter of ≥ 25 cm) and to calculate the density of snags per area for several study sites (cf. Table 2) with the aim of validating the bioenergetic model.

b) Complete field inventory of snags in forest stands

In ten study sites (cf. Table 2) a random sample (n = 16 to 35, depending on the size of the study site) of forest stands of about 0.5 ha have been visited in the field to make a comprehensive inventory of standing dying and dead trees (minimal breast-height diameter 10 cm). The main variables were: diameter, snag decomposition stage, and treetop condition. Other variables describing the stand structure and physical parameters have also been recorded.

c) Relascope point sampling

A systematic grid of 16 sampling plots, 250 m apart, has been put onto each observation unit of 1 km^2 in size. The total number of trees at each sampling plot with a dbh ≥ 10 cm, i.e. wider than the gap in the angle relascope, represented the basal area of the forest at that plot. Basal areas were recorded for snags, logs and living trees. Other variables related to exploitation, physical parameters and Three-toed woodpecker traces have also been recorded.

3.3. Methods used to test the postulates

Postulate 1: *Large standing dead spruce trees can be effectively quantified by a method based on remote sensing and GIS techniques.*

The AP-GIS-method has been developed in a case study using four study sites (cf. Table 2) by interpreting recent (< 2 years old) infrared aerial photos on a scale of 1:10,000 with a stereoscope. All dying and dead spruce trees visible on the photos of the study sites have been marked. After integrating the aerial photos into a Geographic Information System and digitising snag data, snag distribution maps were drawn up. The AP-GIS-method was validated by comparing these maps with complete field inventories of snags that have been made on the same study sites. Details of the development and validation of this method are given in Paper I.

Postulate 2: *The presence of Three-toed woodpeckers shows a non-linear response related to dead-wood quantities in both boreal and Alpine spruce forests.*

This postulate was tested by conducting a case study in Switzerland and central Sweden. We sampled dead-wood data in paired study sites with and without breeding woodpeckers (2x12 in Switzerland and 2x10 in Sweden), using the relascope point sampling method. Other variables describing forest management and important habitat features of this species have also been recorded. To test for differences between the two groups of forests within a country, we mainly used two sample t-tests pair-wise. Logistic regression was used to evaluate the existence of non-linear responses related to different dead-wood quantities. Details of the methods are given in Paper III.

Postulate 3: *The amount of dying/dead trees required for the presence of Three-toed woodpeckers can be predicted by modelling and translated into management recommendations*.

In order to test this postulate, we developed a theoretical mathematical model, known as a bioenergetic model, based on the energy requirements of the Three-toed woodpecker and on different assumptions regarding food selection and prey availability. For estimation of model variables we used literature data. The model output is a prediction of the probability of woodpecker presence as a function of snag density. We analysed the sensitivity of the model and then validated it on ten study sites (cf. Table 2) by quantifying the snags using the AP-GIS-method and comparing the predicted probability of woodpecker presence with its occurrence on these sites. As a second model, known as an empirical model, predicting the probability of woodpecker presence as a function of dead-wood quantities, we used logistic regression models (cf. Postulate 2). By comparing the predictions of the two models, we defined critical dead-wood amounts for woodpecker presence. These critical values were then translated into quantitative dead-wood management targets. The details of the methods used are given in Paper IV.

Postulate 4: *Three-toed woodpeckers are an interesting alternative to bark beetle control using pheromone traps in spruce forests.*

We tested this postulate by the development of different scenarios for woodpecker effectiveness in bark-beetle control and their comparison with available statistical data of bark beetles caught by pheromone traps in Swiss forests. In order to define three scenarios, the energy requirements of Three-toed woodpeckers were estimated based on literature data on its feeding ecology. Details of the methods are given in Paper II.

Chapter 4

Snag quantification by remote sensing and GIS

4.1. Ecological importance of dead wood: a literature review

Dead wood or coarse woody debris (CWD), i.e. snags[2], stumps, logs[3], large branches, is a very complex substrate. Its value for different species depends on the total volume, species, dimension, location, stage of decay and continuity. According to Albrecht (1991), both spatial and temporal continuity of various dead-wood types, each fulfilling different ecological functions, are necessary to maintain dead-wood-dependent species in the long term. Lack of CWD is one of the most crucial factors for many threatened species of bryophytes, lichens, fungi, insects and birds (Nilsson et al. 2001; Utschick 1991). Removal of woody microhabitats is hence considered a major threat to biodiversity and the stability of forest ecosystems. For Europe, Speight (1989) estimates that 40 percent of saproxylic beetle species are endangered in the greater part of their distribution area.

Both large animals and small organisms use logs and snags for hiding and cover, reproduction and feeding sites. Some use them as lookout posts (squirrels), for drumming (woodpeckers) or for sunning themselves (lizards). Small mammals may use CWD as bridges for reaching the opposite side of a small river. Many species of invertebrates are known to depend on CWD, especially beetles (*Coleoptera*). Their possible benefits from CWD are: source of food and breeding site, nesting site, source of construction materials, protection from predators, protection from environmental extremes (e.g. desiccation), over-wintering site, etc.

Epiphytic bryophytes and lichens are the main vegetation components on standing and newly-fallen stems and persist to rather late stages of decay. CWD also provides habitat for an enormous number of species of fungi. In former West Germany, for example, there are approximately 1500 macromycetes which require dead wood (Albrecht 1991). Travé et al. (1999) found in a French nature reserve that one third of the fungi species, i.e. 103 species, are wood decomposers. Recent studies show correlation between densities of

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[2] Snag : in this thesis defined as all standing dead and dying trees

[3] Log : down woody material

dead trees and, for example, richness of wood-beetles (Martikainen et al. 2000; Okland et al. 1996), and wood-fungi (Bader et al. 1995) (cf. Fig. 10).

In mature and old-growth forests, logs also play a role as “nurse logs” for tree regeneration, since tree seedlings are commonly found rooted in or on logs (Harmon 1986).

☞

> Dead wood is of prime importance for numerous plant and animal species in the forest ecosystem.

4.2. Relevance of large snags

In this section we present different reasons justifying why it is important to focus on large snags.

a) Extensive literature data demonstrate the preference of many organisms (cavity nesting birds, wood-dependent beetles, red-listed cryptogams) for large dead trees (cf. examples in Nilsson et al. 2001, Raphael & White 1984, Thomas 1979, Kruys et al. 1999, Samuelsson et al. 1994). For example, for cavity users, a smaller snag may be replaced by a larger one, but the reverse is not true. In particular, woodpeckers prefer larger snags to smaller ones for foraging (Fig. 2). This preference, which we verified on our study sites without differentiation of woodpecker species, is corroborated by literature concerning the Three-toed woodpecker (Hess 1983; Imbeau & Desrochers 2002).

b) Large-diameter snags provide a more stable microclimate for organisms than smaller ones because of wood thickness. For example, thickness of the wood surrounding a cavity is important for thermal regulation, and protection from environmental extremes and predators. Large snags remain moist in their centre even during long droughts, hence preventing small organisms from desiccation.

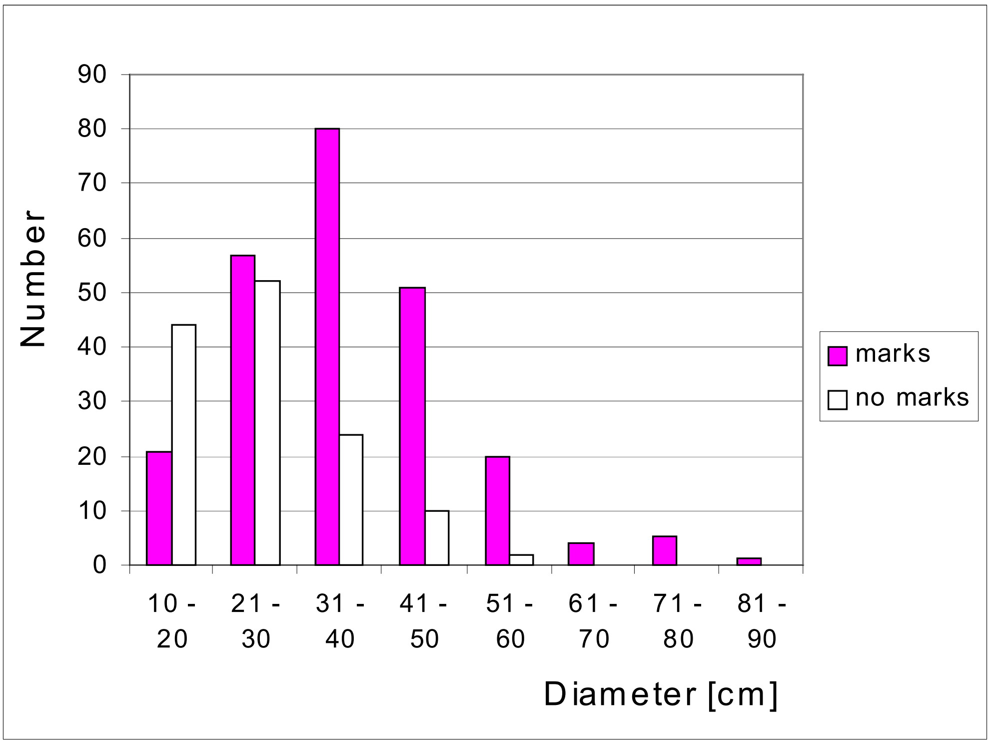

Fig. 2: *Relationship between snag diameter and number of woodpecker beakmarks, signs of foraging. Number of analysed snags = 371 on 3 study sites (cf. Table 2). Woodpecker species were not differentiated.*

c) Longevity, i.e. the length of time a snag stands, is positively correlated with snag diameter (Everett et al. 1999; Morrison & Raphael 1993). A larger snag may therefore have a long(er) use as a wildlife tree. For example, Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) with a dbh of 23 cm reach decay stage 3 (i.e. absence of bark and branches, intact bole with a minimum of top breakage; cf. Fig. 5) 65 years after mortality (Everett et al. 1999).

d) Large, standing declining and recently dead trees are the rarest of the diverse dead wood substrata, especially in managed forests (Fridman & Walheim 2000; Green & Peterken 1997). Since such trees still have a certain economic value, they may be cut when timber is harvested, or they are removed by sanitary logging. As illustrated in Figure 3, the diameter-frequency distribution of the snags on our study sites was clearly skewed towards small diameters. This tendency is less marked in forests with Three-toed woodpeckers, where harvesting is in general less intensive than in the other studied forests.

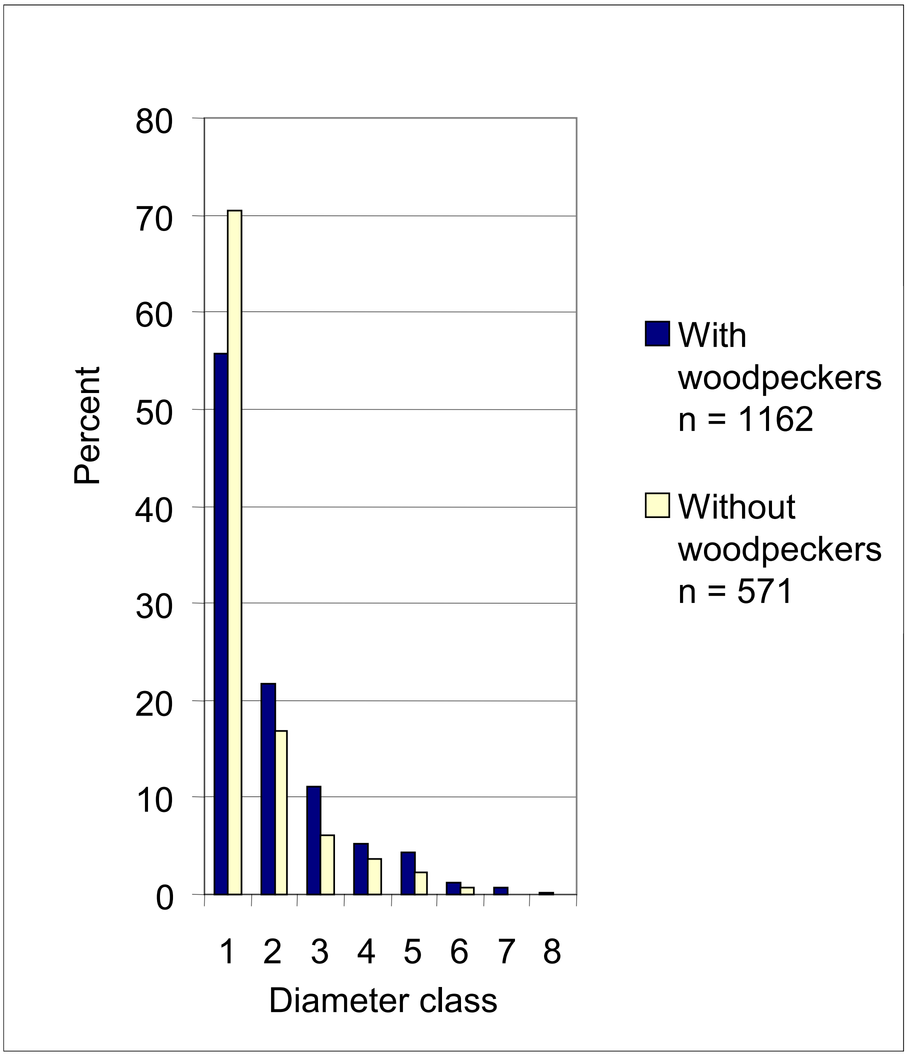

Fig. 3: *Snag-diameter frequency distribution in sub-Alpine forests with (7 sites, n = 1162) and without (3 sites, n = 571) Three-toed woodpeckers, respectively. Distribution is skewed towards small diameters, especially in forests without Three-toed woodpeckers. On the x-axis: diameter class 1 = 10-19 cm dbh, 2 = 20-29 cm, etc.*

e) The number of large dead trees above certain diameters may be crucial rather than the total volume of dead wood. Nilsson et al. (2001) suggest that for a given volume of dead wood, big trees can host more species than the same volume of thinner trees.

f) Dead trees of larger-diameter classes generally account for most of the CWD volume and basal areas in old-growth forests (Nilsson et al. 2002; Siitonen 2001). We found the same relationship in our study sites located in slightly managed forests in the Western Pre-Alps (Pays-d’Enhaut region): the proportion of the total basal area of dead trees with a dbh ≥ 30 cm was 72%, whereas numerically they only accounted for 25% (n = 338). High volumes are important for biodiversity conservation, since it has been demonstrated that the volume and basal area of CWD is positively correlated with saproxylic beetle species richness (Grove 2002; Martikainen et al. 1999; Martikainen et al. 2000; Okland et al. 1996).

Since large snags seem to have particular ecological relevance, we intended to develop a method that is especially efficient for quantification of large snags.

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> Among the different dead-wood types, large snags have a particular relevance for biodiversity, and they are especially rare in managed forests.

4.3. Why a new snag-quantification method?

There are two major reasons justifying the urgent need for new methods of dead-wood quantification.

a) *Growing demand from various users:* Initially, dead-wood data were collected to address wildlife habitat issues. More recently, dead wood is also considered relevant to issues of forest health, site productivity, fuel, and carbon stores. Groups interested in dead-wood inventories include those studying criteria and indicators defined for sustainable forest management (e.g. criteria 1 and 4 in the Helsinki process, i.e. global carbon cycles and biodiversity), wildlife managers or those concerned with forest certification processes. In the future, dead wood will hence be inventoried more and more frequently.

b) *Methodical difficulties in field methods:* Large dead trees are rare objects in managed forests. Most classic sampling designs will not be efficient for rare elements (Yoccoz et al. 2001). A high level of natural variability in rates of creation and amounts of dead wood is typical in unmanaged forests. Large snags may cluster and many plots with no such trees are to be expected. Large sample numbers and plot sizes are therefore required to monitor densities of large snags (Gray 2002). In monitoring programmes for land management, however, money and personnel are limited. A major problem is to ensure adequate sample numbers and plot sizes for field recording of such a patchily-distributed resource. Strip or line transect sampling, which have been proposed instead of plot-based methods (Lämas & Stahl 1998; Ringvall et al. 2000; Stahl et al. 2001), present similar problems. Recent work has focused on adaptive sampling designs (Thompson & Seber 1996), which seem to be promising for rare elements that form clusters (Acharya et al. 2000). In such designs, however, the sample size is not known beforehand, since the intensity of sampling is dependent on initial sampling results. This may be a drawback when evaluating survey costs. A large group size increases the efficiency of systematic adaptive cluster-sampling. When groups become too large, however, such sampling becomes equivalent to (near) full enumeration and survey costs may be extremely high.

☞ For large-snag inventories, classic field-based methods present numerous sampling difficulties and are hardly cost- and time-efficient.

4.4. AP-GIS-method

For both research and management purposes, simple, rapid and accurate methods for dead-wood quantification are required. To date, remote sensing as a data source is only seldom used for European national forest inventories (Köhl et al. 1998), and under-utilised for the assessment of forest biodiversity (Innes & Koch 1998), in spite of its high potential and frequent use in forest research. In this thesis we developed the AP-GIS-method, coupling infrared **A**erial **P**hotos scaled to 1:10,000 and a **G**eographic **I**nformation **S**ystem, in order to map and quantify large standing dying/dead spruce trees. For details we refer to Paper I. Given both the patchy distribution and relative scarcity of large snags, especially in managed forests, air borne data sources, such as aerial photos, facilitate inventories. Our method uses the differences in spectral reflectance in the near-infrared region (wavelength 700-1500 nm) between sound and dying/dead spruce trees. The latter can be detected on colour infrared photos because of their greyish-white colour (cf. Fig. 4). Mathematical processing based on a digital elevation model is necessary to transform the scanned images into so-called digital ortho-photos. These are geo-referenced in a Geographic Information System and prepared for spatial analyses and mapping on various scales.

With the developed method, a map of the spatial distribution of snags with a dbh ≥ 25 cm can be obtained in about 16 hours for an area of 3 km^2 in size (i.e. 3 minutes per ha of map). Quantitative estimations, expressed as number of snags per hectare, can easily be derived.

Field verifications revealed that 90% of the detected snags had a dbh ≥ 25 cm (n = 270). As demonstrated above (cf. § 4.2.), such large snags have a particular ecological relevance. In very good conditions – isolated tree, stand with open canopy - the smallest detected snags measured less than 20 cm. Tree diameter, treetop condition (broken or intact) and the canopy closure of the forest stand significantly affected the success of detection. The AP-GIS-method detected 71% of snags with a dbh ≥ 35 cm (67% for dbh ≥ 25 cm). The main reason for detection failure was a broken treetop. When only snags with an intact treetop were considered, the method detected 93% of the snags with a dbh ≥ 35 cm (90% for dbh ≥ 30 cm; 82 % for dbh ≥ 25 cm). A second reason for undetected snags was that they belonged to the understory and were therefore not visible. The method's main limitation is its inefficiency for the detection of snags in an advanced stage of decomposition (i.e. stages 4 and 5 in Fig. 5), which may be important wildlife trees. Based on our results for snag detection failure, we developed a correction coefficient in order to take into account the bias caused by undetected snags. The accuracy of the AP-GIS-method after application of this correction factor was ≤ 0.6 snags ha^{-1}, when compared with ground-truth field data. Including a security factor, we estimate that the AP-GIS-method gives results lying within 1 snag ha^{-1} of the ground-truth field data for snag densities, i.e. number of snags per hectare.

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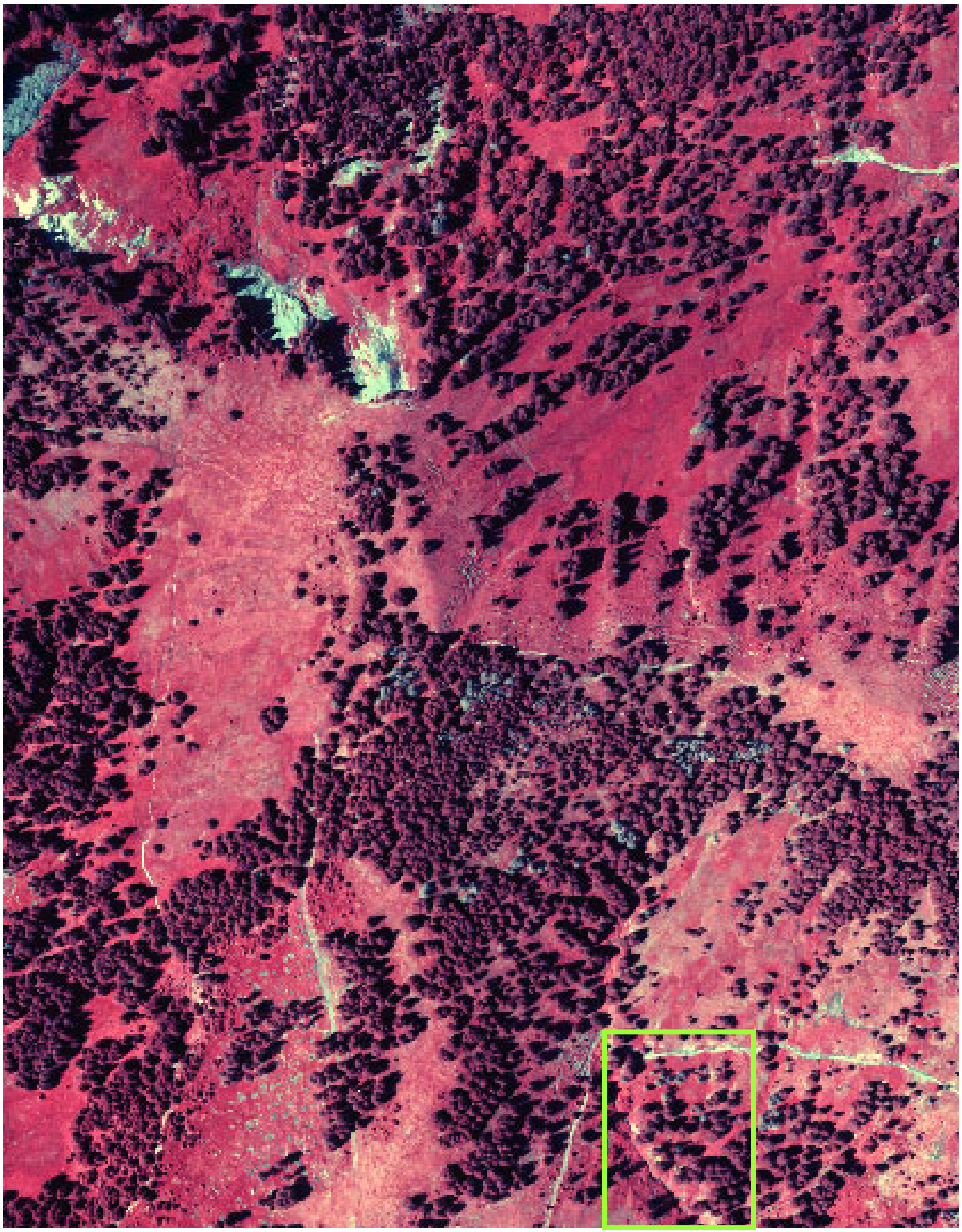
> The new AP-GIS-method enables mapping and time-efficient quantification of snags with a diameter ≥ 25 cm with an uncertainty of ± 1 snag ha^{-1} when compared to the ground truth.



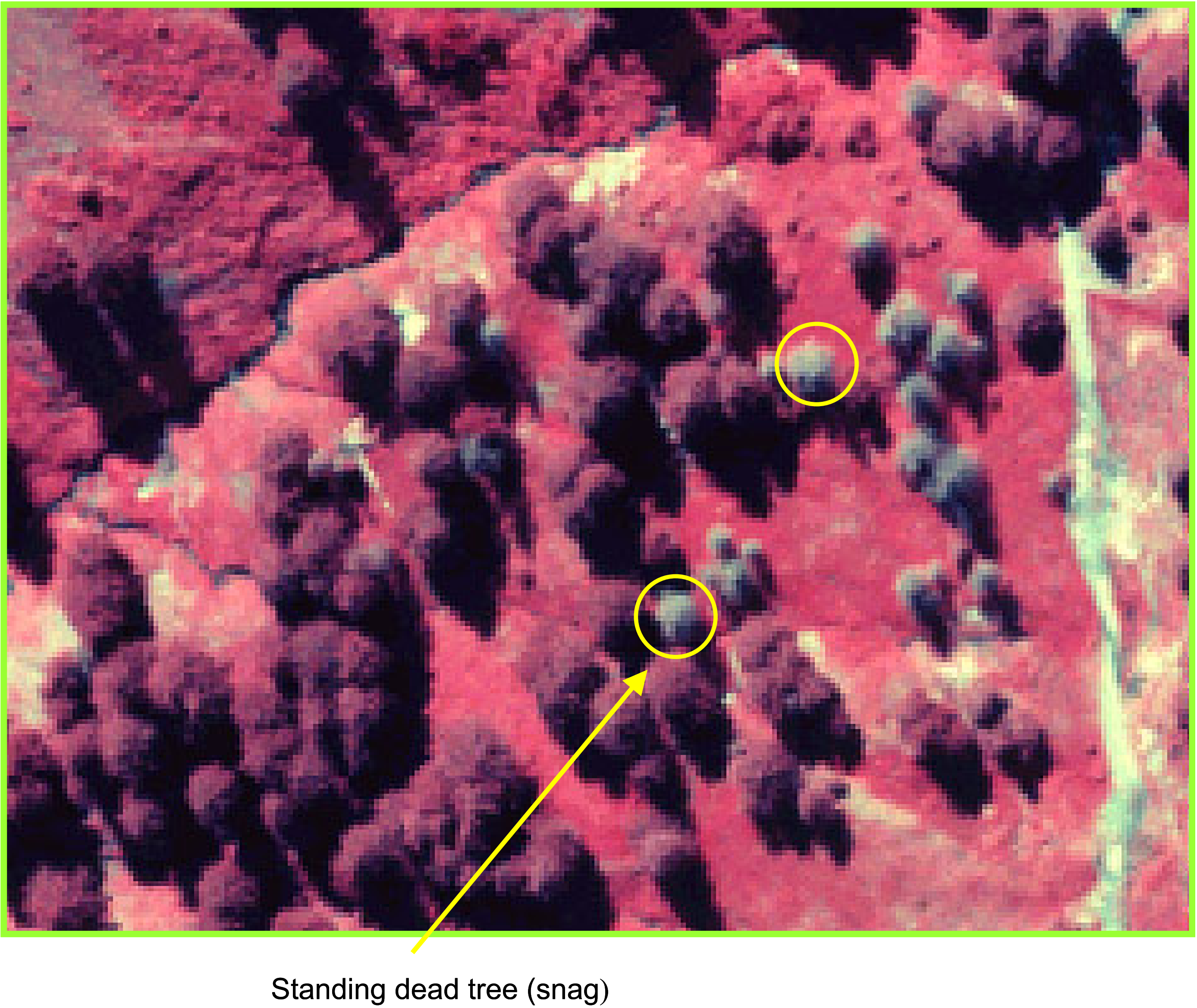


Fig. 4: *Colour infrared aerial photo presenting a forest landscape with sound spruce trees (red-violet) and snags (greyish-white). Bare rocks and tractor tracks also result in greyish colour on such photos.*

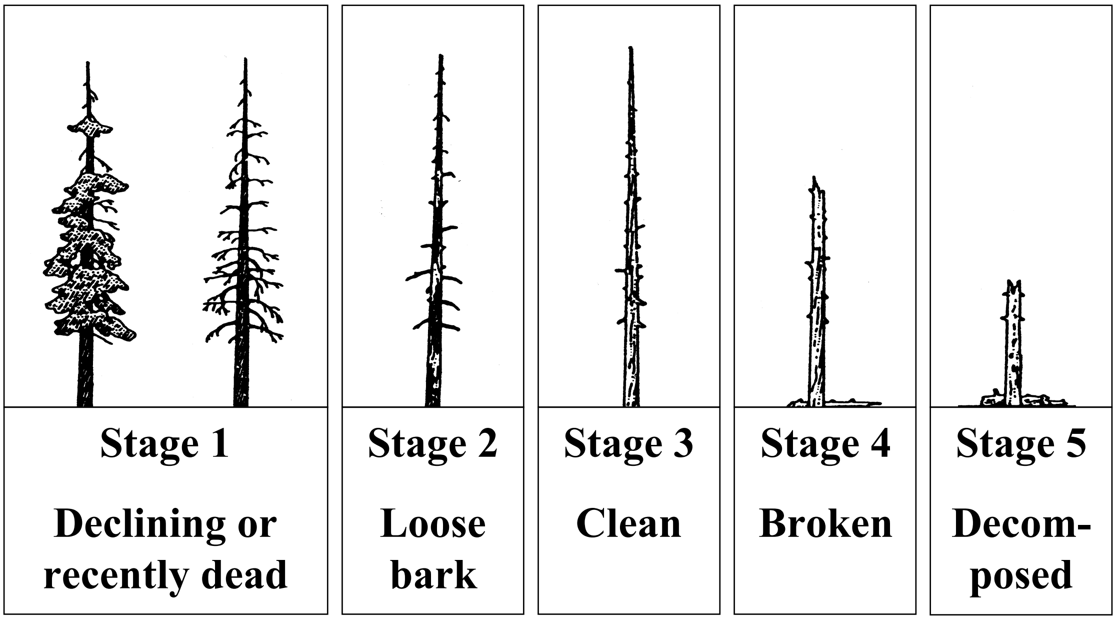


Fig. 5: *Snag decomposition stages, as defined in this thesis (modified from Maser et al. 1979).*

4.5. Prospective applications

A method based on remote sensing offers various advantages for rapid inventories of large snags. It facilitates the study of spatial and temporal variation in snag amounts and distribution in remote and inaccessible areas. In particular, the assessment of spatial arrangement of dead trees within a stand or across a landscape becomes possible thanks to the full enumeration of large snags over large areas (cf. Fig. 6). Another possibility is to represent the spatial arrangement of snags as a snag-density map (cf. Fig. 7). This map highlights the uneven spatial distribution of snags within a forest landscape. The third example shows how the road network may influence the spatial distribution of snags (cf. Fig. 8). Most of the snags are located where the road network density is low, i.e. at a certain distance of forest roads. GIS techniques enable many other types of spatial analyses and cartographic representation of geo-referenced data combined with snag maps. Our AP-GIS-method may be used as a basis to define, for example, an adaptive sampling design for field measurements in hectare or smaller plots. It may also be used for sampling on the landscape scale: one aerial photo couple scaled to 1:10,000, with 23x23 cm dimensions and an overlap of 80 percent, permits investigation of a forest area of 3.5 km^2. Even larger sampling plots would be possible by combining several photos in a composite. The potential of such large plots (3.5 km^2

instead of 1-hectare field plots) for different applications (wildlife studies, forest certification, etc.) may be considerable.

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The new AP-GIS-method may be used for forest inventories, certification processes, wildlife studies, etc.

4.6. Quantity and quality of dead wood in unmanaged versus managed forests

In § 4.7. we present our results of dead-wood amounts measured in forests with and without Three-toed woodpeckers. In order to situate our findings in a wider context, in this section we give a literature review on dead-wood amounts found in unmanaged and managed forests.

a) Unmanaged forests:

The volume of CWD in a natural forest depends on productivity of the site, decomposition rate of dead wood, and disturbances affecting input rate and stand succession (Harmon 1986). Aggregation does occur, since factors such as insects, disease, and wind-throw tend to cause localised mortality rather than random death throughout the stand (Caza 1993). The volume of dead wood varies considerably among forest types, about one order of magnitude (20-200 m^3) in European forests. On many sites, 30-50 m^3 standing and about 100 m^3 downed dead wood were probably commonly occurring amounts before European forests were subjected to human exploitation (Nilsson et al. 2002). For European unmanaged old-growth forests, volumes of > 250 m^3 ha^{-1} have been reported (Korpel 1995), whereas in North America CWD volumes may exceed 1000 m^3 ha^{-1} (Harmon 1986). For Swedish natural forests Siitonen (2001) reported CWD of around 18-40% of the total wood volume. Many studies in North America have demonstrated that CWD volume is highest at early successional stages immediately after the disturbance, lowest in the middle of succession, and high again in old-growth forests (Clark et al. 1998; Lee et al. 1997). Nilsson et al. (2002) synthesised several studies of European old-growth forests and found that among all standing trunks about 10% are dead. This proportion is independent of total basal areas (and site productivity) and may therefore serve as reference value.

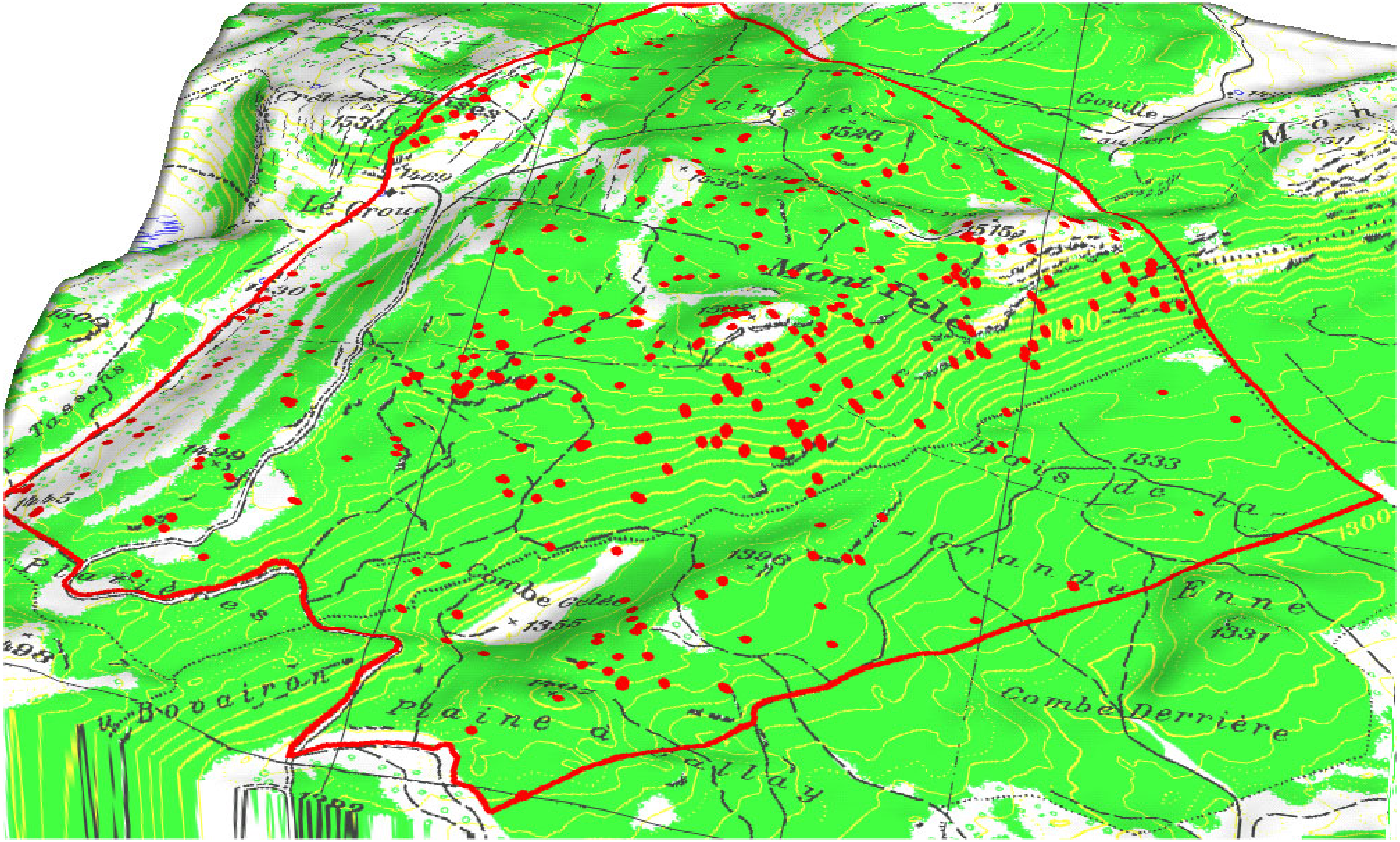

Fig. 6: *Example of a snag-distribution map (red dots) in a 300-ha forest landscape (red line). © Swiss Fed. Office of Topography.*

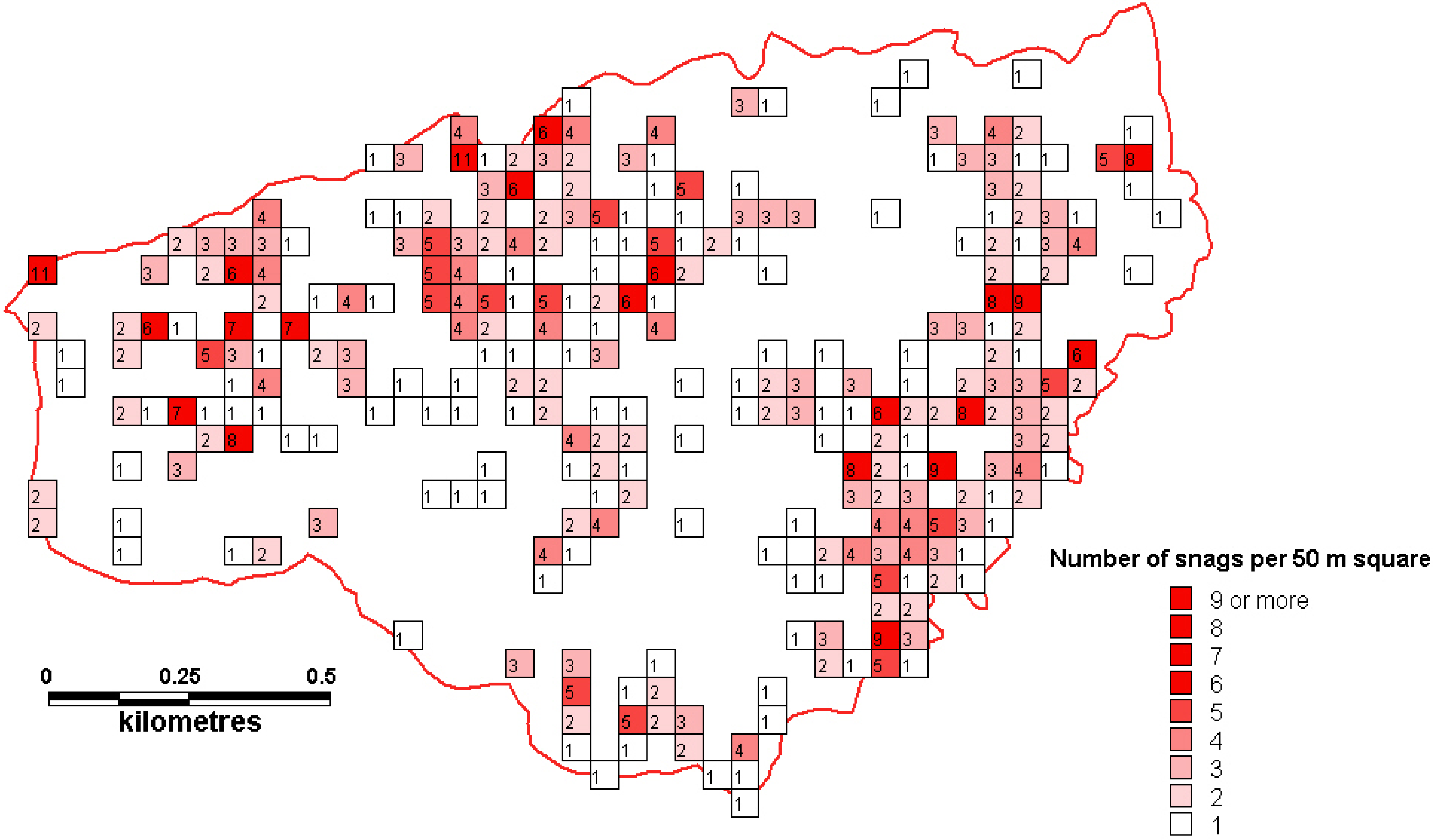

Fig. 7: *Example of a snag-density map.*

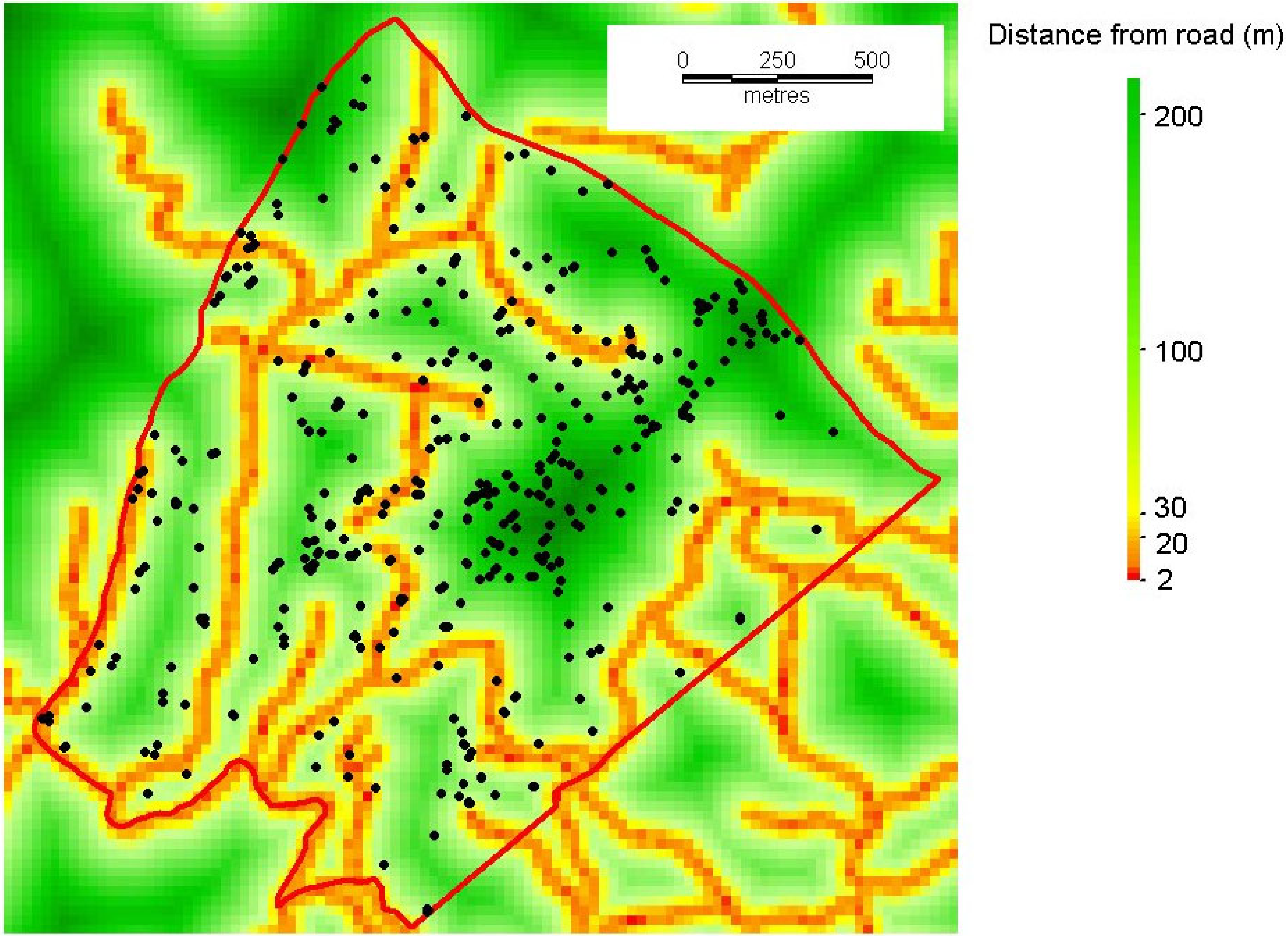

Fig. 8: *Example of a spatial analysis showing the snags (black dots) and their distance from the road network*

In 15 European old-growth forests, the density of standing dead trees with a dbh $\geq$ 20 cm was 34 ± 7 ha^{-1} (mean ± S.E.) and their basal area was 5.1 ± 0.7 m^{2} ha^{-1} (mean ± S.E.; dbh $\geq$ 10 cm) (Nilsson et al. 2002).

b) Managed forests:

Due to intensive forest management (shorter rotation lengths, commercial thinning, etc.), the volume of dead wood has decreased and its quality is less diverse in managed than in naturally-disturbed forests (e.g. Similä et al. 2002, Siitonen 2001). Thinning of managed stands reduces CWD in the mid-successional stages, since dead, damaged and weakened trees are usually removed. If large quantities of CWD are created by natural disturbances, such as wind-throw, snow breakage or insect outbreaks, the dead trees are habitually harvested in salvage or sanitary logging. According to Siitonen (2001), the average amount of CWD has been reduced by 90-98% in managed forests in Fennoscandia, compared to old-growth forests. Forest management does not decrease all CWD uniformly. It reduces densities of large dead trees relatively far more than thinner trunks (e.g. Green & Peterken 1997, Kirby 1998). The spatial distribution of CWD is uneven (cf. Fig. 7 and 8). In Fennoscandia, for example, large parts of the managed landscape contain extremely low amounts of CWD compared to natural stands, while some areas, stands or patches can contain relatively large quantities (Siitonen 2001). For Middle Europe, the few existing studies show similar trends (cf. in Albrecht 1991; Derleth et al. 2000; Erdmann & Wilke 1997; Guby & Dobbertin 1996; Meyer 1999).

