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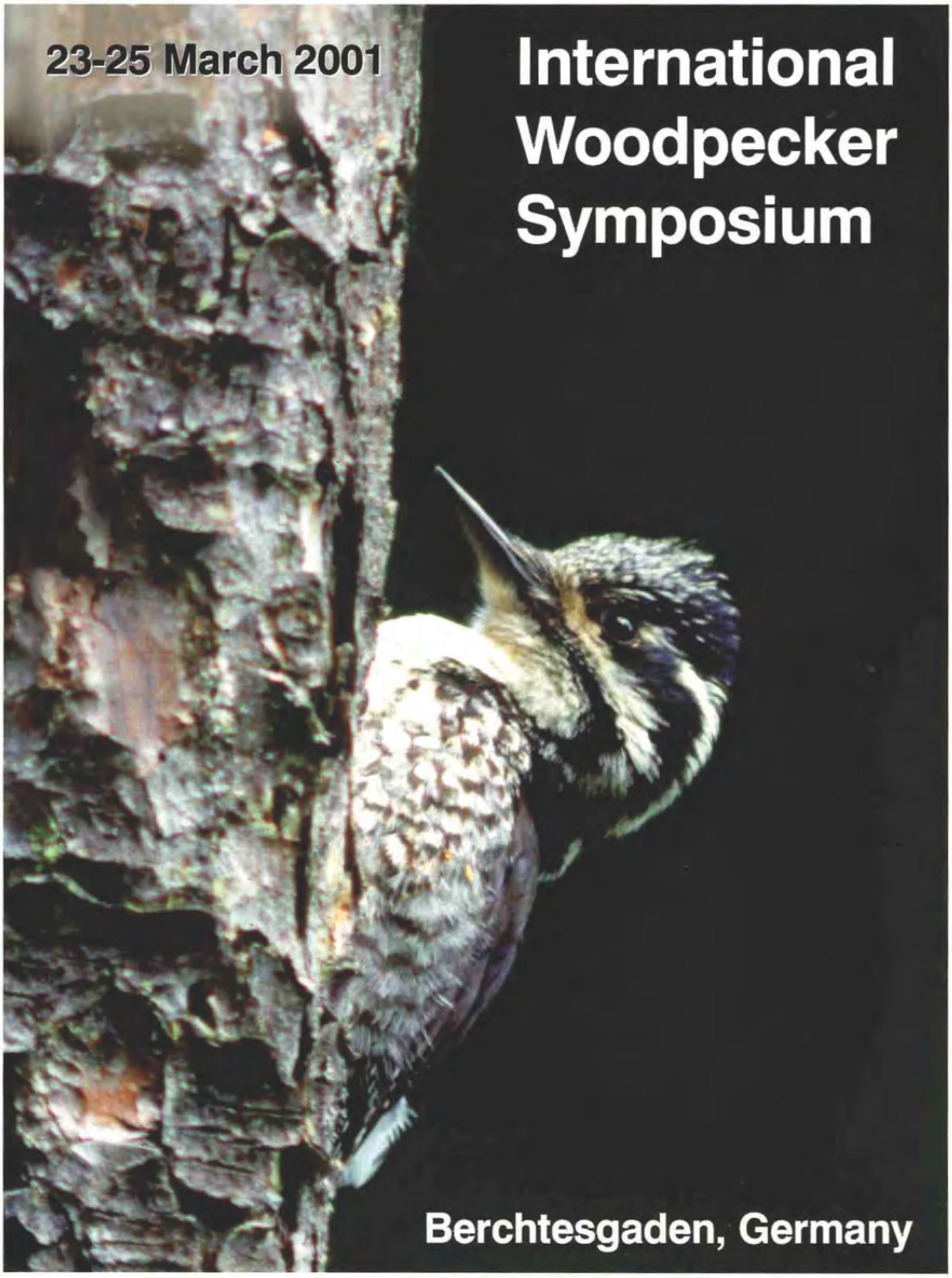

23-25 March 2001

International Woodpecker Symposium

Berchtesgaden, Germany

Forschungsbericht 48

Nationalpark
Berchtesgaden

International
Woodpecker Symposium

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and
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Forschungsbericht 48

Bayerische Landesanstalt
für Wald und Forstwirtschaft

BAYERISCHE
STAATSFORSTVERWALTUNG

Impressum:

Nationalpark Berchtesgaden
Forschungsbericht 48/2002

Herausgeber:
Nationalparkverwaltung Berchtesgaden, Doktorberg 6,
D-83471 Berchtesgaden, Telefon 0 86 52/96 86-0, Telefax 0 86 52/96 86 40,
e-Mail: poststelle@nationalpark-berchtesgaden.de
Internet: http://www.nationalpark-berchtesgaden.de
im Auftrag des Bayerischen Staatsministeriums für Landesentwicklung und Umweltfragen

ISSN 0172-0023
ISBN 3-922325-51-3

Druck: Berchtesgadener Anzeiger, Berchtesgaden

Gedruckt auf chlorfrei gebleichtem Papier

Schriftleitung: Dr. Peter Pechacek und Dr. Werner d'Oleire-Oltmanns

Titelbild: Dr. Peter Pechacek

Fotos:
K. George, R. Hill, T. Hochebner, Dr. J. A. Jackson, H.-J. Kampfenkel,
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International Woodpecker Symposium

Preface

Woodpeckers represent a distinct group of birds characterized by a unique combination of various highly derived features. Their arboreal habits and the attractive coloration of many of their species make woodpeckers well-known and popular birds. Practically all aspects of their morphology and anatomy are influenced by their life style that is closely associated with forests throughout the world. The family is widespread and the ranges of its 214 members cover a wide range of habitats and altitudes including savannas, desert scrub and mountain grasslands. The lack of woodpeckers is only documented for the Australasian region, extreme desert areas and many islands including Madagascar.

More than any other group of birds, woodpeckers are well adapted to their tree dominated environment. The life of most species is based on chiselling out holes in dead or live wood, in which these birds roost and breed, and on gleaning prey from trees, probing into crevices, prying off bark, or excavating for wood–boring insect larvae. Their ability not only to dig various arthropods and their grubs out of holes in trees or in the ground but also to excavate their own nest holes in trees gives them a distant advantage over other birds. In addition, some woodpecker feed on the sugary sap which oozes from specially excavated holes, rob anthills, store food, or use anvils for pounding large prey items, opening nuts or extracting the seeds from cones. Combinations of these activities make woodpeckers important indicator and key-stone species of natural forests. Besides, most of these activities leave traces which can be identified by the observant naturalist, and thus, woodpeckers appear in children songs, cartoons, and scientific work providing them with fascination and sympathy. Yet they may sometimes also run counter to man's own interest or even constitute a nuisance.

Woodpeckers, however, do suffer much more from man as they benefit from this relationship. Loss of habitat is the main reason for decline or even extinction of woodpecker populations. Out of this concern, ecological information on various aspects of woodpecker's biology is the key issue to providing land managers with data essential for stopping or at least slowing-down the process of habitat loss. Serious action to preserve woodpecker habitats to maintain biodiversity can only be taken if we improve our knowledge on woodpecker biology. National Parks have good reason to get primarily involved in research on these animals because their protected status provides information when man's influence has been mostly eliminated. This enables scientists to approach the issue more sophisticated by sorting out data gathered under natural conditions from data collected in forests managed by man. A long-term monitoring of woodpecker populations in Berchtesgaden National Park permanently proves this approach successfully.

Woodpecker ecology and practical approaches in conservation strategies have been chosen to be emphasized during the 5th International Woodpecker Symposium held in Berchtesgaden, Germany 23–25 March 2001. The purpose of this Symposium was to bring together researchers, conservation biologists, ecologists, resource managers, and environmentalists to develop better understanding and conservation management of woodpeckers. During our days together, we have explored many issues of global importance of woodpecker ecology and conservation. We have also strengthened existing partnerships among involved institutions and created new networks for cooperation among woodpecker enthusiasts. This Proceedings provides a permanent record of the ideas and issues presented in Berchtesgaden and represents a very wide diversity of papers, ranging from descriptive and heuristic offerings to tightly designed manuscripts. We believe that contributions to the 5th International Woodpecker Symposium in Berchtesgaden improved our knowledge on ecology of woodpeckers, and that the following papers may help create new management strategies to save these magnificent birds and their habitats for future generations.

About this Proceedings

All presenters were asked to submit manuscripts at the time of the Symposium or one month later. We received the manuscripts, did a brief review and provided authors with editorial comments and suggestions for revision. After receiving revised drafts from the authors, we sent all acceptable papers out for English editing and additional comments. Each paper re-received from the authors was then minimally edited and we prepared a draft of the complete proceedings. Contributions were compiled in alphabetical order following the name of the first author. We then asked authors to check the proofs. After receiving checked papers, we did the final proofreading.

Suggested citation format of this Proceedings is:

Entire book

PECHACEK, P. & W. D'OLEIRE-OLTMANNS, 2003: International Woodpecker Symposium. Proceedings. Forschungsbericht 48, Nationalparkverwaltung Berchtesgaden. 192 pp.

Individual paper in the book

BÜTLER R. & R. SCHLAEPFER, 2003: Three-toed woodpeckers as an alternative to bark beetle control by traps? Pages 13–26 *in* P. PECHACEK & W. D'OLEIRE-OLTMANNS: International Woodpecker Symposium. Proceedings. Forschungsbericht 48, Nationalparkverwaltung Berchtesgaden.

Acknowledgments

We extend our deepest thanks to all of you who were able to participate in the 5th International Woodpecker Symposium. This volume has taken an enormous amount of work to complete. Our thanks goes to all authors for their patience to keep up with our manuscript guidelines. Petra Welz helped to prepare editorial comments. We thank Dr. Jerome A. Jackson and Alison R. Styring for kindly editing the revised manuscript versions, and checking the English language. Katja Polzer did the final proofreading. People from the National Park Administration in Berchtesgaden, in particular its former leader Dr. Hubert Zierl, and employees of the Bavarian State Institute of Forestry, in particular its president Olaf Schmidt provided the main personal and financial support for the Symposium, and this Proceedings. Sponsoring was also provided by the Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen, the Deutsche Forschungsgemeinschaft, the Deutsche Ornithologen-Gesellschaft, the Waldförderverein e.V., and a large number of Symposium participants. We would also like to say a special thanks to Oliver Conz and Dr. Klaus Ruge for their cooperation in the development of the Symposium.

Berchtesgaden, 27 November 2002

Dr. Peter Pechacek
Dr. Werner d'Oleire-Oltmanns

The ecology of the Black Woodpecker in Mont Avic Natural Park (Italian Western Alps)

Die Ökologie des Schwarzspechts im Mont Avic Naturpark (Italienische Westalpen)

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Abstract

In 1996 the Natural Park of Mont Avic began a study on the Black Woodpecker *Dryocopus martius*; in 1999 a more comprehensive study project was coordinated with the Department of Animal and Human Biology of the University of Turin. The aim of the project was to obtain a precise evaluation of the number of territorial adults occurring in the entire sample area and to examine various aspects of species ecology on a local level: habitat selection during every phase of the annual cycle, characterisation of the environmental parameters of nesting sites, evaluation of the reproductive success, determination of individual and pair home-ranges, and roosting use of cavities. The search for trees with nests (26 as of 1999) was carried out by systematically examining the entire area under investigation. The repeated mapping of territorial observations during March-June and the periodic checking of all cavities by a microscopic television camera suggested the presence of at least 6 pairs and 2 unpaired males in an area of 1950 ha. Ecological characteristics associated with nesting clearly emerged from the comparative analysis of the environmental parameters recorded at nesting and control sites. A monitoring programme using radio-tracking was started in February 2000, and is providing an interesting preliminary set of eco-ethological data. From a methodological point of view, it should be observed that a simple check of the nests containing eggs or young was not enough to obtain a reliable evaluation of either the number of territorial birds actually present, or of their reproductive success. It is therefore of interest to conduct a study of contiguous territories, quantifying the frequency of unpaired birds, the percentage of couples that lay eggs and rear their young, and the number of fledglings.

Im Naturpark Mont Avic wurde 1996 mit einer Untersuchung über den Schwarzspecht begonnen; seit 1999 wird die Studie umfassender durchgeführt, in Zusammenarbeit mit dem Institut für Tier- und Humanbiologie der Universität Turin. Das Ziel des Projekts ist es, eine genaue Bewertung der Anzahl von territorialen adulten Tieren im gesamten Untersuchungsgebiet zu erhalten und verschiedene Aspekte der Ökologie der Spechte auf einer lokalen Ebene zu untersuchen: Habitatwahl während jeder Phase des jährlichen Zyklus, Charakterisierung der Umweltparameter von Nistplätzen, Bewertung des Reproduktionserfolgs, Bestimmung der Home Ranges von Individuen und Paaren, Nutzung von Höhlen als Brutstätten. Die Suche nach Bäumen mit Nisthöhlen (26 bis 1999) wurde systematisch auf der gesamten Untersuchungsfläche durchgeführt; das wiederholte Kartieren von Beobachtungen mit territorialem Verhalten von März bis Juni und die regelmäßige Kontrolle aller Höhlen mit einer mikroskopischen Fernsehkamera deutete auf die Anwesenheit von mindestens 6 Paaren und 2 unverpaarten Männchen in dem 1.950 ha umfassenden Gebiet. Die deutlich spezifischen ökologischen Charakteristika der Nestwahl ergeben sich aus der vergleichenden Analyse von Umweltparametern, die an Neststandorten und Kontrollpunkten aufgenommen wurden. Das Monitoringprogramm mit Hilfe der Telemetrie, welches im Februar 2000 begonnen wurde, liefert ein extrem interessantes Grundgerüst an öko-ethologischen Daten. Zum methodischen Ansatz ist hervorzuheben, dass eine einfache Kontrolle der Nisthöhle mit Eiern oder Jungtieren nicht ausreicht, um eine zuverlässige Bewertung der Anzahl von tatsächlich anwesenden territorialen Vögeln und ihres Reproduktionserfolgs zuzulassen: Es ist daher von besonderer Bedeutung, eine Studie in aneinandergrenzenden Territorien durchzuführen, sowie die Zahl der unverpaarten Vögel, den Anteil von Paaren, die Eier legen und ihre Jungen auch aufziehen und die Anzahl von flüggen Jungvögeln zu ermitteln.

Introduction

In 1996 the Natural Park of Mont Avic began a study on Black Woodpeckers *Dryocopus martius* inhabiting a forest area (2000 ha, 900–2200 m a.s.l.) mostly covered by pines *(Pinus uncinata* and *Pinus sylvestris)*. In 1999, a more comprehensive study project was coordinated with the Department of Animal and Human Biology of the University of Turin and the study area was extended to the whole Chalamy and Pialong (two tributary streams of the Dora Baltea) basin (Aosta Valley). The aim of the project was to obtain a precise evaluation of the number of territorial adults occurring in the entire sample area and to examine various aspects of species ecology on a local level. Habitat selection during every phase of the annual cycle, characterisation of the environmental parameters of nesting sites, evaluation of the reproductive success, and determination of individual and pair home-ranges, roosting use of cavities were the primary objectives.

Black Woodpecker **(Photo: Peter Pechacek)**

Materials and methods

The search for trees with nests was carried out by systematically examining the entire area under investigation. Numerical estimates were obtained through the repeated mapping of individuals seen or heard during March-June through the periodic checking of all cavities by a microscopic television camera. Play backs of drumming were used to elicit interactive responses in sectors where no spontaneous drumming or vocalisations were heard during at least two following visits. Line-transect methods (TJERNBERG et al. 1993) were not used because of the complex topography characterised by steep slopes and lack of tracks. Major ecological nesting site characteristics selected by woodpeckers were determined by comparing the environmental parameters (i.e. slope, exposure, forest density and composition, occurrence of leafy branches up to 10 m from the ground) recorded at the nesting and control sites over a circle area of 20 m radius (BOCCA & FALCONE 1999). A radio-tracking monitoring programme began in February 2000. Birds were captured by means of nets mounted on telescopic poles at roosting sites. To avoid any possible disturbance on breeding, captures were made in autumn and winter. Radio-transmitters (7 g) were tail-mounted (KENWARD 1987). Fixes were obtained through triangulation or approaching birds, at intervals no shorter than 30 min.

Results

Forty-one trees with nests and 5 with uncompleted nests were sampled from 1996 to 2000. Most of the trees (36) were still alive; others were dead (8) or withering (2). The majority of trees were clustered (39 grouped in 7 clusters) and only 7 were isolated. Minimum distance between two simultaneously occupied nests was 900 m. Nest site characteristics (Table 1; Fig. 1, 2 and 3) are reported by BOCCA & FALCONE (1999). In steep

Table 1. Ecological characteristics of nesting and control sites.

Parameters	Reproductive sites	Control sites	χ^2 Test P-Level
trees/ha	52	53	n.s
mean diameter (h = 130 cm)	26.6 cm	17.6 cm	$p < 0.01$
Σ diameter (h = 130 cm)	1569 cm	1127 cm	$p < 0.05$
occurence of leafy branches			
layer 0–3 m	44 %	75 %	$p < 0.01$
layer 3–10 m	74 %	90 %	$p < 0.01$
layer > 10 m	68 %	47 %	$p < 0.01$
mean slope	31°	22°	$p < 0.01$
mean altitude	1355 m	1660 m	$p < 0.01$
dominant trees:			
- *Fagus sylvatica*	50 %	3 %	
- *Pinus sylvestris*	36 %	26 %	
- *Pinus uncinata*	7 %	48 %	
- *Larix decidua*	/	23 %	
- *Betula pendula*	7 %	/	

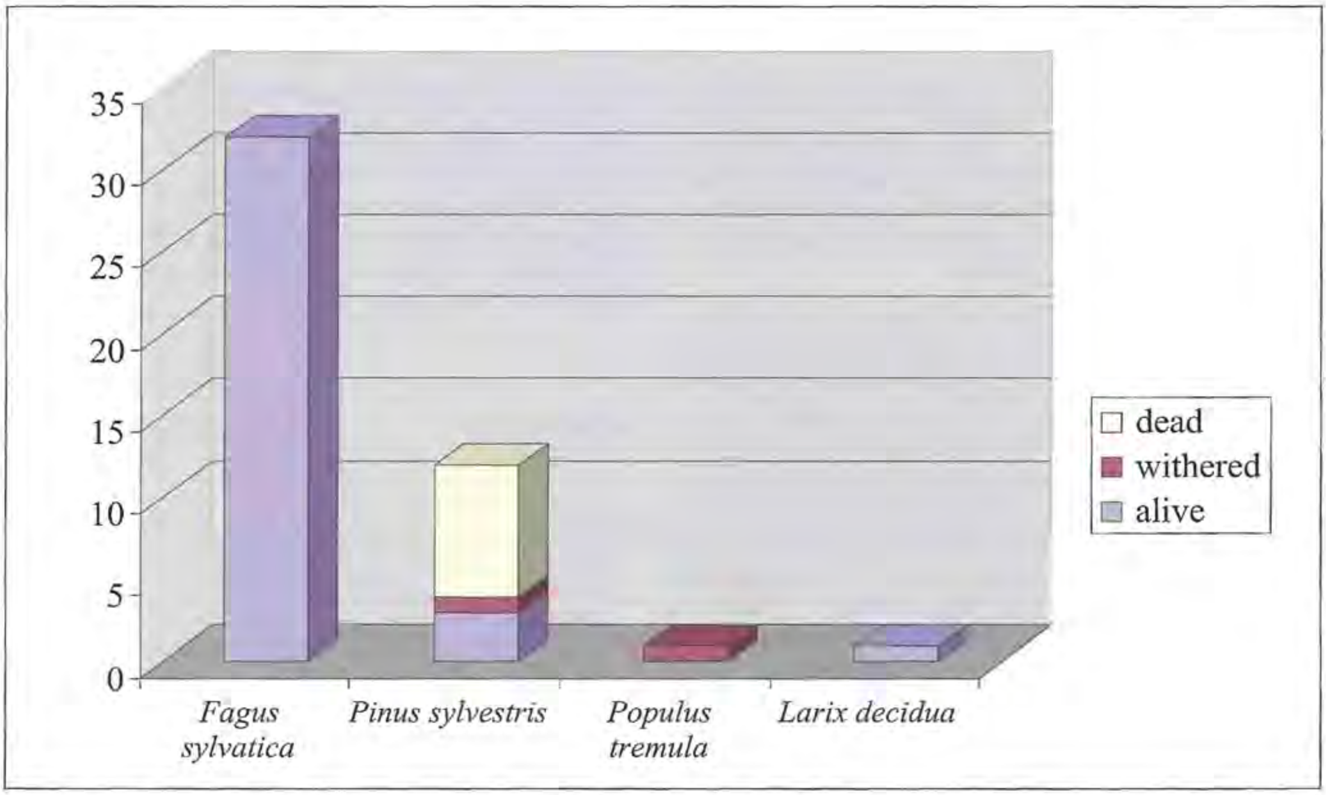

Fig. 1. Trees where cavities (both completed or uncompleted) were excavated.

slope conditions, entrance holes were valley-oriented (maybe an anti-predatory strategy), in keeping with previous observations in Germany (LANGE 1995). Nesting trees were not uniformly scattered over the study area: no nesting holes were found in the South-eastern sector, covered by thick *Pinus uncinata* forests. However, most of the area was used for feeding: Black Woodpeckers were in fact observed from 700 to 2,150 m a.s.l. in 70 % of the forested 500 x 500 m squares studied. Observations carried out from 1986 to 1999 confirmed that young *Pinus uncinata* sectors characterized by small diameter and thick trees were also used for feeding.

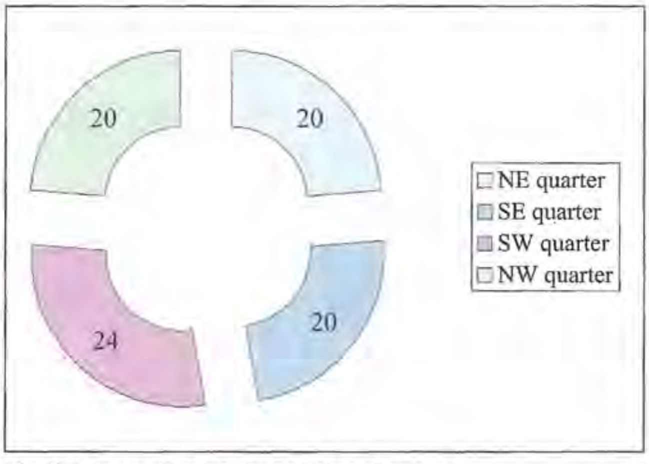

Fig. 2. Exposure of entrance holes of nests.

In 1999, 6 nesting pairs and 2 unpaired males were detected over a sampling area of 1,950 ha. Two pairs successfully bred, three pairs did not lay eggs, and the male of the sixth pair disappeared at the end of April. Mean distance between nearest bordering pairs (CLARK & EVANS 1954) was 1050 m (nearest occupied nest hole; range 800–1,600 m). In 2000, at least five pairs successfully bred in an area of 2,500 ha. Potential nesting sites, however, were poorly monitored.

To date, four birds have been radio-tracked during spring and summer (2000) and seven during winter (2000–2001).

During the non-reproductive period, sometimes the same cluster of trees with holes were used contemporaneously by several roosting birds (up to five individuals along a 200 m linear transect, seven individuals along 550 m. During one night two Black Woodpeckers and one Green Woodpecker *Picus viridis* roosted in holes of the same beech tree).

Discussion

Val Chalamy forests, despite the paucity of large trees, are densely inhabited. Preliminary density estimates suggest one pair/300–370 ha, which is higher than the mean value of one pair/400 ha reported by GLUTZ VON BLOTZHEIM & BAUER (1980) for Central Europe. The clustered distribution of nest sites, which is dependent on availability of suitable trees, is very different from the regular spacing of territories suggested for Pyrenees and Scandinavia forests (FERNANDEZ & AZKONA 1996, TJERNBERG et al. 1993). Radio-tracking data provide additional information on range-overlap, seasonal movements and habitat selection for comparison with work done in previous studies carried out in Scandinavia (ROLSTAD et al. 1998).

From a methodological point of view, it should be observed that a simple check of nests containing eggs or young is not enough to obtain either a reliable evaluation of the number of territorial birds actually present, or a reliable estimate of reproductive success. It is therefore of interest to conduct a study of contiguous territories, quantifying the frequency of unpaired birds, the percentage of couples that lay eggs and rear their young and the number of fledglings. Therefore, as suggested for diurnal birds of prey (MATHIEU & CHOISY 1982), reproductive success must be calculated by considering the number of territorial pairs monitored not the mere number of nests with eggs or nestlings.

Acknowledgments

Our study was supported by the Aosta Valley Autonomous Region – Assessorato Territorio Ambiente e Opere Pubbliche. Captures were co-ordinated by guards of the Mount Avic Natural Park, E. Broglia and M. Gamba. Many people radio-tracked and/or observed birds in the field: M. Ortolan and V. Napoli (Università di Torino); J. Garcel, M. Jacquand and J. Ruel Gallay (I.R.E.O. de Mondy- F), P. Lovato (L.E.G.T.A. de St-Laurent- F), S. Ballesteros and G. Bontemps (L.E.G.T.A. de Vendôme- F), E. Duchenne (Università di Gembloux- B), E. Broglia, M. Gamba, G. Marquis e P. Zappa (Parco naturale del Mont Avic).

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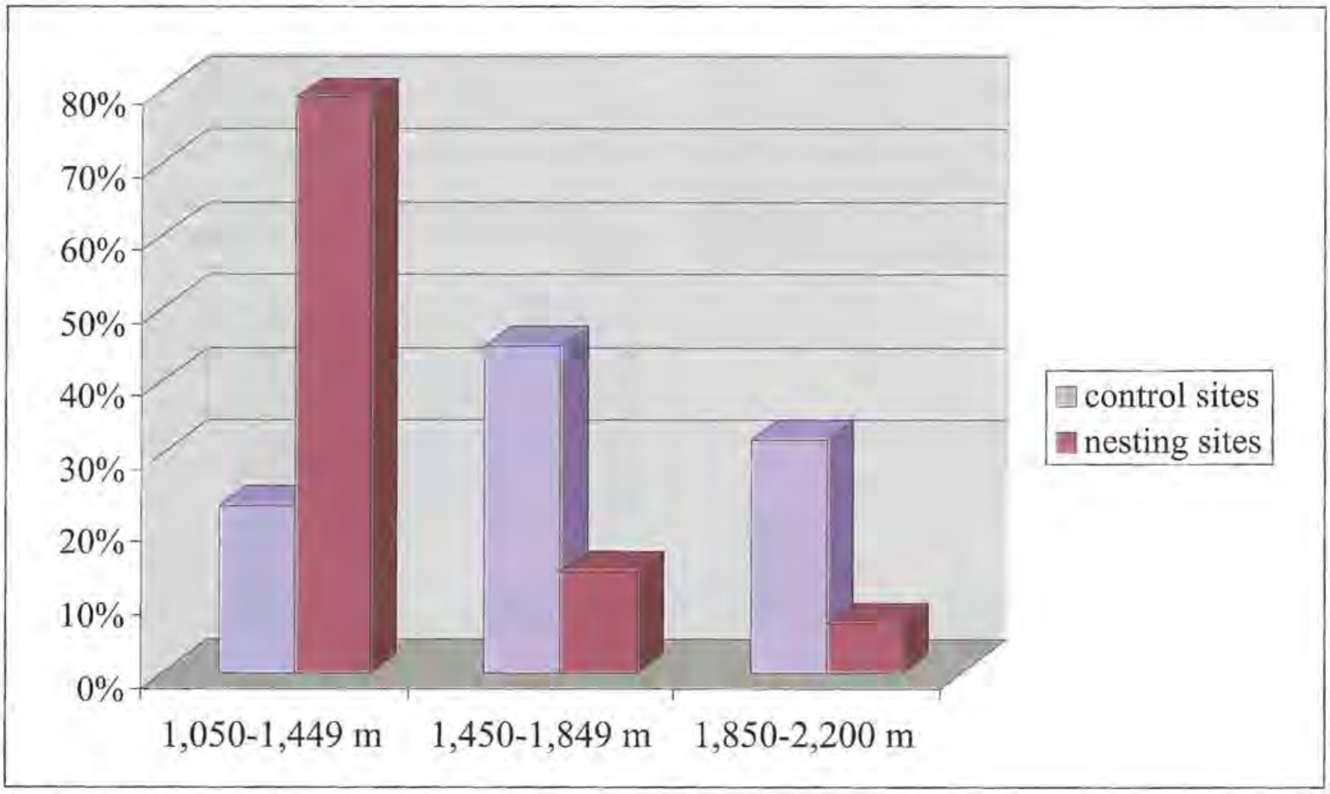

Fig. 3. Altitude of nesting and control sites.

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

Dreizehenspechte als Alternative zur Überwachung von Borkenkäferpopulationen mittels Pheromonfallen?

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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.

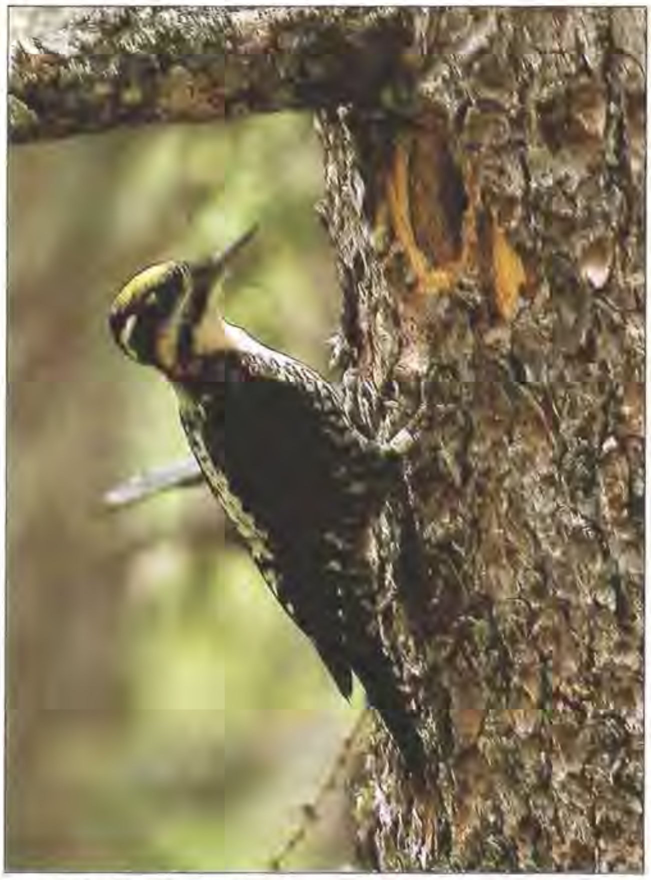
In dieser Studie wurde die Wirksamkeit des Dreizehenspechtes als natürlicher Feind des Borkenkäfers mit Fangzahlen von Pheromon-Borkenkäferfallen verglichen. Der berechnete Energiebedarf des Spechtes und die daraus resultierende Anzahl vertilgter Käfer wurde Daten aus Schweizer Borkenkäferfallen-Statistiken 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 Hektar (Brusthöhendurchmesser ≥ 21 cm) patchworkartig auszuscheiden.

Introduction

The Three-toed Woodpecker *Picoides tridactylus* is a highly specialised bird that feeds on bark beetles (HOGSTAD 1970, 1978, SEVASTJANOW 1959 cited in SCHERZINGER 1982, HESS 1983, FORMOSOW et al. 1950 cited in GLUTZ VON BLOTZHEIM 1994). 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.).



Three-toed Woodpecker **(Photo: Gottfried Reidler)**

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 its 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*?

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.

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 (Fig. 1):

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.

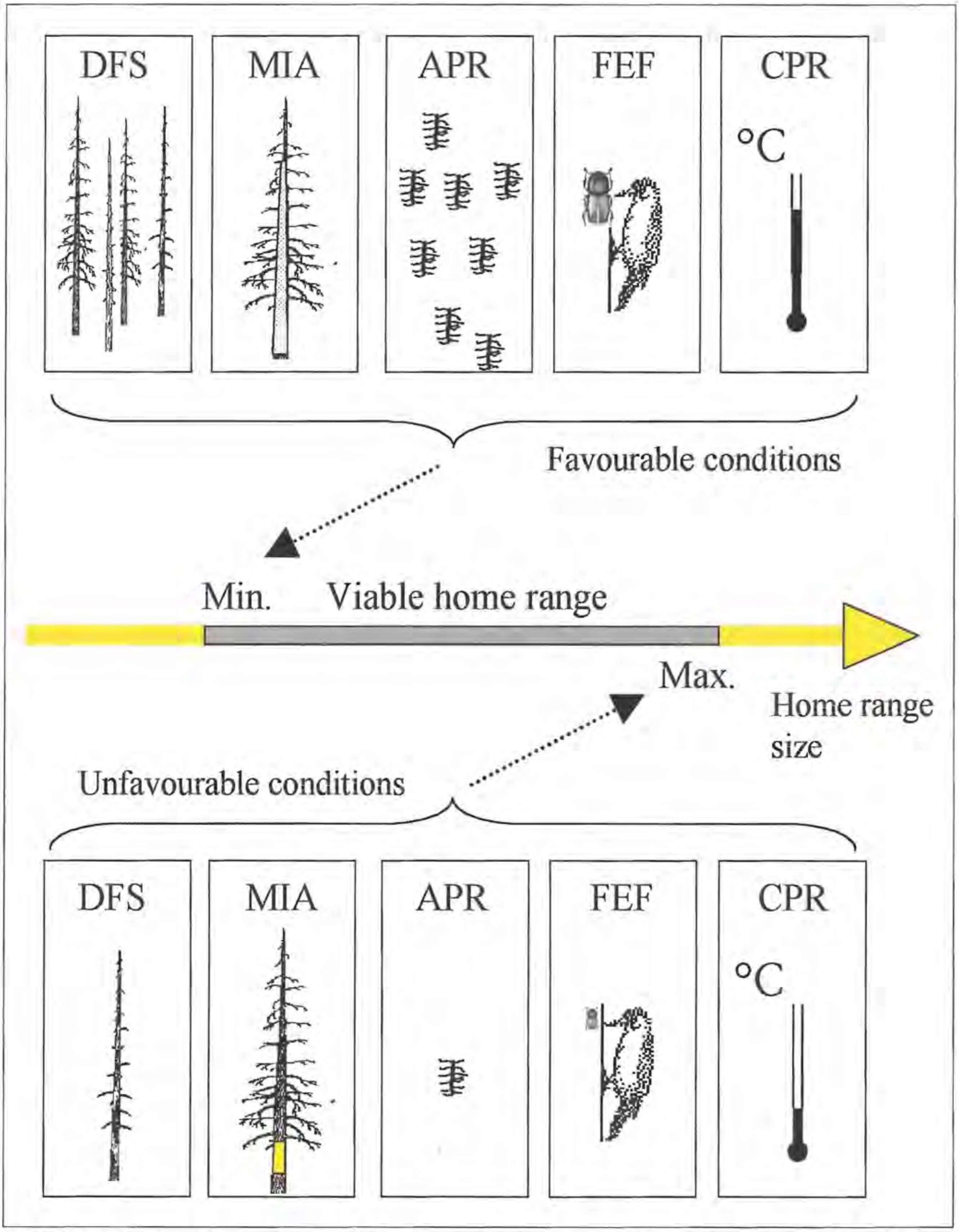


Fig. 1. Different factors influence the potential home range size of a Three-toed Woodpecker. Extremely favourable / unfavourable conditions lead to a minimal / maximal viable home range size. DFS = Density of potential Foraging Substrate, MIA = Mean Infested Area of potential foraging substrate, APR = Available Prey in the foraging substrate, FEF = Foraging Efficiency of the woodpecker, CPR = Consumed Prey during a time unit.

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").

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 infrared 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.

Results and Discussion

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 pers. comm.). 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 $((63.3-0.37 * (0° / (5/9) + 32)) * 4185\ J / 83.7\ J = 2{,}573)$. 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.

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 1,000–1,500 breeding pairs, that is 2,000–3,000 individuals. According to our calculations the whole woodpecker population, i.e. 2,500 individuals, consumes, during one year, about 1,675,000,000 (1675 million) bark beetles.

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	1680	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.

Bark beetle trap statistics

Since 1984 pheromone traps have been installed in Switzerland, in order to control *Ips typographus*. In Fig. 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 6,272 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, pers. comm.). The proportion of larvae and adult beetles in 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.

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 pers. comm.).

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.

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

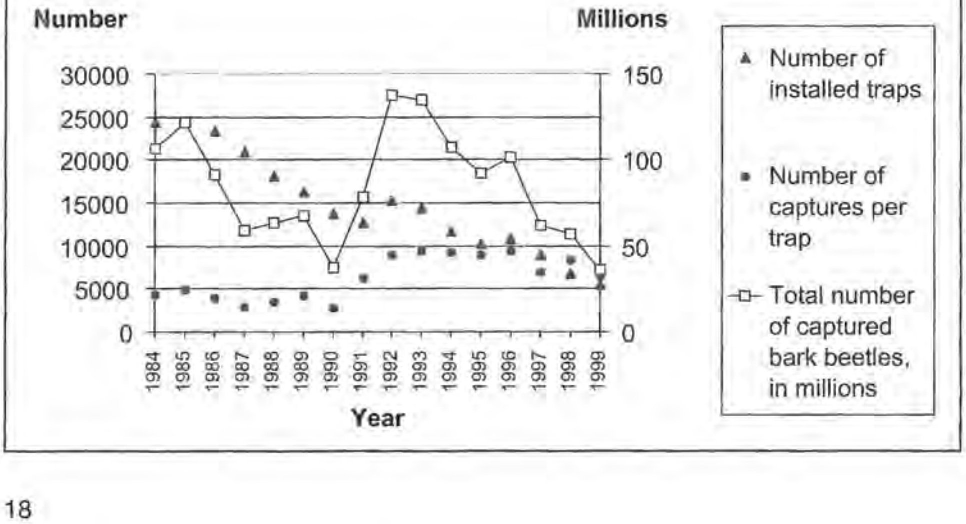


Fig. 2. Number of installed bark beetle *Ips typographus* traps in Switzerland since 1984, number of captures per trap and total number of yearly captured beetles. After the storm "Vivian" of February 1990, an increase, both, of the total number of captured beetles and beetles per trap is visible. Data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

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 < 1,200 new beetle attacks of > 10 spruce trees, i.e. the years 1989–90 and 1998–99. The epidemic level is defined as years with > 3,000 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.

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 re-

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 statistical period for bark beetle traps is from 1984 to 1999.

	Consumend 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	
Scenario *5)*	1 individual	whole pop. (Mio.)	E_W	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	670,000	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	1,172,500	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	3,182,500	7961	1260 F 5040 M	16.9 F 67.7 M	25,200	338	126.3	23.6
Endemic level *3)*										
Low	670,000	1675 L	670,000	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	1,172,500	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	3,182,500	7961	1080 F 4320 M	9.9 F 39.5 M	21,600	198	147.3	40.2
Epidemic level *4)*										
Low	670,000	1675 L	670,000	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	1,172,500	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	3,182,500	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

port 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.

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

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.)

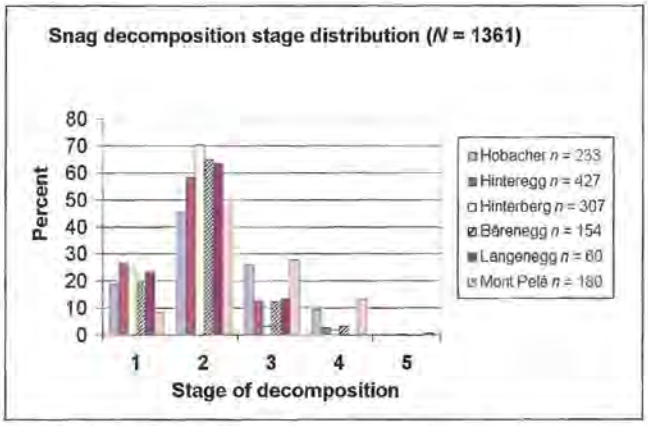


Fig. 3. Percentage of snags in different stages of decomposition: 1: declining or recently dead, 2: loose bark, 3: clean and hard snag, 4: clean and soft snag, 5: broken, decomposed snag.

> 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 (Fig. 3) shows a similar pattern for all study sites with 58 to 94 percent of the snags belonging to stages 1 and 2.

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

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. ≥ 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 subalpine mountain forests, we expect only one beetle generation per season and set the egg laying to the second week of June (NIERHAUS-WUNDERWALD 1995). Fig. 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 (1958), 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}.

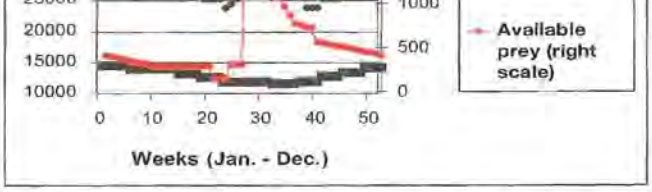


Fig. 4. Estimated number of weekly consumed *Ips typographus* items by one Three-toed Woodpecker and a woodpecker family, respectively. Estimated available *Ips typographus* items per m^2 bark (all development stages without eggs) for an attack density of 150 nuptial chambers per m^2 (endemic level) 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))$^{-1}$.

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 (Table 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, SCHERZINGER 1982, HESS 1983, PECHACEK 1995, DORKA 1996, PECHACEK et al. 1999, RUGE et al. 1999).

For our study sites we get the following PHR:

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

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

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

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

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

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

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?

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
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

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] $Pr(X_a < Z < X_b) = 95$ %

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.

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 Fig. 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).

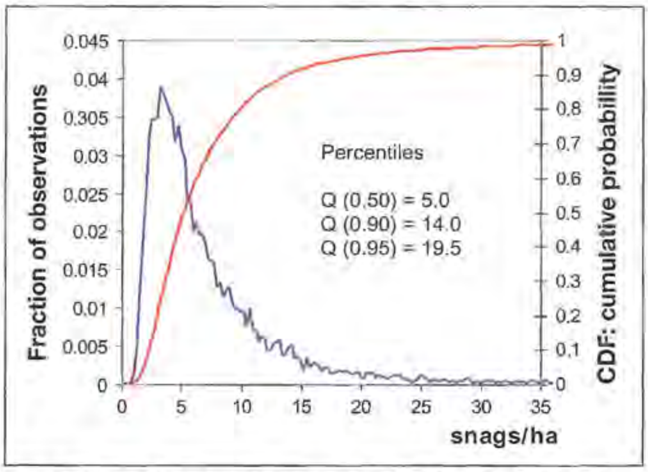


Fig. 5. Simulated probability distribution function of the snag density required to meet the Three-toed Woodpecker's foraging needs and required snag densities for different probability levels. CDF = Cumulative distribution function. The input model is DFS = (PHR * APR * FEF * MIA) –1 * CPR.
DFS = density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

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 (P. PECHACEK pers. comm.). 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.

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

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

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

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.

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 (ANGELSTAM & MIKUSINSKI 1994, AMCOFF & ERIKSSON 1996, 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 benchmarks. 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. ≥ 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. ≥ 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.

Acknowledgments

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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Reaktionsbereitschaft von Kleinspechten auf Klangattrappen

Response of Lesser Spotted Woodpeckers to playbacks

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Kurzfassung

Kleinspechte *Picoides minor* sind wegen ihrer geringen Größe und heimlichen Lebensweise schwierig zu erfassende Vögel. Der Einsatz von Klangattrappen könnte eine wichtige Methode sein, um die Kartierung dieser Spechtart zu erleichtern. Die Reaktion von Kleinspechten auf Klangattrappen ist jedoch nur spärlich dokumentiert. Im Rahmen dieser Untersuchung wurden zwischen Februar und Juni 1999 Klangattrappenversuche an 15 besenderten Kleinspechten (7 Weibchen und 8 Männchen) im Taunus (Hessen) durchgeführt. Ziel der Arbeit war es, Parameter zu finden, die die Reaktion auf Klangattrappen beeinflussen. Beim Einsatz von Klangattrappen war die Reaktionsbereitschaft von Männchen und Weibchen während der Balzzeit am größten (61 %). Die Reaktionsbereitschaft beider Geschlechter hing allerdings von der Art der eingesetzten Klangattrappe ab (Männchenruf, Weibchenruf, Trommelreihe). Andere Parameter hatten keinen signifikanten Einfluss auf die Reaktionsbereitschaft der Kleinspechte. Hinsichtlich der tageszeitlichen Verteilung der positiven Reaktionen war der Anteil in den Morgenstunden aber tendenziell größer.

The Lesser Spotted Woodpecker is a small and inconspicuous species that is easily overlooked. The birds are difficult to map and the use of playbacks could be a helpful method to solve this problem. Response of Lesser Spotted Woodpeckers to playbacks is hardly described in recent literature. Within this study playback-experiments were carried out at 15 radio-tracked Lesser Spotted Woodpeckers (7 females, 8 males) near Frankfurt/Main, Germany. The study was conducted between February and June 1999. The objective was to reveal whether the woodpeckers respond at all and if there were seasonal differences. The highest proportion of response to playbacks was during the mating season for both sexes (61 %). The kind of playback used (call of male, call of female, drumming) influenced the reaction of the sexes in different ways. Other parameter tested had no significant influence although there was a tendency for better responding in the morning.

Einleitung

Der Kleinspecht *Picoides minor* ist nur kleibergroß und damit die kleinste der europäischen Spechtarten (GLUTZ VON BLOTZHEIM & BAUER 1980). Europaweit verläuft der Trend des Kleinspechtbestandes negativ (u.a. MIKUSINSKI & ANGELSTAM 1997). Auch in der Bundesrepublik Deutschland scheinen die Bestände des Kleinspechts zumindest lokal rückläufig zu sein (HAVELKA & RUGE 1993, CONZ 1997). In der Roten Liste der bestandsbedrohten Brutvogelarten in Hessen wird der Kleinspecht als gefährdet eingestuft (Hessisches Ministerium des Inneren und für Landwirtschaft, Forsten und Naturschutz 1997).

Die Bestandsaufnahme ist bei dieser Art sehr problematisch. Aufgrund der geringen Größe und heimlichen Lebensweise des Kleinspechts ist sein Bestand mit den meisten heute üblichen Kartierungsmethoden nicht ausreichend genau zu erfassen (SPITZNAGEL 1993). Daher wird er als „schwierig zu erfassende Art" eingestuft (OELKE 1975).

Angesichts dieser Problematik spielen die artspezifischen Lautäußerungen des Kleinspechts eine wichtige Rolle, um ihn im Freiland dennoch auffinden zu können. Der Einsatz von Klangattrappen ist eine wichtige Methode, die bei anderen Arten bereits mit gutem Erfolg eingesetzt wurde (SCHUSTER 1971, EXO & HENNES 1977, JOHNSON et al.1981, MARION et al. 1981). Auch bei einigen Spechtarten hat sich der Einsatz von Klangattrappen bereits bewährt (SPITZNAGEL 1993, SÜDBECK & GALL 1993, HARTEL 1998, TOMEC & KILIMANN 1998). Die Reaktion von Kleinspechten auf Klangattrappen ist jedoch nur spärlich dokumentiert (ZABKA 1979, MIRANDA-GUT 1998, HÖRENZ 2000). Über Faktoren, welche die Reaktionsbereitschaft der Kleinspechte beeinflussen könnten ist ebenso wenig bekannt wie über geschlechtsspezifische Unterschiede. Um Klangattrappen gezielt einsetzen zu können, ist es besonders wichtig den Einfluss äußerer Faktoren beurteilen zu können. Nur dann ist der Erfolg beim Einsatz von Klangattrappen abzuschätzen.

Im Rahmen dieser Untersuchung standen folgende Fragen im Vordergrund:

- Welche Faktoren beeinflussen die Reaktion der Kleinspechte auf Klangattrappen ?
- Reagieren Männchen und Weibchen unterschiedlich auf Klangattrappen ?
- Ist der Einsatz von Klangattrappen geeignet, um Kleinspechte zu erfassen ?

Kleinspecht (Foto: Hans-Jürgen Kampfenkel)

Material und Methode

Untersuchungsgebiet

Die Untersuchung wurde in Hessen, nordwestlich von Frankfurt/Main durchgeführt (50°9'N, 8°27'E). Das Untersuchungsgebiet umfasst eine Fläche von ca. 70 km^2. Naturräumlich schließt es den Übergangsbereich zwischen Main-Taunus-Vorland und Vortaunus ein (KLAUSING 1988). Im Norden prägen besonders Streuobstwiesen die Landschaft. Daneben lassen sich hauptsächlich forstwirtschaftlich genutzte Flächen finden. Es wechseln sich Laubwald, insbesondere Eichen-Hainbuchenwald, Nadel- und Mischwald ab. Der Süden des Gebietes wird hauptsächlich zum Ackerbau und als Grünland genutzt. Kleinere Bereiche mit Wald- und Streuobstanteil sind in diesem Teil des Untersuchungsgebietes jedoch auch zu finden.

Besenderung

Während des Untersuchungszeitraums von Februar bis Juni 1999 wurden 15 Kleinspechte besendert und individuell markiert. Die 1,15 g schweren Sender vom Typ BD-2 der Firma Holohil Systems (Kanada) wurden an zwei Schwanzfedern der Vögel angebracht. Damit war es möglich die einzelnen Individuen voneinander zu unterscheiden und die Kleinspechte über längere Zeiträume zu verfolgen und zu beobachten.

Klangattrappenversuche

Um einen Klangattrappenversuch durchführen zu können war es erforderlich, dass der Kleinspecht sich im Blickfeld oder in unmittelbarer Nähe des Beobachters befand (Umkreis von 30 m). Dies war notwendig, um die Reaktionen des Spechts wahrnehmen zu können. War diese Bedingung erfüllt, konnte die Klangattrappe mit Hilfe eines Diktiergeräts (Sony) und Aktivboxen (Sony) abgespielt werden. Die Lautstärke betrug ca. 90 dB. Folgende Klangattrappen wurden eingesetzt:

- Rufreihe eines Männchens (Aufnahme von Rochée)
- Rufreihe eines Weibchens (Aufnahme von Höntsch)
- Trommelreihe unbekannten Geschlechts (Aufnahme von Rochée)

Die Versuche wurden von Sonnenaufgang bis 12 Stunden danach durchgeführt.
Die Klangattrappe wurde innerhalb einer Versuchsreihe an einem Individuum in Abständen von ca. 2 Minuten höchstens drei Mal hintereinander abgespielt. Zeigte der Kleinspecht schon beim ersten oder zweiten Abspielen der Klangattrappe eine Reaktion wurde sie kein weiteres Mal abgespielt. Bei einer solchen Versuchsreihe wurde immer die selbe Klangattrappe eingesetzt. Um eine eventuelle Gewöhnung der Kleinspechte oder mögliche Beeinträchtigung zu vermeiden, wurde an einem Individuum höchstens einmal am Tag eine Versuchsreihe durchgeführt. Bei der folgenden Versuchsreihe an diesem Individuum an einem der nächsten Tage, wurde eine andere Klangattrappe angewandt.

Bei den 114 Versuchen wurden folgende Parameter aufgenommen:

- Datum, das in folgende Zeitabschnitte (Perioden) einfloss:
  Winter (1.–28. Februar)
  Balzzeit (1. März – Ablage des 1. Eies)
  Brutzeit (1. Ei – Ausflug der Jungvögel)
  Führungszeit (Führung der Jungvögel – Auflösung des Familienverbands)
- Uhrzeit (MEZ)
- Identität und Geschlecht des Kleinspechts
- Aufenthaltsort in Bezug zum Bruthöhlenstandort
- Art der Klangattrappe (s. o.)
- Art der Reaktion (Ruf, Trommeln)

Ergebnisse

Reaktionsbereitschaft in den verschiedenen Zeitabschnitten

Die Kleinspechte reagierten während des gesamten Untersuchungszeitraums auf die Klangattrappe (Abb. 1).

Die Anteile der Reaktionen waren in den einzelnen Perioden jedoch unterschiedlich (Kruskal-Wallis-Test, $p < 0,05$).

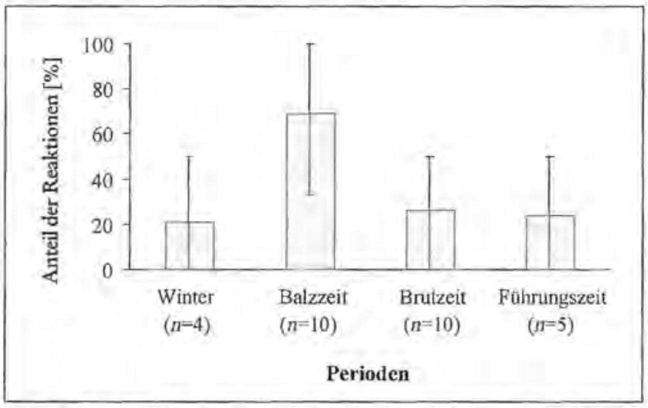

Abb. 1. Anteil der Reaktionen in den unterschiedlichen Perioden (Mittelwerte und Datenbereiche), *n* = Anzahl der beobachteten Individuen.
Proportion of reactions during the different periods (mean and variability), n = number of observed individuals.

In der Balzzeit war die Reaktionsbereitschaft der Kleinspechte besonders gut. Mit durchschnittlich 69 % lag der größte Anteil von positiven Reaktionen in dieser Periode. Die Spechte reagierten in dieser Zeit signifikant häufiger auf die Klangattrappe als in allen anderen Perioden (Mann-Whitney-U-Test, p < 0,02). Einige Individuen zeigten sogar auf jeden Versuch eine Reaktion (Abb. 1).

In den drei anderen Perioden überschritt der Anteil an Reaktionen im Mittel nicht einmal 30 %. Auch Spechte, die in diesen Perioden die größte Reaktionsbereitschaft zeigten, reagierten nur auf jeden zweiten Klangattrappenversuch. Die Anteile der Reaktionen in diesen Perioden unterschieden sich nicht signifikant voneinander (Mann-Whitney-U-Test, p > 0,05) (Abb. 1).

Im Folgenden wird der Einfluss weiterer Faktoren überprüft. Dabei werden nur noch Versuche aus der Balzzeit (*n* = 48) berücksichtigt, da in den anderen Perioden die Reaktionsbereitschaft der Spechte zu gering war.

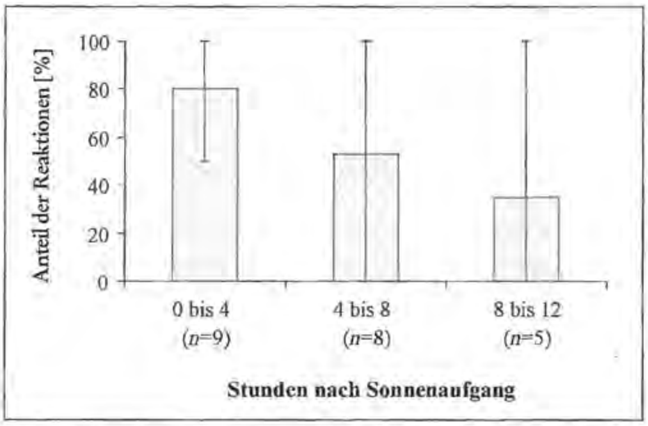

Abb. 2. Anteil der Reaktionen im Verlauf des Tages während der Balzzeit (Mittelwerte und Datenbereiche), *n* = Anzahl der beobachteten Individuen.
Proportion of reactions during the day while the mating season (mean and variability), n = number of observed individuals.

Reaktionsbereitschaft im Tagesverlauf

Die Klangattrappen wurden den Kleinspechten von Sonnenaufgang bis 12 Stunden danach vorgespielt. Die Anteile der Reaktionen im Verlauf dieses Zeitraumes während der Balzzeit sind in Abb. 2 zu erkennen.

In den Morgenstunden (Sonnenaufgang bis vier Stunden später) konnten die meisten Reaktionen auf Klangattrappen feststellt werden. Durchschnittlich 80 % der Versuche wurden mit einer Reaktion beantwortet (Abb. 2). Zwischen vier und acht Stunden nach Sonnenaufgang reagierten die Kleinspechte nur auf etwa die Hälfte der durchgeführten Klangattrappenversuche (Abb. 2). Die Reaktionsbereitschaft zwischen acht und zwölf Stunden nach Sonnenaufgang war am geringsten. Der Anteil der Reaktionen lag hier im Mittel nur bei 35 % (Abb. 2). Die Unterschiede der Reaktionsbereitschaft im Verlauf des Tages waren statistisch nicht zu sichern (Kruskal-Wallis-Test, p > 0,05).

Abb. 3. Männlicher Kleinspecht in seiner Bruthöhle.
Male Lesser Spotted Woodpecker in his breeding cavity.
(Foto: Fritz Kohl)

Reaktionsbereitschaft in unterschiedlicher Entfernung zur zukünftigen Bruthöhle

Kleinspechte bauen jedes Jahr eine neue Höhle, um ihre Jungen darin großzuziehen (Abb. 3). Im Hinblick auf die räumliche Beziehung zur später bekannt gewordenen Bruthöhle wurden die Reaktionen ebenfalls ausgewertet. Abb. 4 zeigt den Anteil der Reaktionen in den unterschiedlichen Entfernungsbereichen zur Bruthöhle.

Die Reaktion der Kleinspechte auf die Klangattrappe war am besten, wenn sich die Vögel im Umkreis von 0 m bis 400 m um die zukünftige Bruthöhle aufhielten. In diesem Bereich zeigten die Spechte auf durchschnittlich 82 % der Versuche eine Reaktion (Abb. 4). Wenn sich die Vögel weiter von ihrer Bruthöhle entfernten, war ihre Reaktionsbereitschaft nicht mehr so hoch. Im Bereich von 400 – 1200 m antworteten sie nur noch auf durchschnittlich die Hälfte der Klangattrappenversuche (Abb. 4). Einige Individuen, die sich in diesem Bereich

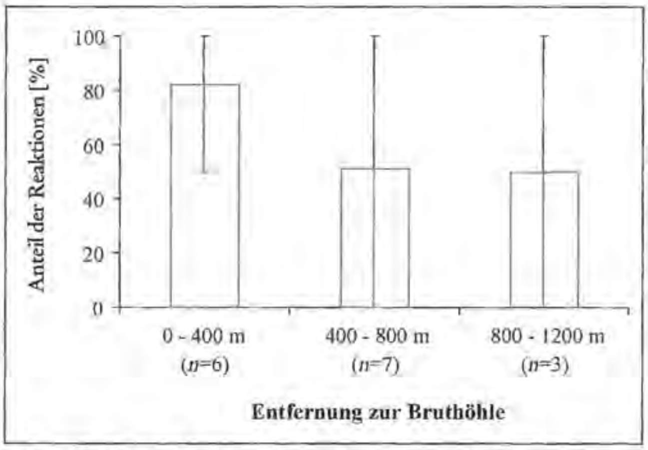

Abb. 4. Anteil der Reaktionen in unterschiedlichen Entfernungsbereichen um die zukünftige Bruthöhle während der Balzzeit (Mittelwerte und Datenbereiche), *n* = Anzahl der beobachteten Individuen.
Proportion of reactions in different distances to the later breeding cavity during the mating season (mean and variability), n = number of observed individuals.

aufhielten regierten sogar auf keine der Klangattrappen, die ihnen vorgespielt wurde. Der Unterschied der Reaktionsbereitschaft zwischen diesen Bereichen war allerdings nicht signifikant (Kruskal-Wallis-Test, p > 0,05).

Reaktionsbereitschaft auf unterschiedliche Klangattrappen

Die Reaktionsbereitschaft der Männchen und Weibchen auf die unterschiedlichen Klangattrappen während der Balzzeit wird in Abb. 5 gegenübergestellt. Dabei konnten zum Teil erhebliche geschlechtsspezifische Unterschiede in der Reaktion auf die unterschiedlichen Klangattrappen beobachtet werden.

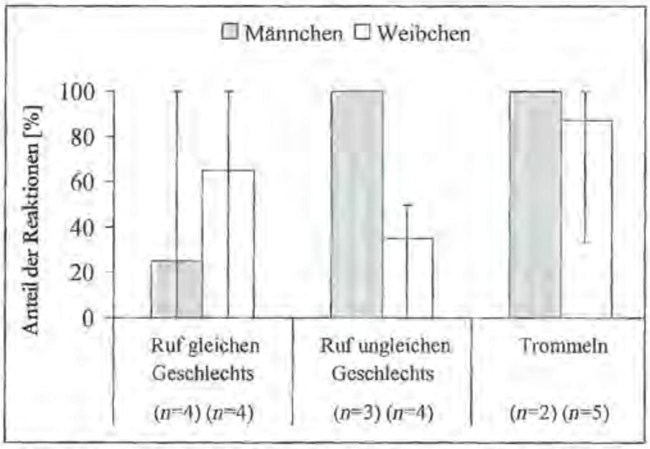

Abb. 5. Anteil der Reaktionen beider Geschlechter auf die unterschiedlichen Klangattrappen in der Balzzeit (Mittelwerte und Datenbereiche), *n* = Anzahl der beobachteten Individuen.
Proportion of reactions of both sexes to the different playbacks during the mating season (mean and variability), n = number of observed individuals.

Bemerkenswert ist, dass die Männchen auf einen weiblichen Ruf und ebenso auf eine Trommelklangattrappe immer eine positive Reaktion zeigten. Spielte man hingegen den Weibchen eine männliche Rufreihe vor, reagierten diese nur auf durchschnittlich 35 % der Versuche (Abb. 5). Der Anteil der positiven Reaktionen auf die Trommelserie war allerdings auch bei den Weibchen sehr hoch (87 %). Die Unterschiede zwischen der Reaktionsbereitschaft der Männchen und Weibchen auf die Klangattrappen mit Ruf ungleichen Geschlechts und Trommelserie konnte nicht getestet werden, da die Stichprobenanzahl zu klein war (Abb. 5). Nur nach dem Vorspielen eines Rufs gleichen Geschlechts reagierten die Weibchen häufiger als die Männchen. Sie reagierten auf durchschnittlich 65 % der Versuche, während die Männchen nur auf 25 % der Versuche eine Reaktion zeigten. Dieser Unterschied war jedoch nicht signifikant (Mann-Whitney-U-Test, p > 0,05) (Abb. 5).

Diskussion

Einfluss der phänologischen Perioden auf die Reaktionsbereitschaft

Untersuchungen der Reaktionsbereitschaft von Kleinspechten auf Klangattrappen sind bisher selten und teilweise widersprüchlich. Laut BLUME & TIEFENBACH (1997) lässt sich der Kleinspecht das ganze Jahr mit Hilfe von Klangattrappen anlocken. Dagegen gibt SPITZNAGEL (1993) für die Zeitspanne von Januar bis Juni eine Erfolgsquote von unter 50 % für die Reaktionen der Kleinspechte an. Bei ZABKA (1979) reagierten Kleinspechte von Anfang bis Mitte Mai sehr gut auf Trommelklangattrappen.

Die vorliegende Untersuchung zeigt, dass die Reaktionsbereitschaft der Kleinspechte deutlich von der phänologischen Periode abhängig ist. In der Balzzeit reagierten die Kleinspechte am besten auf die Klangattrappen. Hier wurden durchschnittlich 69 % der Versuche durch Rufe oder Trommeln beantwortet. In den anderen Perioden lag die Erfolgsquote bei unter 30 % (Abb. 1). Wählt man also die richtige Zeitspanne aus um Klangattrappenversuche durchzuführen, wird die Chance eine Reaktion zu provozieren erheblich gesteigert. Die große Reaktionsbereitschaft während der Balzzeit könnte, ebenso wie die gesteigerte Rufaktivität in diesem Zeitraum, mit der erforderlichen Partnersuche zusammenhängen. Da das Untersuchungsgebiet von Kleinspechten nur dünn besiedelt ist (ca. 0,02 BP/10 ha), die Vögel außerhalb der Brutzeit einen sehr großen Aktionsraum befliegen und die Höhlenzentren weit voneinander entfernt liegen (HÖNTSCH 1996), ist es schwierig einen Partner zu treffen. Deshalb müssen sie in der Balzzeit auf Lautäußerungen reagieren, um auf sich aufmerksam zu machen und ihren Standort zu erkennen zu geben. Des weiteren ist es möglich, dass sie in der Klangattrappe einen potentiellen Rivalen sehen und ihn mit Hilfe von energischem Rufen versuchen zu vertreiben. Aggressives Verhalten und Kämpfe zwischen Kleinspechten konnten hauptsächlich in der Balzzeit beobachtet werden (HURME 1973, HÖNTSCH 1996).

Allerdings war die Reaktionsbereitschaft der Kleinspechte auch während der Balzzeit nicht immer positiv. Die Kleinspechte reagierten auf durchschnittlich 31 % der Versuche nicht. Es ist also wahrscheinlich, dass zusätzliche Faktoren existieren, welche einen Einfluss auf die Reaktionsbereitschaft haben könnten.

Einfluss der Tageszeit auf die Reaktionsbereitschaft

Die vorliegende Studie zeigt, dass die Reaktionsbereitschaft der Kleinspechte nicht zu allen Tageszeiten gleich war. Der Anteil der Reaktionen war in den ersten vier Stunden nach Sonnenaufgang größer, als in den Stunden des restlichen Tages (Abb. 2). Die Motivation auf eine Klangattrappe zu reagieren scheint bei den Kleinspechten in den Morgenstunden größer zu sein, als später am Tag. Es wäre möglich, dass zu den Tageszeiten, zu denen die Kleinspechte schlechter auf die Klangattrappe reagierten, Aktivitäten im Vordergrund standen, die die Motivation zur Reaktion verringerten. OLSSON (1998) stellte fest, dass Kleinspechte morgens weniger Zeit auf die Nahrungssuche verwenden, als am Nachmittag. Da sich die Kleinspechte am Nachmittag hauptsächlich mit der Nahrungssuche beschäftigen, könnte während dieser Zeit die Reaktionsbereitschaft niedriger sein. Auch ZABKA (1979) erwähnt, dass die Reaktionsbereitschaft vom Zustand des Spechtes abhängen kann. Hungermotivierte Tiere sollen danach keine Reaktion auf die Klangattrappe zeigen.

Einfluss der Entfernung des Kleinspechts von der zukünftigen Bruthöhle

Der Standort der zukünftigen Bruthöhle scheint während der Balzzeit Einfluss auf das Reaktionsverhalten der Kleinspechte zu haben. Die Kleinspechte reagierten in der Nähe der Bruthöhle (bis 400 m entfernt) häufiger als in größerer Entfernung (Abb. 4). Das Ergebnis könnte darauf hindeuten, dass Kleinspechte den Bereich um ihre zukünftige Bruthöhle während der Balzzeit vor Konkurrenten verteidigen. Kleinspechte nutzen keine alten Bruthöhlen. Sie bauen jedes Jahr während der Balzzeit eine neue Höhle zur Aufzucht ihrer Jungen (PYNNÖNEN 1939, ROSSMANITH 1999, HÖNTSCH 2001). Sie investieren also jedes Jahr Energie in den Höhlenbau. Es ist deshalb sinnvoll, die Bruthöhle gegen andere Kleinspechte zu verteidigen, um nicht erneut Energie für einen weiteren Höhlenbau aufwenden zu müssen. Nach Fertigstellung der Bruthöhle wird sie deshalb auch von den Brutpartnern bewacht (ROSSMANITH 1999).

Geschlechtsspezifische Unterschiede in der Reaktion auf verschiedene Klangattrappen

In der vorliegenden Untersuchung war die Reaktionsbereitschaft von Männchen und Weibchen in der Balzzeit auf die Trommelklangattrappe in etwa gleich hoch (Abb. 5). Nach ZABKA (1979) scheint Trommeln das Erregungsniveau zu erhöhen. Das bestätigen auch die Ergebnisse der vorliegenden Versuche.

Bei der Reaktionsbereitschaft auf den männlichen und den weiblichen Ruf konnten allerdings tendenzielle Unterschiede festgestellt werden. Die Weibchen reagierten besser auf einen Ruf gleichen Geschlechts, dagegen zeigten die Männchen eine bessere Reaktion auf den Ruf des anderen Geschlechts (Abb. 5). Es kann deshalb angenommen werden, dass die Rufe der Geschlechter unterschiedlich sind und die Kleinspechte hier differenzieren können (K. HÖNTSCH, pers. Mitt.). Für das menschliche Ohr klingen die Rufe der beiden Geschlechter gleich.