In Switzerland the national mean value of CWD in forests is 11.9 m^{3} ha^{-1}, i.e. 3.3% of total wood volume (Brassel & Brändli 1999). Forests in lowland areas contain 4.9 m^{3} ha^{-1} (1.1%) and forests in the Alpine zone 19.5 m^{3} ha^{-1}. In Sweden, the average volume of CWD in managed forests is 6.1 m^{3} ha^{-1} (4.5% of total wood volume) on productive forest land (Fridman & Walheim 2000). In France the mean national volume is 2.2 m^{3} ha^{-1} (Vallauri & Poncet 2002). In production forests, 1-3 m^{3} ha^{-1} has been reported for Bavaria, Germany (Ammer 1991), and 2-10 m^{3} ha^{-1} for Finland (Siitonen 2001).

☞

> Dead-wood amounts, and in particular the densities of large dead trees, are generally much lower in managed (1-12 m^{3} ha^{-1}; < 5% of total wood volume) than unmanaged forests (20-250 m^{3} ha^{-1}; up to 40% of total wood volume).

4.7. Quantity of dead wood in forests with and without Three-toed woodpeckers

In our study we consistently found, for sub-Alpine and boreal regions, that forests with breeding Three-toed woodpeckers, where management intensity is usually low, had significantly more CWD than forests without this species (Table 4). The differences between these two forest types were largest for the basal areas of snags (the foraging substrates preferred by this bird). The total volume of CWD in forests without Three-toed woodpeckers corresponded to the national mean values for Switzerland and Sweden, respectively (cf. § 4.6.), whereas woodpecker forests had more than three times that volume. It should be noted, however, that the differences between these two forest types are small if compared with the decline from unmanaged to managed forests (cf. § 4.6.).

A significant positive linear relationship exists between the basal areas of snags and all standing trees (forests with woodpeckers: $r_{Pearson} = 0.67$, $N = 22$, $p = 0.0007$; without woodpeckers: $r_{Pearson} = 0.67$, $N = 22$, $p = 0.0007$; Fig. 9a). This indicates that basal area (and volume) of CWD is related to site productivity, which is higher in sub-Alpine than boreal forests (Fig. 9a). It explains why the absolute CWD volume and basal area are higher in sub-Alpine than boreal forests (cf. Table 4). By contrast, the snag ratio seems to be independent of site productivity, since no significant linear relationship has been found between the basal area ratio of snags to all standing (dead and living) trees (with woodpeckers: $r_{Pearson} = 0.34$, $N = 22$, $p = 0.12$; without woodpeckers: $r_{Pearson} = -0.15$, $N = 22$, $p = 0.51$). Similar findings have been reported for old-growth forests (Nilsson et al. 2002).

Our study shows that forests without Three-toed woodpeckers have generally $\leq 3\%$ dead standing trees, whereas most forests with this bird species have $\geq 5\%$ up to ratios $> 10\%$, which are comparable with European old-growth forests (Fig. 9b). As illustrated graphically in this Figure, Three-toed-woodpecker forests occupy an intermediate rank between intensively-managed and old-growth forests in terms of dead-tree ratios. Three-toed woodpeckers could therefore serve as a tool to derive dead-tree management

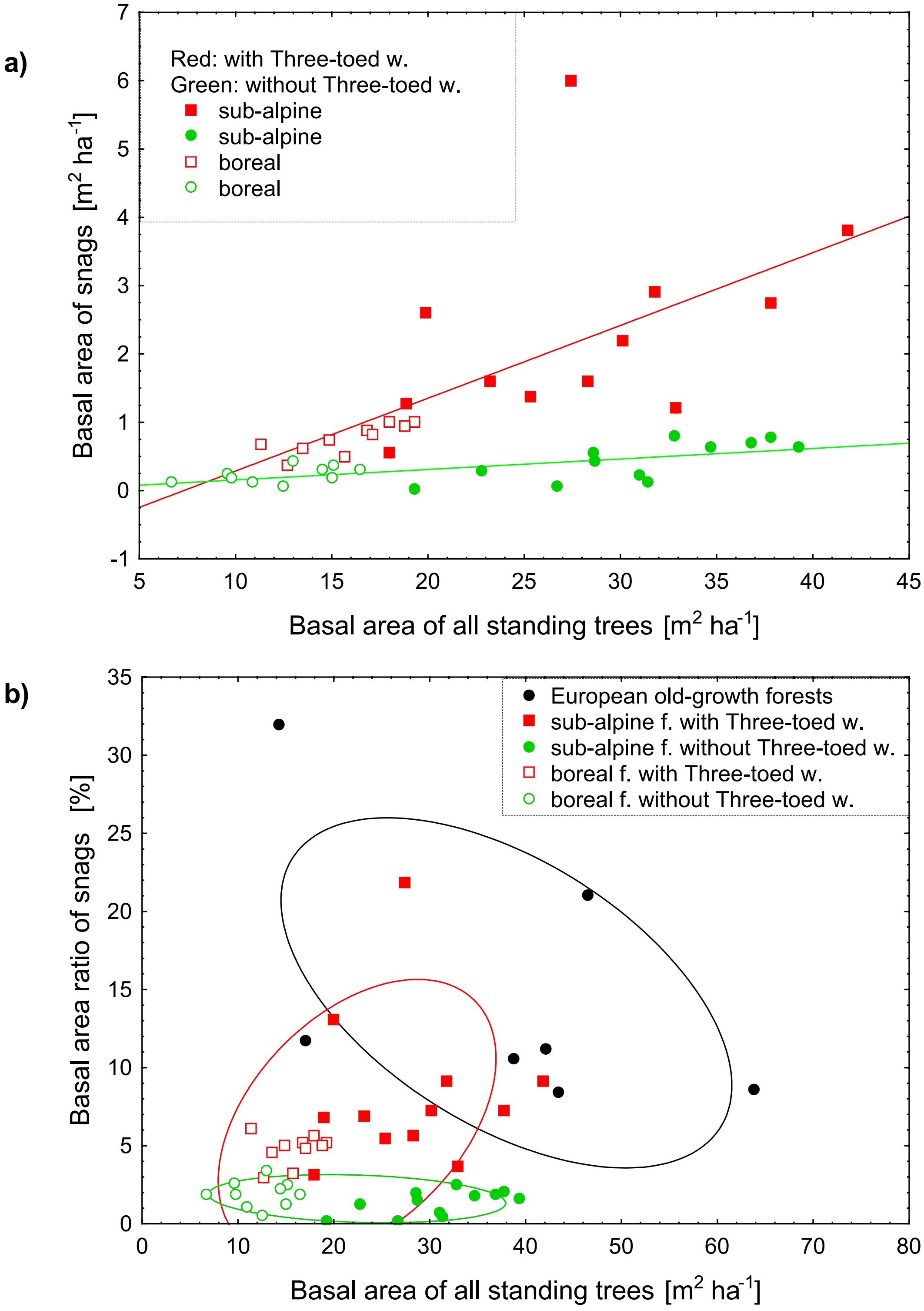

Fig. 9: ***a)*** *Basal area of snags in sub-Alpine and boreal forests with and without Three-toed woodpeckers, respectively. Equation of the linear regression line fitted to forests with woodpeckers:* $y = -0.7785 + 0.1065x$*; without woodpeckers:* $y = 0.0027 + 0.0154x$*.* ***b)*** *Basal-area ratio of snags in three types of forests: European old-growth forests (black dots; data from Nilsson et al. 2002), forests with breeding Three-toed woodpeckers (red squares), and forests without Three-toed woodpeckers (green dots). Range ellipses, whose lengths projected onto the axes are equal to the mean* $\pm$ *0.95 range of the plotted variables.*

targets, if a) a critical dead-wood threshold value exists for its presence; b) it has desirable properties of an indicator species; and c) other species are associated with its presence. In the following three chapters we demonstrate that these requirements are met.

Table 4: *Dead-wood amounts measured on our study sites in Swiss and Swedish forests with and without breeding Three-toed woodpeckers. Mean values and ranges. All differences between forests with and without woodpeckers within a country are significant at a level $p<0.05$.*

Measured feature	Switzerland (sub-Alpine forest)		Sweden (boreal forest)	
	With woodpeckers	Without woodpeckers	With woodpeckers	Without woodpeckers
	n = 6	*n = 4*		
Snags [N ha^{-1}] 1)	6.6 (2.9-11.2)	1.4 (0.8-1.9)	n.a. 3)	n.a.
	n = 12	*n = 12*	*n = 10*	*n = 10*
Snag basal area ratio of all standing trees [%] 2)	8 (3-22)	1 (0-3)	5 (3-6)	2 (0-3)
Snags [m^2 ha^{-1}] 2)	2.3 (0.6-6.0)	0.4 (0.0-0.8)	0.8 (0.4-1.0)	0.2 (0.1-0.4)
Logs [m^2 ha^{-1}] 2)	2.2 (0.9-4.1)	0.6 (0.2-1.2)	1.8 (0.9-2.9)	0.8 (0.4-1.1)
Total dead wood [m^2 ha^{-1}] 2)	4.5 (1.5-10.1)	1.1 (0.5-2.0)	2.6 (1.3-3.8)	1.0 (0.5-1.4)
Snags [m^3 ha^{-1}] 2)	19 (6-34)	5 (0-10)	7 (3-10)	2 (0-3)
Logs [m^3 ha^{-1}] 2)	21 (10-43)	7 (2-16)	16 (7-28)	7 (3-10)
Total dead wood [m^3 ha^{-1}] 2)	40 (16-65)	12 (5-26)	23 (10-37)	7 (3-11)

1) *from AP-GIS-method; dbh $\geq$ 25 cm;*
2) *from fieldwork with relascope sampling; dbh $\geq$ 10 cm;*
3) *n.a.: not analysed.*

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> Forests with Three-toed woodpeckers have significantly more dead wood, and in particular snags (5-15% of the total standing basal area), than managed forests without this species ($\leq$ 3%).

Chapter 5

Snag targets based on Three-toed woodpecker's habitat requirements

5.1. Dependence on dead wood: significant non-linear response

Our data indicate the existence of critical dead-wood thresholds for the presence of Three-toed woodpeckers. Both in Swedish boreal and Swiss mountain forests, snag and log amounts were significantly higher when the Three-toed woodpecker was present than in forests where it was absent (cf. Table 4). In Switzerland mean snag basal area [m^2 ha^{-1}] was 2.3 vs 0.4 (paired t-test, $n = 12$, $t = 4.78$, $p = 0.0006$), whereas mean log basal area was 2.2 vs 0.6 (paired t-test, $n = 12$, $t = 6.23$, $p = 0.0001$). In Sweden we recorded 0.8 vs 0.2 m^2 ha^{-1} of snags (paired t-test, $n = 10$, $t = 7.07$, $p = 0.0001$) and 1.8 vs 0.8 m^2 ha^{-1} of logs (paired t-test, $n = 10$, $t = 5.59$, $p = 0.0003$). The snag ratio of all standing trees was also significantly higher in woodpecker forests. In Switzerland the snags represented 8.3 ± 1.5% (mean ± S.E.) in woodpecker forests against 1.3 ± 0.2% in forests without woodpeckers (Fig. 2 in paper III). In Sweden, the snag proportion was 4.8 ± 0.3% against 1.9 ± 0.3%. These results suggest that Three-toed woodpeckers are clearly confined to forests with high dead-wood amounts. Univariate logistic regression models for snags resulted in significant non-linear responses for the probability of woodpecker presence, indicating the existence of critical ecological thresholds for both sub-species *P. tr. alpinus* and *P. tr. tridactylus* (Fig. 4 and Table 3 in paper III). In these empirical models, the probability of Three-toed woodpecker presence increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m^2 ha^{-1} (Switzerland) and from 0.3 to 0.5 m^2 ha^{-1} (Sweden).

☞ The probability of Three-toed woodpecker presence exhibits a significant non-linear response to varying dead-wood amounts, indicating the existence of a critical dead-wood threshold.

5.2. Is the Three-toed woodpecker a good indicator species?

As demonstrated in the following section, this species meets most of the desirable requirements for indicator species, and, therefore, has a potential to be used as such. According to Hansson (2001) an indicator should have the following characteristics:

1) be specialised in the ecosystem or landscape to be monitored (habitat specialist). The Three-toed woodpecker is one of the species most closely associated with old-growth spruce stands, i.e. > 120 years old (Imbeau et al. 1999; Virkkala 1987; Virkkala et al. 1994a);
2) be sensitive to artificial disturbance in at least one specific factor, over a wide range of natural variability. Its sensitivity to different dead-wood amounts has been demonstrated by this thesis (cf. § 5.1.);
3) consist of populations with rapid density responses to disturbances or habitat changes. Three-toed woodpeckers are known to respond opportunistically to insect outbreaks following fires or windfall in coniferous forests (Koplin 1969; Murphy & Lehnhausen 1998). Among boreal forest bird species, this woodpecker is possibly the most negatively affected by long-term changes induced by commercial forestry in eastern Canada (Imbeau & Desrochers 2002). The ongoing decline of populations in Fennoscandia is directly related to modern forestry's practice of removing old and dead trees (Tucker & Heath 1994; Virkkala 1987, 1991).
4) have fairly large area and resource requirements. It is the only woodpecker occurring in both the New and Old Worlds (Winkler et al. 1995). It has a circumpolar range and some more southern isolated breeding ranges in the mountains, for example in the Alps (Hagemeijer & Blair 1997). Reported home range sizes vary between 44 and 176 ha (Bürkli et al. 1975; Dorka 1996; Hess 1983; Pechacek 1995; Pechacek et al. 1999; Ruge et al. 1999; Scherzinger 1982);
5) be fairly common, easily and cheaply identified and sampled. While being classified as a Species of European Conservation Concern with "Declining" threat status (SPEC Cat 3) (Hagemeijer & Blair 1997), it is a species of least concern, i.e. not threatened, in Switzerland (Keller et al. 2001). Its presence can easily be verified based on ringed trees (cf. § 5.6. and Fig. 11).
6) have continuous and demographically-balanced populations (cf. 4));

7) be a resident species. Alpine populations *P. t. alpinus* are sedentary also in winter (Winkler et al. 1995), whereas the nominate form *P. t. tridactylus* is not completely resident (Hogstad 1970);
8) if their populations are characterised by sinks and sources then the monitored habitat should contain source populations. Populations in Fennoscandia are in an ongoing decline (Angelstam & Mikusinski 1994; Nilsson 1992; Tucker & Heath 1994), whereas Swiss populations have been increasing for some years (Schmid et al. 1998). For this thesis, study sites have been selected in Sweden and Switzerland;
9) the populations examined should not be affected by any conspicuous demographic stochasticity or genetic impoverishment due to long-term marginal population sizes. The history of intensive land use is much shorter in northern than central Europe (Angelstam 1997). The ongoing decline of northern Three-toed woodpecker populations is recent and they are not yet expected to be subject to genetic impoverishment.

Based on this different literature information, we think that the Three-toed woodpecker has good potential as a useful indicator species.

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The Three-toed woodpecker meets most desirable requirements for an indicator species and is therefore an interesting species on which to focus.

5.3. Three-toed woodpecker as indicator of dead wood and habitat quality

We demonstrated with our data the dependence of Three-toed woodpeckers on relatively high amounts of dead trees (cf. § 5.1.) and, therefore, suggest this bird species be considered as indicator of dead wood. If dead-wood thresholds for Three-toed woodpeckers are to be applied as practical management targets, it is necessary to evaluate the umbrella[4] value of this woodpecker species for other taxa. Several links with

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[4] Umbrella species : a species whose conservation confers a protective umbrella to numerous co-occurring species (Fleishman et al. 2000b). A species whose occupancy area (plants) or home range (animals) are large enough and whose habitat requirements are wide enough that, if they are given a sufficiently large area for their protection, will bring other species under that protection. (Heywood, 1995).

biodiversity and habitat quality have previously been demonstrated by other studies (cf. Fig. 10). Mikusinski et al. (2001) found that the number of forest bird species is correlated positively with the richness of woodpecker species and, in particular, with the presence of the Three-toed woodpecker. Suter et al. (2002) demonstrated that the Capercaillie (*Tetrao urogallus*), co-occurring with the Three-toed woodpecker, is an umbrella for red-listed mountain birds. Pakkala et al. (2002) found a positive correlation between the occurrence of breeding Three-toed woodpeckers and territory and landscape quality. In a case study, Derleth et al. (2000) concluded that this species can be considered as an indicator of habitat quality. Since there exists a quantitative link between Three-toed woodpeckers and dead wood, we can assume that the maintenance of sufficient dead wood for this bird's presence may also favour the presence of other dead-wood-dependent species. In addition, this woodpecker is characteristic of naturally dynamic old-growth forests, which have a high biodiversity conservation value *per se*. This is why different authors have already proposed it as "indicator species". Angelstam (1998b) suggested this woodpecker species as an indicator of gap-phase dynamics in *Picea* spruce boreal forests and of the diversity of seral stages (old and old-growth) after large-scale disturbances. This species figures on the list of 32 selected birds suggested as indicators of the functioning of mature forests in the report on criteria and indicators of the Canadian Council of Forest Ministers (Anonymous 1997). Nilsson et al. (2001) propose a preliminary list of species indicating high biodiversity or many red-listed species. This list includes the Three-toed woodpecker, since it requires larger forest patches with a high density of dead *Picea abies* spruce (Amcoff & Eriksson 1996).

Clearly, this species can be qualified as an "indicator of dead wood and habitat quality". Whether it can even function in a broader sense as an "indicator of a high biodiversity" should be tested by systematically analysing its umbrella value in different landscapes. It seems to be potentially qualified, since we demonstrated that it meets most of the desirable requirements for an indicator species (cf. § 5.2.).

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Due to its dependence on dead wood, and to several links with other aspects of biodiversity, the Three-toed woodpecker can be qualified as an indicator of dead wood and habitat quality.

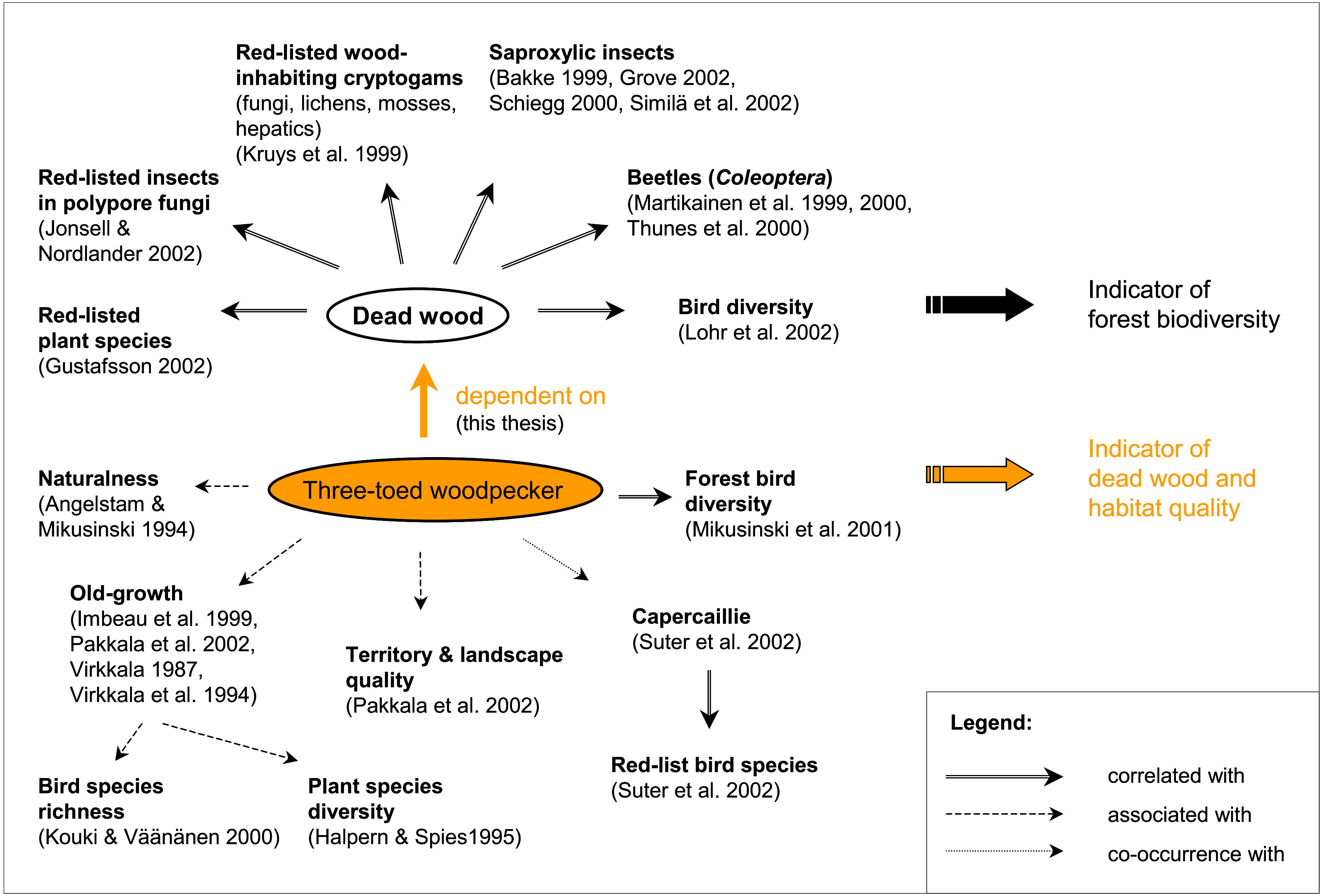

Fig. 10: *An incomplete overview of relationships between dead wood and the Three-toed woodpecker and different aspects of biodiversity (recent literature only).*

5.4. Estimation of snag requirements using a bioenergetic model

We intend to use the Three-toed woodpecker as a tool to derive dead-tree management targets. Striving for reliable target values, we chose two complementary approaches to estimate snag requirements for this woodpecker species: an empirical approach, where we measured dead-wood amounts in forests with and without this bird species (cf. results in § 5.1.) and a theoretical approach by developing a bioenergetic model. In this section we present the basic idea behind this bioenergetic model. For detailed information we refer to Paper IV.

Bioenergetic models are based on quantitative energy budgets of a given species. Such models have above all been used for relatively large-sized animals, for example to estimate the grazing impact of large ungulates on forest ecosystems (e.g. Vivas et al. 1991; Armstrong & Robertson 2000), or the possible concurrence of seabirds with a marine fishing industry (e.g. Gremillet et al. 1995; Wanless et al. 1998). Our application is original, since it uses a small-bird species and estimates the resources required for its protection instead of its possible negative impact on ecosystems or markets. Three-toed woodpeckers occur in old coniferous forests, where *Picea* spruce is the dominant tree species (Imbeau et al. 1999; Pakkala et al. 2002; Virkkala 1987; Virkkala et al. 1994b). Their food consists of 69-97% bark beetles (Fayt 1999, Glutz von Blotzheim 1994; Hess 1983; Hogstad 1970, 1978; Murphy & Lehnhausen 1998; Pechacek & Kristin 1993, 1996). The preferred foraging substrate is large, standing dying and recently dead spruce trees (Hess 1983; Murphy & Lehnhausen 1998; Pechacek 1995). Such trees can be successfully detected by our AP-GIS-method. If we are able to quantify the energy needs of Three-toed woodpeckers, and the available energy sources (i.e. bark beetles) within a given area, then we can predict the probability of woodpecker presence in this area. Since Three-toed woodpeckers are sedentary also in winter, we can assume that they have to find sufficient energy sources to fuel all their activities over the course of a year (reproduction, moulting, over-wintering etc.) within their home-range. The starting point of our model was an equation proposed by Koplin (1972) for the daily energy requirements of free-living woodpeckers, which served as a basis for estimation of yearly energy requirements. We introduced several variables to estimate the abundance of available bark-beetle prey as a function of available snags, measured by the AP-GIS-method. Our model output is the probability of woodpecker presence. The model predictions for 10 study sites (6 sites with woodpeckers and 4 sites without) were compared with woodpecker occurrence on these sites. Snag amounts required for the local continued presence of Three-toed woodpeckers in sub-Alpine forests, as predicted by this bioenergetic model, are presented in § 6.3.

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> The developed bioenergetic model enables estimation of snag amounts required for the local continued presence of Three-toed woodpeckers.

5.5. Natural agent against bark beetles?

Since the Three-toed woodpecker feeds primarily on bark beetles, and since it locally concentrates in areas after natural disturbances (windfall, fire), it may be an interesting species for bark-beetle control in forest management. The importance of woodpeckers as natural control agents was often reported for North America, in particular during epidemic bark-beetle outbreaks (Baldwin 1968; Hutchinson 1951; Knight 1958; Kroll & Fleet 1979). However, the number of bark beetles consumed by Three-toed woodpeckers has never been compared with pheromone-trap statistics. Such traps have been used in Switzerland for bark-beetle control after heavy windfalls and subsequent bark-beetle calamities, and are still being used for bark-beetle population monitoring. We evaluated the effectiveness of woodpeckers during endemic[5] bark-beetle levels, arguing that these birds may contribute to maintaining bark beetles at low levels. It has been recognised that high endemic beetle levels are an important element aggravating beetle outbreaks after natural disturbance. To prevent high endemic levels and reduce the spread of infestation, a common strategy in Swiss forest management is to remove infested dying, damaged and dead trees. But this reduces food resources for woodpeckers, possibly causing population decline, such as in Fennoscandia (BirdLife 2000; Tucker & Heath 1994).

By defining three scenarios for different levels of woodpecker effectiveness, we demonstrated that woodpeckers catch 2-19 times more bark beetles than traps do

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[5] endemic : normal level in opposition to epidemic level during an insect outbreak

(cf. Paper II for details). This result applies for both when one woodpecker is compared with one trap, and when the whole Swiss woodpecker population is compared to all traps installed in Swiss forests. These findings corroborate other studies showing the limited effect of pheromone traps in bark-beetle elimination (Duelli et al. 1997; Wichmann & Ravn 2001). We therefore argue that Three-toed woodpeckers should be considered an interesting alternative to bark-beetle control by pheromone traps. That will mean, however, that a sufficient number of dying and dead trees would have to be maintained in forests in order to meet this bird's foraging requirements. Such a management strategy would bring other biodiversity benefits and would probably also be economically profitable, since removing dying and dead trees is an expensive operation.

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> The Three-toed woodpecker is an interesting alternative to bark-beetle control by pheromone traps, thus playing a role in stimulating conservation awareness among forest managers.

5.6. Ringed trees as indicators of breeding continuity

We have shown that the Three-toed woodpecker is a potentially useful indicator species of good habitat quality (cf. § 5.2. and 5.3.) and an interesting alternative to bark-beetle control by pheromone traps (cf. § 5.5.). If it were to play a role in practical forest management, it would be important to easily be able to establish its presence on a given site. In this section we present the "ringed trees", characteristic signs of its presence and relatively easy to detect (cf. Fig. 11).

Sap-licking is a general habit of European Three-toed woodpeckers (Bürkli et al. 1975; Glutz von Blotzheim 1994; Hess 1983; Pechacek 1995; Ruge 1968; Scherzinger 1982), resulting in characteristic ringed trees. Such trees, most often spruce and pine, have small holes in the bark made by the woodpecker (Fig. 11a), and may sometimes display bulges as signs of continuous use over a long period (Fig. 11b). Therefore, we hypothesised that a long-term presence of this bird species in the same habitat would result in i) a high number of ringed trees and ii) trees with bulges. Our data support this hypothesis. We found more ringed trees in Switzerland than Sweden (Table 2 in paper III), and no trees with signs of very long use in Sweden. These differences in breeding continuity in Swiss and Swedish forests can be explained by the different management regimes and histories of Alpine and boreal forests. In Switzerland, selective tree-cutting creates a dynamic of small gaps within stands, which retain favourable habitat features for the woodpecker over time. By contrast, in Sweden clear-cutting is the general harvesting type since the late 19th century and the rotation time of about 80 years for Norway spruce and 100 years for Scots pine is relatively short. Three-toed woodpeckers need forests with dead wood, either in old-growth stands or in stands subject to stand-replacing disturbance by fire or wind (Angelstam & Mikusinksi 1994). Consequently, in managed forests in Sweden they would not be expected to stay longer than about 10-30 years in the same old-forest patch, too short a time to create numerous signs or signs of long use. Our findings are corroborated by Nilsson & Ericson (1997) who expect species in temperate forests to be more dependent on continuity (i.e. the presence over a long period of features such as high tree cover or big dead trees) than species in boreal forests, due to the different disturbance regimes. Our results suggest that the number and age of ringed spruce and pine trees may be used as indicators of breeding continuity (cf. Fig. 4 in paper III). These signs are easily detectable in forests throughout the whole year and could therefore become a tool for forest managers to verify the presence of breeding Three-toed woodpeckers. However, it must be pointed out that the Great spotted woodpecker *(Dendrocopos major)*, a sympatric species, may occasionally ring spruce and pine trees, even if it prefers deciduous trees. In order to acquire a better knowledge of the differences in ringed trees between these two species, it would be necessary to study the Great spotted woodpecker's ringing habits in different regions.

☞ Ringed trees are indicators of breeding Three-toed woodpeckers and may become a tool to easily establish their presence.

a)

b)

Photos: R. Bütler

Fig. 11:

a) *Ringed tree with fresh signs of woodpecker sap-licking and*

b) *tree that has formed bulges, a sign of continuous woodpecker use over a long period.*

Chapter 6

Forest management and biodiversity

Forest management practices often have a major impact on biodiversity (Larsson 2001). In Finland for example, 43% of all species classified as endangered are thought to be so as a result of forest practices (Kouki & Niemelä 1997). In the lowland areas of Switzerland 30% of forest plant species and 34% of the 83 forest bird species are red-listed (Bolliger 1996; Landolt 1991). Lack of dead wood is one of the main reasons for this decline in biodiversity. As an example of the influence of forest management on dead-tree amounts, we analysed the impact of forest roads.

6.1. Negative impact of forest roads in Switzerland

Management intensity is directly linked with the accessibility of harvesting areas. A high level of road-network development facilitates forest management intensification and salvage cutting, i.e. the removal of diseased and dead trees (cf. Fig. 8), which is often practised in Switzerland. Indeed, we found a significant negative linear relationship between road density on the Swiss study sites and dead-wood amounts ($r = -0.64$, $t = 3.93$, $p = 0.0007$, $n = 24$; Fig. 3 in paper **III**). In addition, road network density had a non-linear negative impact on the presence of Three-toed woodpeckers, with an accelerated drop beyond a density of about 2.6 km per km^2. If the current 10%-per-decade growth of the road network (Brassel & Brändli 1999) continues, this critical threshold could be reached in about 30 years.

Easily-accessible forests, characterised by a high forest-road network density, have significantly smaller dead wood amounts than forests that are difficult to access. The road network therefore has an indirect impact on the spatial distribution of woodpeckers.

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> Since a high road network density facilitates the removal of dying and dead trees in forests, it negatively affects woodpecker presence.

6.2. Remove or not remove dead wood in managed forests?

Although recognised as ecologically important, dead wood is still lacking in most managed forests. For example, after the heavy storm “Lothar” in 1999 in central Europe, during which 12.5 Mio. m^3 of wind-thrown wood was created in Swiss forests, less than 2.5 Mio. m^3 has been left *in situ* (Anonymous 2002). One main reason for removing wind-thrown trees is the possible subsequent damage caused by insect pests. More than 260 Mio. SFr. (of a total of 510 Mio. of public subsidies invested after “Lothar”) has been devoted to removing wind-thrown and insect-damaged trees (Anonymous 2002). This corresponds to 36 SFr. per inhabitant. While this measure may be necessary in forests with a protective function, it is less justified elsewhere. It is important to point out that, from a forest-protection point of view, harmful insects use a tree only the first two years after its death (in Samuelsson et al. 1994, p.43).

It is, however, difficult to predict the possible damage caused to forests if most of the wind-thrown trees had not been removed. Similarly, the possible benefits for biodiversity in the same case are difficult to estimate. It can be expected that in well-functioning forest ecosystems, where the antagonists of harmful insects are present in naturally balanced numbers, the damage would be smaller than in intensively-managed forests that lack suitable habitat for antagonist populations. As we demonstrated in § 5.3. (and Paper II), the Three-toed woodpecker is an effective bark-beetle eater. Favouring its presence in forests would enable better control of infestation by such insects than the currently used pheromone traps. Related to the dead-wood habitat feature, the fundamental question is then: How much dead wood is enough in managed forests to maintain dead-wood-dependent species?

6.3. How much dead wood is enough?

This question is extremely difficult to answer. Generally, scientists prefer giving vague qualitative recommendations to stating absolute figures. “Leave as many large standing dead trees at harvest as possible”, (Mccarthy & Bailey 1994); “It is important to maintain standing dead trees, wherever possible, during harvesting and renewal operations”, (Greif & Archibold 2000); “There is a need to increase the input of large dead trees”, (Kruys et al. 1999). Without clear quantitative guidelines, however, it is impossible to assess progress towards biodiversity maintenance or restoration in managed forests, two challenges which must be taken up by foresters. Aware of the controversial character of quantitative figures, we nevertheless venture to conclude this thesis with such concrete recommendations (cf. § 6.4.), arguing like Hagan & Grove (1999): “If forest ecologists don’t know how much coarse woody debris is needed to maintain biodiversity, how are foresters supposed to know?”

One way to achieve a better understanding of dead-tree requirements for biodiversity preservation is to measure these features in natural forests, and then derive management targets from these reference systems. However, no, or very few, natural forests remain in most parts of Europe. In addition, the amount of dead wood in natural forests may be so extensive – up to 30% of dead stems (Linder et al. 1997) or 25% of above-ground biomass (Bobiec 2002; Nilsson et al. 2002; Siitonen 2001) – that such targets would be incompatible with the economic objectives of multifunctional forestry. Another approach, such as undertaken in this thesis, involves quantification of the ecological preferences of species of special interest (in our case the Three-toed woodpecker) and derivation from their habitat requirements of quantitative target values for management use (Fahrig 2001; Simberloff 1995; With & Crist 1995).

Table 5 presents the snag amounts required in order to achieve a given probability of presence of the Three-toed woodpecker in sub-Alpine and boreal forests, by applying a logistic regression model to our data collected in Switzerland and Sweden. The predicted required volumes and basal areas are considerably lower in boreal than sub-Alpine forests. One reason is that both total volume and basal area depend on site productivity, which is lower in boreal than in sub-Alpine forests (cf. § 4.7.). We therefore also considered the ratio of dead trunks to the total number of trunks, since this ratio is independent of site productivity (cf. § 4.7.). In this case, the values are more similar, even if a difference, although small, between predictions for both forest types still remains. This result may indicate that the boreal sub-species *P. tr. tridactylus* needs a lower density of snags than the Alpine sub-species *P. tr. alpinus*.

We argue, however, that this is not true. Instead the figures must be put into the context of woodpecker population trends, stable or even increasing in Switzerland and declining in Sweden, due to loss of suitable habitat and decrease in the quality of the remaining habitat caused by forest management (cf. Table 6).

Table 5: *Snag amounts required for local continued presence of the Three-toed woodpecker, as predicted by an empirical logistic regression model based on data for Switzerland (sub-Alpine forest) and Sweden (boreal forest). Mean values ± S.E. for snag basal area, volume, and ratio dead/all trees of forests with breeding Three-toed woodpeckers (n = 12 for Switzerland and n = 10 for Sweden).*

P(woodp.)	Basal area [m^2 ha^{-1}]		Volume [m^3 ha^{-1}]		Ratio dead/all[1)] [%]	
	sub-Alpine	boreal	sub-Alpine	boreal	sub-Alpine	boreal
0.50	0.9	0.4	10	3.2	3.4	3.1
0.75	**1.0**	0.5	**12**	3.8	4.1	3.5
0.90	1.2	0.5	14	4.1	4.5	3.7
0.95	1.3	0.6	16	4.4	4.9	3.9
Mean ± S.E.	2.3 ± 0.4	0.8 ± 0.1	19.4 ±3.4	6.8 ± 0.8	8.3 ± 1.5	4.8 ± 0.3

[1)] Ratio of basal areas of standing dead to all standing (dead and living) trees

According to Tilman et al. (1994), metapopulation decline in response to habitat destruction occurs with a time delay, called “extinction debt”. This means that many species may be remaining for a long time in a landscape that has already lost its capacity to support them in the long term. We think that the metapopulation capacity, i.e. the sum of contributions from individual suitable habitat fragments (Hanski & Ovaskainen 2000) of the studied central Swedish landscape may already be below the threshold value required by Three-toed woodpeckers. It is also possible that the central Swedish population is a sink population (Pulliam & Danielson 1991), whose survival hinges on migration from source populations further to the north, where more naturally-dynamic forests with much dead wood remain. In view of these considerations, and referring to the precautionary principle, we suggest that management recommendations for boreal forests be based on the higher values derived from sub-Alpine forests.

Predictions by the bioenergetic model developed for sub-Alpine forests were in the same order as results of the field approach (Table 7). In particular, for p(woodpecker) = 0.75 both approaches predicted the same snag amounts. The similarity in the results of our two completely different approaches enables us to affirm the reliability of predicted snag amounts to achieve a given probability of Three-toed woodpecker presence.

☞ Snag targets should be based on dead-tree requirements of the increasing Alpine, instead of the declining northern, Three-toed woodpecker populations.

Table 6: *Three-toed woodpecker population trends in Switzerland and Sweden*

Switzerland	**Sweden**
Three-toed woodpeckers in Switzerland have been increasing for some years (Schmid et al. 1998). New breeding populations have been detected in the western Pre-Alps (first breeding proved in the Pays-d'Enhaut in 1991; cf. Beaud et al. 1995) and the Jura mountains (first breeding proved in 1994, Chabloz & Wegmüller 1994). As a reason for this population growth in the western Pre-Alps, Derleth et al. (2000) identified a decrease of forest exploitation since World War II accompanied by growing dead-wood amounts.	Populations in Fennoscandia are in a drastic ongoing decline (Angelstam & Mikusinski 1994; Nilsson 1992; Virkkala 1991). Between 1970-1990 the Swedish and Finnish populations, totalling 20,000–35,000 pairs, declined by more than 20% (Tucker & Heath 1994), due to habitat loss caused by intensive forest management (Virkkala 1987, 1991). Virgin forests, over 200 years old and with plenty of dead trees, have been replaced by managed thinned and young forests, where most dead trees have been removed (Virkkala 1991).

Table 7: *Snag amounts required for local continued presence of the Three-toed woodpecker in sub-Alpine forests, as predicted by the bioenergetic model.*

P(woodpecker)	Basal area [m^2 ha^{-1}]	Volume [m^3 ha^{-1}]	Density [N ha^{-1}]1)
	sub-Alpine	sub-Alpine	sub-Alpine
0.50	0.6	7	5.0
0.75	**1.0**	**12**	8.5
0.90	**1.6**	**18**	**14.0**
0.95	2.2	25	19.5

1) trees with a dbh ≥ 21 cm

6.4. Recommendations

Management objectives will define which level of probability of woodpecker presence will be specified. According to the principle of precautionary, the following management recommendations are based on a strategy intended to maximise the probability of woodpecker presence (i.e. probability of woodpecker presence ≥ 0.9 in both approaches). For sub-Alpine spruce forests, we recommend that at least 5% of the standing basal area (or volume) should be dead. Since this ratio is independent of site productivity (cf. § 4.7.), it can be used as a general target for spruce forests in different geographic regions. In Swiss sub-Alpine spruce forests, this target corresponds to a basal area of ≥ 1.6 m^2 ha^{-1}, or a volume of ≥ 18 m^3 ha^{-1}, or a minimum of 14 snags with a dbh ≥ 21 cm per hectare. Such snag-retention levels should be applied to forest patches of about 1 square kilometre, which corresponds to the mean home-range of a woodpecker breeding pair. These recommendations can be relevant in spruce forests with small-scale gap-phase-dominated dynamics, such as those prevailing in the Alpine forests, which is where selective tree cutting is the usual harvesting type.

For boreal forests, we also recommend a snag target of 5% of the standing basal area (or volume) of older forests. However, for boreal forests with large-scale stand replacing by clear-cutting, the relevance of these targets should be further examined both at the stand and landscape level. For example, the usefulness of snag retention in clear-cuts for Three-toed woodpeckers should be assessed. We think that in Sweden the spatial clear-cut patch design (directly affecting the amount of residual dead wood, and indirectly affecting the local density of old-forest patches), and stand-rotation time are closely related to the Three-toed woodpecker's population trends. There is hence a need to analyse the configuration of the landscape mosaic and determine the proportion of forests with dead wood, either old-growth stands or stands subject to stand-replacing disturbance by fire or wind.

Neither the 18 m^3 ha^{-1} recommended as a snag target amount for managed sub-Alpine spruce forests, nor the 7 m^3 ha^{-1} found in the Three-toed woodpecker forests of central Sweden can play the same role as that of 30-60 m^3 ha^{-1}, the volume of snags determined in European old-growth forests (Linder et al. 1997, Nilsson et al. 2002, Siitonen 2001). We nevertheless suggest aiming for our recommended values in managed-forest patches, which are supposed to play the role of stepping stones within a more intensively managed landscape, and, as a complementary measure, for the creation of totally protected forest areas left entirely untouched.

☞ Five percent of the standing basal area, or volume, should be dead. In sub-Alpine mountain forests, this corresponds to a basal area of ≥ 1.6 m^2 ha^{-1}, or a volume of ≥ 18 m^3 ha^{-1}, or a minimum of 14 snags with a dbh ≥ 21 cm per hectare.

6.5. Is it reasonable to base recommendations on one species?

Our recommendations for dead-tree targets in spruce-dominated forests are derived from the habitat requirements of one focal species, the functional indicator Three-toed woodpecker. It is necessary to ask whether it is reasonable to base recommendations on one species. Various shortcuts that rely on identifying key species to be focused on during planning efforts have been developed by conservation biologists since the eighties. Both management approaches based on one single species and multi-species approaches have met with criticism. There is at present a wide debate in the literature on which approach should be suggested for practical management. Clearly, no agreement exists on this question. Use of the keystone[6], indicator, focal and umbrella species concepts (Fleishman et al. 2000a; Lambeck 1997; Pearson 1994; Simberloff 1998) is currently increasing, in spite of many remaining scientific uncertainties regarding certain species being appropriate proxies for others (Landres et al. 1988; Lindenmayer et al. 2000). In this thesis the Three-toed woodpecker has been identified as a suitable species to be focused on for management purposes, provided always that its umbrella value – to be systematically tested – for other species and taxa proves high.

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[6] Keystone species : a species whose loss from an ecosystem would cause a greater-than-average change in other species' populations or ecosystem processes; species that have a disproportionately large effect on other species in a community. (Heywood, 1995). A species that shaped the habitat in which it lives and allows the presence of other species. (Farina, 1998).

We think that no single biodiversity surrogate or management approach will be best. Rather, applying different concepts and management regimes to different places will mean spreading the risk of failure. We argue that management strategies must remain flexible and responsive to new information, such as for example that provided by this thesis. “Management of diversity requires a diversity of management”, (Lindenmayer & Fischer 2002).

Chapter

7

Limitations, outlook and further research

Our newly developed AP-GIS-method for spruce-snag quantification was shown to be efficient for the inventory of unbroken snags. However, for broken snags, which may be important wildlife trees, although they are not preferred by Three-toed woodpeckers, its effectiveness is limited. One way to overcome this drawback would be to enhance knowledge of dead-wood profiles, i.e. the frequency distribution of different snag decomposition stages in various forest types and successional stages. It would then be possible to derive correction coefficients for the bias caused by undected snags in an advanced stage of decomposition, but more difficult for fresh treetop breakage. The AP-GIS-method should be further tested in various spruce-forest landscapes by applying the developed correction coefficient and assessing the accuracy achieved. More differentiated correction coefficients, taking spatial heterogeneity (i.e. topography, canopy closure of forest stands) within a forest landscape into account, would have to be developed if high accuracy is necessary. Applications in forests dominated by other coniferous tree species (for example pine) seem possible.

There is a gradient in the productivity of forests with variation in latitude and altitude, and also within each forest vegetation zone from dry via mesic and moist sites. Hence the average annual input and equilibrium volume[7] of dead wood probably varies accordingly. As we did not explicitely analyse the productivity of our study sites in central Sweden, it is difficult to recommend dead-tree targets expressed as volume or basal area for Swedish, and, more broadly, boreal forests. For sub-Alpine forests, such targets seem justified, since the bioenergetic model was developed and validated in the Alpine zone. A further research question is to analyse if Three-toed woodpeckers respond differently to various volumes and densities of snags, in other words, if the number per hectare of snags, or their absolute volume, is decisive.

One way to evaluate the relevance of the proposed dead-tree targets would be to undertake management experiments. After increasing snag levels in intensively-

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[7] Equilibrium volume of CWD: the hypothetical state in which average input and decay rates are in balance. In old-growth stands, the actual volume is often close to the equilibrium volume, but depends on recent small-scale disturbances and stand development.

managed forest landscapes up to the recommended targets, the impact on Three-toed woodpeckers (and other dead-wood-dependent species) should be assessed. Before the proposed dead-tree targets are widely applied in spruce-forest management, it would be important to evaluate the umbrella value of the Three-toed woodpecker for other species and taxa, in order to know which other species would be brought under its protection by conserving its habitats. Another point to verify is the usefulness to Three-toed woodpeckers of snag retention in clear-cut areas, since currently only few data are available on the effectiveness of such techniques.

Our dead-tree targets are developed for an intermediate scale between the stand and landscape level, since they should be applied to areas of about 1 km^2. To date, little knowledge exists on the amount, spatial density and configuration of suitable forest patches required by Three-toed woodpeckers at the landscape level. Since this species is dependent on a continuous snag supply in space and time, one important question is for example: how far apart can home-range forest patches meeting the dead-tree target be?

We suggest the possible use of ringed trees as indicators of Three-toed woodpecker breeding continuity. It would, however, be necessary to study the ringing habits of the Great-spotted woodpecker, and the difference between trees ringed by these two sympatric woodpecker species.

Chapter

8

Conclusion

In this thesis we developed a method enabling efficient quantification of large unbroken spruce snags. Such trees have a particular relevance for forest biodiversity. In order to provide management guidelines for dead-tree amounts in managed forests, we ascertained quantitative dead-tree targets, based on the habitat requirements of Three-toed woodpeckers. In doing so, this research goes beyond previous works on dead-wood quantification, since it makes ‘hard’ quantitative management recommendations. With 5% of the standing basal area, or volume of trees, being dead over an area of 1 km^2 (home-range size of a woodpecker breeding pair), this woodpecker species is expected to be locally maintained. Since Three-toed woodpeckers are indicators of good habitat quality, many other species dependent on dead wood may be maintained by applying our target value of 5% dead trees. We recommend that forest managers create such dead-tree levels in managed forests as an important contribution towards maintaining or restoring forest biodiversity. This woodpecker is also an effective bark-beetle eater, thus playing an important role in the control of this insect population.

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Paper I

Spruce snag quantification by coupling colour infrared aerial photos and a GIS

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Abstract

Among different dead wood types, large snags have a particular ecological relevance for biodiversity in forest ecosystems. For both research and management purposes, rapid and cost-effective inventories of large snags are required. Due to the great variability within stands and across the landscape, field recording of large snags is labour-intensive and expensive, if adequate sample sizes have to be ensured. We present a new method enabling efficient mapping and quantification of large snags by coupling colour infrared aerial photographs and a Geographic Information System (GIS). The method is validated by comparing the results with the data assessed by field methods in four spruce-dominated mountain forests in Switzerland. The different steps for implementing the method are: 1) stereoscopic interpretation of aerial photos for snag detection; 2) scanning and production of orthophotos; 3) geo-referencing and integration of the orthophotos and other data layers into a GIS; 4) digitisation of detected snags and drawing up of snag distribution maps. With the developed method, a map of the spatial distribution of spruce snags with a dbh ≥ 25 cm can be obtained in about 16 hours for an area of 3 km^2 (i.e. 3 minutes per ha of map). Tree diameter, treetop condition (broken or intact) and the canopy closure of the forest stands significantly affected the success of snag detection. The method detected 82% (93%) of snags ≥ 25 cm (≥ 35 cm) with an intact treetop, and

67% (71%) when broken snags ≥ 25 cm (≥ 35 cm) were also included. Given our encouraging results, the method should be further tested on similar study sites in order to obtain more certainty regarding validity of the coefficient correcting underestimation. The method may become a promising tool, complementing standard field methods, with various prospective applications, such as wildlife studies, forest inventories, certification processes etc.

Keywords: snag, dead tree, inventory, map, infrared aerial photo, CIR, remote sensing, geographic information system, GIS, biodiversity

1. Introduction

Large standing dead trees (snags) are of prime importance for forest biodiversity. Using standard field methods, however, it is difficult to effectively quantify snags, in particular on the landscape scale, such as required for different wildlife management issues. In this paper we describe a new snag quantification method based on colour infrared (CIR) aerial photos and a Geographic Information System (GIS).

Dying and dead trees provide habitats and resources for numerous threatened animal, plant and fungal species (Thomas 1979, Utschick 1991, Morrison and Raphael 1993, Samuelsson et al. 1994, Smith 1997). The lack of dead wood as resource and habitat in forest ecosystems is therefore considered a major threat to biodiversity. Recently, dead wood has been proposed as a new indicator of forest biodiversity, to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (<http://www.minconf-forests.net/> 24.10.2002). Dead wood also figures in modern certification standards for best forestry practices, such as for example those defined by the Forest Stewardship Council FSC (<http://www.fscoax.org/index.html> 24.10.2002). Other international initiatives intended to develop criteria and indicators of sustainable forest management - e.g. Montreal Process, Helsinki Process, or International Tropical Timber Organization ITTO - retained as indicator rare, threatened and endangered species, many of them depending on dead wood.

In spite of the growing awareness of conservation biologists, forest and wildlife managers and political circles of the importance of dead wood as indicator of forest biodiversity, this indicator is not yet operational. For example, no agreement exists on the kind of dead wood pieces to be inventoried: e.g. standing or lying dead wood, from small up to large tree diameters, expressed in volume or number of stems per area? According to Albrecht (1991), both spatial and temporal continuity of different dead wood types, such as snags, stumps, lying dead trees (logs) and large branches, each fulfilling different ecological functions, are necessary to maintain dead wood-dependent species in the long term. However, snags with larger than average diameters have been recognized as being of prime importance for a good forest ecosystem structure and biodiversity (Thomas 1979, Raphael and White 1984, Samuelsson et al. 1994, Kruys et al. 1999).

Dead wood inventories for research and monitoring purposes are currently generally carried out using labour-intensive and expensive field methods (Stierlin et al. 1994, Harmon and Sexton 1996, Anonymous 1998, Buckland et al. 1998, Davis 1998, Hurlburt et al. 1998, Bate et al. 1999, Ganey 1999). The data is collected using sample plots, strips or transects. Because of the naturally high variability of snags through time and across the landscape, sampling is not easy and the sampling intensity must by fairly high to achieve reliable results. The fieldwork is not only cost- and time-consuming (Boyle et al. 1998), but also difficult in remote areas, rough terrain or steep slopes. A more practical, cost-effective, reliable method based on remote sensing techniques - i.e. aerial photo or satellite imagery - to quantify dead trees and stands on large areas would be a relevant contribution to overcome these difficulties. Combined with Geographic Information System (GIS) techniques, it would for example become possible to map the spatial arrangement of snags, useful for various applications, such as dead wood monitoring or the assessment of habitat quality for species depending on large snags. As far back as in 1996, the Intergovernmental Panel of Forests (IPF) of the UN-Commission on Sustainable Development suggested emphasizing the use of modern technologies, and in particular remote sensing, for the assessment of key parameters characterizing sustainable forest management (ISCI 1996).

CIR aerial photos have often been used in forestry, e.g. for management planning, stand description and mapping, time studies, or assessment of forest disease (Huss 1984, Akça et al. 1991, Ekstrand 1994, Kusché et al. 1994, Hildebrandt 1996, Franklin 2001). However, for the study of forest biodiversity, remote sensing has been under-utilized (Innes and Koch 1998). In particular, for dead wood inventories and snag quantification, only few studies have used aerial photos: for example mapping of dead wood in insect outbreak areas (Nüsslein et al. 1997) and windfall areas (Scherrer 1993, Schmidtke 1993, Koch et al. 1998). In both cases damaged stands and not single snags have been assessed. The few existing studies on the assessment of single dead or defoliated trees by CIR aerial photos are based on large-scale images, i.e. 1:6000 to 1:1000 presenting many details (Oester 1991, Ekstrand 1994, Dendron Resource Surveys Inc. 1997, Haara and Nevalainen 2002). For applications at the landscape level, however, smaller scales (less detail, but larger areas) would be preferable. As a contribution towards making the "dead wood" indicator operational, this paper aims: 1) to present a method allowing an efficient quantification of large snags by means of a combination of CIR aerial photos scaled to 1:10,000 and a GIS; 2) to validate it by comparing the results with the ground-truth assessed by field methods.

2. Material and methods

Colour infrared is one of the most frequently used forms of aerial photography. Differences in reflectance create differences in colour and tone on the photographic image that allow discrimination of vegetation types and plant species. The characteristic surface, thickness, internal structure and pigment content of leaves, and the characteristic structure and geometry of the canopy, as determined by orientation of the plants and their leaves, all affect the amount of radiation reflected. Vegetation reflects much more near-infrared (wavelength 700-1500 nm) than visible light, and subtle differences between species in crown characteristics can show up as large differences in infrared reflectance (colour/tone). Typical CIR imagery combines this reflectance information from the near-infrared with information from the green and red visible bands in a "false-colour" display. For example, red tones indicate deciduous vegetation, the ground appears in shades of blue, green, or white depending on soil type, and objects like buildings, roads, or houses will show up on CIR film as dark blue, greyish blue, or black.

Damages in the tree crowns cause changes in the reflectance of trees, especially in the near-infrared region. In our method, the detection of dead trees by means of CIR aerial photos uses these differences in spectral reflectance properties of living, damaged and dead trees. If the near-infrared radiation entered entirely into the plant cell, then temperature would rise, chlorophyll would break down, and photosynthesis would stop.

Water-rich plant cells are very efficient at preventing near-infrared radiation from entering their structure, whereas water-poor cells of decaying or dead trees are not. For detection of the vitality of spruce trees a variety of colour-based interpretation keys for CIR photos have been developed (Gilsa 1984, Oester 1991, Anonymous 1993). During the dying phase of a spruce tree, its colour appearing on the CIR photo changes from intensive dark red (living, sound tree) via light violet and violet-grey (stressed tree) and grey (declining tree) to greyish-white or greyish-green (dead tree). It is hence possible to distinguish on a CIR aerial photo between living, dying and dead spruce trees in a forest stand.

Our approach consisted of the development of a new snag quantification method, which we call Aerial photo (AP) – GIS-method, and its validation by field measurements (Fig. 1). We adopted the snag definition following Thomas et al. (1979) as any dead tree at least 10 centimetres in diameter at breast height (dbh) and at least 1.8 meters tall. We used CIR aerial photos scaled to 1:10,000, 23x23 cm, taken using NAGA-F 7176 and NAGA-F 7171 lenses, respectively, with a focal length of 210 mm. In order to assess the soundness of the method, we chose four topographically different study sites in Switzerland, resulting in different light conditions among different aerial images and within an image. The median surface slope between the sites varied from 8 to 15 degrees (with ranges from 0 to 47 degrees). The aerial photos were taken during the vegetation period in July at about midday, local time.

Table 1: *Study sites and field sampling intensity for validation of the AP-GIS-method.*

Study site	Height above sea level	Total area	Forest area	Verified random forest stands	Verified random snags	Digitised snags	Sampling intensity [2]	Measured snags inside forest stands
	m	ha	ha[1]	Number (ha)	Number (%) [3]	Number	%	Number
Ibergeregg	1280 - 1600	183.9	90.5	35 (10.5)	86 (12)	718	12	235
Mont Pelé	1300 - 1540	300.6	252.0	25 (14.5)	110 (24)	461	6	180
Bärenegg	1360 - 1630	86.5	45.8	16 (3.7)	74 (15)	510	8	158
Langenegg	1300 - 1540	55.6	40.5	16 (4.1)	n.d. [4]	74	10	60
Total	*Min. 1280* *Max. 1630*	*626.6*	*428.8*	*92 (32.8)*	*270 (15)*	*1763*	*Mean 7.6*	*633*

[1] Map data: VECTOR25 © 2000 Federal Office of Topography (DV002210)

[2] Area of verified random forest stands divided by forest area

[3] Percentage of digitised snags

[4] n.d.: no data collected

The study sites had a size of 0.5 to 3.0 km^2 and were located in the sub-alpine vegetation zone between 1280 and 1630 metres above sea level (Table 1). They were dominated by mature spruce (*Picea abies* L.) forests, the natural forest type at this altitude, interspersed with pastures. The fieldwork was done in the same year, during a maximum of twelve months following the flight for aerial photos. No harvesting occurred between these two dates.

2.1. Development of the AP-GIS-method

The AP-GIS-method was based on the following steps (cf. Fig. 1):

Step 1: Stereoscopic CIR aerial photo interpretation

The study sites were delineated on the aerial photo. For each site we used one or several couples of photos for a stereoscopic interpretation that was performed with a Wild Leica Aviopret.

On the aerial photo, we delineated forest stands that were homogenous by age, vertical structure, canopy closure and tree species. First, we described each stand using the Swiss Forest Inventory method (Stierlin et al. 1994) according to the following variables: tree development stage (young growth/thicket; pole wood; young timber; medium timber; old timber); canopy closure (packed; normal; loose; wide-spaced; single trees without contact; packed tree groups) and percent of coniferous trees (< 50%; 51-90%; > 90%). Secondly, all visible dying and dead standing trees were marked on the photos, i.e. trees whose colour was grey, greyish-white or greyish-green and/or whose shadow, a fine dark line, revealed a dead tree without branches (Fig. 2a and Fig. 1).

Step 2: Production of orthophotos

The photos were scanned with a Digital Scanning Workstation DSW200 and stocked with a mean resolution of 50 cm per pixel. For the rectification into vertical frame photographs (orthophotos), we used the ERDAS IMAGINE v8.4® software package. The Digital Elevation Model, based on the height information of the National Map 1:25 000 (basic model) and the resulting interpolated heights arranged in a 25-meter grid (matrix model), was supplied by the Swiss Federal Office of Topography.

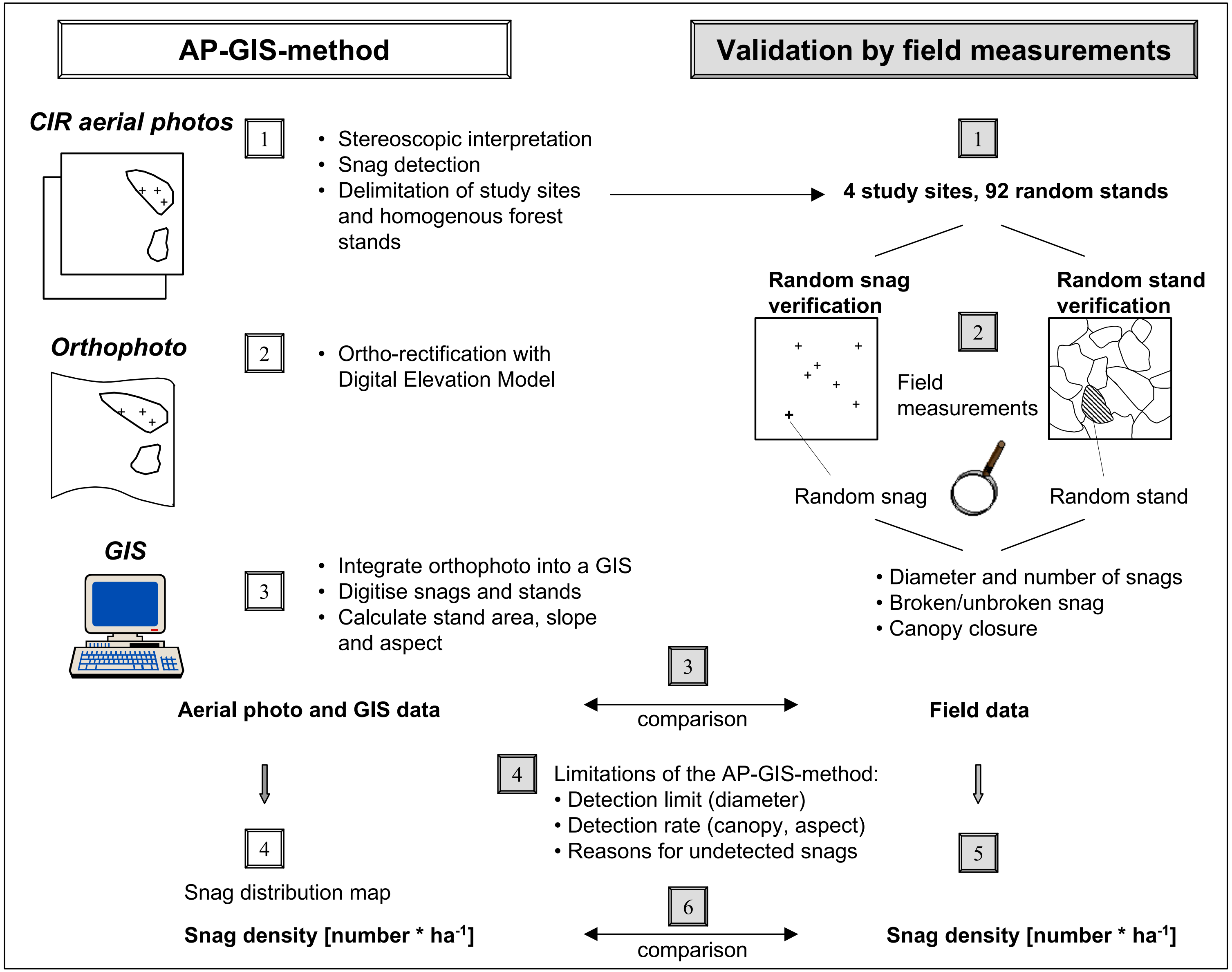

Fig. 1: *Our methodology includes the development of a new method for snag quantification, called the AP-GIS-method, by coupling aerial photo (AP) data and a GIS (on the left), and its validation by field measurements on four study sites (on the right). The limitations of the AP-GIS-method were determined by a comparison between AP-GIS data and field data.*

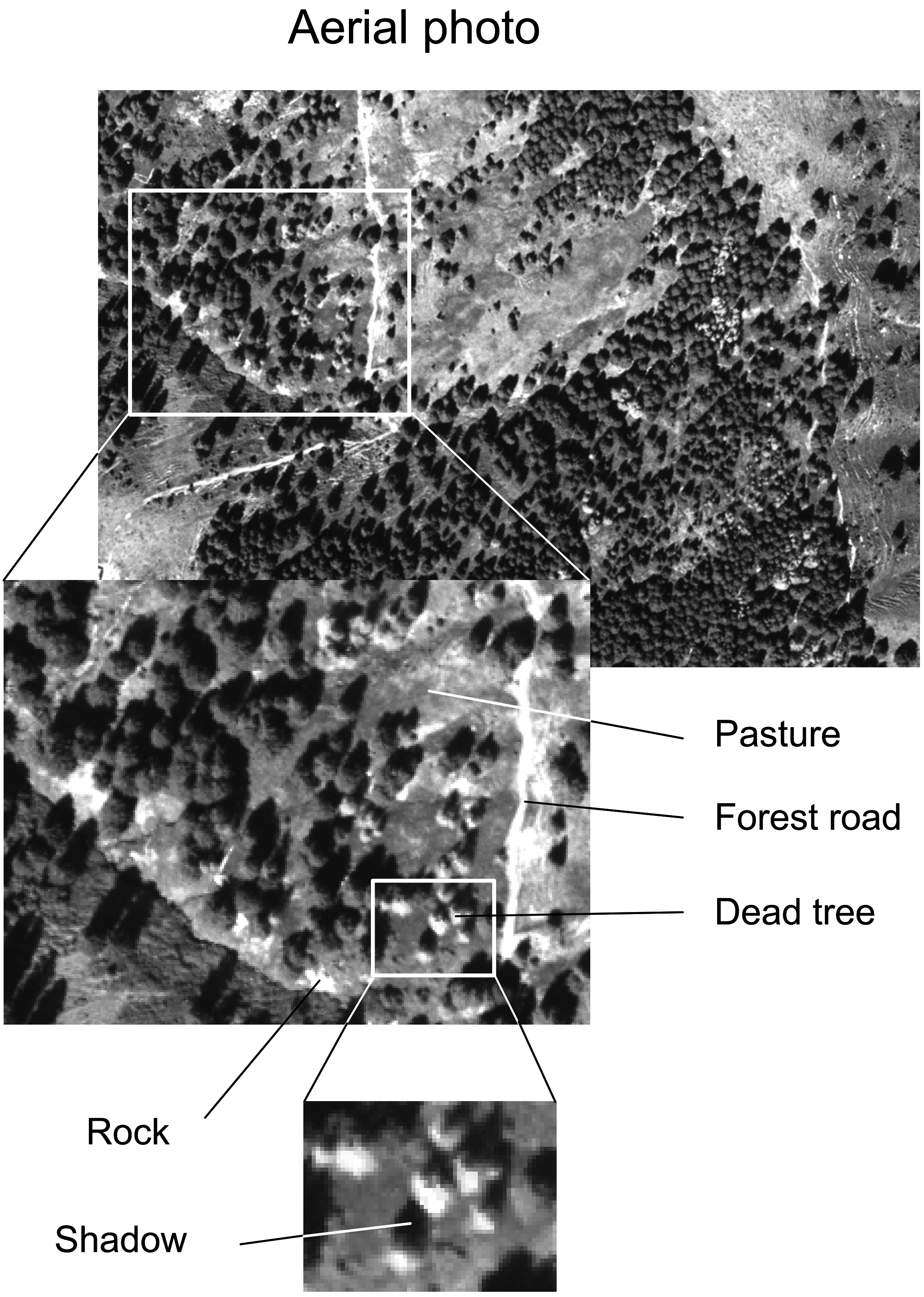

Fig. 2a): *Detection of dead spruce trees on colour infrared aerial photos (here black and white)*

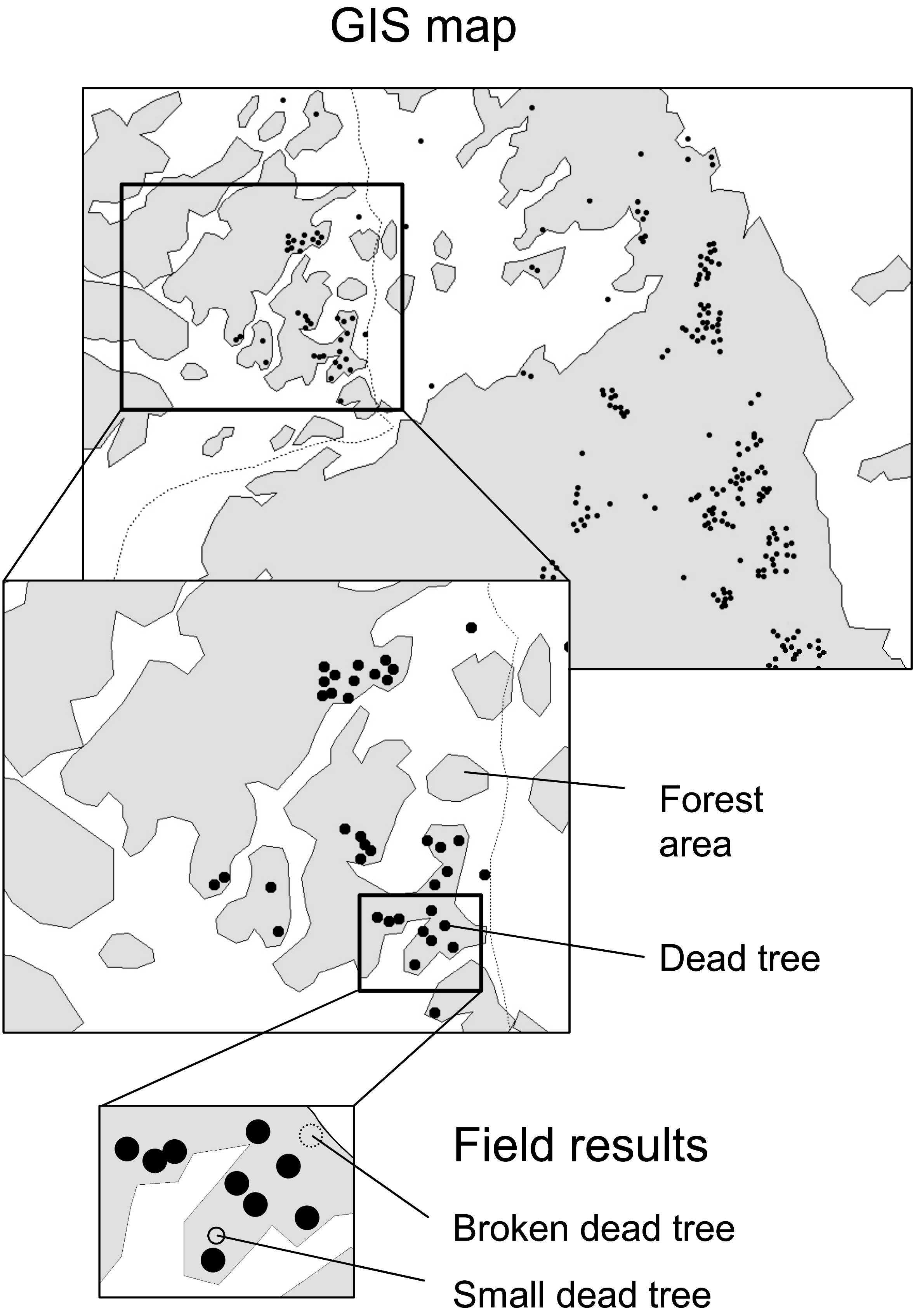

Fig. 2b): *Map of detected dead trees and forest area after data integration into a GIS.*

Step 3: Data integration into a GIS

The orthophotos were geo-referenced and integrated into a GIS, using the MapInfo Professional 5.5® software package. We digitised the previously delineated forest stands and detected snags. The area of the study sites and delineated forest stands was then calculated. We added slope and geographic-aspect maps derived from the Digital Elevation Model, road networks and a layer of the forest areas. The latter were supplied by the Swiss Federal Office of Topography (Vector25).

Step 4: Snag density and spatial distribution

By means of the GIS we drew up snag distribution maps (cf. Fig. 2b) and calculated the density of snags (number * ha^{-1}) both for each study site and for a selection of n random stands in each site (cf. Validation by field measurements).

2.2. Validation by field measurements

Sampling design and data gathering

On each study site we selected i) a random sample of the snags detected by photo-interpretation and ii) a random sample of the delineated forest stands (Fig. 1 and Table 1). In the study site Langenegg we did not sample snags, since too few snags were present on this site (cf. Table 1). Random sampling was preferred to other types of sampling, since the mortality of individual trees is a stochastic, rare, and irregular phenomenon (Eid and Tuhus 2001). The sample size was defined by considering the area of the study sites and available time for fieldwork, in order to achieve similar sampling intensities between study sites. Each random snag was localized in the field and described according to the following variables: snag or other object; dbh in cm; single tree or tree with neighbours within a distance of 2 m; number of treetops; broken or unbroken. Each random stand was visited in the field, and its stand characteristics were verified following the Swiss Forest Inventory method (Stierlin et al. 1994) (cf. Step 1). A complete snag inventory was drawn up (minimum dbh 10 cm) and each snag described by: dbh; broken or unbroken; detected or not by CIR aerial photo-interpretation; reason for undetected snags if dbh ≥ 20 cm, i.e. i) the snag is broken (B); ii) the snag is closely grouped together with a neighbour snag, i.e. ≤ 2 m distance between the individuals (G); iii) the snag splits into two (or several) treetops below breast height and is therefore counted as two (or several) trees by field methods (ST); iv) the snag belongs to the understory and is therefore not visible (NV). If there was a second possible reason for an undetected broken snag, then “broken” was retained as the main reason. The mean values for slope and geographic aspect of the verified stand, derived from the Digital Elevation Model, were attributed to all the snags within a stand.

Data analyses

The validation aimed:

a) to identify the ground-truth of detected objects on the CIR aerial photo and determine the minimal diameter at breast height (dbh_{min}) of the detected snags. We calculated the detection limit or dbh_{min}, defined as the dbh exceeded by 90% of the detected snags, separately for each study site and for the four sites together (N = 270).

b) to test if the variables tree diameter, broken treetop, canopy closure, surface slope and geographic aspect are related to snag detection. All the sampled random stands (N = 92 containing 633 measured snags) were considered as coming from one population. Statistical analyses were performed with the STATISTICA 6.0® software package. Logistic regression (Hosmer and Lemeshow 1989) was chosen as the appropriate method to identify significant variables for snag detection, due to the binary nature of the response variable (detection and failure, coded as 1 and 0). We tested for possible collinearity of the continuous variables slope and diameter. The first step in regression analysis was to calculate univariate models for all variables and test for significance of the coefficients by the Wald statistic. Variables with a p-value < 0.25 (Hosmer and Lemeshow 1989) associated with the Wald statistic were excluded for the second step, corresponding to the calculation of multiple models. The second step was performed by a forward stepwise approach (p-value 0.25 to enter and remove variables), first for all snags (n = 633), secondly for snags ≥ 25 cm (n = 211) and thirdly for unbroken snags ≥ 25 cm (n = 168). The remaining variables were assessed for the significance of their coefficient by the Wald statistic, and each estimated coefficient was compared with the coefficient from the univariate model (Hosmer and Lemeshow 1989).

c) to calculate detection rates for different snag diameters.

We defined:

$$R_d = S_{AP} S_F^{-1} \qquad (1)$$

with: R = detection rate;
d = minimal dbh of snags;
S_{AP} = number of snags detected by aerial photo interpretation;
S_F = number of snags with a dbh ≥ d inventoried by fieldwork.

Detection rates were computed for different minimal tree diameters d and as a function of canopy closure (open, i.e. loose, wide-spaced or single trees without contact – closed, i.e. packed, normal or packed tree groups) and aspect (north, i.e. 280°-360°-80° – south, i.e. 145°-215°). Equation (1) was applied to the random stand sample (N = 92 containing 633 measured snags).

d) to qualitatively explain the probable reasons for undetected snags and their respective contribution to detection failure. All the sampled random stands (N = 92 containing 633 measured snags) were considered as coming from one population.

e) to calculate the accuracy of the AP-GIS-method by comparing for the sampled stands the corrected photo snag density with the snag density resulting from field data.