Die Unterschiede in der Reaktion auf die geschlechtsspezifischen Rufe könnten mit dem Zustand der Paarbindung zusammenhängen. Es könnte sein, dass die Männchen ihre Reviere schon zu diesem Zeitpunkt gebildet haben und deshalb weniger Reaktionen auf die Klangattrappe mit dem männlichen Ruf zeigten. Des weiteren wäre es möglich, dass die Weibchen in der Balzzeit große Flächen abfliegen, um mit ihren Rufen die Männchen zu suchen. Für die Männchen wäre es sinnvoll die Weibchenrufe zu beantworten, um auf sich aufmerksam zu machen. Die Weibchen hingegen müssten nicht unbedingt auf die Männchenrufe reagieren, da ihnen der Aufenthaltsort des Männchens durch seine Rufe damit bekannt wäre. Für die Weibchen wäre es aber von Vorteil auf Rufe von anderen Weibchen zu reagieren, um Konkurrentinnen zu vertreiben, und die Möglichkeit zu erhöhen sich mit zwei Männchen zu verpaaren (vgl. HÖNTSCH 1996, ROSSMANITH 1999). Das Weibchen könnte dann mit zwei Männchen ein Gelege haben und seinen Bruterfolg erhöhen. Die Tatsache, dass in der Balzzeit ausschließlich Weibchenkämpfe beobachtet werden konnten, unterstützt diese Vermutung (eigene Beobachtungen). KOTAKA (1998) konnte auch bei Buntspechtweibchen *Picoides major* aggressives Verhalten feststellen. Er beobachtete während der Balzzeit zwei Männchen und zwei Weibchen. Die Weibchen zeigten ein sehr aggressives Verhalten gegeneinander. Nachdem ein Weibchen das andere vertrieben hatte, verpaarte es sich mit beiden Männchen. Dieses Weibchen hatte später mit beiden Männchen ein Gelege.

BACHMANN (1997) stellte bei Buntspechten ähnliche geschlechtsspezifische Unterschiede in der Revierbildung fest, wie sie oben für die Kleinspechte angenommen wurden. Die Buntspechtmännchen besaßen in der Balzzeit schon die gleichen Reviere wie später in der

Brutzeit, während die Weibchen in großflächigen Gebieten umherschweiften. Die Weibchen glichen im Verlauf der Balzzeit ihre Aktionsräume an die der Männchen an. Es wird vermutet, dass die Buntspechtweibchen im Spätwinter herumschweifen und sich in der Balzzeit für eines der Männchen Reviere entscheiden (BACHMANN 1997, MICHALEK 1998).

Konsequenzen für den Klangattrappeneinsatz

Die vorliegenden Ergebnisse lassen den Schluss zu, die Erfassung von Kleinspechten mittels Klangattrappe als geeignete Methode anzusehen. Die Untersuchung ergab jedoch auch, dass die Reaktionsbereitschaft von verschiedenen Faktoren beeinflusst werden kann. Um die Methode deshalb sinnvoll einsetzen zu können und eine möglichst gute Reaktion auf die Klangattrappe zu erzielen, sind zusammenfassend folgende Punkte zu beachten:

1. Der Einsatz der Klangattrappe sollte in den Monaten März und April durchgeführt werden. Dieser Zeitraum entspricht in etwa der Balzzeit, in der die höchste Reaktionsbereitschaft zu erwarten ist.
2. Eine Probefläche sollte in dieser Zeit häufiger aufgesucht werden. Die Balzstimmung und die Ablage des ersten Eies können individuell zu unterschiedlichen Zeiten beginnen und damit die Reaktionsbereitschaft der Kleinspechte beeinflussen.
3. Die Untersuchung einer Probefläche mittels Klangattrappe sollte in den ersten vier Stunden nach Sonnenaufgang durchgeführt werden, denn der Anteil der Reaktionen war in diesem Tagesabschnitt am größten.
4. Die eingesetzte Klangattrappen sollte immer Trommelserien enthalten. Beim Einsatz von Rufen könnte die Reaktionsbereitschaft von Männchen und Weibchen unterschiedlich sein.

Die Reaktionsbereitschaft der Kleinspechte kann aber auch von Faktoren bestimmt werden, die der Anwender beim Einsatz von Klangattrappen nicht beeinflussen kann. So war die Reaktionsbereitschaft der Kleinspechte z.B. von ihrem Standort in Bezug auf die zukünftige Bruthöhle abhängig. In der Nähe der zukünftigen Bruthöhle (0 m bis 400 m) war der Anteil der Reaktionen am größten. Erhält man bei der Untersuchung einer Probefläche mit Hilfe von Klangattrappe zur Balzzeit mehrfach eine positive Reaktion, ist es wahrscheinlich, dass man sich in der Nähe einer zukünftigen Bruthöhle befindet. Es wäre deshalb zusätzlich sinnvoll, die Orte, an denen der Kleinspecht auf die Klangattrappe reagiert hat, in der Brutzeit nach Bruthöhlen abzusuchen. Die zusätzliche Suche der Bruthöhlen könnte dadurch die Genauigkeit der Bestandserfassung erhöhen.

Abschließend lässt sich sagen, dass der Einsatz von Klangattrappen kombiniert mit einer anschließenden Höhlensuche eine gute Möglichkeit zur Bestandserfassung von Kleinspechten bieten könnte.

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Time of natal dispersal and reproductive decisions of the Three-toed Woodpecker under varying food conditions

Zeitpunkt der Jungenabwanderung und Reproduktionsentscheidungen beim Dreizehenspecht unter verschiedenen Nahrungssituationen

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Abstract

The finding that, among juvenile birds, earlier dispersers contribute more to their parents' lifetime reproductive success justify the study of factors that promote the evolution and explain the timing, rate and extent of natal dispersal movements for understanding the adaptive value of particular traits between populations and individuals. In this study, I examined the hypothesis that change in food availability explains the onset of natal dispersal in the Three-toed Woodpecker *Picoides tridactylus*. In eastern Finland, I studied the life cycle of the spruce bark beetle community (Coleoptera, Scolytidae), its main insect prey from autumn to spring time, by taking bark samples from recent foraging trees in the pre-reproduction, reproduction, post-reproduction and natal dispersal periods of the woodpecker. The natal dispersal period was inferred from information gathered at the landscape level, provided by national ringing records from Finland and Sweden. I also compared the breeding time, brood size, prey provisioning and delivery rates of breeding woodpeckers in relation to timing of the bark beetle life cycle. Adults were then expected to adjust their investment in reproduction and parental effort with prey development if its timing, which is temperature-dependent, would determine the dispersal time and survival prospects of the offspring and if parents would behave in a way that would optimize their inclusive fitness. Juvenile woodpeckers dispersed in Finland and in Sweden when the abundance in bark beetles declined locally. This apparent reduction in food level seemed to result from the dispersal of synchronously developed beetle species over habitats, prior to hibernation. A review of the existing literature on the ecology of wood-boring longhorn beetle larvae (Coleoptera, Cerambycidae), the main food supply of the woodpecker nestlings' diet, emphasised also changes in their availability at the time of the bird natal dispersal, due to gallery excavation from the phloem, before pupation. Female woodpeckers bred earlier and reared larger broods in habitats where the spruce bark beetles reproduced earlier and/or development was faster, and thus the beetles emerged earlier. Unlike males, females fed the offspring from earlier/larger broods with more wood-boring beetle larvae, i.e. prey of higher caloric value than bark beetles, than the nestlings from later/smaller broods. These results support the idea that natal dispersal time and reproductive decisions in Three-toed Woodpeckers are related to the development time of their prey, whether they are bark beetles, longhorn beetle larvae, or both, or to local temperature conditions. They suggest also that, in agreement with the working hypothesis, a sudden change in the spatial distribution of insect prey may lower temporarily their availability for the foraging woodpeckers, which, in turn, determine the propensity of juveniles to disperse.

Ganz allgemein tragen Jungvögel, die sich früher verstreuen, mehr zum lebenslangen Bruterfolg ihrer Eltern bei. Diese Erkenntnis rechtfertigt die Analyse von Faktoren, die die zeitliche Abstimmung, Rate und den Umfang von Zerstreuungsbewegung der Jungvögel nach der Geburt erklären und somit die Evolution fördern. Dies trägt zum Verständnis der besonders anpassungsfähigen Wechselwirkung zwischen Populationen und Individuen bei. Ich prüfte deshalb in dieser Studie in Ostfinnland die Hypothese, dass Änderungen in der Nahrungsverfügbarkeit den Beginn der Zerstreuung der jungen Dreizehenspechte erklären. Da Fichten-Borkenkäfer Coleoptera, Scolytidae als Hauptbeuteinsekten des Dreizehenspechts gelten, untersuchte ich durch Entnahme von Rindenproben aus unlängst genutzten Nahrungsbäumen den Lebenszyklus einer Fichten-Borkenkäfergemeinschaft vom Frühjahr bis Herbst. Ich trennte die Entnahme zeitlich nach vier biologischen Perioden der Spechte: Vor der Fortpflanzung, während der Fortpflanzung, nach der Fortpflanzung und während der Zerstreuung der Jungspechte nach der Geburt. Die Periode der Zerstreuung der Jungspechte leitete ich anhand der finnischen und schwedischen Beringungsdaten auf der geographischen Landschaftsebene ab. Ich verglich außerdem Brutzeit, Brutgröße, Beuteverfütterung an die Jungen und Fütterungsfrequenzen der brütenden Spechte im Verhältnis zur zeitlichen Abstimmung des Entwicklungszyklus der Borkenkäfer. Dabei erwartete ich, dass die erwachsenen Spechte ihre Investitionen in Fortpflanzung und ihre elterlichen Anstrengung mit der Entwicklung der Beute abstimmen würden, wenn (1) der temperaturabhängige Zeitpunkt der Beuteentwicklung die Dispersion und die Überlebenschancen des Nachwuchses bestimmt, und wenn (2) damit die Eltern durch ihr Verhalten ihre eigene Gesamtfitness (Erhöhung des eigenen Gesamtlebensbruterfolg durch erfolgreiche Nachkommenschaft) optimieren können. Jungspechte verstreuten sich in Finnland und Schweden zu der Zeit, als die Abundanz der Borkenkäfer lokal abnahm. Diese auffällige Reduktion auf der Nahrungsebene resultierte *wahrscheinlich aus der Zerstreuung der synchron entwickelten Käferarten vor ihrem Winterschlaf über ihren Lebensraum. Bockkäferlarven Coleoptera, Cerambycidae stellten die Hauptnahrungskomponente in der Ernährung der Nestlinge dar. Eine Literaturrecherche über ihre Ökologie betonte ebenfalls Veränderungen in der Verfügbarkeit der Bockkäferlarven zur Zeit der Zerstreuung der Jungspechte. Dies ging auf die Aushöhlung der Gänge vor der Verpuppung aus dem Phloem zurück. Spechtweibchen in Habitaten mit einer früheren Fortpflanzung der Borkenkäfer und/oder ihrem schnelleren Entwicklungszyklus (d.h. Käfer tauchten früher auf) brüteten früher und zogen größere Bruten auf. Weibchen fütterten im Unterschied zu Männchen ihren Nachwuchs aus früheren/größeren Bruten mit mehr Cerambyciden Larven (= Beute mit größerem Nährwert als Scolytiden) als ihre Nestlinge aus späteren/kleineren Bruten. Dieses Resultat untermauerte die Idee, dass die Zerstreuung der Jungspechte nach der Geburt und die Entscheidungen für die Fortpflanzung bei den Eltern in Beziehung zur Entwicklung ihrer Beute oder zur lokalen Temperaturentwicklung stehen. Dabei war es egal, ob die Beute aus Borkenkäfern, Bockkäferlarven oder aus den beide Beutegruppen bestand. Das Ergebnis legte in Übereinstimmung mit der Arbeitshypothese auch Folgendes nahe: Eine plötzliche Änderung in räumlicher Verteilung der Insektenbeute könnte vorübergehend ihre Verfügbarkeit für die nahrungssuchenden Spechte senken, und somit im Umkehrschluss die Neigung der Jungen zur Dispersion bestimmen.*

Introduction

Both intrinsic and extrinsic factors have been proposed as correlates, proximate causes or consequences of natal dispersal in birds, i.e. movements from the birth place to the site of first reproduction (GREENWOOD et al. 1979). Intrinsic factors include sex (CLARKE et al. 1997, WOLFF & PLISSNER 1998), age (DHONDT & HUBLE 1968, DHONDT & OLAERTS 1981, ADRIAENSEN 1986, NILSSON 1989, FERRER 1993), and body size or condition (NILSSON & SMITH 1985, BROWN & BROWN 1992, FERRER 1992, LENS & DHONDT 1994). Important environmental factors include food availability (MCCALLUM 1990, SUTHERLAND 1996) and population density (HILDEN 1982, NEGRO et al. 1997). On the whole, however, the proximate causes of dispersal are not yet fully understood due to non-independence among factors (DIECKMANN et al. 1999, FERRIERE et al. 2000).

Nevertheless, several lines of evidence stress the paramount influence of food abundance and distribution on dispersal from natal habitat and on population density. First, during favorable food conditions, dispersers have been observed to emigrate over shorter distances and later (ERIKSSON 1970, SONERUD et al. 1988, ARCESE 1989). The autumn and winter densities of sedentary populations have also been found to be adjusted to natural or experimentally controlled food level, with an increase in density due to increased recruitment of juveniles with food supply (HANON et al. 1987, ENOKSSON 1990). Finally, large-scale eruptions of juvenile birds have typically been reported in late summer and autumn during years of high breeding density with subsequent food shortage (PERRINS 1966, ERIKSSON 1971).

Hypothesis and Predictions

In this study, I investigated whether the onset of natal dispersal in the Three-toed Woodpecker *Picoides tridactylus* is related to change in availability of its main insect prey in the boreal environment, the bark beetles (Coleoptera, Scolytidae) living on spruces *Picea abies* (DEMENT'EV 1966, HOGSTAD 1970, MASSEY & WYGANT 1973, FAYT 1999).

At the habitat level, the life cycle of spruce bark beetles was studied after bark samples were collected from recent foraging trees in relation to the pre-reproduction, reproduction, post-reproduction and natal dispersal periods of the woodpecker. Because the time at which young woodpeckers effectively dispersed from the studied habitats was not known, the natal dispersal pe-

Three-toed Woodpecker **(Photo: Peter Pechacek)**

riod was inferred from information gathered at the landscape level, provided by national ringing data files. Thus with a lack of information about the actual timing for dispersal of juvenile woodpeckers out of the study area, however, the working hypothesis allowed me to generate several predictions:

(1) Based on earlier findings (see introduction), bark-beetle availability in the study area should be lower at the time when young woodpeckers disperse across landscapes than earlier.

(2) Since late-hatched birds disperse and search for vacant habitats later than birds from early broods (PINOWSKY 1965), woodpeckers should breed earlier in habitats where the bark-beetle life cycle is in an earlier stage if the food supply proximately influences natal dispersal and if its variation is related to the prey life cycle.

(3) Earlier-dispersing juvenile birds have been noticed to contribute more to their parents' lifetime reproductive success than later-dispersing ones (NILSSON & SMITH 1988, VERBOVEN & VISSER 1998, VISSER & VERBOVEN 1999). Thus, parents should invest more in reproduction and parental care in habitats with earlier prey life cycles if timing of prey development prior to egg laying would determine the dispersal time and survival prospects of the offspring and if parents would behave in a way that would optimize their inclusive fitness. In particular then, they should increase their delivery rate of wood-boring beetle larvae (e.g. longhorn beetle (Coleoptera, Cerambycidae), an important and more energetically rewarding prey compared with the much smaller bark beetles, during the nestling period (PECHACEK & KRISTIN 1996, POWELL 2000).

Study Area and Study Species

This study was conducted in 1998 and 1999 in North Karelia, easternmost Finland (63°N, 31°E). Each year, the study area, which covers some 3600 km^2, consisted of a patchwork of four spruce-dominated old-growth stands and one burnt forest patch. Each habitat patch (70–162 ha), isolated from the others by a surrounding matrix of younger, managed Scots Pine *Pinus sylvestris* stands, was inhabited by a single pair of Three-toed Woodpeckers. In 1998, the five breeding pairs were color-ringed. Individuals were captured after they entered the nest cavity to feed the offspring by placing in front of the nest hole a plastic tunnel prolonged by a hoop net. In 1999, however, to avoid repeated measurements from the same females, two out of the four old-growth stands studied in 1998 were replaced by two different stands, each occupied by another pair of woodpeckers.

The Three-toed Woodpecker is a conspicuous element of the taiga (HOGSTAD 1970), with a circumpolar range of distribution that closely coincides with that of spruce tree species (BALDWIN 1968, BOCK & BOCK 1974). Its occurrence is correlated with the amount of dead wood in individual forest stands (AMCOFF & ERIKSSON 1996) and its density increases with the proportion of forests over 100 years old in boreal forest landscapes (VIRKKALA et al. 1994). In Finland, the Three-toed Woodpecker is now classified as a near- to regionally-threatened breeding bird (RASSI 2000). The main insect prey of the woodpecker in the boreal zone, spruce bark beetles, undergo complete metamorphosis (CHARARAS 1962). This implies the occurrence of three distinct post-embryonic stages: (an early form without wing pads called) the larva, (a quiescent form with wing pads called) the pupa, and the adult (STARK 1982). The adult stage can also be subdivided into juvenile, sub-adult, and adult forms, based on their coloration (P. FAYT, unpubl.). The bark-beetle life cycle includes three phases (STARK 1982). The first is the process of colonization during late spring and summer, when beetles invade trees before they start to reproduce. The second is a reproduction phase, which includes mating, construction of the egg gallery, oviposition, and brood development up to the time of emergence. The third is a natal dispersal phase prior to hibernation. Beetle emergence or timing of natal dispersal depends on the time of reproduction (ANNILA 1969). Ambient temperature has a major influence upon the duration and timing of the different phases (CHARARAS 1962, SALONEN 1973).

Methods

Woodpecker breeding cycle

To understand the possible influence of food availability on the onset of natal dispersal in the Three-toed Woodpecker, each year I compared the life cycle of spruce bark beetles in relation to the nesting cycle of the bird. The breeding cycle of the woodpecker was subdivided into pre-reproduction, reproduction, post-reproduction, and natal dispersal. The first period coincided with late winter and ended with the start of nest excavation; the subsequent reproduction period lasted until fledging. The natal-dispersal period was defined on the basis of information provided by ringing records from the Finnish and Swedish museums of natural history for 1973 to 2000. The dispersal time of young woodpeckers at the habitat level was thus inferred from information gathered at the landscape level. The post-reproduction period was then considered to be the time between fledging and natal dispersal.

Woodpecker reproductive decisions

To ascertain whether parents adjusted their reproductive decisions with their prey life cycle, breeding time, brood size and parental effort were compared for the five annually studied territories in relation to timing of the development of bark beetles. However, in 1999, one of the 10 nests was discovered too late for reliable measurements of food delivery. Breeding time and brood size were related to each other to measure seasonal variation in the reproductive output of the woodpecker, including measurements from 16 additional nests found from 1996 to 1999 in eastern Finland. The study of parental effort in relation to breeding time, brood size, and prey development was complemented with measurements from 7 additional nests found between 1997 and 1999, although then with a lack of information about the local prey development time. Nests were located by nest-excavation noises in early morning, by accidental discovery, usually after the discovery of fresh wood chips on the ground floor, and by the noisy vocalizations of offspring during the second half of the rearing period.

The breeding time of the bird was estimated from the fledging date instead of from the laying date by backward calculation from the date of fledging, to control for between-pair variation in the length of the incubation and rearing periods. Fledging date corresponded to the number of days from the 1st of June to the fledging day. Nests were visited daily once a nestling was seen extending its head from the cavity to beg; fledgling was considered to be when the first nestling had left the nest. Determining brood size of the woodpeckers required climbing the nest tree and using a small mirror and flashlight to investigate the cavity.

Based on 6 hours per nest (with 2 consecutive hours per day during the two last weeks of the rearing period), parental effort was estimated from the feeding frequency per hour and per nestling. Attention was also paid to counting the number of delivered wood-boring beetle larvae (e.g. longhorn beetle). The diet of the offspring was identified and quantified by using spotting scopes. To see whether time of the day may influence the extent of parental effort, a total of 44 and 52 hours of observation were spent before and after noon, respectively.

Bark beetle life cycle

Study of the life cycle of spruce bark beetles involved removal of bark samples from trees showing recent Three-toed Woodpecker foraging tracks (i.e. small pieces of bark surrounding the base of the trunk). Samples (one per tree, 10x15 cm) were taken with a small axe in the immediate vicinity of exploited bark patches, at a height of 2 m above the ground. This method assumed only limited small-scale variation in distribution and composition of insect prey inside the tree bark at a given level above the forest floor. To minimize the potential effect of abiotic factors on beetle distribution, samples were taken only from standing trees, which are characterized by a more even distribution of different bark beetle species along their trunks compared with the abrupt gradations found on uprooted trees (JAKUS 1998). Trees bearing feeding tracks were sought all over the woodpecker territories, i.e. about 70 ha/pair in old-growth spruce stands of eastern Finland (P. FAYT, unpubl.). All territories were visited on the same day and five samples were taken per territory. Insect fauna living in spruce bark was investigated by collection of bark samples 14 times during the study period, on two, four, four, and four sampling days during the pre-reproduction, reproduction, post-reproduction, and natal dispersal periods, respectively. Of 350 bark samples, 50, 100, 100, and 100 were taken during the four respective periods. I collected 250 samples in 1998, but only 100 in 1999, due to time limitation for sampling and identifying insect prey (Table 1).

Timing of insect development was estimated by counting and examining the ratios of the number of adults, pupae, and larvae of bark beetle species from bark samples collected during the reproduction, post-reproduction and natal dispersal periods of the woodpecker. Because of the smaller sample size and of difficulties to es-

Table 1. Bark sample sizes (BS) during the pre-reproduction (1), reproduction (2), post-reproduction (3) and natal dispersal (4) periods of the woodpecker. The yearly clutch size and fledging date (standardized from yearly population medians) are added.

Site	Year	BS (1)	BS (2)	BS (3)	BS (4)	Clutch s.	Fledg. d.
1	1998	5	15	15	15	3	1
2	1999	5	5	5	5	4	3
3	1998	5	15	15	15	2	4
	1999	5	5	5	5	3	7
4	1998	5	15	15	15	4	-4
	1999	5	5	5	5	4	-1
5	1998	5	15	15	15	4	-3
	1999	5	5	5	5	4	1
6	1998	5	15	15	15	2	2
7	1999	5	5	5	5	5	-7

timate reliably the actual development level of beetle larvae (i.e. the predominant stage, see FAYT 1999), this estimate did not take into account the number of beetles that developed before the woodpeckers began nesting. Based on the sequential order in developing beetles (egg-larva-pupa-adult), it was assumed that the earlier/faster the prey reproduction/development is, the more adults and fewer larvae should be collected.

The successive developmental stages of bark beetles, i.e. juvenile, sub-adult, and adult, were identified at the species level and classified according to Silfverberg's proposal for nomenclature (1992). Sub-adults were distinguished from juveniles on the basis of their forehead color, which was darker than the rest of their darkening body. Juveniles, on the other hand, were uniformly light brown; for them, species identification was based on their size and shape.

Statistical analysis

Data were analyzed using SPSS for Windows 1998. To study whether the coexisting bark beetle species developed synchronously in the study area, juveniles and sub-adults of the most abundant species (> 35 individuals) were counted in relation to the pre-reproduction, reproduction, post-reproduction, and natal dispersal periods of the bird. Their numbers were ranked and compared among the four periods with Kendall's test for concordance. When the assumptions of normality were not met, non-parametric tests were used. Kruskal-Wallis and Mann-Whitney U-tests were performed to relate the abundance of the successive development stages of the different beetle species to the breeding cycle of the woodpecker. Linear regression analyses, with the number of individual beetles in successive developmental stages as independent variables, were used to examine the importance of prey development for breeding time, brood size, and parental effort of birds. Fledging dates were standardized from yearly population medians. Association between the parental effort of males and females was analyzed using Kendall rank correlation. Finally, paired-sample *t*-tests were used to compare the extent of male and female parental effort before and after noon. The limited number of birds captured did not allow me to test whether parental age and length of the pair-bond were related to the woodpecker brood size, breeding time, and prey delivery rate.

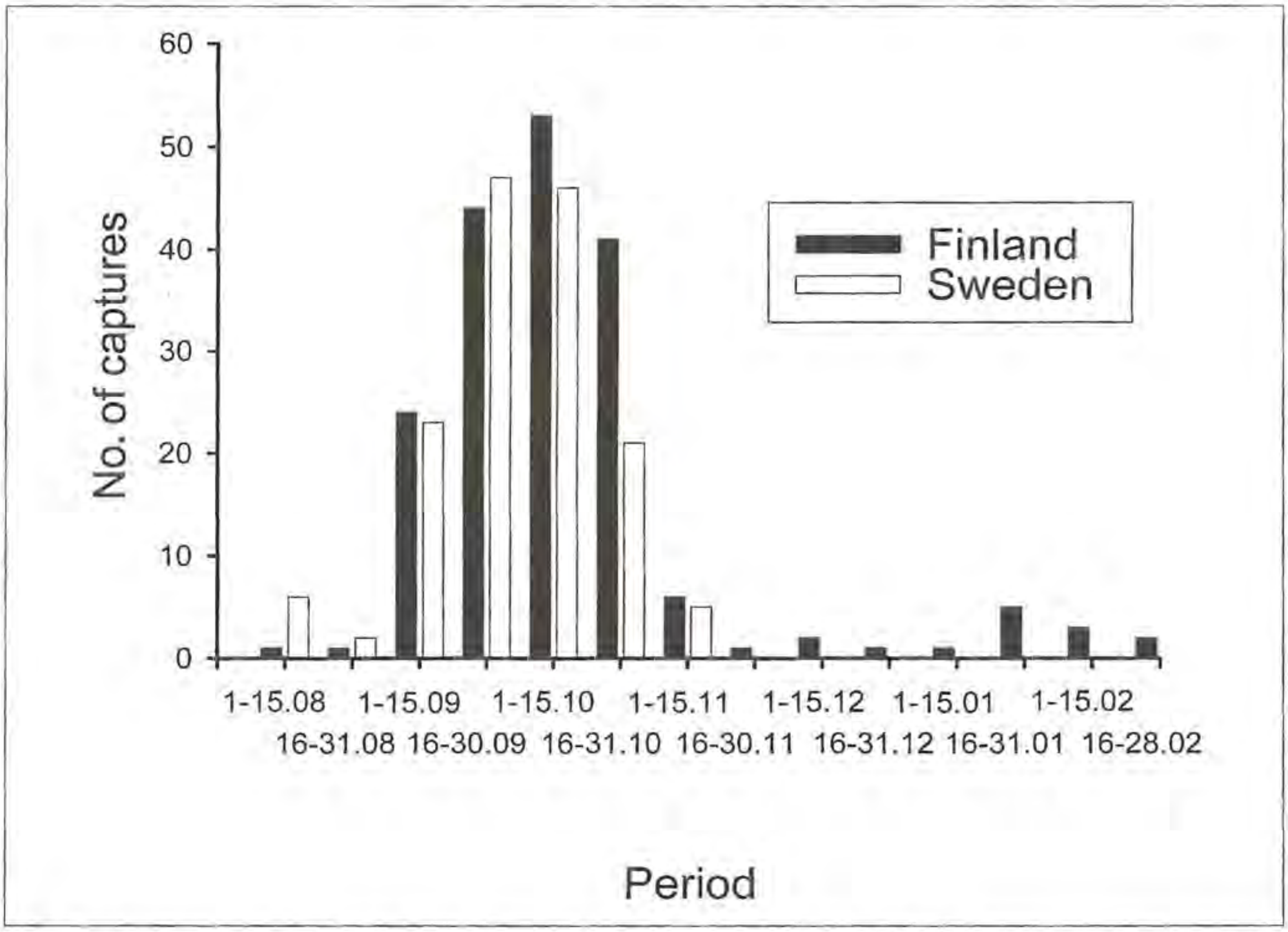

Fig. 1. Natal dispersal period of the Three-toed Woodpecker in Finland and Sweden (1973–2000).

Results

Natal dispersal time of woodpeckers

Of 284 and 160 Three-toed Woodpeckers ringed between August and February in Finland and in Sweden, 257 (90.49 %) and 130 (81.25 %) were juveniles (i.e. individuals hatched during the preceding summer). Although dispersing juveniles were captured from August to February, the main period of dispersal was defined as the period between 1 September – 30 November (Fig. 1).

Bark beetles: species assemblage and development

I counted 8,921 bark beetles in various stages of development from 350 samples of spruce bark. These included 3,383 adults, 1,269 sub-adults, 742 juveniles, 964 pupae, and 2,563 larvae (Appendix). Considering the life cycle of the eight most abundant species (> 35 individuals, excluding larval and pupal stages) among the four study periods, their development was found to be synchronous (Kendall's test for concordance, juvenile: χ^2 = 15.305, df = 7, p = 0.032; sub-adult: χ^2 = 15.227, df = 7, p = 0.033).

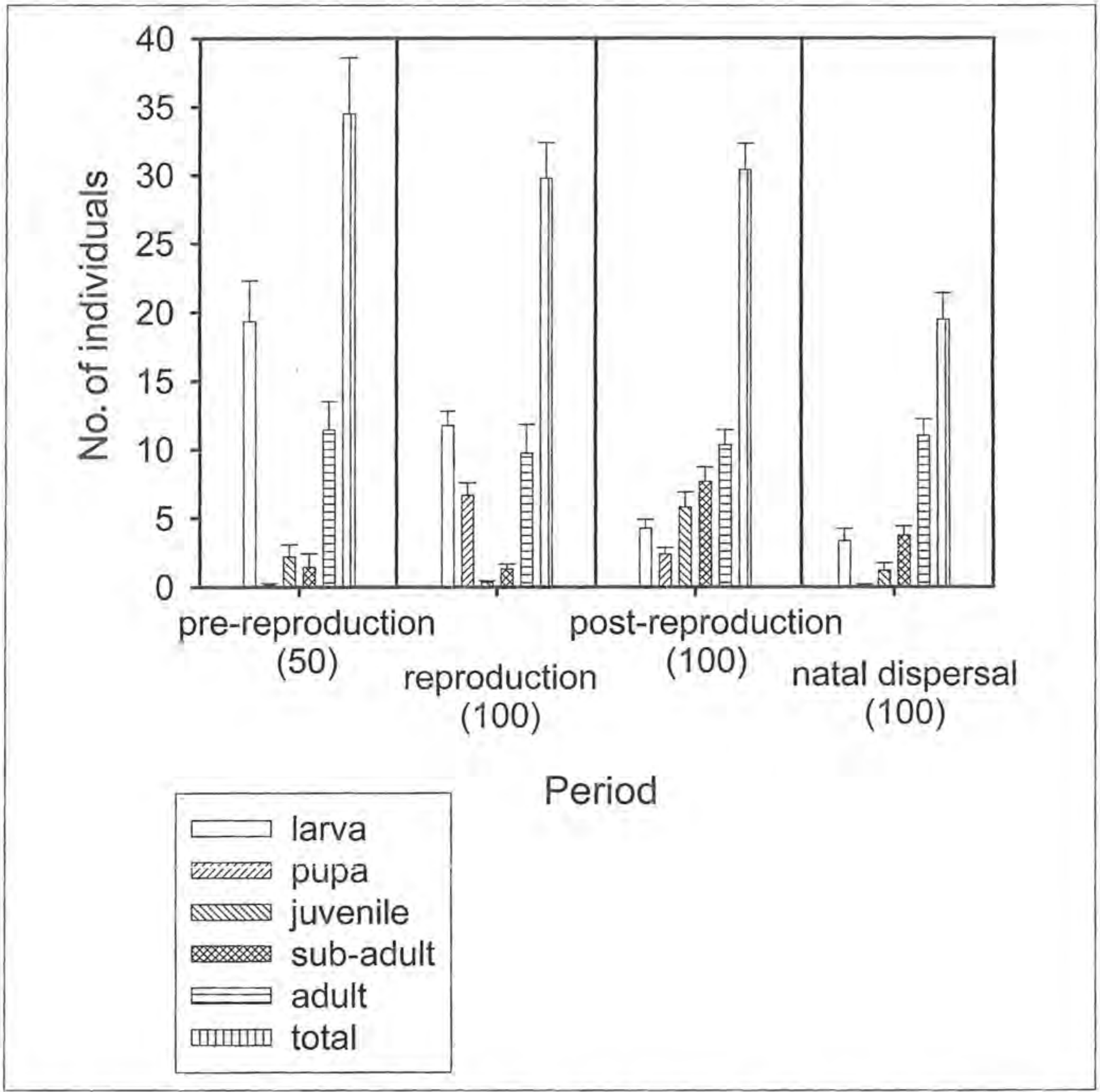

Fig. 2. Abundance of spruce bark beetles in relation to the nesting cycle of the woodpecker, all habitats combined. Mean numbers of individuals in successive stages of development per bark sample are plotted with standard errors and sample sizes. Stages of development include (in chronological order): larva, pupa, juvenile, sub-adult and adult (see text for further details).

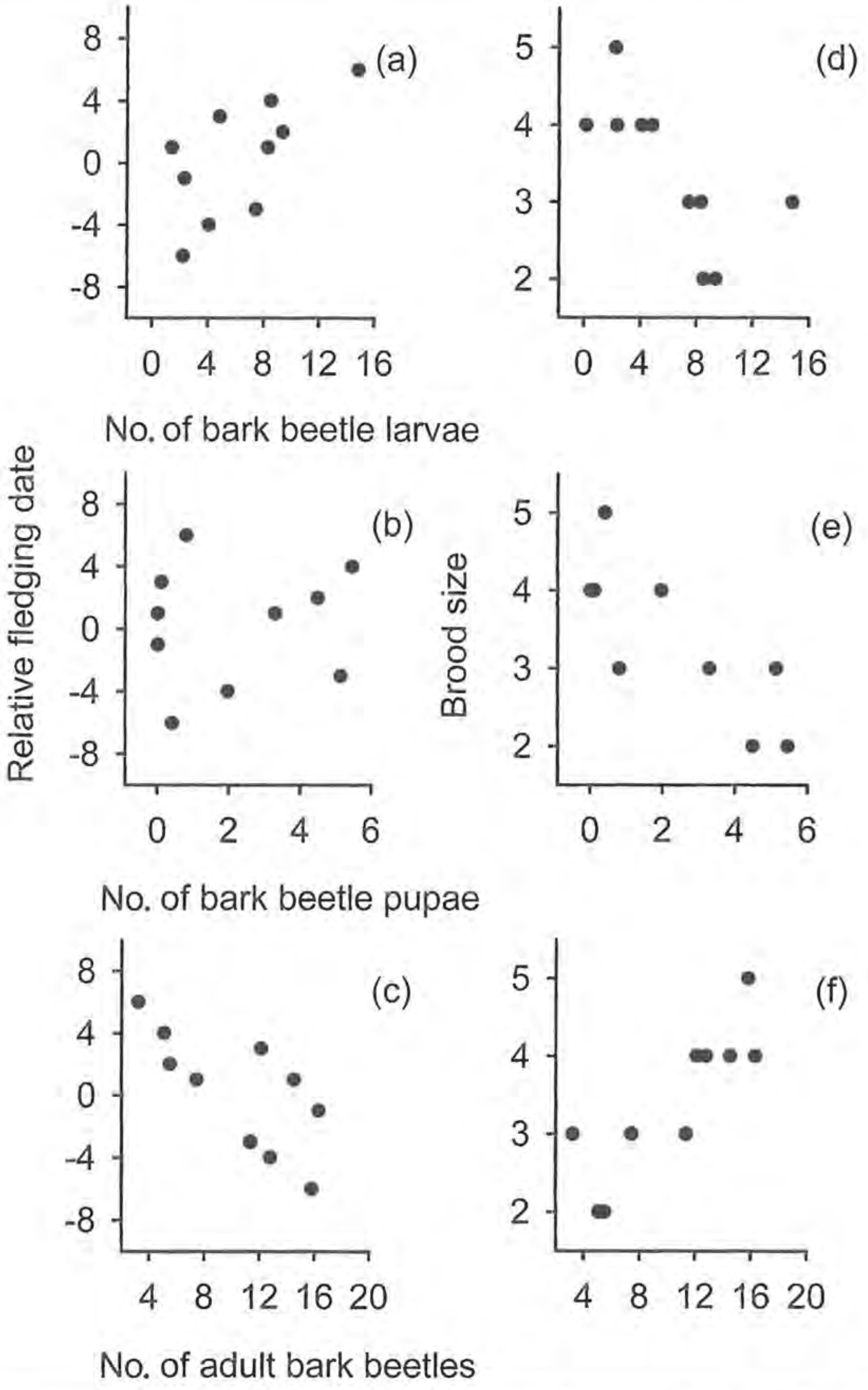

Fig. 3. Breeding time (left) and brood size (right) of the woodpecker in relation to the mean number of spruce bark beetle larvae (a, d), pupae (b, e), and adults (c, f) per bark sample. Bark samples were collected during the reproduction, post-reproduction and natal dispersal periods of the woodpecker. Data from 1998–1999. See Table 1 for sample sizes.

Bark beetle development and the woodpecker breeding cycle

Successive development stages ((1) larva, (2) pupa, (3) juvenile, (4) sub-adult, and (5) adult) were identified in spruce bark beetles from spring to autumn (Fig. 2). The number of bark beetle larvae in spruce was found to peak prior to woodpecker reproduction before decreasing progressively and reaching a minimum value during the woodpecker natal dispersal period (Kruskal-Wallis test, $H = 98.839$, $p = 0.000$). The next stages of development, pupa and juvenile – sub-adult, peaked during the woodpecker reproductive period (Kruskal-Wallis test, $H = 74.190$, $p = 0.000$) and the post-reproduction period (Kruskal-Wallis test, juvenile: $H = 65.952$, $p = 0.000$; sub-adult: $H = 63.789$, $p = 0.000$). In spite of this increase in abundance of juvenile and sub-adult beetles prior to the natal dispersal period of the birds, the number of adult bark beetles in the different periods did not differ (Kruskal-Wallis test, $H = 4.743$, $p = 0.192$). The total number of individual beetles (of all stages), on the other hand, decreased significantly at the time of woodpecker dispersal (Mann-Whitney *U* test, $U = 2721.5$, $p = 0.000$).

Bark beetle development and timing of woodpecker reproduction

The Three-toed Woodpecker bred earlier in habitats with fewer bark beetle larvae ($R^2 = 0.415$, $n = 10$, $p = 0.044$, Fig. 3a) and with more adult beetles ($R^2 = 0.728$, $n = 10$, $p = 0.002$, Fig. 3c) sampled throughout the season. So that, based on the assumption that the earlier/faster the beetle reproduction/development is, the more adults and fewer larvae should be found, the woodpecker nested earlier in forest habitats where the beetles reproduced earlier and/or development was faster, and the beetles emerged earlier.

Bark beetle development and woodpecker reproductive success

Brood size of the woodpecker was inversely related to the number of spruce bark beetle larvae ($R^2 = 0.507$, $n = 10$, $p = 0.021$, Fig. 3d) and pupae ($R^2 = 0.655$, $n = 10$, $p = 0.005$, Fig. 3e). Or, conversely, brood size was larger in forest patches with more adult beetles ($R^2 = 0.722$, $n = 10$, $p = 0.002$, Fig. 3f). Thus, because the woodpecker

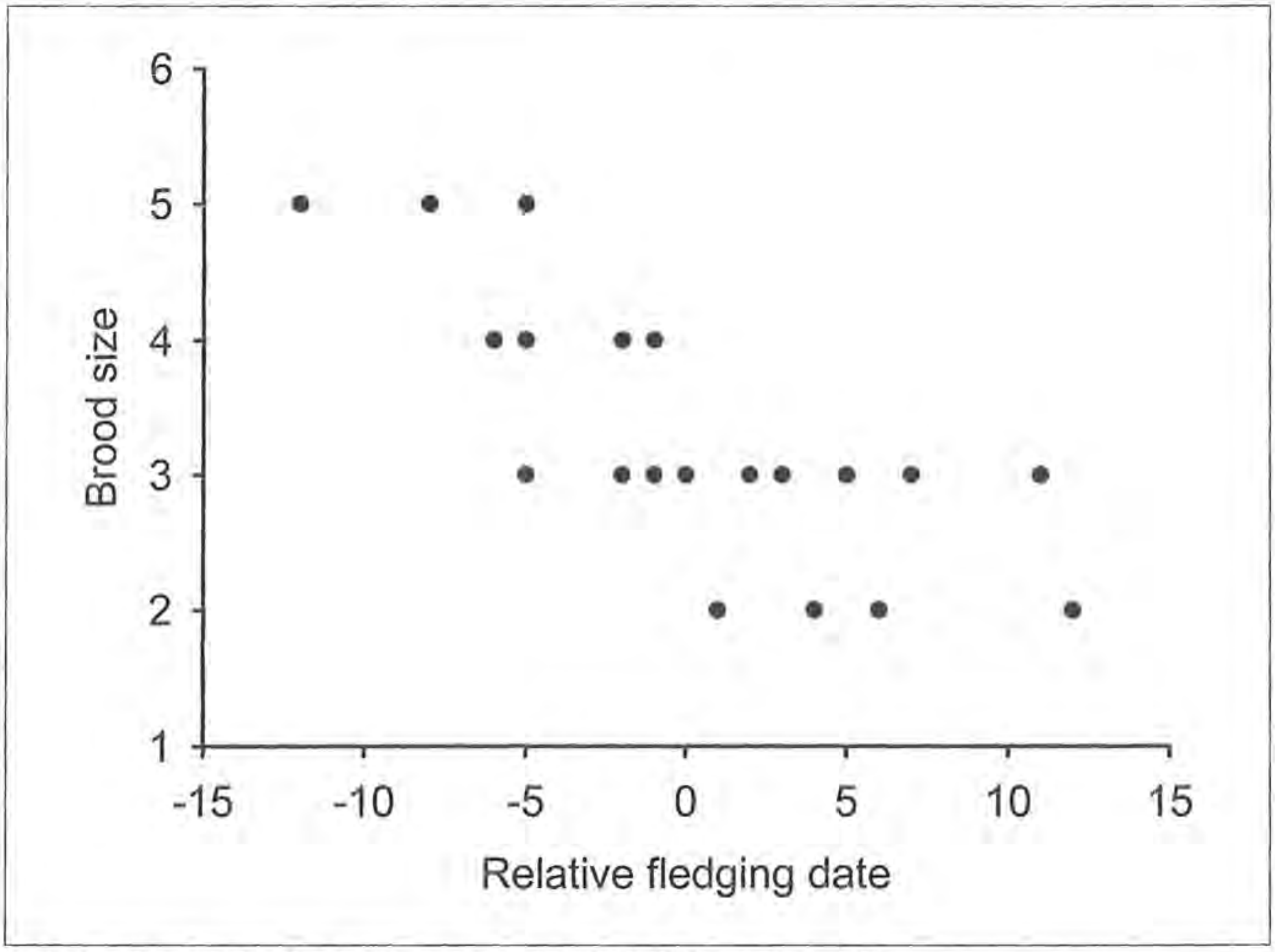

Fig. 4. Brood size in relation to relative laying date. Data for 1996–1999 combined ($n = 26$).

bred earlier in habitats with more adults and fewer beetle larvae, a seasonal decline was observed in the woodpecker brood size ($R^2 = 0.353$, $n = 26$ (including measurements from 16 additional nests found from 1996 to 1999), $p = 0.001$, Fig. 4). The range of relative fledging dates over the years was 24 days, from −12 to +12.

Bark beetle development and woodpecker parental effort

Neither the provisioning rate (visits per hour and per offspring) of the male or that of the female woodpecker was found to be related to timing of the development of spruce bark beetles (Linear regression analysis: larva, pupa, juvenile, sub-adult, adult, $n = 9$, $p > 0.050$) or to breeding time and brood size. Nor did the woodpeckers deliver more energy-rich wood-boring beetle larvae per hour and per offspring to earlier and larger broods or to broods from habitats with earlier and/or faster development of bark beetle. Using a larger nest sample size ($n = 16$), without information on the local time of prey development, both parents still did not change their provisioning rate with brood size or the timing of breeding. However, earlier ($R^2 = 0.490$, $p = 0.003$, Fig. 5a) and/or larger ($R^2 = 0.345$, $p = 0.017$, Fig. 5d) broods experienced a higher wood-boring beetle larva provisioning-rate than later and/or smaller ones. While comparing between the sexes, only females were found to increase the number of wood-boring beetle larvae delivered per hour to individual nestlings from earlier (male: $R^2 = 0.162$, $p = 0.122$, Fig. 5b; female: $R^2 = 0.277$, $p = 0.036$, Fig. 5c) and/or larger (male: $R^2 = 0.005$, $p = 0.802$, Fig. 5e, female: $R^2 = 0.453$, $p = 0.004$, Fig. 5f) broods. Intersexual differences in the adjustment of parental effort was also confirmed by the lack of correlation in provisioning rate (Kendall rank correlation, $\tau = -0.228$, $n = 16$, $p = 0{,}222$) and in wood-boring-beetle-larva delivery rate ($\tau = -0.146$, $n = 16$, $p = 0{,}440$) between males and females.

The feeding frequency and wood-boring beetle larva provisioning – and delivery – rates of both males and females did not differ before and after noon (paired-sample t-tests, $n = 16$, $p > 0.050$).

Discussion

Food availability and woodpecker natal dispersal

In Finland and Sweden, young Three-toed Woodpeckers dispersed mainly from September to November, at the time when the abundance of their main insect prey, the spruce bark beetles, in the study area was lower than during the preceding spring, in the reproductive and post-reproductive periods. Thus, the results support the working hypothesis that a decline in food availability promotes the dispersal of young woodpeckers. Because of a similar number of adult beetles in the bark during the post-reproductive (July–August) and the dispersal periods of the bird, despite a peak in the number of juveniles and sub-adults among the different species of beetles during the former period, this apparent reduction in food level seemed to result from the dispersal of synchronously-developed beetle species within the habitat. Accordingly, various studies on the population ecology of bark beetles in boreal environments have shown that emerging beetles leave their brood trees from late August to November (e.g. CHARARAS 1962, ANNILA 1969). I might suggest that the propensity of juvenile woodpeckers to disperse is causally related to a sudden change in the spatial distribution of their insect prey. This hypothesis, however, together with the finding that most of the dispersing woodpeckers captured between August and February were hatched during the preceding summer, stresses differences in abilities of juveniles and older birds to cope with such a change. Several studies have shown that dominance attributes such as age and sex determine access to food and intake rate of birds under fluctuating food conditions (EDEN 1987, RICHNER 1989). Partially reduced food supplies have been found to explain interference (DOLMAN 1995, CRESSWELL 1998), the decline in intake resulting from the behavior of other individuals (SUTHERLAND 1996), and to promote dispersal of juveniles as a result of adjustments in dominance hierarchies (LUNDBERG 1985, HANNON et al. 1987). Especially, aggressive interactions have been observed to decrease in frequency once dominant adult males can easily monopolize the resources (HENDERSON & HART 1995). This emphasizes the significant role of spatial distribution of food in social interactions. Nevertheless, whether sex-specific natal dispersal in the Three-toed Woodpecker results from aggressive interactions with conspecifics, from adaptive restlessness (ALWAYS & BOAG 1979, RITCHISON et al. 1992), or both, is not known.

Does a change in bark beetle distribution reduce the foraging efficiency of young woodpeckers at the time of dispersal? The fledglings may be able to rely on newly growing bark beetle larvae, which originate from the preceding late spring-summer oviposition, or on alternative prey. Studies of interactions between Three-toed Woodpeckers and spruce bark beetles of North America have shown how woodpeckers ignore very small larvae, younger than $3^{1}/_{2}$ to 4 months of age (KOPLIN & BALDWIN 1970). Three-toed Woodpeckers only minimally prey on the larvae of spruce beetles during the breeding season or during the time of annual molt of the bird, from late May through late September (HOGSTAD 1970, MASSEY & WYGANT 1973). This supports the view that foraging woodpeckers in this study could not start to rely on the growing beetle larvae from a preceding oviposition (i.e. in late May–June) before roughly the second half of the bird dispersal period (i.e. in late September-

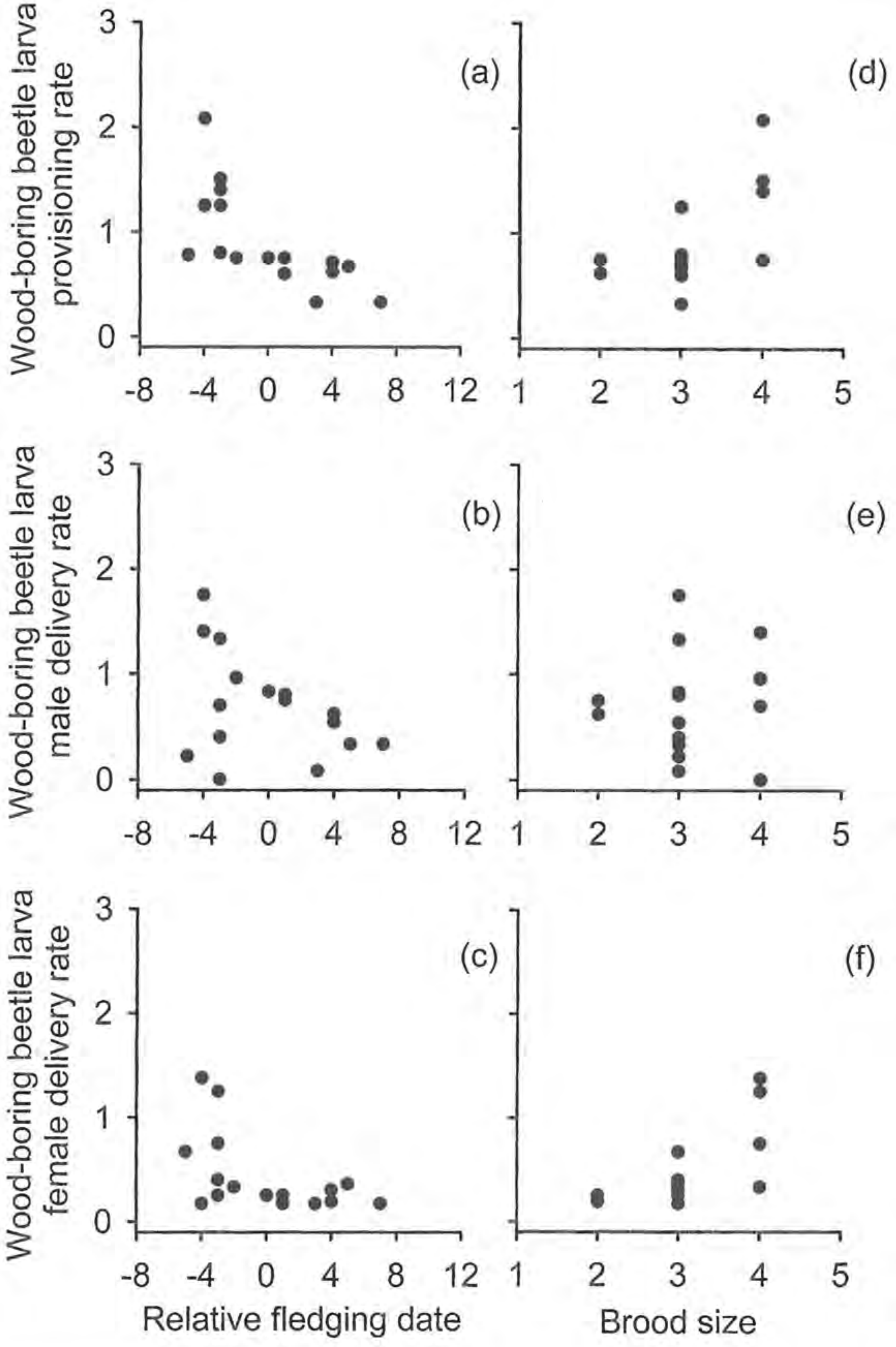

Fig. 5. Provisioning rate (visits per hr and offspring) (a, d), and male (b, e) and female (c, f) delivery rates (items per hr and offspring) of wood boring beetle larvae in relation to the breeding time (left) and brood size (right) of the woodpecker. Six hours were spent per nest. Data for 1997–1999 combined.

October). Wood-boring beetle larvae, on the other hand, and especially longhorn beetle larvae, have been shown to contribute significantly to the diet of nestlings and of fledglings and adults during the summer months (DEMENT'EV 1966, HOGSTAD 1970, PECHACEK & KRISTIN 1996). They have also been noted as a main prey for woodpeckers inhabiting areas (e.g. in the Alps) where bark beetles are only available during outbreaks (P. PECHACEK, pers. comm.). One may thus argue that, although it may promote change in food availability, natal dispersal of bark beetles should not significantly reduce the food intake of foraging Three-toed Woodpeckers since these birds are able to rely also on larger and longer-lasting wood-boring larvae. In contrast to bark beetles whose larvae develop in moist phloem and bark, some longhorn beetle species, whether shallow (e.g. *Tetropium sp.*) or deep (e.g. *Monochamus sp.*) borers, spend a part of their larval and pupal stages inside the wood (xylem) after a first period spent in the phloem (BILY & MEHL 1989). Such wood-boring activity and pupation of larvae does not begin until late August–September of the beetle's first season (ROSE 1957, BILY & MEHL 1989), i.e. at the time when young woodpeckers start to disperse. When they reach the wood by gallery excavation from the phloem, larvae may thus suddenly become unavailable for the Three-toed Woodpecker, which uses bark scaling as its predominant foraging technique (VILLARD 1994). Even if larvae do not bore deep inside the wood, this constraint on foraging may become especially meaningful for a young woodpecker with limited foraging skills and experience. That gallery excavation from the phloem may cause a decrease in the availability of woodborers for a foraging woodpecker is confirmed from analyses of stomach contents of birds collected from the boreal region. In Alaska, MURPHY & LEHNHAUSEN (1998) showed that Three-toed Woodpeckers fed mostly on bark beetles and fed only on wood-boring beetle larvae that were still in the phloem, i.e. in their first instar. In Norway, longhorn beetles were only found from gizzards of birds sampled from late May to September (HOGSTAD 1970). Those observations support the view that a sudden change in the spatial distribution of insect prey, whether they are bark beetles that disperse over habitats before hibernation, wood-boring beetle larvae that excavate deeper inside the wood for pupation, or both, may temporarily lower the foraging efficiency of woodpeckers and promote the dispersal of young individuals. As a comparison, GIBB (1960) found an association between the decline in number of foliage-gleaning passerines and the stock of their invertebrate food. Larvae of the pine looper moth *Bupalus piniarius* were still common in early September, but their pupation in the soil partly accounted for the major decrease in the stock from that time until November.

Bark beetle development and woodpecker reproductive decisions

Earlier bird studies have found that juveniles that disperse earlier are more likely to establish themselves earlier than those that disperse later (e.g. HOGSTAD 1990). Settlement time, in turn, is a major determinant of dominance, survival, recruitment, and parents' lifetime reproductive success (NILSSON & SMITH 1988, SANDELL & SMITH 1991, VERBOVEN & VISSER 1998, VISSER & VERBOVEN 1999). It would thus benefit female Three-toed Woodpeckers to produce variable phenotypes and for both sexes to adjust their parental effort with prey development if its timing prior to reproduction would determine the dispersal time and, in turn, survival prospects of their offspring. Female woodpeckers that I observed bred earlier and reared larger broods in habitats with earlier reproduction of spruce bark beetles and/or faster development, and thus with earlier beetle emergence. Using a larger sample size, but without information on the local time of prey development, only females (not males) fed offspring from earlier and/or larger broods with more wood-boring larvae, and thus with more energetically-rewarding prey compared to bark beetles. That intersexual differences in the adjustment of parental effort were found suggest sex-specific costs and benefits underlying behaviors presumed to maximize lifetime reproductive success. Thus, my results would indicate that the time of the bark beetle life cycle, which is temperature-dependent, or spring temperature per se may serve as a predictable cue for a female woodpecker to assess the benefits of investment in reproduction. Alternatively, under warmer microclimatic conditions, the much larger wood-boring longhorn beetle larvae are also expected to grow faster and reach a profitable size earlier during the spring than under cooler conditions. Before egg-laying, the female bird may use their temperature-dependent profitability as a cue to adjust her reproductive decisions, independently of a parallel but incidental change in the availability and abundance of bark beetle. Based on the relationship between the natal dispersal time of the woodpecker at the landscape level and of its prey at the habitat level, my results prompt me to suggest that timing of prey development or temperature conditions at the time of egg-laying may help female woodpeckers to assess indirectly the survival prospects of the offspring, through dispersal. Females would then allocate resources differently in reproduction and parental care in relation to the predictable timing of dispersal of their offspring. A lower survival among later-dispersing juveniles compared to earlier dispersers would contribute to explain the seasonal decline observed in the woodpecker brood size and parental care.

Acknowledgments

I am especially grateful to Hannu Huuskonen, Louis Imbeau, Harri Kontkanen and Melchert Meijer zu Schlochtern for their companionship and great help in collecting data. Thord Fransson from the Swedish Museum of Natural History as well as Jukka Haapala and Pertti Saurola from the Finnish Museum of Natural History are acknowledged for allowing me to consult ringing data files. I thank Jerome A. Jackson, Jari Kouki, Peter Pechacek, Jorma Sorjonen and Jorma Tahvanainen for comments on the manuscript. This study was funded by the Maj and Tor Nessling Foundation and by the Faculty of Mathematics and Natural Sciences, University of Joensuu.

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APPENDIX

Species assemblage and development stages of bark beetles (Coleoptera, Scolytidae) found in 350 bark samples. The classification is based on nomenclature.

Composition	Total number	Percentage (n=8,921)
Adult	**3,383**	**37.92**
Hylurgops glabratus	34	1.00
Hylurgops palliatus	251	7.42
Xylechinus pilosus	810	23.94
Polygraphus sp. (subopacus – poligraphus)	1,401	41.41
Pityogenes chalcographus	93	2.75
Pityogenes quadridens	1	0.03
Ips amitinus	114	3.37
Dryocoetes autographus	30	0.89
Dryocoetes hectographus	1	0.03
Crypturgus sp. (subcribrosus – pusillus – hispidulus)	425	12.56
Trypodendron lineatum	4	0.12
Trypodendron signatum	3	0.09
Cryphalus saltuarius	201	5.94
Pityophthorus micrographus	15	0.44
Sub-adult	**1,269**	**14.23**
Hylurgops glabratus	5	0.39
Hylurgops palliatus	51	4.02
Xylechinus pilosus	197	15.52
Polygraphus sp. (subopacus – poligraphus)	812	63.99
Pityogenes chalcographus	60	4.73
Ips amitinus	8	0.63
Dryocoetes autographus	2	0.16
Crypturgus sp. (subcribrosus – pusillus – hispidulus)	114	8.98
Cryphalus saltuarius	20	1.58
Juvenile	**742**	**8.32**
Hylurgops glabratus	2	0.27
Hylurgops palliatus	16	2.16
Xylechinus pilosus	92	12.40
Polygraphus sp. (subopacus – poligraphus)	472	63.61
Pityogenes chalcographus	47	6.33
Dryocoetes autographus	5	0.67
Crypturgus sp. (subcribrosus – pusillus – hispidulus)	32	4.31
Cryphalus saltuarius	76	10.24
Pupa	**964**	**10.81**
Larva	**2,563**	**28.73**

Population census and ecology of the White-Backed Woodpecker in the NATURA 2000 area "Ötscher-Dürrenstein" (Lower Austria)

Erfassung und Ökologie des Weißrückenspechtes im NATURA 2000-Gebiet Ötscher-Dürrenstein *(Niederösterreich)*

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Abstract

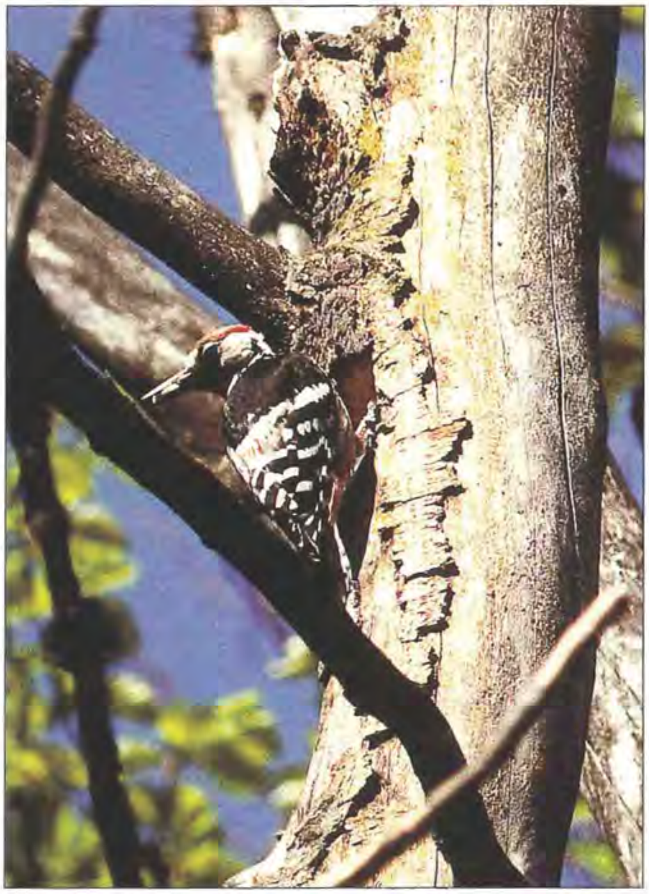
In 1999 and 2000 a quantitative survey of the White-backed Woodpecker *Picoides leucotos* as well as documentation of all other woodpecker species was carried out in the NATURA 2000 area "Ötscher-Dürrenstein" (Lower Austria). Between 69–72 territories of the White-backed Woodpecker were recorded in 43 study plots covering a total area of 5,094 hectares (an abundance of 1.38 territories/100 ha). In adjoining plots that were 233 to 590 ha in size there were between 1.36 and 2.57 territories per 100 hectares. Therefore, in mature mountainous mixed forest White-backed Woodpecker was one of the most common woodpeckers, and in the primeval stands of the "Urwald Rothwald" it was the dominant woodpecker species. The White-backed Woodpecker occurred only in woods dominated by broad-leaved trees with beech accounting for about 68 % of the total trees per stand. Large amounts of dead wood, especially logs in great dimensions (on an average of 38 cm) and snags, seem to be the most important factor in determining what habitats are suitable for the White-backed Woodpecker. Compared with other woodpecker species, the White-backed Woodpecker (as well as the Three-toed Woodpecker) prefers higher altitudes. Steep inclines and southerly slopes are typical characteristics of its territories. Based on the survey, it is estimated that there are a total of 208 territories in the study area, suggesting that the NATURA 2000 area "Ötscher-Dürrenstein" is of international importance for the White-backed Woodpecker. Based of this species' distribution and habitat use, management measurements were proposed.

*Im Rahmen der Bestandserfassung der Spechte im NATURA 2000 Gebiet „*Ötscher-Dürrenstein*" (Niederösterreichische Kalkalpen) konnten in montanen Mischwäldern auf 43 Probeflächen mit einer Gesamtfläche von 5.094 ha 69–72 Reviere des Weißrückenspechtes nachgewiesen werden. Die Siedlungsdichte bezogen auf die gesamte Untersuchungsfläche betrug 1,38 Reviere/100 ha und lag in zusammenhängenden Probeflächen mit Ausdehnungen zwischen 233 und 590 ha bei 1,35–2,57 Revieren/100 ha. In naturnahen Mischwäldern gehörte der Weißrückenspecht neben dem Buntspecht zu den häufigsten Vertretern der Spechtfauna und war im primären Urwaldgebiet „Rothwald" sogar die dominierende Spechtart. Der Weissrückenspecht besiedelte ausschließlich laubholzdominierte Wälder, der Anteil der Buche betrug im Durchschnitt 68 %. Neben einem hohen Angebot an Totholz bevorzugte der Weißrückenspecht Altholzbestände, steile Hangneigungen und südexponierte Wälder. Der Schwerpunkt der Nachweise lag zwischen 900 und 1200 m Meereshöhe, die flächenbereinigte Darstellung zeigte die Präferenz für höhere Lagen. Auf Basis der Kartierungsergebnisse wurde für das gesamte NATURA 2000 Gebiet „*Ötscher-Dürrenstein*" ein Weißrückenspecht-Bestand von 208 Revieren errechnet. Dies bestätigte die internationale Bedeutung der untersuchten Hang- und Schluchtwälder. Die Erfassung der Spechtfauna sowie die Untersuchung der ökologischen Ansprüche des Weißrückenspechtes dienen als Grundlage für Managementmaßnahmen, die abschließend kurz skizziert werden.*

Introduction

The White-backed Woodpecker *Picoides leucotos* is the rarest and the most endangered woodpecker species in

Fig. 1. Female White-backed Woodpecker at the breeding hole in a beech stump at Maiszinken. **(Photo: Alois Thaler)**



White-backed Woodpecker **(Photo: Peter Pechacek)**

Europe. Estimates given for central Europe including Poland and Slovakia are between 2,400–4,300 breeding pairs (BAUER & BERTHOLD 1996), but due to the loss of habitats, the White-backed Woodpecker is further declining across most of its range (AULEN 1988, VIRKKALA et al. 1993, WESOLOWSKI 1995).

Our knowledge concerning the distribution, population size and ecology of the alpine population is very poor (RUGE & WEBER 1974, SCHERZINGER 1982, PECHACEK 1995, KILZER 1996). Systematic census work and monitoring programs are required for conservation and for management plans (BERG 1997, SACKL & SAMWALD 1997). In 1999 and 2000 a quantitative survey of the White-backed Woodpecker as well as a documentation of all other woodpecker species was carried out in the NATURA 2000 area "Ötscher-Dürrenstein" (FRANK & HOCHEBNER 2001).

The results concerning the ecology of the White-backed Woodpecker are presented in the thesis "Brutzeitliche Einnischung des Weißrückenspechtes *Picoides leucotos* im Vergleich zum Buntspecht *Picoides major* in montanen Mischwäldern der nördlichen Kalkalpen" (FRANK 2001). This abstract is only a brief summary of the ecology of the White-backed Woodpecker.

Fig. 2. Breeding habitat of the White-backed Woodpecker. The forest is dominated by beech with large amount of dead wood at Eisgrube. **(Photo: Thomas Hochebner)**

Study Area

The study area includes the NATURA 2000 area "Ötscher-Dürrenstein" with a total area of 42,622 hectares. It is located in the south-west of Lower Austria in the "Nördlichen Kalkalpen" and ranges in altitude from 430 m in the northern parts up to 1,900 m in the highest mountains of the south. Eighty-five percent of the study area is covered by forest. With the exception of the subalpine spruce stands in the higher altitudes, most of the area consists of mixed montane forest dominated by beech, spruce, and fir. Due to intensive forestry, some of the mixed forest is partly replaced by spruce stands with broad-leaf-dominated stands often restricted to steep locations where little or no logging occurs.

In the study area, there are still large mature stands with much dead wood. Some of the mortality is attributed to avalanches and rock slides. The study area also includes primeval stands of the "Urwald Rothwald". Therefore it was possible to compare the abundance and the habitat use of the White-backed Woodpecker in virgin stands and forests.

In addition to the White-backed Woodpecker, the Grey-headed Woodpecker *Picus canus*, Black Woodpecker *Dryocopus martius*, Great Spotted Woodpecker *Picoides major*, and Three-toed Woodpecker *Picoides tridactylus* regularly breed in the study plots.

Methods

The survey was carried out during the breeding seasons of 1999 and 2000. Areas with old deciduous stands were identified using forestry plans and aerial photos. In these potential habitats of the White-backed Woodpecker, 43 plots covering a total area of 5,094 ha were randomly selected. In 1999 plots located in the western part of the area were studied, and in 2000 plots in the eastern part of the study area were examined. Each plot was checked twice: first in March or April, and second in May or June. During this period (mating-, breeding- and feeding period), the White-backed Woodpecker shows the highest activity of drumming and calling (SCHERZINGER 1982). Playbacks of drumming were rarely used because there was no positive effect at the beginning of the survey.

Territory mapping was used and we walked through the plots in vertical intervals of about 100 meters. All records of woodpeckers (drumming, calling, visual observations) were noted on maps or aerial photographs (1:25,000). The behaviour of each woodpecker was recorded as well as parameters of each tree used (species, height, diameter and vitality). We also measured parameters of habitat structure (exposition, forest structure, tree composition, number of logs and lying dead wood and their dimensions, number of stocks) within a radius of 20 meters around the observation point.

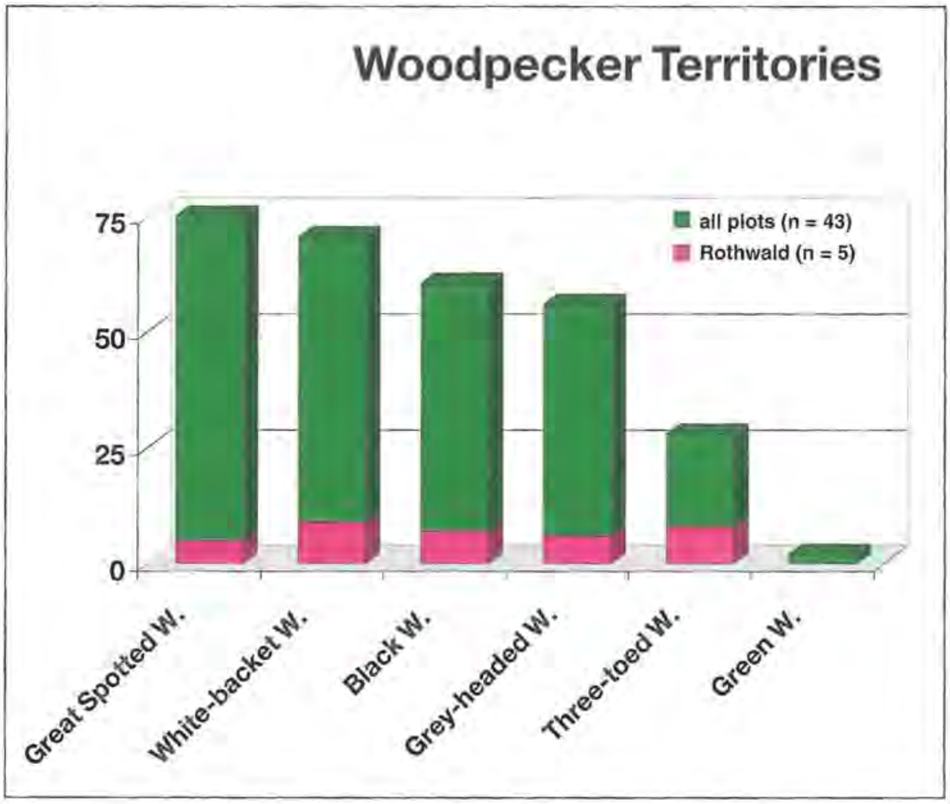


Fig. 3. In 43 plots with a total area of 5,094 hectares 69–72 territories of the White-backed Woodpecker were recorded. In the virgin stands of the "Urwald Rothwald" it is even the most common woodpecker species.