We defined:

$$D_{AP-GIS} = S_{AP} A^{-1} \quad \left[\text{n ha}^{-1}\right] \quad (2) \qquad \text{and} \qquad D_F = S_F A^{-1} \quad \left[\text{n ha}^{-1}\right] \quad (3)$$

with: D_{AP-GIS} = snag density resulting from the AP-GIS-method;
A = total surveyed forest area;
D_F = snag density resulting from ground-truth field data.

We further defined:

$$D^*_{AP-GIS} = \left[S_{AP} + (1 - R_{25}) S_{AP}\right] A^{-1} \quad \left[\text{n ha}^{-1}\right] \qquad (4)$$

with: D^*_{AP-GIS} = corrected photo snag density = snag density resulting from the AP-GIS-method after correction for bias due to underestimation;
R_{25} = detection rate for snags with a dbh ≥ 25 cm;

$1-R_{25}$ = proportion of undetected snags with a dbh ≥ dbh_{min}, i.e. 25 cm (cf. Results).

We further defined:

$$\Delta = D^{*}_{AP-GIS} - D_F \qquad (5)$$

with: Δ = Accuracy = difference between corrected photo snag density and snag density resulting from ground-truth field data.

Applying equations (2) and (3) to the random stand samples, we calculated for each study site snag densities using the AP-GIS-method and the ground-truth field data. We did not calculate the accuracy for the Langenegg study site, since only 2 out of 74 detected snags were located within sampled stands. The minimal dbh corresponded to the detection limit (dbh_{min}) of the AP-GIS-method (i.e. ≥ 25 cm; cf. dbh_{min} results of the detected snags). In order to take into account snag detection failure and the resulting bias of the AP-GIS-method, we then applied equation (4) using the mean R_{25} of the three study sites, and obtained a corrected snag density with the AP-GIS-method. The accuracy of the AP-GIS-method was then calculated with equation (5).

f) to compare snag densities of forest landscapes from the AP-GIS-method (full enumeration of snags) with mean snag densities from the field inventory (extrapolation from random stands to the whole forest area). We calculated the mean snag density resulting from the AP-GIS-method for each studied forest landscape by (4) ± (5), assuming that the accuracy previously determined on sampled stands is representative for the whole forest landscape. For the Langenegg site we assumed the same accuracy as for Bärenegg, since these sites were located in the same management unit. For the field inventory, we then calculated basic statistics for the random stand samples in each study site. The mean snag density obtained was extrapolated to the whole forest landscape, assuming that the random stands were a statistical sample of the whole snag population in the forest landscape. Decreasing plot size is known to negatively affect accuracy for tree density estimations, resulting in greater proportional error from sampling populations with lower densities (Gray 2002). To obtain a mean snag density, each stand was therefore weighted by its area, since the latter was not identical for all stands. Finally, we compared the snag density from the AP-GIS-method with the mean snag density from the field inventory.

3. Results

The main results of the AP-GIS-method presented are GIS maps at the landscape level, showing the spatial distribution of snags (Fig. 2b). Following steps 1-4 of the "Development of the AP-GIS-method", about 16 hours are required to obtain such a map for an area of 3 km^2 (or 3 minutes per ha of map), if the required material is available. The results presented below focus mainly on the comparison between those achieved with the AP-GIS-method and those determined by fieldwork in the corresponding study sites. We will now deal with points a to f (cf. Data analyses).

a) Ground-truth and dbh$_{min}$ of detected snags:

All detected snags on the aerial photo that we verified in the field (n = 270) could be clearly localized and turned out to be snags. None of them were revealed as other objects that may appear on the CIR photo in similar colours as snags: for example stones, rocks, open water or bare ground (cf. Fig. 2a).

For all the verified random snags in three study sites (n = 270), we got a detection limit of 25 cm (22, 26 and 27 cm for each study site). In very good conditions - isolated tree, stand with open canopy etc. - the smallest snags detected by this AP-GIS-method measured less than 20 cm dbh (minimum 11 cm).

b) Significant variables for snag detection:

Possible factors influencing the success of snag detection include snag characteristics (diameter, broken or not), topographic variables (slope, aspect) and stand characteristics (canopy closure). Forest stands with a relatively open canopy are less dense and the visibility of single snags may be better than in closed canopy stands. Flights for CIR aerial photography are usually made in good weather conditions, i.e. low cloud cover. In the northern hemisphere, more "dark zones" (shadow) may be expected on north-oriented than south-oriented or flat terrain. The shadow problem could also influence the tree visibility on steep slopes (Fig. 2a).

Univariate logistic regression models showed that the variable slope was not significant for successful snag detection (Table 2). The variable aspect was significant in univariate models, while not included in multiple models. For both snag categories $\geq$ 10 cm dbh and $\geq$ 25 cm dbh, the significant variables retained by the stepwise forward variable selection

Table 2: *Univariate and multiple logistic regression models and model statistics for the surveyed variables. The dependent variable is success / failure (1 and 0) for snag detection by aerial photo interpretation.*

Variable	Snags ≥ 10 cm (n = 633)			Snags ≥ 25 cm (n = 211)			Snags ≥ 25 cm unbroken (n = 168)		
	β[1] (SE)[2]	Wald	p	β (SE)	Wald	p	β (SE)	Wald	p
<u>Univariate models</u>									
Diameter	-0.11 (0.01)	127.6	< 0.001	-0.02 (0.01)	2.31	0.13	-0.12 (0.03)	13.12	< 0.001
Slope	-0.02 (0.02)	0.75	0.39	-0.02 (0.03)	0.33	0.56	-0.05 (0.04)	1.38	0.24
Aspect	0.29 (0.15)	3.69	0.05	0.56 (0.25)	4.91	0.03	0.57 (0.36)	2.61	0.11
Unbroken	-1.25 (0.21)	34.25	< 0.001	-1.74 (0.26)	45.6	< 0.001	-----	-----	-----
Open canopy	-0.30 (0.09)	11.65	< 0.001	-0.42 (0.15)	7.59	0.01	-0.28 (0.20)	1.94	0.16
<u>Multiple final models</u>									
Diameter	-0.17 (0.02)	124.0	< 0.001	-0.08 (0.02)	11.16	< 0.001	-0.14 (0.04)	13.82	< 0.001
Unbroken	-2.83 (0.36)	61.95	< 0.001	-2.13 (0.34)	40.5	< 0.001	-----	-----	-----
Open canopy	-0.31 (0.13)	6.23	0.01	-0.44 (0.19)	5.11	0.02	-0.47 (0.22)	4.57	0.03

[1] β = regression coefficient

[2] SE = standard error

method, were “diameter”, “unbroken snags” and “open canopy” (Table 2). For “unbroken snags” with a dbh ≥ 25 cm, both variables “diameter” and “open canopy” were significant.

c) Detection rates for different snag diameters:

Since the variable “unbroken” was highly significant for snag detection (cf. Table 2), we calculated detection rates separately for all (including broken) snags and unbroken snags (Table 3). The detection rate rose with increasing tree diameter from 0.27 (for ≥ 10 cm dbh) to 0.71 (for ≥ 35 cm dbh). It was higher for unbroken snags than when all snags were considered (Fig. 3 and Table 3). Our AP-GIS-method detected 93% of the unbroken snags with a dbh ≥ 35 cm.

For snags located in south-oriented stands (145° - 215°) detection rates were higher than for snags in north-oriented stands (280° - 360° - 80°), even if the variable “aspect” showed low statistical significance in logistic regression models. Snags in stands with an open canopy showed a better detection rate than snags in stands with a closed canopy.

Table 3: *Detection rate R_d for snag detection as a function of tree diameter at breast height (dbh), canopy closure and geographic aspect.*

Snag category	Snag dbh ≥ 10 cm (n = 633) R_{10}		Snag dbh ≥ 25 cm (n = 211) R_{25}		Snag dbh ≥ 30 cm (n = 154) R_{30}		Snag dbh ≥ 35 cm (n = 116) R_{35}	
	all $^{1)}$	unbroken $^{2)}$	all	unbroken	all	unbroken	all	unbroken
All snags	0.27	0.35	0.67	0.82	0.73	0.90	0.71	0.93
Open canopy	0.36	0.42	0.76	0.86	0.80	0.92	0.76	0.93
Closed canopy	0.21	0.29	0.58	0.77	0.67	0.89	0.68	0.94
Aspect 280°-80° N	0.16	0.21	0.40	0.64	0.42	0.71	0.45	0.82
Aspect 145°-215° S	0.27	0.39	0.68	0.86	0.72	0.91	0.70	0.94

1) all snags considered

2) broken snags not included

$0 \leq R_d \leq 1$; d = minimal dbh

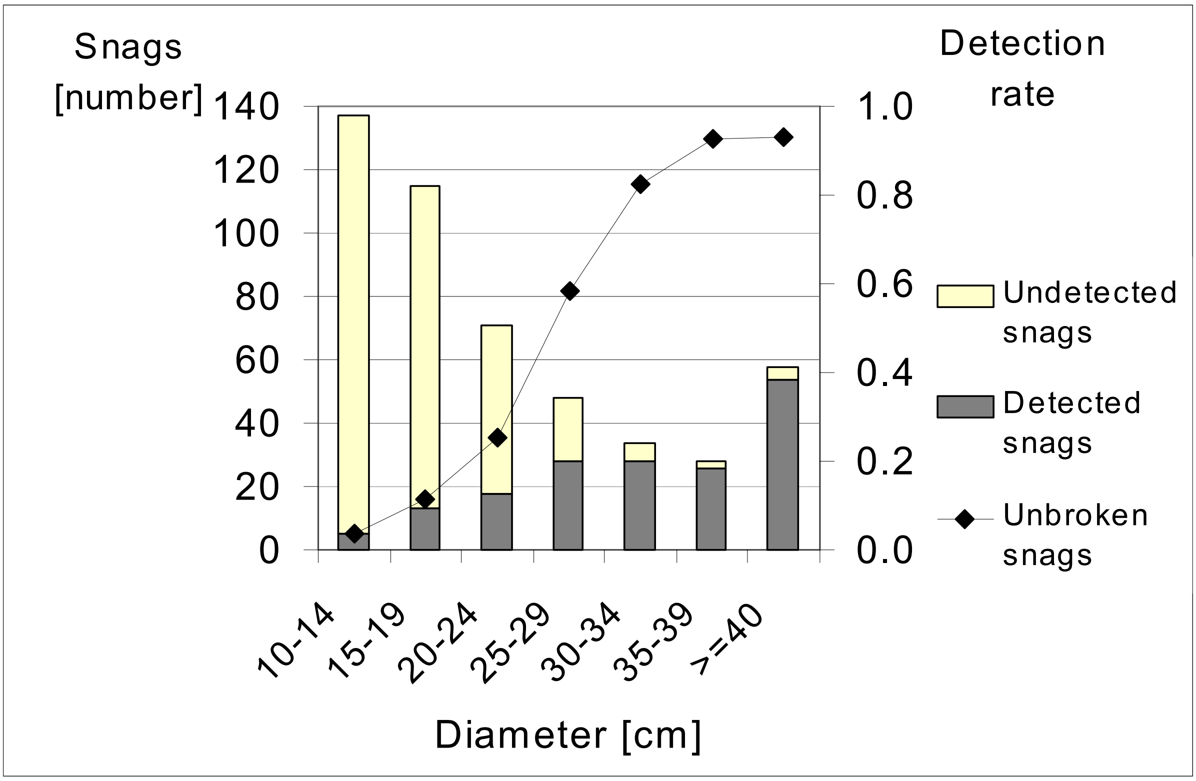

Fig. 3: *Number of detected snags (left scale) and detection rate (right scale) for the AP-GIS-method as a function of the diameter at breast height of the verified snags.*

d) Probable reasons for undetected snags:

The four reasons explaining why a snag was not detected by our AP-GIS-method were: B (broken), G (grouped), ST (several treetops) and NV (not visible) (cf. Sampling design and data gathering). The problems of shadow, canopy closure and topographical location of a forest stand may occur in conjunction with the four probable reasons analysed. For example, a broken tree in an open and south-oriented stand may be detected, whereas the same tree would not be detected if located in a closed and north-oriented stand. In the field, however, it is hardly possible to objectively decide that a snag was not detected because of its topographical location (leading to shadow) or because of the canopy closure of the forest stand. Topographical location and canopy closure were therefore not used to explain the detection failure of an individual snag.

Fig. 4 shows that 67% and 73% of snags with a dbh of ≥ 25 and ≥ 30 cm respectively were detected (cf. also detection rates in table 3). Almost 20% of all snags verified in the field presented broken treetops. This was the main reason for detection failure of snags with a dbh ≥ 25 cm. Only 10% of broken snags (dbh ≥ 25 cm) were successfully detected by the AP-GIS-method. The second reason for detection failure was invisible snags, belonging to the understory. The proportion of invisible understory snags decreased from 11% to 5% when tree diameter increased from 25 to 30 cm. The two other reasons (ST and G) were of less importance, and together concerned less than 5% of snags.

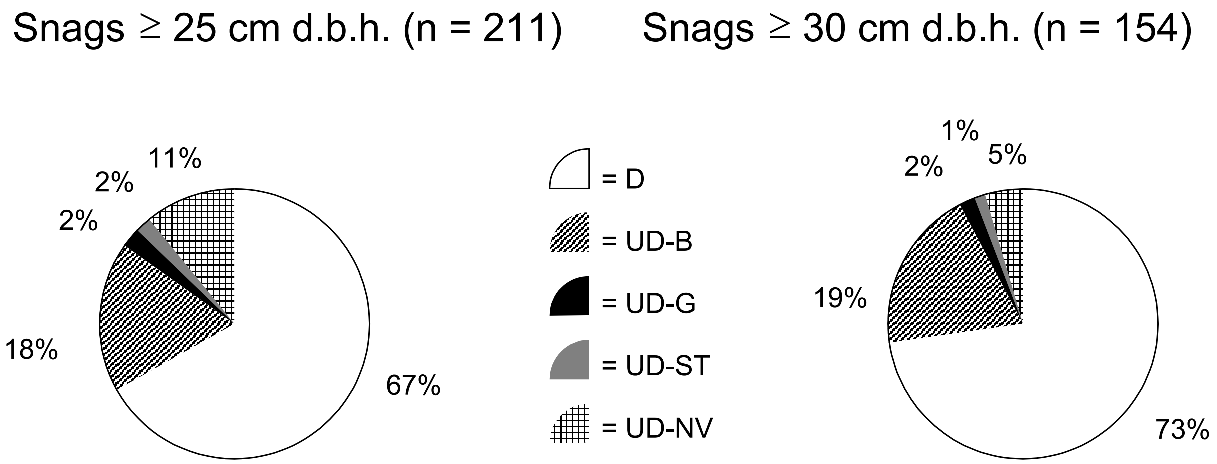

Fig. 4: *Proportion of detected and undetected snags by the AP-GIS-method and probable reason for detection failure. D = detected snag ; UD-B = undetected broken snag ; UD-G = undetected snag grouped together with another snag (distance < 2 m) ; UD-ST = undetected: part of a snag with several treetops ; UD-NV = undetected: snag not visible on aerial photo (understory tree).*

e) Accuracy of the AP-GIS-method:

Snag densities resulting from the AP-GIS-method ($D_{AP\text{-}GIS}$) were smaller or equal to densities from field data (D_F), due to undetected snags as mentioned above (Table 4). The accuracy was ≤ 0.6 snags ha^{-1} for all three study sites. Including a safety factor, we estimate that the corrected AP-GIS-method gives results within 1 snag ha^{-1} of the ground-truth field data.

f) Snag densities of forest landscapes: comparison AP-GIS-method and field inventory:

One prospective application of the AP-GIS-method is the creation of maps showing the spatial distribution of snags (Fig. 2b). Such maps may serve as a basis for calculating

Table 4: *Accuracy of the AP-GIS-method: snag densities [number ha^{-1}] for random forest stands resulting from aerial photo data compared with ground-truth field data and percentage difference.*

Study site	Snag density [number ha^{-1}]			Accuracy
	$D_{AP\text{-}GIS}$ 1)	$D^*_{AP\text{-}GIS}$ 2)	D_F 3)	Δ (%) 4)
Ibergeregg	7.5	9.7	9.4	0.3 (+ 3)
Mont Pelé	2.1	2.7	2.1	0.6 (+ 29)
Bärenegg	14.4	18.6	18.9	-0.3 (- 2)

1) $D_{AP\text{-}GIS}$ Snag density resulting from the AP-GIS-method

2) $D^*_{AP\text{-}GIS}$ Snag density resulting from the AP-GIS-method after correction for bias due to underestimation

3) D_F Snag density resulting from field data ($dbh_{min} \geq 25$ cm)

4) Δ $D^*_{AP\text{-}GIS} - D_F$

Table 5 : *Mean snag densities [number ha^{-1}] of forest landscapes: snag densities resulting from the AP-GIS-method compared with field data extrapolated from random stands to the whole forest area.*

Study site	AP-GIS-method: whole forest area	Field data: Random stands → whole forest area						
	$D^*_{AP\text{-}GIS}$ 1) [number ha^{-1}]	D_F 3) [number ha^{-1}]						
	Mean ± Δ 2)	*n*	Mean ± SE	Min.	1.Qu.	Median	3.Qu.	Max.
Ibergeregg	10.2 ± 0.3	35	9.4 ± 1.2	0.00	3.8	8.0	10.5	52.9
Mont Pelé	2.4 ± 0.7	25	2.1 ± 0.4	0.00	0.0	1.7	2.4	37.4
Bärenegg	14.4 ± 0.1	16	18.5 ± 3.9	0.00	9.9	16.3	32.4	56.5
Langenegg 4)	2.4 ± 0.0	16	3.2 ± 0.6	0.00	0.0	4.1	7.6	28.2

1) $D^*_{AP\text{-}GIS}$ Snag density resulting from the AP-GIS-method after correction for bias due to underestimation

2) Δ Accuracy of the AP-GIS-method

3) D_F Snag density resulting from field data ($dbh_{min} \geq 25$ cm)

4) The same accuracy as for Bärenegg was assumed.

mean snag densities of a forest landscape. For our study sites, the mean snag densities resulting from the AP-GIS-method were between 2.4 and 14.4 snags ha^{-1} (Table 5). Basic statistics on the field data demonstrated a high variability of snag densities within each site, i.e. large standard deviations and ranges (Table 5). The differences between snag densities resulting from both approaches – full enumeration of snags by AP-GIS-method and inference from samples for field data – were higher for study sites where the sample size n of random stands was small.

4. Discussion

Limitations of standard field methods and sampling designs for the inventory of large dead trees

Extensive literature exists on structural and functional characteristics of dead wood and its importance for biodiversity (Caza 1993, Samuelsson et al. 1994). However, quantitative studies are still scarce, in particular for temperate European forests. One reason may be the only recent acknowledgement by researchers, forest and wildlife managers of the importance of dead wood. Another probable reason is the methodological problems involved in making cost- and time-effective dead wood inventories. Although probability sampling methods theoretically ensure unbiased estimation, the precision of the estimates depends largely on spatial patterns. Most standard sampling designs will not be efficient for rare elements, such as large dead trees in managed forests (Yoccoz et al. 2001). In unmanaged forests - on which most studies have been based - a high level of natural variability in the rates of creation and amounts of dead wood is typical. Large snags may cluster and many plots with no such trees are to be expected. Large sample numbers and plot sizes are therefore required to monitor densities of large snags (Gray 2002). Grove (2001), for example, strongly suggests that further sampling would have been desirable to obtain more precise estimates of dead wood in his study, although the sampling intensity used was at least as high as in most other cited studies. On our study sites, with a sampling intensity between 6% and 12% and mean plot sizes of 0.25 to 0.60 hectares (Table 1), we obtained standard errors of 13% to 21% for the mean snag density (Table 5). Higher standard errors corresponded to a smaller sample size (n = 16) and lower errors to a larger sample size (n = 35). Our sampling intensity, although considerably time-consuming with 14 days for a 33-hectare sampled forest area, should have been three times higher (100 hectares needed) in order to obtain standard errors ≤ 10% of the mean on all study sites. Since estimation errors for a given plot size are relatively large and accuracy increases with plot size, Gray (2002) recommends plot sizes of 1 hectare for large snags.

In monitoring programmes for land management purposes, however, money and personnel are usually limited. One of the main problems is to ensure adequate sample numbers and plot sizes for field recording of such an irregularly distributed resource. According to Yoccoz et al. (2001), most estimates of biological diversity are not based on an appropriate spatial sampling type. As a consequence, in most forest monitoring programmes, replication and statistical power are low (Foster 2001).

Since plot-based methods are in most cases inefficient for surveys of rare elements, other methods such as strip or line transect sampling have been proposed as (competitive) alternatives to circular plots. Line transect sampling is based on the probability of detecting an object as a function of its perpendicular distance from the inventory line. An important difficulty is estimation of the parameters of the true probability-of-detection function (Lämas and Stahl 1998), while choice of the model for the detection function is somewhat subjective. The accuracy of line transect sampling depends on how well the detection function can be estimated (Lämas and Stahl 1998). Ringvall et al. (2000) point out that important bias may be caused by systematic and random errors made by the surveyor. These authors suggest considering other reasonable alternatives to line transect sampling for surveying inanimate populations, such as large snags.

Recent work has focused on adaptive sampling designs (Thompson and Seber 1996), which seem to be promising for rare elements that form clusters (Acharya et al. 2000). In such designs, however, the sample size is not known beforehand, since the intensity of sampling is dependent on initial sampling results. This may be a drawback when evaluating survey costs. A large group size increases the efficiency of systematic adaptive cluster sampling. When groups get too large, however, such sampling becomes equivalent to (near) full enumeration and survey costs may become high.

Advantages and prospective applications of the AP-GIS-method

Initially, dead wood data were collected to address wildlife habitat issues. More recently, dead wood is considered relevant to issues of forest health, site productivity, fuels, and carbon stores. In the future, dead wood will hence have to be inventoried more and more frequently. Interest groups for such inventories are for example those studying criteria and indicators (C&I) defined for sustainable forest management (e.g. criteria 4 and 1 in the Helsinki process, i.e. biodiversity and global carbon cycles), wildlife managers or groups concerned with forest certification processes, such as the Forest Stewardship Council FSC. Dead wood is referred to in modern FSC certification standards at national or regional levels (for example United States, United Kingdom, Germany, Sweden, Netherlands, Switzerland, British Columbia etc.).

Both the increasing demand of various users and the discussed limitations of standard field methods and sampling designs emphasize the importance of developing rapid, simple and cost-effective dead wood inventory methods. Up until now, remote sensing as a data source is only seldom used for European national forest inventories (Köhl et al. 1998), in spite of its high potential and frequent use in forest research. A method based on remote sensing offers advantages for rapid inventories of large snags. It facilitates the study of spatial and temporal variation in amounts and distribution of snags in remote and inaccessible areas. In particular, the assessment of spatial arrangement of dead trees within a stand or across a landscape becomes possible thanks to the (almost) full enumeration of large snags over large areas. On the one hand, our AP-GIS-method may be used as a basis for defining, for example, an adaptive sampling design for field measurements in hectare or smaller plots. On the other hand, it may also be used for a sampling on the landscape scale: one aerial photo couple scaled to 1:10,000, with 23x23 cm dimensions and an overlap of 80% offers the possibility of investigating a forest area of 3.5 km^2 in size. Even larger sampling plots would be possible by combining several photos into a mosaic. The potential of such large plots (3.5 km^2 instead of 1-hectare field plots) for different applications may be important. As an example, we mention an ongoing application for the management of the three-toed woodpecker (Bütler et al., unpublished data), an indicator species of spruce forest biodiversity (Nilsson et al. 2001). A sample of 10 three-toed woodpecker home-range areas, each measuring about 0.5 – 1.5 km^2 and representing one sampling plot on the landscape scale, has been entirely inventoried for snags. Our AP-GIS-method allowed the analysis of the density and spatial distribution of snags and the derivation of snag retention levels for the presence of this woodpecker species.

Limitations of the AP-GIS-method

A first limitation is the minimum diameter of snags that are detected. This depends on both forest type and structure and has to be determined before the method can be applied. Since this detection limit is not abrupt but continuous, some uncertainty in relation to the diameter of the detected snags remains. In our study sites, 90% of detected snags had a dbh ≥ 25 cm, but some smaller snags were nevertheless detected in good conditions.

A second limitation is determination of the snag detection rate. This depends on forest type and structure, but some more variables such as geographic aspect, surface slope of the site, weather conditions and hour of flight may influence it. The detection rate transformed into a correction coefficient must be known in order to obtain an accurate quantification. Yet the detection rate may vary within a study site and also depends on tree diameter (cf. Table 3). In this paper, we determined a mean detection rate (0.70 for trees ≥ 25 cm dbh) from three study sites. The difference compared with ground-truth field data was ± 0.6 snags per hectare. The correction coefficient should be further tested on new study sites to acquire more certainty on accuracy and possible generalization. If a lower bias is necessary, more investigation to elaborate subtly differentiated correction coefficients within a site would be required. This problem, however, also affects field methods. All methods, such as fixed-area circular or rectangular plots, or line transect sampling, used to estimate standing amounts of woody debris in coniferous forests lead to a certain degree of error. Ringvall et al. (2000), for example, report an underestimation as high as –22.2% in their study on line transect sampling, partly due to violation of the assumption that all objects on or very close to the survey line are detected. But in many cases, the error is not known or estimated.

A third limitation is the fact that most snags with a broken treetop are not detected. Our detection rate for broken snags larger than the detection limit - i.e. ≥ 25 cm dbh - was only 10%, and the main detection error was due to these broken snags (cf. Fig. 4). Consequently, our method is not efficient for quantifying snags in an advanced decay class, defined by Thomas (1979) as stages 6 and 7 (broken and decomposed). From a biodiversity viewpoint, these broken snags are important, since it has been demonstrated that they may have a higher wildlife value than whole snags. Considering all our study sites, snags ≥ 25 cm dbh that were broken represented a mean value of 20% of total snags.

A fourth limitation is the need for high technology equipment and material, if precise snag distribution maps and density estimations are required: CIR aerial photos, a digital scanning workstation to scan the aerial photo slides and special software to produce orthophotos. For an approximate snag quantification, however, a simple count of the snags on the original photos with an estimation of the forest cover area using topographic maps may be sufficient. In such a case, apart from a stereoscope, no special equipment would be required.

We developed and tested the AP-GIS-method in spruce forests. Since the spectral reflectance properties for other coniferous tree species are similar, our method may not be limited to spruce snag detection. For deciduous trees, however, the method would probably be more limited, due to their different reflectance behaviour and less compact tree crowns.

5. Conclusion

For both research and management purposes, simple, rapid and accurate methods for the quantification of dead wood are required. Our study presents the feasibility and usefulness of a method coupling infrared aerial photos scaled to 1:10,000 and GIS, in order to map and quantify large standing dead spruce trees. In spite of the high ecological value of such trees, few quantitative inventories or maps of their spatial distribution exist, because of the many difficulties arising from the use of standard methods for field inventories. Given both the irregular distribution and relative scarcity of large snags, especially in managed forests, air borne data sources, such as aerial photos, facilitate inventories. With the AP-GIS-method presented, a map of the spatial distribution of snags with a dbh ≥ 25 cm can be obtained in about 16 hours for an area of 3 km^2 in size. Quantitative estimations, expressed as number of snags per hectare, can easily be derived. Considering our encouraging results, the AP-GIS-method may become a promising tool, complementing standard field methods, with various prospective applications: national, regional or local forest inventories; certification processes; wildlife studies of the habitat quality for species depending on dead trees; classification of old-growth stands etc.

Acknowledgements

The authors would like to thank: C. Hunziker (Chair of Photogrammetry, EPFL) and A. Pointet (Geographical Information System Laboratory, EPFL) for their technical help on aerial photo scanning and GIS software; H.-U. Scherrer (GEOPLAN LTDA); R. Ehrbar, N. Walliser, M. Fuchs, F. Laimbacher, A. Annen (Forest Offices). We are grateful to V. Barbezat, I. Iorgulescu, and J.J. Sauvain for wise comments on earlier versions of the manuscript, and to M. Howett for revising the English.

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Paper II

Three-toed Woodpeckers as an alternative to bark beetle control by traps?

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Pages 13-26 in: P. Pechacek & W. d'Oleire-Oltmanns: International Woodpecker Symposium. Forschungsbericht 48, Nationalparkverwaltung Berchtesgaden.

Abstract

The efficiency of the Three-toed Woodpecker (*Picoides tridactylus*) as a natural agent against spruce bark beetles was compared with the number of *Ips typographus* beetles captured in pheromone traps commonly used in Swiss forestry. The woodpecker's energy requirements and statistics derived from use of Swiss bark beetle traps served as input data. Our results demonstrate that one woodpecker destroys more bark beetles than one trap, and the whole Swiss woodpecker population destroys more beetles than all installed traps together.

In a second step, we determined the number of standing declining and dead trees, one of the most important habitat features, required by this woodpecker species. A simple model was developed relating the number of potential foraging substrates per unit area to five variables: the woodpecker's potential home range size in endemic bark beetle population levels, the bark area per foraging substrate infested by bark beetles, the breeding density of bark beetles, the woodpecker's foraging efficiency, and the woodpecker's energetic requirements. Although the model has to be further developed and validated, we have derived a provisional management recommendation. Based on the preliminary Monte Carlo simulation results, we recommend a snag retention level of at least 14 snags/ha (d.b.h. ≥ 21 cm) over 200 ha forest areas, distributed patchily within a forest landscape.

Zusammenfassung

In dieser Studie wurde die Wirksamkeit des Dreizehenspechtes *Picoides tridactylus* als natürlicher Feind des Borkenkäfers mit Fangzahlen von Pheromon-Borkenkäferfallen verglichen. Der berechnete Energiebedarf des Spechtes und die daraus resultierende Anzahl vertilgter Käfer wurde Daten aus Schweizer Borkenkäferfallen-Statistiken gegenübergestellt. Unsere Resultate zeigen, dass ein Specht deutlich mehr Borkenkäfer zerstört als eine Pheromonfalle und die gesamte Schweizer Spechtpopulation mehr als sämtliche Fallen in Schweizer Wäldern. In einem zweiten Schritt bestimmten wir die notwendige Menge eines für diesen Specht wichtigen Habitatelementes: absterbende und tote stehende Bäume. Es wurde ein einfaches Modell entwickelt, das die notwendige Anzahl potentieller Nahrungsbäume in Abhängigkeit von fünf Variablen berechnet: Aktionsraumgrösse während endemischen Borkenkäfer-Populationsniveaus, durch Borkenkäfer befallene Stammoberfläche pro Nahrungsbaum, Borkenkäferbrutdichte, Effizienz des Spechtes bei der Nahrungssuche und sein Energiebedarf. Obwohl das Modell noch Verbesserungen und weiterer Tests bedarf, gestatten die vorläufigen Monte Carlo-Simulationsresultate bereits, eine provisorische Management-Empfehlung abzuleiten. Wir empfehlen, in einer Waldlandschaft extensiv bewirtschaftete Gebiete von ungefähr 200 ha Grösse mit durchschnittlich 14 absterbenden und toten Bäumen pro Hektare (Brusthöhendurchmesser ≥ 21 cm) patchworkartig auszuscheiden.

Keywords: Three-toed Woodpecker, *Picoides tridactylus*, bark beetle, pheromone trap, dead wood, snag.

1. Introduction

The Three-toed Woodpecker (*Picoides tridactylus*) is a highly specialised bird that feeds on bark beetles (Formosow et al. 1950 cited in Glutz von Blotzheim 1994, Hess 1983, Hogstad 1970, 1978, Sevastjanow 1959 cited in Scherzinger 1982). For foraging, this woodpecker prefers standing spruce (*Picea* spp.) trees with a relative large diameter (Hess 1983, Murphy & Lehnhausen 1998, Villard 1994), corresponding to the preferred breeding tree of Europe's most important spruce bark beetle species *Ips typographus* (Schmidt-Vogt 1989).

For some years, the Swiss Three-toed Woodpecker population has been growing (Schmid et al. 1998). In parallel, dead wood volumes in mountain forests have also been increasing, partly due to an increase of unexploited and rarely exploited forest areas due to economic reasons (see Figure 149 in Brassel & Brändli 1999). It is possible that this increase of dead wood in mountain forests has led to an improvement of the Three-toed Woodpecker's habitat conditions. However, if the timber market price increases, what would be the woodpecker's future?

Woodpeckers, and in particular the Three-toed Woodpecker, have been shown to be indicators of forest bird diversity and forests with a high conservation value (Angelstam & Mikusinski 1994, Derleth et al. 2000, Mikusinski et al. 2001). Maintaining habitat features favouring woodpeckers can therefore be a goal for sustainable forest management. In the case of Three-toed Woodpeckers, however, their preferred prey, i.e. spruce bark beetles, are feared by forest managers because of their cyclic outbreaks, especially after natural disturbances (storms, fire, etc.).

A common strategy used in forestry to control bark beetle populations is to install pheromone traps during the flight season of beetles. In addition, salvage harvesting, i.e. the removal of infested dead or damaged trees, is often practised to prevent or reduce the spread of the infestation. But this kind of beetle management artificially diminishes the abundance of potential foraging substrate and thus likely negatively influences woodpecker populations. Finland and Sweden provide examples where the modern forestry practice of removing old and dead trees has caused a decline of this bird (Väisänen et al. 1986 cited in Amcoff & Eriksson 1996, Hagemeijer & Blair 1997).

The importance of woodpeckers as natural control agents of bark beetles has often been reported for North America, in particular during epidemic bark beetle outbreaks (e.g., Baldwin 1968, Hutchinson 1951, Knight 1958, Kroll & Fleet 1979). One reason aggravating *Ips typographus* outbreaks after natural disturbance is a high endemic population level of the beetle. Because of its predatory impact on bark beetles, the Three-toed Woodpecker should be a bird species of interest to foresters because of their potential to maintain bark beetles at low levels -- particularly during endemic phases. Through this study we evaluate the potential value of Three-toed Woodpeckers to forestry and provide forest management recommendations for maintaining Three-toed Woodpecker habitat features. We try to answer the following questions:

1. What is the efficiency of *Picoides tridactylus* in bark beetle control compared with bark beetle traps?
2. How many declining and dead spruce trees per ha are required to meet the foraging needs of *Picoides tridactylus*?

2. Methods

For the first question, we compare Swiss bark beetle trap statistics with the number of bark beetles consumed by Three-toed Woodpeckers. The latter figures were calculated using the model developed by Koplin (1972) for the bird's energetic requirements. Data from the literature, both on the woodpecker's feeding ecology and on capture success of bark beetle pheromone traps served as input to define three scenarios used to evaluate the efficiency of traps and woodpeckers for bark beetle control.

To answer the second question we developed, as a first step, a simple model relating the woodpecker's potential home range size (PHR) in endemic bark beetle levels to five variables (defined below under “Modelling”). In a second step, the model variables were estimated from literature data and our own field data. In a third step, the model was validated against literature home range sizes. Finally, we used our model to estimate the number of declining and dead spruce trees needed by the Three-toed Woodpecker to satisfy its energy requirements.

2.1. Modelling

The home range size of a woodpecker breeding pair lies between a minimal and maximal value. The presence of all habitat elements required by the bird species, in minimal, but sufficient quantities, defines the minimal size. The upper limits of home range size are defined by the size at which too high an energy expenditure is required for moving around. By definition a viable home range lies within these extreme values. The factors influencing food availability and requirement are the most important ones for an insectivorous bird spending most of its time searching for food. The potential home range size (PHR) depends on the following factors (Figure 1):

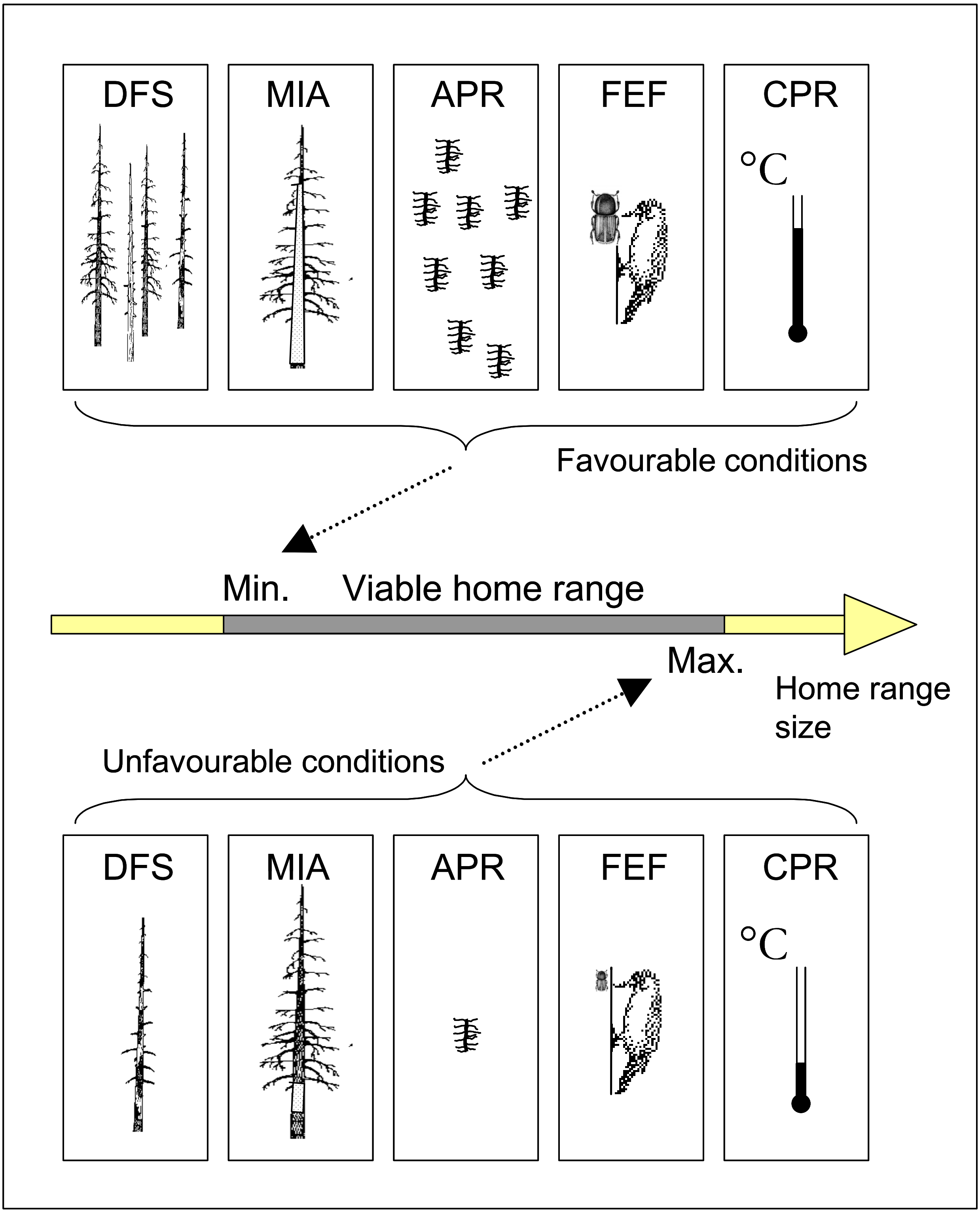

Fig. 1: *Different factors influence the potential home range size of a Three-toed woodpecker. Extremely favourable / unfavourable conditions lead to a minimal / maximal viable home range size. DFS =* ***D****ensity of potential* ***F****oraging* ***S****ubstrate, MIA =* ***M****ean* ***I****nfested* ***A****rea of potential foraging substrate, APR =* ***A****vailable* ***Pr****ey in the foraging substrate, FEF =* ***F****oraging* ***Ef****ficiency of the woodpecker, CPR =* ***C****onsumed* ***Pr****ey during a time unit.*

1) The density of potential foraging substrate (DFS) is the number of trees per hectare, which present a minimal diameter for the woodpecker's foraging and which may contain bark beetles.

2) The mean infested area (MIA) is the mean area of bark surface per foraging substrate (tree) that is infested by bark beetles.

3) The available prey (APR) values are the annual mean number of potential prey items (adult bark beetles and their larvae) per infested square meter of bark.

4) The foraging efficiency of the woodpecker (FEF) is the proportion of APR that is really detected and consumed by the woodpecker.

5) The consumed prey (CPR) values are the number of bark beetles (larvae and adults) consumed by a woodpecker during a year.

Based on these variables, we define the following model:

$$PHR = (DFS * APR * FEF * MIA)^{-1} * CPR$$

with: PHR = **p**otential **h**ome **r**ange size (ha)

DFS = **d**ensity of potential **f**oraging **s**ubstrates (number ha^{-1})

MIA = **m**ean **i**nfested **a**rea of potential foraging substrate (m^2)

APR = **a**vailable **pr**ey in the foraging substrate (number m^{-2} bark)

FEF = **f**oraging **ef**ficiency of the woodpecker (percent)

CPR = **c**onsumed **pr**ey during a time unit (number)

The model variables were estimated (see "Estimation of the model variables") and the model validated (see "Validation of the model"). Then, the same equation, solved for DFS, was used to estimate the number of declining and dead trees required to meet the Three-toed Woodpecker's foraging needs. This estimation was done by a Monte Carlo approach (10 simulations), based on a sample size of N = 10,000 (see "Estimation of the snag density required to meet the Three-toed Woodpecker's foraging needs").

2.2. Case studies for the estimation of the DFS

The variables MIA, APR, FEF, and CPR were estimated mainly by means of data from the literature (see "Energy model to calculate food requirements of Three-toed Woodpeckers" and "Estimation of the model variables"). No literature data being available on DFS, we estimated this variable from field data collected at six study sites.

Study sites

We chose six study sites in different geographic regions of Switzerland between 1280 and 1700 m above sea level. Four sites supported at least one Three-toed Woodpecker breeding pair before and during the two study years: Hobacher (HO), Hinteregg (HE), Hinterberg (HB), and Bärenegg (B). Two sites, presenting the same forest types, but with a more intensive forest exploitation, did not have any breeding pair: Langenegg (L) and Mont Pelé (MP). All sites lie in the sub-alpine vegetation zone. They are dominated by spruce (*Picea abies*) forests, the natural forest type at this altitude, and were interspersed with pastures. Their size was between 0.5 and 3.0 km^2. Mean monthly temperature varied from about - 6 °C in winter to 12 °C in summer, with yearly precipitation of about 1800 - 2600 mm.

Infra-red aerial photo interpretation

For each study site we used pairs of false colour infra-red aerial photos in a 1:10,000 scale, 23 x 23 cm, taken either by an objective NAGA-F 7176 or NAGA-F 7171 with a focal length of 210 mm. After delimitation of the study sites on aerial photos, they were prepared for a stereoscopic analysis done using a Wild Leica Aviopret. Forest stands were delimited, each one homogenous by age, vertical structure, canopy closure, and tree species. All visible declining and dead standing trees (snags) were marked. On the photo, such trees present a grey, greyish-white or greyish-green colour and/or a fine shadow line, which corresponds to a dead tree without branches.

Field measures

At each study site we chose 16 - 35 random stands (N = 152) for field verifications. In each stand a complete inventory of snags (N = 1367) was done in order to collect the following data: (1) diameter at breast height (d.b.h.); (2) detected/not detected by aerial photo; (3) stage of decomposition according to Maser et al. (1979), but slightly modified for our purpose (stage 1= declining or recently dead; 2= loose bark; 3= clean; 4= broken; 5= decomposed); (4) billmarks or other signs of Three-toed Woodpeckers.

GIS and calculations

The photos were scanned using a Digital Scanning Workstation DSW200. For the rectification into vertical frame photographs (ortho-photos), we used ERDAS IMAGINE v8.4 software. The Digital Elevation Model (the Swiss DHM25), based on height information from the National Map at a scale of 1:25,000 and arranged in a 25-meter grid, was supplied by the Federal Office of Topography. The geo-referenced ortho-photographs were integrated in a Geographic Information System (GIS), working with the MapInfo Professional 5.5 software. We digitised the positions of the previously delimited forest stands and snags. The density of snags (number per hectare) was calculated in the GIS for each study site and snag distribution maps were drawn.

3. Results and discussion

3.1. What is the Three-toed Woodpecker's efficiency in bark beetle control compared with traps?

We compare the number of bark beetles (adults and larvae) consumed by one/all Three-toed Woodpecker(s) during one year with the number of beetles captured by one/all Swiss pheromone trap(s) during one season. Statistics on Swiss bark beetle traps from 16 years, provided by the Forest Insect and Disease Survey (FIDS) of the Swiss Federal Research Institute WSL, were used.

Energy model to calculate food requirements of Three-toed Woodpeckers

Koplin (1972) developed a deterministic model in order to predict the predatory impact of the Three-toed Woodpecker on endemic and epidemic populations of larval spruce beetles. This model predicts the number of prey items consumed by the predator under given temperature conditions by the following equation:

$$ER = (63.3 - 0.37 * (T^C / (5/9) + 32)) * 4185\ J$$

with ER = energy requirement in J (Joules) per bird-day (1 cal = 4.185 J)

T^C = temperature in ° Celsius.

The mean caloric content of one bark beetle larva is 83.7 J (0.02 kcal), estimated from 807 items (Koplin 1972). This estimation seems to be realistic, as shown by the following calculation with data from two other sources. The mean energetic content of animals (dry weight) is 23.77 kJg^{-1} (Barbault 1997) and the dry weight of an adult bark beetle *Ips typographus* 4.1 mg (B. Wermelinger, personal communication). Based on these data we obtain an energetic content of 96.3 J (0.023 kcal) for one adult bark beetle.

According to Koplin's equation, a woodpecker needs 2573 larvae per day at 0° C to satisfy its energy requirement ((63.3 - 0.37 * (0° / (5/9) + 32)) * 4185 J / 83.7 J = 2573). If we assume the moisture content of a bark beetle larva as 70% (Bell 1990), this represents 35 g of fresh weight. Considering *Picoides tridactylus'* body weight (male about 70 g and female about 60 g (Hogstad 1970)) and literature data about bird digestion (Karasov 1990), this seems to be a realistic winter daily diet for an insectivorous bird.

Table 1: *Energy requirement per day [kJ] for one Three-toed Woodpecker, calculated for the study sites Mont Pelé (MP), Hobacher (HO), Langenegg (L) and Bärenegg (B), based on the model of Koplin (1972). Number of bark beetles consumed daily and monthly by one Three-toed Woodpecker, calculated with the assumptions that the caloric content of one larva or adult bark beetle is 83.7 J and the proportion of bark beetles in the woodpecker's diet is 75 %.*

	Mean temperature °C			Energy requirement per day [kJ]			Number of consumed bark beetles (larvae and adults) per day			Number of consumed bark beetles (larvae and adults) per month		
	MP	HO	L/B	MP	HO	L/B	MP	HO	L/B	MP	HO	L/B
January	- 6	- 6	- 6	232	232	232	2080	2080	2080	64'480	64'480	64'480
February	- 2	- 6	- 4	221	232	226	1980	2080	2030	55'440	58'240	56'840
March	- 2	- 2	- 2	221	221	221	1980	1980	1980	61'380	61'380	61'380
April	2	2	2	210	210	210	1880	1880	1880	56'400	56'400	56'400
May	6	8	6	199	193	199	1780	1730	1780	55'180	53'630	55'180
June	10	10	10	187	187	187	1680	1680	1680	50'400	50'400	50'400
July	10	12	10	187	182	187	1680	1630	1680	52'080	50'530	52'080
August	12	12	12	182	182	182	1630	1630	1630	50'530	50'530	50'530
September	10	10	10	187	187	187	1680	1680	1680	50'400	50'400	50'400
October	6	6	4	199	199	204	1780	1780	1830	55'180	55'180	56'730
November	2	0	0	210	216	216	1880	1930	1930	56'400	57'900	57'900
December	- 2	- 6	- 6	221	232	232	1980	2080	2080	61'380	64'480	64'480
Total CPR[1)]										**669'250**	**673'550**	**676'800**

[1)] CPR (consumed prey) is the totally consumed bark beetles (larvae and adults) during one year.

The calculated daily energy requirement of one Three-toed Woodpecker (Table 1) is based on Koplin's model (1972) and on monthly mean temperatures for the study sites (Kirchhofer 1982). To calculate the number of consumed bark beetles (larvae and adults) we assumed that the caloric content of one larva or adult beetle is equal (83.7 J) and that the proportion of bark beetles in the woodpecker's diet is 75% (Hutchinson 1951 cited in Baldwin 1968, Formosow et al. 1950 cited in Glutz von Blotzheim 1994, Hess 1983, Hogstad 1970, Pechacek & Kristin 1993, Sevastjanow 1959 cited in Scherzinger 1982).

During one year a Three-toed Woodpecker consumes about 670,000 bark beetles (Table 1). Schmid et al. (1998) estimate the Swiss *Picoides tridactylus* population to be 1000 - 1500 breeding pairs, that is 2000 - 3000 individuals. According to our calculations the whole woodpecker population, i.e. 2500 individuals, consumes, during one year, about 1,675,000,000 (1675 million) bark beetles.

Bark beetle trap statistics

Since 1984 pheromone traps have been installed in Switzerland, in order to control *Ips typographus*. In Figure 2 we show the estimated total number of beetles captured per year, and the mean number of captures per trap (data from the Forest Insect and Disease Survey FIDS of the Swiss Federal Research Institute WSL, Birmensdorf). After the storm "Vivian" of February 1990, the total number of captures increased drastically to a maximum of 137 million in 1992. The number of captures per trap has been growing during outbreaks, probably due to both the increase of the bark beetle population and the improvement of capture techniques. Between 1984 and 1999, a mean of 84.6 million bark beetles have been captured yearly; that is 6272 individuals per trap.

Efficiency of woodpeckers and traps in bark beetle control

Woodpeckers feed on both, bark beetle larvae and adults. Traps, however, only capture adult beetles. To capture an adult female means also to destroy its potential offspring, since this female will not breed any more. In order to compare the efficiency of woodpeckers and traps, respectively, we have thus to take into account the development stage of the captured item (larvae or adult) and also its sex. Traps capture both sexes in a proportion depending on season, outbreak or non-outbreak condition, etc. (B. Wermelinger, personal communication). The proportion of larvae and adult beetles in

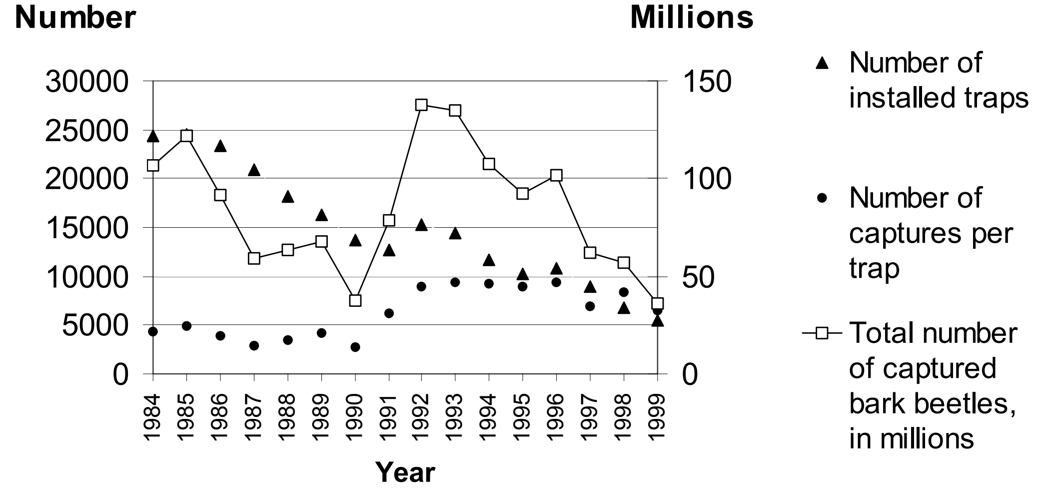

Fig. 2: *Number of installed bark beetle* Ips typographus *traps in Switzerland since 1984, number of captures per trap and total number of yearly captured beetles. After the storm "Vivian" of February 1990, an increase, both, of the total number of captured beetles and beetles per trap is visible. Data from the Forest Insect and Disease Survey FIDS of the Swiss Federal Research Institute WSL, Birmensdorf.*

the woodpecker diet may also vary. These varying conditions (male/female ratio for traps and larvae/adult ratio for woodpeckers) are taken into consideration by defining three different scenarios: low woodpecker efficiency, medium (realistic) woodpecker efficiency, and high woodpecker efficiency.

a) Low woodpecker efficiency scenario: In this scenario, the Three-toed Woodpecker feeds on 100 percent larvae (no adults) and the traps capture only females. The woodpecker completely avoids adult beetles, and in particular adult females. In its view, this scenario is pessimistic. Fayt (1999) for example reports a proportion of 40 percent adult beetles in the Three-toed Woodpecker's diet. In addition, it is not realistic that traps only capture females, since the used pheromone aggregations normally capture both sexes (B. Wermelinger, personal communication).

b) Medium (realistic) woodpecker efficiency scenario: The woodpecker feeds on 90 percent larvae, 5 percent adult females and 5 percent adult males. The traps capture 70 percent females and 30 percent males. This scenario is considered as the most realistic one. Weslien & Bylund (1988) report capture ratios of about 30 percent males. This corresponds to the observations of several authors mentioning a male proportion after hibernation of about 40 percent.

c) High woodpecker efficiency scenario: The woodpecker feeds on 50 percent larvae, 25 percent adult females and 25 percent adult males. The traps capture 80 percent males and 20 percent females. In the woodpecker's view, this scenario is very optimistic, since it is not probable that the traps only capture 20 percent females.

There are some common points in all three scenarios. The Three-toed Woodpecker's diet is based on 75 percent bark beetles and 25 percent other food. All captured or consumed adult beetle females are supposed to breed successfully, if they would not have been destroyed. According to Schmidt-Vogt (1989), the average number of eggs per female is supposed to be 40 and the average egg and larva mortality (without woodpecker predation) 60 percent (Balazy 1968). Thus, the results suggest production of 16 larvae per female.

We define the efficiency E as the number of destroyed bark beetles (adults plus larvae plus theoretical offspring of females). E_W is the efficiency of one woodpecker and E_T the efficiency of one trap. E_{Wtot} is the efficiency of the whole Swiss Three-toed Woodpecker population and E_{Ttot} the efficiency of all installed bark beetle traps in Swiss forests. The efficiency relation is defined as E_W / E_T and E_{Wtot} / E_{Ttot}. First, we calculated efficiency relations for the whole statistical period 1984 to 1999. Then the calculations were done for the endemic level (not outbreak situation) and for the epidemic level (outbreak situation). The endemic level is defined as years with < 1200 new beetle attacks of > 10 spruce trees, i.e. the years 1989-90 and 1998-99. The epidemic level is defined as years with > 3000 new beetle attacks of > 10 spruce trees, i.e. the years 1984-85 and 1992-96.

The results in Table 2 show that the efficiency relation in all tree scenarios is clearly in favour of woodpeckers. In the realistic scenario, one Three-toed Woodpecker is about 16 times more efficient than a trap. The whole woodpecker population is about 3 times more efficient than all installed traps together. In general, during the endemic level, the efficiency relation is higher than during the outbreak. In contrast to the traps that caught more beetles during the outbreak, the woodpecker in our scenario did not increase its bark beetle consumption, since its energetic requirements are not supposed to change.

Table 2: *Efficiency relation for bark beetle control of the Three-toed woodpecker compared to bark beetle traps. One woodpecker individual is compared with one trap, and the total Swiss woodpecker population with the total of installed traps in Swiss forests. The statistic period for bark beetle traps is from 1984 to 1999. L = larvae, F = females, M = males.*

Scenario *5)*	Consumed bark beetles by *Picoides tridactylus* during one year		Number of destroyed items *1)*		Captured beetles in traps during one season *2)*		Number of destroyed items		Efficiency relation	
	1 individual	whole pop. [Mio.]	E_W [Mio.]	E_{Wtot} [Mio.]	1 trap	all traps [Mio.]	E_T	E_{Ttot} [Mio.]	E_W / E_T	E_{Wtot} / E_{Ttot}
Whole statistic period 1984 – 1999 considered										
Low	670'000 L	1675 L	0.67	1675	6300 F	84.6 F	100'800	1354	**6.7**	**1.2**
Medium	603'000 L 33'500 F 33'500 M	1508 L 84 F 84 M	1.17	2936	4410 F 1890 M	59.2 F 25.4 M	72'450	973	**16.2**	**3.0**
High	335'000 L 167'000 F 167'000 M	838 L 419 F 419 M	3.18	7961	1260 F 5040 M	16.9 F 67.7 M	25'200	338	**126.3**	**23.6**
Endemic level *3)*										
Low	670'000 L	1675 L	0.67	1675	5400 F	49.4 F	86'400	790	**7.8**	**2.1**
Medium	603'000 L 33'500 F 33'500 M	1508 L 84 F 84 M	1.17	2936	3780 F 1620 M	34.6 F 14.8 M	62'100	568	**18.9**	**5.2**
High	335'000 L 167'000 F 167'000 M	838 L 419 F 419 M	3.18	7961	1080 F 4320 M	9.9 F 39.5 M	21'600	198	**147.3**	**40.2**
Epidemic level *4)*										
Low	670'000 L	1675 L	0.67	1675	7900 F	114.6 F	126'400	1834	**5.3**	**0.9**
Medium	603'000 L 33'500 F 33'500 M	1508 L 84 F 84 M	1.17	2936	5530 F 2370 M	80.2 F 34.4 M	90'900	1318	**12.9**	**2.2**
High	335'000 L 167'000 F 167'000 M	838 L 419 F 419 M	3.18	7961	1580 F 6320 M	22.9 F 91.7 M	31'600	458	**100.7**	**17.4**

1) Number of consumed / captured larvae plus adults plus theoretical offspring of 16 larvae per female with the assumption that all females would breed successfully, if they were not destroyed;

2) Average number of captured bark beetles by Swiss traps;

3) 1989 – 90 and 1998 – 99, that is years with < 1200 new beetle attacks of > 10 spruce trees;

4) 1984 – 85 and 1992 – 96, that is years with > 3000 new beetle attacks of > 10 spruce trees;

5) Scenario: low, medium and high woodpecker efficiency.

One reason for the high efficiency relation is the fact that woodpeckers consume bark beetles during the whole year, whereas traps work only during a relatively short period between spring and autumn. Several authors report up to 90 percent bark beetles in the woodpecker's diet (Hutchinson 1951 cited in Baldwin 1968, Hogstad 1970, Pechacek & Kristin 1993). We based our calculations on a 75 percent *Ips typographus* proportion, considering that the food could also contain other bark beetle species. It is indeed possible that during endemic bark beetle population levels the Three-toed Woodpecker switches over to other insect prey or other foods. However, data from the literature for the Three-toed Woodpecker's diet during endemic levels are still lacking.

We assumed that the destruction of females would have a strong negative impact on the bark beetle population and made no such assumption for the destruction of males. According to Schmidt-Vogt (1989), a new breeding tree is attacked in a proportion of 1 male to 2-3 females. Polygamy compensates for the high dispersal mortality of males. Even if males are captured in a high number, females are thus supposed to be able to find a polygamous male. The capture of females seems therefore to have a differential negative effect on breeding success.

Based on Thalenhorst (1958 cited in Schmidt-Vogt 1989) and Balazy (1968), we chose a mean egg and larva mortality of 60 percent (without woodpecker predation). In our calculations we assume that all females breed successfully, producing a surviving brood of 16 immature beetles. It is, however, probable that adult females are themselves subjected to mortality factors after flight and before breeding. In this case, the efficiency relationship would even be stressed in favour of the woodpeckers.

Three-toed Woodpeckers have been shown to destroy more bark beetles than their effective consumption. This happens as a consequence of the woodpecker removing bark and exposing numbers of brood to the external environment (Kroll & Fleet 1979). Fungi also invade galleries of bark beetles via openings created by woodpecker foraging.

Considering these arguments, we conclude that Three-toed Woodpeckers are more efficient in bark beetle control than traps. They should be considered as an important natural alternative to bark beetle control by traps.

3.2. How many declining and dead trees are required by the Three-toed Woodpecker?

A forest manager could decide to favour Three-toed Woodpeckers as an alternative to bark beetle control by traps. In this case, he should know which are the important habitat features for this bird. In this study we considered food as the limiting and thus the most important factor. Management decisions influence the availability of declining and dead trees, i.e. the woodpecker's foraging substrate. It is therefore important to determine the necessary density of foraging substrate to guarantee enough food, in particular during endemic bark beetle levels.

Estimation of the model variables

a) Density of potential foraging substrate DFS

As a specialist feeding on spruce bark beetles, the Three-toed Woodpecker strongly selects spruce trees as its foraging substrate (97.5% in Hess 1983, 97.8% in Hogstad 1970, 93.2% in Murphy & Lehnhausen 1998, 88.8% in Pechacek 1995). In concert with the habitat of its preferred prey, this woodpecker forages on declining, dying, and recently dead trees (all three categories 95.5% in Hess (1983) and 97% in Hogstad (1970)). The diameter at breast height of its foraging substrate was > 15 cm in Norway forests (Hogstad 1978), whereas in Alpine forests it was > 40 cm (Hess 1983). In Alaska's boreal forests the mean diameter was 34.6 cm for females and 42.4 cm for males (Murphy & Lehnhausen 1998).

Our aerial photo interpretation suggested that 95% of the detected snags had a breast height diameter ≥ 21 cm (n = 501). According to the literature, smaller trees that were not detected by our method are hardly used by this woodpecker. Field data compared with aerial photo data revealed an underestimation of about 20 percent of the real snag density (≥ 21 cm d.b.h.). This error is due to snags that were not visible on the aerial photo for several reasons (shadow, understory tree, broken tree, etc.). This error of 20 percent was taken into account to calculate the snag density (Table 3).

Snags whose stage of decomposition is ≤ 2 can be considered as potential foraging substrate. The decomposition stage frequency distribution (Figure 3) shows a similar pattern for all study sites with 58 to 94 percent of the snags belonging to stages 1 and 2.

Table 3: *Density of potential foraging substrates, calculated by multiplying the total snag density of the forest landscape (including not forested areas) with the percentage of snags belonging to the snag decomposition stages 1 and 2 (declining, recently dead and loose bark) that are suitable foraging substrates for Three-toed woodpeckers because of their potential presence of bark beetles. The snag density of the forest area is also indicated.*

Study site	Snags in decomposition stages 1 and 2 [2)] [%]	Total snag density Landscape [3)] [number per ha]	DFS Landscape [4)] [number per ha]	Total snag density forest area [5)] [number per ha]
Hobacher	69	4.7	3.2	7.1
Hinteregg	84	8.9	7.5	11.2
Hinterberg	94	2.3	1.9	2.9
Bärenegg	82	7.1	5.8	10.7
Langenegg [1)]	87	1.6	1.4	1.5
Mont Pelé [1)]	58	1.8	1.1	1.9

[1)] Site without Three-toed woodpeckers

[2)] Field data

[3)] Aerial photo data calculated for the forest landscape, i.e. including pastures, meadows, etc.

[4)] Aerial photo data combined with field data

[5)] Aerial photo data calculated for the forest area only (without pastures, meadows, etc.)

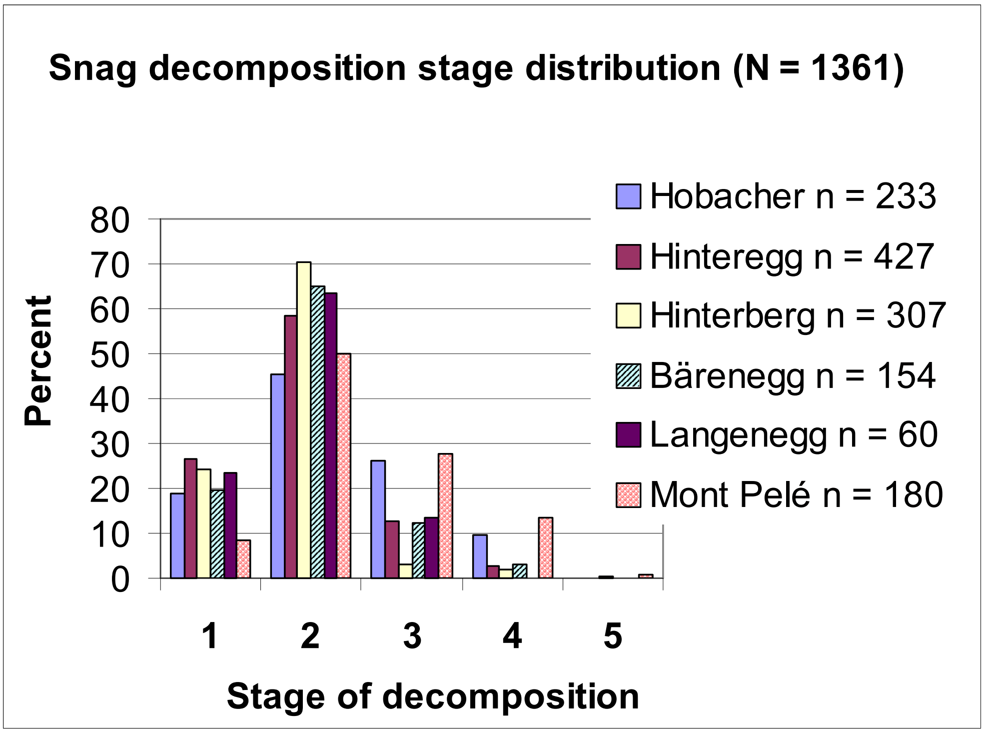

Fig. 3: *Percentage of snags in different stages of decomposition: 1: declining or recently dead, 2: loose bark, 3: clean and hard snag, 4: clean and soft snag, 5: broken, decomposed snag.*

$$\text{We define: DFS} = (S_1 + S_2) * A^{-1}$$

where S_1 = number of snags belonging to decomposition stage 1

S_2 = number of snags belonging to decomposition stage 2

A = total area (in hectares) of the study site (including not forested areas)

The resulting DFS for our study sites are shown in Table 3.

b) Mean infested bark area MIA

There exist only few literature data on the proportion of bark area that is infested by spruce bark beetles (Gonzalez et al. 1996, Weslien 1994, Weslien & Regnander 1990). The mean d.b.h. of the potential foraging substrates (trees with a d.b.h. $\geq$ 21 cm) in our study sites was 35 ± 13 cm (S.D.). During an epidemic level Gonzalez et al. (1996) found a MIA of 21 m^2 for spruce trees with a mean d.b.h. of 46 ± 5 cm. Weslien & Regnander (1990) indicate in endemic populations attacks of 50 percent of the tree height for spruce trees with a mean d.b.h. of 30 cm. Based on these authors, we assume the MIA for an endemic level in our study sites was 12.5 m^2.

c) Available prey APR

As it is shown by literature data, the breeding density of *Ips typographus* is highly variable within a tree, between trees, and in different bark beetle population levels (endemic to epidemic). We had to estimate an annual mean APR for an endemic breeding density. First, we calculated the APR for each week by multiplying the bark beetle attack density by the mean number of eggs per female and by a mortality factor for eggs, larvae, pupae, imagos, and immature beetles, respectively. The annual mean APR was then obtained by adding the weekly APR values and dividing by 52. For sub-alpine mountain forests, we expect only one beetle generation per season and set the egg laying to the second week of June (Nierhaus-Wunderwald 1995). Figure 4 shows the estimated weekly APR values based on the following assumptions:

With an attack density of 150 nuptial chambers m^{-2} (Weslien & Regnander 1990) we expect an average of 27 eggs per nuptial chamber (Thalenhorst 1958 cited in Schmidt-Vogt 1989). According to Balazy (1968) and Thalenhorst, the expected mortality is 25% for eggs, 45% for larvae and 15% for pupae and imagos. (The mortality caused by the Three-toed Woodpecker itself is taken into account.) During maturate feeding, hibernating, flight, and invasion on new trees, another mortality of half of the individuals that reached full development is expected.

The estimated annual mean APR value is 657 m^{-2}.

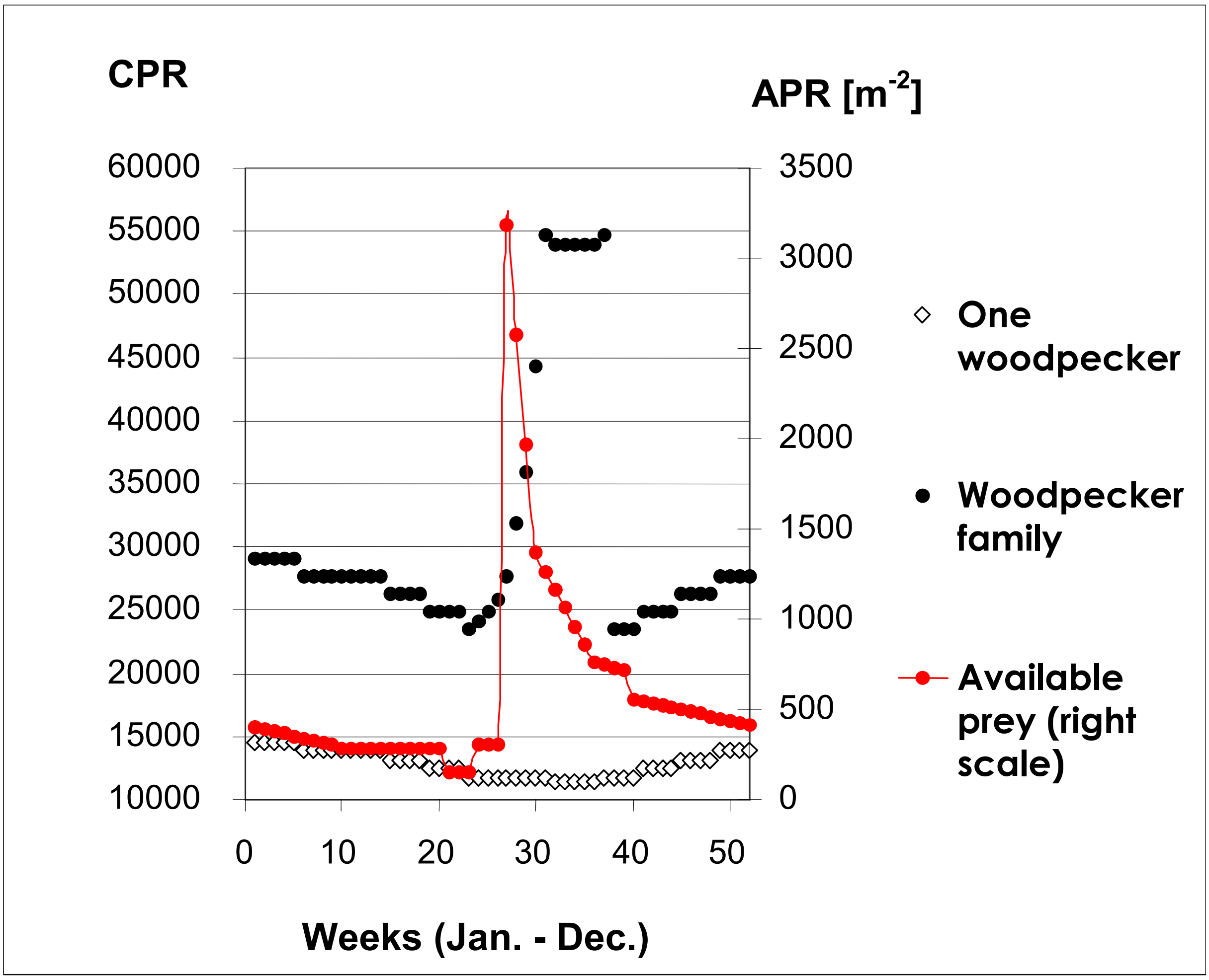

Fig. 4: *Estimated number of weekly consumed Ips typographus items by one Three-toed Woodpecker and a woodpecker family, respectively. Estimated available Ips typographus items per m^2 bark (all development stages without eggs) for an attack density of 150 nuptial chambers per m^2 (endemic level) and 27 eggs per nuptial chamber. CPR = consumed prey items during one week, APR m^{-2} = available prey items per m^2 of bark.*

d) Foraging efficiency FEF

Even if virtually scaling the tree, the woodpecker will not discover one hundred percent of the available prey. Removed bark chips falling to the ground may contain bark beetles or larvae that are not consumed. When the bark beetle breeding density is low, the woodpecker may decide not to inspect any parts of a tree. Capture rates of an insect species vary seasonally in relation to weather and other factors (Wolda 1990). Based on Baldwin (1968), a reasonable assumption for a mean FEF is 50 percent.

e) Consumed prey CPR

We calculated the CPR (i.e. adult bark beetles and their larvae) for one woodpecker during a year (see above). Our PHR-model is defined for a woodpecker breeding pair. Therefore, we have to calculate the CPR for two adult woodpeckers (male and female) and their young. The CPR for an adult woodpecker is obtained by dividing its daily energy requirement (according to Koplin 1972) by the energy content of one bark beetle (larva or adult) and multiplying by the proportion of bark beetles in the diet of an adult woodpecker. For a young woodpecker (nestling, fledgling and until its departure from its parents' home range), the daily CPR is calculated as follows: 0.7 * bird weight * proportion of bark beetles in the bird's diet * (fresh weight of a larva or an adult bark beetle (13.7 mg, both assumed to be equal))$^{-1}$.

Table 4: *Assumed change of the diet of young Three-toed Woodpeckers until their departure from their parents' home range.*

Week	Bird weight (g)	Assumed percent of bark beetles in the bird's diet	Estimated number of consumed bark beetles per bird per day	Estimated number of consumed bark beetles per week by 1.8 young birds
1.	20	5.8	59	743
2.	50	5.8	148	1865
3.	65	5.8	193	2432
4.	65	10	332	4183
5.	65	20	664	8366
6.	65	30	996	12'550
7.	65	50	1661	20'929
8. – 14.	65	75	2491	31'387
Departure of the young birds				Total: 270'777

According to Glutz von Blotzheim (1994), the mean breeding success of Three-toed Woodpeckers is 1.8 young birds. During the nestling period, only about 5.8 percent of the diet is comprised of Scolytidae and *Ips typographus* larvae (Pechacek & Kristin 1996). We hypothesise that the diet gradually changes up to a 75% proportion of bark beetles until the departure of the young from their parents' home range (Table 4). The estimated annual CPR of a woodpecker family is about 1.61 million beetles (Tables 1 and 4).

Validation of the model

The PHR-model is validated against literature home range sizes. The European *Picoides tridactylus* home range sizes reported in the literature vary between 44 and 176 ha (Bürkli et al. 1975, Dorka 1996, Hess 1983, Pechacek 1995, Pechacek et al. 1999, Ruge et al. 1999, Scherzinger 1982).

For our study sites we get the following PHR:

Hobacher: $\text{PHR} = (3.2\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.615 * 10^6 = 123\ \text{ha}$

Hinteregg: $\text{PHR} = (7.5\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.615 * 10^6 = 52\ \text{ha}$

Hinterberg: $\text{PHR} = (2.2\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.615 * 10^6 = 179\ \text{ha}$

Bärenegg: $\text{PHR} = (5.8\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.621 * 10^6 = 68\ \text{ha}$

Langenegg: $\text{PHR} = (1.4\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.621 * 10^6 = 282\ \text{ha}$

Mont Pelé: $\text{PHR} = (1.1\ \text{ha}^{-1} * 657\ \text{m}^{-2} * 0.5 * 12.5\ \text{m}^2)^{-1} * 1.607 * 10^6 = 356\ \text{ha}$

The first four calculated PHR (sites with a Three-toed Woodpecker breeding pair) lie roughly within observed home range sizes (Hinterberg slightly higher). The other PHR (sites without breeding pairs) far exceed observed home range sizes. We cannot exclude the existence of such large home ranges. The energy expenditure for a breeding pair to move around in such a large home range, however, would probably be too high. These first validation results suggest that the model describes our study sites quite well.

Estimation of the snag density required to meet the Three-toed Woodpecker's foraging needs

Our validated PHR model is now used in order to find a response to the question: How many declining and dead spruce trees per ha are required to meet the *Picoides tridactylus'* foraging needs?

We use the same equation, solved for DFS: $DFS = (PHR * APR * FEF * MIA)^{-1} * CPR$

We hypothesise that during bark beetle outbreaks, the woodpecker is not subjected to a scarcity of food. In contrast, during endemic bark beetle population levels, it may have difficulty in satisfying its foraging needs. It is important that forest management maintains sufficient habitat features, i.e. potential foraging substrate, during endemic bark beetle population levels, too. For variables related to bark beetle infestation (APR, MIA), we therefore chose probability distributions whose mean values describe an endemic bark beetle population level (Table 5). For variables assumed to be normally distributed, we chose relevant limits in a way to get 95 percent of the values within those limits and then calculated the corresponding standard deviations.

Table 5: *Probability distribution functions chosen for the variables in the model used to estimate the snag density required to meet the Three-toed woodpecker's foraging needs.*

Variable [unit]	**Type of distribution**	x_{min} / x_{max}	μ / σ [1)]	x_a / x_b [2)]
PHR [ha]	uniform	44 / 176		
APR	normal		657 / ± 216	234 / 1080
FEF	normal		0.5 / ± 0.1	0.25 / 0.75
MIA [m^2]	normal		12.5 / ± 3.8	5 / 20
CPR	uniform	$1.605*10^6$ / $1.623*10^6$		

1) μ = mean; σ = std dev.

2) $Pr(x_a < Z < x_b) = 95\ \%$

After sampling of each variable (n = 10,000) the output probability distribution for DFS was simulated by a Monte Carlo approach. The results presented in Figure 5 are based on 10 simulations. The snag density is DFS/0.8, i.e. DFS divided by the mean value (for our study sites) of snags in decomposition stages 1 and 2 (see Table 3). The resulting snag density values are related to the forest area. The expected mean value is 7.5 ± 0.24

snags/ha (mean and S.E.). With ≥ 5 snags/ha (d.b.h. ≥ 21 cm), the probability to provide sufficient foraging substrate is 50 percent. In order to attain a 90 percent probability, ≥ 14 snags/ha are necessary, and > 19 snags/ha for a 95 percent probability. Expressed as basal area (m^2/ha) or volume (m^3/ha), the snags ≥ 21 cm d.b.h. have to represent > 0.5 m^2/ha and > 4.3 m^3/ha ($p = 0.5$), > 1.3 m^2/ha and > 12.0 m^3/ha ($p = 0.9$) and > 1.8 m^2/ha and > 16.3 m^3/ha ($p = 0.95$).