Results

Presence, number of territories, and abundance of the White-backed Woodpecker

The White-backed Woodpecker was present in 90.7 % of the study plots. Only the Black Woodpecker had a higher presence and was recorded in 93 % of the plots. So it appears that, in suitable habitats, the White-backed Woodpecker is evenly distributed over the study area.

Across 43 plots and 5,094 ha, 69–72 White-backed Woodpecker territories were recorded, which translates into an abundance of 1.38 territories per 100 ha. In adjoining plots that were 233 ha to 590 ha in size, we found between 1.36 and 2.57 territories per 100 ha (FRANK & HOCHEBNER 2001).

The White-backed Woodpecker is beside the Great Spotted Woodpecker the dominant woodpecker species in the study plots. In the primeval stands of the "Urwald Rothwald" it is the most common woodpecker species (Fig. 3).

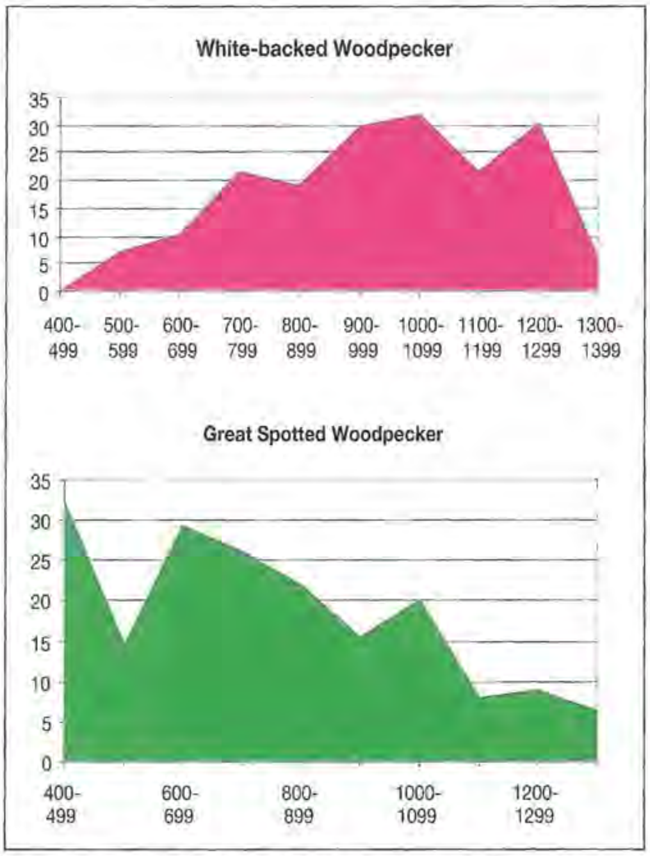


Fig. 4. The White-backed Woodpecker showed a relative preference for higher altitudes with a peak between 900 and 1,200 metres. This was contrary to the vertical distribution of the Great-spotted Woodpecker which was less abundant in higher elevations. The preference of different altitudes seemed to be a way to avoid interspecific competition.

Altitude distribution

The distribution of the White-backed Woodpecker ranged from 540 m to 1,320 m with most observations between 900 and 1,200 m, suggesting that the White-backed Woodpecker preferred higher altitudes than for example the Great Spotted Woodpecker (Fig. 4).

Slope and aspect

The White-backed Woodpecker was found most frequently on steep slopes that ranged between 30°and 40°, the median of all observations was 29°. This differs from the average slopes found in the sample plots with 24° with a most areas between 26–29°.

The preference for south exposed slopes by the White-backed Woodpecker was significant, about 70 % of all observations were in south-east, south and south-west facing slopes (Fig. 5).

Deciduous trees

The White-backed Woodpecker mainly occurred in forests with a high portion of broad-leaved trees. In the NATURA 2000 area "Ötscher-Dürrenstein," the habitat was dominated by beech (Fig. 6).
Beech, on which 50 % of all foraging White-backed Woodpeckers were observed using, was the most important substrate for foraging. Spruce was used in the study area, but it was used less frequently than expected given its relatively high abundance of about 70 %. On the other hand, ash *Fraxinus excelsior* and fir *Abies alba*, both of which occurred in low numbers, were, in relation to their low abundance, strongly preferred.

All breeding cavities ($n = 11$) were excavated in deciduous trees (1 breeding hole in ash tree, 10 cavities in beech).

Dead wood

In comparison with other woodpecker species, the White-backed Woodpecker inhabits forest with large amounts of dead wood. For example, the number of logs is two times higher in habitats of the White-backed Woodpecker than in territories of Great Spotted Woodpecker (FRANK 2001). About 55 % of foraging White-backed Woodpeckers were observed on dead wood, primarily on beech (about two thirds of all observations).

Especially logs in great dimensions (on an average of 38 cm) were important structural elements in its habitat. Snags already were used in smaller dimensions (with about 20 cm in diameter).

For the excavation of the nest-hole rotten trees of beech and ash ($n=11$) were exclusively used.

Old stands

In accordance to SCHERZINGER (1982) and PECHACEK (1995), the White-backed Woodpecker is preferen-

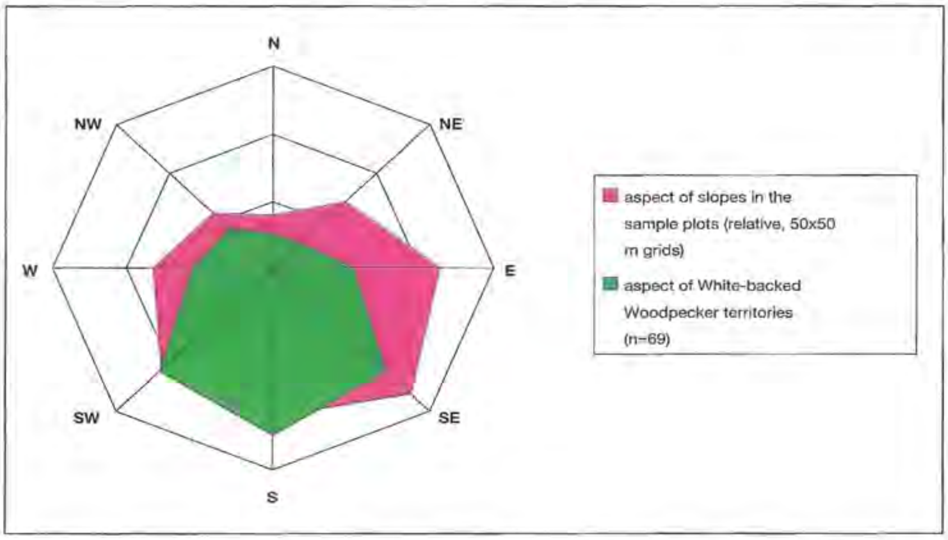


Fig. 5. The White-backed Woodpecker prefered south-exposed forests. Beside the higher portion of broad-leaved trees, in particular beech, climatic factors make these locations attractive for the White-backed Woodpecker.

tially using old stands. The inhabited stands in the study area were in average 195 (!) years old, only 4 % of the observations were in forests younger than 100 years (FRANK 2001).

Discussion

Based on our mapping (69–72 territories of the White-backed Woodpecker in the study plots and 11 territories outside) we have estimated 208 territories in the NATURA 2000 area "Ötscher-Dürrenstein" (FRANK & HOCHEBNER 2001).

Considering the population estimates of 2,400–4,300 pairs given for central Europe (BAUER & BERTHOLD 1996) and 200–300 pairs (ZUNA-KRATKY cited in BERNONI 1994, KARNER et al. 1997) for Austria, the population we examined is of international importance.

This study is the first survey for central Europe, which shows that in suitable habitats, the White-backed Woodpecker can be the dominant woodpecker species. This is in accordance with a statement by S. HOFFMANN (in MURR 1975/77), which identifies White-backed Woodpecker as a very common woodpecker in the Loferer and Leoganger Steinberge/Salzburg.

Actually, we have to consider that there are some mature stands with extensive forestry where the abundance of the White-backed Woodpecker is higher than in the virgin stands of the "Urwald Rothwald" due to climatic factors and because of the preference of White-backed Woodpecker for lightly closed forests.

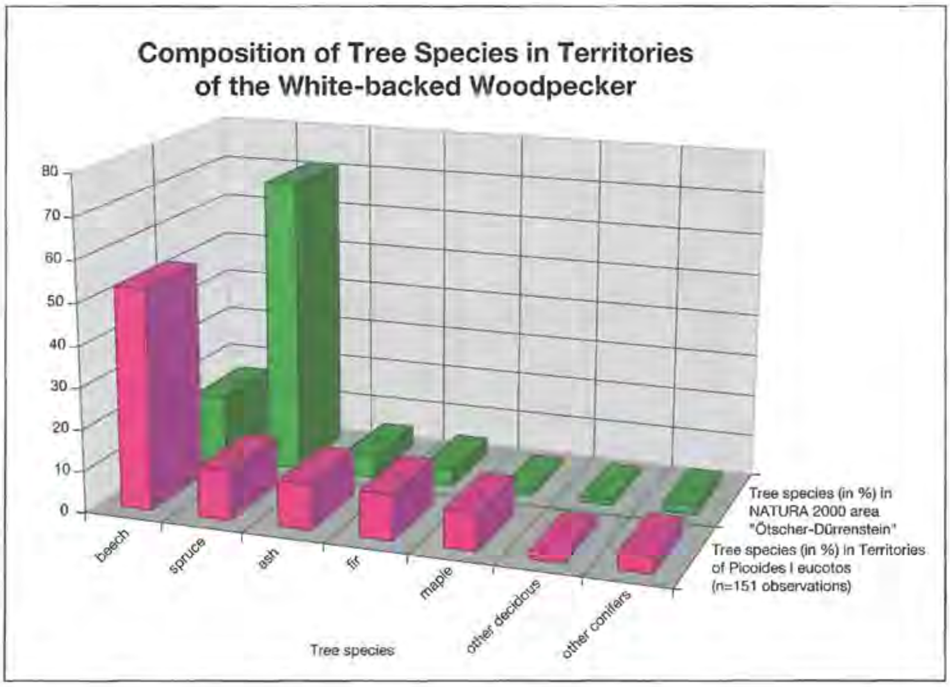


Fig. 6. In the NATURA 2000 area "Ötscher-Dürrenstein" the White-backed Woodpecker inhabited only forests with a high portion of deciduous trees, in particular beech. In comparison with the availability (BÜCHSENMEISTER, pers. comm.) Spruce seemed to be of less importance while ash, fir and maple were important elements in the habitat of the White-backed Woodpecker.

This work confirms the importance of the White-backed Woodpecker as an indicator for mature, old growth and decidous stands. These stands are of high quality especially for the Grey-headed Woodpecker, but also Black Woodpecker and even Three-toed Woodpecker can reach very high abundance in the forests of the study plots (FRANK & HOCHEBNER 2001). Only the Great Spotted Woodpecker seemed to be regionally less abundant, perhaps due to competition with the White-backed Woodpecker (FRANK 2001).

In accordance with PECHACEK (1995), the evidence suggests that the White-backed Woodpecker and the Three-toed Woodpecker prefer higher altitudes than other species. This is especially interesting in comparison with the Great Spotted Woodpecker (Fig. 4), which probably competes with the White-backed Woodpecker.

The preference of steep slopes by the White-backed Woodpecker is likely a result of forestry practices in which steep slopes are generelly avoided.

However, in the primeval stands in the "Urwald Rothwald," the White-backed Woodpecker also prefers steep slopes. These locations are more strongly exposed to the sun and are warmer than the "cold basins" in the valleys which receive much less sunlight. Such conditions lead to a higher portion of deciduous trees, and also makes these locations free of snow earlier in the year, while in the cold basins there is a closed snow cover until April/May. This fact is apparently of high importance for the White-backed Woodpecker, which forages on lying dead wood more often than any other woodpecker species in the study area. Therefore, in early spring White-backed Woodpeckers are regularly observed on clear-cuttings foraging on stocks.

These factors may also be the reason for the preference of south-exposed slopes by the White-backed Woodpecker (Fig. 5).

A large amount of dead wood that is in adequate quality (FRANK 2001) seems to be the most important factor determinig which forests are suitable for the White-backed Woodpecker (RUGE & WEBER 1974, GLUTZ & BAUER 1980). Due to the closed snow cover until April/May, standing dead wood ("snags") is an important structural element which is available also in winter and early spring.

While snags and stumps are already used in small dimensions (about 20 cm in diameter), lying dead wood must be thicker to be intensively used by foraging White-backed Woodpeckers. Thus, small windfalls were very valuable in producing additional foraging habitat for hits species.

For the conservation of the White-backed Woodpecker in the NATURA 2000 area "Ötscher-Dürrenstein" as one of the most important populations of White-backed Woodpecker in central Europe, concrete conservation measurements are suggested by FRANK & HOCHEBNER (2001) and are briefly summarised in the following points:

I. Preserving large wilderness refuges and primeval stands as central habitats

One wilderness refuge is already realised in the south of the NATURA 2000 area. The preserved area of 805 ha includes at least 16 breeding pairs of the White-backed Woodpecker.

FRANK & HOCHEBNER (2001) have proposed further large wilderness refuges with areas of at least 300–400 ha. Therefore, it would be possible to ensure the habitats for about 13 % of the population in the study area.

II. Network consisting of small old growth stands ("stepping stones")

If there are adequate rests of old growth deciduous stands, the White-backed Woodpecker is tolerant of forestry and fragmentation by forestry roads. We suggest creating a network of small old growth stands of at least 10–20 ha each. The patches should be close enough to one another to allow ready dispersal.

For extensive areas, an average of about 30 % old growth stands (older than 100 years) seems to be the minimum requirements of the White-backed Woodpecker. Therefore, per 100 ha forest at least 2 or 3 old growth stands should be preserved.

III. Adequate practice of forestry

In some plots with extensive forestry, the White-backed Woodpecker can reach abundances as high as in virgin stands. Therefore, it is beneficial to improve the amount of dead wood, to increase the portion of deciduous trees in each stand (e.g., by natural succession instead of reforestration with spruce), and to avoid large clear-cuttings.

Acknowledgements

My major debt is to Thomas Hochebner for the great teamwork and Hans-Martin Berg for his permanent personally support. I am also grateful to Dr. Wolfgang Scherzinger who attends to this project, to Josef Pennerstorfer for his support concerning data analysis and to Mag. Gabor Wichmann for many helpful discussions. Thank you to DI Alois Thaler who makes the photos of White-backed Woodpecker available to me.

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Woodpeckers visit on the island of Greiswalder Oie

Spechte als Gastvögel auf der Insel Greiswalder Oie

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Abstract

The Greifswalder Oie is a Baltic Sea island of 62 ha. The island is located in the Pommersche Bucht, 12 km west of the Rügen Island. Pastures (interspersed with bushes) that were once used for agriculture characterize the island today, and these pastures are maintained by ponies and sheep to prevent forestation. In areas of ongoing succession young ashes grow and form dense patches in the northeast of the island. These patches are adjacent to an old deciduous forest that is almost 10 acres and consist of oak *Quercus spp.*, lime *Tilia spp.*, hornbeam *Carpinus betulus*, beech *Fagus silvatica*, and elm *Ulmus spp*. Since 1994, the Jordsand Society for the Protection of Seabirds and Nature (Verein Jordsand zum Schutze der Seevögel und der Natur e. V.) has operated a ringing station on the island. In 1995, a systematic census of the population density of breeding birds began. Woodpeckers do not breed on the Greifswalder Oie, therefore, woodpeckers that are netted on the island provide useful migration and dispersal information. The Great Spotted Woodpecker *Picoides major*, and Wryneck *Jynx torquilla*, are the most common visitors, passing through every year. The Black Woodpecker *Dryocopus martius*, Green Woodpecker *Picus viridis*, and Lesser Spotted Woodpecker *Picoides minor*, are irregular visitors. The phenology and numerical variation associated with yearly visits is also discussed.

Die Greifswalder Oie ist eine 62 ha große Ostseeinsel in der Pommerschen Bucht 12 km westlich von Rügen. Die Insel wird heute weitgehend von ehemals landwirtschaftlich genutztem Offenland geprägt, welches durch extensive Beweidung mit Ponys und Schafen vor einer Bewaldung bewahrt werden soll. Diese Flächen sind teilweise von Sträuchern durchsetzt. Wo die Sukzession weiter fortgeschritten ist, finden sich Eschen, die sich im Nordosten der Insel zum sogenannten „Jungwald" verdichten. Dort grenzt unmittelbar ein etwa 4 ha großer alter und artenreicher Laubwald (Eiche, Linde, Hain- und Rotbuche, Ulme) an. Seit 1994 betreibt der Verein Jordsand zum Schutze der Seevögel und der Natur e. V. eine Beringungsstation auf der Insel, und im Jahr 1995 begannen systematische Erhebungen des Brutvogelbestandes. Spechte gehören nicht zu den Brutvogelarten der Greifswalder Oie. Alle Beobachtungen von Spechten können somit zweifelsfrei Auskunft über Zug bzw. Dismigration geben. Buntspecht und Wendehals gehören zu den alljährlichen Durchzüglern. Unregelmäßig wurden auch die Arten Schwarzspecht, Grünspecht und Kleinspecht nachgewiesen. Der Vortrag gibt unter anderem Auskunft zur Phänologie und zu jährlichen Schwankungen.

Introduction

With the exception of the Wryneck and some New World species, migration in woodpeckers is almost unknown. Therefore, small islands without breeding populations of woodpeckers make a useful setting for documenting movement: every observed woodpecker is something special. This has been the case at Greifswalder Oie, an island nature reserve established in August 1993, and cared for by the care of Jordsand Society for the Protection of Seabirds and Nature (SCHNEIDER 1993). It has a ringing station that operates year round, and analysis of ringing lists and observations (complemented by biometric data) enables us to follow the occurrence of woodpeckers and gain insights into seasonal movements.

Study Area

The Greifswalder Oie is a small island (about 62 ha) in the Baltic Sea situated in the Pommersche Bucht (54°15'N, 13°55'E). The closest breeding woodpeckers are more than 12 km west on the island of Rügen and about 11 km southwest on the island of Usedom (KLAFS & STÜBS 1987). Greifswalder Oie is about 1,640 m long and reaches an altitude of 17 m above sea level (SCHNEIDER 1997). Pastures that were once used for agriculture characterize the island today, and these pastures are maintained by ponies and sheep to prevent forestation (ABRAHAM 2000). Pastures are interspersed by old fruit trees and various species of shrubs (primarily hawthorn *Crataegus*, sloe *Prunus spinosa* and blackberry *Rubus fructicosus*). In areas of ongoing succession, young ashes form dense patches of young growth in the northeast of the island. These patches are adjacent to an old patch (almost 4 ha) of deciduous forest with oak *Quercus* spp., lime *Tilia* spec., hornbeam *Carpinus betulus*, beech *Fagus silvatica*, and elm *Ulmus* spp. The ground vegetation in spring is dominated by Bärlauch *Alium ursinum*. Beech trees are large enough in diameter for the Black Woodpecker *Dryocopus martius* to use for nesting. The island's east coast is characterized by an open, unprotected landscape and an actively eroding cliff (Fig. 1). Some parts of the coastline that are protected by stone walls, have shallow water and reed beds. Cliffs that have eroded are covered with woods.

Methods

In the 1930s, Walter Banzhaf, the pioneer of ornithological research on the island of Greifswalder Oie, ran a small biological station on the island for the museum of natural history in Stettin. In 1994, a ringing program began on the island in cooperation with the European-African Songbird Migration Network (GEORGE 1999a). Several lines of nets are operated during spring migration (between April 1st and May 31st). During fall migration (between August 1st and October 31st), a large, funnel-shaped net is also used (Fig. 2). Data collection of breeding birds started in 1995 (HEINICKE 1996). The island farm is inhabited throughout the year and scientists and visitors of the Jordsand Society keep a diary about all observations. All this material, including personal observations and unpublished yearbooks of observations, are presented in this paper.

Results

Five species of woodpeckers have been observed on the island of Greifswalder Oie.

Wryneck *Jynx torquilla*

This transpalearctic species, has local populations above the Arctic Circle and migrates to winter habitats in west and central Africa (SCHERNER 1994). It has an interesting temporal pattern of migration on the island of Greifswalder Oie. It appears for just three decades during summer and winter migration (Fig. 3). Summer migrating birds occurred as early as April 22nd (von RÖNN, Fig. 4), and numbers of individuals steadily increased until mid May with the latest catch on May 18th (BANZHAF 1938). Winter migration also started slowly. The earliest observations were made on August 19th in 1997 (GEORGE & SCHILZ unpubl. data). The number of individuals increased to a migration peak in early September and dropped off afterwards. BANZHAF (1936) recorded the latest observation on September 24th, 1932. One individual that appeared on September 1st 1997 was ringed with three other birds the day before, suggesting a short rest period. Another Wryneck ringed on Greifswalder Oie appeared at the following location:

Fig. 1. View of the island Greifswalder Oie including the old deciduous forest and the open unprotected east coast cliff. **(Photo: Klaus George)**

Fig. 2. The funnel-shaped net construction, opened in northeastern direction on the island of Greifswalder Oie. **(Photo: Klaus George)**

HIDDENSEE OA 68139

August 27th, 1997 not from the same year on Greifswalder Oie (54°15'N; 13°55'E),

August 30th, 1997 at Galenbecker Lake (53°37'N; 13°44'E) three days later and 71 km south of Greifswalder Oie and August 31st, 1997 at Galenbecker Lake 4 days after ringing.

Winter migration starts at the island of Greifswalder Oie in August with Redstart *Phoenicurus phoenicurus*, Spotted Flycatcher *Muscicapa striata,* and Pied Flycatcher *Ficedula hypoleuca* and ends in October with Goldcrest *Regulus regulus*, Chaffinch *Fringilla coelebs* and Greenfinch *Carduelis chloris*. Sparrowhawks *Accipiter nisus,* migrate or rest regularly on the island. HEINICKE et al. (1995) mentions as many as 285 individuals between August 7th and October 28th, 1994. Therefore it is not surprising that Sparrowhawks caugth Wrynecks on the island of Greifswalder Oie (HEINICKE 1995). The number of caught or observed individuals during the migration periods varies considerably (Fig. 5). According to measurements of BANZHAF (1936), mean wing length of 32 birds is 90.5 mm (range = 87–95 mm). Mean partial feather (KAISER 1993) length for 25 individuals was 68.4 mm (range 66–71 mm). The distribution of wing measurements is shown in Fig. 6. Mean weight of 30 birds was 34.5 g (range = 30.1–39.9 g, Fig. 7)

Green Woodpecker *Picus viridis*

A few observations were made on August 21st and 22nd, 2000 (VON RÖNN unpubl. data) and August 28th, 2000 by GAUGTER (unpubl. data).

Black Woodpecker

The following list includes all observations:
August 1st, 1998 – early in the morning at the nets (SCHLAWE unpubl. data),

April 10th, 1998 – in old growth forest (KUNERT unpubl. data), July 15th, 2001 – in old growth forest (GEORGE unpubl. data), August 2nd, 20th/ 21st (PFEFFER unpubl. data) in old growth forest and on August 29th – September 11th (GEORGE et al. 2001). It is possible that all observations in 2000 were made of the same bird.

Great Spotted Woodpecker *Picoides major*

This species is less frequently observed on the island of Greifswalder Oie during spring migration than in fall (Fig. 8). The earliest observation was made on March 8th, 1995 (HEINICKE 1996). According to data from 1994 – 2000, spring migration ends in early May. In summer, the earliest data for this species is from the middle of June (SCHLAWE unpubl. data – 17 June 1997). The

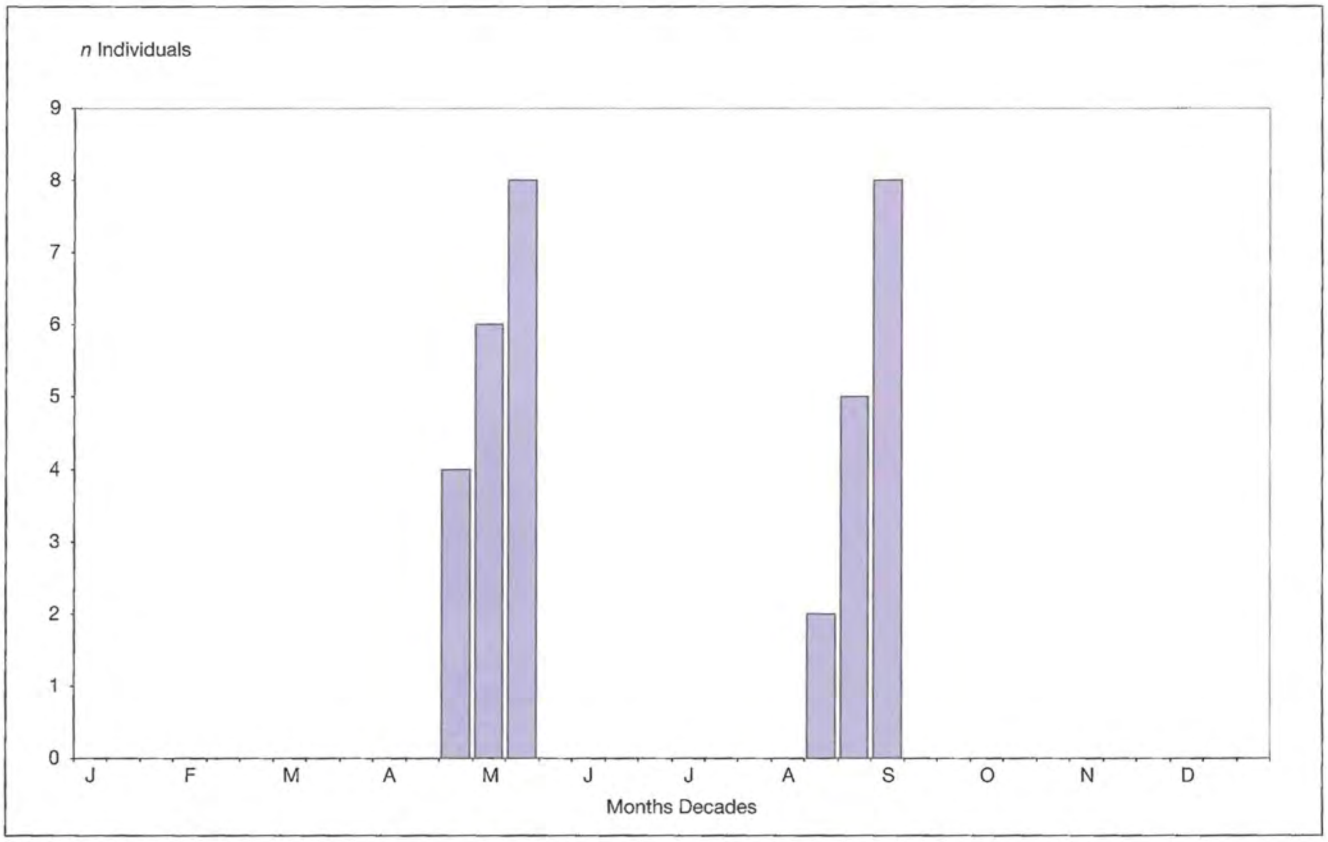

Fig. 3. Phenology of migrating Wrynecks on the island of Greifswalder Oie between spring 1994 and 2000.

Fig. 4. Wryneck on the island of Greifswalder Oie at April 22nd, 2000. **(Photo: Jan von Rönn)**

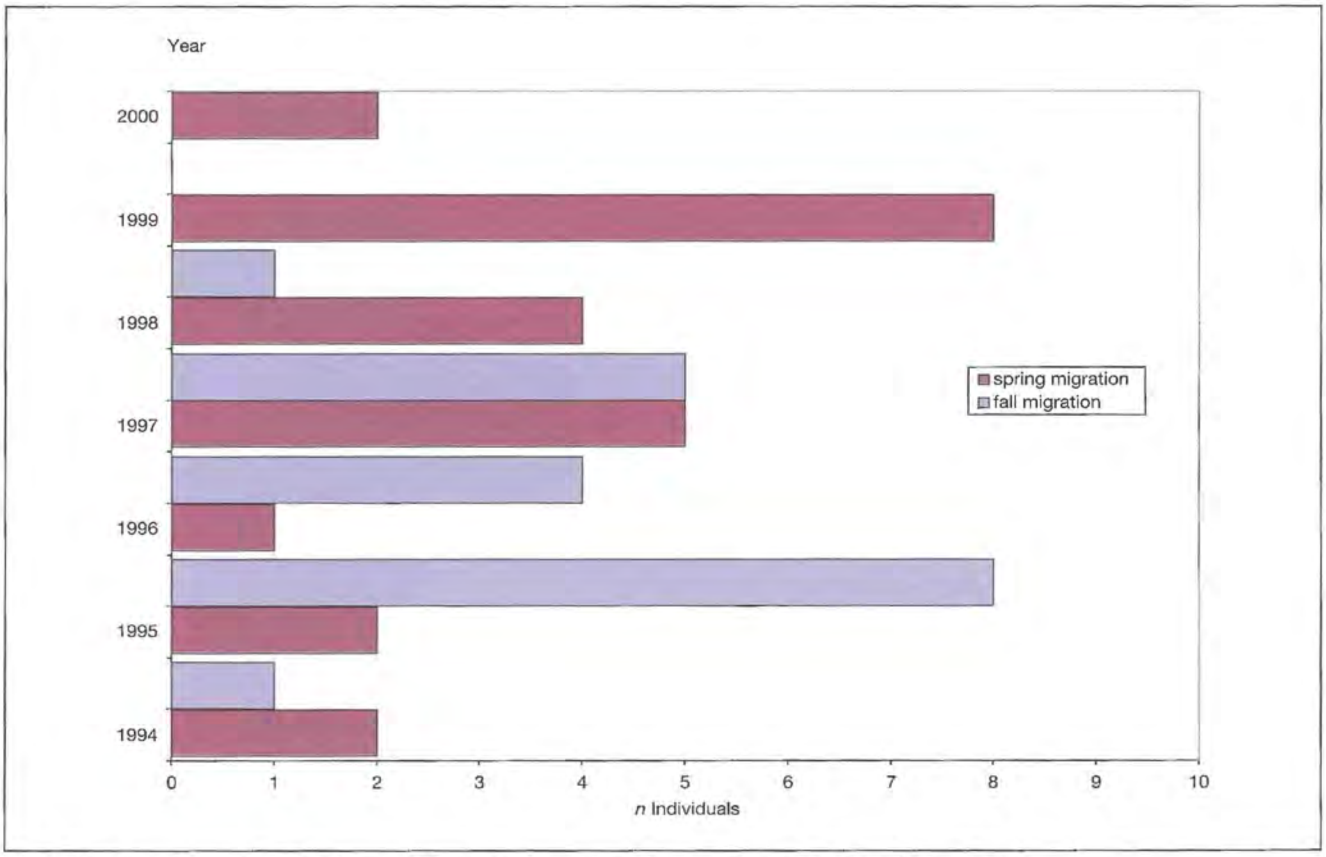

Fig. 5. Number of caught and observed Wrynecks during migration on the island of Greifswalder Oie.

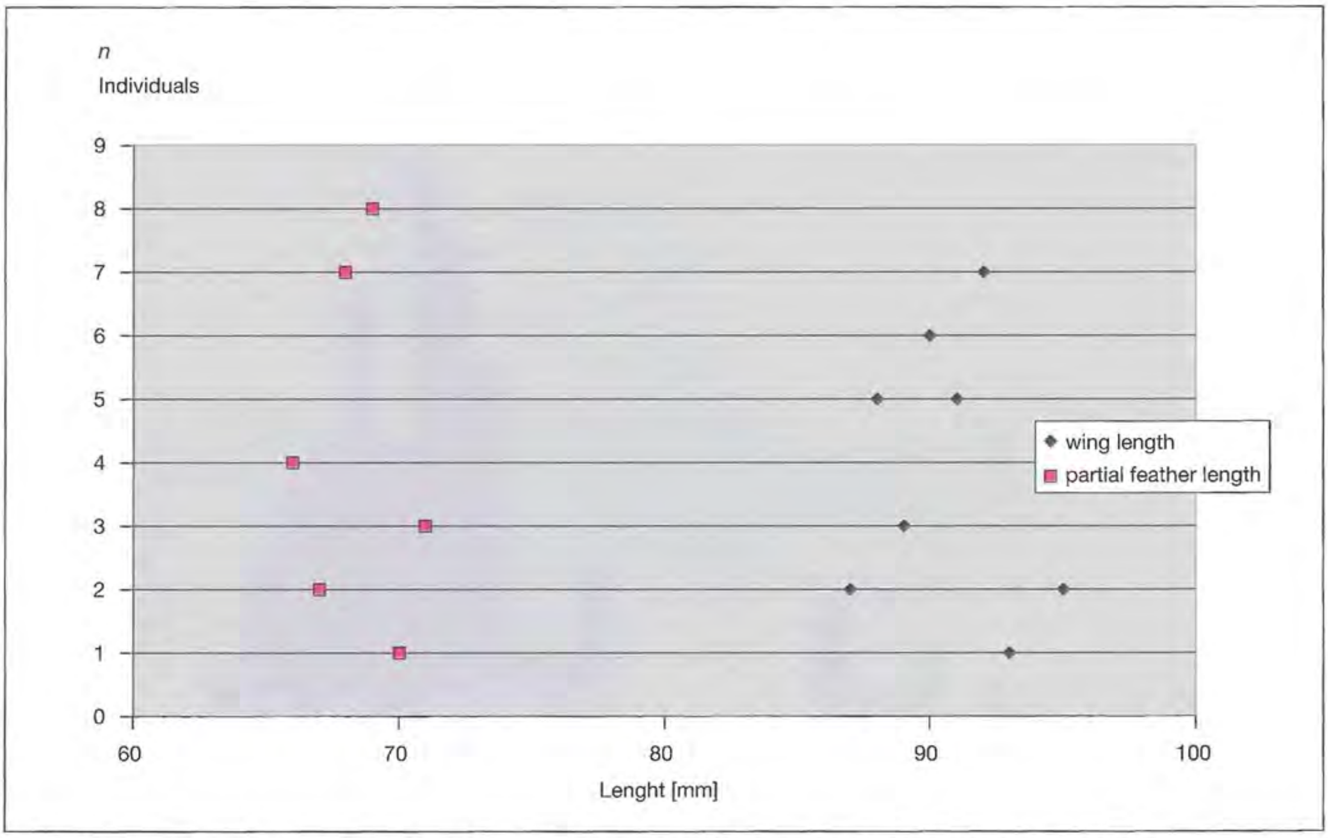

Fig. 6. Wing length distribution of the Wryneck caught on the island of Greifswalder Oie between 1932 and 2000.

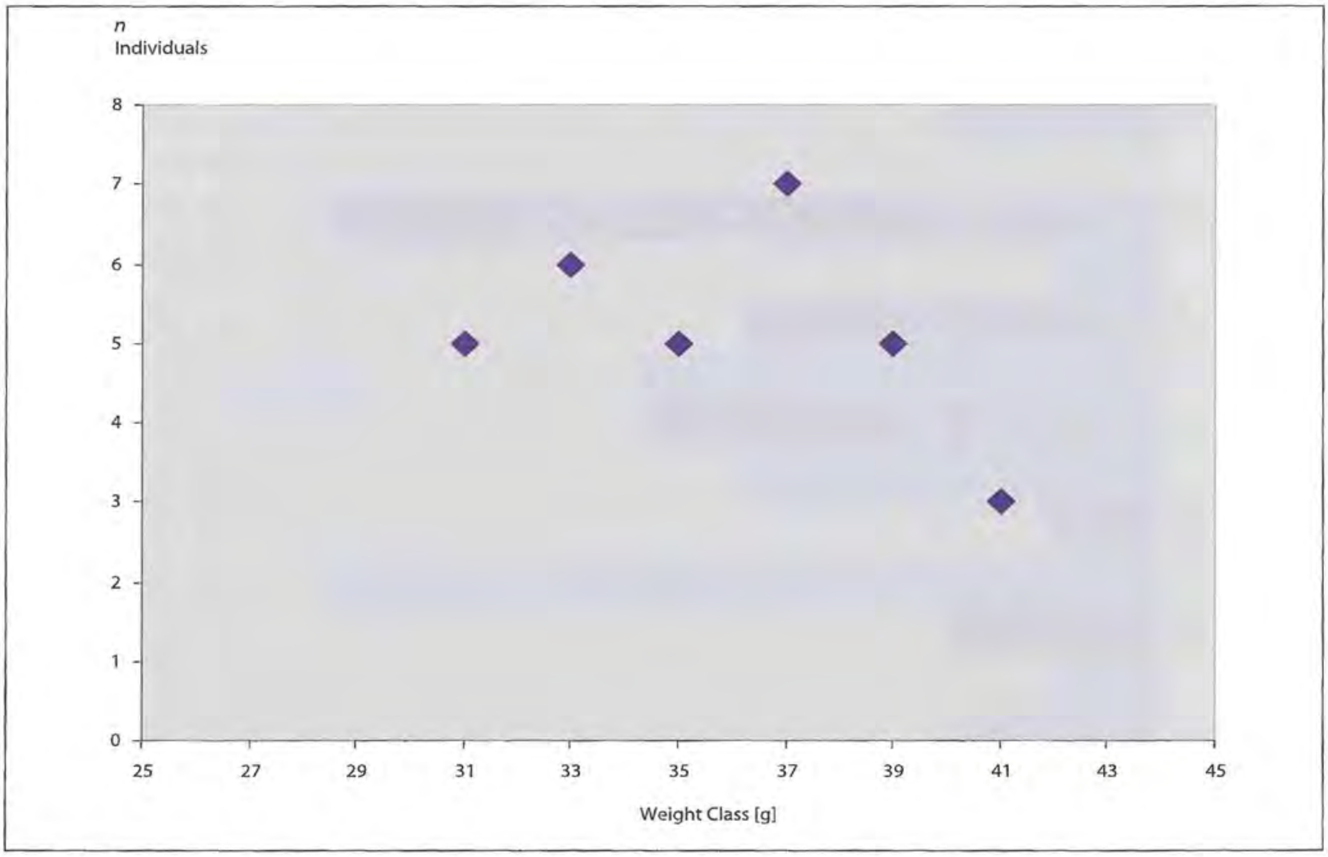

Fig. 7. Weight distribution of Wrynecks caught on the island of Greifswalder Oie between 1932 and 2000.

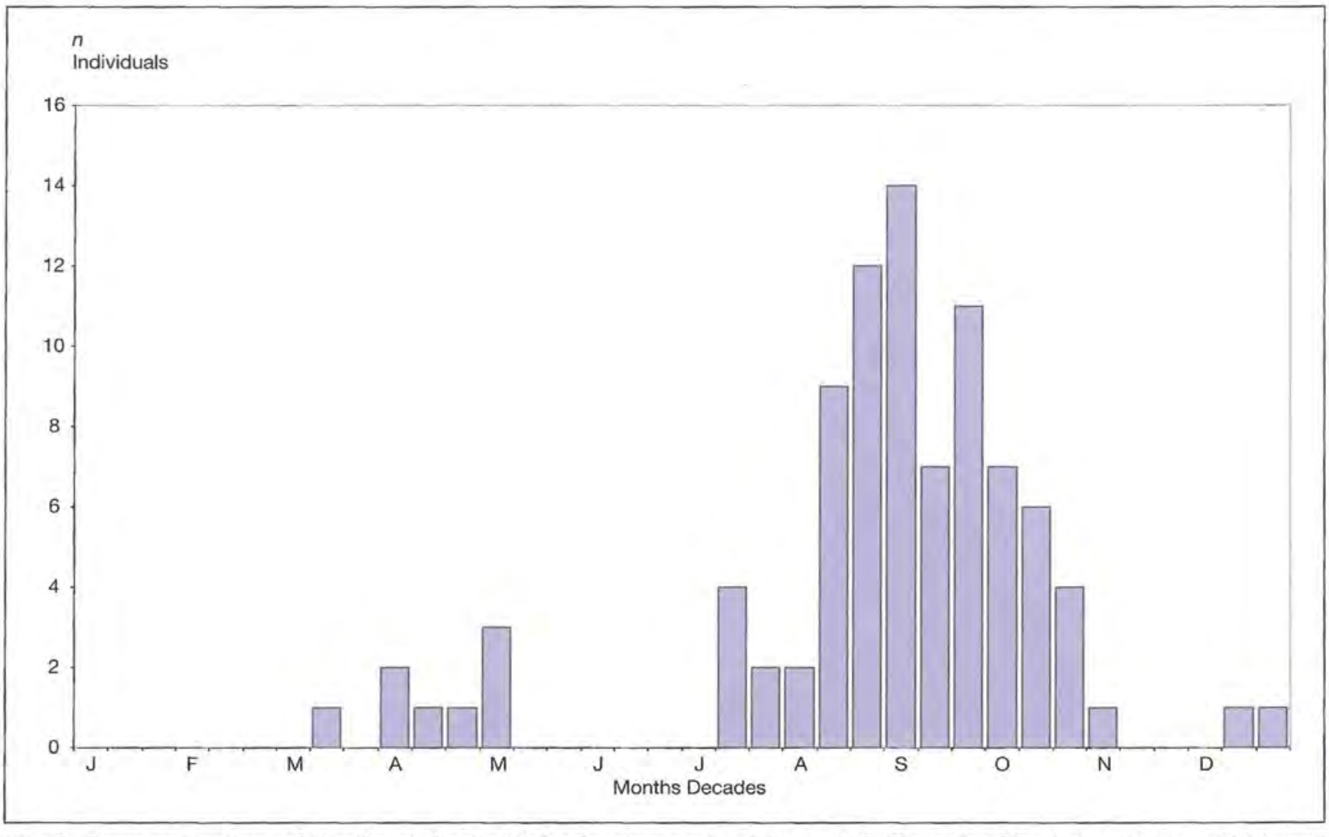

Fig. 8. Temporal pattern of the Great Spotted Woodpecker on the island of Greifswalder Oie during summer 1994 until spring 2000.

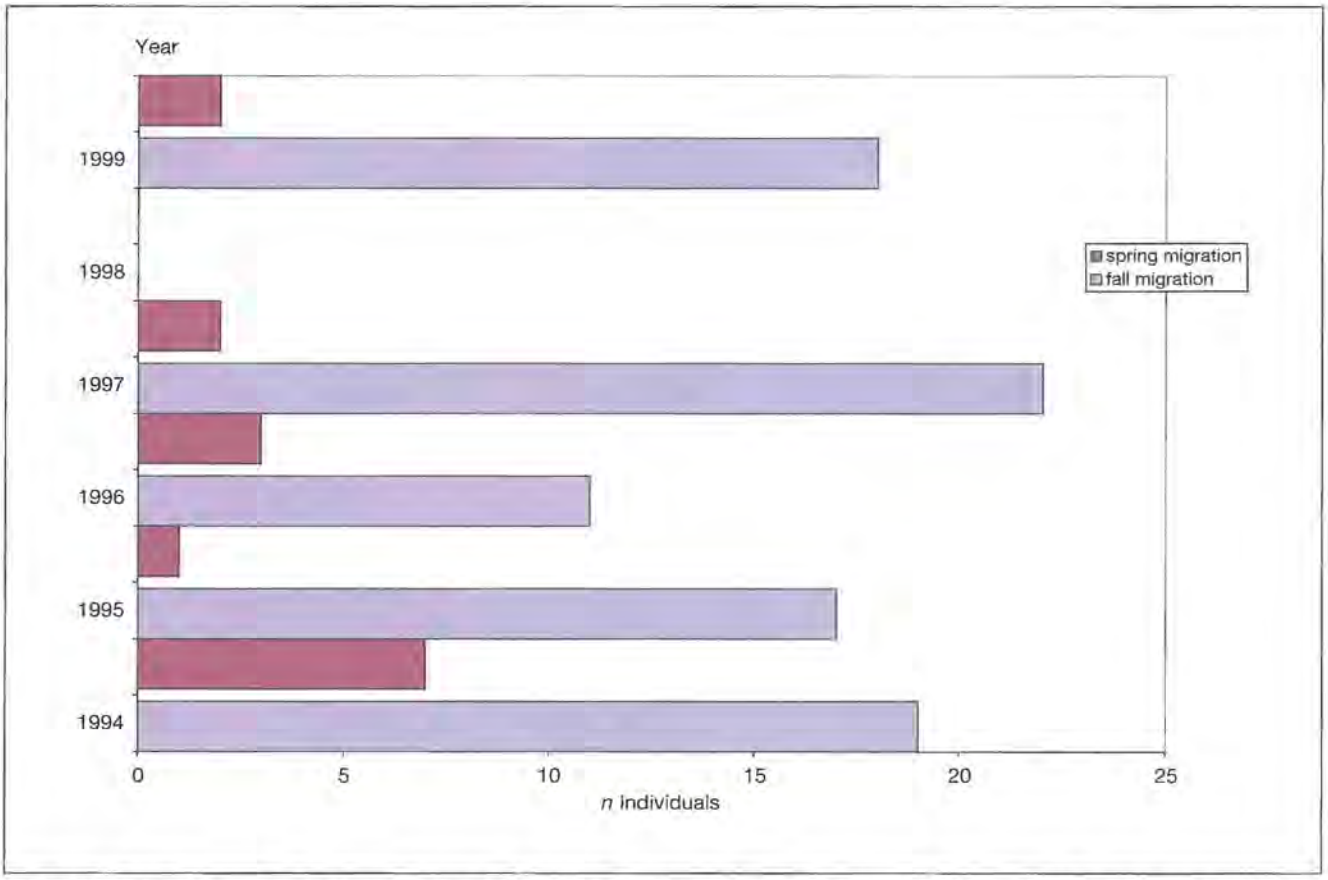

Fig. 9. Number of caught and observed Great Spotted Woodpeckers on the island of Greifswalder Oie during six periods of spring and fall migration between 1994 and 2000.

height of the season is in August/September and ends in the early November. Ringed birds were observed resting on the island of Greifswalder Oie during fall migration three times for at least one day, once for each two and three days. One Great Spotted woodpecker stayed at least a fourth night, gaining 8.4 g during this time.

HIDDENSEE NA 072894
September 14th 1999 young bird from that year at 11:00 a.m., weight = 69.2 g
September 25th 1999 at ringing position at 3:00 p.m., weight 75.6 g,
September 28th 1999 at ringing position at 3:00 p.m., weight 77.6 g.

HEINICKE (1996) assumes that birds also rest during spring migration. The observation of a ringed female on April 21st, 1998 (SCHLAWE unpubl. data) could be evidence of this. Another yearling female was caught and ringed in April 19th, 1998. In winter, the species was only observed twice:

December 31st, 1994 – in the old growth forest (HEINICKE et al. 1995) and

December 16th, 1999 – one female (VON RÖNN unpubl. data).

Great Spotted Woodpeckers were recorded in just one out of six fall/spring migratory seasons (1988/89) (Fig. 9). Except for one individual, all 35 birds caught during fall migration had fledged the same year (97 %). The two birds caught during spring migration were also in their first year (Fig. 10).

Wing length was measured for 22 birds: The mean was 135.5 mm (range 125–142 mm). Partial feather length was measured for 34 individuals (mean = 105.7 mm, range = 92–116 mm) (Fig. 11).

Mean weight of 39 birds was 80.2 g (range = 66.5–99.1 g., Fig. 12).

Mean wing length and body mass was (BANZHAF 1938 data not used): Male, April 15th, 1936: wing length: 148 mm, weight: 106 g; female, April 17th, 1936: wing length: 143 mm, weight: 90 g.

Lesser Spotted Woodpecker *Picoides minor*

Two recordings: September 18th, 1996 – one juvenile bird caught and ringed (HIDDENSEE PA 52371);
October 15th, 1999 – (SCHLAWE unpubl. data): wing length = 95 mm, partial feather length = 73 mm, weight = 21.1 g.

Fig. 10. Great Spotted Woodpeckers first year, caught on the island of Greifswalder Oie. **(Photo: Jan von Rönn)**

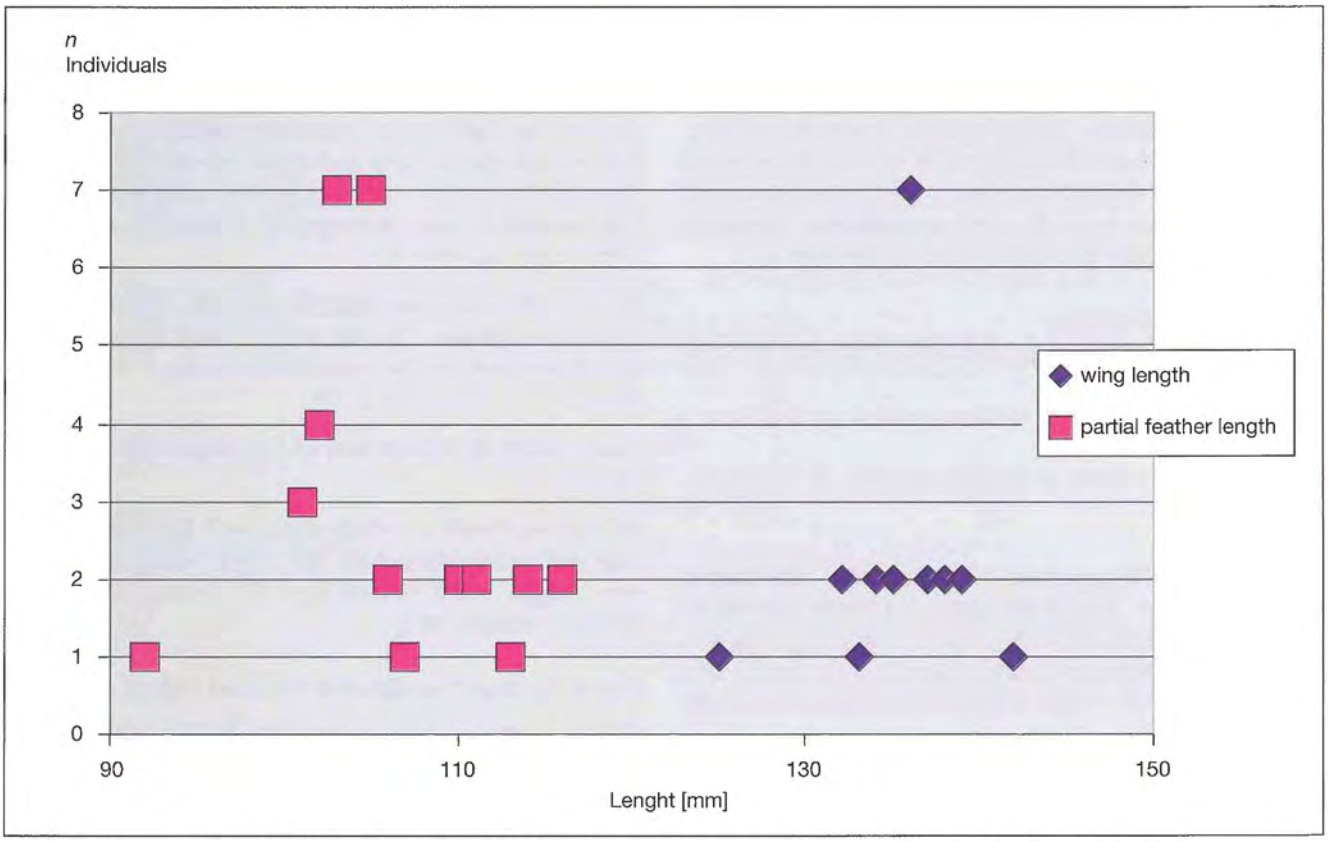

Fig. 11. Wing length distribution of the Great Spotted Woodpecker caught on the islands of Greifswalder Oie between 1994 and 2000.

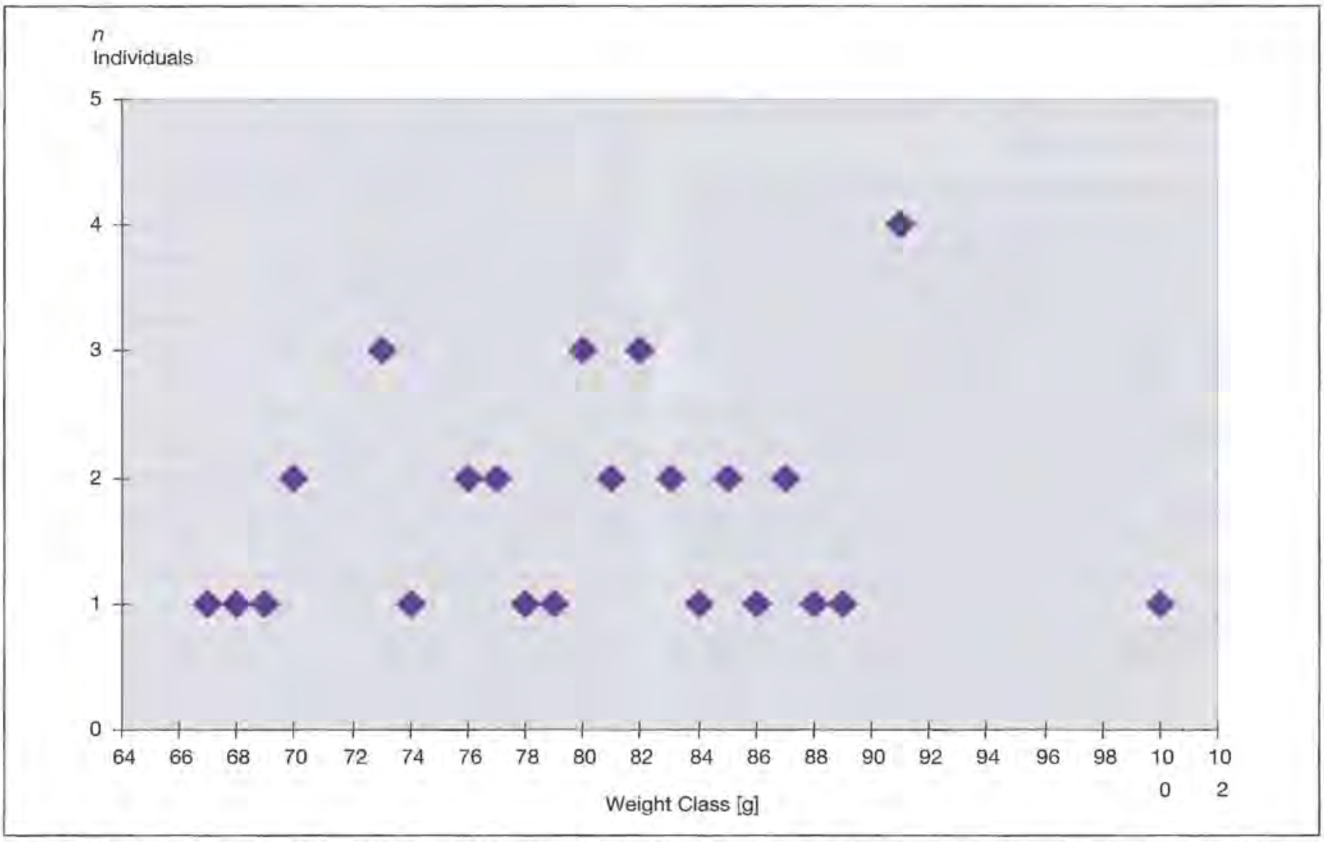

Fig. 12. Weight distribution of Great Spotted Woodpecker caught on the islands of Greifswalder Oie between 1994 and 2000.

Discussion

Despite the fact that only a few Wrynecks stop over at the island of Greifswalder Oie and that no birds were observed during the fall migration of 1999, the species is considered an annual visitor. According to the definition of BERTHOLD (1992), the Wryneck migrates annually, making seasonal movements between breeding and winter ranges. The beginning of migration is not followed by a peak and a slow drop out (which is common), but by a continuous increase and abrupt end. During migration, young Wrynecks were observed on Greifswalder Oie starting in mid July.

The long and pointed wings of the birds netted on Greifswalder Oie, which are about 2 mm longer than German bread birds, indicate that the birds may migrate to far northern breeding areas. According to measurements from NIETHAMMER (1938) and CREUTZ (1964) the ave-rage wing length of 34 measured birds is 88.5 mm (range: 86–94.5 mm).

It is assumed that the Black Woodpecker once bred on Greifswalder Oie. In 1966, first birds settled at the island of Bornholm (Denmark) and have increased in numbers since then (BLUME 1994). The expansion of this species continued in the 1990s (BAUER & BERTHOLD 1996). In the late 1960s/early 1970s, the breeding population in a 25 ha isolated forest in Thuringia was still not very common (LIEDER 1986). A few years later, BRIESEMEISTER et al. (1988) reported that every fifth forest patch in the regions of Staßfurt and Magdeburger Börde (Saxony-Anhalt) had a breeding pair almost every year between 1978 and 1982. The forest patches on the island of Greifswalder Oie are very small, but the Black Woodpecker is known to breed in even smaller areas as long as there are old growth beeches for nest trees. The old forest of the island of Greifswalder Oie has some large beeches with a DBH of 80 cm. For example, in a 0.44 ha old park in the area of Ditfurt, region Quedlinburg (Saxony-Anhalt), which consists of only a small stretch of riverine forest and mostly open landscape, Black Woodpeckers breed.

The Great Spotted Woodpecker is distributed up to the tree line in northern, subarctic areas. Several geographical subspecies are distinguished; such as *Picoides major pinetorum* (C. L. BREHM 1831) found Central Europe and is known as a migratory bird. In Northern Europe, *Picoides major major* breeds from the Norwegian Atlantic coast and Kattegat over to the Ural. It feeds almost exclusively on conifer seeds in winter and moves irregularly according to the availability of the food resources.

An invasion occurred on the North Sea island of Helgoland in 1962. 34 Great Spotted Woodpeckers have been ringed there in 1962 (VANK 1964). During other years only a few Great Spotted were observed and ringed. On the island of Greifswalder Oie, BANZHAF (1938) recorded an invasion in 1935 (see Vogelzug 6, 1935: 69–72; BLUME 1997).

Comparing this information with the data collected from 1994 to 2000 (Figs. 8 and 9); it is apparent that spring migration takes place from mid March to the beginning of May. There is a striking discrepancy between the number of woodpeckers caught in spring compared to the number caught in summer/fall. A possible reason for the higher catch frequency between July and November could be due to a combination of dispersal and fall migration. Both observations in December may be due to dispersal of young birds. According to BERTHOLD (1992), this period lasts far into winter for short distance migratory birds. GLUTZ VON BLOTZHEIM (1994) suggested that numbers observed during spring migration often fluctuate between years, and that there is a closer relationship between spring and fall migration in a given year than there is between spring migration in consecutive years. Fall migration exhibits a more or less regular temporal pattern (Fig. 8). Taking the shift from north to south into consideration, the start and end of migration is similar to the pattern seen in Estonia (end of July–October, LEIVITS 1994) and in Baden-Württemberg (August/September–November, GATTER 1973). Data from SCHILDMACHER & BERGER (1957) on the Island of Hiddensee between 1948 and 1957, where no breeding pair existed, showed that some Greater Spotted Woodpeckers migrated more regularly than expected. Wing measurements of 7 individuals from 1956/57 (mean = 139.6 mm, range = 135–145 mm) suggest that not all Great Spotted Woodpeckers on the Baltic Sea island should be considered of the subspecies *Picoides major major* (SCHILDMACHER & BERGER 1957). Of the 45 birds caught and ringed at the island of Helgoland during an invasion (VAUK 1964) members of both subspecies were present. This could explain the double peak seen during fall migration in 1972 (between July 17th – September 10th until end of October) (GATTER 1973). There is a possible mix in the populations of *Picoides major major* and *Picoides major pinetorum* during migration and at wintering areas. Both birds caught by BANZHAF (1938) in the spring of 1936 (after the 1935 invasion) were larger than any birds caught between 1994 and 2000 where no invasion took place. Also the long spring migration period until the end of May in 1936 possibly shows that some birds from the far North joined in.

At Ladoga Lake in Russia, which is northeast of the island of Greifswalder Oie, an irregularly occurring spring migration of the subspecies *Picoides major major* takes place between the end of March and the beginning of June. Both young and old birds of both sexes take part. In vacant areas following unsuccessful breeding the population numbers may add up easily after an invasion (KOVALEV 1996).

The pattern for the Central European subspecies, *Picoides major pinetorum*, (which can also be found east and northeast of the islands of Greifswalder Oie) is notably different (TOMIALOĆ 1990). During times of low food abundance, only young birds migrate. As described for *Picoides major major* (PULLIAINEN 1963), young Greater Spotted Woodpeckers of the subspecies *Picoides major pinetorum* may try to occupy breeding areas in summer, but if these are not sufficiently available (high breeding success, low mortality of old birds, large home ranges due to low food availability), the young birds disperse. They apparently prefer to move in a westerly direction (GATTER 1973). Other evidence for the importance limited breeding areas is made for chaffinches in the Harz Mountains. Young birds ringed in their nest areas were more often observed there again in the following year if the population density in the ringing year was especially low. When the population density stayed at the same level, ringed birds generally did not return to their former nest areas (GEORGE 1999b).

The small number of observations for the Lesser Spotted Woodpecker on the island of Greifswalder Oie does not allow for any analysis. According wing measurements, the species that do stopover on the islands of Greifswalder Oie probably belong to the northern subspecies, *Picoides minor minor* (LINNAEUS 1758), occurring from the Danish islands and northward (see GLUTZ VON BLOTZHEIM 1994). The subspecies *Picoides major hortorum* (C. L. BREHM 1831), which occurs in Central Europe up to southern Jutland, northern Germany and central Poland, may also stopover.

Acknowledgments

I would like to thank the Jordsand society, especially the managing director Uwe Schneider (Ahrensburg) and all the ringers for the permission to conduct research on the island of Greifswalder Oie and for their hospitality and help. For the support during the talk and the translation I would also like to thank Irene Fischer (Frankfurt/Main) for the support and translation of my oral presentation and written manuscript.

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Habitatnutzung und Nahrungserwerb von Mittelspecht und Buntspecht in bewirtschafteten und unbewirtschafteten Buchenwäldern des nordostdeutschen Tieflandes

Habitat use and foraging activity of the Great Spotted Woodpecker and Middle Spotted Woodpecker in managed and semi-natural beech forests of the north-eastern German lowlands

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Kurzfassung

Im Rahmen einer Diplomarbeit an der Universität Essen wurde auf zwei je 40 ha großen Probeflächen in bewirtschafteten (45–) 100–165-jährigen Buchenwäldern im Biosphärenreservat Schorfheide-Chorin im nordöstlichen Brandenburg eine vergleichende Analyse der Habitatnutzung von Buntspecht *Picoides major* und Mittelspecht *Picoides medius* von März bis Juli sowie von November bis Dezember 2000 durchgeführt. Als Referenzflächen diente der 25 ha große Altbestand des NSG „Heilige Hallen", ein seit längerem forstlich völlig ungenutzter, bis zu 350-jähriger Buchenbestand im südlichen Mecklenburg-Vorpommern und in eingeschränktem Maße der zum Teil über 200-jährige Altbestand des Totalreservats „Fauler Ort" im Nordteil des Biosphärenreservates. Gegenstand der Untersuchung war das Verhalten der Spechte bei der Nahrungssuche, insbesondere die Technik des Nahrungserwerbes und die dabei genutzten Strukturen und Substrate sowie die sich daraus ergebenden Unterschiede und Präferenzen (zum Beispiel die Rolle des Totholzes). Von besonderem Interesse war dabei die Frage nach der unterschiedlichen Ressourcennutzung des nach gängiger Ansicht hauptsächlich an Eichenwälder gebunden geltenden Mittelspechts in den untersuchten reinen Buchenwäldern. Die mittels Sichtbeobachtung aufgenommenen Spechtaktivitäten wurden als Zeitdauer ausgewertet, um anteilige Nutzungen bestimmter Parameter für jede Art und jedes UG zu erhalten. Die von den untersuchten Arten vornehmlich genutzten Strukturen wurden den tatsächlich vorhandenen aus einer forstlichen Strukturaufnahme der Untersuchungsgebiete gegenübergestellt. So nutzten beide Spechtarten bei der Suche nach tierischer Nahrung den vorhandenen Totholzanteil der Buchen überproportional, der Buntspecht saisonal überwiegend das liegende, der Mittelspecht das stehende Totholz. Dabei spielten auf der Referenzfläche neben den Buchenstümpfen die fast toten Bäume eine entscheidende Rolle. In den Wirtschaftswäldern wurden die in sehr geringen Anteilen vorhandenen Eichen von allen Arten verhältnismäßig stark genutzt, beim Mittelspecht saisonal sogar mehrheitlich. Der Mittelspecht beschränkte in der Referenzfläche seine Nahrungssuche am lebenden Substrat ausschließlich auf Bereiche mit hoher Oberflächendiversität, sogenannten „Rindenstörstellen". Die vom Buntspecht bevorzugten Strukturen, wie liegendes Totholz, tote und fast tote Buchen ermöglichen es ihm, auf den Referenzflächen mit deutlich höheren Siedlungsdichten zu brüten. Beim Mittelspecht bildet der hohe Anteil stehender Totholzbereiche und die hohe Strukturdiversität der Buchenoberflächen in Verbindung mit dem Fehlen jeglicher, selektiver forstlicher Eingriffe in die Bestände überhaupt erst die Grundlage für dessen Vorkommen in reinen Buchenwäldern. Daraus leitet sich die Hypothese ab, dass der Mittelspecht früher weite Teile der Tiefland-Buchenwälder besiedelt hat. Es werden einige waldbauliche Maßnahmen zur Förderung des Mittelspechtes im Zuge der Buchenbewirtschaftung vorgeschlagen.

In this diploma thesis at the University of Essen a comparative study of habitat utilization by the Great Spotted Woodpecker and the Middle Spotted Woodpecker was carried out. Data was gathered from March to July and from November to December 2000 in two study areas of 40 ha in managed (45–) 100 to 165–year-old beech forests in the Biosphere Reserve "Schorfheide-Chorin" in the north-east of Brandenburg. As reference area the Nature Reserve "Heilige Hallen" (25 ha) situated in the south of Mecklenburg-Vorpommern, an up to 350-year-old beech forest which has been left uncultivated by forestry for more than 150 years and, to a restricted degree, the strict Nature Reserve "Fauler Ort" in the northern part of the biosphere reserve was chosen. This study focussed on the woodpeckers foraging behaviour, especially the foraging technique, the used structures and substrates and finally the resulting differences and preferences (for example the role of dead wood). In this aspect the question of the varying usage of resources in the examined nearly pure beech forests by the Middle Spotted Woodpecker, which is thought to be mainly associated with oak forest habitats, was of special interest. The results concerning the predominantly used structures were compared to the actual forest structure of the study areas. Searching for animal food, both woodpecker species used the available dead wood of the beech more than expected, P. major seasonal mostly lying, P. medius standing dead wood. Beside the tree-stumps, the almost dead beech trees played a crucial role in the reference sites. The small proportion of oak trees in the managed forests was used predominantly, P. medius even preferred oak trees seasonally. Searching for food on living substrate on the reference sites, P. medius ex-

clusively used areas with high surface diversity („damaged bark"). The structures, like lying dead wood, i.e. dead and almost dead beech trees preferred by P. major obviously enabled the species to inhabit the natural reference areas with clearly higher abundance. In case of P. medius, a high proportion of standing dead wood (as a part of living trees) and a rich surface structure diversity of mature beech trees, supported by the absence of any selective thinning, enabled the occurrence in pure beech forests. Therefore we can assume, that in former times lowland beech forests were widely inhabited by P. medius. Specific silvicultural recommendations for the support of P. medius within the beech forest management are drawn.

Einleitung

Die vorliegende Arbeit stellt einen Teilbereich meiner Diplomarbeit an der Universität Essen dar. Sie war im Rahmen des seit Ende 1999 laufenden und vom Bundesamt für Naturschutz geförderten Forschungs- und Entwicklungsvorhabens der Brandenburgischen Landesanstalt für Großschutzgebiete in Eberswalde „Biologische Vielfalt und Forstwirtschaft – Naturschutzstandarts für die Bewirtschaftung von Buchenwäldern im nordostdeutschen Tiefland" angesiedelt.