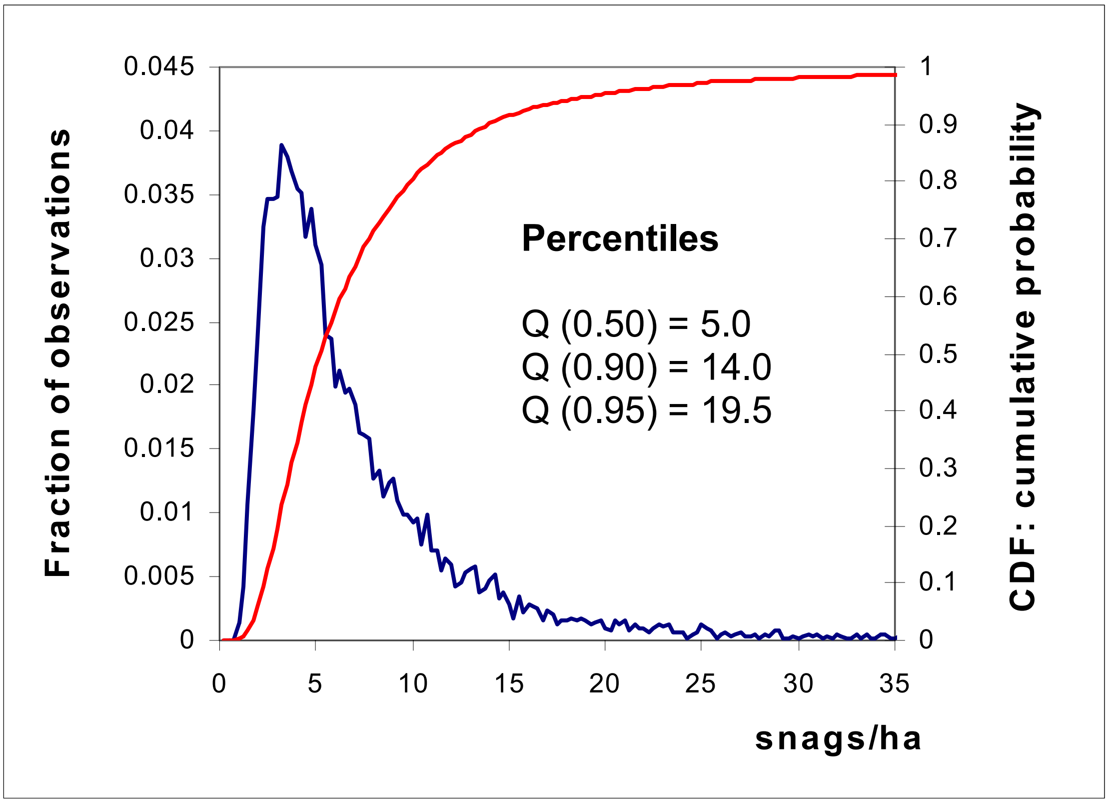

Fig. 5: *Simulated probability distribution function of the snag density required to meet the Three-toed Woodpecker's foraging needs and required snag densities for different probability levels. CDF = Cumulative distribution function. The input model is DFS = (PHR * APR * FEF * MIA)*$^{-1}$ ** CPR.*

DFS = density of potential foraging substrates [number ha^{-1}*], PHR = potential home range size needed by a woodpecker breeding pair [ha], APR = available prey under 1 m*^{2} *of bark [number m*$^{-2}$*], FEF = foraging efficiency of the woodpecker [percent], MIA = mean infested bark area of a potential foraging substrate [m*^{2}*], CPR = consumed prey items by a woodpecker family during a time unit [number].*

With their current snag densities (Table 3) our study sites without woodpecker breeding pairs present only a rather low chance for woodpecker settling (sites with woodpeckers: Hobacher 7.1 snags/ha ($p = 0.65$), Hinteregg 11.2 snags/ha ($p = 0.84$), Hinterberg 2.9 snags/ha ($p = 0.18$), Bärenegg 10.7 snags/ha ($p = 0.83$); sites without woodpeckers: Langenegg 1.5 snags/ha ($p = 0.02$), Mont Pelé 1.9 snags ($p = 0.04$)).

A recommendation for forest management can, for example, be based on a $p = 0.9$ level. Comparisons with recommendations for other cavity nesting birds from literature data are not easy, due to differences in considered minimal tree diameter, decomposition stages, tree species, forest type, age, and structure, etc.

Limitations of the model

The model presented in this paper is a simple and theoretical model intended as being a first approach to answer the question: How many declining and dead spruce trees per ha are required to meet *Picoides tridactylus'* foraging needs? Some limitations of the present model are discussed here in order to show how it could be improved in a next step.

i) At present, this model is mainly based on literature data. Measuring bark beetle breeding density, infested bark area and Three-toed Woodpecker home range sizes in our study sites during endemic bark beetle levels could be a further validation step. Indeed, only few bark beetle studies have been conducted on endemic populations. Most studies report outbreak conditions. Our assumptions for the Three-toed Woodpecker's diet are based on the available literature results, essentially obtained during outbreaks (Pechacek, personal communication). The bark beetle proportion in the woodpecker's diet during endemic levels could be lower than in cited literature. If future research findings indicate that other insect groups are important prey for the Three-toed Woodpecker, they will have to be integrated into the presented model.

ii) The uncertainty of values for the variables MIA and FEF is rather high, since literature data on these topics are still scarce.

iii) Another limitation is the validity of Koplin's model (1972), developed for American Three-toed Woodpeckers and not for European populations.

iv) Validation was done for six study sites. It should be repeated for other sites, if possible in different Alpine regions with spruce mountain forests.

v) It is hardly possible by aerial photo interpretation to detect a tree that is freshly attacked by bark beetles (just before decomposition stage 1). Needle loss or other stress symptoms appear slightly later. To handle with this problem, we considered spruce trees with bark loss (decomposition stage 2) as potential foraging substrate, although such trees are probably not inhabited by bark beetles any more. We argue that these trees could have been bark beetle breeding trees some time ago. Breeding trees, being continuously created in a dynamic forest ecosystem, this time-related delayed snag inventory can be justified. It was therefore important to choose study sites where the state of presence and absence of Three-toed Woodpeckers has been constant for some years.

4. Conclusion

By our comparison of bark beetle *Ips typographus* trap statistics for Switzerland with the energetic requirements and the resulting bark beetle consumption of Three-toed Woodpeckers, we demonstrated that woodpeckers capture more insects than traps. These birds could therefore be an important alternative to bark beetle control by traps. In addition to their role as natural agents against bark beetles, they are considered to be indicators for forest bird diversity (Mikusinski et al. 2001) and natural forests (Amcoff & Eriksson 1996, Angelstam & Mikusinski 1994, Derleth et al. 2000). Removing of infected, declining and dead trees from the forest is not always cost-effective. Apart from this drawback, this management practice is also detrimental to many other dead wood dependent species (Samuelsson et al. 1994). By the potential economic benefit that the presence of Three-toed Woodpeckers instead of traps may induce, this species demonstrates that biodiversity and economic forestry can be complementary goals.

Nature protection organisations often call for more dead wood in managed forests. Due to the lack of scientific information, it is, however, difficult to give quantitative targets. Dead wood quantification is only a recent research field in ecology. Our study is an attempt to give quantitative management recommendations for snag retention in spruce forests. Even if the developed model is mainly literature based and needs some further validation, we can already use it to derive some provisional management recommendations. Based on our preliminary simulation results, we recommend the retention of a mean of > 14 declining or dead spruce trees per hectare (d.b.h. $\geq$ 21 cm) over about 200 hectares (home range of a Three-toed Woodpecker breeding pair), in order to create favourable habitat features for this species. This value corresponds to a basal area of > 1.3 m^2/ha and a volume of > 12 m^3/ha (d.b.h. $\geq$ 21 cm). Forests with such snag levels should be distributed patchily within the landscape. The closer the patches, the higher the Three-toed Woodpecker population density may become (examples presented in Scherzinger (1982)). A snag management following our recommendations also favours many other dead-wood-dependent species (fungi, mosses, lichens, invertebrates, secondary cavity nesting animals, etc.). During all decomposition stages from a hard towards a soft snag and, after falling down, as a log, a dead tree plays an important ecological role.

Acknowledgements

The authors thank I. Iorgulescu, J.-J. Sauvain, B. Frochot, and J.A. Jackson for several suggestions that have substantially improved this paper.

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Paper III

Dead wood threshold values for the Three-toed Woodpecker in boreal and sub-Alpine forest

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submitted to: Conservation Biology

Abstract

Predicting species' responses to habitat loss is a significant challenge facing conservation biologists. We examined the response of the Three-toed Woodpecker *Picoides tridactylus* to different amounts of dead wood, one of the most important habitat features of old-growth forests. We studied the dependence between two Palearctic subspecies of this woodpecker (*P. tr. tridactylus* and *P. tr. alpinus*) and dead wood in a boreal and a sub-Alpine coniferous forest landscape in central Sweden and Switzerland, respectively. Habitat variables were measured by fieldwork in forests with breeding woodpeckers ($n = 10+12$) and in control forests without breeding woodpeckers ($n = 10+12$) in the same landscape. Logistic regression analyses revealed steep thresholds for the amounts of dead standing trees and the probability of Three-toed Woodpecker presence in both Sweden and Switzerland. The probability of the presence of Three-toed Woodpeckers increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m^{2} ha^{-1} in Switzerland and from 0.3 to 0.5 m^{2} ha^{-1} in central Sweden. In Switzerland, a high road network density negatively affected the presence of woodpeckers ($r = -0.65$, $p = 0.0007$).

The higher volumes of dead wood in Switzerland, where population trends are more positive, than in central Sweden, where the population is declining, would suggest that the volumes of dead wood in managed forests in Sweden are too low to sustain Three-toed Woodpeckers in the long-term. In terms of management implications, we suggest a quantitative target of at least 5% of standing trees in older forests being dead over at least 100 ha large forest areas. This corresponds about to ≥ 1.3 m^2 ha^{-1} (basal area) or ≥ 15 m^3 ha^{-1} (volume), still depending on site productivity.

Keywords: *Picoides tridactylus*, habitat thresholds, dead wood, forest management, biodiversity conservation

1. Introduction

Loss of habitat is the major reason for local extirpation and, ultimately, the extinction of species. While habitat loss is often a continuous change in the process of habitat fragmentation in ecological systems, the response of different components of ecosystem integrity to habitat loss may be non-linear (Fahrig 2001; Muradian 2001). Both models and empirical studies have demonstrated the existence of ecological thresholds of habitat proportions for different species at the landscape scale (e.g., Andren 1994; Jansson & Angelstam 1999; With & Crist 1995; Fahrig 2001). Thus, an answer to the question “How much habitat is enough?”, or in other words knowledge of ecological thresholds for the amount of habitat area or habitat features required at different ecological scales, is necessary to prevent further local and regional loss of species (Fahrig 2001). Consequently, ecological thresholds are a key feature that should be taken into consideration (Muradian 2001; Simberloff 1995; With & Crist 1995) in the context of forest biodiversity maintenance, both by nature conservation *per se*, and by sustainable forest management and forest certification processes.

The usefulness of keystone species (Paine 1966) and umbrella species (Fleishman et al. 2001; Fleishman et al. 2000) for biodiversity conservation is gaining increasing acceptance among ecologists and conservation biologists (Simberloff 1999; Roberge & Angelstam in press). Among vertebrates, woodpecker species are a particularly interesting group to be studied with respect to non-linear responses to habitat loss. They are of special importance due to their key-stone role in supplying forests with tree-cavities, that serve secondary users as nesting or roosting holes (Saari & Mikusinski 1996). Moreover, among area-demanding species specialised in natural forest components such as old trees, dead wood and structural diversity (Angelstam 1990; Angelstam & Mikusinski 1994; Mikusinski & Angelstam 1997), they are also considered to be the most demanding guild in terms of their ecological requirements. Furthermore, a positive relationship has been reported between woodpecker species richness and the number of other forest species (Martikainen et al. 1998; Mikusinski et al. 2001).

In the case of conifer-dominated forests, the Three-toed Woodpecker is a potential umbrella species for which habitat threshold values could be developed (Angelstam 1998; Mikusinski et al. 2001; Nilsson et al. 2001; Angelstam et al. in press). Moreover, Imbeau (2001) defined the Three-toed Woodpecker as a keystone species (*sensu* Thompson and Angelstam (1999)). In addition to its qualities as a potential umbrella and keystone species, other reasons justify its suitability as an important candidate for the development of habitat threshold values for the purpose of forest biodiversity management. It is the only woodpecker occurring in both the New and the Old Worlds (Winkler et al. 1995), thus showing a large geographic distribution. Consequently, habitat threshold values translated into management recommendations could be applied over a wide geographic area. Moreover, Alpine populations are also sedentary in winter (Winkler et al. 1995), and Swedish populations mostly sedentary (Svensson et. al. 1999). Local reasons, such as forest management practices, must, therefore, be considered to explain population fluctuations. For example, the ongoing decline of populations in Fennoscandia is directly related to the modern forestry practice of removing old and dead trees (Angelstam & Mikusinski 1994; Nilsson 1992; Tucker & Heath 1994). Finally, Three-toed Woodpeckers are important predators of insects that are prone to outbreaks. Examples of these insects include *Polygraphus* and *Ips* in Eurasia and spruce bark beetle *Dendroctonus obesus* in America. Thanks to their ability to concentrate locally in burned sites or windfall areas (Koplin 1969; Murphy & Lehnhausen 1998), Three-toed Woodpeckers can be considered as natural agents against insect plagues (Bütler & Schlaepfer in press).

Three-toed Woodpeckers mainly feed on the larvae of scolytid beetles and other insects found in dying and dead trees (Fayt 1999; Murphy & Lehnhausen 1998; Pechacek & Kristin 1993) and, in spring, they occasionally lick sap from tree trunks in which they make small holes (Glutz von Blotzheim 1994; Pechacek 1995). Consequently, dead trees are one of the most important habitat features for foraging (Hess 1983; Hogstad 1970; Murphy & Lehnhausen 1998; Pechacek 1995; Ruge et al. 1999). Dead wood amounts in woodpecker habitats, however, have rarely been quantified (Derleth et al. 2000), and the existence of a dead wood threshold value for this species has never been tested using dead wood as a resource (but see Pakkala et al. 2002).

The aims of this study were to search for possible dead wood threshold values playing an important role in the local continued presence of Three-toed Woodpeckers in boreal and mountain forests, and to derive quantitative targets for management implications. We chose an original approach replicated in two different landscapes and with two palearctic subspecies *P.t.tridactylus* (in Northern Europe) and *P.t.alpinus* (in the mountains of Central, Southern and South-East Europe).

2. Material and methods

2.1. Study areas

We conducted our study in two coniferous forest regions, one located in central Sweden (SE) and one in Switzerland (CH) (Fig. 1). Whereas Norway spruce (*Picea abies*) is the main tree species in the Swiss sub-Alpine mountain forest landscape, the Swedish forest landscape is characterised by boreal forests dominated by a mixture of Scots pine (*Pinus sylvestris)* and Norway spruce. In order to take into account the heterogeneity arising from the topography of Swiss mountain regions, data was collected in three areas (Fig. 1) situated in the eastern/central and the western Lower Alps and in the Jura Mountains. In 1993 a small population of Three-toed Woodpeckers was detected the first time in the Swiss Jura (Chabloz & Wegmüller 1994), where the species was not present before. As the Swiss Three-toed Woodpecker population is obviously in expansion (Schmid et al. 1998), it seemed interesting to us to include such a newly colonised area. In contrast, boreal forests in central Sweden are homogenous and population trends are generally negative (BirdLife 2000). For this reason, there was no sub-division into different areas.

2.2. Study design

In each region pair-wise sampling units of 1 km squares were studied (10+10 units in Sweden and 12+12 in Switzerland). Each pair consisted of one unit where the Three-toed Woodpecker had been breeding (called “presence”) in the years of field work (1998 to 2001) and one randomly selected unit where it was not observed (called “absence”). In accordance with the criteria of probable breeding as defined in the International Onithological Atlases (Sharrock 1973), presence was indicated where nests were found or birds observed. The selection of presence/absence of breeding Three-toed Woodpeckers in the field units was based on data provided by the Swiss ornithological station (Sempach) and by local amateur ornithologists in Switzerland and Sweden. In Switzerland, the study areas were located at altitudes between 1200 and 1700 m a.s.l. and in Sweden between 100 and 300 m a.s.l.

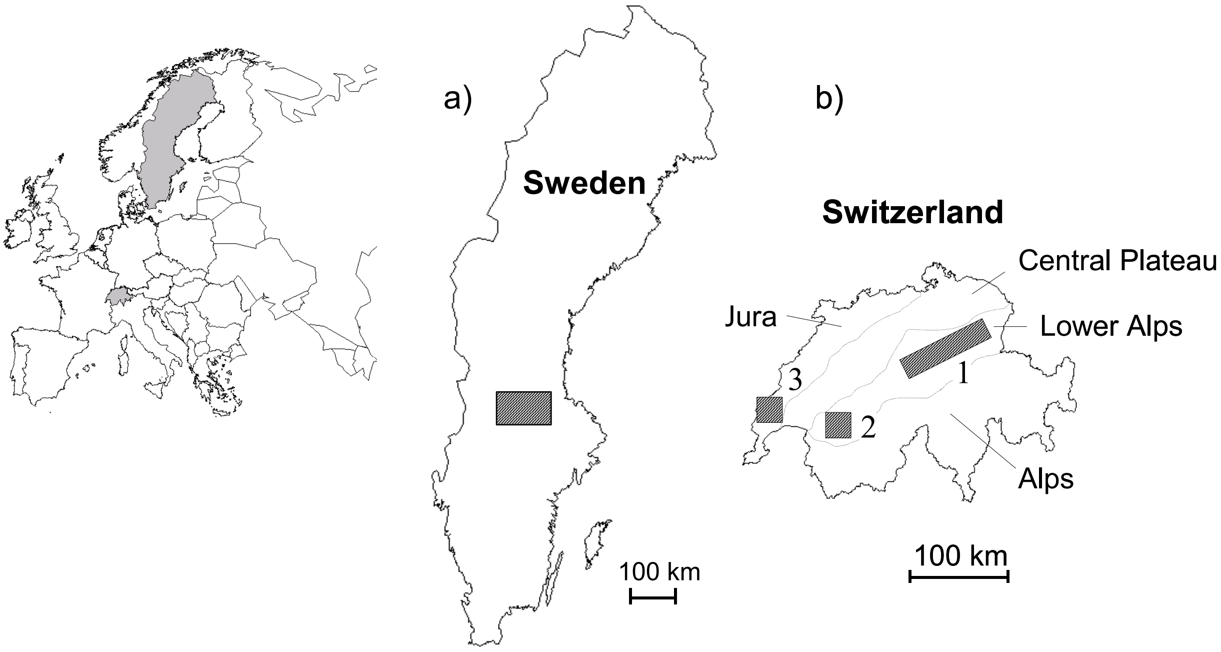

Fig. 1: *Study sites:* ***a)*** *a boreal landscape located in central Sweden and* ***b)*** *a Swiss sub-Alpine landscape, sub-divided into three areas, situated in the eastern/central (1) and western Lower Alps (2) and in the Jura Mountains (3).*

2.3. Data gathering

In each 1 sq. km sampling unit a total of 16 systematically placed sampling plots were used to sample the amount of dead wood. The distance between sampling plots was 250 m. Four types of variables were defined (Table 1). Measurements of the basal area of trees were made using a relascope. A snag was defined as any standing dead tree with a minimal height of 1.7 m. The minimal diameter for recording snags, logs (laying dead trees) and living trees was 10 cm dbh., and the measurement unit was stand basal area (m^2 ha^{-1}). Slope and aspect were measured in degrees. Road/track density was the total length of roads and tracks in the field unit accessible by a tractor. Roads and tracks were measured using topographical maps. Harvesting intensity was defined as the density of tree stumps within the plot. It was classified in two categories: ≤ 3 stumps per plot (extensive harvesting) and ≥ 10 (intensive harvesting). Harvesting time was also a dichotomous variable used to date the harvesting period into recent (tree stumps are hard, uncovered by mosses or vegetation) or past (tree stumps are soft or decomposed and/or covered by mosses or vegetation). A plot could, therefore, present both recent and past harvesting.

Table 1: *Measured variables in 1x1 km field units (n = 12+12 in Switzerland (CH) and n = 10+10 in central Sweden (SE)), in which the Three-toed Woodpecker was present and absent, respectively. Each field unit contained 16 systematic sampling plots.*

Type	**Variable**	**Unit**	**Type of measure**	**Level**	**Landscape**
Habitat features	Snags	m^2 ha^{-1}	Relascope	Plot	CH / SE
	Logs	m^2 ha^{-1}	Relascope	Plot	CH / SE
	Living trees	m^2 ha^{-1}	Relascope	Plot	CH / SE
	Spruce trees	% of living trees	Relascope	Plot	CH / SE
	Pine trees	% of living trees	Relascope	Plot	SE
	Deciduous trees	% of living trees	Relascope	Plot	SE
	Tree height	m	Heightmeter	Plot	CH / SE
Topography	Slope	degrees	Clinometer	Plot	CH
	Aspect	degrees (0 –360°)	Compass	Plot	CH
Management	Road/track density	km km^{-2}	Topographical maps	Field unit	CH / SE
	Intensive harvesting	% of occurrence	Visual appreciation	Field unit	CH / SE
	Extensive harvesting	% of occurrence	Visual appreciation	Field unit	CH / SE
	Recent harvesting	% of occurrence	Visual appreciation	Field unit	CH / SE
	Past harvesting	% of occurrence	Visual appreciation	Field unit	CH / SE
Continuity	Snags with bark	% of occurrence	Visual appreciation	Field unit	CH / SE
	Snags without bark	% of occurrence	Visual appreciation	Field unit	CH / SE
	Hard logs	% of occurrence	Visual appreciation	Field unit	CH / SE
	Soft logs	% of occurrence	Visual appreciation	Field unit	CH / SE
	Ringed trees	Number, age	Visual appreciation	Field unit	CH / SE

Ringed trees are trees having small holes made in the bark by woodpeckers (and in particular by Three-toed Woodpeckers), typically distributed as horizontal lines on the trunk (Glutz von Blotzheim 1994; Ruge 1968; Scherzinger 1982). The total number of ringed trees in the 1 km squares was counted by walking on transect lines between the plots (total distance 6 km per sampling unit), and their approximate age determined using the following categories: i) fresh signs (transparent, sticky and flowing resin in the holes); ii) quite fresh signs (white or yellow resin not flowing any more); iii) old signs (no resin, only small holes); iv) signs of long use (the tree has formed bulges). Because two different persons did the fieldwork in Switzerland and Sweden, we estimated the between-person difference of basal area measurement. This estimation was based on data from 209 plots, measured twice separately by two different persons.

2.4. Statistical analyses

For the statistical analyses we used STATISTICA 6.0® statistical software. The analyses were carried out separately for Switzerland and Sweden, except for ringed trees, where all data were merged. For dichotomous variables (i.e. intensive/extensive harvesting, recent/past harvesting, snags with/without bark, hard/soft logs; cf. Table 1), we calculated the proportion of sampling plots per field unit where the observed characteristic occurred. For each 1 sq. km sampling unit, we calculated mean values for all variables measured in the sampling plots. The field units were then separated into two groups (woodpecker forests and control forests, i.e. without woodpeckers) and group means and ranges were calculated for all variables. The continuous variable aspect was transformed into a categorical variable (eight categories of 45 degrees from 0 to 360 degrees), and a Chi-square goodness-of-fit test was conducted on plot data frequency distribution (n = 192 for presence and n = 192 for absence plots) to test for differences between groups (Zar 1999).

Because of the binary nature of the response variable for the Three-toed Woodpecker ("presence" and "absence", coded as 1 and 0), logistic regression (Hosmer & Lemeshow 1989) was chosen as the appropriate method to evaluate the existence of dead wood threshold values. Following Hosmer and Lemeshow (1989), the potential predictor variables were first assessed for significance in a univariate analysis by a pair-wise two-sample t-test. Thus, variables in percentages (cf. Table 2) were arcsine square-root transformed in order to normalise the data distribution (Zar 1999).

A correlation matrix was calculated between all significant independent variables to examine possible co-linearity. After this we calculated univariate logistic regression models. The resulting models were assessed using goodness-of-fit based on maximum likelihood estimates, and the overall rate of correct classification of the response variable (“presence” and “absence”). For the regression models for snag basal area, we calculated the first derivative function to compare the steepness of the slopes between the models for Sweden and Switzerland. The x-values of the inflexion points of the two models were tested for statistical difference at a level of $\alpha = 0.01$ by calculating its standard errors.

To enable comparison with other studies reporting dead wood amounts in forest stands, which are usually expressed as volume per hectare (m^3 ha^{-1}), we also calculated the dead wood volumes (V) by a formula: V = basal area * tree height * shape index (correction factor for tree shape of trees estimated as the ratio between the actual volume of the cone-shaped tree and an assumed cylinder with constant diameter corresponding to the basal area at breast-height) (Anonymous 1982:213). While shape indices range from 0.55 to 0.75 in well-managed forests, to be conservative, we used a shape index of 0.5. This means that our volume estimates are in the low range.

3. Results

3.1. Factors explaining the presence/absence of the Three-toed Woodpecker

For Switzerland:

A strong positive linear relationship existed between the amounts of logs and snags ($r = 0.86$, $t = 8.01$, $p = 0.0000$, $n = 24$). Snag and log amounts differed significantly between woodpecker forests and control forests (Table 2). The basal area of snags was more than five times higher in woodpecker forests than in control forests, whereas the basal area of logs was more than three times higher. The proportion of snags compared to all standing trunks was significantly higher in woodpecker forests (presence: 8.3 ± 1.5 %; absence: 1.3 ± 0.2 %; mean ± SE; Fig. 2). Tree height and the percentage of spruce trees did not differ in the two groups. The basal area of living trees was lower in woodpecker forests.

Table 2: *Variable means and ranges for the 1x1 km field units in which the Three-toed Woodpecker was present and absent, respectively. Highly significant p-values ($p \leq 0.01$) in bold. n.d.: no data collected.*

Variable	Presence mean (range) n = 12	Absence mean (range) n = 12	t-statistics		Presence mean (range) n = 10	Absence mean (range) n = 10	t-statistics	
			t	p			t	p
Habitat features [unit]		**Switzerland**				**Sweden**		
Snags [m^2 ha^{-1}]	2.3 (0.6-6.0)	0.4 (0.0-0.8)	4.78	**0.0006**	0.8 (0.4-1.0)	0.2 (0.1-0.4)	7.07	**0.0001**
Logs [m^2 ha^{-1}]	2.2 (0.9-4.1)	0.6 (0.2-1.2)	6.23	**0.0001**	1.8 (0.9-2.9)	0.8 (0.4-1.1)	5.59	**0.0003**
Living trees [m^2 ha^{-1}]	25.6 (17-38)	30.4 (19-39)	-2.54	0.0273	15.0 (11-18)	12.1 (7-16)	2.42	0.0386
Spruce [%]	91 (81-95)	86 (78-95)	2.02	0.0683	45 (30-67)	34 (14-59)	1.97	0.0805
Pine [%]	n.d.	n.d.	n.d.	n.d.	45 (30-65)	59 (29-86)	-2.68	0.0252
Deciduous [%]	n.d.	n.d.	n.d.	n.d.	11 (4-36)	7 (0-21)	1.38	0.2169
Tree height [m]	23 (19–26)	23 (19-27)	-0.24	0.8115	17 (14-23)	14 (10-16)	3.66	**0.0053**
Topography								
Slope [°]	21 (8-36)	13 (4-30)	2.45	0.0322	n.d.	n.d.	n.d.	-----
Management								
Road/track density [km km^{-2}]	1.8 (0.0-3.6)	5.3 (2.9-7.3)	- 7.32	**0.0000**	1.1 (0.0-2.1)	1.2 (0.0-2.9)	-0.46	0.6569
Intensive harvesting [%]	27 (0-50)	54 (13-94)	-2.42	0.0342	19 (0-44)	35 (19-50)	-2.61	0.0282
Extensive harvesting [%]	28 (6-63)	3 (0-13)	5.08	**0.0004**	69 (56-88)	68 (56-100)	-0.26	0.7975
Recent harvesting [%]	46 (19-88)	52 (19-81)	-0.58	0.5742	13 (0-31)	30 (0-56)	-2.17	0.0583
Past harvesting [%]	84 (56-100)	90 (69-100)	0.01	0.9908	75 (50-88)	78 (56-100)	-0.99	0.3472
Continuity								
Snags with bark [%]	69 (44-80)	30 (0-50)	6.25	**0.0001**	19 (0-38)	11 (0-19)	1.74	0.1164
Snags without bark [%]	23 (13-31)	7 (0-19)	5.55	**0.0002**	19 (0-31)	7 (0-19)	3.00	0.0149
Hard logs [%]	79 (56-94)	47 (19-69)	6.85	**0.0000**	53 (31-75)	26 (0-44)	3.61	**0.0057**
Soft logs [%]	37 (6-60)	15 (6-25)	5.19	**0.0003**	36 (25-50)	23 (13-38)	3.46	**0.0071**
Ringed trees [n]	9 (0-35)	1 (0-4)	2.36	0.0377	4 (0-16)	0 (0-0)	2.33	0.0450

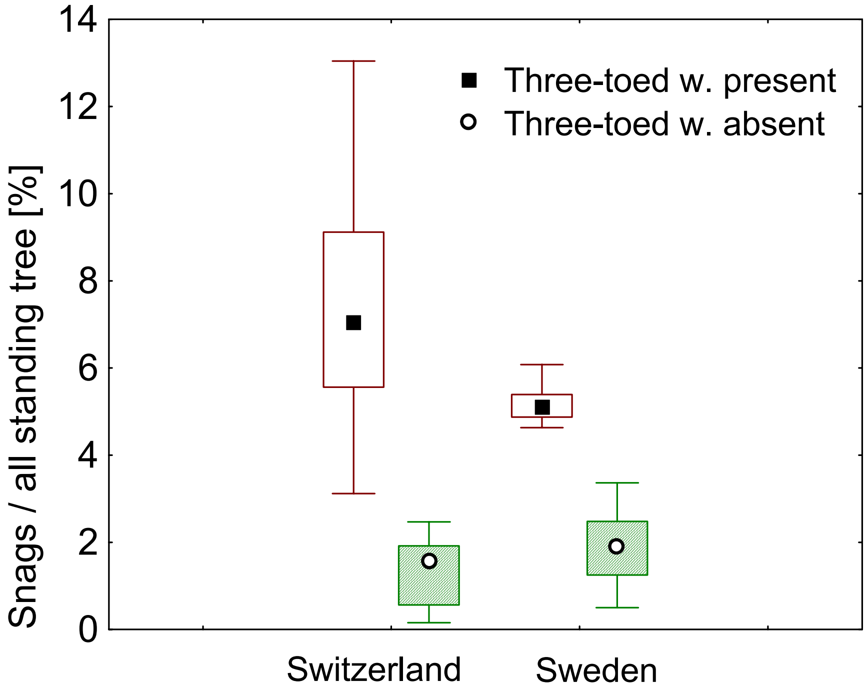

Fig. 2: *Box-plots for the basal area proportion of snags compared to all standing (living and dead) trunks, shown separately for forests with Three-toed Woodpeckers versus forests without this bird species. Box-plots represent median, 25, 75 percentiles, non-outlier min, non-outlier max. The two boxes on the left present data from Switzerland (distribution of mean values for field units of 1 square kilometre; n = 12 each, presence and absence) and the two boxes on the right present data from central Sweden (n = 10).*

The topographical situation was not identical in both groups. In woodpecker forests, the slope was steeper than in control forests, although the difference was not highly significant (Table 2). Woodpecker forests were more SE oriented than control forests, where the most frequent orientation was NW to NE (Chi-square = 82.30, df = 7, $p < 0.000$).

Extensive harvesting was significantly more frequent in woodpecker than in control forests (Table 2). The road/track density was three times higher in control forests than in the woodpecker forests. It negatively affected dead wood amounts (Fig. 3). A positive linear relationship existed between the variables extensive harvesting and snags ($r = 0.64$, $t = 3.93$, $p = 0.0007$, $n = 24$) and a negative relationship between road/track density and snags ($r = -0.64$, $t = 3.95$, $p = 0.0007$, $n = 24$). There was no difference in management history (i.e. recent/past harvesting) between the two groups.

Snags with or without bark and hard or soft logs (i.e. variables measuring the continuity over time of food resources) occurred more frequently in woodpecker forests than control forests (Table 2). These variables were positively correlated with the two quantitative variables snag and log basal area, as they described the quality of dead wood.

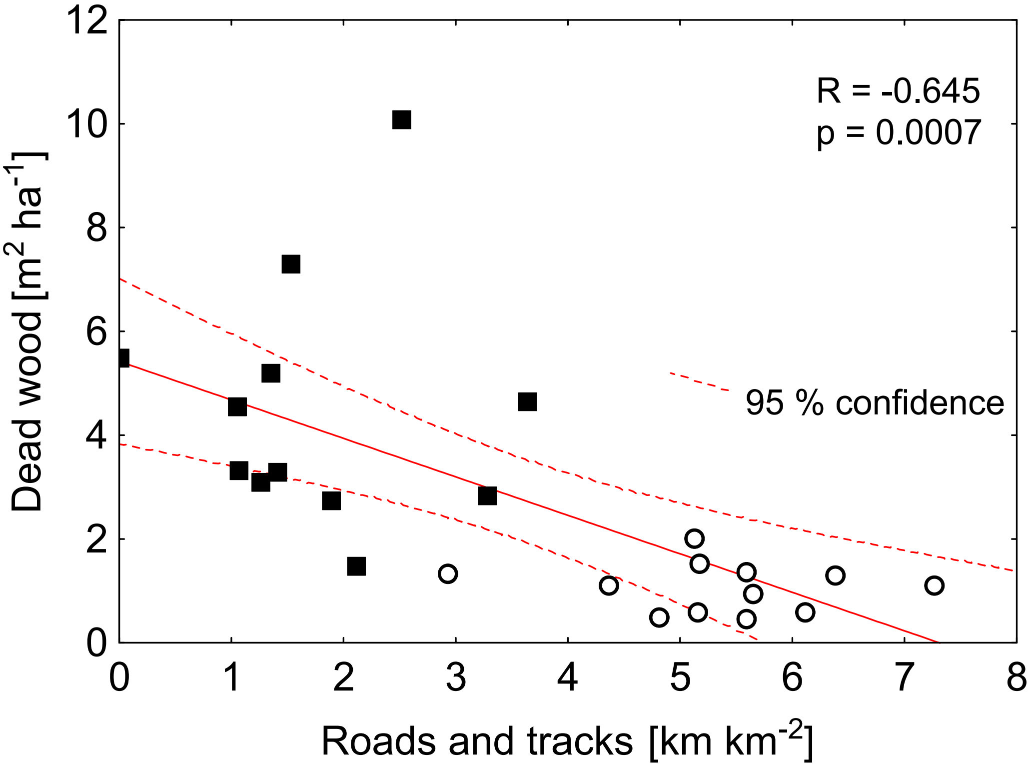

Fig. 3: *Negative linear correlation between dead wood amount and road network density for Switzerland. On the x-axis, the total length per square kilometre of roads and tracks suitable for trucks or tractors to convey harvested wood. On the y-axis the basal area of all standing and lying dead wood (minimal dbh 10 cm).*
Black squares: units with breeding Three-toed Woodpeckers; white circles: units without Three-toed Woodpeckers.

<u>For Sweden:</u>

In accordance with the results for Switzerland, snag and log basal area showed the most significant between-group differences for all measured habitat variables (Table 2). A strong positive linear relationship existed between log and snag basal area (r = 0.80, t = 5.58, p = 0.0000, n = 20). The basal area of snags was four times higher in woodpecker forests compared to control forests, and the basal area of logs twice as high. Between-group differences for snags and logs were less marked than in Swiss forests. In

Sweden, snag amounts in woodpecker forests were smaller than in Switzerland (0.8 ± 0.1 m^2 ha^{-1} and 2.3 ± 0.4 m^2 ha^{-1}; mean ± SE), whereas this was not the case for logs (1.8 ± 0.2 m^2 ha^{-1} and 2.2 ± 0.3 m^2 ha^{-1}). As in Switzerland, the proportion of snags compared to all standing trunks was significantly higher in woodpecker forests (presence: 4.8 ± 0.3%; absence: 1.9 ± 0.3 %; mean ± SE; Fig. 2). In contrast to Switzerland, the basal areas of living trees was significantly higher in woodpecker forests compared to control forests (Table 2). The percentage of pine trees was smaller in woodpecker forests, whereas the proportion of spruce trees, even if slightly higher in woodpecker forests, did not differ significantly between groups. There was no difference between the groups for deciduous trees.

Intensive harvesting occurred more frequently in control forests as compared with woodpecker forests, however the difference was not highly significant (Table 2). The road/track density between groups was not different, and no correlation was found between dead wood amounts and road/track density. As was the case for Switzerland, there was no between-group difference for management history (i.e. recent/past harvesting).

Both hard and soft logs occurred more frequently in woodpecker forests than control forests (Table 2). Snags without bark occurred more often in woodpecker forests, whereas snags with bark did not exhibit any difference between the groups. As for Switzerland, these variables describing dead wood quality were positively correlated to the basal areas of snags and logs.

3.2. Road network and ringed trees

Road/track density negatively affected Three-toed Woodpecker presence in Switzerland. We found a non-linear relationship indicating a threshold between 2.6 and 3.5 km km^{-2} (x-values at $p = 0.9$ and $p = 0.5$; Table 3). More ringed trees were found in Switzerland than in Sweden (Table 2). The number of ringed trees exhibited a significant non-linear relationship with the probability of woodpecker presence in Switzerland and Sweden (Table 3), and also when all data were merged ($\chi^2 = 16.68$, df = 1, $p = 0.00004$; odds ratio = 9.1; CC = 72.7%; Fig. 4).

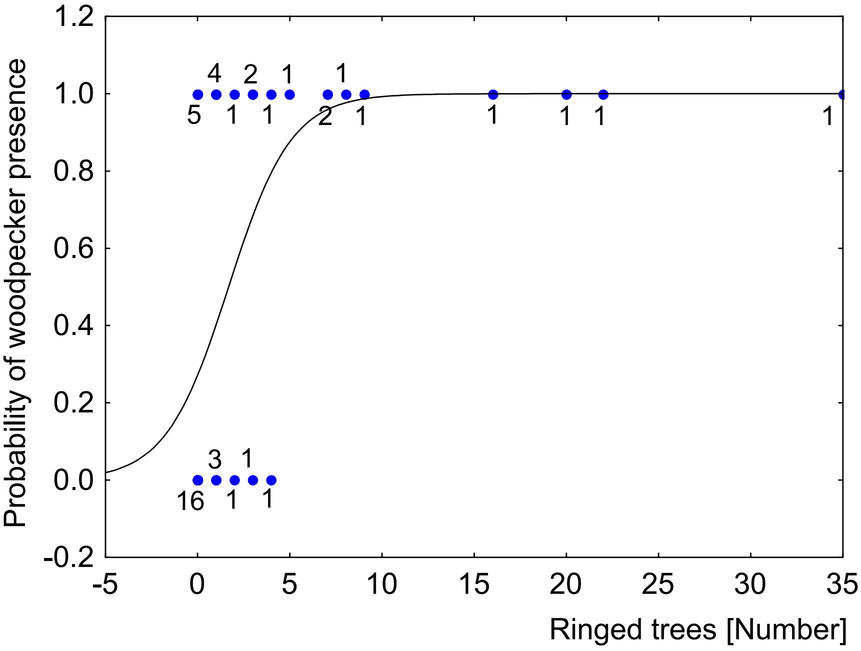

Fig. 4: *Logistic regression showing a significant relationship between the number of ringed trees in boreal and sub-Alpine forest and the probability of Three-toed Woodpecker presence. Samples from Sweden and Switzerland matched (n = 44). Figures: number of samples.*

3.3. Critical dead wood threshold values for the Three-toed Woodpecker

Several variables associated with snag amounts were highly inter-correlated (in Switzerland: basal area of snags versus snags with bark, road/track density, logs, hard logs, soft logs, harvesting intensity; always $r > 0.60$, $p < 0.001$, $n = 24$; in Sweden: snags versus living trees, tree height, logs and hard logs; always $r > 0.65$, $p < 0.002$, $n = 20$). Univariate logistic regression models for snags reached a good fit and high accuracy, both for Sweden and Switzerland (Table 3).