Mittelspecht **(Foto: Gilberto Pasinelli)**

Unter den „holzbewohnenden" Vogelarten gelten die stammkletternden Arten und hier im besonderen ein Großteil unserer heimischen Spechte wegen ihrer ganz auf Bäume fixierten Lebensweise als besonders geeignete Bioindikatoren für Zustand und Veränderungen von Wäldern (vergleiche BLUME & TIEFENBACH 1997, SCHERZINGER 1998). Daraus resultiert die Eignung dieser Vogelgruppe für die Frage nach der Minimumausstattung von Wäldern mit bestimmten Requisiten. Im allgemeinen korreliert die Spechtdichte positiv mit der Totholzmenge (SCHERZINGER 1997, HOHLFELD 1997, KREUZIGER 1999).

Während der Buntspecht als Ubiquist praktisch alle Waldformen besiedelt (BLUME & TIEFENBACH 1997), gilt der Mittelspecht allgemein als typische Leit- und Charakterart von Eichen(misch)wäldern (zum Beispiel GLUTZ VON BLOTZHEIM & BAUER 1980, HOLZINGER 1987, FLADE 1994). Dennoch führt FLADE (1994) ihn gleichzeitig als Leitart für Tiefland-Buchenwälder auf. Es stellt sich die Frage, welche Voraussetzungen hierfür gegeben sein müssen. Folgende Fragestellungen werden behandelt:

- Welche Präferenzen bezüglich Baumart, Substratkondition der Unterlage etc. zeigen die beiden Spechtarten bei der Nahrungssuche und welche Rolle spielt dabei das Totholz?
- Welche Strukturen erlauben dem Mittelspecht das Vorkommen im Buchenwald?
- Welche waldbaulichen Konsequenzen leiten sich daraus ab?

Untersuchungsgebiete

Die Auswahl der vier verschiedenen Untersuchungsgebiete (UG) erfolgte aus dem Kollektiv der Probeflächen des oben genannten Projektes. Bei den zwei Wirtschaftswäldern, Melzower Forst und Choriner Wald, handelt es sich um je 40 ha große, (45–) 100–165-jährige Buchenbestände im südlichen Teil beziehungsweise nordwestlichen Teil des Biosphärenreservates Schorfheide-Chorin (vergleiche Abb. 1 und Tab. 1).

Als Referenzfläche diente der Altbestand des NSG „Heilige Hallen", ein seit circa 150 Jahren forstlich völlig ungenutzter, bis zu 350-jähriger Buchenbestand im südlichen Mecklenburg-Vorpommern (vergleiche Abb. 1). Das Naturschutzgebiet „Heilige Hallen" ist dafür besonders geeignet, denn es enthält nicht nur den ältesten Buchenwald Deutschlands, es besitzt auch durch die lange, nutzungsfreie Periode den stärksten Urwaldcharakter. Der 25 ha große Altbestand der „Heiligen Hallen" befindet sich überwiegend in der Alters-, Zerfalls- und Verjüngungsphase und ist vor allem durch großen Totholzreichtum und hohe Strukturdiversität gekennzeichnet (vergleiche BORRMANN 1996, JESCHKE 1997, TABAKU 2000).

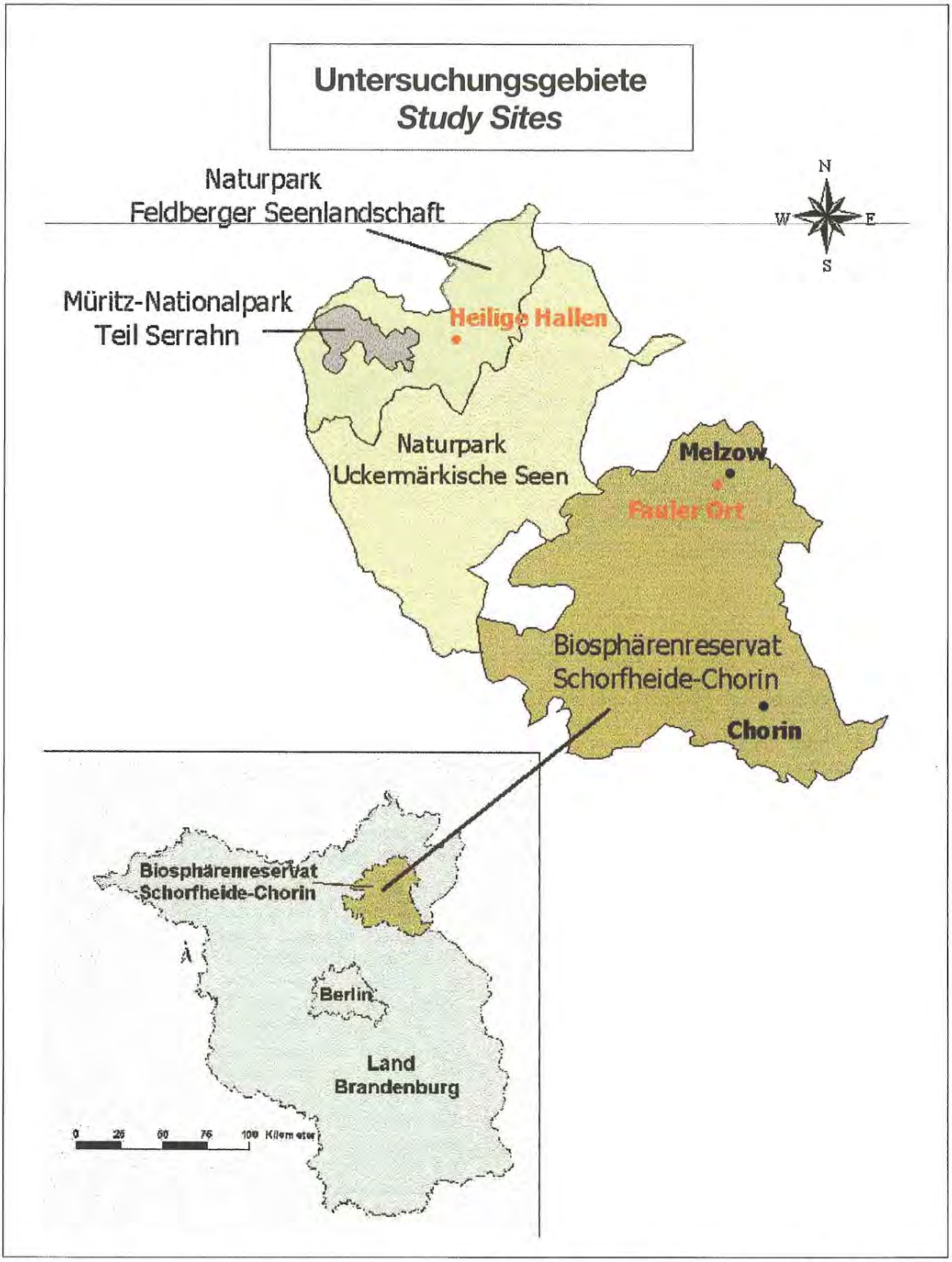


Abb. 1. Die Lage der vier Untersuchungsgebiete in den verschiedenen Schutzgebieten und im Großraum; die Referenzflächen sind rot, die Wirtschaftswälder schwarz beschriftet. *Location of four study areas in various protected areas. Red = unmanaged forest, Black = managed control sites.*

Tab. 1. Größe, Alter, Anteil der Baumarten, stehende Holzgrundfläche und Totholzanteil der Untersuchungsgebiete (WINTER 2001). ***Description of study sites (S. WINTER unveröff.).***

	Größe/ *Size*	Alter des Hauptbestandes/ *Age of dominant stand*	Anteil/ *Percentage Fagus s.*	Anteil/ *Percentage Quercus p.*	Holzgrundfläche*/ *Basal area*	Anteil Totholz*/ Percentage of dead wood
	ha	*Jahre*	*%*	*%*	*m^2 / ha*	*%*
Heilige Hallen	24,9	~ 350	~ 100	0	31,3	23,6
Fauler Ort	13,6	~ 100–210	~ 80	~ 0	33,7	21,9
Melzow	40,1	~ 125–145	94,4*	5,6*	21,2	0,0
Chorin	40,3	~ 45–165	95,4*	4,6*	18,8	0,6

* Datenerhebung mittels Winkelzählprobe nach BITTERLICH. *Data collected by angle count method after BITTERLICH.*

Ergebnisse aus einer zweiten Referenzfläche, dem Totalreservat „Fauler Ort" finden bei der hier behandelten, speziellen Fragestellung keine Verwendung, da es sich bei diesem Bestand um keinen reinen Buchenwald, sondern teilweise um einen Mischbestand handelt (vergleiche SCAMONI 1955).

Der Totholzanteil liegt in den „Heiligen Hallen" bei circa 24 % der gesamten Holzgrundfläche (siehe Tab. 1). In den Wirtschaftswäldern beträgt der Anteil stehenden Totholzes 0,0 % beziehungsweise 0,6 % der Grundfläche (WINTER 2001).

Methoden

Die nahrungsökologischen Aufnahmen fanden im Zeitraum vom 9.3. bis zum 19.12.2000 an 91 verschiedenen Tagen statt. Dabei handelt es sich um folgende, drei zeitlich getrennte Blöcke, die auch separat zur Auswertung gelangten:
Frühjahrsblock: Anfang März bis Ende April 2000 (Zeitpunkt des Laubaustriebs)
Sommerblock: Ende April bis Anfang Juli 2000
Herbstblock: Anfang November bis Mitte Dezember 2000

Die Daten aus dem Sommerblock sind wegen der gewählten Methode weniger repräsentativ als die aus den laubfreien Perioden und bleiben hier unberücksichtigt.

Die Aufnahme der nahrungsökologischen Daten erfolgte per Sichtbeobachtung mit dem Fernglas. Gleichzeitig zur Beobachtung erfolgte das Aufsprechen der Spechtaktivitäten auf ein Diktiergerät. Inhaltlich orientierten sich die aufgenommenen Informationen an den vorher festgelegten Parametern:

- **Baumart**
- **Vitalität des Baumes:** Die Klassifizierung der Vitalität des jeweiligen stehenden Einzelbaumes erfolgte in vier Stufen: *völlig tot, fast tot,* grün, aber nicht völlig vital (*geschädigt*) und *vital* beziehungsweise gesund.
- **Substratkondition der Unterlage:** Unterschieden wird, ob der jeweilige Untergrund (der Stamm oder Ast) *lebend* oder *tot* ist.
- **Kronenposition:** hierbei wird die Position des Vogels im Baum in Bezug auf die Baumkrone angegeben. Die Einteilung erfolgt in vier Klassen: im Baum *ohne Krone, unterhalb der Krone, untere Kronenhälfte* und *obere Kronenhälfte*.
- **Nahrung:** Art der pflanzlichen und tierischen Nahrung, sofern diese identifiziert werden konnte.
- **Nahrungssucheverhalten (NSV) selten:** beschreibt den Fall, dass der Vogel während des Vorgangs der Nahrungssuche, gemessen an der Zeit, weit weniger häufig zum Beispiel pickt oder hackt als er dies sonst tut. Das Verhältnis vom „normalen NSV" zu „NSV selten" beträgt ungefähr 1:2 oder schlechter, d.h. während eines Suchvorgangs mit dem Zusatz „selten" wird nur halb so oft gepickt, gehackt oder ähnliches wie bei dem „normalen NSV".

Daneben wurde noch eine ganze Reihe weiterer, hier nicht aufgeführter Parameter aufgenommen, zum Beispiel Erstkontakt, Brusthöhendurchmesser des Baumes, Astdurchmesser, Höhenschicht, Technik der Nahrungssuche, Art der Oberfläche, Oberflächenbeschaffenheit der Rinde, Sitzposition, Bewegungsrichtung und -verhalten des Vogels.

Zur Auswertung der so gewonnenen Daten wurden die Zeitdauer der einzelnen Datensätze nach bestimmten Parametern geordnet aufsummiert, zum Beispiel anteilige Nutzungen verschiedener Substrate durch Addition sämtlicher Zeiten auf gleichem Substrat. Die sich daraus ergebenden Zeitanteile (vom Gesamtzeitbudget der Art in einem UG) lassen sich so nach Parametern geordnet für die jeweiligen UG darstellen und miteinander vergleichen. Die zeitliche Untergrenze für eine Sequenz wurde bei 10 sek. festgelegt. Alle Datensätze einer Vogelart in einem bestimmten Gebiet in einem der drei Zeitblöcke entsprechen einer Gesamtstichprobe. Die Summe der registrierten und ausgewerteten Nettokontaktzeit während der Nahrungssuche beträgt beim Buntspecht circa 11 Stunden und beim Mittelspecht circa 8,5 Stunden.

Die verwendete Methode hat eine ganze Reihe von Fehlerquellen, eine davon ist die zum Teil sehr niedrige

Tab. 2. Anzahl der Reviere und Abundanzen von *Picoides major* und *P. medius* in den Untersuchungsgebieten.
Number of territories and abundances (breeding pairs/10 ha) of P. major and P. medius in the study sites.

	breeding season 2000			
	P. major		*P. medius*	
	number bp	bp/10 ha	number bp	bp/10 ha
Heilige Hallen	9	3,6	3	1,2
Fauler Ort	4	2,4	2	1,2
Melzow	3	0,8	2	0,5
Chorin	8	2,0	–	–

bp = breeding pair

Individuenzahl der Vogelarten auf den Untersuchungsflächen. Je weniger Individuen bei den Stichproben vertreten sind, desto höher ist die Wahrscheinlichkeit, dass sich abnorme Verhaltensweisen beziehungsweise bestimmte Vorlieben einzelner Individuen bei der Nahrungssuche spürbar im Ergebnis auswirken. Die geringste Zahl registrierter Individuen betrug vier im Falle des Mittelspechts im UG Melzow, die höchste Zahl der Individuen pro UG lag (theoretisch) bei 18 Individuen im Falle des Buntspechts in den „Heiligen Hallen“ (siehe Tab. 2).

Ergebnisse

Im Folgenden ist eine Auswahl von Ergebnissen dargestellt. Im Falle des Mittelspechts beschränken sie sich auf die UG Melzow und „Heilige Hallen“, da er in Chorin nicht Brutvogel war und Daten von hier deshalb nur für den Herbst vorliegen.

Buntspecht *Picoides major*

Nahrung:

Im Frühjahrsblock überwiegt der Anteil der Suche nach tierischer Nahrung und ist in den „Heiligen Hallen“ mit 83 % signifikant höher als in Melzow und Chorin mit je circa 65 % (siehe Tab. 3). Im Herbst dagegen ist das Verhältnis zwischen tierischer und pflanzlicher Nahrung unklar, denn dann verließen die Buntspechte die UG regelmäßig zur Zapfenernte.

Folgende Ergebnisse beziehen sich auf die Suche nach tierischer Nahrung:

Baumarten:

Die beobachteten Buntspechte hielten sich bei der Suche nach tierischer Nahrung in Melzow zu 33 % im Frühjahr beziehungsweise zu 47 % im Herbst an Eichen auf. Der Eichenanteil beträgt nach WINTER (pers. Mitt.) im UG Melzow allerdings nur circa 6 % und circa 5 % im UG Chorin (vergleiche Tab. 1). Demnach fand hier eine überproportionale Nutzung der Eiche statt. In Chorin trifft dies nur auf das Frühjahr zu (siehe Abb. 2). Dort konzentrieren sich die vorhandenen Eichen auf wenige Stellen.

Substratkondition/Totholz:

In den „Heiligen Hallen“ verbrachten die Buntspechte bis zu 92 % an totem Substrat, größtenteils an liegendem Totholz, in Melzow zu 86 % im Frühjahr beziehungsweise zu 70 % im Herbst an totem Substrat (vergleiche Abb. 2). In Chorin ist eine große jahreszeitliche Differenz erkennbar (zu 47 % im Frühjahr und zu 100 % im Herbst an totem Substrat).

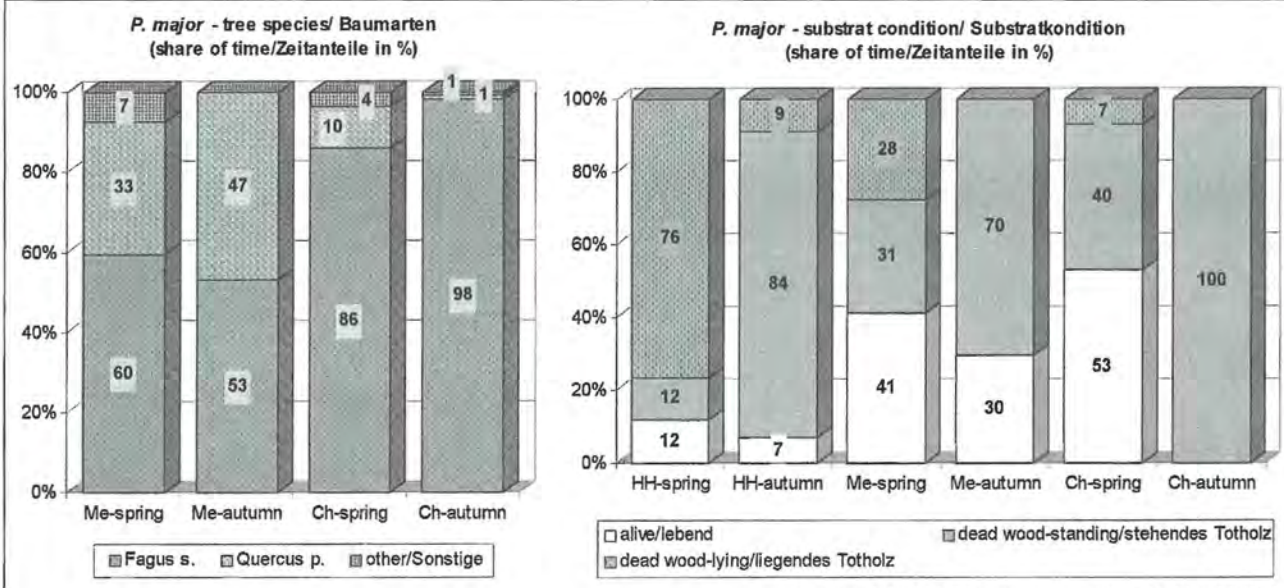
In allen UG ist eine mehr oder minder deutliche Bevorzugung von totem Substrat festzustellen. Im Frühjahr präferierte der Buntspecht offenbar liegendes Totholz, soweit es ihm zur Verfügung stand. Dies kommt stark in den „Heiligen Hallen“ zum Ausdruck, wo er bei der Nahrungssuche $^3/_4$ seiner Zeit auf liegendem Totholz verbrachte (vergleiche Abb. 2).

Vitalität des Baumes:

Im Frühjahr war der Buntspecht in den „Heiligen Hallen“ zu 60 % an toter beziehungsweise fast toter Buche anzutreffen, im Herbst zu einem etwas geringeren Anteil

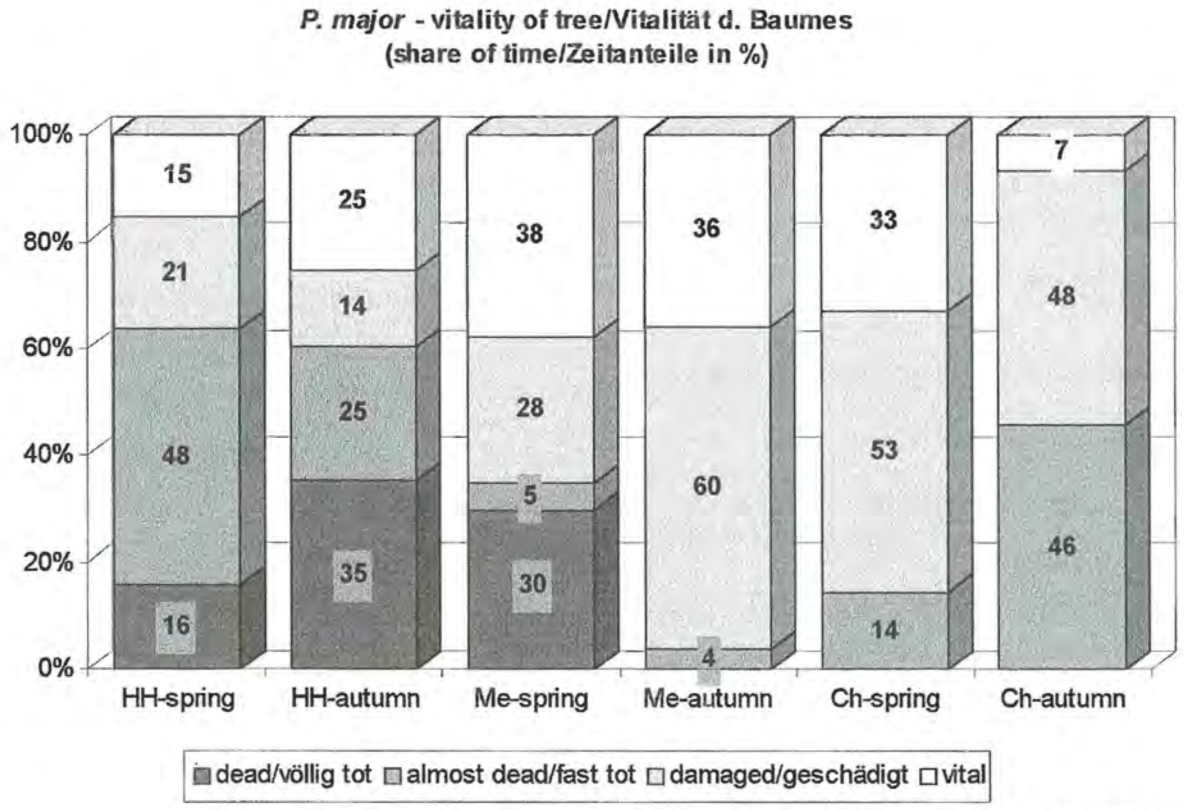
Tab. 3. Nahrung von *Picoides major* im Frühjahr (Zeitanteile in %).
Food of P. major in spring (proportion of time in %).

	tierisch/ *animal*	pflanzlich/ *vegetable*	unbekannt/ *unknown*	*n* in seconds
Heilige Hallen	83	5	12	9161
Melzow	69	1	30	3112
Chorin	63	14	23	4948



Verwendete Abkürzungen: HH = Heilige Hallen
Me = Melzow
Ch = Chorin

Abb. 2. Zeitanteile der Suche nach tierischer Nahrung durch den Buntspecht, dargestellt sind die dabei genutzten Baumarten (links) und deren Substratkondition (rechts). *Foraging upon animal prey by the Great Spotted Woodpecker. Shown is proportion of time spend on tree species (left) with various condition (right).*



Verwendete Abkürzungen: HH = Heilige Hallen
Me = Melzow
Ch = Chorin

Abb. 3. Zeitanteile der Suche nach tierischer Nahrung durch den Buntspecht, dargestellt sind die verschiedener Vitalitätsklassen der dabei genutzten Bäume. *Foraging upon animal prey by the Great Spotted Woodpecker. Shown is proportion of time spend at trees in various vitality stages.*

(siehe Abb. 3). In den Wirtschaftswäldern fiel die Nutzung toter beziehungsweise fast toter Bäume wesentlich geringer aus, da diese weitgehend fehlen. Der Spitzenwert in Melzow basiert auf der intensiven Nutzung einzelner, weniger Bäume.

Kronenposition:

Im Frühjahr ist ein deutliches Gefälle zwischen der Nutzung des Kronenraumes und der Schicht darunter in den „Heiligen Hallen" und Chorin zu erkennen (vergleiche Abb. 4). 83 % der Zeit der Nahrungssuche verbrachten die Buntspechte in den „Heiligen Hallen" unterhalb der Krone beziehungsweise an den vorhandenen Stümpfen (siehe Abb. 4).

In Melzow hielten sie sich im Frühjahr zu 55 %, und in Chorin zu 82 % im Kronenraum auf. Für den Herbst gilt die gleiche Abstufung, nur ist sie hier weniger deutlich ausgeprägt.

Mittelspecht *Picoides medius*

Nahrung:

Der Mittelspecht wurde ausschließlich bei der Suche nach tierischer Nahrung angetroffen, lediglich im Frühjahr im UG Melzow konnte ein Anteil von 6 % pflanzlicher Nahrung (Saftlecken) registriert werden.

Folgende Ergebnisse beziehen sich auf die Suche nach tierischer Nahrung:

Baumarten:

Im UG Melzow war der Mittelspecht bei der Nahrungssuche zu 38 % im Frühjahr und zu 62 % im Herbst an vornehmlich lebender Eiche anzutreffen (siehe Abb. 5). Dieses Ergebnis stammt allerdings von nur zwei Brutpaaren (vergleiche Tab. 2), in deren Revieren der Eichenanteil bei circa 10 % einzuschätzen ist.

Substratkondition/Totholz:

Das liegende Totholz spielte bei der Nutzung durch den Mittelspecht nur eine geringe Rolle und lag bei maximal 12 % im UG Melzow im Frühjahr (siehe Abb. 5).

Beim stehenden Totholz wurden die Totholzbereiche vornehmlich der lebenden Buchen in allen Untersuchungsgebieten überproportional genutzt. In den „Heiligen Hallen" fand sich der Mittelspecht zu 58 % im Frühjahr beziehungsweise zu 85 % im Herbst an toten

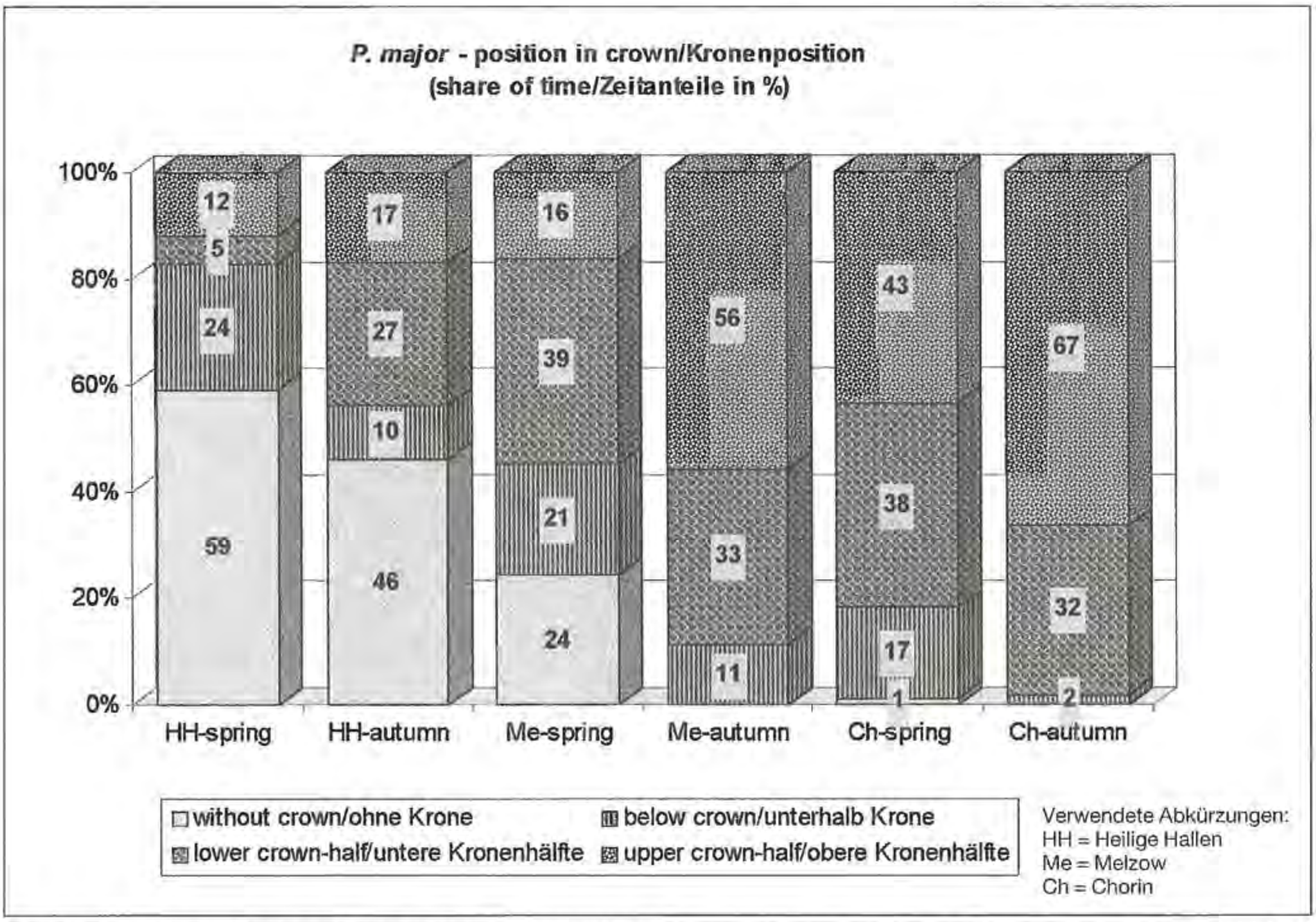
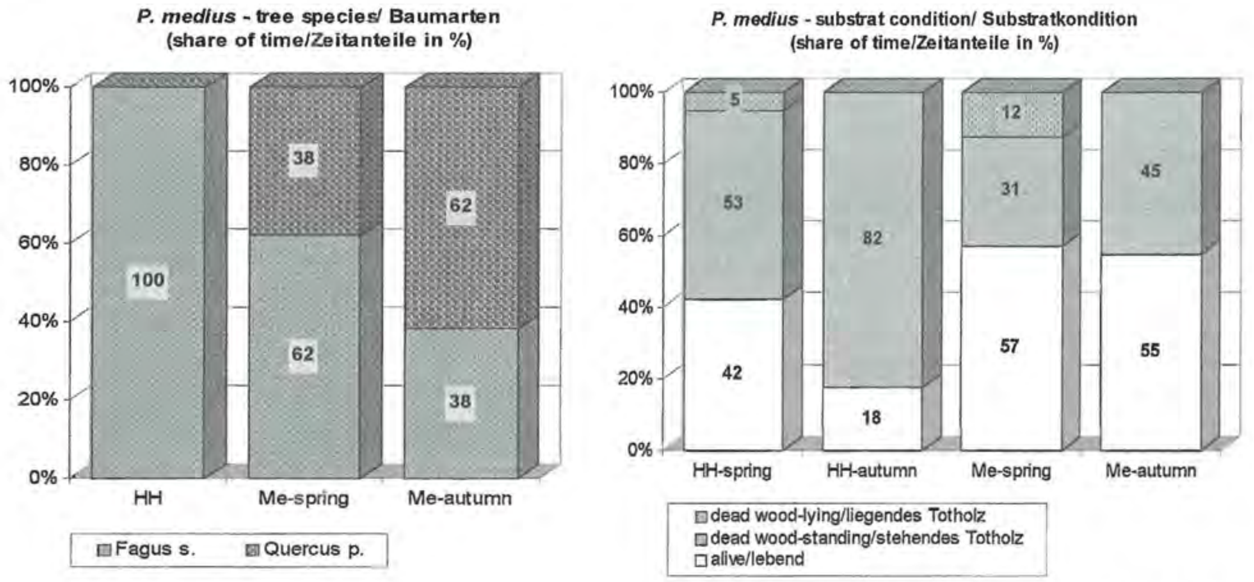
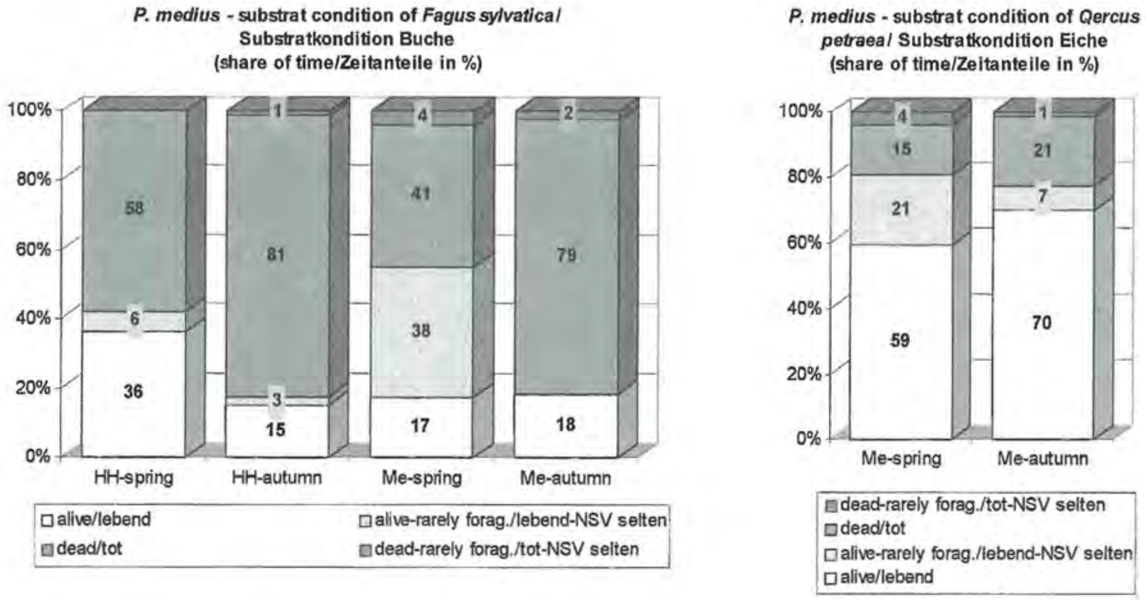


Abb. 4. Zeitanteile der Suche nach tierischer Nahrung durch den Buntspecht, dargestellt sind die verschiedener Zonen innerhalb des Baumes, welche die Position des Vogels wiedergeben. *Foraging upon animal prey by the Great Spotted Woodpecker. Shown is proportion of time spent in various parts of the tree crown.*



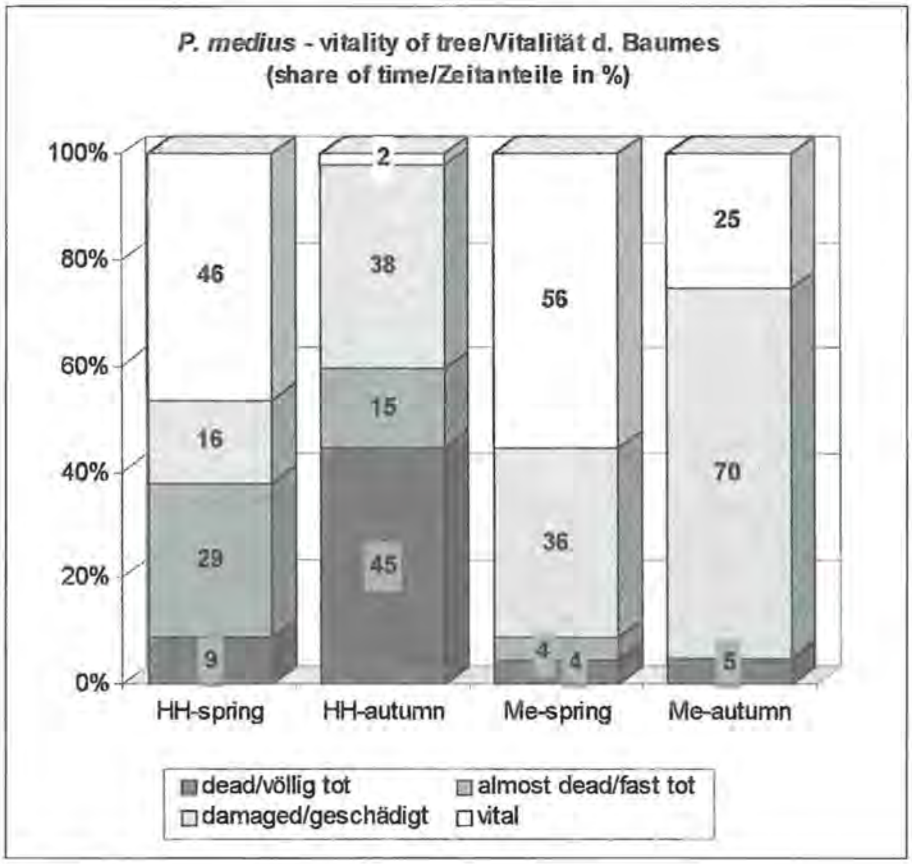
Verwendete Abkürzungen: HH = Heilige Hallen
Me = Melzow
Ch = Chorin

Abb. 5. Zeitanteile der Suche nach tierischer Nahrung durch den Mittelspecht, dargestellt sind die dabei genutzten Baumarten (links) und deren Substratkondition (rechts).
Foraging upon animal prey by Middle Spotted Woodpecker. Shown is proportion of time spent on tree species (left) with various condition (right).



Verwendete Abkürzungen: HH = Heilige Hallen
Me = Melzow Ch = Chorin
forag. = foraging NSV = Nahrungssucheverhalten

Abb. 6. Zeitanteile der Suche nach tierischer Nahrung durch den Mittelspecht, dargestellt ist die Substratkondition der dabei genutzten Buchen (links) und Eichen (rechts).
Foraging upon animal prey by Middle Spotted Woodpecker. Shown is proportion of time spent at beeches (left) and oaks (right) with various vitality stages.



Verwendete Abkürzungen:
HH = Heilige Hallen
Me = Melzow
Ch = Chorin

Abb. 7: Zeitanteile der Suche nach tierischer Nahrung durch den Mittelspecht, dargestellt sind die verschiedener Vitalitätsklassen der dabei genutzten Bäume.
Foraging upon animal prey by Middle Spotted Woodpecker. Shown is proportion of time spent at all trees combined that were in various condition stages.

Substrat, in Melzow zu 43 % im Frühjahr beziehungsweise zu 46 % im Herbst (siehe Abb. 5).

Abb. 6 zeigt die anteilige Nutzung toter und lebender Bereiche auf Buche und Eiche durch den Mittelspecht. Dabei wird zwischen dem „normalen Verhalten bei der Nahrungssuche" und dem „Nahrungssucheverhalten selten" unterschieden (vergleiche Kapitel Methode). Im UG Melzow im Frühjahr beispielsweise hielt sich der Mittelspecht 17 % der Zeit der Nahrungssuche an Buchen an lebenden Substrat auf, weitere 38 % am selben Substrattyp, jedoch wesentlich seltener pickend. Im Falle der toten Bereiche sind dies nur 4 % der Zeit. Bezieht man diesen Aspekt bei der Interpretation des Ergebnisses mit ein, so überwiegt in diesem Falle die Nutzung des toten Substrates. Abb. 6 zeigt demnach eine Bevorzugung abgestorbener Bereiche bei der Buche und lebender Bereiche bei der Eiche auf der Referenzfläche (hier sind allerdings keine Eichen vorhanden) und im UG Melzow.

Vitalität des Baumes:

Der Mittelspecht hielt sich bei der Nahrungssuche in den „Heiligen Hallen" zu 38 % (Frühjahr) und zu 60 % (Herbst) an abgestorbenen oder fast toten Buchen auf (vergleiche Abb. 7). Im Wirtschaftswald (Melzow) betrug die anteilige Nutzung am Gesamtzeitbudget der Nahrungssuche aufgrund des Mangels solcher Bäume nur 8 % im Frühjahr und 5 % im Herbst. Der Anteil toter und fast toter Buchen wurde somit überproportional vom Mittelspecht genutzt.

Kronenposition:

Auf der Referenzfläche lag im Frühjahr der Schwerpunkt der Raumnutzung eher unterhalb der Krone beziehungsweise an den Stümpfen, in Melzow hingegen im unteren Kronenbereich. Im Herbst war eine Umkehrung der Verhältnisse zu beobachten (vergleiche Abb. 8).

Diskussion

Beide Spechtarten nutzten bei der Suche nach tierischer Nahrung den vorhandenen Totholzanteil der Buche überproportional, der Buntspecht saisonal überwiegend das liegende, der Mittelspecht das stehende Totholz. Eine Bevorzugung von liegenden Totholz fand JENNI (1983) beim Buntspecht für das zeitige Frühjahr auch in Eichenwäldern. In den Wirtschaftswäldern wurden die in geringen Anteilen vorhandenen Eichen von beiden Arten verhältnismäßig stark genutzt, beim Mittelspecht saisonal sogar überwiegend.

Der Mittelspecht ist im Gegensatz zum Buntspecht ganzjährig auf die Verfügbarkeit tierischer Nahrung angewiesen (zum Beispiel JENNI 1983). Diese gewinnt er überwiegend stochernd aus grobrissiger und somit arthropodenreicher Oberflächenstruktur. Daher ist die Eiche besonders attraktiv für den Mittelspecht (zum Beispiel GLUTZ VON BLOTZHEIM & BAUER 1980, JENNI 1983, FLADE & MIECH 1986, RUGE 1986, GUNTHER 1992 und 1997, BRULAND 1993, BUHLMANN 1993, BLUME & TIEFENBACH 1997, KONIG 1998, PASINELLI 1999). Die hier festgestellte überproportionale Nutzung der Eichen deutet darauf hin, dass zumindest in Wirtschaftswäldern der Eichenanteil entscheidend ist für das Vorkommen des Mittelspechts im Buchenwald (vergleiche auch SCHINDLER 1996).

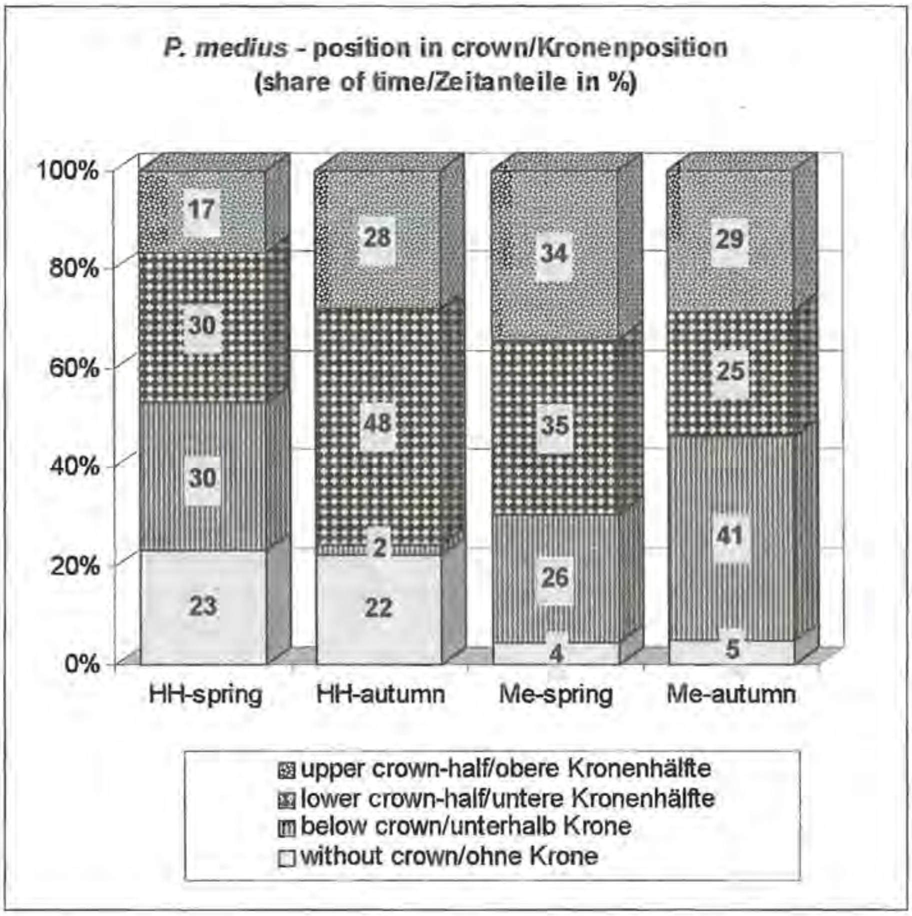
In der vorliegenden Untersuchung spielen für den Buntspecht neben den toten Buchen in noch stärkerem Maße die fast toten Buchen eine wichtige Rolle bei der Nahrungssuche. Dabei sind Buchenstümpfe neben liegendem Totholz die bevorzugten Strukturen auf der Referenzfläche. Eine hohe Attraktivität für die Nutzung durch den Buntspecht weisen auch die vorhandenen fast toten Bäume auf. PECHACEK (1995) zufolge nutzt der Buntspecht eine breite Palette von Totholzformen.

Beim Mittelspecht fand in den Wirtschaftswäldern die bevorzugte Nutzung der Eiche ausschließlich an lebendem Holz statt, während bei den Buchen die toten Substrate stärker frequentiert waren. Erstes wird durch Untersuchungen am Mittelspecht in Eichenwäldern bestätigt (JENNI 1983 und HOHLFELD 1997).

Der Mittelspecht suchte in den „Heiligen Hallen" die meiste Zeit am toten Substrat nach Nahrung, am lebenden Substrat ausschließlich an Bereichen mit hoher Oberflächendiversität („Rindenstörstellen"). Dieses Ergebnis deckt sich mit den Beobachtungen von GUNTHER & HELLMANN (1997) im selben Gebiet. Weiterhin bevorzugte *Picoides medius* saisonal den Stammbereich und tote beziehungsweise fast tote Buchen. Im eichenfreien Buchenwald kann offenbar ein gewisser Totholzanteil beziehungsweise Anteil fast toter Bäume die ansonsten für den Mittelspecht fehlende Attraktivität der Buche kompensieren.

Buchen mit hoher Strukturdiversität im Stammbereich sind attraktiv für den Mittelspecht. Dies zeigen Beobachtungen aus den „Heiligen Hallen". Dort wurde er im Stammbereich nie an glatter Buchenrinde angetroffen.

Im Untersuchungsgebiet „Heilige Hallen" reicht das Spektrum der Rindenstruktur der Altbuchen von völlig glatt bis tief rissig. Die meisten Stämme weisen eine leichte bis starke Rauheit der Rinde auf. Wirklich tief rissige Berei-che, bei denen es oft zur Ausbildung einer groben Borke kommt, beschränken sich auf Bereiche am Stammfuß, an Stammverzweigungen sowie auf Rinden-



Verwendete Abkürzungen:
HH = Heilige Hallen
Me = Melzow
Ch = Chorin

Abb. 8. Zeitanteile der Suche nach tierischer Nahrung durch den Mittelspecht, dargestellt sind die verschiedener Zonen innerhalb des Baumes, welche die Position des Vogels wiedergeben.
Foraging upon animal prey by Middle Spotted Woodpecker. Shown is proportion of time spent in various parts of the tree crown

knollen und Krebsgeschwüre. GUNTHER & HELLMANN (1997) diskutieren ausführlich den Zusammenhang zwischen der Rindenstruktur der Buchen in den „Heiligen Hallen“ und dem dortigen Vorkommen des Mittelspechts.

Für den Mittelspecht bedeutsame Merkmale sind neben der mehr oder minder stark aufgerauten Rinde der Altbuchen auch das häufige Auftreten von „Rindenstörstellen”. Mit diesem Begriff sind alle größeren Unebenheiten auf der ansonsten relativ glatten Rinde der lebenden Buchenstämme gemeint. Hierzu zählen insbesondere Krebsgeschwüre in z.T. gigantischen Dimensionen, kleinräumig gehäuft auftretende Astnarben, sog. Chinesenbärte, Rindenknollen sowie mehr oder wenig stark verwachsene Rindenverletzungen aller Art (zum Beispiel durch Wurf des Nachbarbaumes oder durch Schädigungen wie Rindenbrand, Frostrisse und Schleimfluss verursacht). Diese Rindenstörstellen sind im Altbestand der „Heiligen Hallen“ sehr häufig und an nahezu jedem starken Stamm anzutreffen. Die Hauptursache dieser Häufigkeit liegt sicherlich schlicht im hohen Alter der Bäume, da es dann sowohl zu einer vermehrten Borkenbildung als auch mit schwindender Vitalität zu einer höheren Anfälligkeit gegenüber Schaderregern kommt. Allerdings dürften hierbei neben genetischen Prädispositionen einzelner Individuen auch die fehlende forstliche Bestandeserziehung eine entscheidende Rolle spielen. Bei der regulären forstlichen Bewirtschaftung der Buche werden im Zuge einer gestaffelten Durchforstung schon im Jungwuchsstadium bis wenige Jahrzehnte vor der Endnutzung (Hochdurchforstung) durch Pflegeeingriffe selektiv alle unerwünschten Bäume entfernt. Diese Auslese führt dazu, dass ein in Bezug auf Standort und Pflege durchschnittlicher Buchenbestand von über 100 Jahren im Vergleich zu den „Heiligen Hallen“ sehr arm an oben genannte Rindenstörstellen ist (zum Beispiel UG Melzow). Hinzu kommt noch das nur sehr vereinzelte Auftreten von Individuen mit aufgerauter Rinde; zur Ausbildung einer Borke kommt es hier in der Regel nicht. Die Störstellen gehören neben den toten Stammbereichen, die durch den Wechsel von Rinde und Holz oft durch eine raue, unebene Oberflächenstruktur gekennzeichnet sind, zu den vom Mittelspecht bei der Nahrungssuche bevorzugten Strukturen.

Zudem ist der Mittelspecht nicht in der Lage, am senkrechten Stamm auf glatter Buchenrinde zu klettern und meidet sie daher meist ganz. Kleinflächige Bereiche mit glatter Rinde überspringt er flatternd oder überbrückt sie fliegend (eigene Beobachtungen). Wegen der fehlenden Unterschlupfmöglichkeiten beherbergen solche Bereiche zudem kaum tierische Nahrung (Arthropoden), sind also für den Mittelspecht doppelt unattraktiv. Aber dass selbst reine Buchenwälder ohne die Beimischung von Baumarten mit grob rissiger Rinde eine hohe Anziehungskraft auf den Mittelspecht ausüben können, zeigt eindrucksvoll das Beispiel „Heilige Hallen“.

Aus den Ergebnissen kann zusammenfassend für den Buntspecht gefolgert werden, dass die von ihm bevorzugten Strukturen wie liegendes Totholz, tote und fast tote Buchen es ihm offenbar ermöglichen, die Referenzflächen mit deutlich höheren Siedlungsdichten zu besiedeln (siehe Tab. 2 und H. SCHUMACHER unveröff.). Beim Mittelspecht hingegen ermöglicht erst der hohe Anteil stehender Totholzbereiche und die hohe Strukturdiversität der Buchenoberflächen in Verbindung mit dem Fehlen jeglicher selektiver Eingriffe in die Bestände das Vorkommen in reinen Buchenwäldern. Es liegt daher der Schluss nahe, dass der Mittelspecht früher weite Teile der Tiefland-Buchenwälder besiedelt hat. Das Vorkommen des Mittelspechts in den untersuchten circa 100–160-jährigen bewirtschafteten Buchenwäldern scheint zur Zeit an das gleichzeitige Vorhandensein eines gewissen Eichenanteils gebunden zu sein.

Aus den Ergebnissen können folgende waldbaulichen Konsequenzen zur Förderung des Mittelspechts bei der Buchenbewirtschaftung abgeleitet werden (vergleiche auch BAUER & BERTHOLD (1996)):

- Anhebung der Zielstärke bei der Endnutzung der Buche zur Erhöhung der durchschnittlichen Stammdimensionen der Altbestände
- Sicherung stark dimensionierter Totholzanwärter und toter Bäume (zum Beispiel Stümpfe)
- Grundsätzliche Schonung von „Steinbuchen" (Buchen mit der Veranlagung zur Ausbildung einer rissigen Rinde)
- Vereinzeltes Belassen von Bäumen mit der Veranlagung zur Bildung von Rindenknollen, besonders großen Krebsgeschwüren u.ä. im Zuge von Durchforstungsmaßnahmen.

Buntspecht **(Foto: Peter Pechacek)**

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Three-toed Woodpecker ecology in a managed Engelmann spruce forest

Ökologie des Dreizehenspechts in einem bewirtschafteten Engelmann-Fichten-Wald

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Abstract

The Three-toed Woodpecker *Picoides tridactylus* is an uncommon bird of the boreal forest that is dependent on recent burns and Spruce Bark Beetle *Dendroctonus rufipennis* infestation for foraging (Fig. 1). Populations of Three-toed Woodpeckers in south-central Utah have increased recently due to the large scale spread of spruce bark beetle infestation. Subsequently, much of this area has been targeted for salvage logging. We studied habitat use and behavior of Three-toed Woodpeckers in logged and unlogged portions of beetle-infested Engelmann spruce *Picea engelmannii* forest on Monroe Mountain, Utah, Fishlake National Forest, from May to August 2000. Micro and macro-habitat data and bird behavior were recorded at 60 sites where Three-toed Woodpeckers were observed. Comparisons of habitat parameters were made between feed, nest, and drum trees. Engelmann spruce was used most heavily for feeding and comprised 97 % of feed trees. Forty-four percent of nest trees were in Aspen *Populus tremuloides*, with the remaining 56 % in broken top conifers. Average forest canopy cover differed between the three types of trees ($p < 0.05$), with feed trees having the highest canopy cover (69.7 ± 16 %) (mean ± SD), and nest trees the lowest (19.9 ± 18 %). Canopy cover was also less in logged than in unlogged areas ($p < 0.001$). Outer debarking was significantly greater ($p > 0.05$) on feed (55 ± 27 %) and drum trees (31 ± 34 %) than on nest trees (6 ± 10 %). Nest trees were found to occur in less aggregated stands of surrounding random trees than were feed and drum trees ($p < 0.05$). Distance to habitat edge was less in logged areas than in unlogged areas ($p < 0.10$). These findings suggest that according to certain habitat parameters, Three-toed Woodpeckers use different types of trees for feeding, nesting, and drumming, and in logged and unlogged areas. This indicates that perpetuation of mature aspen and old-growth Engelmann spruce is important in maintaining Three-toed Woodpecker populations.

Der Dreizehenspecht ist ein seltener Vogel der borealen Wälder, dessen Vorkommen von akuten Waldbrandfolgen oder Borkenkäferbefall abhängt. Die Populationen des Dreizehenspechts im Süden Utahs haben aufgrund einer Borkenkäferkalamität in den vergangenen Jahren stark zugenommen. Aufgrund des Befalls mit Borkenkäfern waren große Teile des Gebietes Ziel von Zwangsnutzungen. Wir untersuchten Habitat und Verhalten von Dreizehenspechten in unberührten und eingeschlagenen Beständen befallener Engelmann-Fichtenwälder am Monroe Mountain Region, Fishlake National Forest, in der Zeit von Mai bis August 2000. Mikro- und Makrohabitat Daten und Vogelverhalten wurden an 60 Stellen innerhalb des Untersuchungsgebietes aufgenommen, in denen Dreizehenspechte zu beobachten waren. Die Habitatparameter wurden bei den Bäumen mit Bedeutung für die Nahrungssuche, das Nisten und das Trommeln verglichen. Zur Nahrungssuche wurde überwiegend die Engelmann-Fichte (97 %) genutzt. Nestbäume waren zur 44 % Zitterpappeln, der Rest bestand aus abgebrochenen Nadelbäumen. Der durchschnittliche Kronenschluss variierte zwischen den unterschiedlich genutzten Bäumen ($p < 0,05$). Die zur Nahrungssuche genutzten Bäume hatten mit 69.7 ± 16 % (mean ± SD) den höchsten Kronenschluss, während Nistbäume mit 19.9 ± 18 % den niedrigsten Kronenschluss aufwie-

Fig. 1. Male Three-toed Woodpecker
(Photo: Kreig Rasmussen)

sen. Ein unterschiedlicher Kronenschluss (p < 0,001) wurde auch beim Vergleich der unberührten und eingeschlagenen Wäldern festgestellt. Die Ent-rindung der Nahrungsbäume war mit 55 ± 27 % signifi-kant größer als die der Trommelbäume (31 ± 34 %) und der Nestbäume (6 ± 10 %). Nestbäume wurden in lichteren Beständen mit weniger zufällig umgebenden Bäumen gefunden, als die Nahrungs- und Trommelbäume (p < 0,05). Die Entfernung zum Waldrand war in den Wäldern mit Einschlag kleiner als in den unberührten Wäldern (p < 0,10). Die Ergebnisse deuten mit Rücksicht auf bestimmte Habitatparameter darauf hin, dass der Dreizehenspecht in unberührten und bewirtschafteten Wäldern unterschiedliche Nahrungs-, Nest-, und Trommelbäume nutzt. Dies zeigt, dass die mittelalten Zitterpappelbestände und alte Engelmann-Fichte-Bestände für den Erhalt der Dreizehenspecht-Populationen eine hohe Bedeutung besitzen.

Introduction

The Three-toed Woodpecker *Picoides tridactylus* (Fig. 1) is historically uncommon (BENT 1939), and follows the geographic distribution of spruce circumborealy (CRAMP 1985, WINKLER 1995). It is the most arboreal

Fig. 2. Feed Tree **(Photo: Kreig Rasmussen)**

Fig. 3. Nest Tree **(Photo: Rebecca Hill)**

Fig. 4. Drum Tree **(Photo: Rebecca Hill)**

woodpecker (WINKLER 1995), and specialized in its preference for feeding on adult and larval Spruce Bark Beetle *Dendroctonus rufipennis* (CRAMP 1985, WINKLER 1995). Endemic populations of Three-toed Woodpeckers have low densities, (MURPHY & LEHNHAUSEN 1998), with local irruptions occurring in response to increased food availability caused by bark beetle infestation, extensive wild fires, or forest disease (YUNICK 1985). As a result of a long-term regional drought cycle, spruce bark beetle infestation has increased to epidemic levels in parts of Utah since 1997. Pursuant to this, the Forest Service has targeted much of this area for intensive salvage logging. Prior to this study, Three-toed Woodpecker habitat use had not been studied thoroughly in Utah. Likewise, the effects of salvage logging on Three-toed Woodpecker habitat have not been studied in this area, but have been documented by other researchers to be detrimental (MURPHY & LEHNHAUSEN 1998). Our first study objective was to quantify habitat characteristics of feed, nest, and drum trees used by Three-toed Woodpeckers. Our second study objective was to compare habitat use of Three-toed Woodpeckers in logged and unlogged areas.

Study Area and Methods

Our research was conducted on Monroe Mountain, Utah, Fishlake National Forest, from May to August 2000. The study area encompassed approximately 6,000 acres of Engelmann spruce *Picea engelmannii* dominated forest on a broad north-facing slope, with an elevational range of 2,985–3,311 m. In this late successional forest, Sub-alpine Fir *Abies lasiocarpa* is co-dominant, with isolated patches and individual Aspen *Populus tremuloides* interspersed irregularly.

Birds were located opportunistically, using audio cues. Their presence was confirmed visually, by walking roads, skid-trails, and cross-country routes through harvested and unharvested areas during daylight hours. At each tree, bird behavior was observed and recorded using all occurrences sampling (ALTMAN 1974). Behavior was then classified into one of three focal types, feeding (Fig. 2), nesting (Fig. 3), or drumming (Fig. 4). The following micro-habitat parameters were recorded at each tree; tree species, diameter at breast height (DBH), canopy cover, and debarking. Canopy cover was

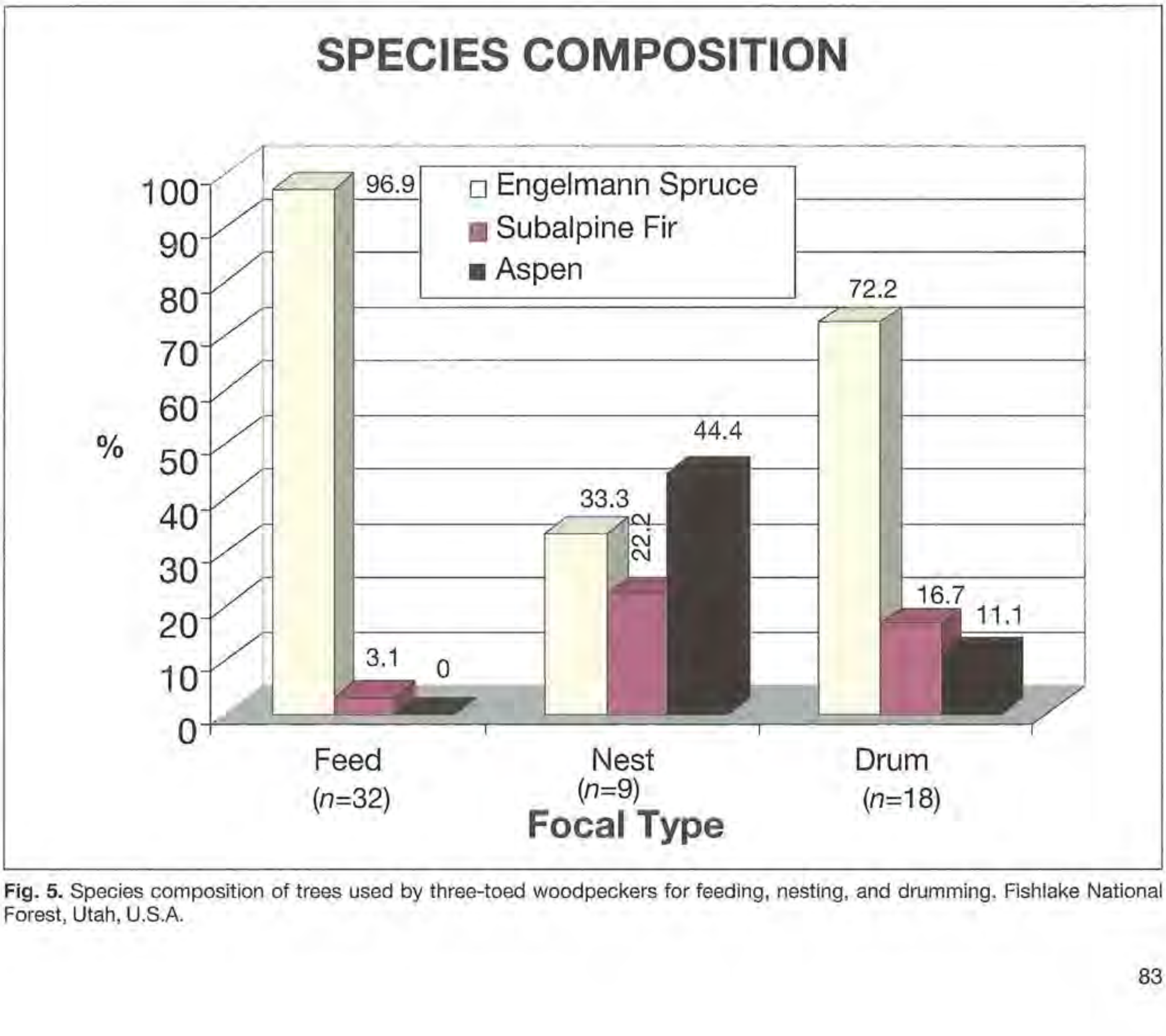

Fig. 5. Species composition of trees used by three-toed woodpeckers for feeding, nesting, and drumming, Fishlake National Forest, Utah, U.S.A.

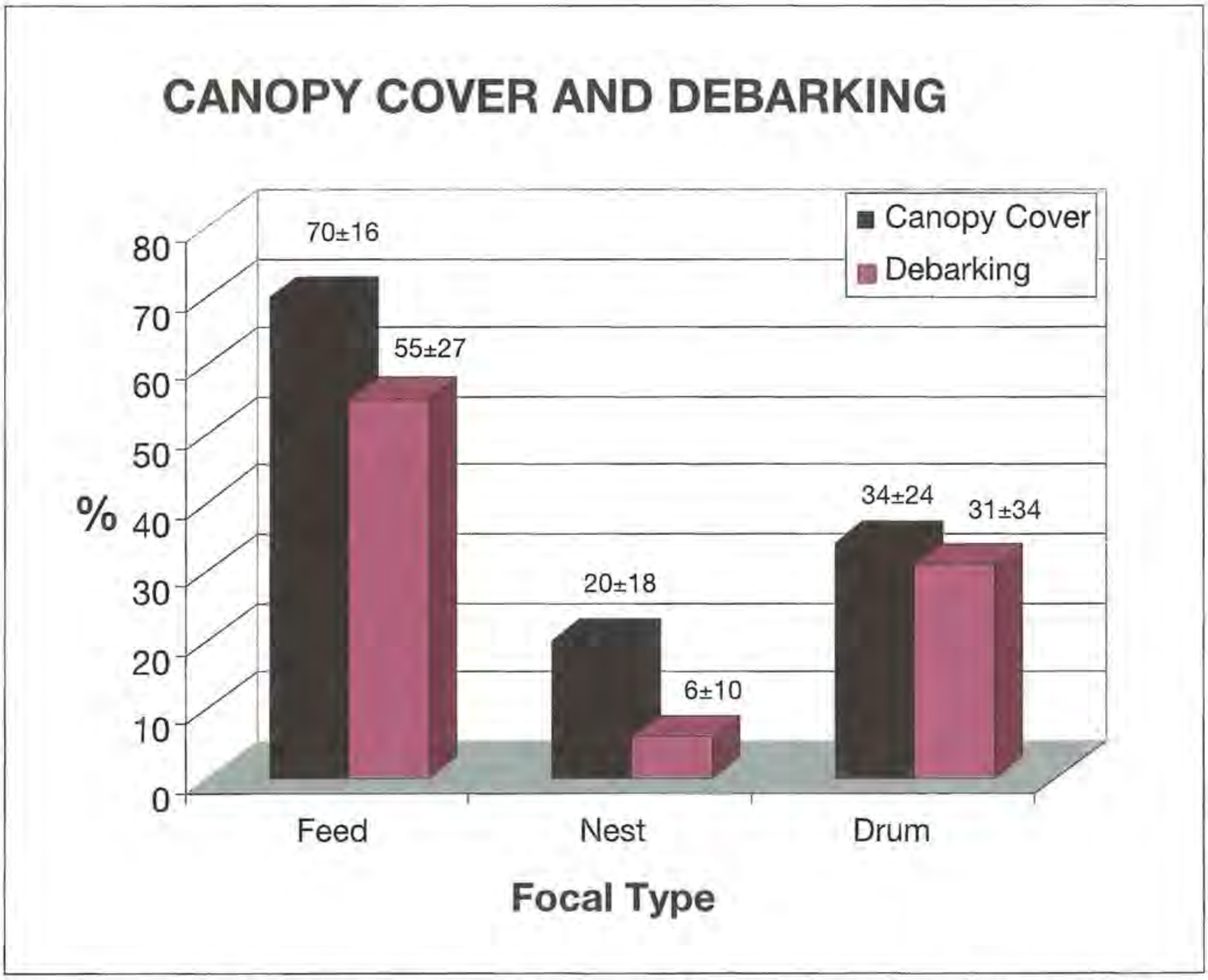

Fig. 6. Canopy cover and debarking (mean ± SD) on al focal trees used by three-toed woodpeckers. Fishlake National Forest, Utah, U.S.A.

measured using a convex spherical densiometer and debarking was estimated ocularly according to BERGIVINSON & BORDEN (1992); 0 (no debarking), 0.025 (< 5 %), 0.075 (5–10 %), 0.15 (10–20 %), 0.30 (20–40 %), 0.50 (40–60 %), 0.80 (> 60 %).

Macro-habitat parameters were also measured for each focal tree. The spatial pattern of proximal trees was determined using a modified T^2 method, which measured nearest neighbor distances to two feed trees and to two trees of any kind (LUDWIG & REYNOLDS 1966). Distance to habitat edge was measured with a metric tape, or laser rangefinder, if greater than 15 m.

A general linear model (GLM) was used in comparisons between the three types of focal trees and between logged and unlogged areas. P-values were derived from expected values created in the model.

Results

Engelmann spruce was used most heavily for feeding and comprised 97 % of feed trees. Forty-four percent of nest trees were in aspen, with the remaining 56 % in broken top conifers (Fig. 5).

Canopy cover differed significantly between feed, nest, and drum trees ($p < 0.05$) (Fig. 6). Canopy cover also differed significantly between logged and unlogged areas ($p < 0.001$). Average canopy cover for logged areas was 31± 22 % (mean ± SD), and 75 ± 8 % for unlogged areas.

Outer debarking on nest trees was significantly less than on feed and drum trees ($p < 0.05$) (Fig. 6). This is because 44 % of nest trees occurred in aspen, which is not fed on by woodpeckers. Feed trees were the most heavily debarked as a result of the woodpeckers' primary method of feeding, which is removing or scaling bark.

The spatial pattern of nest trees to surrounding random trees was significantly less aggregated than the spatial pattern of feed and drum trees ($p < 0.05$) (Fig. 7). There was no significant difference in the spatial pattern from all focal trees to nearest feed trees.

DBH of feed trees differed significantly from DBH of nest trees ($p < 0.10$). Feed trees average DBH was 46 ± 15 cm, nest trees 33 ± 7 cm, and drum trees 38 ± 14 cm. Distance to habitat edge differed significantly between logged and unlogged areas ($p < 0.10$). Distance to edge from logged areas averaged 2.0 ± 2.3 m. Distance to edge from unlogged areas averaged 27.8 ± 38.1 m.

Discussion

Our results indicate that Three-toed Woodpeckers feed primarily on large diameter beetle infested Engelmann spruce trees occurring in aggregated groups. Mature aspen with low canopy cover occurring in forest openings, and broken top conifers are critical nesting habitat. Additionally, snags or dead trees of all species are an important component for drumming habitat. This indicates that Three-toed Woodpeckers are highly habitat specific. Consequently, large-scale removal of any of these classes of trees may have long term effects on woodpecker population density or viability.

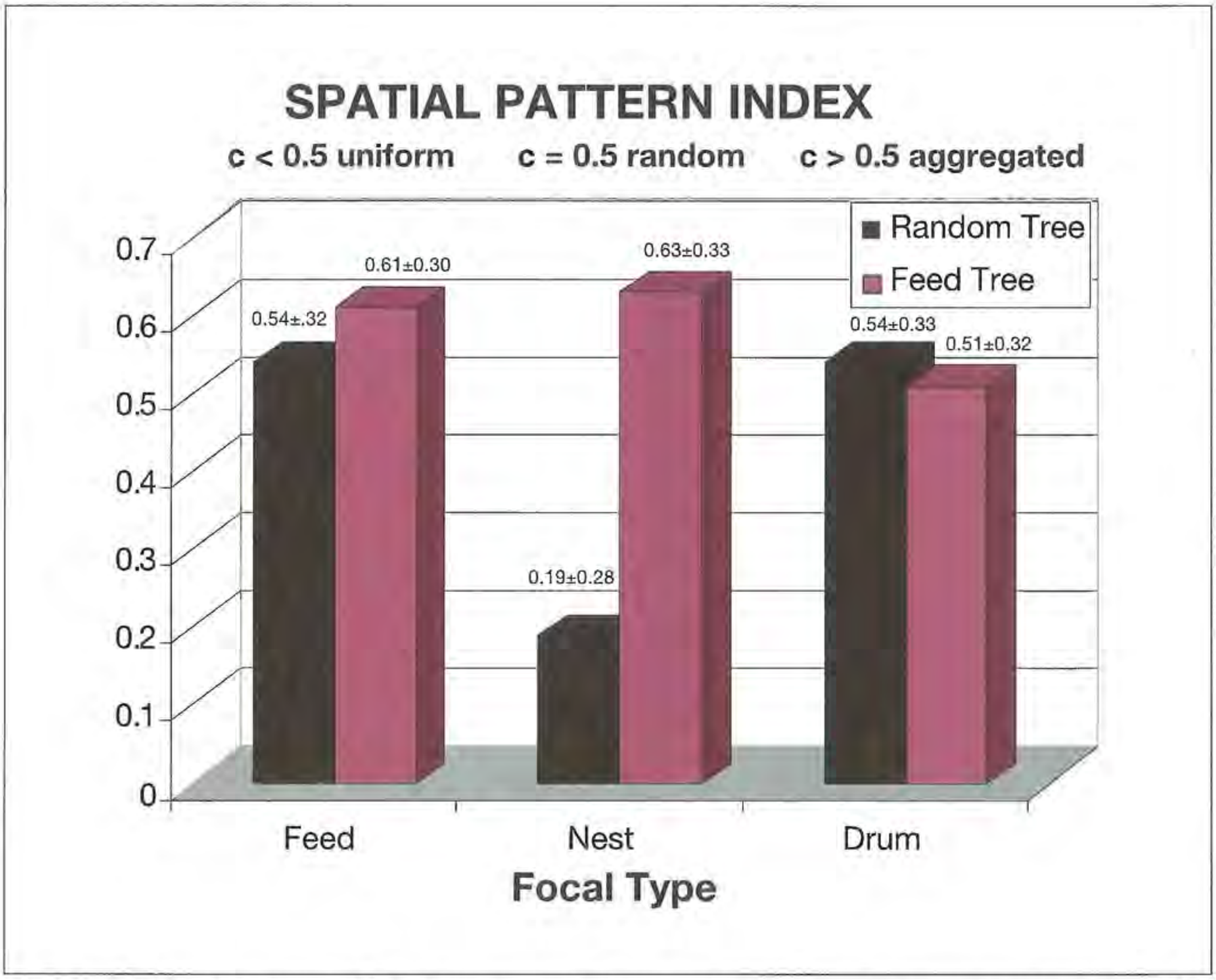

Fig. 7. Spatial pattern index (mean ± SD) for focal trees used by Three-toed woodpeckers. Fishlake national forest, Utah, U.S.A. This is a measure of the distance to the nearest neighboring tree from the focal tree and indicates stand uniformity, randomness, or stand aggregation.

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Niche concepts and woodpecker conservation: understanding why some species are endangered

Das Nischenkonzept und Schutzbemühungen für Spechte: Warum manche Arten gefährdet sind

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Abstract

Recognition that a species is endangered is often easy, evidenced by rapidly declining populations. Understanding why a species is endangered is often not so easy. Simple solutions are often sought and efforts are focused at the species level without understanding the species' past history, ecosystem dynamics, interspecific interactions, and seasonal, age-specific, sex-specific, habitat specific, and geographic-specific needs. In this paper I will address oversimplification of woodpecker conservation problems and discuss how lack of understanding of the species' niche relates to endangerment and how developing an understanding is an important first step to successful conservation. My discussion will focus on two endangered species: the Red-cockaded Woodpecker *Picoides borealis* and the Ivory-billed Woodpecker *Campephilus principalis*, while drawing examples from several less troubled species.

Zur Erkenntnis, dass Arten gefährdet sind, kommen wir leicht, wird dies doch durch rapide sinkende Populationen deutlich. Zum Verständnis dagegen, warum eine Art gefährdet ist, kommen wir nicht sonderlich leicht, denn für das Management von Wildtieren werden einfache Lösungen gesucht und eine Reihe wichtiger Einflussfaktoren bleibt dabei unberücksichtigt. Die Aufmerksamkeit konzentriert sich oft ausschließlich auf die Artebene, ohne die ursprüngliche Situation der Art zu berücksichtigen, Dynamik des Ökosystems zu verstehen, interspezifische Interaktionen, saisonale, altersspezifische und geschlechtsspezifische Bedürfnisse der Art zu beachten oder geographische und habitatbedingte Variationen in Betracht zu ziehen. In diesem Beitrag werde ich die Probleme der zu großen Vereinfachung von Schutzbemühungen für Spechte nennen und diskutieren, wie die Nische der Arten mit der Gefährdung zusammenhängt. Die Entwicklung des Verständnisses der ökologischen Nische einer Art stellt einen ersten Schritt für ein erfolgreiches Schutzprogramm dar. Meine Diskussion wird sich hauptsächlich auf zwei vom Aussterben bedrohte Arten beziehen, nämlich den Kokardenspecht und den Elfenbeinspecht, während ich auch auf Beispiele anderer, wenig bedrohter Arten eingehen werde.

"Five, four, three, two, one..." Those were the words not heard at the Kennedy Space Center in Florida in June 1997 when the Space Shuttle Discovery was scheduled to be launched. The delay was due to a woodpecker – the Yellow-shafted Flicker *Colaptes auratus*. Video was broadcast around the world of a Yellow-shafted Flicker that had excavated more than 200 holes in the insulation of the external fuel tank of the space shuttle (Fig. 1). The estimated costs of repairs and delays exceeded a million dollars. The true story, however, was not as simple as implied (JACKSON 1997a).

The insulation on the external fuel tanks is a foam-like material that is light-colored when applied, but which changes to reddish-brown on the outside when cured. It has a consistency much like rotted wood. Flickers were nesting in the general area and it is likely that the perpe-

Fig. 1. The Space Shuttle Discovery on its launch pad following repair of 208 holes that had been made in the insulation by a Northern Flicker. The repaired holes can be seen as light spots in the rust colored insulation.

(Photo: Jerome A. Jackson)

trator of the damage was trying to excavate a nest cavity. Unfortunately, the thickness of the insulation layer was inadequate to contain a normal flicker cavity and each time the bird got started, it quickly hit metal and had to start over again. Hence there was a multitude of false starts.

Why did the bird do this? Several factors come into play. First, in constructing the launch pad and adjacent facilities, most of the palms and other trees that the birds usually use as nest sites in the area had been removed. Second, to prevent wildfires near the launch pad, grass was very closely mowed, creating perfect foraging habitat for the ground-feeding flickers. Third, European Starlings *Sturnus vulgaris* were abundant at the site, also attracted to the closely mowed habitat for their foraging. While they no doubt competed vigorously for the few available flicker nest sites and usurped new cavities as they were excavated, they also nested in protected sites on the nearby buildings and other structures. Finally, the rusty color of the foam insulation on the shuttle fuel tank was precisely the same color as found on the upper part of many of the palms used for nesting by flickers in the area. Could the shuttle fuel tanks have been super releasers?

NASA's desire was to solve the problem and prevent a recurrence. Their initial goal was to capture and remove the bird involved – perhaps an understandable, but over-simplified and inadequate response. A more appropriate response was one that comes through understanding the species' niche and the nature of its interactions with European Starlings: let the grass grow so that there is inadequate foraging habitat for either the flickers or the starlings, and institute a starling control program to reduce competition for the flickers.

In this case an understanding of woodpecker and starling niche dynamics was used to help solve a serious, high profile, economic problem. However, successful efforts to solve conservation problems involving woodpeckers should also focus on understanding of niche dynamics.

Basic Niche Concepts

A **niche** as it is usually defined – is the role of the species in its environment. One of the basic tenets of ecology is that no two species can occupy the same niche. Segregation of species by niches that vary in habitat types, seral stages of habitats, foraging methods, foraging sites, prey species, and nesting phenology allow coexistence of about 10 species to coexist in both eastern North America (SHORT 1982, JACKSON unpublished data) and central Europe (WESOLOWSKI & TOMIALOJC 1986, PECHACEK 1995, SCHERZINGER 2001).

I emphasize here the multi-dimensional nature of a woodpecker's niche. Morphology, physiology, social structure, season, climate, food availability, habitat, past history, other species, and many other factors influence a woodpecker's niche. Furthermore, it is often the interactions among these factors that are the ultimate arbiters of a woodpecker's role in nature, its success, and survival as a species. For example, JACKSON (1976b) found that Red-headed Woodpeckers *Melanerpes erythrocephalus* typically nest in more open habitats, whereas Red-bellied Woodpeckers *Melanerpes carolinus* nest more within a forest. JACKSON & NICKOL (1979) demonstrated that as a consequence of this difference, Red-bellied Woodpeckers were subject to infestation with an acanthocephalan parasite, whereas Red-headed Woodpeckers were not susceptible to it.

I also emphasize the distinction between the **fundamental niche** of a species and the **realized niche** of the local population, sex, age group, or individual. The fundamental niche is the total breadth of the role that a species might play within the environments in which it occurs. The realized niche is the role played by the specific group or individual at a particular time and place.

Niche breadth is a function of the limits of tolerance of a species. Typically those species that are endangered or threatened are ones that have one or more aspects of the niche with narrow limits of tolerance – they are in some way specialists. Downy Woodpeckers *Picoides pubescens* and Great Spotted Woodpeckers *Picoides major*, for example, have broad niches that include compatibility with a great diversity of habitats and climatic conditions. They accept a diversity of potential nest sites, and food resources are varied and ubiquitous. Red-cockaded Woodpeckers, in contrast, are usually limited by their narrow choice of fungal-infected living pines in extensive open forests as sites for cavity excavation, and by preferences for foraging on pines. Ivory-billed Woodpeckers are certainly limited by their need for very large trees in which to excavate nest and roost cavities and probably also by the availability of large wood-boring beetle larvae (TANNER 1942, JACKSON 1996). ***Every aspect of a species' niche is a potential management problem.***

The Problem of History

In order to fully understand today's conservation problems, it is essential to have a sense of historical change in a species' niche and environment. A lack of an historical perspective can lead to false assumptions about the niche of a species, incorrect assessment of the conservation problems, and fruitless conservation efforts.

In North America, for example, Red-bellied Woodpeckers may be experiencing a shift in nesting phenology and may now be competing more for nest sites with Red-headed Woodpeckers as a result of competition with the introduced European Starling (JACKSON 1997c).

HOGSTAD & STENBERG (1997) acknowledged that most data concerning habitat selection in the endangered White-backed Woodpecker *Picoides leucotos* have been collected in recent decades and "may not be relevant to its natural habitat." Both the Red-cockaded and Ivory-billed woodpeckers provide case histories of failure to consider an historical perspective. All too often we make assumptions about habitat requirements based on recent studies of habitats that are far different from natural habitats of a century or more ago.

Critics of endangered species efforts often grasp at the idea that extinction is a natural process and that species should be allowed to follow the natural course to extinction. Extinction is a natural process, one that is essential to evolution. It is, in many cases, the ultimate result of evolution. Species facing extinction have, through the processes of natural selection, become so fine-tuned, so specialized, so wonderfully adapted to their environment, that they have lost the flexibility to change with a rapid change in that environment. Both the Red-cockaded and Ivory-billed woodpeckers fit that mold. The key, of course, is that today it is humans, and humans alone, that have brought about the rapid habitat changes.

Red-cockaded and Ivory-billed woodpeckers are intimately adapted to lives in extensive old-growth forests. Both are species dependent on severe ecological disturbances. The Red-cockaded is dependent on frequent fire to maintain its open, fire climax, pine forest ecosystem. The Ivory-bill is dependent on fires, floods, and other severe ecological disturbances to provide a continuing supply of recently dead, large, old trees that serve as the source of its food supply, e.g., very large cerambycid beetle larvae.

In the case of the Red-cockaded Woodpecker, some argue that we should simply provide them with vast areas of wilderness and that nature would take care of its own. This view is wrong. While the frequency of lightning-started fires could potentially be similar to that prior to the arrival of humans in the New World, the extent to which those fires would burn would not be similar. Natural fires might once have burned for hundreds of miles; those today would be stopped either by roads or by human efforts. Thus fire cannot play its natural role and human management intervention is essential for "natural" functioning of wilderness ecosystems (JACKSON et al. 1986).

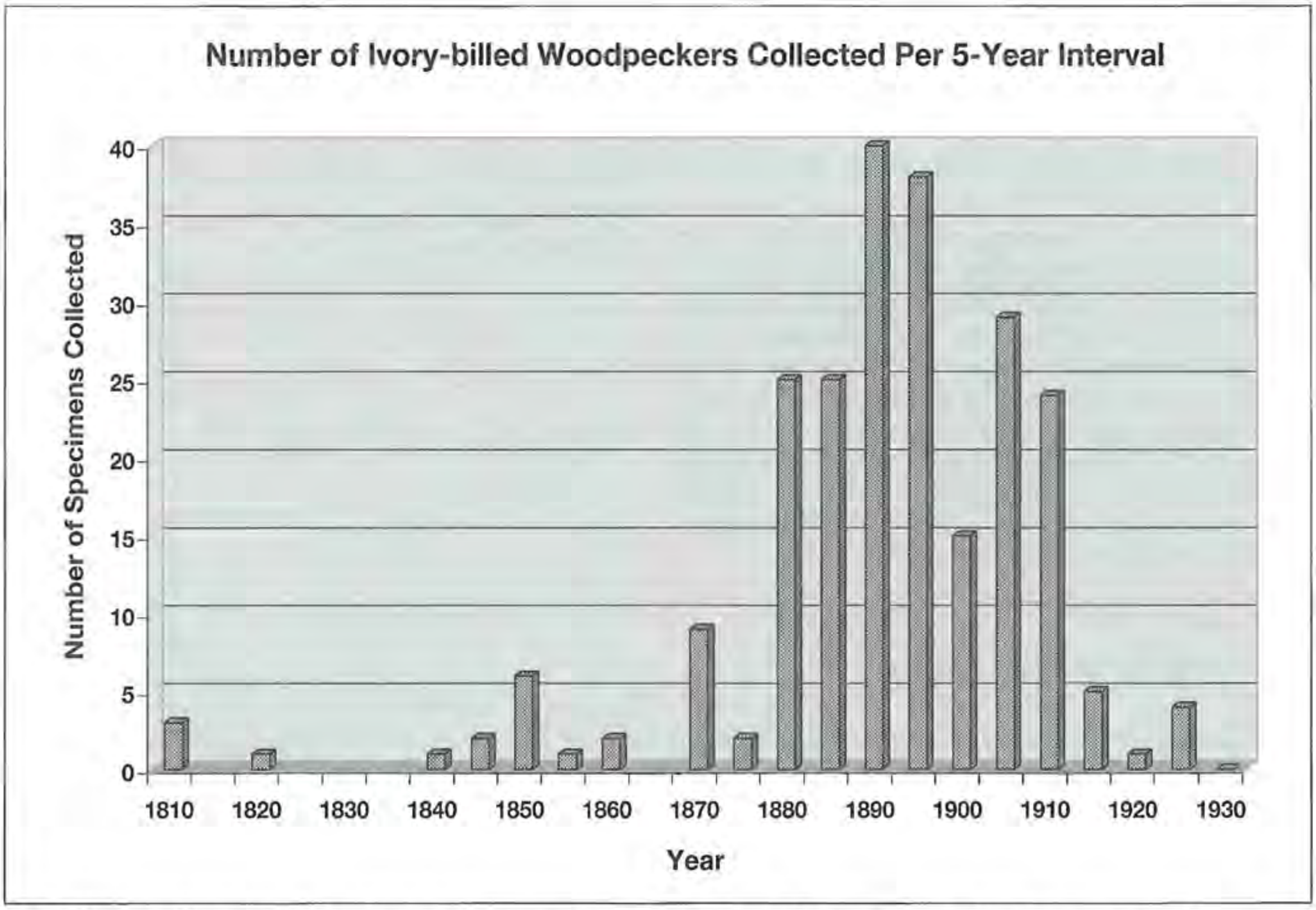

Fig. 2. Number of Ivory-billed Woodpecker specimens present in collections that were collected per five-year interval.

A lack of a historical perspective in the case of the Ivory-billed Woodpecker has resulted in a warped view of both its habitat preferences and the causes of its demise. The known range of the Ivory-billed Woodpecker was limited, but includes two disjunct populations: one in the southeastern United States, and one on the main island of Cuba. The U.S. population is generally described as being associated with mature swamp forests (TANNER 1942), whereas that of Cuba is associated with mature montane pine forests (SHORT 1982, JACKSON unpublished data).

The Ivory-billed Woodpecker suffered greatly during the late 1800s from killing by humans. It had long been revered – and killed – by native Americans, but primitive weapons probably limited the impact of such killing. With the introduction of guns to North America, killing of Ivory-bills became easier and increased for many reasons. Some were eaten, some were killed no doubt out of curiosity, but by the 1880s, they were perceived to be of value and were killed for sale to museums and private collectors. Over 400 specimens exist in museums today (Fig. 2), most collected between 1880 and 1910.

To blame the demise of the Ivory-bill on collectors, however, is an unreasonable oversimplification. The primary cause for the decline in this species was the destruction of its habitat. The extensive killing came at a time when the birds were already rare and the impact of that killing was enhanced by the habitat destruction that fragmented populations and provided access to collectors.

Understanding of the decline, endangered status, and possible extinction of the species has suffered as a result of these generalizations.

A review of historical records suggests that the Ivory-bill was a species of both upland and lowland old growth forests in both the United States and in Cuba – the major characteristic being old growth. The virgin forests of the uplands were the first to go in the southeastern U.S., providing fiber and fuel, and creating farmland for a growing nation (WILLIAMS 1989). In Cuba, the reverse was true, the lowland forests were cleared during early colonial days for sugar cane and other crops (BARBOUR 1945) and the birds persisted in old growth on mountain slopes too steep for farming.

The Problem of Geography

We often characterize the habitat and the niche of a species on the basis of a few studies in a few areas and assumptions are made that habitat preferences and use of habitat are uniform across the species' range. Some woodpeckers are very widespread. The Great Spotted Woodpecker in Eurasia, and the Hairy Woodpecker *Picoides villosus* in North America, and the circumboreal Three-toed Woodpecker *Picoides tridactylus* are among the most widespread of species. The Hairy is resident from the tree line in the far north to western Panama and some islands of the Bahamas. Geographically it ranges in mass from over 130 grams to less than 40 grams, and in color from white-breasted to brown-breasted, and it occupies a diversity of habitats (JACKSON 1970a, JACKSON et al. in press). Even with such variation, the habitat of the Hairy Woodpecker is often described in simple terms, giving little suggestion that there might be regional differences in the niche of the species (e.g., SOUSA 1982).

The Red-cockaded Woodpecker is much more limited in distribution, occurring only in the southeastern United States. As a resident species, however, it has adapted to local conditions and shows clinal variation in size following classic ecogeographic generalizations such as Bergmann's Rule (MENGEL & JACKSON 1977). It is reasonable to suppose that there might also be regional variation in aspects of the species' niche.

Indeed, in coastal plain habitats the Red-cockaded Woodpecker has been found to forage most of the time (> 90 %) in pines (e.g., RAMEY 1980, HOOPER & LENNARTZ 1981). In contrast, on the Daniel Boone National Forest in south-central Kentucky, JACKSON et al. (1976) and KALISZ & BOETTCHER (1991) found that active Red-cockaded Woodpecker cavity tree clusters were in habitat dominated by trees other than pines (52 % non-pine, 48 % pine). The species was found to use hardwood trees for foraging to a much greater extent – on average 14 % of the time in winter and 44 % of the time during nesting (HINDS & KALISZ 1995). HINDS & KALISZ (1995:109) warned: "Our results suggest that management based primarily on removal of hardwoods to improve Red-cockaded Woodpecker habitat contributes to loss of biodiversity and may ultimately lead to the extirpation of the local population of the species."

In establishing management guidelines for this endangered species, biologists relied solely on coastal plain foraging habitat data that suggested the presence of a hardwood understory was unacceptable to the species. The Daniel Boone National Forest began systematically removing all hardwood midstory within 15.2 m of Red-cockaded Woodpecker cavity trees and intensive removal and control elsewhere within Red-cockaded Woodpecker habitat (SCHMALTZ 1981, ANONYMOUS 1997). With the hardwoods removed, the U.S. Forest Service then sponsored further research on habitat use by the birds in Kentucky; that research was specifically designed to study foraging of Red-cockaded Woodpeckers in the areas where hardwoods had been intensively controlled (ZENITSKY 1999). With most hardwoods removed, it was not surprising that ZENITSKY (1999) found that the birds used pines for foraging to the same extent as Red-cockaded Woodpeckers on the coastal plain. The U.S. Fish and Wildlife Service Red-cockaded Woodpecker Recovery Coordinator (COSTA 1999) ignored the pre-hardwood removal findings of HINDS & KALISZ (1995) that the birds made extensive use of hardwoods. He also did not acknowledge that the more recent results might have been expected with extensive hardwood removal. Further confounding the issue, most of the birds under study by Zenitsky were ones that had been translocated from the sandhills region of South Carolina (REED 1999), where Red-cockaded Woodpecker reliance on pines for foraging is greater. Both the Forest Service and Fish and Wildlife Service chose to use Zenitsky's findings to support their management, while Zenitsky herself (1999:64) noted that "limitations prevent me from concluding whether midstory reduction benefited or harmed Kentucky RCWs."

The ramifications of the intensive hardwood control on the Daniel Boone National Forest were much greater than a simple shift in relative use of pines as foraging substrate. Southern pine forests exist on the coastal plain because of frequent fire. The fires occur with regularity because of a high incidence of electrical storm activity. Both electrical storm and fire frequency decline rapidly north of the Gulf coast, such that natural fire is much less frequent on the Cumberland Plateau. Pines survive there, more or less limited to ridges, where KALISZ & BOETTCHER (1991) found 90 % of Red-cockaded Woodpecker cavity trees. This distribution of pines – and consequently the birds – is in part as a result of occasional fire, but likely more so because of topography that allows exposure of young pines to the sun on ridges.

When the U.S. Forest Service instituted management to remove hardwoods from Red-cockaded Woodpecker habitat on the Daniel Boone National Forest, they failed to consider the adaptive significance of the pine-hardwood mix that had been present. The presence of the hardwoods there was important as a buffer in two ways. First, unlike flat coastal plain forests, the ridge-top forests of the Cumberland Plateau are regularly subjected to extreme winter winds. As winds strike the plateau region, they are funneled up valleys that become increasingly narrow towards the ridges. As the winds are funneled into ever-narrower channels, their velocity increases tremendously – a simple manifestation of physics known as the Bernoulli principle. The hardwood trees mixed with the pines buffered the spindly pines from the brunt of these winds. Once the hardwood trees were removed, the full force of the winds hit the pines and almost all Red-cockaded Woodpecker cavity trees were snapped off.

The hardwood trees also served another buffer function for the pines: they slowed the dispersal of southern pine beetles *Dendroctonus frontalis*, thus greatly reducing the potential for devastating infestations. With the hardwoods removed, and with pines injured by winds, southern pine beetle populations soared to epidemic proportions, destroying so much of the remaining pine habitat that survival of the birds was deemed impossible and the decision was made to remove the remaining birds from Kentucky. Clearly there was a need for understanding of potential geographic variation in the niche of the Red-cockaded Woodpecker and management consistent with that variation. Endangered species management should not be done with a single recipe for all populations and community types!

In managing for the nest-site-limited Red-cockaded Woodpecker, an approach that has helped the species is the development and deployment of artificial cavities known as "cavity inserts" (ALLEN 1991). Essentially these are birdhouses that are inserted into a hole cut into a living pine with a chainsaw. With the entrance of the cavity insert flush with the tree surface, the woodpeckers readily accept the inserts as if they were naturally excavated cavities. These have the disadvantage that they are not initially protected by the gum barrier that the birds develop around a cavity, thus they are at first more vulnerable to climbing predators. In time the birds excavate resin wells and the cavity becomes quite similar in appearance to a naturally excavated cavity (Fig. 3). However, there is another disadvantage that has not been acknowledged. The wood at the entrance to the insert is often only 2–3 cm thick, whereas in excavating a cavity, the birds characteristically go in 6–8 cm or more before excavating the nest chamber. Thus in the inserts, nestlings and roosting adults are more vulnerable to predators that can reach into a cavity or that can enlarge a cavity entrance. The lesser thickness of wood at the front of the insert also likely means less protection from thermal extremes. The significance of this thermal protection likely varies geographically. Lack of adequate insulation associated with cavity inserts may have been a factor contributing to a drastic reduction in the population of Red-cockaded Woodpeckers on the Cumberland Plateau of Kentucky. This northernmost population of the species is subject to much colder winters than other populations. After these birds had suffered extensive cavity tree loss due to winds, they had been provided with cavity inserts. Most birds had only cavity inserts for roosting and the population decline seems to have occurred during cold winter weather.

The Problem of Seasonal Variation in the Behavioral Ecology

Perhaps the single greatest focus of scientific study of birds is the nest site. It is fixed in space and time and offers ease of study and quantification. For academics, the breeding season generally falls in summer when the greatest time is available for research. When a species is recognized as potentially threatened or endangered, initial efforts – and often the greatest efforts – are focused on the nest site and breeding season. Breeding is of paramount importance because of its link to our understanding of many basic parameters of population dynamics.

However, conservation efforts must not be so myopic as to limit the focus of management efforts to the breeding season or to assume that niche parameters revealed during the breeding season reflect the limits of niche parameters for the species. The Red-cockaded Woodpecker presents a clear picture of problems that can ensue with a primary conservation focus on the breeding season.

When this species was first declared endangered, there was little known of its biology. Its unique cavities, excavated into living pines, were easily recognized and forest managers knew that these were often cut as "cull" trees. In addition, LIGON (1968, 1970) had just completed studies of the species in Florida. His efforts provided important baseline information on home range, habitat use, and differential niche use by the sexes.

Of critical importance, he found that Red-cockaded Woodpeckers that were feeding nestlings had home ranges of little more than 12 ha (30 acres). His data were immediately put to use in managing for the birds, focusing protection and management efforts on about 12 ha associated with cavity trees. What wasn't realized at the time was that adults are limited in the distance they can travel to find food for nestlings. Traveling any greater distance would not allow sufficient food to be brought to the nest. In the weeks prior to nesting, the birds rarely forage near the cavity trees and as soon as the young fledge they are led to foraging areas far from the cavity trees. Resources near the cavity trees are more or less reserved for the critical nesting period. During the rest of the year, home ranges are commonly 81 ha (200 acres) or more (e.g., JACKSON 1994, JACKSON & PARRIS 1995). Management plans developed on the basis of data from only the nesting season were grossly inadequate and Red-cockaded Woodpecker populations continued to plummet.

Fig. 3. Red-cockaded Woodpecker at its nest in an artificial cavity, Note the outline of the cavity "box" still evident, although the bird has since pecked resin wells and the flow of gum now makes the cavity very similar in appearance to cavities the birds excavate. **(Photo: Jerome A. Jackson)**

The foraging niche of woodpeckers – including diet, foraging sites, and foraging behavior – often varies considerably with season and this variation needs to be considered when contemplating conservation efforts or evaluating the impact of woodpeckers on forest insect pests (e.g., BUTLER & SCHLAEPFER 2001). In North America, Red-headed Woodpeckers, for example, may feed largely on fruit in spring, insects during the summer, and acorns in winter – using quite different foraging methods in seasonally different habitats (SHORT 1982, J. A. JACKSON unpubl. data). Even use of the same resource can require different efforts at times: PFLUMM (1979), for example, found that in Great Spotted Woodpeckers handling time for retrieving seeds from dry larch *Larix* sp. cones was significantly longer than for retrieval from wet larch cones. Thus during a particularly dry season, there might be increased energetic costs associated with foraging even though the same quantity of food was available.

In Red-cockaded Woodpeckers, seasonal differences in choice of foraging substrate have been reported by SKORUPA & MCFARLANE (1976), HOOPER & LENNARTZ (1981) and HINES & KALISZ (1995).

Potential For Problems Resulting From Differential Niche Use by the Sexes

Patterns of niche variation have usually been thought of in terms of species differences. However, following a seminal paper by SELANDER (1966), researchers focused on patterns of sexual dimorphism and quantification of the foraging niches of the sexes of woodpeckers. Selander and others have argued that by using different food resources or using the same resources in different ways, members of a pair compete less with one another and thus maintain a stronger pair bond.

Many species illustrate such differential niche use, and the nature of differences between sexes varies with species and in concert with many other parameters. For example, male Downy Woodpeckers *Picoides pubescens* forage significantly more often on small branches or even weed stems, whereas the females forage more on larger branches and the trunk of trees (JACKSON 1970b, Kansas; KISIEL 1972, New York). While these behavioral differences between the sexes are widespread, OUELLET (1997) found some evidence in eastern Canada of a reversal in the pattern: there male Downy Woodpeckers may forage more on tree trunks and females more on branches.

In the Red-cockaded Woodpecker, males forage significantly more in the crowns of pines and on peripheral branches, while females forage more on the trunks of larger pines (LIGON 1968, RAMEY 1980). This pattern has been found across the range of the species and, because of the species' endangered status, the differential niche use takes on a special significance: management for this species must provide for the different foraging habitat needs of the sexes. Studies of the Red-cockaded Woodpecker at the Savannah River Plant in South Carolina and at Ft. Polk, Louisiana, provide evidence of the consequences of management that neglects consideration of differences between the sexes. Young pines may be able to provide adequate foraging habitat for males, but they provide neither the surface area nor the bark surface texture that the trunk of a large, old pine provides (JACKSON 1979).

At the Savannah River Plant I studied the behavioral ecology of a declining population of Red-cockaded Woodpeckers in forests with few old trees and considerable areas of young pine plantations. Home ranges of birds increased dramatically in younger forests, often exceeding 400 ha (1000 acres) in forests dominated by 16–20-year-old pine plantations. Similarly, at Fort Polk, Louisiana, JACKSON & PARRIS (1995) found typical home ranges (about 80 ha) for Red-cockaded Woodpeckers prior to removal of older pines for a new tank range, and home ranges exceeding 400 ha after removal of the older trees.

Aspects of differential niche use by the sexes other than foraging ecology must be considered as well. For example, in the Red-cockaded Woodpecker, males are strongly philopatric, characteristically remaining at their natal cavity cluster, thus potentially inheriting the valuable site, while females characteristically disperse from their natal cavity cluster, thus lessening the potential for inbreeding in the species. As a result of these niche differences, efforts to move Red-cockaded Woodpeckers are usually successful for young females (which would normally disperse), and usually unsuccessful for males. Males that have been moved often return to their natal site from great distances (JACKSON 1997b).

Differential niche use by the sexes of a species can vary geographically, perhaps a function of availability of habitat, nature of food resources, or presence or absence of competitors – and almost certainly a function of the past history of the species' populations. For example, differential niche use by the sexes is characteristic of the North African race of the Great Spotted Woodpecker *Picoides major numidus*, but not in European races. WINKLER (1979) suggests isolation of the North African race during the Mindel glaciation as a contributing factor.

Potential For Problems Resulting From Age-specific Niche Variation

In considering threatened species we also need to be concerned about niche variation with age from hatching through adulthood. Needs, interactions, and interdependencies vary greatly with age and thus habitat characteristics. Events that take place within a very short time – such as nestling life or post-fledging dependencies – have potential for limiting a species. Woodpeckers are among the most altricial of birds, naked and with closed eyes for the first few days of life. Attainment of thermoregulatory abilities comes with plumage development and takes more than a week, making young nestlings vulnerable to cold and dependent on brooding adults. As a neonate, a woodpecker has an exceptionally long neck and large head, no doubt facilitating feeding, but perhaps creating potential for other problems. A typical neonate brood of 3–5 nestlings will cluster in the center of the cavity. Siblings, as well as nest structure, influence a nestling's niche. Each nestling faces the others, draping its long neck and head over a sibling, thus decreasing the distance the head must be raised for the next feeding (Fig. 4; JACKSON 1970c, 1976a). It also gains a thermoregulatory advantage from reduced surface-area exposure. This interaction among nestlings is likely significant for brood survival. Brood reduction to one or two nestlings, such as might occur with reduced habitat quality of the adults, likely reduces individual nestling survival potential as a result of increased energy loss through exposure and energy expenditure in raising the head to feed.

Another nestling characteristic that is important to consider is sexual dimorphism. In the White-backed Woodpecker HOGSTAD & STENBERG (1997) found that fledgling females had significantly less mass than fledgling males. I found that female Red-cockaded Woodpecker nestlings at 15 of 18 nests with nestlings aged 7 to 22 days averaged less mass than sibling males of the same age (Table 1). Larger size is generally advantageous in sibling rivalry for food and, in circumstances where food is limited, smaller nestlings are generally the ones that die. Thus, nestling female Red-cockaded Woodpeckers may be at a disadvantage and suffer differential mortality in less productive habitats. Nestling sex ratios favoring males have been found for the species in South Carolina (GOWATY & LENNARTZ 1985, Jackson unpublished data) and Mississippi and Louisiana (J. A. JACKSON unpubl. data).

Discussion

Investigations of seasonal, habitat-specific, sex-specific, and age-specific variation in niches of woodpeckers have been minimal, but have been increasing. Indeed, such studies may be more common for woodpeckers than for other groups of birds. The Red-cockaded Woodpecker may be the most intensively studied woodpecker in the world (JACKSON 1995) and it provides clues as to the potential niche variation in other species. The fundamental niche of the Red-cockaded Woodpecker is characterized by its cooperative breeding, differential niche use by the sexes, differential dispersal by the sexes, a long dependence of fledglings on their parents, use of living pines for cavity excavation, and adaptations to fire climax ecosystems. Its realized niche varies geographically, seasonally, and with habitat variability. Problems associated with all aspects of the species' niche have contributed to its demise and must be dealt with in conservation efforts.

Fig. 4. Day-old nestlings of the Red-headed Woodpecker showing how nestling woodpeckers arrange themselves in the center bottom of the nest cavity. By resting against one another, they conserve heat and the head and neck are partially raised, reducing energy expenditure when they raise the head to beg. **(Photo: Jerome A. Jackson)**

The fundamental niche of the Ivory-billed Woodpecker has not been well understood. A more complete understanding of the niches of other species, recent field work in the United States and Cuba, existing historical descriptions of Ivory-billed Woodpecker habitats, and examination of 200+ Ivory-billed specimens, provide additional insight into the behavioral ecology and fate of this species. A long juvenile dependence, a limited food resource, and need for very large trees for nest and roost cavity excavation may have contributed to the species decline as original habitats were destroyed, altered, and fragmented.

For many woodpecker species the evidence needed for sound management is available, but neither understood nor acted upon because of seemingly conflicting results of scientific studies. Such should be re-examined. Have

Table 1. Sex differences in weights of Red-cockaded Woodpecker nestlings.

Nest #	Weights (g)		Difference
	males	females	(males – females)
Savannah River Plant, South Carolina			
1	14.3	12.3	2.0
2	42.5	40.7	1.8
3	21.4	19.9	1.5
4	32.5	36.5	- 4.0
5	38.3	34.2	4.1
	37.8		3.6
6	40.6	38.3	2.3
	41.0		2.7
Fort Polk, Louisiana			
1	37.8	35.4	2.4
		34.6	3.2
Noxubee National Wildlife Refuge, Mississippi			
1	45.3	43.9	1.4
2	32.3	32.3	0
3	48.3	44.8	3.5
4	47.2	43.9	3.3
	45.0		1.1
5	37.6	30.9	6.7
	34.5		3.6
6	38.7	32.2	6.5
7	40.4	32.9	7.5
8	37.4	35.0	2.4
		20.9	16.5
9	36.8	37.8	-1.0
10	40.0	40.7	-0.7
11	39.2	38.0	1.2

the possibilities of geographic, habitat, seasonal, sex, and age variation in the species niche been considered? Were the studies the result of sound science or were important possibly niche-related differences ignored in their design?

Our lack of understanding of the complexity of woodpecker niches has hampered conservation efforts for declining species. Our failure to make use of the understanding that is available has been tragic.

Acknowledgments

I thank Peter Pechacek for inviting me to participate in this woodpecker workshop and Peter and the many woodpecker biologists who made the workshop such a stimulating event. This manuscript has benefited much from the discussions at the workshop and since and from Peter's helpful editorial suggestions.

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A study of mechanisms underlying habitat fragmentation effects on the Middle Spotted Woodpecker: A progress report

Eine Untersuchung zu den Mechanismen, die den Effekten der Habitatfragmentierung beim Mittelspecht zugrunde liegen: ein Zwischenbericht

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Abstract

A previous study of habitat fragmentation effects on a Middle Spotted Woodpecker *Picoides medius* population in the Nerussa-Desna woodland (52°18'–52°50' N, 33°28'–34°40' E) has shown that breeding density and some reproduction indices may be lower in habitat fragments than in continuous habitat (KOSSENKO & KAYGORODOVA 1998, 2001). In order to understand mechanisms underlying the effects of habitat fragmentation, the most important population processes such as density fluctuations, reproduction, mortality and dispersal were followed in subpopulations at two forested areas differing in degree of fragmentation of the main habitat (oak-dominated forest) from 1997 to 2000. Over this period, the difference in density between continuous habitat (on average 1.22 pairs/10 ha) and fragmented habitat (0.20 pairs/10 ha) was significant with density variation being low in both habitat types. Among reproduction indices, only the proportion of eggs fledged for all nests was significantly lower in fragmented compared to continuous habitat in 1997. The rates of nest and egg failures did not differ in continuous habitat and fragments. Due to cases of nest abandonment nestling losses for all years combined were significantly higher in fragments (25 %) than in continuous habitat (7 %). A rate of annual mortality of adults determined from percentage of young birds among breeders did not differ significantly between continuous and fragmented habitat (33 % and 25 %, respectively). Although data on dispersal are yet insufficient for detailed analysis, the distances of breeding dispersal in continuous and fragmented habitats did not differ statistically and usually did not exceed 0.5 km or 1–2 breeding territories. A maximum distance of natal dispersal of 10.5 km was recorded in fragmented habitat. Abundance of larval Lepidoptera was higher in continuous habitat than in fragments in 1999, but in 2000, it was higher in fragments than in continuous habitat. The variation of food abundance was significantly lower in continuous habitat than in fragments. The woodpeckers tended to occupy habitat patches with higher food supply. In general, the differences between continuous and fragmented habitats in breeding performance, mortality of adults and breeding dispersal seem to be too minor to explain significant difference in density. Mechanisms behind effects of habitat fragmentation are likely to be related to habitat quality variation and success of dispersal.

Eine frühere Untersuchung des Einflusses der Habitatfragmentierung auf die Mittelspechtpopulation in den Waldungen von Nerussa-Desna (52°18'–52°50' N, 33° 28'–34°40' O) zeigte, dass die Brutdichte und einige Reproduktionsmerkmale in den fragmentierten Habitaten kleiner sein dürften, als in den nicht-fragmentierten Habitaten (KOSSENKO & KAYGORODOVA 1998, 2001). Um die Mechanismen zu verstehen, die dem Effekt der Habitatfragmentierung zugrunde liegen, wurden folgende Populationsmerkmale in zwei bewaldeten Gebieten mit unterschiedlichem Grad der Fragmentierung zwischen 1997 bis 2000 untersucht: Abundanzschwankungen, Reproduktion, Mortalität und Dispersion. Während dieser Periode wurde eine signifikante Differenz zwischen der Abundanz des Mittelspechts in nicht-fragmentierten (im Durchschnitt 1,22 Paare/10 ha) und fragmentierten (0,20 Paare/10 ha) Habitaten festgestellt. Die Abundanzschwankungen waren dabei in den beiden Habitaten niedrig. In Bezug auf die Merkmale der Reproduktion konnte nur beim Anteil der geschlüpften Eier festgestellt werden, dass 1997 in den in den fragmentierten Habitaten weniger Eier schlüpften als in den nicht-fragmentierten Wäldern. Die Anteile erfolgloser Bruten und ungeschlüpfter Eier unterschieden sich in den beiden untersuchten Habitaten nicht. Die Nestlingsverluste aufgrund von Verlassen der Brut waren zusammen in allen Jahren höher in den fragmentierten Habitaten (25 %) als in den nicht-fragmentierten Teilen (7 %). Die jährliche Mortalitätsrate der Altvögel ermittelt anhand der Anteile der Jungvögel unter den Brutvögeln unterschied sich in den beiden Habitattypen nicht signifikant (33 % und 25 %). Die Daten zur Dispersion sind für eine detaillierte Analyse zwar noch nicht ausreichend vorhanden, doch die Brutdispersion in fragmentierten und nicht-fragmentierften Flächen unterschied sich statistisch nicht und überstieg gewöhnlich nicht mehr als 0,5 oder 1 bis 2 Brutreviere. Die maximal registrierte Abwanderungen eines Jungen wurde mit 10,5 km in einem fragmentierten Habitat belegt. Abundanz der Lepidopteren-Larven war 1999 in den nicht-fragmentierten Gebieten höher als in den fragmentierten, doch im Jahre 2000 hat sich die Situation umgedreht. Allerdings variierte die Abundanz der Nahrung weniger in den nicht-fragmentierten als in den fragmentierten Wäldern. Mittelspechte tendierten zur Besiedelung von Habitatstellen mit einem hohen Nahrungsaufkommen. Insgesamt konnte festgestellt werden, dass die Unterschiede zwischen den fragmentierten und nicht-fragmentierten Habitaten in Bezug *auf Bruterfolg, Mortalität der Altvögel und Brutdispersion zu klein waren, um damit die signifikanten Abundanzschwankungen zu erklären. Mechanismen, die dem Effekt der Habitatfragmentierung zugrunde liegen sind vermutlich abhängig von der Variation in der Habitatqualität und vom Dispersionserfolg.*

Introduction

Habitat fragmentation appears to be one of the principal threats to many species in the temperate zone (WILCOVE et al. 1986). It has a variety of negative consequences such as a general loss of habitat area, reduced size of habitat remnants, separation of habitat patches, an increase in the resistance to dispersal movements, etc. (OPDAM et al. 1995, WIENS 1995).

The Middle Spotted Woodpecker *Picoides medius* seems to be a species with strict habitat requirements confined to oak-dominated forests (PETTERSSON 1984). It is highly vulnerable because of habitat loss and fragmentation throughout its range. As a non-migratory, medium-sized habitat specialist with a relatively small breeding territory, it is an ideal subject to study the effects of habitat fragmentation. Although the Middle Spotted Woodpecker was included in the Russian Red Data Book as a species with decreasing numbers (ILYASHENKO & ILYASHENKO 2000), in our study area known as Nerussa-Desna woodland, its numbers are still high, estimated at 500 breeding pairs (KOSSENKO & KAYGORODOVA 1999).

The first results of our study showed that breeding density and some reproduction indices may be lower in fragmented habitat than in continuous habitat (KOSSENKO & KAYGORODOVA 1998, 2001). In order to understand mechanisms underlying habitat fragmentation effects, the most important population processes such as density fluctuations, reproduction, mortality and dispersal were followed in two subpopulations inhabiting two different forest landscape areas: one with continuous and one fragmented habitat. In this paper the results of our ongoing research are presented in general.

Study area

The Nerussa-Desna woodland (52°18'–52°50' N, 33° 28'–34°40' E) with an area of approximately 250,000 ha is located in the European southwest of Russia within the Bryansk administrative region along the left bank of the Desna River (Fig. 1). This is one of the least undisturbed areas within the forested zone of European Russia, with forests covering more than 60 % of the area. About 16,000 ha of this area consists of oak-dominated forests. These forests are preserved in a near natural state as broad continuous tracts along the rivers. However, in some watersheds they are clearcut or highly fragmented by forestry.

Material and Methods

We conducted the study in 1997–2000. During this period, we surveyed study plots annually (total habitat = 345 ha), and followed the reproduction of 62 breeding pairs. We also marked 305 individuals with metal and colour rings, determined the age of 72 breeding individuals, and obtained 39 ringing recoveries. Abundance of food resources was also measured in 1999 and 2000 in continuous and fragmented habitats.

For comparative studies, we established two adjacent study areas differing in their degree of fragmentation of the main habitat (KOSSENKO & KAYGORODOVA 2001). The first area was a 96 ha study plot established as a reference area within a large (280 ha) continuous oak-dominated forest in the Nerussa River floodplain. The other study plot was represented by 30 fragmented oak-dominated woods ranging from 3 ha to 19 ha in size (total area 249 ha) scattered over a forested watershed with an area of about 70 km^2. The fragments are situated at 0.8–8.2 km from a broad continuous tract of oak-dominated forest.

Within the study plots, we determined woodpecker densities by mapping the sightings and tracking movements during the period of pair formation, nest building and egg laying. Once a bird was encountered within a plot it was followed as long as possible to define its territory outline. Particular attention was paid to the search of nests. With the exception of 1997, we used the playback technique on a limited basis in order to detect the woodpeckers while trying to avoid attracting them from their territories.

In order to monitor reproduction, we recorded the breeding behaviour of adults and inspected nesting cavities using a mirror and a lamp. Before the young fledged, we opened the nests by cutting a hole in the nest chamber to count, measure and ring the nestlings. After this, the young were put back and the hole was closed.

We attempted to mark all adult birds and nestlings observed within our study plots with metal and colour rings for individual field identification. Dispersal was investigated by obtaining ringing recoveries. The age of breeding birds was established on the basis of ringing data or plumage characteristics depending on whether tertials, secondaries and greater upper primary coverts were moulted or unmoulted (CRAMP 1985). Each bird was categorized as young (1-year-old) or as adult (≥ 2-year old).

In the Nerussa-Desna woodland, the Middle Spotted Woodpecker nestling diet consists primarily of caterpillars gathered from foliage (KAYGORODOVA & KOSSENKO 2000). This resource is characterized by periodic irruptions that provide abundant food. Larvae of a butterfly known as *Ptilophora plumigera* (Family *Notodontidae*) are most abundant among defoliating Lepidoptera in the area (KAYGORODOVA & KOSSENKO

Fig. 1. Location of the Nerussa-Desna woodland.

2000). It specialises on the maples *Acer platanoides* and *Acer campestris*. We estimated the abundance of larval Lepidoptera directly on foliage by visually searching 100-leaf samples. Each sample was taken from five different trees (20 leaves each) in a plot. Sample plots were positioned regularly at the intersections of a 100 x 100 m grid. In 1999, 36 samples were taken in continuous habitat and 62 samples taken in twelve fragments. In 2000, 104 samples were taken in continuous habitat and 124 samples taken in fifteen fragments. We counted larvae of Lepidoptera in the second half of May when most of them are half-grown to full-grown. This period coincides with the nestling phase of the Middle Spotted Woodpecker. We counted larvae on the maple *Acer platanoides* foliage only because this tree species is well presented in the forest understory, easily accessible from the ground, and hosts larvae of *Ptilophora plumigera*. The index of food abundance for a site was calculated (mean number of larvae per 100 leaves) from a range of sample plots.

Results

Breeding density

According to the censuses conducted in the springs of 1997–2000, the density of the Middle Spotted Woodpecker (Fig. 2) in continuous habitat varied from 1.05 to 1.36 pairs/10 ha (on average 1.22 pairs/10 ha). In the fragmented habitat of 30 small oak woods surveyed, this species occurred at 10 fragments at least once over the four year study period. However, the Middle Spotted Woodpecker bred in only five of these fragments with densities ranging from 0.16 to 0.24 pairs/10 ha (average, 0.20 pairs/10 ha). This represents a significant difference in density (on average more than six times lower in fragments than in continuous habitat), with a low amount of variation in both continuous and fragmented habitats (variation coefficient 11.1 % and 16.3 %, respectively).

Reproduction

The mean clutch size in continuous habitat for all years combined was 6.5 ($n = 32$) and ranged between 4 and 9. The overall number of young fledged per nest where eggs were laid was 5.0 ($n = 37$). Nesting success (percentage of nests fledging at least one young) was 93 % ($n = 43$), and fledgling success (percentage of eggs giving rise to fledglings) 77 % ($n = 210$ eggs). In fragmented habitat, clutches averaged 6.6 eggs varying from 5 to 8. The number of fledglings per nest was 4.2 ($n = 17$), and nesting and fledgling success was slightly lower at 83 % and 67 % ($n = 105$ eggs), respectively.

Fledgling success for all nests in continuous habitat was significantly lower in 1999 than in 1997 (Chi-square test $p < 0.05$ considering all nests, and successful nests only). In fragmented habitat, there were significant between-year differences in clutch size (1-way ANOVA $p < 0.05$). Fledgling success for all nests was significantly higher in 2000 than in both 1997 and 1999 (Chi-square test $p < 0.05$ for both comparisons).

Two-way ANOVA did not reveal any significant influence both of fragmentation and year on the reproductive success. Pairwise comparisons of reproductive success indices for each year between continuous habitat and all fragments, where breeding birds were found, revealed a significant difference in fledgling success for all nests in 1997 only. It was lower in fragmented habitat than in continuous (Chi-square test $p < 0.002$). These results suggest that differences in reproductive success between continuous and fragmented habitats are pronounced in particular years only.

Mortality

There was no significant difference between continuous and fragmented habitats in percentage of nest and egg

Fig. 2. Middle Spotted Woodpecker feeding young at its breeding cavity. **(Photo: Igor Shpilenok)**

failures for all years combined. In continuous habitat, three of the 43 nests with eggs failed to produce offspring. Of them, two nests containing eggs were destroyed during stormy weather. The third unsuccessful nest contained presumably inviable eggs. Of the 18 nests with eggs found in fragmented habitat, three nests containing nestlings were abandoned (one in 1997, 1998 and 1999). At least one of these cases was apparently caused by the failure of parents to provide young with food during the 2-day period of heavy rains. In both continuous and fragmented habitat, most egg loss was a result of hatching failure.

Nestling losses were significantly lower in continuous habitat (7 %, $n = 179$ nestlings) than in fragmented habitat (25 %, $n = 94$ nestlings; Chi-square test $p < 0.001$). In continuous habitat, starvation had a major impact and accounted for all of nestling mortality. In fragmented habitat, six of 23 nestlings that were lost perished from starvation although adults still delivered food to the nest. The other 17 nestlings were lost due to the three cases of nest abandonment mentioned previously.

Assuming that the population of a bird species is stable and that all adult birds return to their breeding areas, annual mortality of adults should be equal to proportion of young (1-year-old) birds among breeders (PAYEVSKY 1985). Low variation of the breeding densities in the Middle Spotted Woodpecker subpopulations in both continuous and fragmented habitats suggests that the first assumption is reasonable. The available data on the breeding site tenacity of this woodpecker (PASINELLI 1999; MICHALEK et al. 1999; see also 'Dispersal' section in this paper), though being scarce, characterize it as a philopatric species supporting the second assumption. In the Middle Spotted Woodpecker population we studied, young birds comprised 33 % ($n = 48$) of breeding birds in continuous habitat and 25 % ($n = 24$) in fragmented habitat for all years combined (Chi-square test $p = 0.469$). Therefore, our data suggest no significant difference between the habitats in annual mortality of adults.

Dispersal

Preliminary analysis of 30 ringing recoveries related to breeding dispersal (19 in continuous habitat and 11 in fragmented habitat) suggests that most adult individuals in both continuous habitat and fragments do not disperse over distances exceeding 0.5 km (1-way ANOVA $p = 0.640$) or 1–2 breeding territories. The data on natal dispersal are yet insufficient for detailed analysis. In continuous habitat, seven young birds dispersed over the distances less than 3.5 km from their birthplaces. There are still only two ringing recoveries related to natal dispersal in habitat fragments, but both are remarkable. In the first case, a 1-year-old female established a pair with her father and bred successfully in her natal territory. In the second case, another young female was recovered at 10.5 km from the place of birth. The latter case was the only one when a bird was ringed in one habitat type and seen again in another.

Food abundance

The level of food abundance measured by the index of abundance of larval Lepidoptera was lower in 2000 than in 1999. This, however, did not affect general breeding performance (probably because of more favourable weather conditions in the breeding season of 2000 compared with 1999 and availability of other important food sources). Within breeding territories of the Middle Spotted Woodpecker, food abundance in 1999 was 1.4 times higher in continuous habitat than in fragments (1-way ANOVA $p = 0.251$), but in 2000, on the contrary, 2.3 times lower in continuous habitat than in fragments (1-way ANOVA $p < 0.01$). In both years, variation of food abundance (according to variation coefficients) was significantly lower in continuous habitat than in fragments. In 1999, food abundance within breeding territories was significantly higher than outside them (including empty habitat patches in fragmented habitat) in both continuous and fragmented habitats (1-way ANOVA $p < 0.05$ and $p < 0.01$, respectively); but in 2000, food abundance was higher only in fragments (1-way ANOVA $p < 0.01$). This implies that the woodpeckers tend to occupy habitat patches with higher food supply.

Although no relationship was found between variation of food abundance across years and general breeding performance, in 1999, food abundance within breeding territories was positively correlated with fledging success in fragmented habitat. However, the opposite was true in 2000, with food abundance being positively correlated with fledging success in continuous habitat (i.e., positive correlation was found in those habitats, where food abundance was lower).

Discussion

The Middle Spotted Woodpecker appears to be sensitive to habitat fragmentation. In our case this was demonstrated most significantly by the difference in breeding density between continuous and fragmented habitats. While considering this over six fold difference, some fragments within our study plot may be supposed to be unsuitable for the Middle Spotted Woodpecker. In order to take this into consideration, we recalculated density in fragmented habitat using only those fragments where pairs or single individuals occurred during the breeding season at least once over the four year study period (i.e. habitat that is suitable for the Middle Spotted Woodpecker). The density in continuous habitat was still 2.6 times higher than in fragments.

OPDAM et al. (1995) proposed comparing of reproduction rates in habitat fragments with those in continuous habitat in order to understand factors regulating processes in fragmented populations. Our data suggest that reproductive success of the Middle Spotted Woodpecker is affected by habitat fragmentation only in particular years due to higher nestling mortality in fragments. This is primarily due to nestling abandonment (probably, by unfavourable coincidence, for example, of low food abundance and extreme weather conditions). Productivity of fledglings in habitat fragments appears to be sufficiently high to saturate all vacant territories. Therefore, reproductive success seems unlikely to be responsible for the low breeding density in fragments compared with continuous habitat.

Our study covers only a four year period and may be subject to the problems associated with sample size. Nevertheless, the differences between continuous and fragmented habitats in other population processes such as mortality of adults and breeding dispersal seem to be too minor to explain significant difference in density. Although available data on natal dispersal distances are yet insufficient to discuss them in detail, we found the maximum distance in fragmented habitat (10.5 km) to be three times higher than in continuous habitat (3.4 km). This suggests that absolute dispersal distances may increase, rather than decrease with fragmentation.

Reduced habitat quality might account for lower breeding density in fragments compared to continuous habitat. Provided that variation of some important resources in fragments is higher, and that woodpeckers tend to avoid habitat patches with low supply of these resources, we expect that some proportion of habitat in fragments may remain unoccupied for this reason. Food abundance patterns revealed in our study seem to support this suggestion.

Significant difference in the breeding density between continuous and fragmented habitats is apparently associated with different occupancy of suitable habitat patches. Within study plot representing fragmented habitat, there are at least 11 habitat sites where a Middle Spotted Woodpecker pair bred or could breed, and carrying capacity of the study plot in continuous habitat is estimated at 15 breeding territories. Assuming these figures to represent the number of suitable habitat patches, the mean occupancy in continuous habitat over the four year period was 1.7 times higher than in fragmented habitat (72 % and 45 %, respectively).

The frequent occurrence of woodpeckers in continuous habitat as opposed to fragments demonstrates indirectly the effects of habitat fragmentation on dispersal (MATTHYSEN & GRUBB 1998), which is thought to be the key to survival in fragmented landscapes (OPDAM 1990). As a mobile animal species, the Middle Spotted Woodpecker apparently is able to cross fragmented landscape and colonise distant empty patches within our study plot, all of which are situated < 9 km from continuous habitat (see MÜLLER 1982). In addition, outside the breeding season the Middle Spotted Woodpecker occurred in fragments where it never was found during the breeding season. Therefore, any obvious barriers or gaps inhibiting dispersal movements of the species are absent from our study plots. At the same time, we observed a number of cases in which single individuals were seen displaying in habitat fragments, but those were not resulted in a pair formation and colonisation of the fragments. These observations suggested that meeting a potential mate may be hindered in fragments because of spatial separation. Other plausible causes proposed in related studies on the Nuthatch, *Sitta europaea* (MATTHYSEN et al. 1995, MATTHYSEN & CURRIE 1996, MATTHYSEN 1999), are a higher loss of dispersers in fragmented landscape (as a result of long absences from suitable habitat during the dispersal phase) and asymmetry in dispersal flow between continuous habitat and fragments (net immigration in continuous habitat and net emigration out of fragments). Effects of fragmentation on dispersal are still poorly known (OPDAM 1991, FOPPEN & GRAVELAND 1998, MATTHYSEN & GRUBB 1998). They should be investigated further to understand mechanisms behind the effects of habitat fragmentation.

Acknowledgements

The study is supported financially by the Russian Foundation for Basic Researches (grant No. 99–04–49159). Logistical support is given by the Bryansky Les State Nature Reserve (Zapovednik Bryansky Les). I thank Evguenia Kaygorodova for help in the fieldwork and preparation of the paper, and Alison Styring for useful comments on an earlier manuscript.

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Use of geographic information systems (GIS) for the evaluation of the Great Spotted Woodpecker's breeding habitat in the urban area of Sapporo City

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Abstract

To evaluate the potential breeding habitat of Great Spotted Woodpecker *Dendrocopos major*, we proposed a habitat suitability index (HSI) model, taking spatial distribution of the wood lots into account. For constructing the HSI model applicable to the urban area of Sapporo City which has the population of nearly 1.8 millions and is located in Hokkaido, the northern part of Japan Islands, we compiled the home range data of Great Spotted Woodpecker obtained through our field work and remote sensing techniques on geographic information system (GIS) database. The HSI model well conformed to the Sapporo City planning and management for preservation of the environment comfortable not only for the human inhabitants but also for woodpeckers living in the urban area of the City.

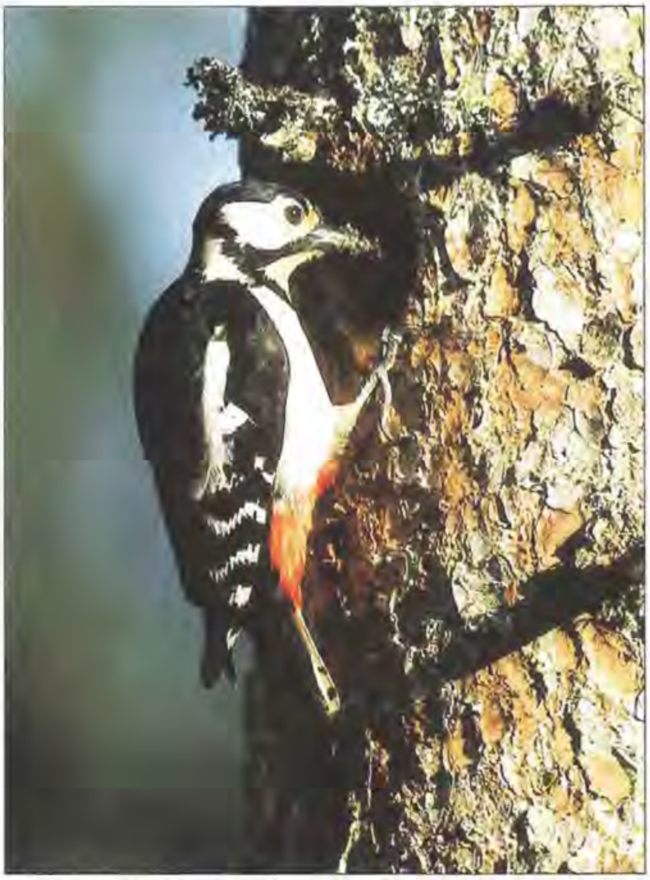
Um den potentiellen Brutlebensraum des Buntspechts zu bewerten, erstellten wir unter Berücksichtigung von räumlicher Verteilung der Waldflächen ein Habitateignungsmodell (HIS). Das Modell bezieht sich auf das urbane Sapporo City, eine 1,8 Millionen Stadt auf der nördlichen japanischen Insel von Hokkaido. Wir nutzten ein geographisches Informationssystem (GIS), um Home-range-Daten, gewonnen durch Feldarbeit und Fernerkundung, zusammenzuführen. Das Modell trug gut zur Planung von Sapporo City bei und verbesserte das Schutzmanagement der Stadtumwelt. Die Stadtumwelt sollte nicht nur zum Wohle der Einwohner, sondern auch der dort lebenden Spechte geschützt werden.

Introduction

In recent years many wildlife species and their habitats have been threatened, endangered and being adversely affected by human activities and resulting disturbances. It is thus increasingly important to understand the habitat requirements, delineate remaining suitable habitats, and effectively manage those units for the survival of these endangered species in an urban area (MAEDA 1993).

The Great Spotted Woodpecker *Dendrocopos major* is distributed throughout the palearctic and eastern Oriental faunal regions (SHORT 1977, CRAMP 1985, WINKLER et al. 1995). It is one of the most omnivorous woodpeckers and it occupies a wide range of habitats throughout boreal and temperate forests (CRAMP 1985). ROLSTAD et al. (1995) suggested that Great Spotted Woodpecker were flexible in their choice of feeding habitat during breeding season. The Great Spotted Woodpecker is one of the five different sympatric woodpecker species which are found widely in west part of Hokkaido. At present, Great Spotted Woodpecker is the only species abundantly found in the urban area of Hokkaido (KAWATA 1985, ITOU & FUJIMAKI 1990 and YAMAUCHI et al.1997).

Because the Great Spotted Woodpecker is a key species as a potential provider of nesting hole, the wide distribution of this species is very important and essential in keeping diversity and population size of secondary cavity-nesting species in the urban areas. Unfortunately at present, large forests and woodlands once suitable for the nesting, breeding and feeding habitats of Great Spotted Woodpecker have been split up into small fragments, thus threatening and endangering the habitat suitability of the environment toward this



Great Spotted Woodpecker (Photo: Peter Pechacek)

species. CRAMP (1985) and YAMAUCHI et al. (1997) suggested that Great Spotted Woodpecker could breed in a small wood lot if there were some suitable foraging area around the nesting site. Not only wood lot size but also wood lot density around the nest site seems to be more important.

Thus, in this study, we first describe the distribution and the present status of the breeding Great Spotted Woodpecker in the highly fragmented forests in the urban area of Sapporo City. Second, we propose a habitat suitability index (HSI) model, taking spatial distribution of the species habitable forests into account. Finally, applying the HSI model to the urban area of Sapporo City, we attempt to delineate the remaining potential habitats for the breeding Great Spotted Woodpecker in the City.

Methods

Study area

The survey was conducted in the central part of Sapporo City covering approximately 65 km square area. The City of Sapporo located in the alluvial plain called Sapporo Alluvia where the river Toyohira, a branch of the Ishikari, merges to the main stream. The plain is nearly flat and only about 9 m elevation from the sea level. Before the beginning of Meiji era in 1867, the most part of today's downtown Sapporo was covered with huge deciduous broad-leaved forests and marshes (HARUKI et al. 1989). However, in the present days, the population of Sapporo City has grown nearly 1.8 million and is still increasing with its urban area rapidly expanding towards the outside, as seen in Fig. 1.

Field survey

During nestling period of Great Spotted Woodpecker from May 20 to July 10 in 1997, we made an extensive survey on the distribution of their successful nest sites by monitoring the begging call of the nestlings throughout the study area. A week before fledgling, nestlings were noisy that can be easily heard from as far as 100 m distance. If we found a woodpecker's nest with no less than 20 days old young in the hole, the hole was classified as successful. We recorded the characteristics of the discovered nest sites such as the type, height and diameter at breast height (DBH) of the nest trees and also whether the trees were dead or alive. The height of the nest holes from the ground was also recorded. Then we marked the locations of the nest sites on a map of 1/15,000 scale, and measured and recorded the distances between the nearest neighbor nest sites.

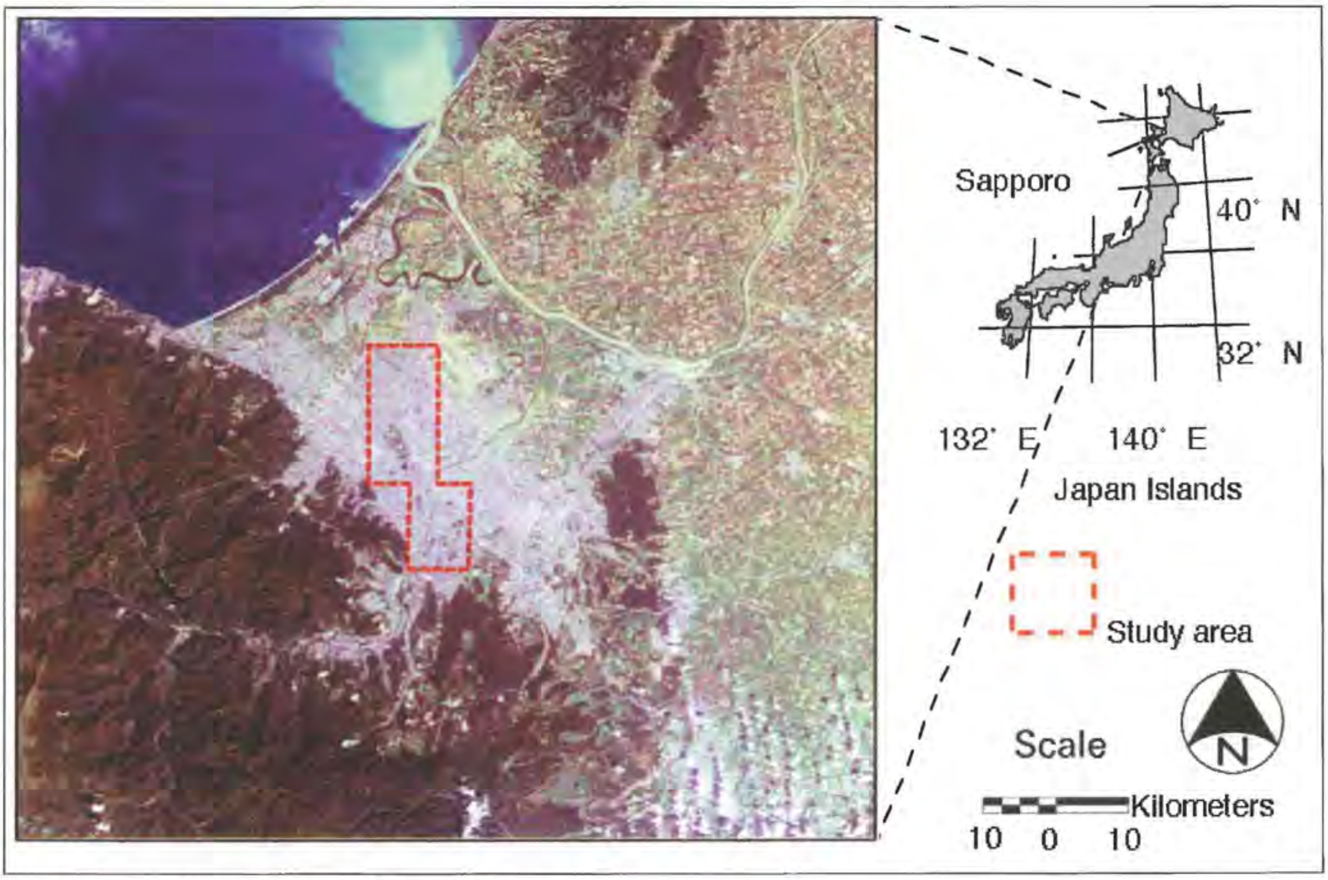


Fig. 1. Location of the study area in Sapporo City, northern Japan.