Critical values, expressed as a minimal amount of snags (m^2 ha^{-1}), below which the probability of Three-toed Woodpecker presence drops quickly, were not identical for Switzerland and Sweden (Fig. 5a). The means and standard errors of the independent values for the inflexion points of the logistic regression function (at $p = 0.5$) were 0.91 ± 0.14 m^2 ha^{-1} (Switzerland) and 0.42 ± 0.05 m^2 ha^{-1} (Sweden). These means differed significantly at a level of $\alpha = 0.01$. The estimated between-person difference for the

Table 3: *Model statistics for all variables (df = 1). β = parameter estimate, SE = standard error, CC = correct classification.*

Variable	**β (SE)**	**χ^2**	**p**	**Odds ratio**	**CC (%)**	**β (SE)**	**χ^2**	**p**	**Odds ratio**	**CC (%)**
	Switzerland					**Sweden**				
Snags	7.03 (3.44)	25.04	0.000	-----	95.8	-23.28 (15.04)	21.93	0.000	81.0	90.0
Logs	7.85 (3.86)	25.11	0.000	121.0	91.7	-9.60 (6.83)	18.68	0.000	-----	90.0
Living trees	-0.12 (0.07)	3.29	0.070	4.0	66.7	-0.41 (0.21)	5.26	0.022	3.5	65.0
Spruce	0.13 (0.09)	2.59	0.107	5.0	70.0	-0.08 (0.04)	3.71	0.054	3.5	65.0
Pine	-----	-----	-----	-----	-----	0.07 (0.04)	4.40	0.036	5.4	70.0
Deciduous	-----	-----	-----	-----	-----	-0.07 (0.07)	1.24	0.266	1.6	55.0
Tree height	-0.07 (0.18)	0.16	0.687	-----	60.0	0.69 (0.35)	9.35	0.002	9.3	75.0
Slope	0.07 (0.05)	2.34	0.126	1.4	54.2	-----	-----	-----	-----	-----
Road/track density	-2.49 (1.19)	26.64	0.000	121.0	91.7	0.22 (0.58)	0.14	0.706	0.7	45.0
Int. harvesting	-0.05 (0.03)	7.36	0.007	10.0	75.0	0.08 (0.04)	5.57	0.018	3.5	65.0
Ext. harvesting	0.23 (0.10)	18.06	0.000	15.0	79.2	-0.01 (0.03)	0.45	0.832	1.6	65.0
Recent harvesting	-0.01 (0.02)	0.30	0.582	1.4	54.2	0.09 (0.04)	6.32	0.012	16.0	80.0
Past harvesting	-0.02 (0.04)	0.24	0.623	1.4	54.2	0.02 (0.03)	0.36	0.548	1.0	50.0
Snags with bark	0.26 (0.13)	25.51	0.000	-----	95.8	-0.07 (0.05)	2.86	0.091	4.0	65.0
Snags without bark	0.48 (0.21)	24.06	0.000	121.0	91.7	-0.14 (0.06)	7.09	0.008	9.3	75.0
Hard logs	0.21 (0.09)	21.02	0.000	55.0	87.5	-0.14 (0.06)	12.74	0.000	9.3	75.0
Soft logs	0.18 (0.07)	16.09	0.000	33.0	83.3	-0.14 (0.07)	7.42	0.006	3.5	65.0
Ringed trees	0.53 (0.28)	9.79	0.002	10.0	75.0	-28.14 (---)	13.68	0.000	-----	85.0

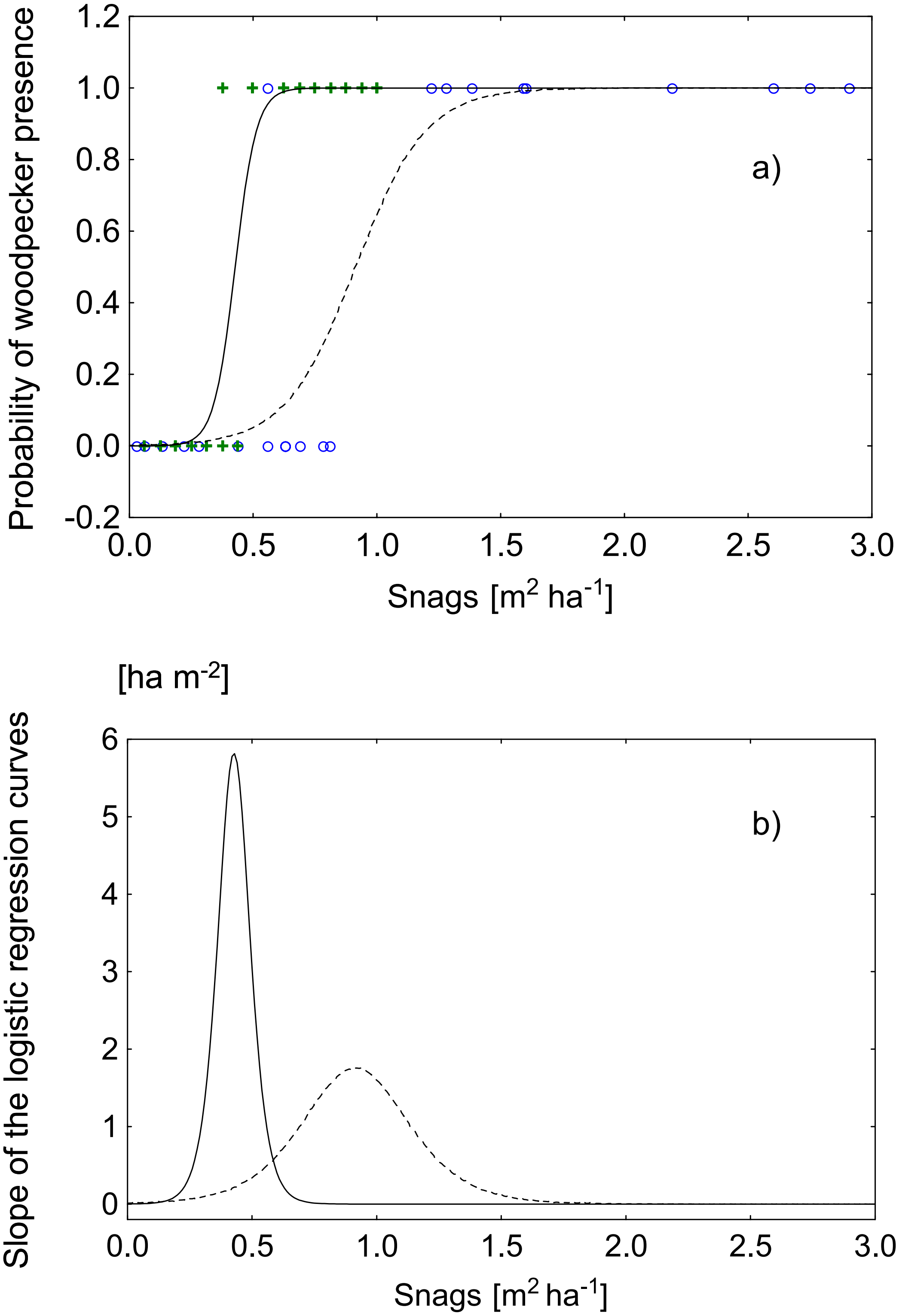

Fig. 5: *Univariate logistic regression models for Switzerland (broken line) and Sweden (whole line) showing significant relationships between the amounts of snags and the probability of Three-toed Woodpecker presence* ***(a)****. First derivative function of these two regression curves* ***(b)****. Crosses: Swedish sample units (n = 20); circles: Swiss sample units (n = 24).*

measurement of snag basal area (field unit mean ± 9.6 %) was too small to invalidate this result. This also applies to the propagated error for the proportion snags/all standing trees (field unit mean ± 11 %). The first derivative function of the regression model resulted in a narrow and high peak for Sweden and a larger and lower peak for Switzerland (Fig. 5b), indicating the existence of an abrupt threshold with a steep slope for Swedish forests. In the model, the probability of Three-toed Woodpecker presence increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m^2 ha^{-1} for Switzerland and from 0.3 to 0.5 m^2 ha^{-1} for central Sweden.

4. Discussion

Critical dead wood threshold

Several authors have demonstrated that Three-toed Woodpeckers forage on dying and dead trees, and, in particular, on recently-dead standing spruce trees (Hess 1983; Hogstad 1970; Murphy & Lehnhausen 1998; Pechacek 1995; Ruge et al. 1999). Accordingly, in our study the basal area of snags, which was highly correlated with the basal area of logs, was the best predictor of Three-toed Woodpecker presence in both Switzerland and Sweden. The probability of presence exhibited a significant non-linear response to different amounts of dead wood, thus indicating that below a critical minimal amount, breeding woodpeckers may disappear from the habitat.

Our results suggest that the amount of standing dead trees related to a given probability of woodpecker presence is smaller in Sweden than in Switzerland (Fig. 2 and 5). Does this mean that Alpine Three-toed Woodpeckers need a higher density of snags than boreal birds? We think not. Instead, the figures should been put into the context of woodpecker population trends in the two study areas. The Swiss Three-toed Woodpecker population is stable or even increasing (Schmid et al. 1998), possibly due to an under-exploitation of marginal mountain forests since World War II (Derleth et al. 2000), a factor that is related to a rapid increase of wood harvesting costs (Brassel & Brändli 1999). Under such conditions, the amounts of dead trees and the availability of food resources are likely to increase. By contrast, the Swedish population is decreasing (BirdLife 2000), due to the loss of suitable habitat and the decline in the quality of the remaining habitat caused by forest management. Considering the fact that the occurrence of a species is expected to track environmental changes with a time delay ("extinction debt" Tilman et al. 1994), the current situation in central Sweden may already be below the landscape threshold for the woodpecker metapopulation capacity (Hanski & Ovaskainen 2000). It is possible that the central Swedish population is a sink population whose survival hinges on migration from source populations further to the north where more naturally dynamic forests remain.

Results from extinction models and some empirical data for vertebrates indicate that regional species extinction starts to accelerate when the suitable habitat area drops below 20-30% of the original suitable habitat area (cf. (Andren 1994; Carlson 2000; Jansson & Angelstam 1999)). Thus, Nilsson et al. (2001) suggested that at least 20% of original densities of large dead trees are needed at the landscape level for biodiversity preservation. Central Swedish dead wood amounts in Three-toed Woodpecker habitats may be close to or below 20% of the amounts found in naturally dynamic forests (cf. Table 4). In addition, our data suggest a higher sensitivity to changes in dead wood amounts for boreal Three-toed Woodpeckers than their sub-Alpine counterparts; i.e. the peak of logistic regression model is narrow and the slope sharper (Fig. 5b), which means, for example, that a small decrease in dead wood amounts results in a quick drop of the probability of woodpecker presence.

For the purpose of the precautionary principle, we suggest, therefore, that forest management recommendations be based on a strategy maximising the probability of woodpecker presence. For example, to achieve a level of probability of $p = 0.95$, our model predicted necessary snag amounts of 1.3 m^2 ha^{-1} for Switzerland and 0.5 m^2 ha^{-1} for Sweden (Fig. 5a). For the studied sub-Alpine forests, a basal area of $\geq$ 1.3 m^2 ha^{-1} corresponds to a volume of $\geq$ 15 m^3 ha^{-1} or $\geq$ 5% of the standing basal area being dead trees. Both basal area and volume depend on the site productivity, which is probably lower in boreal forests than in sub-Alpine forests. Thus, consideration of the ratio of dead trunks to the total number of trunks, independently of the site productivity, is a better way of providing general recommendations. With the aim of reversing the negative population trends in central Sweden, we would suggest aiming for $\geq$ 5% of standing dead trunks in older forests, as is the case in Switzerland. This corresponds approximately to a mean volume of $\geq$ 15 m^3 ha^{-1}, still depending on site productivity, over at least 100 ha large forest areas.

Whereas many studies on dead wood requirements of different woodpecker species have been conducted in North America (e.g., Bull et al. 1997; Keisker 2000; Samuelsson et al. 1994), few literature data are available for Northern Europe, and even fewer for European sub-Alpine forests. The critical value of at least 5% dead trunks in older forests that we determined for Three-toed Woodpecker requirements lies within the range of 5-10 percent recommended by Utschick (1991) as an optimal snag proportion for forest birds.

The comparison with other studies shows that for both studied landscapes, dead wood amounts measured in forests without Three-toed Woodpeckers correspond well to the amounts that have been found in other managed forests by different methods (Table 4). Fridman and Walheim (2000) report around 2-3 m^3 ha^{-1} dead wood in the lowland part of central Sweden where our study was carried out. It should be noted that the differences in the amount of dead wood within our study areas are small compared with the difference between naturally dynamic forests and our study areas, especially for central Sweden (Table 4). Siitonen (2001) reviewed publications of the amount of dead wood in unmanaged boreal forests and found it to vary from 18% to 37% of the total wood volume. Nilsson et al. (2002) reported for old-growth boreal and temperate forests that around 10% of all standing trunks are dead. The dead wood volume in recently disturbed forest is often considerably larger. In general, the amount of dead wood in managed boreal forests is 2% to 5% of the amount found in naturally dynamic forests (Siitonen 2001; Angelstam unpublished data). When considering that remaining unmanaged reference areas where dead wood can be studied generally are located on sites with poorer than average productivity (e.g. Yaroshenko et al. 2001), and that dead wood should be divided into different categories of diameter and decay stage (Stokland 2001), it is likely that the decline in certain types of dead wood (e.g. large and decayed) from natural to managed landscapes is even greater.

To recommend critical dead wood thresholds for Three-toed Woodpeckers as a practical management target, however, it is necessary to evaluate the umbrella value of this woodpecker species for other taxa in conifer-dominated boreal and mountain forest (Angelstam et al. in press; Roberge & Angelstam in press). Several links with biodiversity and habitat quality have previously been demonstrated. Mikusinski et al. (2001) found that the number of forest bird species is correlated positively with woodpecker species richness and, in particular, with the presence of the Three-toed Woodpecker. Suter et al. (2002) demonstrated that the Capercaillie (*Tetrao urogallus*), co-occurring with the Three-

Table 4 : *Dead wood amounts in European sub-alpine and boreal conifer forests.*

Country	Site selection type	Stand age [years]	Logs [m^3 ha^{-1}]	Snags [m^3 ha^{-1}]	Snag proportion of stems [%]	Total CWD [m^3 ha^{-1}]	Authors
			mean (range)	mean (range)		mean (range)	
European sub-alpine spruce forests							
Switzerland	managed		3.9-21.6	0.0-4.2		3.9-25.8	Guby & Dobbertin 1996
Switzerland	managed	> 100	7	12	7	19	Derleth et al. 2000
Germany	unmanaged	140-260	~[1] 56	~ 28		84 (10-180)	Rauh & Schmitt 1991
Germany	unmanaged	old			5-10	20-60	Utschick 1991
Switzerland	unmanaged	> 100	31	32	20	63	Derleth et al. 2000
Poland	unmanaged	all age classes	73	59	~ 14	131	Holeksa 2001
Slovakia	unmanaged	all age classes				80-273	Korpel 1995
Slovakia	unmanaged	all age classes				42	Korpel 1995
Slovakia	unmanaged	all age classes			~ 9	80-220	Korpel 1995
Switzerland	with *Picoides trid.*	> 100	21 (10-43)	19 (6-34)	8 (3-22)	40 (16-65)	this study
Switzerland	without *Picoides trid.*	> 100	7 (2-16)	5 (0-10)	1 (0-3)	12 (5-26)	this study
European boreal conifer forests							
Southern Finland	managed	mature				14 (2-28)	Siitonen et al. 2000
Southern Finland	managed	overmature				22 (7-38)	Siitonen et al. 2000
Central Sweden	managed	all age classes	2.8	1.2		4.0	Fridman & Walheim 2000
Central Sweden	managed	101-140				7.2	Fridman & Walheim 2000
Central Sweden	managed	> 140				11.7	Fridman & Walheim 2000
Southern Finland	unmanaged	old-growth	~ 78	~ 33		111 (70-184)	Siitonen et al. 2000
Central and northern Sweden	unmanaged	88-270			~ 30	89 (27-201)	Linder et al. 1997
Northern Sweden	unmanaged	old-growth	17-65	0.5-13			Jonsson 2000
Northern Finland	unmanaged (pine)	old-growth	~ 11-13	~ 6-8	~ 19	19	Sippola et al. 1998
Northern Finland	unmanaged (spruce)	old-growth	~ 36-42	~ 18-24	~ 19-27	60	Sippola et al. 1998
Central Sweden	with *Picoides trid.*	mature	16 (7-28)	7 (3-10)	5 (3-6)	23 (10-37)	this study
Central Sweden	without *Picoides trid.*	mature	5 (3-8)	2 (0-3)	2 (0-3)	7 (3-11)	this study

[1] ~ calculated by the authors of this study

toed Woodpecker, is an umbrella for red-listed mountain birds. Pakkala et al. (2002) found a positive correlation between the occurrence of breeding Three-toed Woodpeckers and territory and landscape quality. In addition to these findings, it would be important to analyse systematically the umbrella value of this species in different landscapes.

Ringed trees as indicators of breeding continuity

We observed more ringed trees in Switzerland than in Sweden. Assuming that sap licking is a general habit of European Three-toed Woodpeckers (Glutz von Blotzheim 1994; Pechacek 1995; Ruge 1968; Scherzinger 1982), a longer presence of this bird species in the same habitat would result in a higher number of ringed trees. Also, the estimated age of ringed trees does not refute this hypothesis. Indeed, we found no signs of very long use (i.e. the tree has formed bulges) in Sweden, whereas in several breeding forests in Switzerland such trees have been observed. Based on these findings, we therefore expect a longer breeding continuity in Swiss forests as compared to Swedish forests. This hypothesis may be explained by the different forest management regimes in Alpine and boreal forests. In Switzerland, selective tree cutting creates a dynamics of small gaps within stands, which retains favourable habitat features for the woodpecker over time. Hence, the Three-toed Woodpecker’s presence in the same habitat may be continuous over a very long time and many and very old signs can be found. By contrast, in Sweden clear-cutting has been the general harvesting type since the late 19th and the rotation time of around 80 years for Norway spruce and 100 years for Scots pine is relatively short. Three-toed Woodpeckers need forests with dead wood, either in old-growth stands or in stands subject to stand-replacing disturbance by fire or wind (Angelstam & Mikusinski 1994). Consequently, in managed forests in Sweden they would not be expected to stay longer than about 10-30 years in the same old forest patch, a too short a time to create numerous signs or signs of long use. The introduction of variable retention in forestry (Angelstam & Pettersson 1997) is likely to increase the time with sufficient amount of dead wood during a rotation by about 10 years at the beginning of the succession. Our findings are corroborated by Nilsson and Ericson (1997) who expect species in temperate forests to be more dependent on spatial and temporal forest continuity than species in boreal forests, due to the different disturbance regimes.

Our data suggest the existence of a non-linear relationship between the number of ringed trees and the probability of woodpecker presence. Thus, the number and age of ringed trees may be used as indicators of breeding continuity. However, it is not easy to differentiate the ringed trees of Three-toed Woodpeckers from those of the Great Spotted Woodpecker (*Dendrocopos major*), a sympatric species, which, although it prefers making rings in deciduous trees, may occasionally do so on spruce and pine trees. In addition, while the presence of a breeding species can be easily demonstrated, it is difficult to establish its absence. Hence, we cannot exclude the presence of breeding Three-toed Woodpeckers in our control forests. We are aware of this limitation of our study design.

Influence of management intensity and accessibility

In managed forests, dead wood amounts are closely related to the intensity of forest management, which is also linked to the accessibility of harvesting areas, as demonstrated in this study. Because of Switzerland's difficult terrain, in about 80% of the area, trees are felled by hand using chainsaws and then they are transported by tractors or cable cranes to the nearest forest road. In addition to regular selective tree cutting, diseased and dead trees are removed by salvage cutting (Guby & Dobbertin 1996). In our study, the road network density negatively affected dead wood amounts, and, indirectly, the spatial distribution of Three-toed Woodpeckers in Switzerland (Fig. 3).

In Switzerland, the network of forest roads grew by about 10% or 2.5 m ha^{-1} over the past ten years (Brassel & Brändli 1999). Thus, the forest in the Alps and Lower Alps has become more accessible, whereas accessibility in the Central Plateau has only improved slightly. If this trend in forest road growth in mountain areas continues, and if the management goals do not change in favour of more dead wood in the forests, we can expect a negative influence on woodpecker populations. The predicted threshold value, beyond which road density has a strong negative impact on Three-toed Woodpecker presence, was between 2.6 and 3.5 km per km^2. Assuming that the current growth of the forest road network of 10% per decade continues, the critical threshold of 2.6 km per km^2 could be reached in about 30 years (based on the current mean value of road density in Three-toed Woodpecker forests of 1.8 km per km^2).

In Sweden the road network density was generally lower than in Switzerland and did not explain the presence or absence of Three-toed Woodpeckers. Indeed, for the range of road network density found in Sweden (i.e. 0-2.9 km per km^2; cf. Table 2 and Fig. 3), we found no significant correlation between dead wood amounts and road/track density in Switzerland either. In Sweden the presence of a dense road and track network has been easy to establish due to the flat topography. It was variation in the intensity of forest owner's management practices rather than variation in road density that determined the amount of dead wood in Sweden.

Perspectives

Based on the observed differences between the Swedish and Swiss study areas, we suspect that Three-toed Woodpeckers in central Sweden have to move around considerably in the search for adequate forest patch islands within a generally intensively managed forest landscape. In contrast, Three-toed Woodpeckers in Switzerland are likely to be more sedentary, often located in areas on steep slopes and difficult to access (Bütler & Schlaepfer 1999), i.e. where the road network is poorly developed. Two important management consequences follow from this hypothesis: in Sweden clear-cut patch design (directly affecting the amount of residual dead wood and indirectly affecting the local density of old forest patches), and stand rotation time are likely to be closely related to the trend in the Three-toed Woodpecker population; and in Switzerland, the level of road network development that facilitates forest management intensification and salvage cutting, whereby declining and dying trees are removed, is likely to affect Three-toed Woodpecker populations. Testing these hypotheses would necessitate studies of the detailed use of habitat by Three-toed Woodpeckers using radio-telemetry.

The accuracy of the recommended targets for dead tree volumes and basal areas should be verified in other sub-Alpine and boreal forests with various site productivity conditions and forest management types. Some further work has to be done in order to account for the large scale succession, for example assessment of the usefulness of snag retention in clear-cuts for the Three-toed Woodpecker.

5. Conclusion

We demonstrated the dependence between Three-toed Woodpecker presence and high dead wood amounts, both in Switzerland and central Sweden. Thresholds related to dead wood amounts, and, in particular, to standing dead trees existed for both the nominate *P.t. tridactylus* and *P.t. alpinus* subspecies of this bird. In Switzerland the high road network density, a measure for the good accessibility of the forest stands for harvesting, negatively affected the woodpecker's presence. We suggest that a quantitative target for Three-toed Woodpeckers is at least 5% standing dead trees in forest stands over about 100 hectares. This proportion corresponds to about ≥ 1.3 m^2 ha^{-1} (basal area) or ≥ 15 m^3 ha^{-1} (volume), still depending on site productivity. Because of its dead wood dependence, the Three-toed Woodpecker may also be considered as an indicator species for sites with a high value for other specialised species dependent on dead wood, many of which are red list species. Our results suggest that the number of ringed spruce or pine trees resulting from sap drinking, a characteristic habit of this woodpecker, can be used as an indication of the continuity of its presence.

Acknowledgements

We would like to thank P. Adenäs, L. Bütler, K. Eklund, E. Hellberg, R. Lundmark, J. Palm, T. Petterson, I. and M. Richter, J.J. Sauvain, F. Schweingruber, and G. Sengül for field assistance. For helpful comments on statistics and earlier versions of the manuscript we are grateful to I. Iorgulescu, P. Derleth, and C. Glenz. Our thanks also to S. Cox for revising the English.

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Paper IV

Quantitative snag targets for the three-toed woodpecker, *Picoides tridactylus*

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accepted in: Ecological Bulletins

Abstract

Sustainable forest management goals include the conservation of biological diversity and its constituent elements. Dying and dead trees, in particular, have been recognised as being of prime importance as resource and habitat for numerous animal and plant species. Nevertheless, few quantitative target values have been defined for dead wood management purposes, and they often lack well-founded scientific bases.

In this study we developed such quantitative targets for standing dying and dead trees (defined as snags), based on the habitat requirements of the three-toed woodpecker *Picoides tridactylus*, a keystone species whose presence is considered an indicator of the properties of naturally dynamic forests. First we developed a theoretical model based on energy requirements and with predictions for woodpecker breeding probabilities as a function of available snag quantities. Then an empirical field study was conducted in Switzerland with the aim of verifying the model predictions. For this purpose, 12 pairs of sites of 1 km^2 in size and comprising one site with and one without a breeding woodpecker, were sampled for snags. We compared these sites using logistic regression. Finally, the comparison of the theoretical model with the field approach enabled the derivation of quantitative snag targets for spruce forests.

Both our theoretical model and the logistic regression analyses resulted in similar snag quantities for predicted woodpecker occurrence. For management purposes, we recommend the observation of the precautionary principle by striving for target values of 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) or 14 (dbh $\geq$ 21 cm) snags per hectare in an area of 100 ha, corresponding to a probability of $\geq$ 0.9 for woodpecker occurrence in both approaches. Maintaining or achieving such optimal snag levels allows the local persistence of three-toed woodpeckers in forest patches and may serve to define strategies for the maintenance of local populations.

1. Introduction

The conservation of biodiversity has become one of the key goals of sustainable forest management (Lindenmayer et al. 2000). At a certain level of forest management intensity, the lack of habitat components causes once naturally occurring species to decline to the level where they risk extinction. Habitat destruction and degradation is currently considered as the major cause of species extinction (e.g., Tilman et al. 1994, Dobson et al. 1997, Fahrig 2001). In Switzerland, for example, in addition to selective logging of large trees, diseased and dead trees are often systematically removed for sanitary reasons by means of salvage cutting (Guby and Dobbertin 1996) causing a lack of habitats and resources for species that depend on dead wood. Quantitative target values may be derived from reference systems, such as naturally dynamic forests, with the aim of restoring dead wood and other important habitat components in managed forests. However, none or very few natural forests remain in most parts of Europe. Also, the amount of dead wood in natural forests may be so extensive – up to 30% of dead stems (Linder et al. 1997) or 25% of above ground biomass (Siitonen 2001, Nilsson et al. 2002, Bobiec in press) – that such targets would be incompatible with the economic objectives of multifunctional forestry. Another approach involves the quantification of the ecological preferences of species of special interest and derivation of quantitative target values for use in management (Simberloff 1995, With and Crist 1995, Fahrig 2001). One difficulty here, however, is the definition of species of special interest and justification of their role as biodiversity surrogates (Thompson and Angelstam 1999). The use of the keystone, indicator, focal and umbrella species concepts (Pearson 1994, Lambeck 1997, Simberloff 1998, Fleishman et al. 2000) for management considerations is currently increasing, in spite of many remaining scientific uncertainties in relation to certain species being appropriate proxies for others (Lindenmayer et al. 2000).

Among vertebrates, woodpeckers are of special importance due to their key role in supplying forests with tree-cavities, serving secondary users as nesting or roosting holes (Saari and Mikusinski 1996). In terms of their ecological requirements, woodpeckers are considered as being the most demanding guild among resident bird species (Angelstam 1990, Mikusinski and Angelstam 1997). The occurrence of several species of woodpeckers is indicative of the properties of naturally dynamic forests (e.g. old trees, dead wood, structural diversity) (Mikusinski and Angelstam 1997). The three-toed woodpecker *Picoides tridactylus*, in particular, has recently been proposed as a keystone species (Imbeau 2001) and a possible indicator of high biodiversity, i.e. old trees and large dead trees (Mikusinski et al. 2001, Nilsson et al. 2001).

One of the most important habitat features for three-toed woodpeckers are large, standing dying and recently dead trees (Hogstad 1970, Hess 1983, Pechacek 1995, Murphy and Lehnhausen 1998, Ruge et al. 1999b). Such dead wood pieces are the rarest of the diverse dead wood substrata, especially in managed forests (Green and Peterken 1997, Fridman and Walheim 2000). They still have a certain economic value and may, therefore, be cut when timber is harvested. Ecological studies on dead wood have demonstrated the prime importance of large diameters and standing compared to lying dead trees (Samuelsson et al. 1994). They provide habitats and resources for numerous threatened animal, plant and fungal species (Thomas 1979, Utschick 1991, Morrison and Raphael 1993, Samuelsson et al. 1994, Smith 1997, Jonsson and Kruys 2001). Recently, dead wood has been proposed as a new indicator of forest biodiversity to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (<www.minconf-forests.net> 29 April 2002). Dead wood also figures in modern certification standards for best forestry practices, as defined, for example, by the Forest Stewardship Council (FSC). With its requirement of forests with relatively high dead wood amounts (Derleth et al. 2000) and demonstration of threshold responses related to dead wood (Bütler et al. unpubl.), the three-toed woodpecker is directly linked with the structure-based biodiversity indicator ‘dead wood’.

In spite of the growing agreement between conservation biologists, forest managers and political circles on the importance of dying and dead trees, the few existing quantitative dead wood management targets for European forests often lack well-founded scientific bases. Without sound quantitative targets, however, the achievement of management goals and progress towards sustainable forestry cannot be assessed. Due to its specific requirements for standing dying and dead trees (defined as snags), and due to its qualities as a keystone species and biodiversity indicator, the three-toed woodpecker was used in this study to define quantitative snag target values for sustainable management of spruce forests. The aims of this paper are: 1) to develop and validate a theoretical model based on the energy budgets of the three-toed woodpecker, thus predicting the spatial densities of snags required to meet this woodpecker's energy requirements; 2) to test these predictions by carrying out a subsequent field study and 3) to derive quantitative management recommendations through the definition of snag target values.

2. Methods

The probability of presence of the three-toed woodpecker *Picoides tridactylus* was predicted as a function of the snag density (*SNAG*) by developing a simple model based on the energy requirements of the three-toed woodpecker, and on different assumptions with respect to food selection and prey availability. After a sensitivity analysis, this theoretical model was validated on ten study sites in Switzerland. In order to verify the model predictions concerning snags, a field study, aimed at measuring the quantities of snags actually available in sites where three-toed woodpeckers do and do not breed, was subsequently carried out at 24 sites. A logistic regression analysis on the "presence – absence" data in these sites also resulted in a prediction of the probability of woodpecker presence as a function of the snag density. Through comparison of both probability predictions, quantitative snag target values were then derived for this woodpecker species.

2.1. The bioenergetic model

The basic idea behind our model is that a three-toed woodpecker breeding pair has to find sufficient energy sources within its home-range so as to fuel all its activities over the course of one year (reproduction, moulting, over-wintering etc.). According to Glutz von Blotzheim (1994), the mean reproduction of a successfully breeding pair is 1.8 young birds. Such a bird group (2 adults and 1.8 young) is defined as a family. Thus, we included in our model the energy needs of the young birds over 14 weeks, after which they are supposed to leave the home-range definitely. Following Hess (1983) we defined the number per area unit of foraging trees as the most important habitat feature, while regarding the availability of trees for nesting, drumming etc. as not being limiting factors. For practical management considerations, the density of all snags, and not only potential foraging trees, was defined as key variable in the model (Fig. 1). As an insectivorous bird, the three-toed woodpecker gains its energy through insect predation. According to the literature, bark beetles (above all *Ips typographus*) were considered as the most important energy source (Hutchinson 1951 cit. in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 cit. in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 cit. in Glutz von Blotzheim 1994). Bark beetles occur only in a certain phase in the gradual change in the properties of a dying and dead tree. Hence, only a given proportion (*b*) of snags, trees which have still some bark left, are potential foraging trees. Koplin (1972) estimated the daily energy requirements of free-living three-toed woodpeckers by measuring gross energy intake and energy in excrement. In his model, the energetic requirement is a function of air temperature, considered as the most important metabolic factor. This model served as basis for the estimation of the yearly energy requirements of woodpeckers in our model, defined as the number of consumed prey during one year (*CPR*). As a substitute for lacking data on movements and energy expenditure by woodpeckers, we used the potential home-range size (*PHR*), defined as a home-range within a minimum and maximum size, facilitating the viability of the woodpecker family. The size range was based on home-range sizes reported in the literature.

The available prey number (*APR*) of the most important energy source, i.e. bark beetles, was estimated on the basis of reproduction and mortality rates from the literature (cf. Variable estimation). Since bark beetles live beneath the tree bark, the mean bark area infested by beetles (*MIA*) was a further variable included in the model. Finally, we defined the woodpecker's foraging efficiency (*FEF*) as a variable that takes into account a certain loss of prey during foraging. Indeed, even when virtually scaling the bark of a foraging tree, the woodpecker will not capture all available prey items, since bark chips that fall to the ground may contain undetected items. In addition, other insectivores may consume bark-living insects.

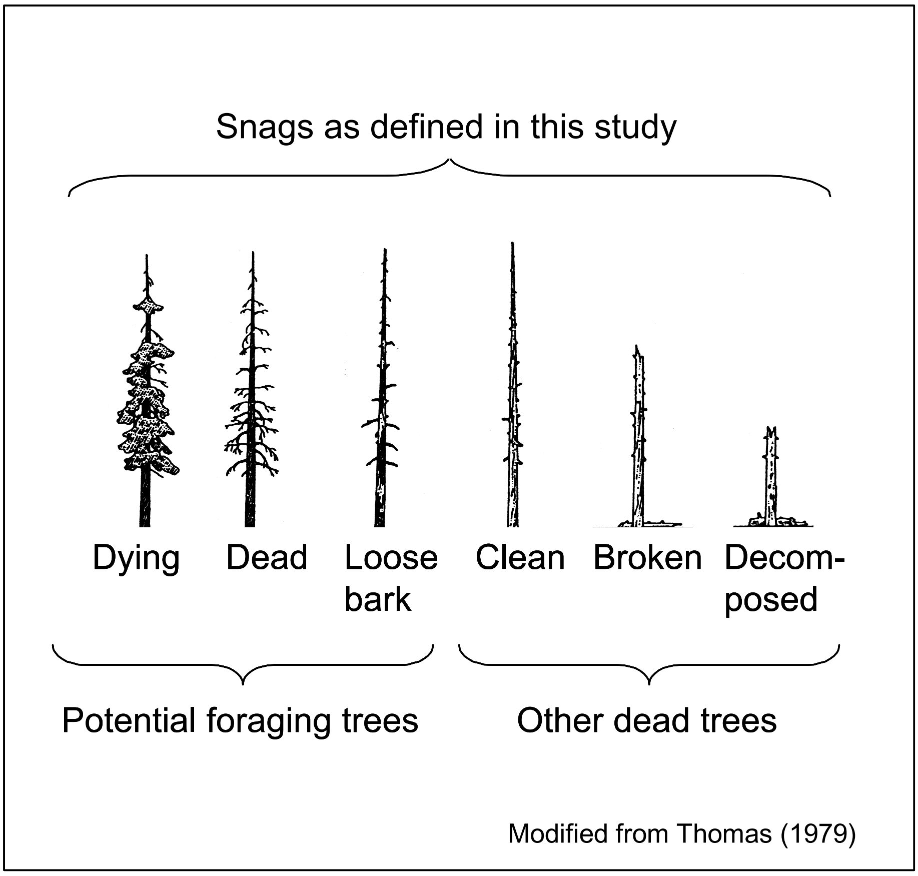

Fig. 1: *Definition of snags and potential foraging trees for the three-toed woodpecker, as used in this study.*

Based on the above considerations, the snag density needed to meet the woodpecker's energy requirements can be estimated by calculating:

$$SNAG_{21} = \frac{CPR}{b * PHR * APR * MIA * FEF} \qquad (1)$$

where

$SNAG_{21}$ = density of snags with a diameter at 1.3 m (dbh) ≥ 21 cm (cf. Validation of the bioenergetic model) required to meet the annual energy requirements of a woodpecker family [snags * ha^{-1}],

CPR = bark beetle prey consumed in the course of one year by a woodpecker family [consumed beetles * $year^{-1}$],

PHR = potential home-range size of a woodpecker breeding pair [ha],

APR = available prey over one year per square meter of bark on potential foraging trees in the woodpecker's home-range area [available beetles * m^{-2} * $year^{-1}$],

MIA = mean infested bark area of a potential foraging tree [m^2 * foraging $tree^{-1}$],

FEF = foraging efficiency of an adult woodpecker [consumed beetles * available $beetles^{-1}$].

b = proportion of potential foraging trees to all snags [foraging trees * $snags^{-1}$].

Since a woodpecker breeding pair consists of two adult birds and is supposed to produce 1.8 young birds annually,

CPR is further defined by

$$CPR = 2 * CPR_a + 1.8 * CPR_y \qquad (2)$$

where

CPR_a = bark beetle prey consumed over one year by 1 adult woodpecker,

CPR_y = bark beetle prey consumed over 14 weeks by 1 young bird.

CPR_a is further defined by

$$CPR_a = \sum_{i=1}^{12} 30 * \frac{GEI(T_i)}{e} * p_a \qquad (3)$$

where

GEI = gross energy intake in Joule per day = $(51.46 - 0.67 * T_i) * 4185$ J, according to Koplin (1972),

T_i = mean monthly temperature in °C

e = energy content in Joule of 1 bark beetle item,

p_a = proportion of bark beetles in the diet of an adult woodpecker.

CPR_y is further defined by

$$CPR_y = \sum_{j=1}^{14} 7 * \frac{BW(j) * p_y(j) * p(BW)}{w_f} \qquad (4)$$

where

$BW(j)$ = body weight in week j [g]

$p_y\,(j)$ = proportion of bark beetles in the diet of a young bird in week j

$p(BW)$ = proportion of body weight a young bird is eating per day,

w_f = fresh weight of a bark beetle larva or adult [g].

APR is further defined by

$$APR = \frac{1}{52} * a * n_a * \sum_{j=1}^{52} 1 - m(j) \qquad (5)$$

where

a = bark beetle attack density, i.e. the number of nuptial chambers per square meter of bark [m^{-2}],

n_a = mean number of eggs per nuptial chamber,

$m(j)$ = cumulative mortality rate of eggs, larvae, pupae, imagos, immature and adult beetles in week j.

2.2. Variable estimation

CPR

In order to estimate the consumed prey *CPR* we assumed a moisture content of 70% for *Ips typographus* larvae or adults (Bell 1990), a mean caloric content of 83.7 J for one item (Koplin 1972, Barbault 1997) and a dry weight w_d of 0.0041 g (Wermelinger pers. comm.) and, thus, fresh weight $w_f = w_d /0.3$. Following Koplin's *GEI*-model, at 0 °C an adult woodpecker was supposed to consume prey whose fresh weight represents about 0.5 times the woodpecker's body weight. Based on the consideration of the data available on bird digestion (Karasov 1990) and energy requirements for different bird sizes (Kendeigh 1970), this appeared to be a realistic winter daily diet for an insectivorous bird. The proportion of bark beetles in the diet of an adult woodpecker p_a was assumed to be 0.75 (Hutchinson 1951 cit. in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 cit. in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 cit. in Glutz von Blotzheim 1994).

The body weight in week j $BW(j)$ of young woodpeckers was estimated according to the growth curve of Pechacek and Kristin (1996), in which the body weight is 20 g in the first week, 50 g in the second week and 65 g from the third week on. Since the nestlings' growth is fast and the energy cost of growth is high, and considering data for other bird species (Westerterp 1973), we assumed that a young bird consumes 0.7 times its body weight per day. The proportion of bark beetles in the diet of a young bird in week j $p_y(j)$ was defined as 5.8% during weeks 1-3 (Pechacek and Kristin 1996), 10% in week 4, 20% in week 5, 30% in week 6, 50% in week 7 and 75% from week 8 on.

Based on the above assumptions and on mean monthly temperatures T_i between –6 and +12 °C, the estimated *CPR* varied between $1.605*10^6$ and $1.623*10^6$ bark beetle items per year (Table 1). Its probability distribution was assumed to be uniform (cf. Monte Carlo simulation).

PHR

The potential home-range size *PHR* was assumed to vary uniformly between 44 and 176 ha, corresponding to the maximum and minimum home-range size reported in the literature for *Picoides tridactylus alpinus* (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999b).

APR

The breeding density of *Ips typographus* is highly variable within a tree, among trees and at different bark beetle population levels (endemic to epidemic). Our estimation was based on data for endemic (no outbreak) population levels in natural sub-Alpine spruce forests. Only one beetle generation per season was expected and the egg laying was set to the second week of June (Nierhaus-Wunderwald 1995). With an attack density a of 150 nuptial chambers per m^2 (Weslien and Regnander 1990) we expected an average n_a of 27 eggs per nuptial chamber (Thalenhorst 1958). The duration of the development cycle was defined as 3 weeks for eggs, 3 weeks for larval stage and 6 weeks for pupal and imago stage. The mortality rate $m(j)$ in week j was expected to be linear during each development stage and to reach 25% of the initial population in week 3, 70% in week 6 and 85% in week 12 (Thalenhorst 1958, Balazy 1968). During the 40 weeks of maturate feeding, hibernating, flight and invasion on new trees, another linear mortality of 50% of the individuals that reached full development was expected.

Based on the above assumptions, we estimated the *APR* as 657 ± 216 (mean ± SD) and normally distributed within $x_a = 234$ and $x_b = 1080$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

MIA

Very little data exists on the proportion of spruce tree bark area, *MIA*, infested by *Ips typographus*. Gonzalez et al. (1996) reported a *MIA* of 21 m^2 for spruce trees with a mean dbh of 46 cm for an endemic population level. Weslien and Regnander (1990) indicated attacks of 50% of the tree height for spruce trees with a mean dbh of 30 cm.

Based on Gonzalez et al. (1996) and Weslien and Regnander (1990) and our own data on the diameter frequency distributions of spruce trees (Bütler unpubl. data), we estimated the *MIA* as 12.5 ± 3.8 m^2 (mean ± SD) and normally distributed within $x_a = 5$ and $x_b = 20$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

FEF

Capture rates of insect prey vary seasonally, mainly in relation to weather (Wolda 1990). No data was found on the foraging efficiency of bark beetle predation by woodpeckers. Bark chips removed by the woodpecker fall to the ground and may contain bark beetle items that are not consumed. Based on Baldwin (1968), we estimated the *FEF* as normally distributed with 0.50 ± 0.13 (mean ± SD) within $x_a = 0.25$ and $x_b = 0.75$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

b

The proportion of potential foraging trees to all snags (*b*) was determined by field measurements of randomly selected snags (N = 1392) at six study sites (Bütler unpubl. data). The decomposition stage of each tree was determined using the method described in Thomas (1979). Only trees with the decomposition stages "dying", "dead" and "loose bark" were considered as potential foraging trees (Fig. 1). As we observed small variations of *b* between the six study sites, we defined it as a constant (*b* = 0.8).

2.3. Monte Carlo simulation and sensitivity analysis

The input variables (*CPR, PHR, APR, MIA* and *FEF*) do not have one determined value, but are defined as independent random variables. In order to calculate the outcome variable $SNAG_{21}$, we undertook a random experiment by means of ten Monte Carlo simulations, based on a sample size of N = 10'000 for each input variable. The variables *PHR* and *CPR* were supposed to have a uniform probability distribution. The largest and smallest home-range sizes reported in the literature for European three-toed woodpeckers were used to define the upper and lower limits x_{max} and x_{min} for *PHR* (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999a). For *CPR*, the definition of x_{max} / x_{min} was based on lowest/highest monthly mean temperatures within the range of the three-toed woodpecker's geographic distribution. We assumed a normal distribution for the variables *APR, MIA* and *FEF*. The mean values of the variables related to bark beetle infestation (*APR, MIA*) corresponded to an endemic bark beetle population level (cf. Table 1). Ecologically relevant limits x_a and x_b were chosen in such a way as to obtain 95% of the values within those limits, and the corresponding standard deviations were then calculated. Finally, we plotted the probability density function of the simulated output random variable $SNAG_{21}$ and its cumulative distribution function.

Table 1: *Probability distribution functions defined for the variables in the bioenergetic model used to estimate the density of dying and dead trees required to meet the three-toed woodpecker's energy needs.*

Variable [unit]	Type of distribution	x_{min} / x_{max}	μ / σ 1)	x_a / x_b 2)
PHR [ha]	uniform	44 / 176		
APR [m^{-2}]	normal		657 / ± 216	234 / 1080
FEF [percent]	normal		0.50 / ± 0.13	0.25 / 0.75
MIA [m^2]	normal		12.5 / ± 3.8	5 / 20
CPR [number]	uniform	$1.605*10^6$ / $1.623*10^6$		

1) μ = mean; σ = standard deviation

2) $P(x_a < Z < x_b) = 0.95$

The parameter estimation of the input variables (x_{min}, x_{max}, x_a, x_b, mean and standard deviation) for the model variables is subject to uncertainties. A sensitivity analysis changing each variable in turn by ± 20% revealed the extent of changes of the predicted *SNAG*-value. A simultaneous change of ± 20% for all variables was undertaken to demonstrate an extreme situation.

2.4. Validation of the bioenergetic model

The bioenergetic model was validated at 10 study sites in Switzerland, where the three-toed woodpecker was present (n = 6) and absent (n = 4), respectively. Woodpecker presence was determined by visual and aural detection and fresh foraging signs. All of the study sites were dominated by sub-Alpine spruce forests and the surveyed areas varied between 0.6 and 3.0 km^2. The snags were measured at each site using a recently developed method that is further described elsewhere (Bütler and Schlaepfer unpubl.). This method quantifies snags by coupling remote sensing techniques with a Geographic Information System. The dbh of snags that can be quantified by this method is ≥ 21 cm. With the model eq. (1), and with the defined probability distribution functions as input values (Table 1), the p-value (probability of woodpecker presence) associated to each measured $SNAG_{21}$-value was then calculated and compared with information on the presence/absence of the woodpecker.

2.5. Study sites and design for the empirical model

The field study was conducted between 1998 and 2001 at 24 sites located in Switzerland in the eastern/central and western Pre-Alps and in the Jura Mountains. Regional pairs of field plots of 1 km^2 in size were selected (2x12 units). Each pair of plots consisted of one plot where the three-toed woodpecker was present during the breeding season of the study years (referred to as “presence”) and one where it has never been observed (referred to as “absence”). Breeding was proven for three plots, whereas it was probable for the others, according to the definition in the International Ornithological Atlases (Sharrock 1973). The selection of presence/absence field plots was based on data provided by the Swiss ornithological station of Sempach (cf. Schmid et al. 1998) and local bird watchers in Switzerland, and was subject to the following criteria: a) spruce tree dominated forests; b) the majority of the forest stands more than 100 years old, i.e. mature to over-mature, the stand age preferred by three-toed woodpeckers; c) between 1200 and 1700 m a.s.l., where the probability of three-toed woodpecker occurrence is highest (cf. Schmid et al. 1998).

In each field plot, a 4 x 4 sampling grid was established, with sampling points 250 m apart.

2.6. Data gathering and statistical analyses

Data was collected by fieldwork at the sampling points using angle relascope, clinometer and compass. The minimal inventory diameter for snags was 10 cm dbh ($SNAG_{10}$) and their minimum height 1.7 m. The number of trees being wider than the gap in the relascope at each point represented the basal area (i.e. the area of the cross section of a tree stem at 1.3 m inclusive of bark; m^2 ha^{-1}) of the forest at the sampling point.

For statistical analyses we used the STATISTICA 6.0® software package. The mean basal area of $SNAG_{10}$ at the sampling points was calculated for each field plot. The plots were then separated into two groups (“presence” and “absence”) and group means and ranges were calculated. We checked for between-group differences by calculating t-statistics. Logistic regression (Hosmer and Lemeshow 1989) was chosen as the appropriate method to predict the probability of the presence or absence (coded as 1 and 0) of three-toed woodpeckers as a function of the $SNAG_{10}$-densities.

3. Results

3.1. The bioenergetic model and its validation

The simulated model solution predicted a probability of < 50% for presence of the three-toed woodpecker, if the density of standing $SNAG_{21}$ (dbh $\geq$ 21 cm) is less than five trees per hectare (Fig. 2). For densities rising from five to fourteen trees, the expected probability increased from 50 to 90%.

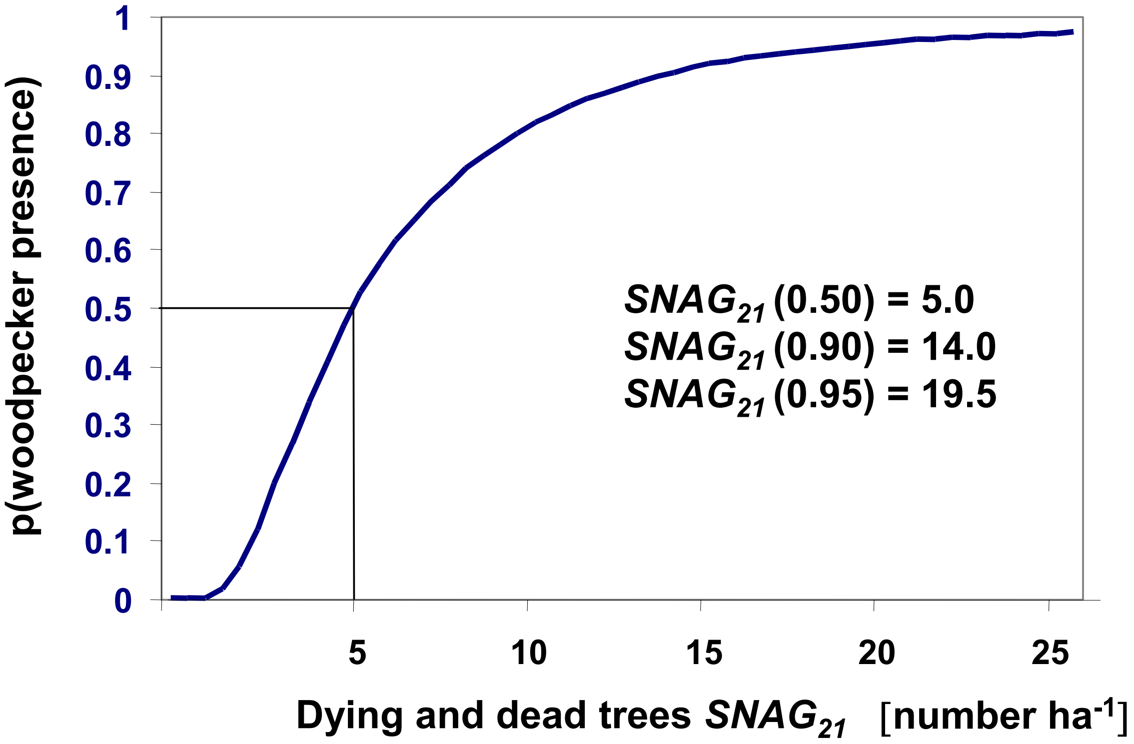

Fig. 2: *Simulated solution of the bioenergetic model predicting the probability of three-toed woodpecker presence as a function of the density of dying and dead trees with a dbh* $\geq$ *21 cm.*

Table 2: *Sensitivity analysis for the output value of the bioenergetic model: changes in predicted $SNAG_{21}$-values for p(woodpecker presence) = 0.5 after 20% changes of input variables.*

Changed variable	New $SNAG_{21}$[1] (+ Δ)	New $SNAG_{21}$ (- Δ)	Deviation [2]
CPR	6.2	4.1	- 0.9 to + 1.2
PHR	4.3	6.5	- 0.7 to + 1.5
APR	4.2	6.4	- 0.8 to + 1.4
MIA	4.3	6.5	- 0.7 to + 1.5
FEF	4.2	6.5	- 0.8 to + 1.5
CPR, PHR, APR, MIA, FEF	2.9	10.3	- 2.1 to + 5.3

1) Original $SNAG_{21}$-value for p(woodpecker presence) = 0.5 was 5.0

2) Deviation is the change in predicted upper and lower limits for the $SNAG_{21}$-value

The results of the sensitivity analysis (Table 2) show the deviation of the $SNAG_{21}$-values (for p(woodpecker presence) = 0.5) due to changes of ± 20%, in turn, of each input variable. The original $SNAG_{21}$-value (p = 0.5) was 5.0. Deviations of the output $SNAG_{21}$-value varied between – 0.9 and + 1.5. For example, changing the number of consumed prey *CPR* by + 20% (i.e. assuming lower air temperatures), increased the required $SNAG_{21}$-density from 5.0 to 6.2 trees per hectare. Positive shifts in $SNAG_{21}$-values were always larger than negative shifts.

Table 3: *Validation of the bioenergetic model for 10 study sites. The $SNAG_{21}$-value was measured for each study site and the associated p-value calculated with the bioenergetic model equation and the defined probability distribution functions (Table 1) as input values.*

Site with three-toed woodpeckers	$SNAG_{21}$ [n ha^{-1}]1)	P(Woodpecker)2)
Hobacher	7.1	0.7
Hinteregg	11.2	0.8
Bärenegg	10.7	0.8
Hinterberg	2.9	0.2
Bois des Fayes	4.5	0.4
Bödmeren	3.4	0.3
Site without three-toed woodpeckers		
Langenegg	1.5	< 0.02
Mont Pelé	1.9	< 0.05
Schraewald	1.2	< 0.01
Les Arses	0.8	< 0.01

1) measured $SNAG_{21}$- value

2) predicted probability of three-toed woodpecker presence by the bioenergetic model

The validation of the model resulted in predicted probabilities of three-toed woodpecker presence ≥ 0.2 for sites where the species was actually present and $p < 0.05$ for those where it was absent (Table 3).

3.2. Results of the empirical model

The mean basal area of *SNAG*$_{10}$ showed significant differences between the one km^2 field plots with and without woodpeckers. For "presence" plots we obtained 2.3 (0.6 – 6.0) m^2 ha^{-1} (mean; range) and for "absence" plots 0.4 (0.0 – 0.8) m^2 ha^{-1} (DF = 22, t = 4.37, p = 0.0002).

Indeed, the probability of woodpecker presence increased significantly with *SNAG*$_{10}$ (Fig. 3; $\chi^2 = 25.04$, $p < 0.000$, DF = 1). In this empirical model the probability of three-toed woodpecker presence increased from 0.10 to 0.95 when the basal area of *SNAG*$_{10}$ rose from 0.6 to 1.3 m^2 ha^{-1}.

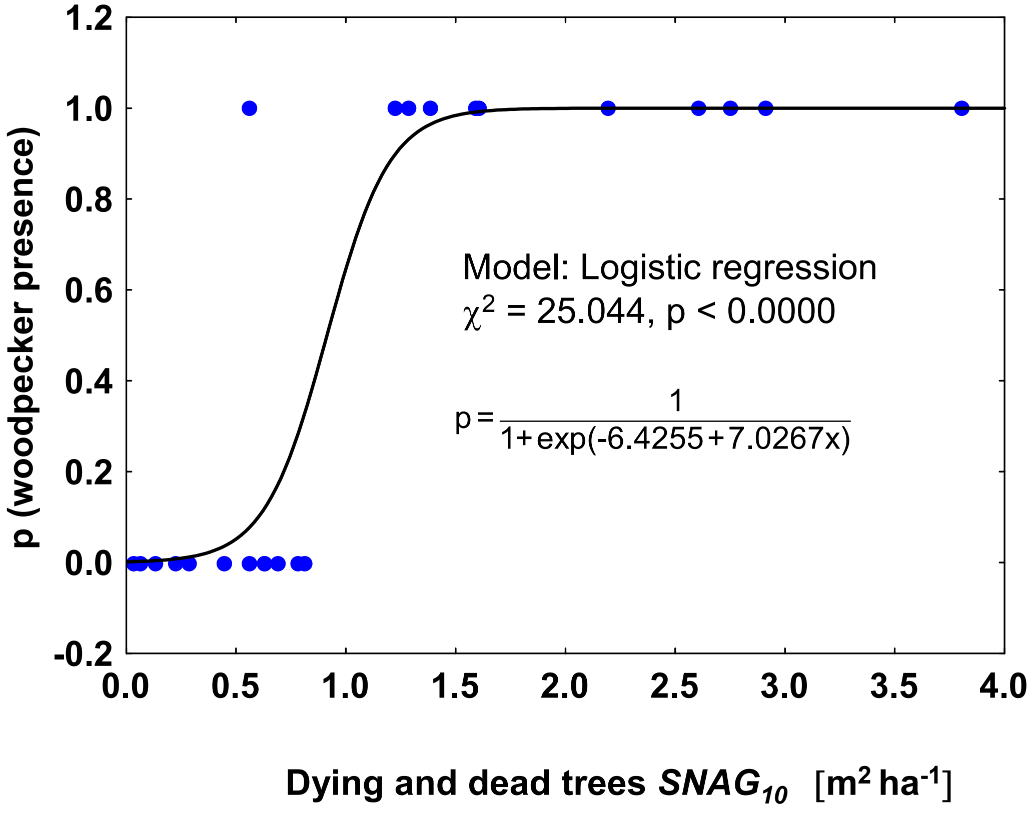

Fig. 3: *Logistic regression model showing a significant relationship between the stand basal area of dying and dead trees and the probability of three-toed woodpecker presence.*

3.3. Comparison of the bioenergetic with the empirical model

In order to compare the results of the bioenergetic model with those of the field study, a data transformation was necessary, since both the measurement units and minimum dbh for snags differed. For this transformation we used an experimental curve of tree diameter distributions from field data from six study sites (Bütler unpubl. data; Fig. 4).

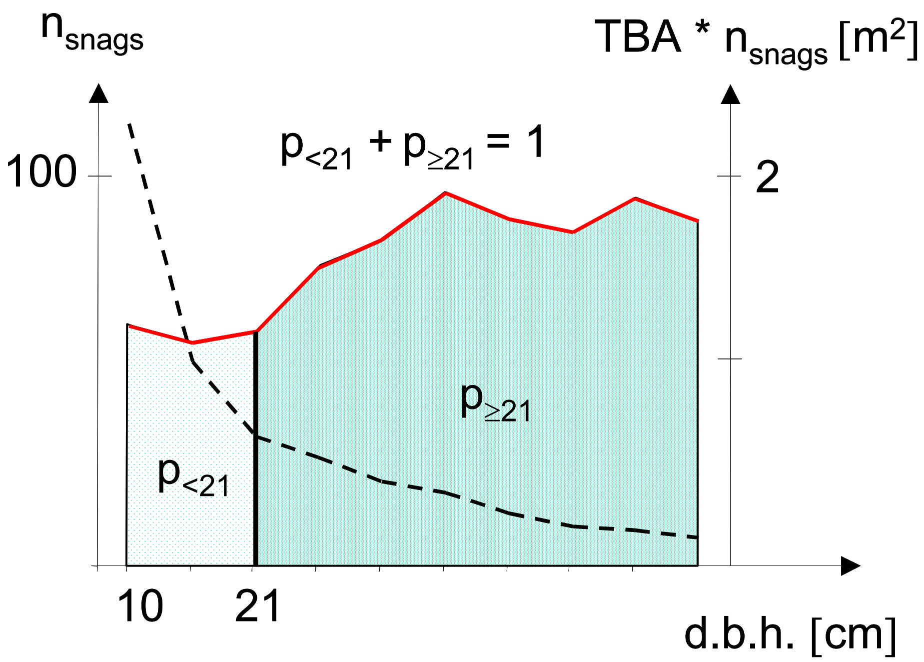

Fig. 4: *Experimental determination of the proportion of the total tree basal area for snags with a dbh ≥ 21 cm and < 21 cm, respectively. Number of snags (n_{snags}) – the broken line – on the left axis and tree basal area multiplied with n_{snags} ($TBA * n_{snags}$) on the right axis. See text for details.*

The predicted $SNAG_{21}$-value, given as tree density ($n\ ha^{-1}{}_{\geq 21\ cm}$), was translated into stand basal area ($m^2\ ha^{-1}{}_{\geq 10\ cm}$) in two steps:

$$\text{a)}\qquad \left[n\ ha^{-1}{}_{\geq 21cm}\right] * TBA_{\overline{dbh}} = \left[m^2\ ha^{-1}{}_{\geq 21cm}\right]$$

with: TBA = tree basal area [m²] = $(0.5\ dbh)^2 * \pi$

$TBA_{\overline{dbh}}$ = tree basal area of the mean-sized tree with a dbh ≥ 21 cm

$$\text{b)} \qquad \left[m^2\ ha^{-1}{}_{\geq 21cm}\right] * \frac{1}{p_{\geq 21cm}} = \left[m^2\ ha^{-1}{}_{\geq 10cm}\right]$$

with: $p_{\geq 21}$ = proportion of total basal area of trees with a dbh ≥ 21 cm

The mean-sized tree with a dbh ≥ 21 cm was 33.5 ± 12.1 cm (mean ± standard deviation; N = 485), corresponding to a $TBA_{\overline{dbh}}$ of 0.09 m^2. The resulting $p_{\geq 21}$ was 0.77.

Figure 5 and Table 4 show the direct comparison between the solution of the bioenergetic model and the results of the logistic regression. Both probability functions lie close together, in particular for p(woodpecker presence) between 0.7 to 0.8. A *SNAG₁₀*-density of less than 0.6 m^2 ha^{-1}, i.e. p(woodpecker presence) < 0.5 in both, theoretical modelling and empirical field approaches, is considered as unfavourable for the woodpecker, whereas a density in excess of 0.9 m^2 ha^{-1}, i.e. p(woodpecker presence) > 0.5 in both approaches, is considered as favourable.

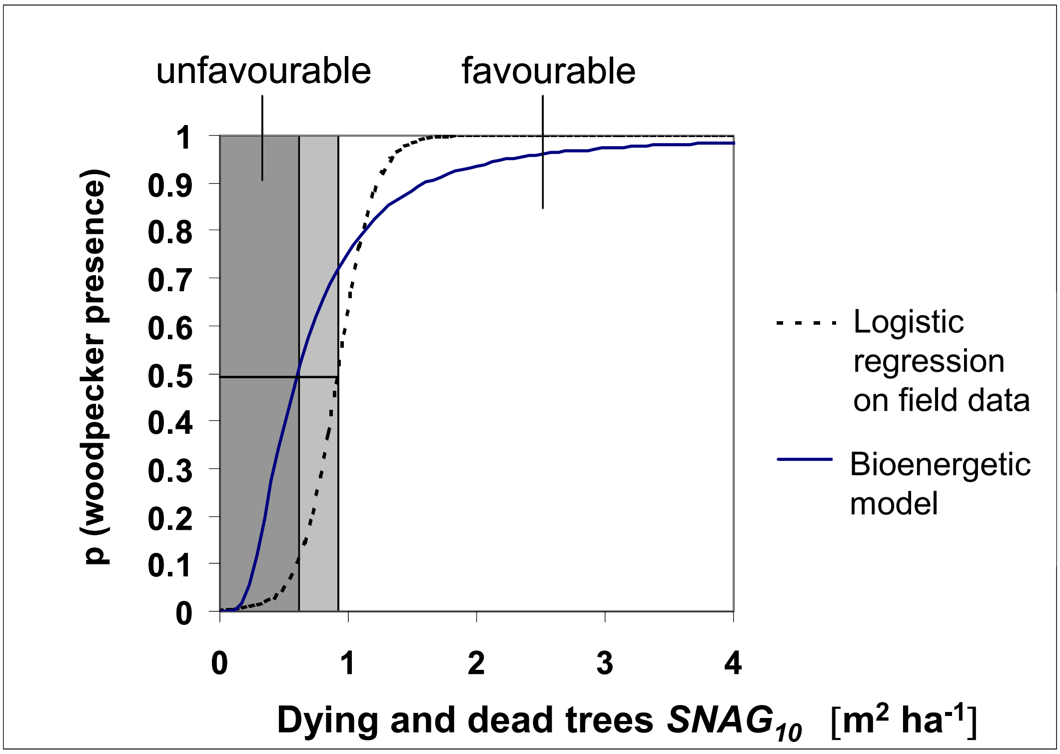

Fig. 5: *Comparison of the solution of the bioenergetic model and the regression results of the empirical model. Predicted probability of woodpecker presence as a function of the stand basal area [m^2 ha^{-1}] of dying and dead trees with a dbh ≥ 10 cm.*

Table 4: *Necessary amounts of standing dying and dead trees required for predicted probabilities of the three-toed woodpecker presence. Comparison between the bioenergetic model results and the results of the logistic regression on field data.*

p(woodpecker presence)	Results	$SNAG_{10}$ 1) [m^2 ha^{-1}]	$SNAG_{10}$ [m^3 ha^{-1}] 2)	$SNAG_{21}$ 3) [n ha^{-1}]
0.50	*SNAG*-model	0.6	7	5.0
	Logistic regr.	0.9	10	
0.75	*SNAG*-model	1.0	12	8.5
	Logistic regr.	1.0	12	
0.90	*SNAG*-model	1.6	18	14.0
	Logistic regr.	1.2	14	
0.95	*SNAG*-model	2.2	25	19.5
	Logistic regr.	1.3	16	

1) $SNAG_{10}$ standing dying and dead trees with a dbh ≥ 10 cm

2) approximate volume calculated with (stand basal area * tree height * shape index) according to Lindroth (1995)

3) $SNAG_{21}$ standing dying and dead trees with a dbh ≥ 21 cm

4. Discussion

In North America, some land-management agencies have defined standards requiring the retention of specified numbers and kinds of snags to provide habitats for wildlife. For ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests, for example, US Forest Service recommendations call for retention of 4.9 and 7.4 snags ha^{-1} with a minimum dbh of 46 cm and minimum height of 9 m (Ganey 1999). This author demonstrated, however, that these snag standards were seldom met even in unlogged forests and concluded that current standards may be unrealistic and should be reconsidered. One reason is that no solid scientific basis was provided for the recommended snag densities, thus highlighting the great need for additional work in these areas. The lack of scientific bases would also appear evident for European forest standards, as illustrated for example by the English national initiative of the Forest Stewardship Council (FSC): “Due to lack of scientific evidence it is not possible at present to give precise guidance on the amount, distribution and composition of dead wood that is appropriate to the individual site” (Anon. 1999). Several national FSC initiatives (e.g. Sweden, Germany, Switzerland) therefore provide only vague qualitative dead wood recommendations, such as “standing dead wood should be created" or "in general, forest owners should maintain some dead trees in a stand". The conclusions of numerous scientific papers emphasising the ecological importance of dead wood only seldom suggest quantitative recommendations (Table 5). Being careful, they remain generally qualitative: "There is a need to increase the input of large dead trees" (Kruys et al. 1999); "It is important to maintain standing dead trees, wherever possible, during harvesting and renewal operations" (Greif and Archibold 2000); "Leave as many large standing dead trees at harvest as possible" (Mccarthy and Bailey 1994).

Quantitative recommendations, however, are essential as operational management goals. Without quantitative targets neither the verification of the progress towards sustainable forest management nor a sound adaptive management is possible. Sippola et al. (1998) argue that quantitative recommendations are too rigid to imitate the variation occurring in natural forests. For example, whereas 5 m^3 ha^{-1} of dead wood may be enough for some species, it would, however, always be too little for other species. The patchy distribution of snags observed in numerous studies argues against the application of uniform targets for snag retention across the landscape (Ganey 1999, Meyer 1999). Thus, in accordance with Sippola et al. (1998) and Ganey (1999), we suggest that a more reasonable goal might be to maintain high snag densities across portions of the landscape, while allowing a smaller than average investment in other areas. Hence quantitative recommendations should be associated with a distribution of the values representing species with different quantitative requirements. In this way the specialised species' requirement regarding the local resource density within the home-range size of a breeding pair could be satisfied even if the recommended mean is considerably lower. Mikusinski et al. (2001) showed that the presence of three-toed woodpeckers was strongly associated with the presence of other forest bird species. Consequently, in spite of remaining uncertainties and an awareness that quantitative targets will never obtain the full endorsement of the various scientific, political and practical management viewpoints, in this paper we still propose provisional snag target values for the maintenance of biodiversity in spruce forests at the stand scale.

Table 5: *Amounts of dead trees in European sub-Alpine spruce forests* ***(a)*** *and recommended quantitative values for standing dead trees in North American and European forests* ***(b)****.*

a)	Stand age [years]	Standing dead trees [m^3 ha^{-1}] Mean (range)	Total lying and standing dead trees [m^3 ha^{-1}] Mean (range)	Authors
Managed forests				
Switzerland		0.0 – 4.2	3.9 – 25.8	Guby & Dobbertin (1996)
Switzerland	> 100	12	19	Derleth et al. (2000)
Switzerland	all age classes	9	16	Brassel & Brändli (1999)
Unmanaged forests				
Germany	140 - 260	28	84 (10 – 180)	Rauh & Schmitt (1991)
Germany	old		20 - 60	Utschick (1991)
Poland	all age classes	59	131	Holeksa (2001)
Slovakia	all age classes		80 - 273	Korpel (1995)
Slovakia	all age classes		42	Korpel (1995)
Slovakia	all age classes		80 - 220	Korpel (1995)
Switzerland	> 100	32	63	Derleth et al. (2000)

b)	Recommendation	Managed organism	Authors
North America			
California	1 clump per 2 ha of 15 snags > 23 cm d.b.h.	Cavity-nesting birds	Raphael & White (1984)
Oregon	0.35 sound snags > 51 cm d.b.h. per ha	Pileated woodpecker	Bull & Meslow (1977)
Oregon	≥ 8 snags per ha	Pileated woodpecker	Bull & Holthausen (1993)
Oregon	≥ 14 snags per ha	Cavity-nesting birds	Schreiber & Decalesta (1992)
Washington	6 hard and 3 soft snags per ha	Cavity-nesting birds	Zarnowitz & Manuwal (1985)
Europe			
Germany	≥ 2.5 – 5 m^3/ha (medium term) ≥ 7.5 – 15 m^3/ha (long term)		Ammer (1991)
Germany	5–10 m^3/ha, i.e. 1-2 % of stems (target value); 20-60 m^3/ha, i.e. 5-10 % of stems (optimal value)	Birds	Utschick (1991)
Sweden	> 10 snags per ha	Lesser spotted woodp.	Olsson et al. (1992)
United Kingdom	11-50 snags per ha, all d.b.h. (medium target) > 50 snags per ha, all d.b.h. (high target)		Kirby et al. (1998)

Limitations and further development of the bioenergetic model

The model presented in this paper was based on literature data for bark beetle breeding density, infested tree bark area and woodpecker home-range sizes. Our assumption about the preferred diet of the woodpecker as consisting mainly of bark beetles, i.e. *Ips typographus*, is a simplified view of a real diet that might be much more diverse, especially in the case of endemic bark beetle population levels. Since most studies on woodpecker diets have been conducted during bark beetle outbreak conditions, however, only very little data is currently available on diet components other than bark beetles.

Another point to discuss is the validity of Koplin's (1972) model for the gross energy intake that served as the input for our bioenergetic model. According to Blem (2000), the metabolised energy and the consequent food requirements of birds vary in relation to a complex number of factors, including body size, level of reproductive, digestive and physical activity, phase of moult cycle, radiation, air temperature, wind etc. Koplin's model, considering only air temperature as the most important metabolic factor, is hence a simplified way to calculate energetic requirements. In addition, Koplin developed it for American three-toed woodpeckers and not for European populations. Different energy requirements between woodpecker subspecies cannot be excluded, even if no data is available on this question.

Our model is based on the assumption that three-toed woodpeckers are completely resident in winter and do not leave their breeding home-range during a whole year. While this hypothesis is true for the Alpine subspecies *Picoides tridactylus alpinus* (Glutz von Blotzheim 1994), the nominate subspecies *Picoides tridactylus tridactylus* may undertake a partial migration to winter territories (Hogstad 1970). However, the size of measured winter feeding territories (5.5 to 8 ha in Hogstad 1970) is so much smaller than breeding home-ranges that the assumption of 'all energy sources within the home-range' seems to be acceptable for the nominate subspecies also.

Our model exhibits an asymptotic curve (Fig. 2 and 5), suggesting an increase, even if diminishing, of the probability of woodpecker presence with increasing availability of snags. Raphael and White (1984) found that the density of all cavity nesting birds in the Sierra Nevada increased with the density of large snags (> 38 cm dbh) until reaching a snag density of about 7.5 ha^{-1}. Above this snag density level, bird densities were evidently limited by other factors. Considering these findings, we believe that there is an upper limit of snag density favouring woodpecker presence. Therefore, our model should not be over-interpreted at the upper end. We suggest that it should not be used where the p-value for occurrence is >>0.95.

Snag targets for the three-toed woodpecker

Our two approaches, undertaken in order to define quantitative snag target values based on three-toed woodpecker habitat preferences, were different. The bioenergetic model was mainly based on theoretical considerations, and its validation performed by a method using remote sensing techniques, i.e. aerial photo interpretation and Geographic Information System (Bütler and Schlaepfer unpubl.). Because of the limitations of these techniques, the results produced involved densities of snags with a minimum dbh of 21 cm (i.e. numbers of trees per hectare). In contrast, the empirical model started from field measurements executed with the angle relascope technique and resulted in stand basal areas of snags with a minimum dbh of 10 cm (i.e. m^2 ha^{-1}). Due to the different measurement units and a different minimum dbh obtained by each approach, a transformation from n ha^{-1} to m^2 ha^{-1} was necessary for comparison purposes (Fig. 4). In spite of the different approaches, the predicted amounts of required snags were similar at a 70-80% probability of woodpecker presence (Fig. 5, Table 4). This fact allows us to strengthen the reliability of the derived snag targets.

We considered a basal area higher than 0.9 m^2 ha^{-1} (p(woodpecker presence) > 0.5 in both approaches) as favourable for the woodpecker. However, in order to maximise the probability of local woodpecker presence and following the precautionary principle, for management purposes we suggest a higher snag target value. For the last ten years, Swiss three-toed woodpecker populations have been stable or even increasing (Schmid et al. 1998). Among the possible reasons for population growth figures the under-exploitation of marginal mountain forests since the Second World War (Derleth et al. 2000), which is related to a rapid increase in timber harvesting costs (Brassel and Brändli 1999). In such conditions, the amount of dying and dead trees and the available food resources are likely to increase. A possible economic recovery of the timber market, leading to a harvesting intensification of marginal forests, however, could rapidly cause a reversal of the currently positive trend for the woodpecker population. Such considerations emphasise the usefulness of the precautionary principle. Spruce forests favourable to three-toed woodpecker breeding must contain, among other features, sufficient amounts of dying and dead trees. We recommend the following target values for dying and dead trees: about 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) of trees with a dbh $\geq$ 10 cm, corresponding to 14 standing trees per hectare with a dbh of $\geq$ 21 cm within an area with a size of an average home-range size (44–176 ha); i.e. corresponding to our sampling area of 100 ha. For such levels, the probability of three-toed woodpecker presence in our study was $\geq$ 0.9. As demonstrated in Figure 4, large snags are generally rare in managed forests (main mortality of small trees by stem exclusion processes), whereas their contribution to the total basal area is substantial. Considering the prime importance of large snags, we would argue that management recommendations either be given as basal area, or, if expressed in n ha^{-1}, should specify the minimum tree diameter, and the area in ha for which this recommendation applies. Density targets without diameter precision and area of application may fail to fulfil the ecological objective they aimed for (Table 5).

Our targets are higher than the dead wood amounts that have been measured in managed Swiss sub-Alpine forests, while they do not reach amounts measured in unmanaged forests (Table 5). Considering mean values for living trees in Swiss forests of 32.3 m^2 ha^{-1} and 354 m^3 ha^{-1} (Brassel and Brändli 1999), the suggested snag target values represent not more than 5% of the living wood stock. We argue that, even in production forests, such a loss in favour of biodiversity should be acceptable.

Our values are of the same order as the snag retention recommendations for North American and European forests that are based on cavity-nesting birds or other woodpecker species (Table 5). They are higher than Ammer's (1991) recommendations, which were not, however, based on ecological preferences of birds. Many snag requirements for different woodpecker species are based only on their use of snags as nesting trees (Imbeau and Desrochers 2002). They implicitly assume that snags required for nesting are an important limiting factor to woodpecker populations. Imbeau and Desrochers (2002) argued that such models are highly unlikely to be successful in predicting long-term habitat needs, considering the extensive use of snags for foraging. Unlike these models, our snag retention prescriptions are designed to ensure a continuous supply of foraging trees and go beyond the aim of maintaining a supply of potential nesting trees.

So far quantitative recommendations for forest management have been made mainly for the scales of trees and stands, but rarely for forest management units and landscapes. However, maintenance of viable populations involves the provision of targets at multiple spatial and temporal scales (Larsson 2001, Angelstam et al. unpubl.). Using area-demanding birds as modelling tools stresses the need for formulating targets at the levels of individuals, populations as well as metapopulations. For Alpine and boreal forests, bird groups such as woodpeckers (e.g., Pechacek and d'Oleire-Oltmanns, in press), grouse (e.g., Angelstam et al. 2001) and resident tits (e.g., Jansson and Angelstam 1999) are important focal species to begin with.

Hence, for a species as the three-toed woodpecker, which is dependent on a continuous supply in space and time of snags of a particular quality, there still remains work to be able to formulate targets within the framework of sustainable forestry for the following issues: 1) How far apart can home-range sized areas exceeding the stand scale target be? 2) What proportion of a landscape needs to be in what phase of successional development of snags to maintain a local viable population? 3) Finally, in regions with other forest dynamics than the gap-phase dominated one prevailing in Alpine forests, the large-scale succession after stand-replacing disturbances need to be accounted for.

5. Conclusion

In this study we presented a model based on energetic needs of three-toed woodpeckers. Although simple, it enabled the quantification of snag requirements for this woodpecker species, which has been corroborated by a field study approach. The results made it possible to identify the snag quantities of local forest patches that are necessary to maximise the probability of local three-toed woodpecker presence. Forest patches presenting optimal quantities may be mapped and integrated into management planning concepts in order to define strategies for the maintenance of local populations of this bird species. Since the three-toed woodpecker is an indicator of forest biodiversity, management aimed at the maintenance of this species will also enable the fulfilment of other biodiversity goals.

Acknowledgements

We are grateful to L. Bütler, I. and M. Richter, J. J. Sauvain, F. Schweingruber, G. Sengül and C. Vignon for their assistance in the field. We also would like to thank I. Iorgulescu for statistic and modelling advice; C. Hunziker (Chair of Photogrammetry, EPFL) and A. Pointet (Geographical Information System Laboratory, EPFL) for their technical help on aerial photo scanning and GIS software; P. Derleth, C. Lundström, J. J. Sauvain and four anonymous reviewers for their helpful comments on earlier versions of this manuscript, and Susan Cox for revising the English.

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Acknowledgements

I would like to sincerely thank my PhD advisor Prof. Rodolphe Schlaepfer, who gave me the opportunity to develop and accomplish a new research project in his laboratory. I thank him especially for his confidence in me, and for the freedom he has given me in this project. His continuous encouragement and advice, dynamism and enthusiasm have greatly contributed to this work.

I would also like to thank Prof. Per Angelstam, who kindly welcomed me in Sweden, and generously offered me his time, experience and extensive knowledge in biodiversity conservation. I also express my gratitude to the other members of the PhD jury for their interest in my work and all their helpful comments: PD Dr M. Bolliger, Prof. H. Harms, and Dr C. Neet.

Special thanks go to Peter Ekelund, who collected all data in Sweden, and kindly placed them at my disposal for this PhD. I would also acknowledge Pascale Derleth and Cécile Vignon, who provided me with dead-wood data from their diploma work. I am particularly indebted to the Swiss ornithological centre (Sempach), to P. Beaud, R. Hess, L. Maumary, P. Wegmüller, and other local birdwatchers for data on woodpecker breeding.

For their assistance in the field, I thank: I. Bütler, L. Bütler, I. and M. Richter, J.J. Sauvain, F. Schweingruber and G. Sengül.

For technical help with aerial photos, GIS and statistics I would like to thank: R. Furrer, C. Hunziker, Prof. O. Kölbl, C. Mosimann, A. Pointet, M. Riedo, and H.-U. Scherrer (GEOPLAN LTDA).

I would also like to thank all my colleagues and friends from the Laboratory of Ecosystem Management for the great working atmosphere they were able to establish. In particular, I thank Ion Iorgulescu for his multiform help and numerous valuable suggestions! I also thank Christian Glenz, Vincent Gorgerat, Natalia Hasler, and Corinne Lundström.

For helpful comments on the manuscripts and revising the English, I thank V. Barbezat, S. Cox, Prof. B. Frochot, M. Howett, and J.A. Jackson.

I am grateful to many people at different Forest Offices for providing information, in particular A. Annen, R. Ehrbar, M. Fuchs, F. Laimbacher, and N. Walliser.

I would like to thank my friends in Sweden and Austria M. Breuss, P. Ekelund, and G. Mikusinski, for their warm reception.

I especially thank my husband Jean-Jacques Sauvain for his patience and great moral and scientific support!

There are many other people who have directly and indirectly, through remarks, constructive critique, or scientific discussion, contributed to this work. May these lines express all my gratitude to them.

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