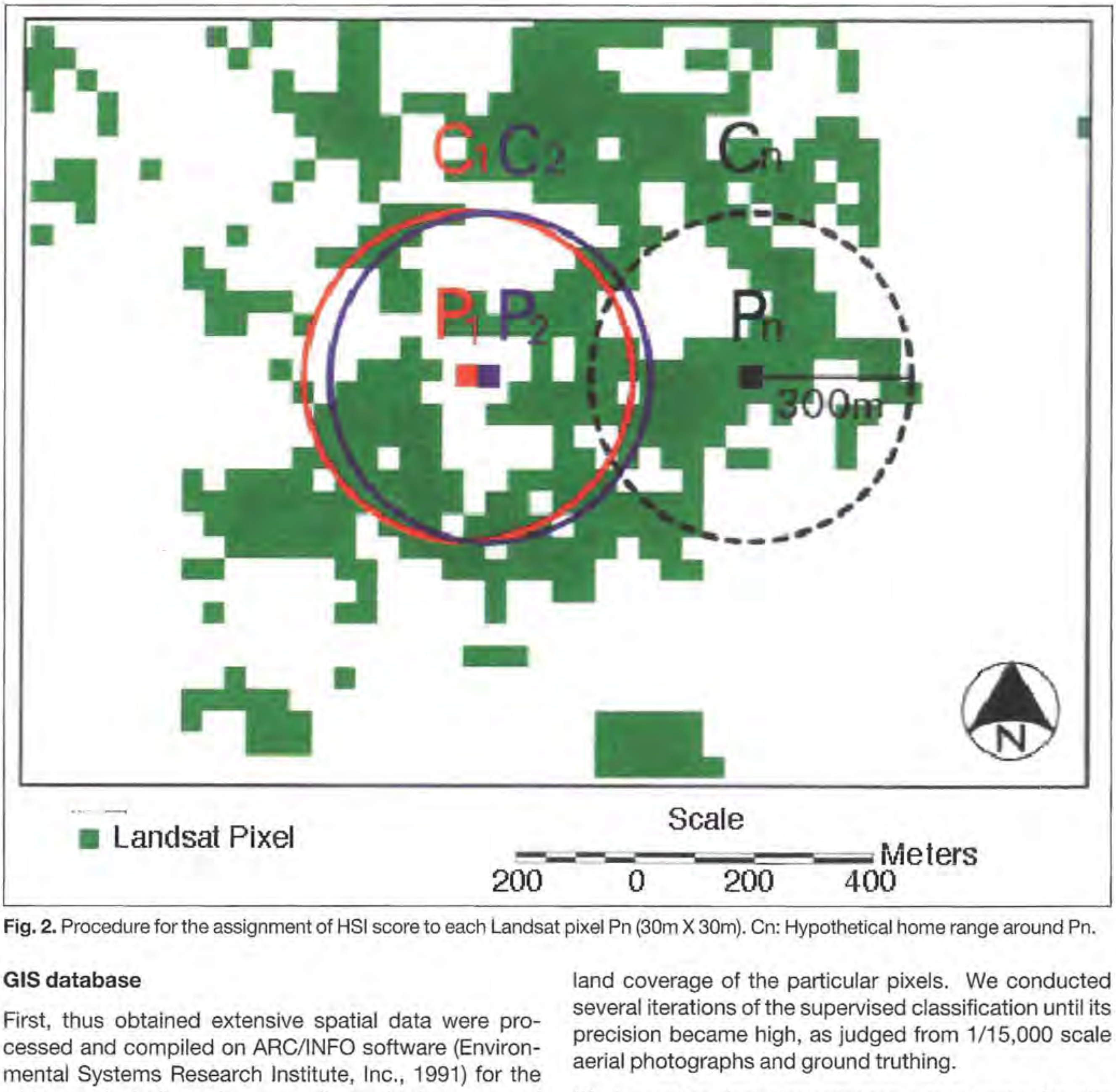


Fig. 2. Procedure for the assignment of HSI score to each Landsat pixel Pn (30m X 30m). Cn: Hypothetical home range around Pn.

GIS database

First, thus obtained extensive spatial data were processed and compiled on ARC/INFO software (Environmental Systems Research Institute, Inc., 1991) for the wide area including urban as well as suburban areas of Sapporo City. The database contained environmental information and the locations of successful nest sites of the Great Spotted Woodpecker compiled from the data derived, respectively, with a remote sensing technique and direct observation through our field survey. This database provided the basis for the HSI modeling described in this study.

Procedures of data processing and analyses

(1) In this study, we constructed a wood lot area map of Sapporo City, using a satellite picture. For this purpose, a Landsat TM picture of the City taken on September 1st, 1992 and July 8th, 1993 was divided into 30 m square pixels, each of which the index 1 (= woodland) or 0 (= otherwise) was assigned according to the modes of land coverage of the particular pixels. We conducted several iterations of the supervised classification until its precision became high, as judged from 1/15,000 scale aerial photographs and ground truthing.

(2) Assuming that the resources necessary for the breeding of a Great Spotted Woodpecker is a certain amount of area of wood lot contained in its home range, we constructed a model of a suitable breeding habitat unit. To do this, assuming the home range of a Great Spotted Woodpecker of the nestling period can be approximated with a circle around the nest, we assigned the area of the wood lot included in the circle as the model index representing the hypothetical home range. Then from the home-range data (N. KOTAKA unpubl.), we determined (hypothetical) radius of the hypothetical home ranges and finally constructed an HSI model (Fig. 2) according to the following procedures.

(3) All the pixels were already indexed as 1 (= wood lot) or 0 (= otherwise). Then, for each pixel (Pn) in the Landsat forest map given in the above Section (1), we as-

sumed a circle (Cn) of a radius r around it, assigned another index 1 to all the pixels within Cn (≦ r) and 0 to the pixels out side of Cn (> r) to be multiplied by their indices, and summed up all these multiplied indices to determine the score of each pixel Pn. In other words, the score is in fact the sum of the indices, which are either 1 for a wood lot pixel or 0 for a non-woodland pixel within the circle Cn (≦ r). Thus the score of HSI represents habitat suitability/unsuitability of each pixel Pn found at the center of each hypothetical home range circle Cn. We

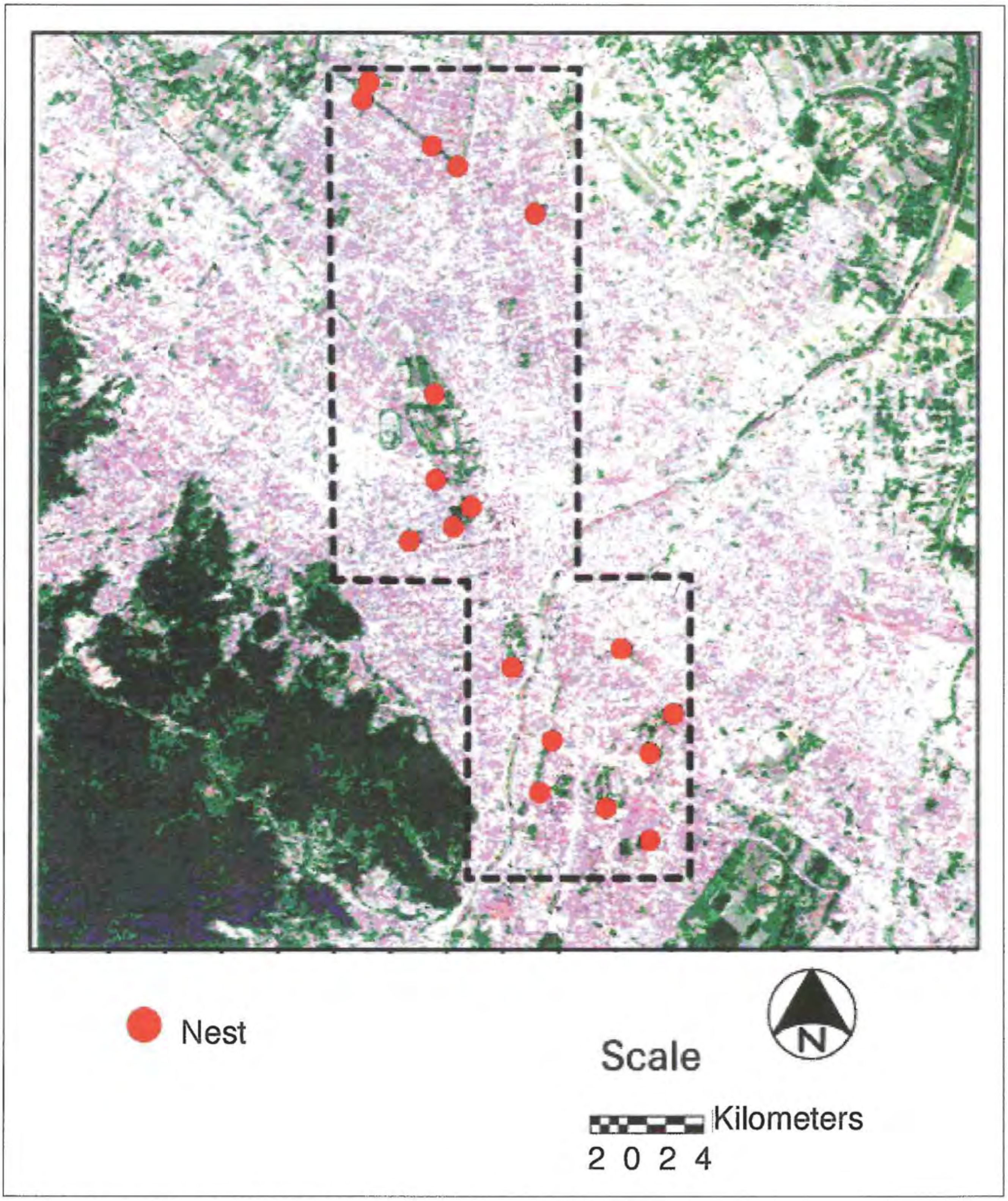


Fig. 3. Locations of the successful nest sites (the red circles) found in 1997 survey.

repeated this assignment the HSI score to all the pixels Pn in the map shown in Figure 2. Through these procedures, we drew a new picture, which has the scores HSI assigned to all the pixels in the map. In this study we employed these scores HSI for judging the habitat suitability of the circles Cn in the later analyses.

(4) From the home range data, we determined the threshold value of the habitat suitability index as the minimum wood lot area required for the successful breeding of a Great Spotted Woodpecker. With this HSI model, we extracted, by using GIS technology, the potential Great Spotted Woodpecker breeding habitats in the urban area of Sapporo City.

Results and Discussion

Status of the breeding Great Spotted Woodpecker in the urban area of Sapporo City

During the survey in 1997 in the urban area of Sapporo City, we found altogether 18 nest trees at the locations shown in Fig. 3 and their characteristics are listed in Table 1. The population densities were only 0.28 nests per 1 square km in the survey area. Nest tree species were 14, among which *Fraxius mandshurica* was 16.7 % or 3 out of 18 and was the largest in number (Table1). Planted exotic trees such as *Pinus densiflora*, *Larix leptolepis*, *Populus nigra* and *Chamaecyparis pisifera* were also utilized as a nest tree. The diameter at breast height (DBH), the tree height and the nest height were, on the average, 36.7 cm (20.6–55.4 cm), 11.2 m (4.8–11.5 m) and 5.1 m (1.1–11.5 m), respectively. As to the status of the nest trees, 22.2 % (4 out of 18) were dead trees. The average nearest-neighbor distance (NND) of the nest trees was 825 m (282–1,938 m). Five nest sites were found to be separated at more than 1 km distance from the nearest neighbor nest.

Application of the HSI model

(a) Evaluation of the urban area of Sapporo City with the HSI model.

From the average area of 29.1 ha (14.9–39.7 ha) of the home range of a successful Great Spotted Woodpecker pair in the nestling period (N. KOTAKA unpubl.), we assigned the value of 300 m to the radius r of the home range circle for the present HSI model (N. KOTAKA unpubl.). Then we applied the model to the wood lot map (Fig. 4) of Sapporo City obtained from the Landsat picture and listed the scores of all the hypothetical home range circles in the map. We assigned the HSI value of 75 (corresponding to wood lot density of *ca.* 23.8 %) as the threshold value, which is the minimum score or the minimum wood lot area included in the home range where we actually recognized a breeding Great Spotted Woodpecker (N. KOKATA unpubl.). Then we assigned all the circles Cn with the score larger than 75 as the Great Spotted Woodpecker suitable breeding habitats as shown in Fig. 5.

Table 1. Estimated potential breeding habitat, HSI score for each nest and nest tree characteristics

Estimated Potential Breeding Habitat	Area (ha)	tree species	tree height	DBH	nest height	dead or alive	HIS
Tonden Nishi Park	19.5	*Juglans ailanthifolia*	6.6	33.6	2.0	alive	80
		Populus nigra	20.0	53.9	14.0	alive	85
Tonden Popula Dori Park	14.1	*Fraxinus mandshurica*	18.0	55.4	11.5	dead	79
		Fraxinus mandshurica	7.1	21.8	5.6	dead	80
Hinomaru Park	8.8	*Salix babylonica*	6.6	28.6	3.5	alive	76
Hokkaido University and Botanic Garden	207.4	*Acer mono*	7.8	43.0	4.7	alive	141
		Larix leptolepis	15.0	28.0	2.5	alive	79
		Morus binbycis	10.5	46.0	7.7	alive	133
		Kalopanax pictus	15.0	68.0	7.7	alive	147
The Official Residence of the Governor	12.2	*Prunus sargentii*	9.5	36.7	1.1	alive	83
Nakajima Park	47.7	*Pinus densiflora*	7.3	21.4	3.2	alive	106
Toyohira Park	18.4	*Ailanthus altissima*	15.0	38.9	5.1	alive	106
Shoujin River Side Park and Hiragishi Semetary Park	117.0	*Ailanthus altissima*	8.5	52.0	6.2	dead	81
		Fraxinus mandshurica	12.0	28.5	5.0	alive	93
		Prunus sargentii	11.5	31.8	4.6	alive	132
		Chamaecypairs pisifera	16.0	28.0	4.5	alive	105
Tukisamu Park	84.0	*Acer japonicum*	4.8	25.5	2.3	dead	134
Nishioka Chuo Park	23.9	*Prunus mazimowiczii*	10.7	20.6	3.6	alive	82
Sumikawa Park	13.1						
Yurigahara Park	6.8						
Daigakumuranomori	2.3						

According to the above procedures, we assigned 14 locations as the breeding suitable habitats in the urban area of Sapporo City (Table 1). All of the nest sites found in the year 1997 survey can be superposed onto the breeding suitable habitats defined in this HSI model. At three locations among the 14 locations defined in the HSI model, we could not find active nest trees during the 1997 survey. However, we recognized the Great Spotted Woodpecker and/or found abandoned nest holes in these three locations. Because this survey was limited only one year in 1997, we expect a rather high possibility of finding active nests in later surveys on these three locations.

Among the 14 breeding suitable habitats deduced in this HSI model, 12 were found in the City Parks, two in the Campus of Hokkaido University and the remaining one around the official residence of the Governor and the Museum of Modern Art (Table 1). Conceivably, these areas have fortunately escaped from deforestation by the activities of housing site developers and thus relatively good environment has been preserved as the Great Spotted Woodpecker breeding suitable habitats. However, the actual number of active nests in each suitable habitat is 0 to at most 4, which fact indicates that in the urban area of Sapporo City the Great Spotted Woodpecker breeding communities are severely fragmented into small localized groups.

Among the pixels of actual nested sites being recognized during this survey, the lowest HSI score was 76 found at Hinomaru Park and the largest, 147 found at Hokkaido University Botanical Garden. In the present HSI model, the score = 1 corresponds to the forest area of 0.09 ha. Thus in Hinomaru Park, deforestation of as small as 0.09 ha within the circle of 300 m radius around the nest tree will make the Great Spotted Woodpecker breeding impossible (Fig. 6). Similarly, deducing from this HSI model, we speculated that for the 9 active nest sites, 50 % of those found during the year 1997 survey, deforestation of more than 1 ha (that accounts to the HSI score of –11.1) in the 300 m circle around the nest tree made the Great Spotted Woodpecker breeding impossible.

In this study, we constructed a habitat suitability index (HSI) model from the home range data of Great Spotted Woodpecker obtained through our fieldwork and the remote sensing technique and compiled on geographic information systems (GIS) database. Then, applying this

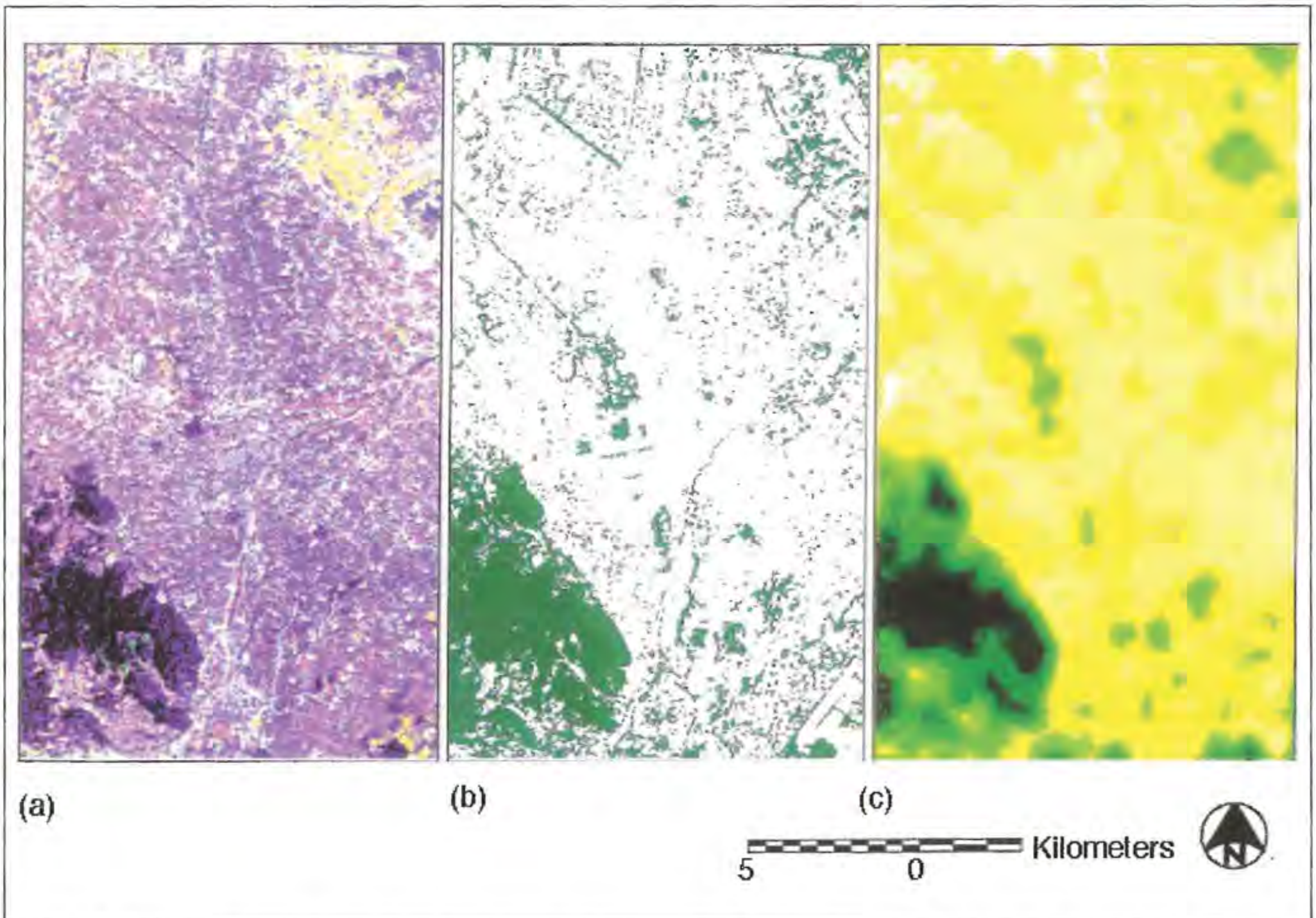


Fig. 4. (a) A Landsat true color image, (b) a wood lot map which was constructed from the satellite picture (a) and (c) an HSI map was drawn by applying the model on the wood lot map (b).

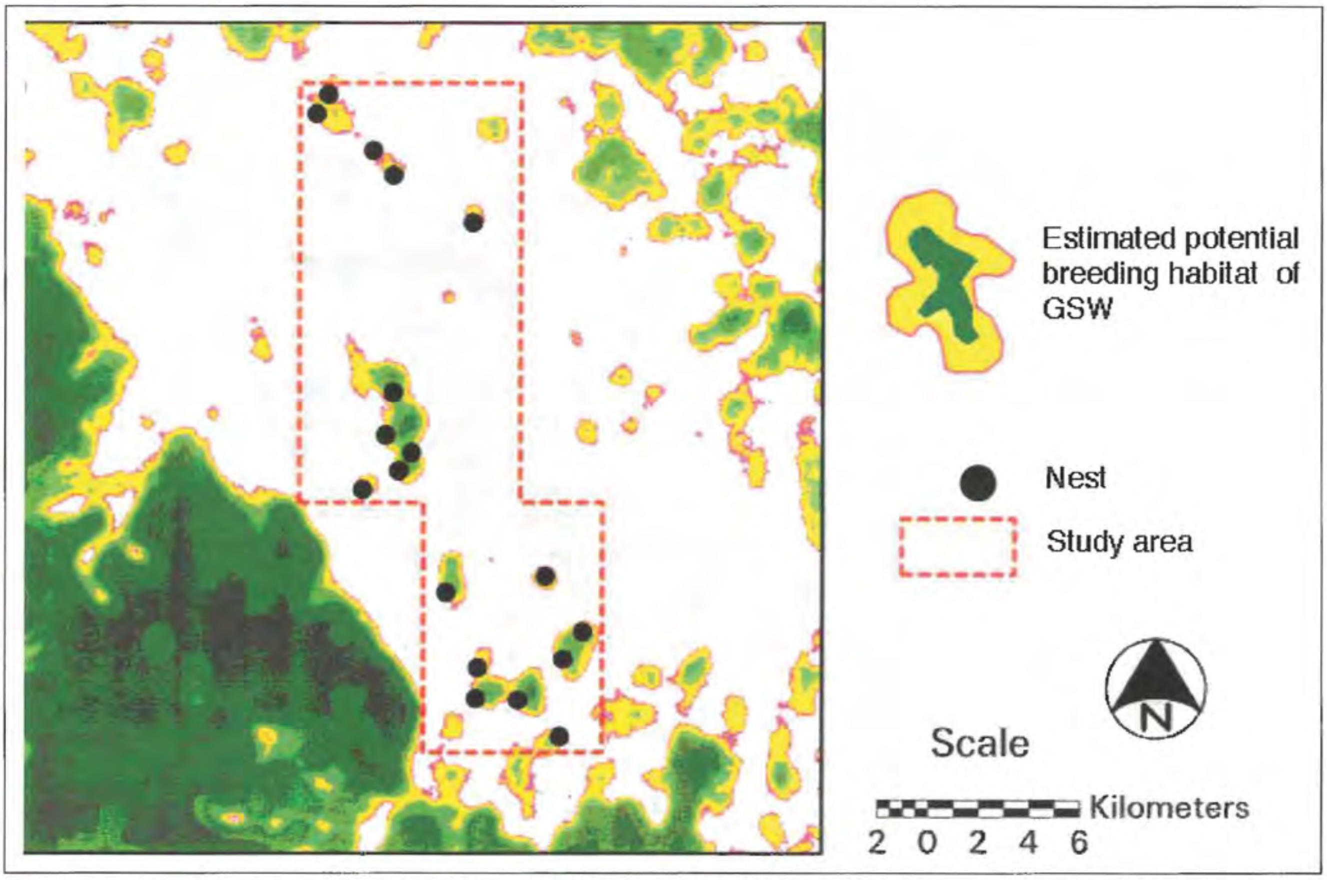


Fig. 5. Estimated potential breeding habitat of Great Spotted Woodpecker and the locations of successful nest sites.

Fig. 6. Location of the nest site in Hinomaru Park.

HSI model to the urban area of Sapporo City, we were able to evaluate the Great Spotted Woodpecker habitat suitability of the area, in which the habitat suitable wood lots had been fragmented and distributed in a complex mosaic shape. This model is indeed a simple model but, we believe, very well represents the complicated features of the spatial distribution of habitat suitable forests and the present status of the potential Great Spotted Woodpecker breeding habitat area. Moreover, by conducting a long-term monitoring and simulation based on the appropriate HSI model, we can assess and evaluate the changes in the habitat suitability induced by environmental management including forestation and/or deforestation.

Acknowledgements

We thank Ms. Takada Yukiko, Mr. Kadoya Shigemasa, Sakai Tomotake and Koroishi Takuya for their help in the field. Dr. Yugo Ono Yuzo Fujimaki and Tadao Kotaka kindly revised an earlier version of the manuscript. Mr. Masami Kaneko provided us facilities to carry out analysis with GIS. Thanks also to Dr. Peter Pechacek and Petra Welz, who suggested many improvements to the manuscript.

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Distribution and habitat preferences of the Three-toed Woodpecker in Šumava National Park

Verbreitung und Habitatpräferenzen des Dreizehenspechts im Nationalpark Šumava

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Abstract

Even though the Three-toed Woodpecker *Picoides tridactylus* is a typical inhabitant of the Sumava mountains it has not been studied systematically there. Our aims were to describe its occurrence and habitat preferences in this region. Because we used recorded playback to attract birds, we were also interested in the response of this species to playback experiments. We determined the presence of Three-toed Woodpeckers in two different areas in the highest parts of the Sumava mountains: Březník (5 km^2), Horská Kvilda (4 km^2). Square grids 500 x 500 m were established at these sites, and recordings of woodpecker calls or drums were continuously played at designated points for five minutes. This fieldwork was conducted at three week intervals for an entire year (April 2000–March 2001). Four pairs of Three-toed Woodpeckers were found in Březník and only one pair in Horská Kvilda. From the distribution of single records it is clear that this species prefers patches of forest that have been attacked by bark beetles. The Three-toed Woodpecker occurred in healthy forests only during the non-breeding period. Response to playback varied seasonally, being weak and infrequent during the non-breeding period except September to November, and becoming intense and frequent during the breeding season (May–July). Males seemed to respond more frequently to playback, although the difference was not statistically significant.

Obwohl der Dreizehenspecht zu den typischen Vogelarten der Sumava Berge gehört, wurde er hier noch nicht systematisch untersucht. Daher war unser vorrangiges Ziel, sein Vorkommen zu beschreiben und die bevorzugten Habitate zu finden. Da wir mit einem Kassettenrecorder gearbeitet haben, um Vögel anzulocken, haben wir außerdem Daten zu den Playback-Versuchen gewonnen. Das Vorkommen wurde in zwei unterschiedlichen Gebieten in den höchst gelegenen Bereichen der Sumava Berge durchgeführt: Březník, 5 km^2; Horská Kvilda, 4 km^2. Dort wurden Untersuchungsquadrate von 500 x 500 m angelegt. Eine Aufnahme von Rufen oder Trommeln wurde an jedem Punkt für fünf Minuten abgespielt. Die Feldarbeit wurde das ganze Jahr in dreiwöchentlichen Abständen durchgeführt. Vier Dreizehenspechtpaare wurden in Březník und nur eines in Horská Kvilda gefunden. Die Verteilung der einzelnen Beobachtungen machte es deutlich, dass Dreizehenspechte vor allem den durch Borkenkäfer befallenen Wald bevorzugten. Im gesunden Wald kamen sie nur außerhalb der Aufzuchtsperiode vor. Die Reaktionen auf die Klangattrappen waren saisonal unterschiedlich. Außerhalb der Brutzeit mit Ausnahme von September bis November wurde eine schwache und wenig häufige Reaktionsbereitschaft festgestellt. Dagegen war die Reaktion während der Brutzeit (Mai–Juli) intensiv und häufig. Männchen schienen stärker zu reagieren als Weibchen, der Unterschied war allerdings nicht signifikant.

Introduction

The Three-toed Woodpecker *Picoides tridactylus* is characterised as an uncommon but regular breeder in the mountain spruce forests in Sumava National Park, Czech Republic. It likely spread to this region from the Alps after the last glacial period because it does not

Three-toed Woodpecker **(Photo: Peter Pechacek)**

breed in any other Bohemian mountains (PECHACEK 1994).

Although this species is a unique resident to this part of the Bohemian Mountains, no systematic field study has been conducted in this region. All published data are based on occasional observations (HUDEC et al. 1983), or were written using a descriptive, non-scientific approach (ANDRLE 1978, 1984). The only source of information on the distribution of the Three-toed Woodpecker in the Czech Republic is a national map of breeding bird distributions (ŠŤASTNÝ et al. 1997)

The lack of detailed information regarding this species determined the main aims of our work.

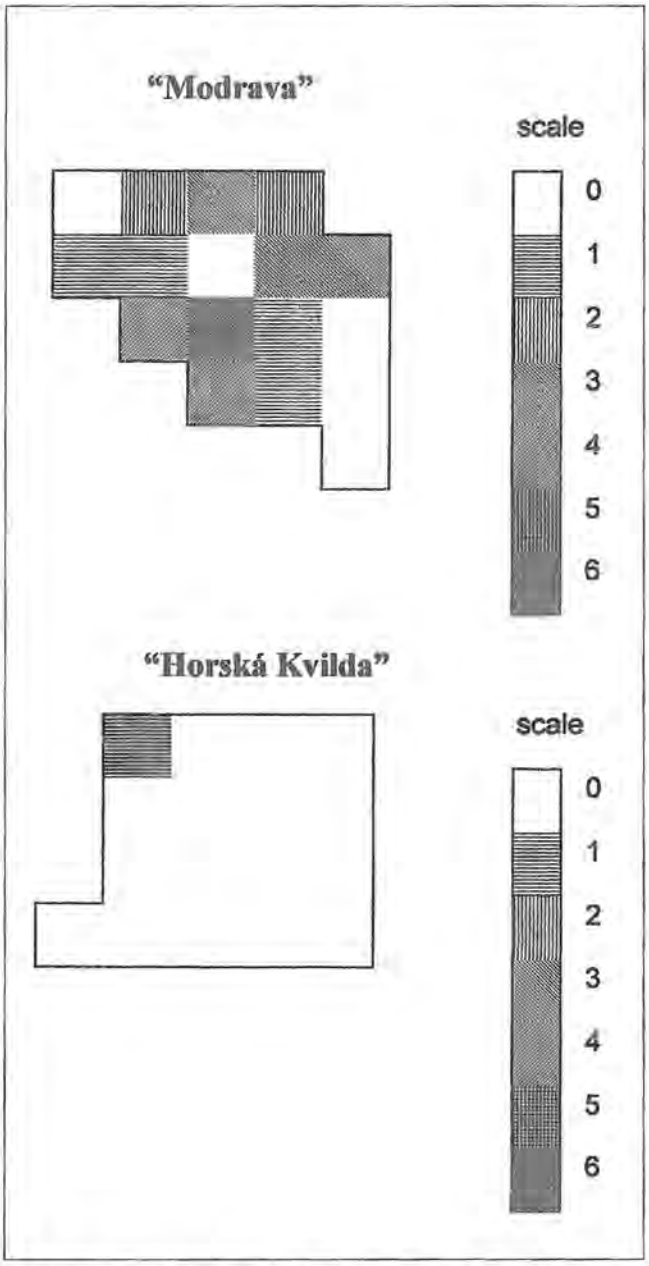

Fig.1. Number of the Three-toed Woodpeckers *Picoides tridactylus* recorded throughout the year in both model areas.

1) Determine the distribution of the Three-toed Woodpecker in Sumava National Park
2) Verify habitat preferences of the Three-toed Woodpecker in this region, and compare the results with those from the other parts of this species' range.
3) Determine variation in the response of this species to playback.

Methods

Transect counts

Transect counts were conducted in order to provide basic information about the distribution of Three-toed Woodpeckers in the Sumava National Park (N 48°50' – 49°10', E 13°–14°). Fourteen routes totalling more than 150 km were established across a broad area from "Železná Ruda" to "Borová Lada". Transect counts were carried out on the 4-5th March 2000. On each route, five minutes were spent at every 500 m interval, and playbacks of calls/drumming were played during the five minute period.

Mapping woodpecker distributions on model areas

We have two model areas where we conducted year-round research. One site was an 4 km^2 area east of the village "Horska Kvilda" (elevation 1,000–1,150 m a.s.l.). The second site was a 5 km^2 area, situated 7.5 km south of the village "Modrava" (elevation 1,130–1,350 m a.s.l.). These areas differed in the general health of the forests there. At "Horska Kvilda" the forest is generally healthy, but at "Modrava", nearly all the trees are dead because of a bark beetle *Ips typographus* infestation.

At each site, we made a square grid (square size 500 x 500 m, 17 squares – see Fig. 1). In the centre of each square, recordings of Three-toed Woodpecker calls and drumming were played for five minutes. Each area was visited every 3 weeks for an entire year (from 8.4.2000 to 27.3.2001).

Description of the habitat in the model areas was based on satellite photos received from the Šumava National Park Administration. They show the health conditions of these forests in 1995 and 1998. We defined a mean degree of wood damage for each square on both model areas from them (Fig. 2). The scale of damage has six degrees (1 healthy tree… 6 dead trees).

Results and Discussion

Transect counts

We found only eight Three-toed Woodpeckers across 150 km of surveys. Four of the sitings were located near

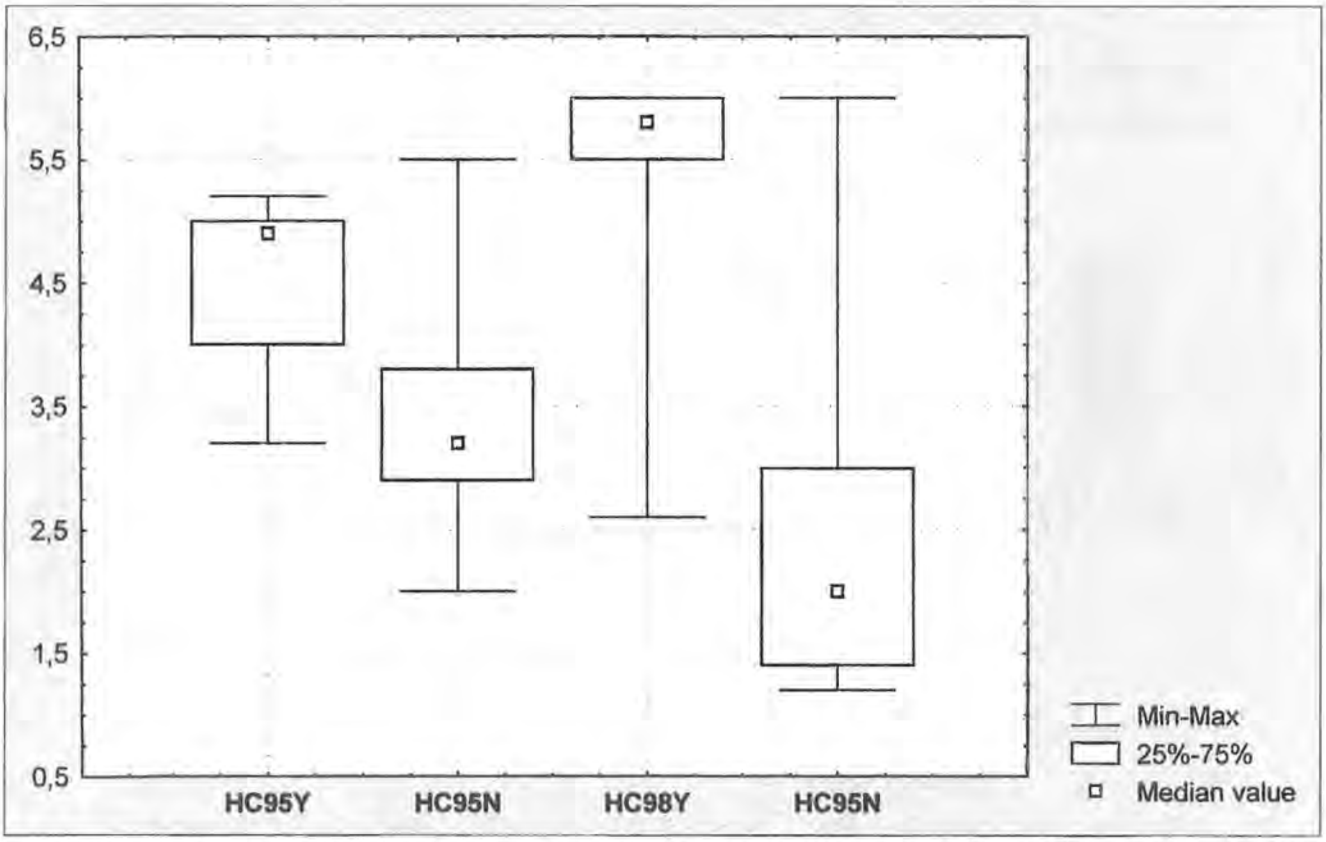

Fig. 2. Changes in forest health condition for individual squares of the model areas between 1995 and 1998 with (Y) or without (N) records of the Three-toed Woodpecker *Picoides tridactylus* in 2000.

the forests at "Horska Kvilda"; the others were distributed over the whole area. With the exception of one individual, all sitings were at elevations over 1,000 m.

There are two possible explanations for the scarcity of Three-toed Woodpeckers across the transect area. The counting date was based on varied information (HUDEC et al. 1983) about the vocal activities of the Three-toed Woodpecker. According to our results from playback experiments (conducted after transect counts were conducted) we now know that the maximum vocal activity is between April and June. Another reason could be the concentration the Three-toed Woodpecker population in areas of trees affected by the bark beetle outbreak. Larvae of the bark beetles (Scolytidae) are an important food source for the Three-toed Woodpecker (NEUFELDT 1958, CRAMP 1985).

The bark beetle outbreak area is situated near the border with Germany. The infestation began about 10 years ago, and the afflicted area is now approximately 50 km^2 (less then 10 % of total Park area). Transects did not include this area. It was sufficiently covered by a study plot for mapping. If we can rely on the results of transect counts; the distribution of the Three-toed Woodpecker in the Sumava mountain range is very unbalanced. These results differ from the published ones. According to HUDEC et. al. 1983 "the three-toed woodpecker is known from the whole Sumava mountains and it is frequent on some places". ŠŤASTNÝ et al. (1986) declared confirmed or probable breeding from 16 mapping squares (each 10 x 12 km). The differences support our hypothesis that Three-toed Woodpecker population is concentrated in areas affected by bark beetle outbreak. This could be due to the increase in food availability in these infested areas, or/and because of decreasing number of damaged or destroyed trees in other areas due to preventative forestry measures.

Mapping on model areas

The number of the Three-toed Woodpeckers recorded throughout the year at both sites is shown in Fig. 1. The absence of the Three-toed Woodpecker in the area "Horska Kvilda" may be explained by the absence of trees infested by bark beetles. Fig. 2 shows the changes in the health-conditions of the trees at both sites during the years 1995–1998. At the "Modrava" site "the number of damaged and dead trees increased. (Wilcoxon test, p = 0,000438). However, at "Horska Kvilda" the number of damaged and dead trees decreased (Wilcoxon test, p = 0,00039). This decrease in damaged and dead trees at "Horska Kvilda" is due to the removal of those trees from the area (excepting the first zone of the national park) as a prevention measure. Three-toed

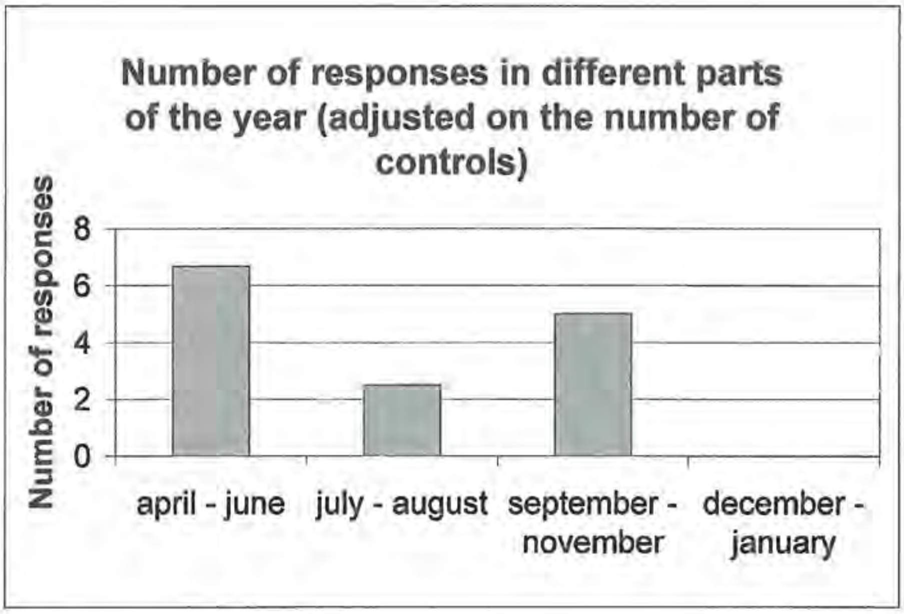

Fig. 3. Response of the Three-toed Woodpecker *Picoides tridactylus* to play-back experiments throughout the year.

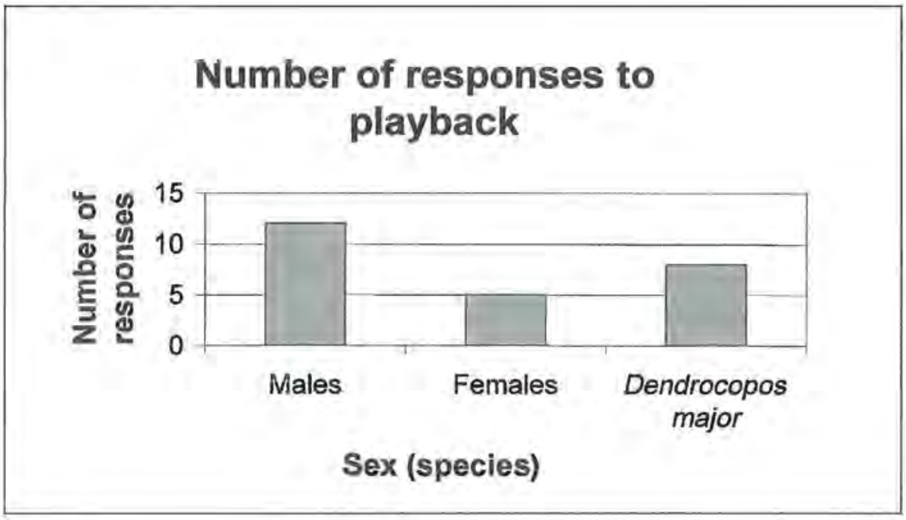

Fig. 4. Response of the Three-toed Woodpecker *Picoides tridactylus* to play-back experiments by sex.

Woodpecker is heavily dependent on dead or decaying trees. This dependence is connected with its requirements for foraging microhabitats. According to HOGSTAD (1971) from 270 spruces where the three-toed woodpecker foraged 247 were dead, 17 were dying, and only 6 were living. The proportion of dead trees in the forest could be relatively low. 20–40 trees with a diameter of 40 cm per 1 ha is enough (PECHACEK 1995). Our results suggest a stronger dependence on large concentrations of dead trees. The causes could be due to the increase in food availability in infested areas, or/and because of decreasing number of damaged or destroyed trees in other areas due to preventative forestry measures.

Playback experiments

Playback responses of the Three-toed Woodpecker to calls or drumming were nearly equal in frequency. The frequency of responses to playback exhibited two peaks during the year-long study period (Fig. 3). The first peak corresponds with the breeding period, and the second peak occurred at a time when young birds were dispersing. During this time, territorial conflicts between old and young males are likely to occur. A similar increase of territorial behaviour in autumn was described for other sedentary birds such as owls (CRAMP 1985). The number of the responses according to sex is shown in Fig. 4. Although differences between the sexes were not significant, males responded with slightly higher frequency. An unexpected result was the frequent response of the Great Spotted Woodpecker *Picoides major* to Three-toed woodpecker calls and drums. This result may indicate some inter-specific territoriality between these two species where they coexist.

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Woodpecker distribution and abundance along a vertical gradient in the Pol'ana Mts. (Central Slovakia)

Verbreitung und Abundanz der Spechte entlang eines Vertikalgradienten von Pol'ana Gebirge (Mittelslowakei)

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Abstract

The breeding distributions of nine woodpecker species were evaluated along a 10 km vertical gradient on south-southwest exposed transects from (460 to 1,458 m a.s.l.) in Pol'ana Volcanic Biosphere Reserve. Five main habitats were investigated (four forest types, older than 90 years: oak 460–650 m a.s.l., beech 750–900 m, mixed beech-fir-spruce 900–1,250 m, and natural spruce 1,250–1,458 m; as well as traditional farming orchards with solitary standing houses 480–850 m a.s.l.) during four checks surveys in April–May 1995 and 1999. Abundance was estimated by mapping territories on transects in each habitat (forest = 50 ha) in each type and in orchards = 300 ha). The Great Spotted Woodpecker *Picoides major* was the most frequent and abundant woodpecker in forests at all elevations. Its abundance decreased with altitude and forest type from 11 pairs/100 ha (oak forests) to 3.7 pairs/100 ha (spruce forests). The Syrian Woodpecker *Picoides syriacus* was the only species that bred exclusively in old, traditional farming orchards, usually near houses (mean = 2.5 pairs/100 ha at 480–850 m a.s.l.). Wrynecks *Jynx torquilla* (6.2 pairs/100 ha, resp. 2.5 pairs/100 ha) and Green Woodpeckers *Picus viridis* (1.2 pairs/100 ha, resp. 0.7 pairs/100 ha) were concentrated mainly at the foot of the volcano in orchards and oak forests (460–850 m a.s.l.). The Middle Spotted Woodpecker *Picoides medius* also visited the same areas where Wrynecks and Green Woodpeckers were commonly found, from neighbouring areas, but its breeding was not documented. White-backed Woodpeckers *Picoides leucotos*, Grey Woodpeckers *Picus canus*, and Black Woodpeckers *Dryocopus martius* were most frequently found in beech- and mixed beech-fir-spruce forests, but bred in all forest types and altitudes of the study area. Lesser Spotted Woodpeckers *Picoides minor* bred only in orchards, oak, and beech forests, but also regularly visited higher elevation habitats outside of the breeding period. The Three-toed Woodpecker *Picoides tridactylus* is associated with spruce and fir forests and preferred these higher elevation forest types where it occurred sympatrically with the Great Spotted Woodpecker. Mean density of woodpeckers in forests decreased with increasing altitude with 17.5 pairs/100 ha (total mean abundance) in oak forest (460–650 m a.s.l.), 14.5 pairs/100 ha in beech forest (750–900 a.s.l.), 12.7 pairs/100 ha in mixed beech-fir-spruce (900–1250 a.s.l.), and 7.5 pairs/100 ha in natural spruce forests (1,250–1,458 a.s.l.). Seven species inhabited oak forests, whereas five species bred in the other three forest types and in orchards. Woodpecker density in traditional farming orchards was similar to that found in oak forests, although diversity was slightly lower. Altitudinal distributions of nine woodpecker species were analysed, and the importance of all associated habitats for woodpeckers was compared to data from Central Europe. Species replacement across an altitudinal/habitat gradient is considered, and the role of woodpeckers as indicators in various habitats is discussed.

Brutverbreitung und Abundanz von neun Spechtarten wurde entlang eines 10 km langen Vertikalgradienten in einem S-SW exponierten Transekt von 460 bis 1458 m ü. NN in Biosphärenreservat Pol'ana analysiert. Die fünf wichtigsten Habitate wurden untersucht (vier Waldhabitate älter als 90 Jahre: Eichen- 460–650 m ü. NN, Buchen- 750–900 m ü. NN, gemischte Buchen-Tannen-Fichten- 900–1250 m ü. NN und naturnahe Fichtenwälder 1250–1458 m ü. NN sowie alte Streuobstgärten 480–850 m ü. NN), alle während vier Kontrollgängen in April–Mai 1995 und 1999. Die Spechtabundanz wurde mit Hilfe einer Revierkartierung entlang der Transekte in Wäldern (jede Transektfläche 5000 x 100 m = 50 ha) und in Obstgärten (300 ha) ermittelt. Der Buntspecht war die am häufigsten vorkommende Waldspechtart entlang des vertikalen Gradienten. Seine durchschnittliche Abundanz sank parallel mit der Meereshöhe und Waldtyp von 11 Paaren (Eichenwälder) bis 3,7 Paare/100 ha (Fichtenurwald). Der Blutspecht repräsentierte die am höchsten spezialisierte Art und brütete nur in Streuobstsiedlungen, gewöhnlich in der Nähe der Häuser (durchschnittlich 2,5 Paare/100 ha, 480–850 m ü. NN). Wendehals (6,2 Paare/100 ha, resp. 2,5 Paare/100 ha) und Grünspecht (1,2 Paare/100 ha, resp. 0,7 Paare/100 ha) brüteten hauptsächlich auf dem Gebirgsfuß in Obstgärten und Eichenwäldern (460–850 m ü. NN). Der Mittelspecht besuchte diese Habitate vom benachbarten Gebiet, doch es wurde kein Brutnachweis gefunden. Weißrücken-, Grau- und Schwarzspecht waren charakteristische Brutarten in Buchen- und gemischten Buchen-Tannen-Fichtenwäldern, die in allen Waldtypen und Meereshöhen im Gebiet brüteten. Der Kleinspecht brütete nur in Obstgärten, Eichen- und Buchenwäldern. Er besuchte jedoch außerhalb der Brutperiode regelmäßig auch höher lokalisierte Habitate. Der Dreizehenspecht war an das Vorkommen der Fichte und Tanne gebunden und bevorzugte höher lokalisierte Waldtypen, wo er neben dem Buntspecht zu den dominanten

Spechtarten gehörte. Die durchschnittliche Abundanz der gesamten Spechtgemeinschaft nimmt mit der wachsenden Meereshöhe von 17,5 Paare/100 ha in Eichen-, 14,5 in Buchen-, 12,7 in gemischten Buchen-Tannen-Fichtenwäldern auf 7,5 Paare/100 ha in den Fichtenurwäldern ab. Sieben Spechtarten brüteten in Eichenwäldern, in anderen drei Waldtypen und Obstgärten brüteten fünf verschiedene Arten mit einer auffälligen artspezifischen Abundanz. Die alten Streuobstgärten bildeten wichtige Habitate für die Spechte und ihre Abundanz ist dort ähnlich hoch wie in den Eichenwäldern. Die hypsometrische Verbreitung von allen neun Spechtarten wurde analysiert und die Bedeutung der studierten Habitate für die Spechte wurde mit den bekannten Angaben von Mitteleuropa verglichen. Die charakteristischen Begleitbrutarten in einzelnen Habitaten und Meereshöhen wurden erwähnt und die Rolle der Spechte bei der Bewertung der Habitatsqualität diskutiert.

Introduction

Forest structure and altitude are key factors influencing the distribution and abundance of animals (ZACH et al. 1995). In mountainous areas, species that overlap regionally may have differing distributions along elevational gradients (WIENS 1989). Bird communities are known to change in terms of species composition and abundance along altitudinal gradients (with their associated habitat gradients) (KRISTIN 1991, KROPIL et al. 1995). TERBORGH (1971) and ABLE & NOON (1976) found that species occurring at higher elevations had the broadest altitudinal amplitudes. VUILLEUMIER & EWERT (1978) suggested that the changes in community structure along an altitudinal gradient in the mountains of Venezuela were caused by major habitat or plant community changes, whereas DIAMOND (1986) attributed the abutting elevational ranges of related species to direct competition.

European woodpeckers are bark- and ground-foraging birds, mostly resident, which breed most often in trees with diameter more than 15 cm (CRAMP 1985). A spectrum of species and abundances can be found in various forest types (KRIŠTÍN 1993, KROPIL 1996a,b, PAVLÍK 1998, 1999a,b SANIGA 1990,1995). Density may also differs broadly within the same forest type and elevation, and are dependent on many microhabitat factors, (i.e. Great Spotted Woodpecker *Picoides major* –

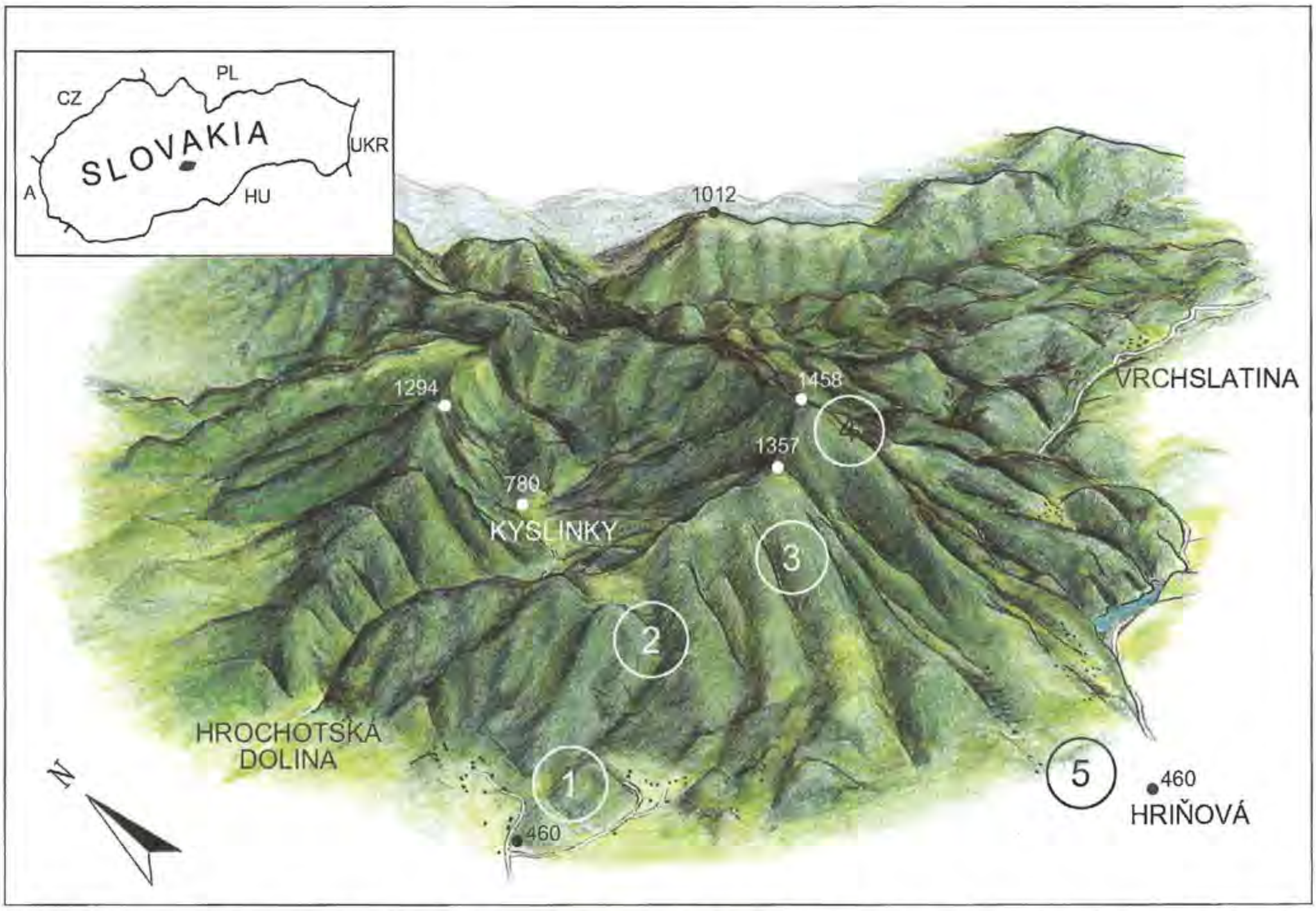

Fig. 1. Study area with study plots (1: oak, 2: beech, 3: beech-fir-spruce, 4: spruce forest, 5: orchards) and location within Slovakia.

PAVLIK 1999b). Many woodpecker species are somewhat specific in their preferences for a certain type of forest or altitude (i.e. Middle Spotted Woodpecker *Picoides medius* – PAVLIK 1996, KOSSENKO & KAYGORODOVA 1998, White-backed Woodpecker *Picoides leucotos* – PAVLIK 1999, Three-toed Woodpecker *Picoides tridactylus* – PACENOVSKY 1999). We expect that in different altitudinal ranges and vegetation types of the same area, woodpecker assemblages and abundances should differ.

The main goals of this project were to identify i) density of nine woodpecker species along an altitudinal vertical gradient that encompassed five habitats on one mountain, ii) the importance of four forested habitats and orchards as breeding habitat for woodpeckers.

Material and Methods

Breeding distributions of nine species of woodpecker were evaluated along a 10 km altitudinal gradient using five south-southwest exposed transects (5,000 x 100 m) that ran from 460 to 1,458 m a.s.l. in Pol'ana Volcanic Biosphere Reserve (Fig. 1). Five habitats were investigated: (1) oak forest (460–650 m a. s. l.), (2) beech forest (750–900 m a.s.l.), (3) mixed beech-fir-spruce forest (900–1250 m a.s.l.), natural spruce forest (1,250–1,458 m a.s.l.), (4) and traditional farming orchards with solitary standing houses (40–120 years old and 480–850 m a. s. l.). All forested habitats had been left undisturbed for at least 90 years and exhibited characteristics of interior forest. All habitats were censussed once in April and May of 1995 and 1999 (four times total). Each census lasted 3–4 hours, usually between 7 and 10 in the morning in favourable meteorological conditions (without rain and mist). All acoustic and visual registrations, nest findings, or other important data relating to bird presence were recorded onto maps during each visit. A territory was distinguished by either finding a nesting birds or observing nesting behavior. All territories were considered to have a breeding pairs (hereafter p). Territories with at least half of their area situated within the study plot were included in the total number of territories. Abundance was estimated by mapping territories on transects in each habitat (each forest type = 50 ha, and orchards = 300 ha). Mean density/100 ha (+ SE) was calculated for each species and for all woodpecker species present in each habitat type and altitude (see Fig. 3–7).

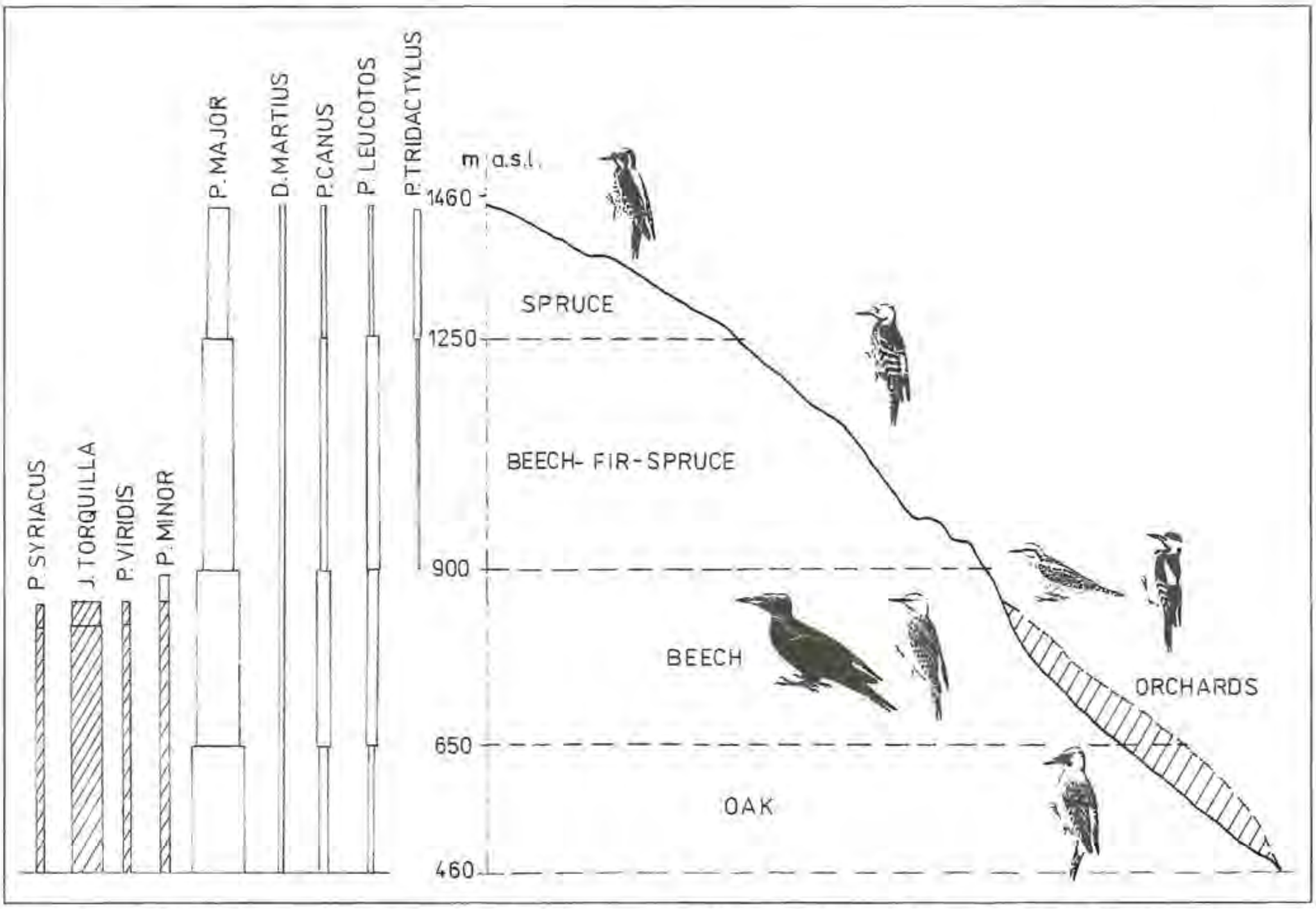

Fig. 2. Schematic distribution of nine woodpecker species between 460 and 1458 m a.s.l. in five habitats (width of bars = approximate abundance along vertical gradient; hatched bars = abundance in orchards (characteristic species are shown in each habitat).

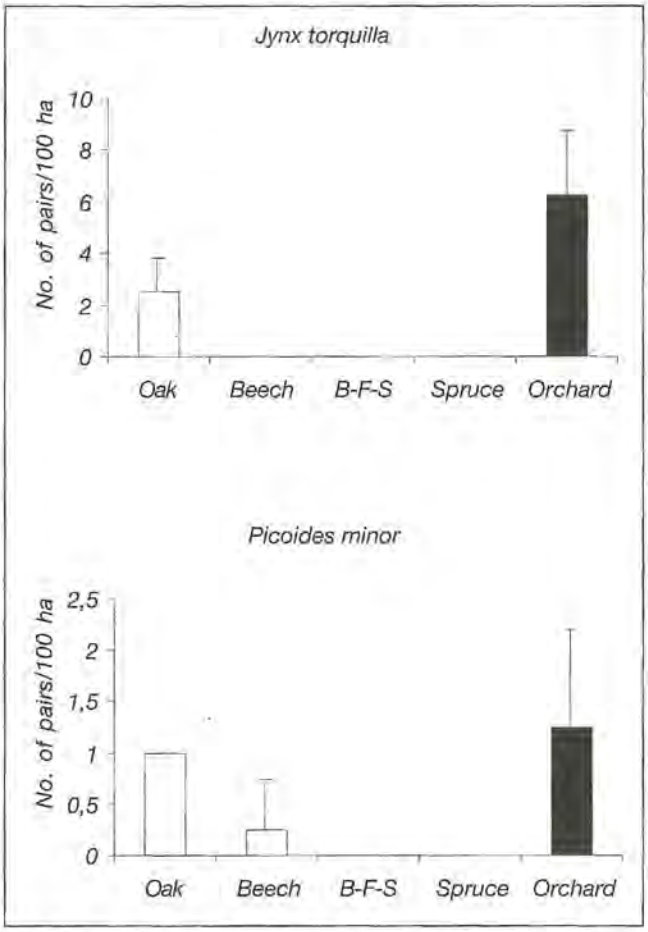

Fig. 3. Abundance (mean ± SE) of Wryneck and Lesser Spotted Woodpecker in studied habitats.

Results and Discussion

Mean woodpecker density decreased with increasing altitude in forested habitats, with 17.5/100 ha in oak, 14.5 p/100ha in beech, 12.7 p/100 ha in mixed beech-fir-spruce, and 7.5 p/100 ha in natural spruce forests. The Great Spotted Woodpecker was the most common species in these habitats, and it showed a similar trend in density ranging from (11 p/100 ha in oak forests to 3.7 p/100 ha in spruce forests, (Figs. 2 and 7). However, previous research indicates that the within habitat variation in density for this species is broad. For example, in 13 mature oak forests with various canopy and tree structure, density ranged between 0 and 5.3 p/10 ha (PAVLÍK 1999). So, for our purposes, it was very important to work in plots of similar age across all habitat types and altitudes (vegetation stages). Decreasing bird density from oak to spruce forests along altitudinal gradients is well established in various areas including other Slovakian primeval forests (85 p/10 ha in oak, 71 p/10 ha in beech, 63 p/10 ha in beech-fir and 53 p/10 ha in spruce forests (KROPIL et al.1995).

The Syrian Woodpecker *Picoides syriacus* was the only species in this study that bred exclusively within traditional farming orchards, usually near houses (Fig. 5). Its mean density (2.5 p/100 ha) was comparable to that found in urban and suburban parks in the town of Kosice (1–17 p/100 ha, MOŠANSKÝ & MOŠANSKÝ 1999).

The Wryneck *Jynx torquilla* (mean = 6.2 p/100 ha in orchards, resp. 2.5 p/100 ha in oak forest, Fig. 3) and the Green Woodpecker *Picus viridis* (mean = 1.2 p/100 ha in orchards, resp. 0.7 p/100 ha in oak forest, Fig. 4) were concentrated at the foot of the volcano (460–850 m a. s. l.) in orchards and oak forests. Mean density of Green Woodpecker in oak forests was similar in this study to studies in oak forests in Southern Slovakia (0.5 p/100 ha, PAVLÍK 1998). The Middle Spotted Woodpecker also visited study plots from neighbouring areas, but breeding was not documented. The White-backed Grey, and Black Woodpeckers were most frequently found in beech and mixed beech-fir-spruce forests (mean density 2.5, 1.5, and 1 p/100 ha respectively), but they bred in all forest types and altitudes of the study area (Fig. 4 and 6). In the oak forests of southern Slovakia, they reached a mean density 0.01, 0.7, and

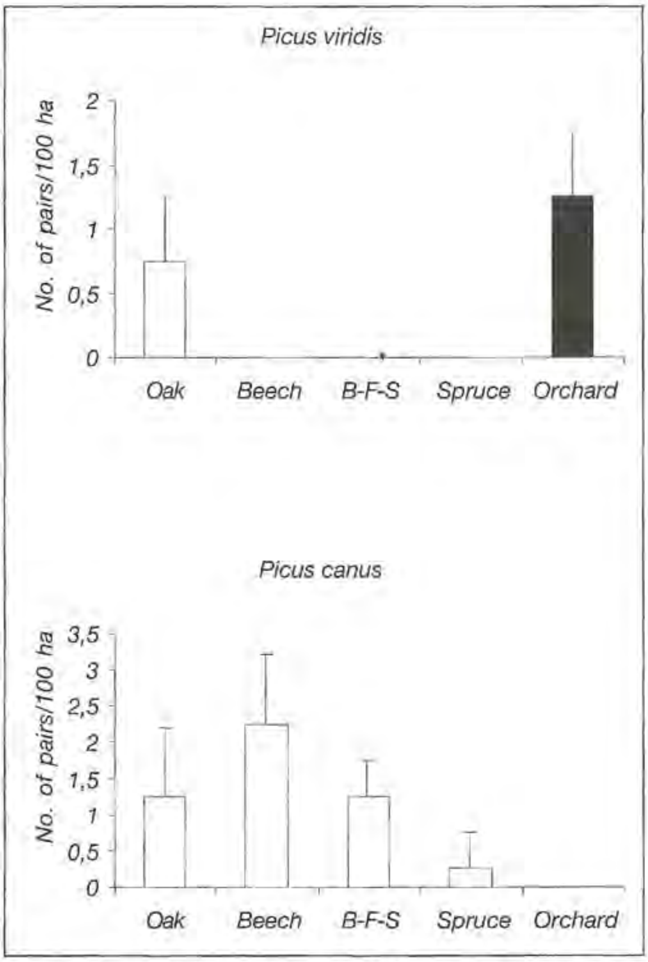

Fig. 4. Abundance (mean ± SE) of Green Woodpecker and Grey Woodpecker in studied habitats.

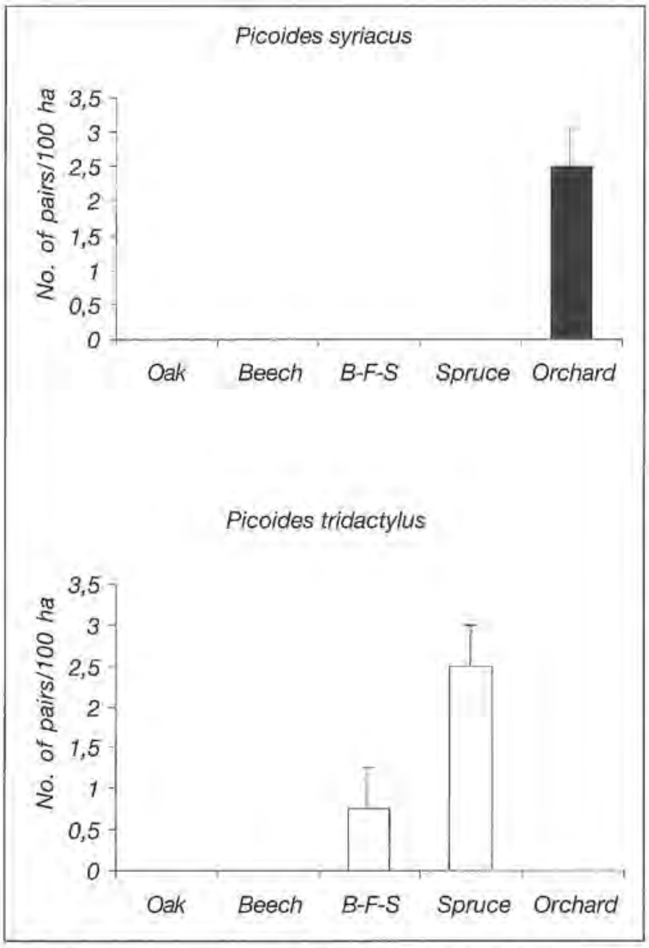

Fig. 5. Abundance (mean ± SE) of Syrian Woodpecker and Three-toed Woodpecker in studied habitats.

0.8 p/100 ha respectively (PAVLÍK 1998). The Lesser Spotted Woodpecker bred only in orchards, oak, and beech forests (Fig. 3), but also regularly visited higher elevation habitats outside of the breeding period. Its highest mean density was in orchards (1.2 p/100 ha). This is very low in comparison to other Slovakian forests, which were censused at smaller study plots than 20 ha (oak = 0.7 p/10 ha (PAVLÍK 1998), fir-beech = 0.4 p/10 ha (KROPIL 1996b), floodplain Danube forests = 0–1.2 p/10 ha (BOHUŠ et al. 1999). The Three-toed Woodpecker is connected with the distribution of spruce and fir forests in the study area, like in all areas of Europe. It prefers higher elevation forest types where it belongs beside Great Spotted Woodpecker as the dominant woodpecker species (Fig. 5 and 7).

Oak forest was the richest habitat for woodpeckers with seven breeding species. PAVLÍK (1998) found the same number of species in oak forests in his study, but his study area lacked Wryneck, which was replaced by Middle Spotted Woodpecker. This difference could be due to differences in forest structure. In the other three forest types and orchards, five different species with characteristic densities bred (Fig. 2). Traditional farming orchards were used extensively by many woodpecker species and had mean densities similar to those found in oak forests (Fig. 7).

In comparison with known data, it seems that some of the differences in woodpecker densities we observed could be caused by the use of different size of study plots. The majority of quantitative studies on woodpeckers were done on plots smaller than 20 ha with densities being calculated for 10 ha. We mapped territories in larger plots (50–300 ha). Mapping territories on smaller study plots may lead to overestimation of density because at small plots may be only part of territory. Furthermore, we expected that the number of species would decrease with increased altitude. This hypothesis was not supported by our data because five species were found in all vegetation stages above the oak forests.

Conclusions

i) Woodpecker density significantly decreased along a 10 km altitudinal gradient (Fig. 7).

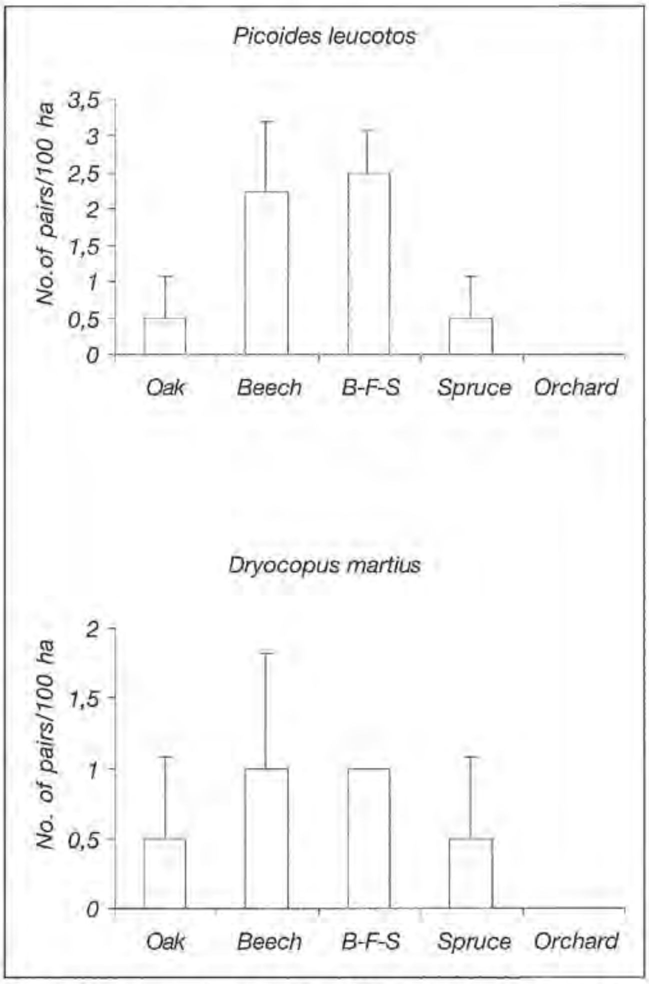

Fig. 6. Abundance (mean ± SE) of White-backed Woodpecker and Black Woodpecker in studied habitats.

ii) Number of breeding woodpecker species during April–May is relatively stable in each habitat, but each habitat has its own characteristic species (Fig. 2).

iii) Woodpeckers appear to be useful indicators forest change (in terms of species composition and relative abundance). Other species, besides woodpeckers, that seem to indicate some degree of habitat quality were:

Oak forests: *Oriolus oriolus* (5.8 pairs/100 ha), *Upupa epops* (1.2 pairs/100 ha), *Ficedula albicollis* (45 pairs/100 ha)

Beech forests: *Columba oenas* (8.5 pairs/100 ha), *Strix uralensis* (0.5 pairs/100 ha), *Phylloscopus sibilatrix* (3.8 pairs/100 ha)

Beech-fir-spruce forests: *Ficedula parva* (6.5 pairs/100 ha), *Tetrao urogallus* (0.8 males/100 ha)

Spruce forests: *Glaucidium passerinum* (0.7 pairs/100 ha), *Tetrao urogallus* (0.5 males/100 ha), *Turdus torquatus* (22pairs/100 ha)

Orchards: *Lanius minor* (9 pairs/100 ha), *Oriolus oriolus* (4.5 pairs/100 ha), *Turdus pilaris* (54 pairs/100 ha).

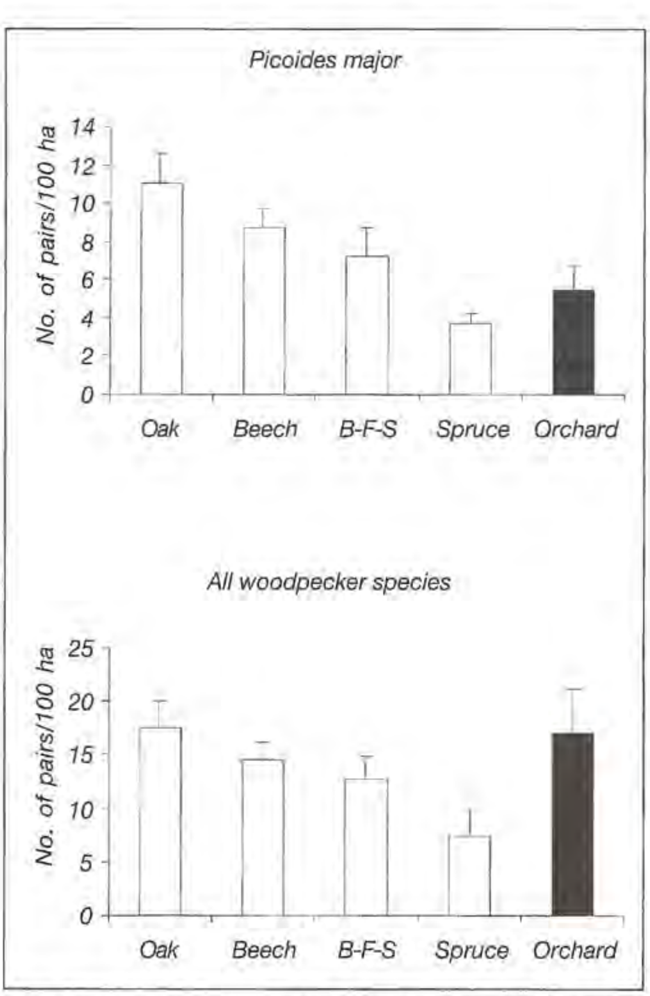

Fig. 7. Abundance (mean ± SE) of Great Spotted Woodpecker and of the total woodpecker breeding assemblage.

Acknowledgements

This research was partially supported by VEGA project No 2/7025/1999. I would like to thank J. Anderson and A. Styring for their help translating this manuscript and valuable comments.

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Age determination in woodpeckers

Altersbestimmung bei Spechten

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Abstract

Specimens of 3282 European woodpeckers were examined to assess flight-feather and wing-covert replacement patterns and their use in aging. Secondaries and primary coverts are retained in post juvenal moult. Typically adult post-breeding moult is not totally complete: some primary coverts and secondaries are retained. By combining retention patterns with differences in colour and shape pattern and relative wear between juvenal and adult feathers, most of the woodpeckers can be reliable aged through their third or fourth year of life; some individuals even into their fifth year.

Balge von 3282 europäischen Spechten wurde untersucht, um die Eignung des Musters beim Austausch von Flugfedern und Deckgefieder für die Altersbestimmung zu evaluieren. Armschwingen und das erste Deckgefieder bleiben beibehalten in der post-juvenilen Mauser. Die Mauser der Adulten nach dem Brüten ist normalerweise nicht vollständig: Einige Armschwingen und das erste Deckgefieder werden beibehalten. Anhand der Kombination des beibehaltenen Musters mit Unterschieden in Farbe und Form sowie mit dem Abnutzungsmuster zwischen den juvenilen und adulten Federn ist eine zuverlässige Altersbestimmung bis zum 3. bis 4., manchmal sogar bis zum 5. Lebensjahr möglich.

Introduction

Age of individuals is a central parameter in bird population ecology. This is because younger individuals have generally been shown to have a lower social status than older ones, which, in turn, has major consequences on their foraging efficiency, territory ownership, breeding success, extent and timing of dispersal, and ultimately habitat selection.

Earlier studies trying to differentiate first calendar year woodpeckers from older birds did not rely on wing moult patterns but rather on obvious traits such as head and eye colour and length of the 10th. (outermost) primary. As a result, ageing was not found possible once the post-juvenal moult had finished (HAARTMAN et al. 1967, BAKER 1980).

The post-juvenal moult is a partial moult: secondaries, primary coverts and some or all greater coverts and bastard wing remains unmoulted (STRESEMAN & STRESEMANN 1966, GEORGE 1972, GINN & MELVILLE 1983, CRAMP et al. 1985). This information has been used to age woodpeckers after the post-juvenal moult (GEORGE 1972, CRAMP et al. 1985, MIETTINEN et al. 1986) and ageing was said to be possible until first complete moult when woodpeckers are about one year old.

In the end of 1980s ringing activities in eastern Finland promoted the recapture of birds during consecutive years, allowing the continuous study of wing moult in birds older than one year old. Accordingly, it was always found possible to differentiate among three age groups: first/second calendar-year, second/third calendar-year and older than third/fourth calendar-year birds. At least in some individuals, it was also possible to age them as

Table 1. Number of studied woodpeckers in skin collections of: H = Helsinki, Finland, S = Stockholm, Sweden and C = Copenhagen, Denmark and number of catches in the fieldwork = F.

Species	H	S	C	F	Total
Eurasian Wryneck *Jynx torquilla*	–	88	50	8	146
Lesser Spotted Woodpecker *Picoides minor*	33	60	69	153	310
Middle Spotted Woodpecker *Picoides medius*	–	12	21	–	33
White-backed Woodpecker *Picoides leucotos*	24	29	28	37	118
Great Spotted Woodpecker *Picoides major*	157	146	215	1346	1853
Syrian Woodpecker *Picoides syriacus*	–	14	3	–	17
Three-toed Woodpecker *Picoides tridactylus*	64	88	50	25	227
Black Woodpecker *Dryocopus martius*	75	150	42	4	271
Eurasian Green Woodpecker *Picus viridis*	–	85	81	–	166
Grey-headed Woodpecker *Picus canus*	56	20	33	11	120
Total	409	653	644	1576	3282

third/fourth calendar year or as older than third/fourth calendar year. PYLE & HOWELL (1995) found that many woodpeckers in North America could be reliably aged through their third or fourth year of life.

In this paper age determination of 6 European woodpecker species, which either breed and/or winter in Eastern Finland, are discussed. Museum skin collections of some other European species (Wryneck, Green Woodpecker, Syrian Woodpecker and Middle Spotted Woodpecker [see Table 1 for scientific names]) were also examined and it seems probable that they can be reliably aged using the same criteria (see also CRAMP et al. 1985). Confirmation through study of captive or recaptured, known-aged birds is desirable. I would be interested in having information (description, photos) about woodpecker recaptures to assist in my preparation of an identification guide about woodpeckers.

Materials and Methods

Fieldwork was started in the autumn of 1981 and is continuing. Thus far I have made more than 1,500 captures. Woodpeckers were captured through the year. Breeding adults were captured from nests during summer, migrating birds were mist-netted at the Höytiäisen kanavan suiston bird-ringing station during summer and autumn, and at feeding places birds were mist-netted from autumn to spring. Animal fat (mainly pig) was provided at feeding places. Most of the field work was carried out in North Carelien, the eastern province of Finland.

During 1985–1989 skin collections of three museums were examined (Table 1). Specimen tag data, including sex, subspecies, date and location of collection, and any notation regarding age, were noted. Measurements taken included: wing-length (maximum method, see e.g. SVENSSON (1992), length of bill, and in live birds weight and length of tarsus.

On each specimen the flight feathers (primaries, secondaries, and tertials) and wing-coverts were carefully examined. Evidence of incomplete replacement and differences in colour pattern, shape and/or wear between juvenal and moulted feathers were recorded. Birds in active moult were noted, all retained flight feathers were aged and recorded by wing and position. At the museum skin collection usually only the outer seven primary coverts were analysed as examination of the inner coverts could not always be performed without risking damage to the specimens. However from individuals that were expected to belong to age-group 2Y (autumn)/3Y (spring) or older, all primary coverts were examined.

By considering all flight-feather information, each woodpecker was assigned an age code following the calendar-based system (SVENSSON 1992). Codes included: FL/+1Y/+2Y for a bird of unknown age; 1Y/2Y for birds in either first calendar year or spring of second calendar year (before first adult post-breeding moult), 2Y/3Y for birds after their first adult post-breeding moult either in autumn or in spring, 3Y/4Y for birds in their second adult post-breeding plumage, +2Y/+3Y for birds after their second adult post-breeding moult and +3Y/+4Y for birds after third adult post-breeding moult.

Table 2. Sample size of 2356 specimens of six European woodpecker examined, according to age-code assignment, and group categories of each species mainly according to primary coverts replacement patterns. On brackets number of controls recovered in the field (not included first figure).

Species	1Y/2Y	2Y/3Y	3Y/4Y	+2Y/+3Y	+3Y/+4Y	Unaged (FL/+1Y/+2Y)	Σ
Lesser Spotted Woodpecker *Picoides minor*	195	12 (1)	4 (2)	4 (1)	1	73	285 (4)
White-backed Woodpecker *Picoides leucotos*	69	5	1	12 (1)	– (5)	22	109 (6)
Great Spotted Woodpecker *Picoides major*	796 (14)	183 (30)	10 (22)	101 (7)	12 (24)	182	1284 (97)
Three-toed Woodpecker *Picoides tridactylus*	159	11	– (1)	1	1	52	224 (1)
Black Woodpecker *Dryocopus martius*	115	18	–	18	1	123	275
Grey-headed Woodpecker *Picus canus*	37	5	–	1	– (1)	27	70 (1)
Σ	1371 (14)	234 (31)	15 (25)	137 (9)	15 (30)	479	2247 (109)

Primaries (p1–p10) were numbered distally (outward or away from the body) and secondaries (s1–s11) proximally (inward or toward the body). Both wings were examined on birds of age-groups other than 1Y/2Y.

The main purpose of field work was to recapture woodpeckers of known age (ringed as nestlings or fledglings) or after the next moult. Through the end of March 2001 I had recaptured 109 woodpeckers of four species (Table 2).

Results and Discussion

Both juvenile and adult woodpeckers have a single annual moult that usually occurs in late summer and fall. In migratory species the moult can be suspended or protracted, active replacement continuing until the following winter, spring, or summer (REE 1974, VIKBERG 1974, PYLE & HOWELL 1995, WINKLER et al. 1995). Most woodpeckers follow the same sequence of flight-feather replacement. Replacement of the primaries starts with the innermost, p1, and continues in sequence to the outermost, p10. In some species, post-juvenal moult already begins in the nest and the first primaries are dropped before they have ever been used (RUGE 1969, WINKLER et al. 1995).

During adult post-breeding moult, replacement of the secondaries usually proceeds both distally and proximally from s8. In many individuals a second series of replacement proceeds proximally from the outermost secondary, s1, such that the last secondaries replaced are often s3 and s4. Just as often, such second replacement seems not to occur and the outermost secondary (s1) is the last replaced (GEORGE 1972, GINN & MELVILLE 1983, PYLE & HOWELL 1995). Often some secondaries are retained in the adult post-breeding moult.

Secondaries are usually all retained in the post-juvenal moult. All European woodpecker species we examined in the field or as museum skins usually retained secondaries. Very few exceptions were found and all of them had replaced one or two feathers accidentally on one wing (MIETTINEN et al 1986). According to the literature three species replace at least some secondaries: *Jynx torquilla, Picoides major and Picoides tridactylus* (CRAMP et al. 1985, LEHIKOINEN & NIEMELÄ 1985).

Both juvenile and adult woodpeckers replace only part of the wing coverts (GEORGE 1972, GINN & MELVILLE 1983, CRAMP ET AL 1985, MIETTINEN et al. 1986). Retained coverts in the post-juvenal moult include primary coverts, all or part of the greater coverts and alula, and some or none of lesser or median coverts. According to CRAMP et al. (1985), juveniles replace some of the primary coverts (2–4 outer ones), but I have not been able to confirm this.

During the post-breeding moult, adults usually retained a few primary coverts.

Determination of age of Great Spotted Woodpecker *Picoides major*

Of all birds examined during the last 20 years, 56 % were Great Spotted Woodpeckers (Table 1 and 2), and 14 % of them were not aged. Most of these birds were either handled by other ringers or data associated with the museum skin were inadequate. In practice during the last 15 years, all birds captured in the field were aged. Most (89 %) captured birds of known age were Great

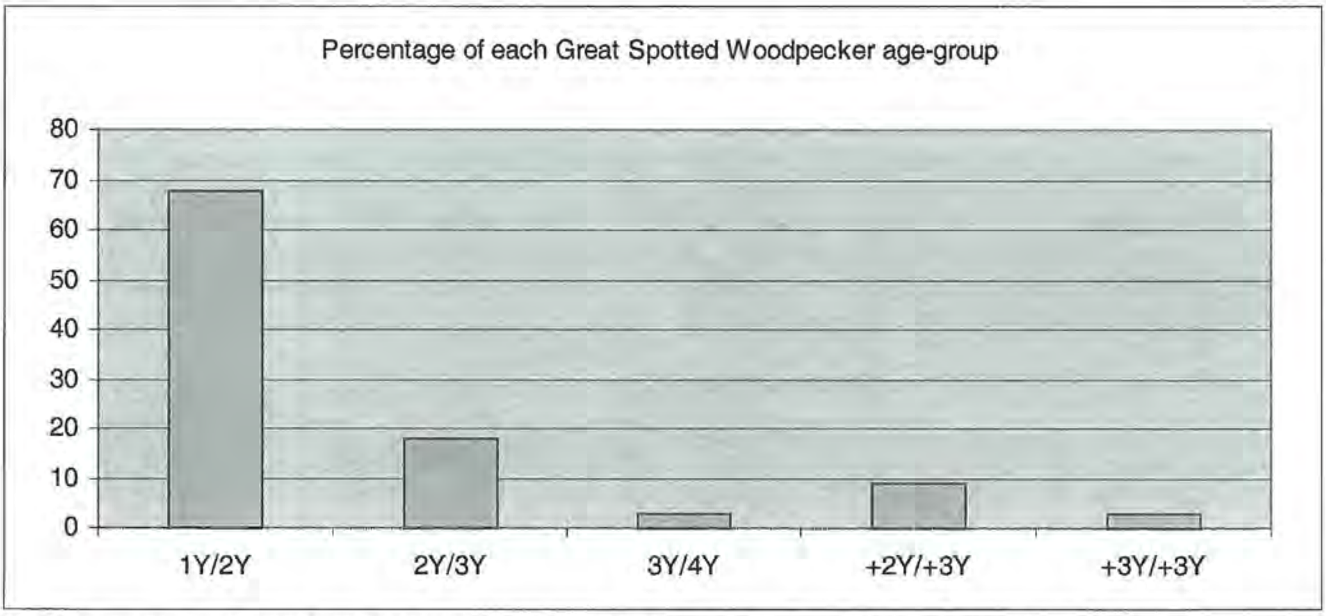

Fig. 1. Examined and aged Great Spotted Woodpeckers *Picoides major* (n = 1199) and proportion of each age-group (see also Table 2)

Spotted Woodpeckers (Table 2). In the summary of ageing criteria below, I use the Great Spotted Woodpecker as an example for ageing woodpeckers.

1Y (autumn)/2Y (spring)

After the post-juvenal moult there is usually a very clear contrast between retained, greyish-brown, wing coverts (all primary coverts, some or all great coverts and alula and some or none median and lesser coverts) and moulted black or blackish coverts. All secondaries are retained but contrast (colour or in wear) to replaced primaries is slight. Colour of the iris is brown or slightly reddish-brown until March or April (at least in Finland; HAARTMAN et al 1967, MIETTINEN et al 1986). According to CRAMP et al. (1985) iris colour could be the same as that of adults even during a bird's first summer. Findings with other species suggest that seasonal, sexual, and geographical variation should be better investigated (GEORGE 1972). I found that 67 % of birds examined (and aged) belonged to this age-group (Fig. 1, Table 2).

2Y/3Y

First adult post-breeding moult is not complete: middle primary coverts and usually some of the secondaries are retained. For example CRAMP et al. (1985) suggest that the adult post-breeding moult is complete, and that replacement of primary coverts is not simultaneous with primaries. Retained primary coverts usually include numbers 3 to 5 and these show very clear contrast in shape, wear, and colour. Juvenile coverts are pointed and narrower, more worn and browner than replaced ones. Shape contrast is clearest in inner ones (for example 1 or 2); primary coverts tend to become more pointed in more distal feathers. Hence differences are much more difficult to see on distal coverts. Retained juvenal secondaries are usually clearly browner and often more worn and bleached than replaced feathers. White spots on the outer web of typical juvenal secondaries are closer to the feather tip. The difference is about 2–5 mm and usually on lower spots it is even greater. Usually spots on adjacent feathers form a kind of line across the secondaries. These lines are not straight on second/third calendar-year birds. About 18 % of Great Spotted Woodpeckers I examined were from this age-group (Fig. 1, Table 2).

+2Y/+3Y

The second adult post-breeding moult is very rarely complete. A bird that has replaced all primary coverts and all secondaries can be aged only as +2Y/+3Y. Usually during the second adult post-breeding moult, a 3Y woodpecker replaces any primary coverts that remained from the first adult post-breeding moult. Also nearly always all outer (8–10) primary coverts are replaced, but some of the inner ones retain. Contrast in colour and wear is slight between old and new coverts; especially in autumn and/or in bad light, contrast easily can be missed. Moreover no differences in covert shape can be detected. Occasionally all secondaries are replaced, but usually 1–3 are retained. Contrast in colour and wear between old and new secondaries is very slight. White spots on the outer web are helpful: light colour areas of a feather wear sooner than dark areas. About 9 % of birds examined belonged to this age-group (Fig. 1, Table 2).

3Y/4Y and +3Y/+4Y

During the second adult post-breeding moult, quite often, maybe even in 30 % (10 out of 32 birds of 3Y/4Y and 12 out of 36 of +3Y/+4Y, Table 2) of Great Spotted Woodpeckers, one or two primary coverts are retained a second time during the adult post-breeding moult. In such cases it is possible to recognize primary coverts belonging to three different age groups and, for the oldest one, it is possible to identify the bird as belonging either to the group of 3Y/4Y (if the twice-retained primary covert is juvenal type) or +3Y/+4Y if the oldest primary covert is adult type. However it should always be kept in mind that the more exposed outer primary coverts wear sooner than inner ones.

About 3 % of birds examined belonged to both of each of these age-groups (Fig. 1, Table 2).

Determination of age of other European woodpecker species.

Age determination of other woodpecker species is possible using the criteria described here for the Great Spotted Woodpecker (e.g. GEORGE 1972, CRAMP et al. 1985, MIETTINEN et al. 1986, PYLE & HOWELL 1995). At least it is always possible to differentiate 1Y/2Y woodpeckers from older ones, but probably all *Picoides* species and the Black Woodpecker *Dryocopus martius* can be aged up to their fourth calendar year and at least some *Picus* species and the Wryneck *Jynx torquilla* can be aged after their first post-breeding moult. Determination of age is, however, more difficult in some species because contrast in shape and colour between juvenile and replaced feathers and among adult feathers of different generations is weaker than in the Great Spotted Woodpecker.

Acknowledgements

Fieldwork was started when my friend Mr. Jukka Pusa suggested that we examine variation we had seen in flight feather colours of some Great Spotted Woodpeckers which were visiting feeders in east Finland during winter. Such study, he suggested might aid in ageing specimens. Together we examined the study skin collection at the Helsinki Zoological Museum in January 1986.

Mr. Pekka J. Nikander similarly studied ageing of the Grey Headed Woodpecker and during April 1987 we examined woodpecker skin collections at Stockholm and Copenhagen.

I am very grateful to both for the interesting and inspiring times we shared in studying woodpeckers.

During the long course of my studies I have had worked with many birdringers and other ornithologists. I mention here only Mr. Kimmo Martiskainen, Mr. Harri Koskinen and Mr. Hannu Huuskonen but I thank for all of them for helping, providing information, and for inspiring my work with woodpeckers.

I also thank Mr. Göran Frisk and other very helpful staff of Naturhistoriska Riksmuseet in Stockholm. We had also a very nice and useful visit to Zoolological Museum of Copenhagen.

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Nesting interaction between woodpeckers and starlings – delayed commensalism, competition for nest sites or cavity kleptoparasitism?

Interaktionen am Nest zwischen Spechten und Staren – verzögerter Kommensalismus, Konkurrenz um Nisthöhlen oder versteckter Kleptoparasitismus?

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Abstract

Primary cavity nesters (PCN's), e.g. woodpeckers are able to excavate their own nesting cavities. During subsequent breeding seasons, the holes are used by secondary cavity nesters (SCN's). Therefore, interactions between these two groups of birds are called delay commensalism. However, the majority of woodpecker species reuse holes for breeding purposes. Thus, competition for the nesting sites may occur between woodpeckers and SCN species. The Great Spotted Woodpecker *(Picoides major)* frequently reusing old holes, and the Starling *(Sturnus vulgaris)* – its most powerful competitor were chosen for the study. The study was carried out in mixed-deciduous forests in Warsaw (Central Poland). Great Spotted Woodpecker rarely reused old holes in small forests, but frequently in large ones where relative abundance of Starlings was lower. In old holes, woodpeckers bred earlier, and fledged more young. Individually marked birds that lost nest holes from previous breeding season were forced to excavate new ones, otherwise they used their old holes. Woodpeckers never used old holes in presence of any pieces of nest material brought there by SCN's. Starlings preferred holes without the nest material, i.e. not used previously by any SCN species. In such cavities, starlings started breeding earlier and fledged more young. Thus, woodpeckers and starlings interact with regard to old, existing holes. If previously occupied nest sites are lost, woodpeckers pay some additional costs, as they have to excavate new cavities, while starlings benefit from good breeding sites every year. Generally, such interspecific interaction should be classified as parasitism, defined as cavity kleptoparasitism, according to KAPPES (1997).

Primäre Nestnutzer (PCN), z.B. Spechte, sind in der Lage, ihre eigenen Nisthöhlen zu bauen. In nachfolgenden Brutsaisons werden diese Höhlen von sekundären Höhlennutzern verwendet (SCN). Daher können diese Interaktionen zwischen den beiden Gruppen als verzögerter Kommensalismus bezeichnet werden. Allerdings nutzen die meisten Spechtarten ihr alten Höhlen wieder als Brutstätten. Dadurch ergibt sich ein Wettbewerb um die Nistplätze zwischen Spechten und SCN-Arten. Für die Untersuchung wurde der Buntspecht ausgewählt, weil er häufig alte Höhlen erneut nutzt und der Star vermutlich sein größer Konkurrent dabei ist. Die Untersuchung wurde in einem Laubmischwald in Warsaw (Zentralpolen) durchgeführt. Es konnte herausgefunden werden, dass Buntspechte in einem kleinen Wald selten ihre alten Bruthöhlen wieder benutzen, aber dies häufig in größeren Wäldern tun, wo das relative Vorkommen der Stare niedriger war. In alten Höhlen brüten die Spechte früher und mehr Jungtiere schlüpfen. Individuell markierte Vögel, die ihre Nisthöhlen der vergangenen Saison verloren hatten, waren gezwungen sich neue zu bauen, oder andere Höhlen zu verwenden. Spechte nutzten niemals alte Höhlen, wenn irgendeine Menge Nistmaterial von SCN eingebracht wurde. Stare bevorzugten Höhlen ohne Nistmaterial, welche z.B. vorher nicht von irgendwelchen SCN-Arten benutzt wurden. In solchen Höhlen brüteten sie früher und es schlüpften ebenfalls mehr Jungtiere. Es gibt daher Interaktionen zwischen Spechten und Staren um alte, vorhandene Höhlen. Spechte haben einen höheren Aufwand, wenn sie Nisthöhlen verlieren und gezwungen sind, neue zu bauen. Stare profitieren generell davon, indem sie jedes Jahr gute Nistplätze zur Verfügung haben. Generell sollte eine solche zwischenartliche Interaktion als eine Art Parasitismus klassifiziert werden, der nach KAPPES (1997) als Höhlen-Kleptoparasitismus definiert wird.

Introduction

Interspecific interactions between species result from exploitation of the same environmental resources, such as food, space, place for breeding, etc. Such interactions between different species of birds very frequently relate to nesting sites, because various species use the same nest sites or even nests in subsequent years. It is true not only for hole nesters (WESOŁOWSKI 1989, SEDGWICK 1997), but also for birds building open nests (FINCH 1982, BERGIN 1997).

Birds that breed in tree holes are generally divided into two groups. Primary cavity nesters (PCN's) – mostly woodpeckers *Picidae* – are able to excavate their own breeding holes. Secondary cavity nesters (SCN's) are unable to excavate their nests, and have to use existing holes. Thus, the former group of birds produces some environmental resources (holes) that are further used by the latter group. Therefore, some relationships have to occur among individuals belonging to these groups.

Interactions between individuals or species are generally considered with respect to their effects they have on population size, or individual fitness (ABRAMS 1987). These could be generally defined as „0" – no effects in relation to particular individuals or whole population; „+" – positive effects, for example a greater number of fledgings, and „- " – negative effects – smaller number of fledgings or deterioration of their condition which determine their later survival.

Because PCN's and SCN's individuals affect one another, pairs of interactions can be analysed. According to general typology of interspecific relations (ODUM 1982), there are three types of interactions between PCN's and SCN's, which should be considered:

1. Commensalism (PCN's 0; SCN's +)
If excavation of new holes every year is a typical behaviour of PCN's, use of the holes by SCN's in next breeding seasons does not produce any extra costs for PCN's. In this case, SCN's would not affect hole producers (PCN's 0). Tree holes can be a factor limiting SCN's abundance (review in NEWTON 1994). As a result of excavatory behaviour of woodpeckers, SCN's have an access to new holes every year, and increasing number of accessible holes enables pairs of SCN's to choose the most favourable breeding sites. In this case, PCN's would affect SCN's positively (SCN's +).

2. Competition (PCN's – ; SCN's –)
Nesting interactions between woodpeckers and SCN's are usually described as competition for nest sites or holes (TROETSCHLER 1976, INGOLD 1989, KERPEZ & SMITH 1990). If cavities are scarce, birds may compete for them. Strong competition for holes newly excavated by PCN's is very frequently observed (SHORT 1979, INGOLD 1989, 1994, 1996, RESTREPO & MONDRAGON 1998).

Woodpeckers lose their holes, and therefore delay breeding and fledge less young (INGOLD 1996). Their eggs are sometimes even thrown away from the holes by competing SCN's birds (KEVE 1963). Thus, SCN's can affect holes producers negatively (PCN's –).

However, there are no data describing the impact of woodpeckers on SCN's. According to interaction approach, both species or individuals involved in competition should suffer some costs (SCN's –). These would include fights for holes, chasing away its owners, and other activities leading to overtaking the holes.

3. Parasitism (PCN's –; SCN's +)
In parasitic interactions, SCN's affect hole produces negatively (see above; PCN's –), while SCN's can benefit due to activity of PCN's (SCN's +). Such positive impacts can be observed at two levels.

Overtaken holes provide SCN's with breeding sites, and some other benefits. Because woodpeckers do not use nest material, ectoparasites are unlikely to occur, overwinter and reproduce in the nest sites (RENDELL & VERBEEK 1996a). New holes are presumably less exposed to predators (SONERUD 1985). Therefore, hole usurpation seems to be a strategy of successful breeding, and should not be related to limited number of accessible holes, especially that a surplus of tree holes is frequently found (EDINGTON & EDINGTON 1972, WATERS et al. 1990, WALANKIEWICZ 1991).

The objective of this work was to find which of the nesting interactions defines best the relations between representatives of PCN's and SCN's.

Studied Species

Two species of similar body size were chosen for the study – the Great Spotted Woodpecker *Picoides major* from the PCN's group and the Starling *Sturnus vulgaris* as a representative of SCN's.

The Great Spotted Woodpecker is the most abundant woodpecker species in Europe (HAGEMEIJER & BLAIR 1997). It may reuse its own cavities or holes excavated by other woodpeckers. The holes excavated by Great Spotted Woodpeckers are used by a few SCN's species, primarily by Starlings (MAZGAJSKI 1994). In this way, both chosen species can use the same resources.

Starling is the most powerful competitor in SCN's group, and it is able to usurp the holes of many bird species (ALLEN & NICE 1952, BUSSE & GOTZMAN 1962, WEITZEL 1988, INGOLD 1994, 1996). Interactions between Starlings and woodpeckers have been very frequently studied in North America where Starling was introduced in Washington in the end of 19th century and then spread over almost the whole continent (HOWELL 1943, WEITZEL 1988, KERPEZ & SMITH 1990, INGOLD 1994, 1996).

Study Area and Methods

The studies were carried out in two wooded areas – Bielański and Kabacki Forests (later BF and KF) situated in outskirts of Warsaw (Central Poland 52° N, 21° E). Both areas are nature reserves, with old-growth deciduous tree stands and stable populations of Great Spotted Woodpecker and Starling. A large number of various holes can be found in old trees in both areas. There are practically no other (artificial) nest sites for hole nesting birds.

The two forest areas differ in size and population size of both species. In the smaller forest (BF of approx. 145 ha) 10–16 pairs of Great Spotted Woodpecker and about 250–300 pairs of Starlings breed every year (MAZGAJ-

SKI 1997, MAZGAJSKI et al. 2001). The larger forest (KF – about 980 ha) supports much bigger bird populations, amounting to more than 100 pairs of Great Spotted Woodpecker and more than 500 pairs of Starling (LUNIAK et al. 1990). Thus, starlings were almost 3 times more abundant than woodpeckers in the case of the former forest, and consequently Starlings are likely to affect woodpecker population more strongly there.

A detailed description of the study areas and nest holes of the Great Spotted Woodpecker can be found elsewhere (MAZGAJSKI 1998).

Additionally, 86 nest boxes suitable for Starling were hung in two younger forest stands (Park Mlociński – PM and Las Mlociński LM).

The studies started in 1992, and during the next few years, the study areas were searched for active nests of woodpeckers. Therefore age of particular holes was known, and referred to as N – for a year of hole excavation, N + 1 – for one breeding season after the hole excavation, etc. The pattern of hole use by birds was observed in consecutive breeding seasons.

Various aspects of birds' breeding biology, such as date of egg laying, clutch size, number of fledgings etc., were studied for both Great Spotted Woodpecker and Starling. This was however confined to KF, where Woodpeckers and Starlings breed relatively low in height (MAZGAJSKI 1998). Contents of holes were checked using a ladder, small light and mirror. Nests were inspected every second-third day during egg-laying and just before fledging, while less frequently in other phases of the breeding cycles. All sorts of nest material in old, unused holes or woodpecker nests were noted.

In KF forest, about 50 woodpecker individuals were colourly ringed, and their nests were searched for in consecutive breeding seasons, and the history of their nest-holes was noted.

To study the relationship between breeding biology of Starling and presence of old nest material in their nest sites, the experiment with nest boxes was carried out.

Results

In the study areas, Great Spotted Woodpecker reused up to 20 % of holes excavated in previous year. However, the rate of hole reuse differed between seasons and areas. It was found that the frequency of hole reoccupation by Great Spotted Woodpeckers and hole use by Starlings differed depending on the size of wooded area ($\chi^2 = 4.11$, $p < 0.05$) (Table 1). In the smaller forest (BF), almost all N + 1 holes were used by Starlings, whereas woodpeckers were able to reuse their holes extremely rarely. In contrast to the larger forest area, where less N + 1 holes were occupied by Starlings and other hole nesting species, a few Great Spotted Woodpecker pairs reused old holes in BF almost every season (Table 1). In the larger forest, one of the holes was successfully used by woodpeckers during three consecutive seasons.

Table 1. Percentage utilisation of N + 1 holes by Great Spotted Woodpecker (GSW) and Starling (Star) in relation to the size of forest area (*N* – sample size).

Season	Small forest (BF)			Large forest (KF)		
	GSW	Star	*N*	GSW	Star	*N*
1993	8	54	13		Lack of data	
1994	–	89	12	6	50	15
1995	–	80	10	–	54	11
1996	–	85	13	17	58	12
1997	20	60	5	20	27	15
Totally	4	76	53	11	45	53

Table 2. First egg laying dates (%) of Starling (Star) and Great Spotted Woodpecker (GSW).

	Breeding season			
	1996		1997	
	Star (*N*=11)	GSW (*N*=8)	Star (*N*=22)	GSW (*N*=12)
25–27 April	82		45	
28–30 April	18	(25)* + 25	45	
1–3 May		38	10	(17)*
4–6 May		12		(17)* + 25
7–9 May				42

*( ) – woodpeckers which bred in old holes

New holes were usually excavated after the old ones had been lost in favour of SCN's species (59 %), or when the hole became unavailable for other reasons (33 %). Only one hole (8 %) seemed to be available for reuse though woodpeckers excavated new one.

Woodpeckers never reused holes containing even traces of nest material brought there by SCN's. Of 24 old holes inspected containing no nest material, 42 % were reused, but none of 17 holes with pieces of nest material or old nests. Also newly excavated holes with fresh vegetation brought there by Starlings were abandoned by woodpeckers.

The pairs of woodpeckers able to breed in existing holes started laying their eggs earlier then pairs from freshly excavated holes (Table 2). When compared with Starlings, woodpeckers started breeding a few days later, however the period of egg laying of the two species partially overlapped (Table 2). Early start of egg laying is very important for woodpeckers, because time of breeding affects the number of woodpecker fledging. The pairs that bred and fledged later, produced significantly less young than those fledging young earlier (early nests: 1997 – 3.21 ± 0.73, 1998 – 4.5 0.53; late nests 1997 – 2.37±0.74, 1998 – 3.75±0.71; Mann-Whitney U test 1997 $z = -2.37$ $p < 0.02$; 1998 $z = 2.06$, $p < 0.04$). Unfortunately, the data from old and fresh holes could not be examined separately, due to differences in number of fledging in 1997 and 1998 (Mann-Whitney U test $z = -3.92$ $p < 0.001$). However, the results suggest that the pairs which bred in old holes might produce more young.

Table 3. Starling occupation of old Great Spotted Woodpeckers' holes in relation to age of the holes. Sample size in parenthesis.

Age of holes (N – the year of hole excavation)		Occupation rate (%)
N + 1	(53)	76
N + 2	(45)	57
N + 3	(31)	45
N + 4	(21)	33
N + 5	(11)	27

Table 4. Breeding parameters of Starling which bred in nest sites with / without old nests. PM, LM – study areas, * – p < 0.05, ** p < 0.01.

		Nest boxes with old nests		
		absent	present	
Occupation rate (%)	PM + LM	79	50	**
Clutch size	PM	4.9	4.4	*
	LM	5.4	5.2	ns
Number of fledging	PM	2.8	2.4	ns
	LM	4.2	3.7	**
Breeding success (fledging/eggs)	PM + LM	69	57	*

It was found that Starlings preferred holes N + 1 for breeding, and utilisation rate of holes decreased with increasing age of the holes (Table 3). The holes N + 1 were used more frequently than N + 2 ($\chi^2 = 4.32$, $p < 0.05$), whereas N + 2 and older were used with similar frequency ($\chi^2 = 4.57$, df = 3 ns).

A possible reason of such results could be presence of old nest material. Starlings avoided nest boxes containing old nests, and its breeding was also more successful in holes without old nests (Table 4).

Discussion

Interaction between PCN's and SCN's classified as commensalism assumes that woodpeckers excavate new holes every year, and old holes are left for SCN's. These holes are available in the next breeding season after their excavation, and such an interaction is termed delayed commensalism (GUTZWILLER & ANDERSON 1988).

Scientific papers and monographs on breeding biology of woodpeckers show that most of these species may reuse old existing holes (SHORT 1982, CRAMP 1985, WINKLER et al. 1995). Such findings are however rare. Therefore, a question can be addressed, why PCN's do not reuse their own holes more frequently?

Great Spotted Woodpeckers may reuse 4–70 % of old holes, and holes are sometimes exploited over 3–5 breeding seasons (BLUME 1977, WESOŁOWSKI & TOMIALOJĆ 1986, HANSSON 1992, MAZGAJSKI 1994). Results of this study confirmed such findings. Differences in frequency of hole reoccupation might be primarily an effect of strong pressure of SCN's. In the small forest, holes were reused sporadically, whereas in the large forest – rather frequently.

Thus, woodpecker species do not have to excavate breeding holes every year. However, they invest their time and energy in the hole excavation due to competitive pressure of other hole nesting species. Therefore, commensalism as an interaction that assumes no extra costs for PCN's should be rejected.

In competition or parasitism, PCN's should suffer some costs due to activity of SCN's. Results of this study confirmed these assumptions:

It was found that woodpeckers were forced to excavate new holes every year, because old holes were not available accessible for them, and were usually occupied by SCN species. The hole once used by SCN's is lost for woodpeckers, because the latter species does not tolerate any nest material (SHORT 1982), and the hole would not be reused.

Woodpeckers occupying old holes start to breed earlier (LANGE 1996, Table 2), whereas nest hole excavation delays breeding, and eventually decreases the number of fledging. If woodpeckers could have bred in old holes, instead of investing in hole excavation, their breeding would be more successful.

Similar data were obtained in studies conducted in North America, where Starlings were introduced. The native woodpecker species also delayed their breeding, and therefore fledged less young (INGOLD 1989, 1996). It was not only an effect of old cavity losses, but also usurpation of freshly excavated holes. Such usurpations are observed in Europe less frequently (TRACY 1938, LÖHRL 1956, BUSSE & GOTZMAN 1962), because woodpeckers co-evolve with Starlings here and may develop some strategies to reduce losses of newly excavated holes. In some areas of North America, Starling pressure can even lead to extinction of native hole nesters, including woodpeckers (WEITZEL 1988).

More frequent penetration of existing holes by predators, instead of SCN's pressure, might explain every-year excavation of new holes by woodpeckers. Reuse of old holes do not decrease breeding success of Great Spotted Woodpecker (own data). Similar studies for other species of woodpeckers are extremely rare and their results are not so certain (LANG & ROST 1990, NILSSON et al. 1991, LANGE 1996).

To sum up, SCN's affect hole producers negatively. An effect of such an interaction is reduced number of fledgings (PCN's -).

Excavatory activity of woodpeckers increases number of available cavities, and this is the most frequently emphasized benefit to SCN's populations. However, the results of this study show also other advantages of new holes in wooded environment. Starlings used usually holes N + 1 with no nest material. Older, already used holes (presumably by SCN's), were occupied less frequently. It could be an effect of presence of old nest material and/or ectoparasites. Starlings, like many SCN's, prefer to breed in clean, empty or parasite free nest sites (OPPLIGER et al. 1994, MERINO & POTTI 1995, RENDELL & VERBEEK 1996b). More or less similar nesting parameters in tree holes and nesting boxes suggest that Starlings breed more successfully in N + 1 holes. The preferences for N + 1 holes can thus be considered as beneficial for Starling, rather than resulting from lack of nesting sites in general.

A conclusion can be drawn that there are strong interactions between the species examined with regard to holes N + 1 or holes without nest material. Both species could breed there, more successfully. However, woodpeckers are poor competitors, and suffer a cost of new hole excavation (PCN's -), whereas SCN's win and benefit from breeding there (SCN's +).

Therefore, parasitism seems to define most adequately the interactions between PCN's and SCN's. The interaction consisting in production of resources by one species and their use by other one is considered as parasitism in a broad sense of this term (BERNARD & BEHMKE 1990), and according to KAPPES (1997), the term cavity kleptoparasitism should be used.

Acknowledgements

I wish to thank Prof. KAZIMIERZ A. DOBROWOLSKI for support, advice and comments during the whole studies, Jerzy Mazgajski for all his logistic support and Aleksander Kedra for his field assistance in nest box part of studies. The studies were financially supported by KBN (Polish Committee for Scientific Research) grant No. 6P04F04313 and Warsaw University grant No. 1385/97/12. The English version was kindly verified by Tomasz Ogledzki and Taida Tarabuła. I am very grateful to the Deutsche Forschungsgemeinschaft (DFG) for the financial support which enable me to participate in the International Woodpecker Symposium.

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Niche seperation in European woodpeckers – reflecting natural development of woodland

Nischendifferenzierung europäischer Spechte im Spiegel natürlicher Waldentwicklung

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Abstract

On the one hand woodpeckers show a nearly uniform appearance – with a strong, chisel-like bill on a relatively bulky head; short, strong wings; stiffly feathered tail; and zygodactyl toes for support of climbing. On the other hand the ten species, found in Europe, are differentiated markedly in respect to their techniques of food gathering and in their degree of specialization for climbing, probing in bark crevices, and excavating the wood of trees. Even when differences in specific behaviour seem to be slight, habitat preferences usually show a comparatively clear interspecific niche separation. Some are more or less linked to open, steppe-like woodland with sparse tree stands (Syrian *Picoides syriacus*, Grey-headed *Picus canus* and Green Woodpecker *Picus viridis* mostly), others to park-like landscapes, fragmented by clearings (Lesser Spotted Woodpecker *Picoides minor*), others to forests, rich in gaps (Great *Picoides major* and Middle Spotted Woodpecker *Picoides medius*), and still others such as the Black *Dryocopus martius*, White-backed *Picoides leucotos* and Three-toed Woodpeckers *Picoides tridactylus* evolved the most narrowly-defined linkage to certain age classes and phases of woodland development. Although woodpeckers usually are classified as typical forest-dwelling species, they only can colonize forest habitats under specific pre-conditions, even in natural woodland. Knowledge of essential characters determining habitat quality – like age of trees, diameter of trunks, structure of bark, supply of dead and down wood – and the strategy to integrate them into forest management are the key to maintaining these birds, as index-species for current protection of tree stands and woodland-ecosystems.

Wenn Spechte auch ein sehr einheitliches Erscheinungsbild zeigen – mit kräftigem Meißelschnabel am relativ großen Kopf, mit kurzen, harten Schwingen, steifgefiedertem Stützschwanz und zygodactylem Kletterfuß –, so unterliegen die zehn in Europa verbreiteten Arten doch einer deutlichen Differenzierung hinsichtlich der Techniken zum Nahrungserwerb, der Fähigkeit zu Klettern, zu Ringeln, zu Schmieden und Bruthöhlen aus dem Holz von Bäumen zu hacken. Scheinen die artspezifischen Verhaltensunterschiede auch nur graduell abgestuft, so lassen die Habitatspräferenzen eine meist recht klare zwischenartliche Abnischung erkennen, entsprechend einer mehr/minder engen Bindung an jeweils offene, waldsteppenartige Landschaften mit schütterem Baumwuchs (vor allem Bodenspechte, Blutspecht), an lichtungsreiche Parklandschaft (z.B. Kleinspecht) oder an lückig-durchbrochene Wälder (Bunt-specht, Mittelspecht), wobei Schwarz-, Weißrücken- und Dreizehenspecht die jeweils engste Bindung an bestimmte Alters- bzw. Entwicklungsphasen im Wald eingegangen sind. Obwohl im Allgemeinen typische Waldarten können Spechte selbst natürliche Waldlebensräume nur unter ganz bestimmten Voraussetzungen besiedeln. Die Kenntnis der essentiellen Qualitätsmerkmale – wie Baumalter, Stammquerschnitt, Borkenrauigkeit, Totholzangebot – und deren Integration in forstliche Bewirtschaftungssysteme ist der Schlüssel zur Erhaltung dieser indikatorisch wichtigen Leitarten für einen zeitgemäßen Schutz von Baumbeständen bzw. Waldökosystemen.

Introduction

The sub-family of *Picinae* includes 182 species worldwide. These can use quite different habitats, even treeless semi-desserts and grass-steppe. In this paper I will focus on only a few of these and look at the ecological situation of typical woodpeckers in central European woodlands – those with more or less intensive linkage to trees, at least for building a nest hole. These birds are highly specialized tree-climbers, characterized by a chisel-like bill, zygodactyl climbing foot, supporting tail feathers, and a smooth, tight plumage.

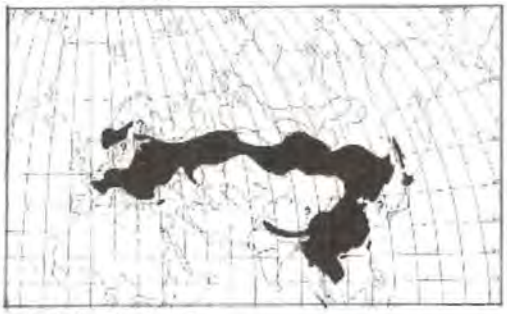
In comparing the distribution maps of the 10 species occurring in central Europe, an east-west extension of species distribution areas is typical and likely a heritage of the ice ages. During the ice ages most of these woodpeckers found safe retreat in far eastern Asia, some in the mediterranean area, and others in the near east. No species are restricted to Europe, but the Green *Picus viridis* and the Middle Spotted Woodpecker *Picoides medius* show quite limited areas of distribution, but with a center in central European forests. The Syrian Woodpecker *Picoides syriacus* is invading central Europe from the near east, and is still expanding its breeding area to the west.

The huge land between Japan and Great Britain is covered not only with forest, but with a high diversity of landscapes: ranging from virgin forests, forest steppe, and boreal taiga to very open country with only small patches of trees. Provided with an optimum climate for

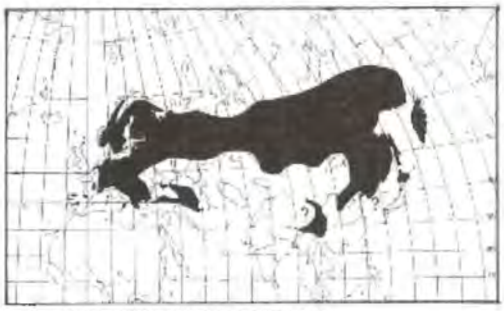
PICOIDES TRIDACTYLUS

JYNX TORQUILLA

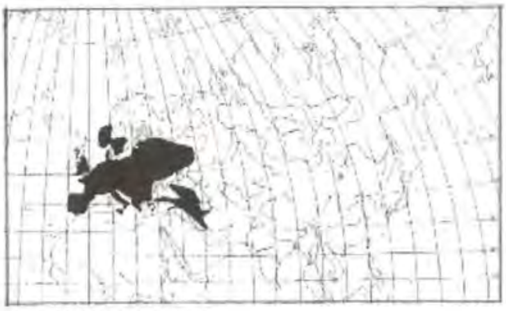
DENDROCOPOS MINOR



PICUS CANUS

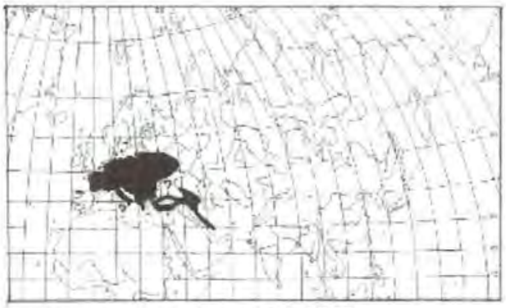


DRYOCOPUS MARTIUS



PICUS VIRIDIS

DENDROCOPOS MAJOR



DENDROCOPOS MEDIUS

DENDROCOPOS LEUCOTOS

DENDROCOPOS SYRIACUS

Fig. 1. Distribution of 10 European woodpecker species: Only Green and Middle-Spotted Woodpecker find their center of distribution in Europe; distribution areas of most species extend to far east of Asia, where they have retreated during the ice-ages (maps following VOOUS 1962).

tree-growing, central Europe would be covered with rich and dense forests under natural conditions. In central Europe we find the ten species in more or less forested habitats; 5 of them are „real“ forest-dwelling species. European woodpeckers may occupy a high variety of habitats: for example, ant-eating species prefer open country. Those with the broadest ecological valency include adaptable species – like the Great Spotted Woodpecker *Picoides major*; the narrowest valency is found in the Middle-Spotted and the White-backed woodpecker *Picoides leucotos*. The highest diversity can be found in open, old stands, rich with clearings (e.g., park-like habitats, forest-steppe) and in natural old growth. The highest density of woodpeckers can be found in riverine, alluvial forests, because soft-wood is preferred by a great number of species (e.g., Little Spotted *Picoides minor*, Great Spotted, Grey-headed *Picus canus* and Green Woodpeckers), and trees grow there very quickly. Huge areas in central Europe are covered by mixed forest of deciduous trees (like oak, hornbeam, lime, ash, maple, beech), which harbour a great number of woodpecker species (and are of special interest for Middle Spotted, Black *Dryocopus martius* and Green Woodpecker). In stands of cooler climate or with soils less rich in nutrients, beech trees may dominate the forest. Pure *Fagetum* is a typical habitat for the powerful

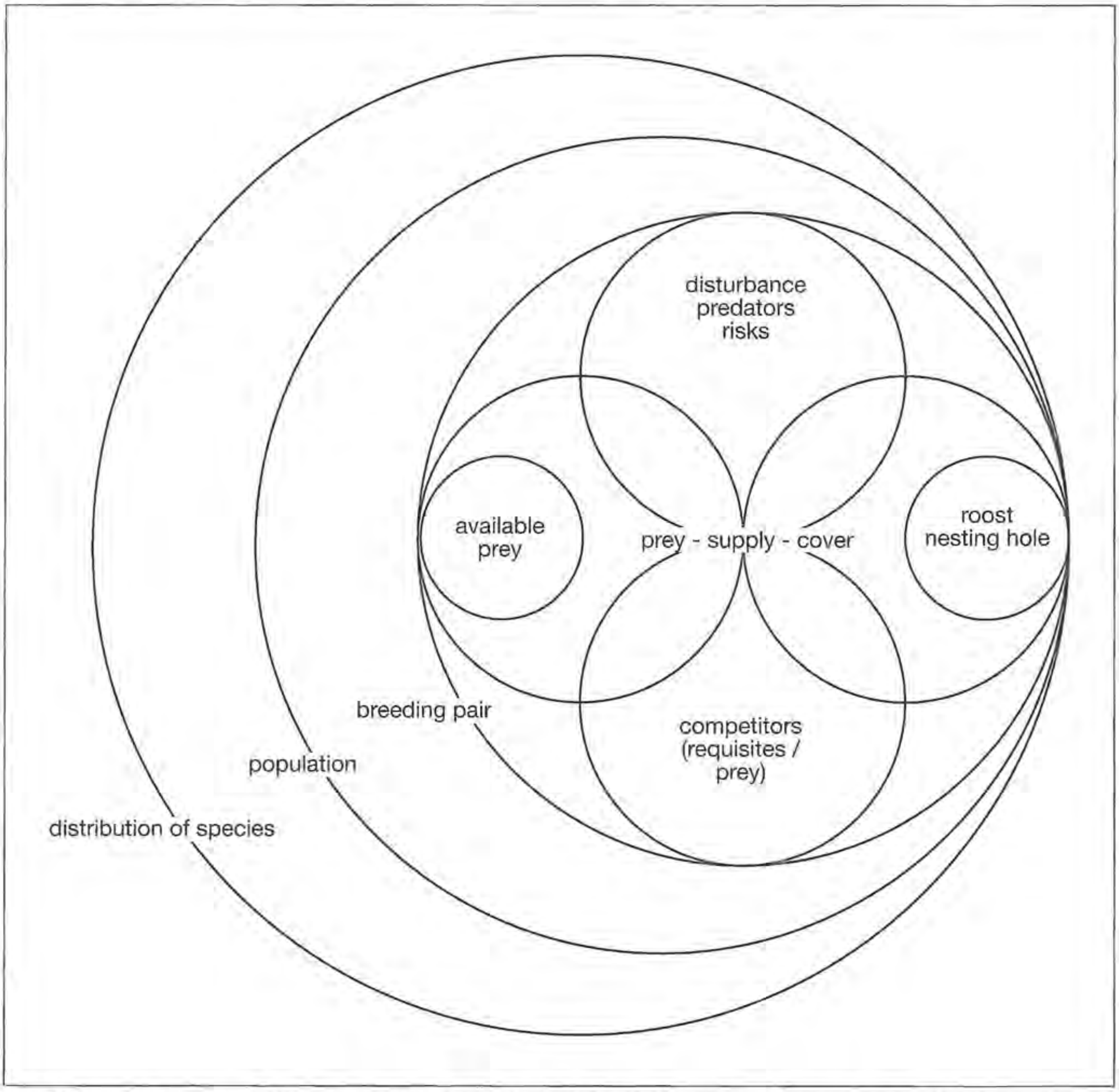
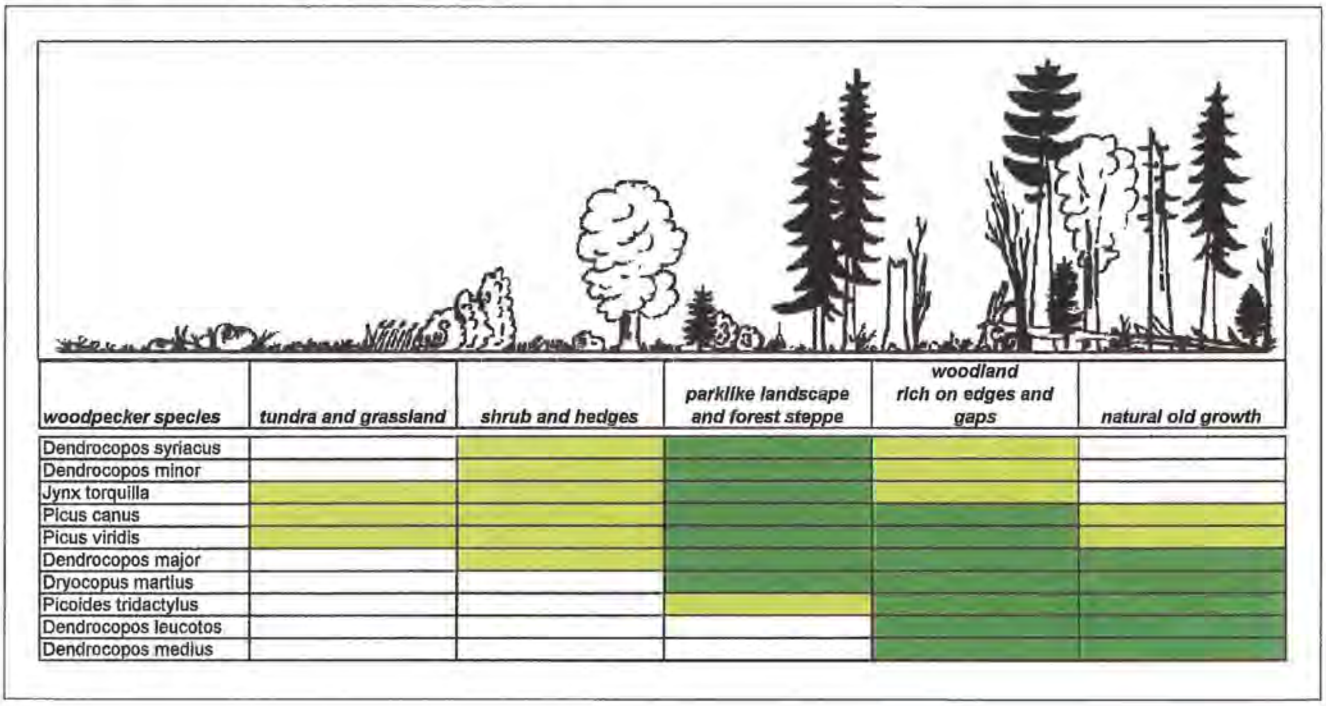


Fig. 2. Dominant parameters, determining quality of woodpecker habitats: Management for conservation of endangered woodpeckers should focus at four functional cycles in their habitat at least; whereby supply of available food and nesting sites seem to be predominant.

Table 1. Main habitat types in distribution: All 10 European woodpeckers are forest dwelling species, preferring markedly old growth, rich on edges, gaps and openings, but some species even may disperse in nearly open grassland, especially the ground-hunting types, feeding mostly on ants.



woodpecker species	*tundra and grassland*	*shrub and hedges*	*parklike landscape and forest steppe*	*woodland rich on edges and gaps*	*natural old growth*
Dendrocopos syriacus		🟨	🟩	🟨	
Dendrocopos minor		🟨	🟩	🟨	
Jynx torquilla	🟨	🟨	🟩	🟨	
Picus canus	🟨	🟨	🟩	🟩	🟨
Picus viridis	🟨	🟨	🟩	🟩	🟨
Dendrocopos major		🟨	🟩	🟩	🟩
Dryocopus martius			🟩	🟩	🟩
Picoides tridactylus			🟨	🟩	🟩
Dendrocopos leucotos				🟩	🟩
Dendrocopos medius				🟩	🟩

Black, the White-backed, and the Great Spotted Woodpeckers; but usually they are dependent on decayed trees, as healthy wood of beech trees is extremely hard. In mixed forest at montane elevations, woodpecker species linked to deciduous trees (e.g., White-backed) occur side-by-side with species linked to conifers (e.g., Three-toed Woodpecker *Picoides tridactylus*). In Bavarian Forest National Park such a mosaic of patches of conifers and deciduous trees (including beech, spruce, fir, and maple) harbours 7 species of woodpeckers (SCHERZINGER 1982). Woodpeckers occur up to timber-line in mountains and alps, where especially the Three-toed Woodpecker is a characteristic species in pure coniferous forest (like spruce, larch, stone pine).

All species of woodpeckers share a similar function in woodland ecosystems and this is reflected by a striking accordance in morphological and behavioural characters (SHORT 1982). Nevertheless there is a shallow differentiation within the European diversity of woodpecker species. All of them avoid tree stands with a closed canopy (because too cool, moist, and dark stands will depress abundance of prey-arthropods); instead of this they prefer gaps, edges and clearings. On the other hand very open areas, created i.e. by catastrophic disaster, are of low attractiveness for all but a few species (e.g., Middle Spotted Woodpecker). Fallen trees and decayed wood may be used by the large species like Black Woodpecker, and the Grey-headed Woodpecker hunts on the ground in sunny areas for ants.

Essential criteria of woodpecker habitats

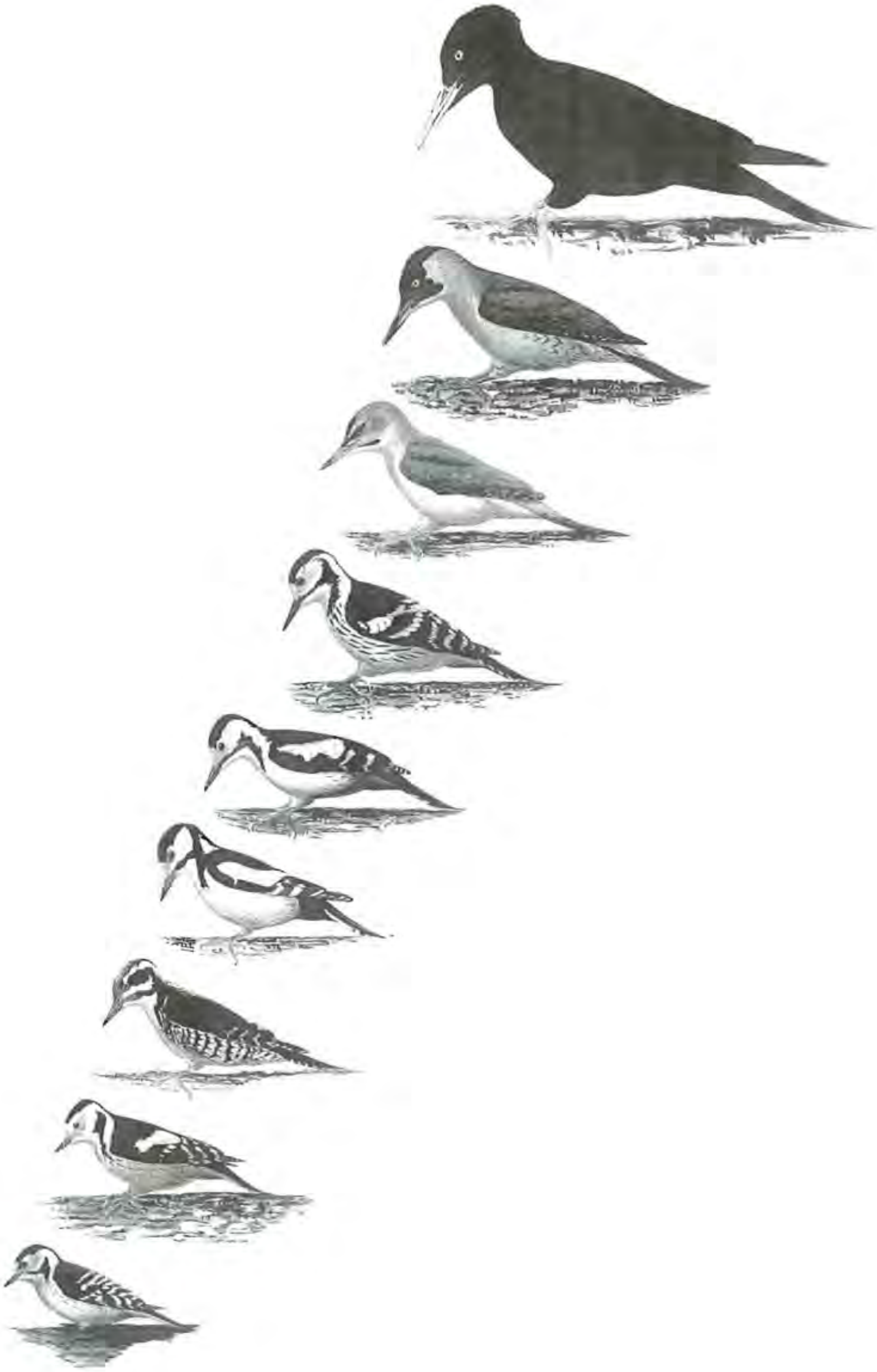
Discussion of niche-separation in woodpeckers is enhanced by analysis of the dominant parameters that determine the quality of woodpecker habitats. Within the main four functional zones (available resources, required requisites, predators, and competitors) we should concentrate on two essential cycles – those concerning prey (especially availability of food) and those concerning habitat structure (like cover and nesting site).

Supply of available food

Woodpeckers may drink tree-sap, open nuts, or – sporadically – even feed on bird eggs or small vertebrates, but the European species mainly feed on arthropods and are specialized to search for prey on tree surfaces. Density and diversity of prey differ with the micro-structural architecture of tree surfaces (e.g., JACKSON 1979): rough-barked trees harbour more insects, spiders and other arthropods because of their greater surface area and abundance of crevices. This is especially the case in oak, lime, ash, and fruit-trees. Very old trees also can develop other surface irregularities and arthropod habitats (like rank growth, crevices, fractures, or decaying hollows), which might be of interest for an arboreal hunter. Broad branches in a tall crown are of high value for all insectivorous mammals and birds, as insects are attracted to the high production of herbal biomass in full sunshine. Epiphytic vegetation also enriches

Table 2. Techniques of food gathering in European woodpeckers: The simplest way to find prey-items is gleaning, probing and pecking, while hammering, chiseling and anvil use need morphological specializations. The most complex behaviour is divided into plucking, carrying and dressing nuts or cones, to open the seeds (vocabulary following WINKLER et al. 1995).

		beak Schnabel	tongue Zunge	foot Fuß	wing Flügel	throat Schlund	breast Brustgefieder
scratching	scharren			■			
sweeping (flaking)	fegen	■					
gleaning	klauben	■	▒				
probing	stochern	■	▒				
tapping	klopfen	■					
digging	in Erde graben	■	▒				
pecking	picken, hacken	■					
hammering	kräftig hacken	■					
prying	hebeln	■					
chisseling	stemmen	■					
stripping (scaling)	schälen	■					
pulling	zerren	■					
plucking	pflücken	■		■			
carry	transportieren	■		?	■	■	
caching	horten (deponieren)	■					▒
anvil use	schmieden	■		▒			■
ringing (driling)	ringeln	■	▒				
sucking (drinking, licking)	lecken		■				
hovering	rütteln				■		
flycatching (screening)	Wartenjagd	■			■		
scally	Flugjagd	■			■		



D. minor	***D. medius***	***P. tridactylus***	***D. major***	***D. syriacus***	***D. leucotos***	***P. canus***	***P. viridis***	***D. martius***	***species***
20	58	68	72	75	110	137	175	300	weight g
99	127	125	136	133	146	146	165	244	winglng mm

Fig. 3. Size-classes of European woodpeckers: Corresponding to a scale of body mass from 20–300 g the species-specific requirements on quality of wood and diameter of nesting trees differ broadly. But size of body is not correlated with ability to excavate a hole, as the most powerful hammering and chiseling types are Three-toed, White-backed and Black Woodpeckers.

niches for tree-dwelling organisms. All these characters are indices of over aged trees such that the attractiveness of tree stands to woodpeckers continuously increases with tree age.

Despite the availability of such habitats, temperate and boreal forest winter conditions create a bottleneck-situation for woodpeckers, as useable surfaces of trees and litter of downed wood are reduced markedly. Some woodpecker species risk climbing under the level of snow-cover (like Three-toed and Black Woodpecker) to reach the root collar, or even burrow long tunnels to open hibernating ant-colonies (like the Green Woodpecker; WINKLER et al. 1995). Black Woodpeckers will excavate on downed timber, when reachable above

Table 3. Species-specific techniques of food gathering in European woodpeckers: The ground-types collecting ants are separated well from the powerful hammering types. In its ability to harvest seeds and open them on anvil the Great Spotted Woodpecker shows a quite complex behaviour on the one hand, but on the other hand this species is characterized as an „universalist" in food-gathering techniques. The least plasticity is demonstrated in the Middle Spotted Woodpecker (details following WINKLER et al. 1995).

	*Dendrocopos minor*	*Dendrocopos medius*	*Jynx torquilla*	*Picus viridis*	*Picus canus*	*Dryocopus martius*	*Picoides tridactylus*	*Dendrocopos leucotos*	*Dendrocopos major*	*Dendrocopos syriacus*
scratching									🟦	
sweeping				🟦				🟩		
gleaning	🟦	🟪	🟪	🟪	🟪	🟦	🟩	🟪	🟪	🟦
probing	🟪	🟪	🟪	🟪	🟦		🟩		🟦	🟦
tapping										
digging					🟪					
pecking	🟦	🟦	🟦	🟪	🟪		🟦		🟪	
hammering	🟦					🟪	🟪	🟪	🟪	
prying						🟦	🟩			
chisseling						🟪	🟦			
stripping						🟩	🟪	🟦	🟪	
pulling									🟦	
plucking									🟪	
caching									🟩	🟪
anvil use		🟩			🟩				🟪	🟪
ringing		🟦				🟦	🟪		🟪	
sucking	🟦		🟦	🟦	🟦	🟦	🟪		🟪	🟦
hovering									🟦	
flycatching	🟦	🟦								🟦
sally								🟩	🟦	

snow cover, or will dig even deeper to find hidden anthills. But in late winter, as food resources are depleted, Black Woodpeckers will invest hard work, to open the trunks of heart-rotted trees, where giant ants *Camponotus* spp. can be found. In Europe, only this woodpecker is able to penetrate even healthy splint-wood. It seems that it would be easier for it to turn its nutrition to vegetable food, like the Great Spotted Woodpecker, which collects seeds of trees. But this strategy demands specific techniques for harvest and transport of seeds, nuts or even big cones, and also an „anvil" on which to open them. – Great numbers of spruce cones will get stapled under preferred working-trees!

Dead wood as a key-factor

Comparing the substrate, chosen by woodpeckers for food gathering, nearly all strata of trees are used – from root collar to the outermost twigs. Small woodpecker species use branches more, larger species use trunks. Five species mostly search for ants on the ground. Dead, downed, and decaying wood plays a central part

Table 4. Substrates of main food gathering in European woodpeckers: Overall the 10 European species can use nearly all strata of a tree, but the individual species are more or less differentiated in habitat use by body size and specific techniques of food gathering. Great Spotted and Three-toed Woodpeckers use the broadest range of substrates; Green and Lesser Spotted Woodpeckers use the smallest spectrum of strata.

	*Jynx torquilla*	*Picus canus*	*Picus viridis*	*Dendrocopos syriacus*	*Dryocopus martius*	*Dendrocopos leucotos*	*Dendrocopos major*	*Picoides tridactylus*	*Dendrocopos medius*	*Dendrocopos minor*
rocks, walls		▦	■							
ground, soil	■	■	■							
litter	▦	▦	■	■	■	░	░	░		
shrubs, bushes				░						░
root collar				▦	▦			▦		
lower trunk		■	▦	■	■	■	■	■		░
middle trunk			▦	▦		■	▦	■	▦	░
upper trunk			▦	░		▦	▦	■	■	░
central crown			■	▦	▦	▦	▦	▦	■	
inner crown	■		▦		▦		■			
outer crown							▦	▦	▦	■
treetop							▦	▦		■
downd dead wood		■			■	▦	▦	■		
dead snags					▦	■	▦	■	▦	
dead branches					░	■	■		▦	
large branches	▦				░	■	▦	▦	■	
thin branches						░	▦	▦	░	▦
prunings								▦		■
rough bork									■	

in woodpecker food supplies. Some species seem clearly dependent on this substrate. But dead wood itself may have quite different value as habitat for wood-boring insects: the worst conditions are offered by the dead trunk of a small diameter coniferous tree laying on cool, moist ground in heavy shadow under a closed canopy; optimum conditions for providing a woodpecker food supply might be found in a dead trunk of soft wood from a large diameter broad-leafed tree that is mostly exposed to sun.

The incredible life expectancy of some hundreds years for some tree species means that often woodpeckers will find only scattered individual snags. But as trees will die at any time, e.g. caused by "intrinsic" factors (like overaged stage, exploitet soil), dead wood constitutes is a very natural and important part of the biomass ("necromass" respectively) in natural forests: on average the biomass of a primary forest will include 10–30 % of dead wood that is of high interest to woodpeckers. Quite a striking change in proportions of dead wood is true, when „extrinsic" factors act as disturbance, and kill clusters of trees or even large areas of forest. Strong winds are the most common abiotic catastrophic disturbance factor in European forests. Large forest areas can also be affected by avalanches in high mountains, which may even destroy old growth forest. Individual trees often die after being struck by lightning and neighboring trees are also often killed as a result of interconnecting roots. When lightning ignites fires in huge areas of coniferous forest, as was the case in Yellowstone National Park in North America in 1988, specialized woodpeckers, such

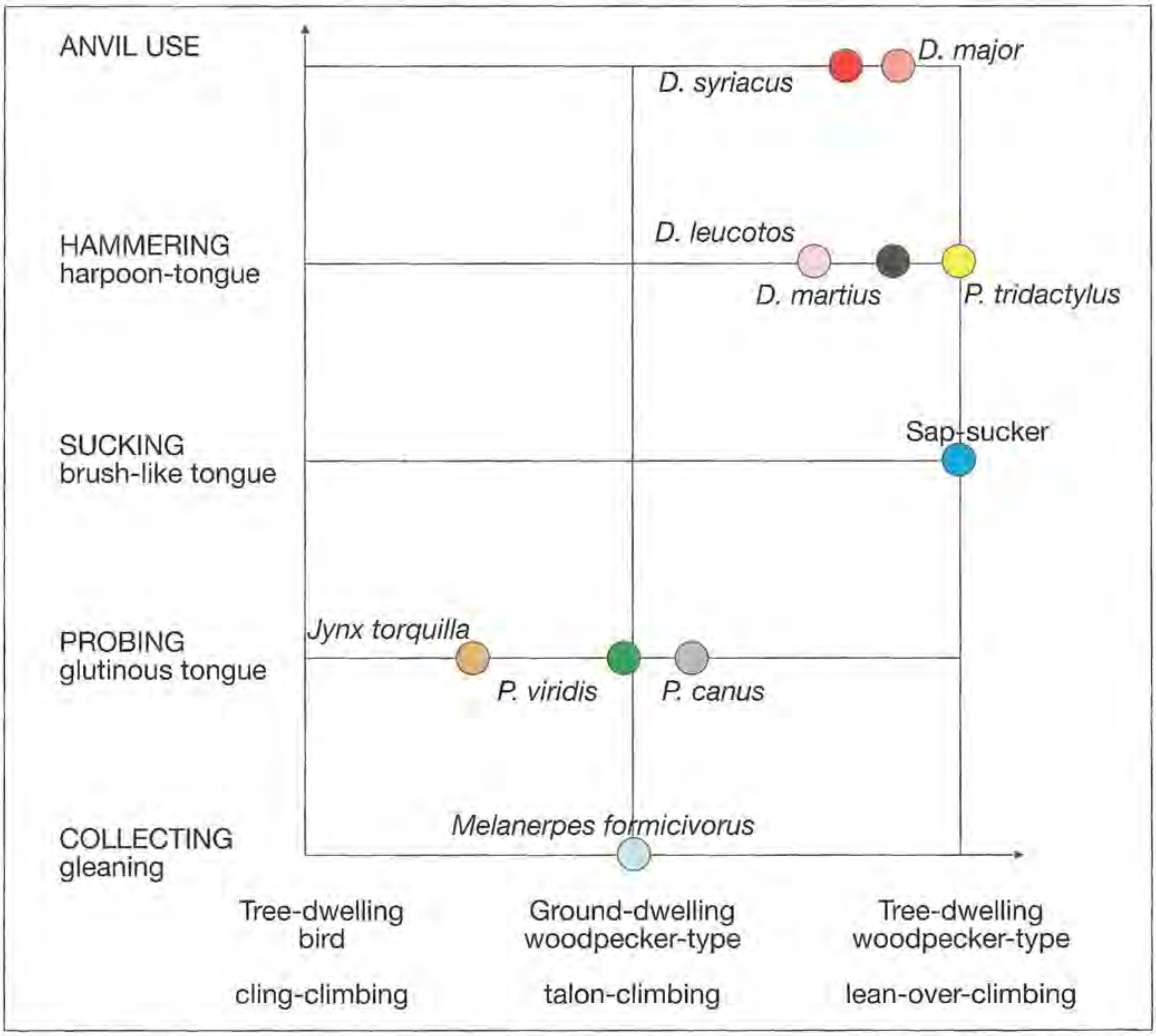


Fig. 4. Grouping of European woodpeckers concerning to their specific performance: Supported by bill and tongue, techniques of food gathering have evolved parallel to techniques of treating wood and climbing (from SCHERZINGER 1989; based on data from POSNANIN and BLUME).

as the Three-toed Woodpecker, profit from the ensuing insect-infestations, and increase their abundance.

Also biotic impact may weaken – or even kill – tree stands by catastrophic infestations. Fungi e.g. can wear down even the hardest tree species, and in consequence facilitate excavation by woodpeckers. Fungi also modify the nutrient value of rotting wood for xylobiontic organisms by permeating the wood with their hyphae that enrich the decaying wood with protein. Well known and alarming are catastrophic outbreaks of pest insects that devastate hundreds of hectares of trees, such as bark-beetle infestations in spruce forest. For a brief period woodpeckers find a super-abundance of prey (SCHERZINGER 1998).

Even vertebrates are able to produce „dead wood" attractive to woodpeckers, like the beaver *Castor fiber*, which causes heavy damage to tree stands by damming small creeks and thus flooding adjacent forest. Drowned trees become snags, favored by many birds for nesting because, surrounded by water, they offer safe breeding sites. Other impacts trees have to suffer come from big herbivorous ungulates, which damage bark, twigs, and buds by their activities. This damage can facilitate invasion by fungi, followed by heartrot and colonisation by *Camponotus* ants. The Black Woodpecker is usually the profiteer.

As prey abundance is dependent on local climate, and because warmth is a necessity for insects, openings in

Table 5. Habitat preferences of European woodpeckers: Although all species are linked to trees or wood respectively, only a few woodpecker-species live in deep forests, fully shadowed by a closed canopy. In contrast they markedly prefer woodlands rich on gaps and clearings, even scattered tree stands in a park like mosaic. But also the opposite extreme of an open landscape, free of cover and roosting trees, like clearcuts, is not attractive for these birds.

	*Dendrocopos medius*	*Dendrocopos syriacus*	*Dendrocopos minor*	*Jynx torquilla*	*Dryocopus martius*	*Picus viridis*	*Picus canus*	*Dendrocopos major*	*Dendrocopos leucotos*	*Picoides tridactylus*
closed canopy								🟧	🟧	🟧
rich of gaps		🟨	🟨	🟧	🟥	🟨	🟥	🟥	🟥	🟥
fragmented patches			🟥	🟥	🟨	🟧	🟥	🟧		🟨
park-like forest		🟧	🟥	🟥	🟧	🟧	🟥	🟥		🟨
forest edges		🟧	🟥	🟥	🟧	🟧	🟧	🟧	🟨	
group of trees		🟥		🟥		🟧	🟧	🟨		
avenue		🟥	🟧	🟧		🟧	🟧	🟧		
orchard	🟧	🟥	🟥	🟥		🟧	🟧	🟧		
catastrophic clearing					🟧	🟧	🟥	🟧	🟧	🟥
clearcut					🟨	🟨	🟧	🟨	🟨	🟨
treeless grassland				🟨		🟨				
coniferous woodland		🟨	🟨		🟧	🟨	🟨	🟧		🟥
mixed woodland			🟨	🟨	🟥	🟧	🟧	🟥	🟧	🟧
deciduous woodland	🟥	🟧	🟧	🟧	🟧	🟥	🟧	🟧	🟥	
riverine woodland	🟥		🟥	🟧	🟧	🟧	🟧	🟧	🟧	
soft-wood trees			🟥					🟧	🟧	
dead trunks, snags					🟧		🟧	🟧	🟥	🟥
old growth	🟥				🟥	🟥		🟥	🟥	🟨

	*Dendrocopos minor*	*Dendrocopos medius*	*Picoides tridactylus*	*Dendrocopos major*	*Dendrocopos syriacus*	*Dendrocopos leucotos*	*Picus canus*	*Picus viridis*	*Dryocopus martius*
diameter of trunk									> 35 cm
main elevation	2 - 8 m	5 - 10 m	4,5 - 5 m	3 - 8 m	2 - 4 m	8 m	2 - 8 m	2 - 10 m	8 - 15 m
diameter entrance	3,2 cm	3,2 - 4,5 cm	4,2 - 4,5 cm	4,5 - 5,7 cm	3,5 - 5,0 cm	5,5 cm	5,7 cm	6,5 cm	8,5 x 13 cm
diameter inner hole	10 - 12 cm	12 cm	10 - 13 cm	13 cm	11,4 cm	15 - 18 cm	9 - -12 cm	15 - 20 cm	> 25 cm
depth inner hole	10 - 18 cm	21 - 34 cm	26 - 30 cm	35 cm	34 cm	25 - 37 cm	29 - 50 cm	25 - 55 cm	31 - 55 cm
soft wood	🟥	🟥		🟥	🟨		🟥	🟥	
deciduous tree	🟥	🟥		🟥	🟥	🟥	🟥	🟥	🟥
coniferous tree	🟨	🟨	🟥	🟥		🟨	🟨	🟨	🟥
healthy tree			🟨	🟨	🟨		🟨	🟨	🟥
backward tree	🟥	🟥	🟥	🟥	🟥	🟥	?	?	🟥
infected by funghi	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
heartrott in tree	🟥	🟥	🟥	🟥	🟥	?	?	🟥	🟨
brokentree-top	🟥	🟥	🟥	🟥	🟨	🟥			
dead trunk, snag	🟥	?	🟥	🟥		🟨	?	?	
hole in trunk	🟨	🟨	🟥	🟥	🟥	🟥	🟥	🟥	🟥
plain bark on trunk			🟨	🟥	?	🟥	🟨		🟥
rough, chappy bark	🟥	🟥	🟨	🟥	🟥	?	?	?	
trunk free of branches									🟥
resinous bark			🟥	🟨					🟨
branch in crown of tree	🟥	🟥		🟥	🟥	🟥	?	?	
dead branch	🟥	?		🟥	🟥	🟥	?	?	

Table 6. Specific tree-type preferences for excavating nesting holes, in European woodpeckers: Despite the powerful Black Woodpecker, most of woodpecker species prefer weakened wood, infected by fungi or insects, rotten by heartrot or somehow broken and decayed; whereas wood of deciduous trees is much more attractive than that of coniferous trees. Only the Three-toed Woodpecker, adapted to the boreal forest, usually excavates its nest hole in spruce, pine or fir trees, even if the trees are sticky with resin (details following GLUTZ VON BLOTZHEIM & BAUER 1980).

the forest canopy that allow the warming sun to reach lower strata will support more insects – and hence more woodpeckers. Gaps and clearings created by grazing cattle e.g. are highly attractive to woodpeckers, especially when they include snags, old trees, and short vegetation in the understory. Ants profit from openings in the canopy big enough for the sun to warm the soil. Sunny edges also support sap flow under tree bark. That is why woodpeckers prefer such exposed trunks when ringing trees. Another phenomenon at sunny edges is „sunburn" of exposed tree trunks. Beech is sensitive to this impact and will develop an exquisite situation for woodpecker excavation of nest and roost holes on the hurt side of the trunk.

In Europe the White-backed Woodpecker is called a "dead-wood-specialist" par excellance, as it shows extraordinarily high requirements for a natural supply of old and dead trees (mostly birch and aspen in boreal forest; beech, maple and fir in montane woodland). In consequence this species, which is highly dependent on dead and dying wood, is extremely vulnerable to large scale timber harvest. As a result, in most countries the White-backed Woodpecker is listed in the highest category of endangered species. Examination of the areas of White-backed Woodpecker distribution on a larger scale, however, suggests a surprising gradient from north to south – a varying regional importance of dead wood for this species. The White-backed Woodpecker is a specialist of true old growth in Fenno-Scandian countries, strictly dependent on xylobiontic insects in dead and decayed wood (AULEN 1988). But this rare and sensitive woodpecker not only lives in astonishing high abundance in mixed forests of deciduous trees in southern parts of Europe, but also in quite inconspicuous forests of younger age, lacking any noteworthy amount of dead wood (e.g., in Abruzzo National Park/ Italy; BERNONI 1994)!

In a favorable climate (warm, mesic) within stands of beech trees, rich with sunny gaps, the supply of insects seems to be sufficient, and dead wood seems to be dispensable. Cool and moist, the woodland habitats in the far north force the White-backed Woodpecker to use prey in decaying wood, and to dwell on a very narrow niche; but the drier, warm, broadleaved forests in the far south enables the bird to greatly expand its niche. So the fundamental niche of White-Backed Woodpeckers allows for quite differing realized niches in local habitats and requirements of the species should not be generalized on a broad European scale.

If all the woodpeckers share a similar morphology and behavior, what possibilities are there for ecological niche separation? Differences in body mass and size provide a place to begin. European woodpeckers range from 20 g (Lesser Spotted Woodpecker) to 300 g (Black Woodpecker). These differences result in a great difference in ability to dress bark and to excavate wood. Different species have also evolved different tools, with highly specialized bills, skulls, and tongues. For example, the tongue varies from harpoon-like in form in Lesser, Middle and Great Spotted Woodpeckers (BLUME 1963), to brush-like for sap drinking, to glutinous (as a result of copious saliva) for catching ants. The latter tongues also show a fascinating flexibility, when in use. An arrangement of woodpeckers by functional group, shows a gradation from ant-eating types (with a less specialized ability to climb) to highly arboreal types equipped with techniques for anvil use and powerful hammering, using a harpoon-tongue to obtain insect larvae from tunnels in wood (SCHERZINGER 1989). There is also a linkage between techniques of excavation and preferred wood quality of the trees.

Patterns of treating bark, wood, seeds or foliage of trees by woodpeckers show a great diversity and are species-specific to some extent. They range from chipping or flaking away bark to chiseling of deep holes with powerful strokes at a small angle to the trunk. For example, the Black Woodpecker typically splits decayed wood and chisels deep holes in weakened trunks. The Three-toed Woodpecker superficially chips bark and chisels with slanting blows of the beak and digs shallow holes. The result of a hard day's work might be a totally scaled trunk and a ring of fragmented bark pieces round the root collar. An extreme effort of chiseling is done in horizontal strokes by Black and White-backed Woodpecker, even on hard, dry wood (like oak). Specific treating techniques may involve use of the bill, tongue, foot, and even breast feathers. The most complicated behaviour is required of those woodpeckers that collect cones, transport them, and use an "anvil" to open them to retrieve seeds (vocabulary following WINKLER et al. 1995). Techniques of food gathering are species-specific. In a synoptic view ground-foraging woodpeckers (which mostly collects ants by probing or digging in soil) are well separated from hammering types (which evolved specialized climbing techniques, and mostly search for bark-dwelling prey), and from birds using an anvil in a very complex performance. But it is also important to recognize that all woodpeckers are opportunists and will use simple gleaning if possible at anytime.

Woodpeckers are characterized by a high level of both inter- and intra-specific aggression. This is an adaptive behavior for living in a habitat of widely dispersed food, avoiding direct competitors. But in years of insect abundance, woodpeckers not only abandon their specific niches (SHORT 1982), but congregate in clusters of feeding individuals. During a bark-beetle disaster in Bavarian Forest National Park, the heavy work of scaling infected spruce-trees was done mostly by the powerful Black Woodpecker, while smaller woodpecker species – and even songbirds – made use of this opportunity to feed on the uncovered food supply in a commensal way (SCHERZINGER 1998)!

Vertical stratification and horizontal patchiness – as important structures in forests

The second essential parameter of quality in a woodpecker's habitat is the structure of the forest that determines cover, breeding, and feeding sites. Woodpeckers prefer weakened, hurt, or even dead parts of a tree for feeding and excavating, but they are exposed to a strong conflict. If increase in dead wood (and consequently prey density) is synchronized with a dramatic decrease of cover – as was the case in spruce stands of the Bavarian Forest National Park, following a bark-beetle outbreak, woodpeckers will leave the "land of milk and honey" when dead trees (lacking any cover) dominate the stands on a large scale (SCHERZINGER 1998).

Another aspect of structure in the forest is the supply of optimum drumming sites; woodpecker prefer trees with dried wood that has a good acoustic resonance.

From the view of nature conservation, discussion of woodpeckers focuses on their function as "carpenters of the forest," as these birds provide a supply of tree holes of high value for a diversity of creatures including dor-mice, bats, songbirds, small owls, honeybees, and others. In contrast to their powerful faculty to build holes even in hard trunks, woodpeckers usually invest only a minimum effort, when excavating a sleeping-hole; they seem to prefer semi-rotten snags, which might break down with the next wind-blow! Infiltrating rainwater facilitates degradation of wood in broken trunks, thus also facilitating the excavations of woodpeckers. As the process of rotting proceeds downward from year to year, woodpeckers will build new holes below those of previous years (e.g., see photo in JACKSON 1976), leading to a perforated "woodpecker-tree" or so called "woodpecker-flute". Investment is mostly greater when constructing a nest cavity, as some species will use them for more than one year. The Black Woodpecker, for example, can reuse its nest cavities because it excavates even in healthy hardwood like beech.

A comparison of specific nest cavity site preferences, the Black Woodpecker seems to have the highest demands among European species: a minimum diameter of tree-trunk (usually > 35 cm), a trunk with smooth bark, trunk free of branches, and sound wood – an important factor that reduces the risk of predation by the pine marten *Martes martes*. But most species prefer trees weakened by fungal infections, with dead branches, semi-rotten trunks, or other weakening, such as especially found in deciduous trees. The least desirable substrate seems to be healthy coniferous wood, with strong flow of resin. But it should be pointed that there are limits to the range of wood that can be used by woodpeckers that must excavate large holes in big trunks. Stand conditions in the forest influence suitability of trees for cavity excavation. For example, oak trees growing on dry and poor soil will produce a extraordinarily hard wood

woodpecker species	re-juven.	thicket	c osed canopy	even aged mature forest	uneven aged old growth	"steady state"	collapse	break down
Jynx torquilla							🟨	🟫
Dendrocopos syriacus							🟨	🟫
Dendrocopos minor						🟨	🟫	🟫
Picus canus						🟨	🟫	🟫
Dendrocopos medius					🟨	🟫	🟫	🟨
Picus viridis					🟨	🟫	🟫	🟫
Picoides tridactylus				🟨	🟫	🟫	🟫	🟫
Dendrocopos leucotos			🟨	🟫	🟫	🟫	🟫	🟫
Dendrocopos major		🟨	🟨	🟫	🟫	🟫	🟫	🟫
Dryocopus martius		🟨		🟫	🟫	🟫	🟫	🟫

Table 7. Linkage of European woodpeckers to structural types of tree stands: Over the long-term of development of natural woodland, tree stands pass through variable phases. Forced by natural dynamics, these permanently change affects structural characters, age classes, supply of dead wood and gaps – thus creating a permanent change of habitat quality for woodpeckers also. The very late phases, with „collapse" and „breakdown" offer the most attractive requisites, and may harbour all 10 species of European woodpeckers.

with fine-pored growth rings; such wood cannot be excavated even by the Black Woodpecker. In contrast, trees on soils rich in water and nutrients will produce suitable wood for most woodpeckers – especially when there is a mutualistic association between the woodpeckers and wood-rotting fungi which facilitate nest building for woodpeckers (BRÜNNER-GARTEN & SCHMIDT 1994). Dead wood is important, but even the White-backed Woodpecker – called an index-species of primary forests – will be satisfied with dead branches or a dead top in a living tree (GLUTZ VON BLOTZHEIM & BAUER 1980).

The shape and size of the entrance hole of a woodpecker cavity is often species-specific. In general, the diameter is as small as possible in order to defend against mammalian predators (SHORT 1982). But the form of a cavity entrance shows some variation depending on quality of wood. The entrance of a Three-toed Woodpecker cavity chiseled in fresh coniferous wood, looks quite circular, but in dry wood it is usually more square in form. When White-backed Woodpeckers excavate their hole at a slanting angle to take advantage of the softer wood in peripheral "splint" (*Alburnum*), the entrance takes on a broad oval shape rather than the typical circular shape found in vertical cavities (SCHERZINGER 1982).

Natural dynamics of forest succession continuously change habitat quality

How can we find a synoptic view of all these single aspects of habitat preference and niche differentiation in European woodpeckers in a context to natural development of woodlands? Long-time monitoring of development in primary forest have taught us that successional dynamics will never stop – even in the so called "climax" or "steady state." In a schematic sequence of development in a montane mixed forest, LEIBUNDGUT (1982) points out a minimum of four main stages, which may proceed in a long-term cycle lasting for centuries. While growing older, the forest will change structures of vertical stratification and horizontal patchiness, age class' and species' diversity of trees, also supply of dead wood, number of openings, density of snags or even probability of catastrophic events. This turnover does not affect the whole area of woodland at the same time, but runs – patch by patch – in an asynchronous cycle. Natural development leads to a coarse-grained mosaic (see REMMERT 1991). All the wood patches develop individually, while the growing forest changes habitat quality for woodpeckers in time. Supply of prey and cover for woodpeckers fluctuate continuously and the birds must find the best situations in this long-term run. The attractiveness of woodland habitat reaches a maximum in the very late phases of stand development, especially during the "collapse" and "break-down" of tree stands. Here the birds find an overlap of supply with very old trees with dead wood, cover, sunny openings in gaps and small clearings. The individual species of woodpeckers show differences in preference of stand structural phases. But the best use of all the different phases is managed by Black, White-backed and Great-Spotted Woodpeckers. The least flexible species are the Lesser-Spotted and the Grey-headed Woodpeckers.

Conclusions drawn for management of commercial forests seem to be quite clear: European woodpeckers show a high potential of ecological adaptability. This enables a successful integration of woodpecker conservation even under a regime of economic wood production. Despite the difficulties of conservation and promotion of old growth stands with sufficient dead wood within the framework of silviculture and forestry, it should be possible to maintain adequate refugia of woodpecker habitats not only in strict reserves, but also in commercial forests. As long as the essential requisites of habitat, the preferred tree species, suitable age-classes of trees, a useful number of snags or dead wood, and the continuity of non-fragmented woodland areas are considered in management planning, our woodpeckers may have a good chance to prosper. This means, however, that traditional goals of "clean" and "tidy" "mopping up" operations are out of place in a multifunctional forest, where sustained production of timber has the same value as sustained maintenance of species-diversity (SCHERZINGER 1996). For this effort, woodpeckers are the best indicator species!

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Woodpeckers in southern Lower Saxony
Screen shots from a video

Spechte in Süd-Niedersachsen: Bilder aus einem Video

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The video (Fig. 1–5) showed a hybrid-female between Grey-headed Woodpecker *Picus canus* and Green Woodpecker *Picus viridis*. The hybrid-female attempted to breed with a male Green Woodpecker in 1991. After the loss of the partner presumably by Goshhawk *Accipiter gentilis* or Sparrowhawk *Accipiter nisus*, the hybrid-female occupied a Grey-headed Woodpecker brood located in a distance of 75 m. The hybrid-female only provided parental care (breeding and feeding) up to the successful fledging of the young.

Der Film (Abb. 1–5) zeigte ein Bastard-Weibchen zwischen Grau- und Grünspecht, bei einem Brutversuch mit einem Grünspecht-Männchen. Nach dem Verlust des Partners durch Habicht oder Sperber vertrieb das Weibchen ein 75 m entfernt brütendes Grauspechtpaar Picus canis, brütete das Gelege der Grauspechte aus und zog die jungen Grauspechte allein auf.

Fig. 1. Hybrid-female near freshly excavated cavity in an alder *Alnus glutinosa. Bastard-Weibchen an frisch geschlagener Höhle in Erle.* **(Photo: Heinz-Waldemar Senge)**

Fig. 2. Hybrid-female at the cavity of the Grey-headed Woodpecker *Picus canus* in a willow-tree *Salix* ssp. *Bastard-Weibchen an der Grauspecht-Höhle in einer Weide.* **(Photo: Heinz-Waldemar Senge)**

Fig. 3. Hybrid-female feeds young Grey-headed Woodpeckers. *Bastard-Weibchen füttert junge Grauspechte.* **(Photo: Heinz-Waldemar Senge)**

Fig. 4. Hybrid-female feeds a young male of Grey-headed Woodpecker. Bastard füttert junges Grauspecht-Männchen. **(Photo: Heinz-Waldemar Senge)**

Fig. 5. Hybrid-female between Grey-headed Woodpecker and Green Woodpecker. *Bastard-Weibchen zwischen Grau- und Grünspecht.* **(Photo: Heinz-Waldemar Senge)**

Temporal use patterns of woodpecker nest trees in British Columbia

Zeitliche Nutzungsmuster von Specht-Brutbäumen in British Columbia

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Abstract

Conservation of woodpecker habitat within British Columbia's 50 million hectares of productive forest land relies primarily on the retention of forest patches and single trees during forestry operations. Trees selected for retention are recommended to have suitable habitat value for woodpeckers and other wildlife tree users. To provide background information for the development of wildlife tree retention strategies in southern British Columbia, we monitored active woodpecker nest trees from 1994 to 2000. Here we describe the characteristics and temporal use patterns of 408 woodpecker nests in 258 individual trees. We located seven sympatric woodpecker species (Red-naped Sapsucker *Sphyrapicus nuchalis*, Northern Flicker *Colaptes auratus*, Pileated Woodpecker *Dryocopus pileatus*, Downy Woodpecker *Picoides pubescens*, Hairy Woodpecker *Picoides villosus*, Three-toed Woodpecker *Picoides tridactylus*, and Black-backed Woodpecker *Picoides arcticus*) breeding in seven different tree species. Forty-two percent of all nest trees were dead, 40 % had visible sign of stem rot and 40 % had broken tops when first recorded as an active nest tree. Eleven percent of all active nests were part of simultaneous double or triple nesting events within single trees. Annual reassessments of all previously active nest trees from 1996 to 2000 revealed that 40 % were reused by woodpeckers and other cavity nesters (chickadees, nuthatches, bluebirds and squirrels). Complex patterns exist in the reuse of woodpecker nest trees by the same and other woodpecker species, and by other cavity-using species. We provide recommendations for conservation of woodpecker nest-tree habitat within the context of wildlife tree management in British Columbia.

Der Schutz von Spechthabitaten in einem 50 Millionen Hektar großen ertragreichen Waldgebiet in British Columbia beschränkt sich hauptsächlich auf den Schutz von Waldinseln und Einzelbäumen vor forstlichen Eingriffen. Die ausgewählten Bäume sollten dabei für die Nutzung durch Spechte und andere Wildtiere besonders geeignet sein. Um Grundlagenwissen für die Entwicklung von Schutzstrategien für solche Bäume in South British Columbia zu erhalten, haben wir besetzte Specht-Brutbäume von 1994 bis 2000 beobachtet. Hier beschreiben wir die Charakteristika und den zeitlichen Verlauf der Nutzung von 408 Spechthöhlen in 258 Einzelbäumen. Wir fanden sieben sympatrisch vorkommende Spechtarten (Sphyrapicus nuchalis, Colaptes auratus, Dryocopus pileatus, Picoides pubescens, P. villosus, P. tridactylus, and P. arcticus), die in sieben unterschiedlichen Baumarten brüteten. Als sie das erste Mal als Brutbäume registriert wurden, waren bereits 42 % der Bäume tot, 40 % zeigten sichtbare Zeichen von Stammfäulnis und 40 % wiesen abgebrochene Kronen auf. Elf Prozent aller besetzten Bruthöhlen wurden Zweit- oder Drittnutzungen ein und desselben Brutbaumes. Die jährliche Neubegutachtung (1996–2000) aller vormals besetzter Brutbäume erbrachte, dass 40 % von Spechten bzw. anderen Höhlenbewohnern (Meisen, Kleibern, Berghüttensängern und Eichhörnchen) erneut genutzt wurden. Komplexe Muster existierten bei der erneuten Nutzung von Spechthöhlen und -brutbäumen durch dieselbe oder eine andere Spechtart sowie hinsichtlich anderer Höhlenbrüter. Wir machen Aussagen zum Schutz von Specht-Brutbäumen im Allgemeinen und im Zusammenhang mit dem Wildtier-Baum-Management in British Columbia.

Introduction

Concern regarding the conservation of woodpecker habitat is increasing in British Columbia and other jurisdictions worldwide because woodpeckers require large standing dead and decaying trees, habitat components which are experiencing widespread reduction in forested landscapes. As primary cavity excavators, woodpeckers play important ecological roles in forested ecosystems by providing nesting and roosting opportunities for a variety of other species that require tree cavities (MACHMER & STEEGER 1995, MARTIN & EADIE 1999). Furthermore, because of their tree excavating habits, some woodpecker species have been suggested to function as ecological keystone species (DAILY et al. 1993, POWER et al. 1996).

Trees with woodpecker cavities are often used repeatedly over time, either by the same breeding pair, by different pairs of the same species, or by multiple species, either sequentially or simultaneously (DAILY et al. 1993, SEDGWICK 1997, MARTIN & EADIE 1999). Trees repeatedly used by cavity nesters may require special protection within managed forests, if populations of woodpeckers and other cavity nesters are to be maintained. However, little information is available on the type, condition and frequency of trees that are used repeatedly over time. In 1996, we initiated a study on the dynamics of cavity nest trees in forests of southern British Columbia. Here we report on the part of the study that addresses temporal use patterns of woodpecker nest trees from 1996 to 2000. Our primary objectives were to examine the use of woodpecker nest trees over time and to provide management recommendations for nest-tree retention in operational forestry.

Study Area

We conducted surveys for breeding cavity nesters in the Deer Creek watershed of Arrow Forest District, southern British Columbia (49°30'N, 118°00'W; Fig. 1). Elevation of the area surveyed ranges from 500 to 1,450 meters, and the area is generally south-west facing. Most of the stands surveyed are managed for industrial forestry and consist of mature 85 to 95 year-old trees, with some younger patches of Lodgepole Pine *Pinus contorta*. Dominant conifer species are Douglas-fir *Pseudotsuga menziesii*, Lodgepole Pine, and Western Larch *Larix occidentalis*, with a minor component of localized Western Redcedar *Thuja plicata*, Western Hemlock *Tsuga heterophylla*, Western White Pine *Pinus monticola*, and Ponderosa Pine *Pinus ponderosa*. Broad-leafed trees are also present as a minor component, consisting primarily of Trembling Aspen *Populus tremuloides* and Paper Birch *Betula papyrifera*. The most significant forest health agents are endemic populations of Mountain Pine Beetle *Dendroctonus ponderosae*, the Root Disease *Armillaria ostoyae*, and Larch Dwarf Mistletoe *Arceuthobium laricis*. Common heart rot fungi responsible for the wood decay that facilitates cavity excavation by primary cavity nesters include White Spongy Trunk Rot *Fomes fomentarius*, Hardwood Trunk Rot *Phellinus igniarius* and Aspen Trunk Rot *Phellinus tremulae* on broad-leafed trees, and Red Ring Rot *Phellinus pini* and Brown Crumbly Rot *Fomitopsis pinicola* on coniferous trees.

Materials and Methods

Nest Searches

We searched approximately 4,500 hectares of the watershed for active nests of woodpeckers between May and early July 1996 to 2000 by inspecting trees for cavities, examining the ground for fresh wood chips, following adult birds, and listening for begging chicks. We did not search the area evenly and systematically as parts of the watershed are inaccessible; instead, we preferentially targeted accessible areas where woodpeckers are likely to occur, to obtain as high a sample size of active nest trees as possible. We considered a nest cavity to be active if a bird or mammal was observed incubating eggs or caring for young.

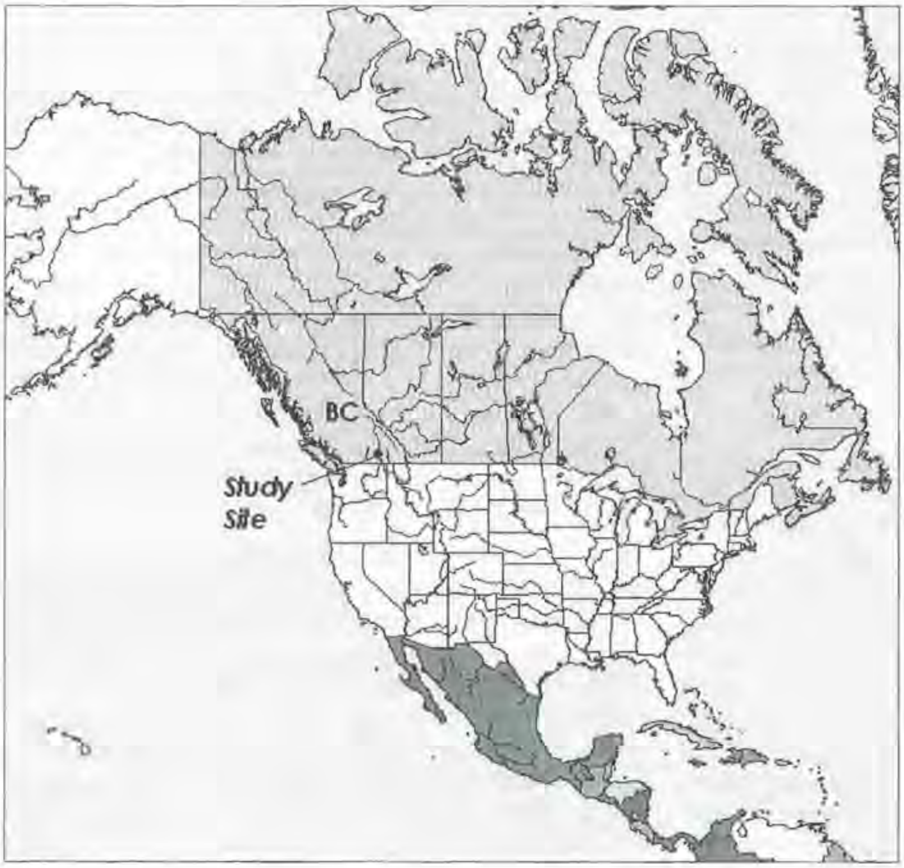

Fig. 1. Location of study area.

Nest Tree Assessments

For each confirmed active nest tree, we recorded tree species and presence of broken tops or stems, fungal decay (on the basis of visible fruiting bodies), and old excavated woodpecker cavities. We also identified the cavity-nesting species using the tree. We revisited nest trees at least twice during the survey periods to confirm active use of cavities and repeated use of previously occupied trees. Although re-assessment of active nest trees commenced in 1996, some nest trees in the study area had initially been located as part of a different study during 1994 and 1995.

Data Analysis

We provide standard summary statistics for most comparisons. We used a chi-square model to compare the frequency of broad-leafed and coniferous nest trees that were dead when first detected with an active nest and performed the analysis with JMP statistical software (SALL & LEHMAN 1996).

Results

Woodpeckers and the species and condition of their nest trees

From 1994 to 2000, we observed 408 active nests of seven woodpecker species in 282 trees (Table 1). The latter number includes multiple occupancies of the same trees by different woodpecker species but excludes multiple occupancies by the same woodpecker species over the study period. Exclusion of all multiple occupancies resulted in a total of 258 individual nest trees. The sample is dominated by Red-naped Sapsucker *Sphyrapicus nuchalis* nests which account for more than 50 % of all nests and nest trees. A total of seven tree species were used, with broad-leafed species (Trembling Aspen and Paper Birch) accounting for 72 % of all nest trees. The most frequently used coniferous tree species were Western Larch and Douglas-fir. Western Redcedar and Lodgepole Pine were used only by Three-toed Woodpeckers *Picoides tridactylus*, while Trembling Aspen was used by six of the seven woodpecker species. For most species, aspen accounted for half or more of all nest trees. We observed Pileated *Dryocopus pileatus*, Black-backed *Picoides arcticus*, and Downy Woodpeckers *Picoides pubescens* nesting in only two tree species (possibly related to small sample size), Red-naped Sapsuckers, Northern Flickers *Colaptes auratus*, and Hairy Woodpeckers *Picoides villosus* in five tree species and three-toed woodpeckers in six tree species (Table 1).

Approximately 40 % of all nest trees were dead, with the same proportion exhibiting broken stems and stem rot (Fig. 2). There was no difference between broad-leafed and coniferous nest trees in the proportion of trees with broken stems and stem rot. However, significantly more conifers were dead when first detected as an active nest tree (63 %) relative to broad-leafed species (28 %) (chi-square = 19.1, d.f. = 1, $p < 0.0001$; Fig. 2).

Table 1. Number of active nests and nest trees, and proportion of nest tree species by woodpecker species, Deer Creek watershed, southern British Columbia.

	No.	No.	Nests tree species[1] (% of total nest trees)						
Woodpecker Species	nests	nest trees	DF	WL	LP	PP	WC	TA	PB
Red-naped Sapsucker *Sphyrapicus nuchalis*	239	147	8	3	0	1	0	50	37
Northern Flicker *Colaptes auratus*	63	40	10	18	0	13	0	50	10
Hairy Woodpecker *Picoides villosus*	56	49	2	27	0	2	0	51	18
Three-toed Woodpecker *Picoides tridactylus*	27	24	8	29	42	4	4	13	0
Pileated Woodpecker *Dryocopus pileatus*	14	13	0	0	0	23	0	77	0
Black-backed Woodpecker *Picoides arcticus*	6	6	33	67	0	0	0	0	0
Downy Woodpecker *Picoides pubescens*	3	3	33	0	0	0	0	67	0
Totals	408	282	8	13	4	4	0.4	48	24

[1] DF = Douglas-fir, WL = Western Larch, LP = Lodgepole Pine, PP = Ponderosa Pine, WC = Western Redcedar, TA = Trembling Aspen, PB = Paper Birch

Use of nest trees within years

Eighty-nine percent of the 408 woodpecker nesting events involved single woodpecker pairs occupying a tree while 10 % involved double nesting events with various species combinations (Table 2). We observed only one triple nesting event by a Red-naped Sapsucker, Northern Flicker, and Mountain Chickadee *Poecile gambeli* pair within a single tree. The simultaneous double nesting events can be divided into (i) two woodpecker pairs nesting in the same tree and (ii) a single woodpecker pair together with a non-woodpecker species (Table 2). All five cases of double woodpecker occupancy involved the Northern Flicker. We observed 16 double nesting events involving woodpecker and non-woodpecker pairs, nine of which involved Northern Flying Squirrel *Glaucomys sabrinus* and Red-naped Sapsucker (Table 2), accounting for 100 % of all observed simultaneous nesting events of Northern Flying Squirrel in our study area. Other non-woodpecker species observed in simultaneous nesting events with woodpeckers included Chestnut-backed Chickadee *Poecile rufescens*, Black-capped Chickadee *P. atricapillus*, Red-breasted Nuthatch *Sitta canadensis*, and Red Squirrel *Tamiasciurus hudsonicus*.

Table 2. Simultaneous double nesting events (n = 21 or 42 nests) by cavity nesters within individual trees, Deer Creek watershed, southern British Columbia.

Species combinations	No. of double nesting events	Percent of total
Woodpecker – Woodpecker	5	24
Northern Flicker – Pileated Woodpecker	3	14
Northern Flicker – Red-naped Sapsucker	2	10
Woodpecker – Non-Woodpecker	16	76
Red-naped Sapsucker – Northern Flying Squirrel	9	43
Red-naped Sapsucker – Red Squirrel	1	5
Red-naped Sapsucker – Chestnut-backed Chickadee	2	10
Red-naped Sapsucker – Black-capped Chickadee	1	5
Three-toed Woodpecker – Red Squirrel	1	5
Three-toed Woodpecker – Red-breasted Nuthatch	1	5
Northern Flicker – Chestnut-backed Chickadee	1	5

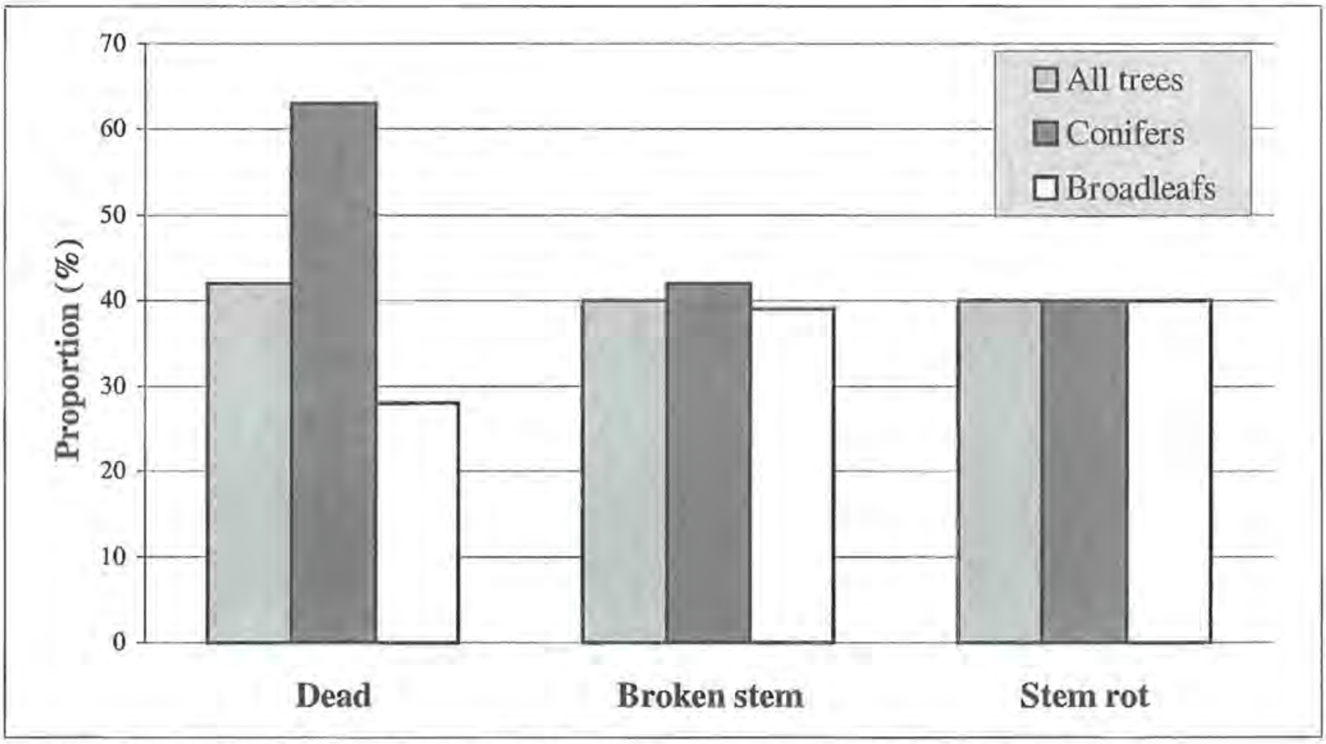

Fig. 2. Condition of woodpecker nest trees (n = 257), Deer Creek watershed, southern British Columbia.

Use of nest trees across years

Total reuse of woodpecker nest trees by all groups of cavity nesters during the year following a documented nesting event was 40 %. Pairs of the same woodpecker species, different woodpecker species and non-woodpecker species accounted for 27, 5, and 8 %, respectively. In addition to the six non-woodpecker species listed in Table 2, a Mountain Bluebird *Sialia currucoides* also reused a woodpecker nest tree in a subsequent year. Reuse of available nest trees (*n* = 256) over the different time periods of the study (maximum = 5 years, 1996–2000) shows a steady increase with number of years available for reuse (Fig. 3).

Indirect evidence of repeated use of trees for nesting or roosting in cavities is provided by the multitude of woodpecker cavities we detected in individual trees. For the tree species observed in this study, the broad-leafed species Trembling Aspen and Paper Birch showed the highest mean and maximum number of cavities per tree. Ponderosa Pine and Western Larch also showed relatively high numbers of cavities, while Douglas-fir showed intermediate and Lodgepole Pine the lowest values (Table 3). Note that when we located active nests, the nest trees showed a variety of decay conditions and previous woodpecker use in the year of detection. Forty percent of all nest trees had broken stems (see Fig. 2) and these trees might have had cavities in the parts that had broken off before we detected the first active nest cavity. Therefore, the values in Table 3 are likely underestimates of the number of cavities that woodpeckers excavated within individual trees.

Table 3. Mean (SE) and maximum number of woodpecker nest cavities observed on individual trees by tree species, Deer Creek watershed, southern British Columbia.

Tree species	*n*	Mean (SE)	Maximum
Trembling Aspen	116	3.8 (0.3)	14
Paper Birch	63	3.6 (0.4)	14
Ponderosa Pine	11	3.2 (1.1)	13
Western Larch	34	2.7 (0.4)	11
Douglas-fir	22	2.1 (0.4)	7
Lodgepole Pine	10	1.1 (0.1)	2

Discussion

The frequency of tree species used by nesting woodpeckers clearly indicates the importance of Aspen and Birch as nest trees. Although Red-naped Sapsuckers nesting in broad-leafed trees accounted for a large proportion of all nests in our dataset (45 %), most of the other woodpecker species also showed extensive use of aspen and birch. Although we did not systematically collect data on availability of potential nest trees and can therefore not address preference by woodpeckers for particular tree species, other studies in the Pacific Northwest have documented a preference for broad-leafed nest trees (for example, HARESTAD & KEISKER 1989, MARTIN & EADIE 1999). In our study area, forest

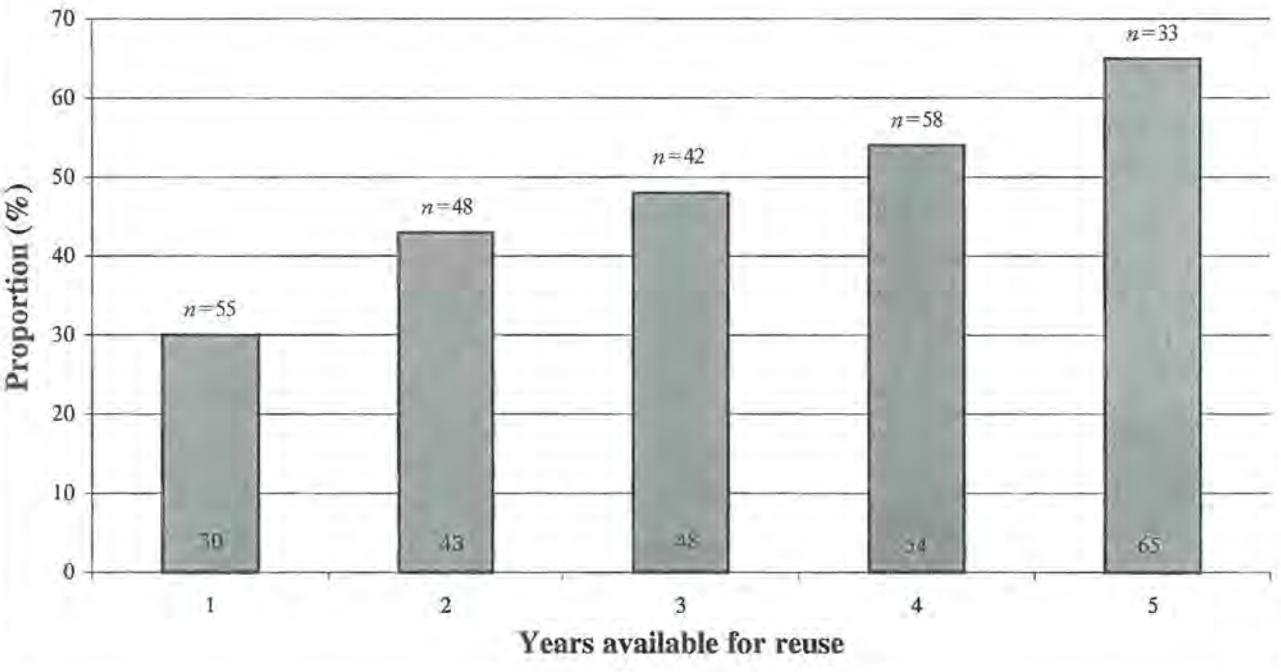

Fig. 3. Proportion of reuse of woodpecker nest trees over time, Deer Creek watershed, southern British Columbia.

stands are primarily Coniferous (> 80 %). These coniferous areas received higher sampling effort than did groves of aspen and birch; the high use of broad-leafed trees by cavity nesters may therefore indicate preference for these tree species in our study area as well.

A large proportion of the nest trees we located had broken stems and visible sign of heartwood decay fungi which is consistent with results from other investigations on the presence of heart rot in cavity nest trees (for example, McCLELLAND 1977, RAPHAEL & WHITE 1984, HARESTAD & KEISKER 1989, BULL et al. 1997). Broken stems allow fungi to enter tree trunks and visible fruiting bodies are an indication of well-established stem rot. Because we were only able to infer stem rot on the basis of visible fruiting bodies, our values for nest trees containing heart rot are likely underestimates as rot establishes inside stems well before fruiting bodies are visible on the outside of stems (MANION 1991). It is therefore likely that the susceptibility of aspen and birch to certain heart-rot fungi (for example, *Phellinus tremulae* and *Phellinus igniarius*, respectively) facilitates cavity excavation and accounts for the high proportional use of these tree species.

While broad-leafed trees in our study were most often used by nesting woodpeckers while the trees were still alive, coniferous nest trees were most often dead when first detected as active nest trees. The importance of standing dead trees for cavity nesters has been well established (MACHMER & STEEGER 1995, WINKLER et al. 1995, BULL et al. 1997) but large-scale industrial forestry can drastically reduce the density of standing dead trees within forest stands. Worker safety regulations in British Columbia result in the removal of most dead and decaying trees during forestry operations and firewood cutting in rural areas also contributes to the decline in dead trees. These pressures potentially threaten the conservation of woodpecker populations and entire species. In northern Scandinavian landscapes where the majority of natural forests (especially broad-leafed stands) have been removed, ANGELSTAM & MIKUSINSKI (1994) documented local extirpations or serious population declines in several woodpecker species. Forest management must ensure an adequate supply of dead and decaying trees (both broad-leafed and coniferous species) if woodpecker populations are to be sustained over the long term.

To meet wildlife conservation goals, forest managers require guidance on the types and densities of trees that should be retained in harvesting and silviculture. This study demonstrated considerable reuse of nest trees. We therefore recommend that active nest trees and trees with evidence of past woodpecker nesting or roosting be included in wildlife tree retention prescriptions. However, because woodpecker nest trees are generally either alive and decaying or dead, most will not remain standing for long periods of time. STEEGER & DULISSE (unpubl.) showed that approximately half of 66 cavity nest trees detected during the 1994 breeding season (this dataset includes some of the woodpecker nest trees presented in this paper) fell within five years of being detected as nest trees due to forestry-related and non-human causes. This lack of longevity necessitates planning for a sustainable supply of dead and decaying trees over the long term and retention of habitat trees must include presently suitable trees as well as future wildlife trees. In British Columbia, the retention of wildlife trees in patches and/or as single trees is required within all cutblocks (Province of British Columbia 2000). Patch retention in forestry operations is useful in two ways: (1) dead and potentially hazardous nest and roost trees can be left without compromising the safety of forest workers and (2) patches can be established such that they also contain important woodpecker feeding substrate (insect-infested trees) and future wildlife trees. Identification and subsequent protection of woodpecker nest trees will facilitate the conservation of woodpecker species and secondary cavity-using species (for example, ducks, owls, swallows, bluebirds, squirrels, bats; STEEGER et al. 1996, BONAR 2000) that depend on woodpecker cavities to meet their life requisites.

Acknowledgements

Aside from the authors, the following people participated in the field data collection: Marc-André Beaucher, Rachel Holt, Carl Savignac, and Maryann McDonaugh. Marlene Machmer reviewed the manuscript. The study was funded by Forest Renewal British Columbia and administered by Darryl Atkinson of the Science Council of British Columbia.

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Effects of selective logging on a guild of 13 syntopic woodpecker species in a Malaysian forest reserve

Auswirkung des selektiven Holzeinschlags auf eine Gilde von 13 syntopisch lebenden Spechtarten in einem Malaysischen Wald-Reservat

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Abstract

Woodpeckers, Family *Picidae*, are considered sensitive to logging and deforestation because they nest in tree cavities and often forage on large trunks or standing dead trees. The diverse woodpecker community found in the lowland rainforests of Peninsular Malaysia was investigated in 5 and 10 year old selectively logged forest and in unlogged forest using census, foraging, and habitat availability data. Relative abundance differed significantly both between logged and unlogged forest and between logged stands. Although members of this guild did not respond uniformly to logging, woodpeckers were generally less abundant in the 10 year old forest. This trend, supported by an earlier study in 45 year old managed forest, reflects a lack of heterogeneity in managed stands with relatively few snags and treefall gaps. Important foraging substrates were identified, and, combined with substrate availability data, were effective in predicting changes in abundance of individual species across forest types. The current practice of maintaining patches of virgin forest within logging concessions appears to be an effective way of maintaining a diverse community of woodpeckers and other cavity-nesting birds. Maintaining a portion of snags and "overmature" trees in logged stands may help increase the abundance of dead wood dependent species across the reserve.

Man nimmt an, dass Spechte sehr sensibel gegenüber Holzeinschlag und Abholzung sind, weil sie in Baumhöhlen nisten und häufig an großen Stämmen oder stehendem Totholz ihre Nahrung suchen. Die verschiedenartige Spechtgruppe, die in den tiefliegenden Regenwäldern der malayischen Halbinsel vorkommt, wurde durch Census-Zählungen und Daten zur Nah-rungssuche und Nahrungsverfügbarkeit in Beständen untersucht, in welchen vor 5 und vor 10 Jahren selektiver Holzeinschlag durchgeführt wurde, sowie in primären Urwäldern. Das relative Vorkommen unterschied sich erheblich, sowohl zwischen Wald mit und ohne Einschlag als auch zwischen verschiedenen Standorten mit Einschlag. Obwohl die Mitglieder in dieser Gilde nicht gleich auf die Holznutzung reagierten, gab es generell weniger Spechte im vor zehn Jahren eingeschlagenen Wald. Dieser Trend, der durch Ergebnisse früherer Studien in 45-jährig genutztem Wald unterstützt wird, zeigt die fehlende Heterogenität in genutzten Beständen mit relativ wenig stehendem Totholz und Öffnungen durch das Umfallen einzelner Stämme. Wichtige Substrate zur Nahrungssuche wurden identifiziert und konnten zusammen mit ihrer Verfügbarkeit als ein effektives Instrument dienen, um Veränderungen in der Häufigkeit einzelner Arten in verschiedenen Waldtypen vorauszusagen. Die derzeitig gängige Praxis, dass nämlich Primärwald zwischen den genutzten Bereichen belassen bleibt, scheint ein effektiver Weg zu sein, um eine mannigfaltige Specht- und Höhlenbrütergemeinschaft zu erhalten. Die Erhaltung eines Teils der abgebrochenen Stämme zusammen mit dem Erhalt der überalteten Bäumen in den Einschlagsbereichen könnte die Dichte der auf Totholz angewiesenen Arten im Gebiet erhöhen.

Introduction

The rapid destruction and alteration of the world's tropical rainforests is well known. In Southeast Asia, exploitation of forests for timber harvesting is a major cause of habitat destruction and degradation. Although this form of forest use is often considered sustainable, the long term effects of selective logging on plant and animal communities are not well known. Research into the short term effects of logging has raised questions about effective management of logged forests (JOHNS 1988, VINCENT 1995). Studies of bird communities in peninsular Malaysia and Borneo indicate that bird diversity and species composition are affected by selective logging (WONG 1985, JOHNS 1989, JOHNS 1996, LAMBERT 1992). Understory insectivores, such as babblers, disappear or become rare after logging, and edge species, such as bulbuls, increase in abundance and penetrate the interior of logged stands.

Woodpeckers are often considered sensitive to logging because most species excavate nests in tree cavities and many forage on dead wood. Studies in temperate regions indicate that snags (standing dead trees) are less common in logged forest compared to unlogged or old growth forest (ROSENBERG et al. 1988). Research in the tropics indicates that snags may be less common at lower latitudes (GIBBS et al. 1993) and that tree cavities are less common in logged compared to unlogged tropical forest (PATTANAVIBOOL & EDGE 1996). Studies of rare or endangered woodpeckers often indicate that these species need a substantial number of mature, "overmature" or dead and dying trees upon which to forage or excavate cavities (NELSON 1898, ALLEN &

KELLOGG 1937, TANNER 1942, DENNIS 1948, TANNER 1964, GREENWAY 1967, JACKSON et al. 1979, COLLAR et al. 1994, HANULA & FRANZREB 1998).

Woodpeckers are extremely diverse in Southeast Asian rainforests. In peninsular Malaysia, as many as 15 species of woodpecker can be found in a single patch of lowland rainforest, representing the highest alpha diversity for woodpeckers in the world (SHORT 1978, WELLS 1999). They comprise a higher percentage of the total avifauna than in other tropical regions, and may therefore be important for conservation (Table 1). Diversity of form and appearance within this group is also high. Extremes in body size are represented by the Great Slaty Woodpecker (*Mulleripicus pulverulentus* – weighing up to 550 g) and the Rufous Piculet (*Sasia abnormis* – weighing as little as 7 g), and a variety of plumage and color patterns can be found (SHORT 1982).

The goal of this study was to document possible changes in the structure of the woodpecker community by determining the relative abundance of species in different forest types. I also wanted to know how availability of important foraging resources related to changes observed due to logging. A secondary purpose of this study was to assess the effectiveness of Virgin Jungle Reserves at preserving a diverse and abundant woodpecker community.

Field Site

For approximately 7 months, I worked at a Sungai Lalang Forest Reserve in the state of Selangor, West Malaysia. Three research sites were located in the reserve. The first site, Compartment 18 (hereafter referred to as 5 year logged forest), was logged from November 1993 to September 1995. The forest at Compartment 18 appeared highly disturbed, but foraging resources such as large stumps, snags, and logs left behind after logging were abundant. The second site, Compartment 33 (hereafter referred to as 10 year logged forest), was logged from January 1990 to March 1991 and looked much more like primary forest structurally. However, certain resources such as snags and logs seemed low in abundance. The third site was located in a patch of unlogged forest designated as a protected area known as a Virgin Jungle Reserve (hereafter referred to as unlogged forest). These reserves are designated in logging concessions throughout peninsular Malaysia and are meant to preserve sensitive wildlife species. Trees in the Virgin Jungle Reserve are very large in girth and height, and snags seemed abundant.

Methods

My first task was to determine differences in woodpecker abundance among the three sites using line transect surveys. Four kilometers of transects were established at each site, and each transect was walked 6 times at a rate of approximately 0.5 km/h. Every woodpecker seen or heard along a transect was counted. Distributional differences in species were determined using a likelihood ratio Chi square (G statistic), and differences between forest types for individual species and overall woodpecker abundance were determined using binomial tests.

The next step was to identify foraging preferences and determine differential use of substrates among forest types. Woodpeckers were followed opportunistically during the study period and their foraging behavior observed. In this paper, only one aspect of behavior is discussed – substrate choice. I conducted a correspon-

Table 1. Woodpecker diversity vs. overall bird diversity at 12 tropical forest sites. WP = woodpecker.

	Location	Total no. of WP species	Total no. of bird species	Precent of avifauna comprised by WPS	Source	Forest Type
NEO-TROPICAL SITES	Barro Colorado Island, Panama	5	197	**2.5**	KARR 1990	Seasonal lowland rainforest
	La Selva, Costa Rica	5	170	**2.9**	KARR 1990	Aseasonal lowland rainforest
	Manaus, Brazil	12	293	**4.1**	COHN-HAFT 1997	Seasonal lowland rainforest
	Manu, Peru	10	311	**3.2**	KARR 1990	Seasonal lowland rainforest
AFRO-TROPICAL SITES	Basse Cassamance NP, Senegal	2	64	**3.1**	THIOLLAY 1985	Semi-deciduous wet (lowland)
	Makokou-Belinga area, Gabon	7	250	**2.8**	THIOLLAY 1985	Lowland rainforest
	Tai NP, Ivory Coast	5	233	**2.1**	THIOLLAY 1985	Lowland rainforest
	Budongo Forest Reserve, Uganda	2	73	**2.7**	OWIUNJII 1998	Lowland rainforest
SOUTH EAST-ASIAN SITES	Danum Valley Cons. Area, Sabah	16	254	**6.2**	LAMBERT 1990	Aseasonal lowland rainforest
	Pasoh Forest Reserve, Malaysia	15	186	**8.1**	ICKES unpubl. data	Aseasonal lowland rainforest
	Sungai Tekam, Malaysia	11	193	**5.7**	JOHNS 1986	Aseasonal lowland rainforest
	Similajau, Sarawak	10	193	**5.2**	DUCKWORTH et al. 1996	Aseasonal lowland rainforest

dence analysis of substrate preference and forest type. This analysis ordinates substrate variables in respect to the forest types in which they were most frequently used.

Finally, I wanted to determine if the relative abundance of woodpeckers correlated roughly with the abundance of preferred substrates, and if certain substrates were more important than others were in determining total abundance. At each study site, three one hectare plots were established for an unrelated floristic study. Each one ha plot was divided into 100 10 x 10 m subplots. At each site, 100 subplots were randomly sampled among the three ha of plots for the following variables: arboreal ant and termite nests, snags, logs, dead wood patches, and dead lianas. In each 10 x 10 m subplot every tree, log, and liana was scanned carefully using binoculars. Every variable seen was documented and measured so that an estimate of surface area could be calculated.

To determine if a substrate was used preferentially in respect to its abundance, I constructed use vs. availability profiles for each forest type. I calculated use vs. availability by subtracting the proportional availability of a given substrate (in comparison to the other substrates sampled) from the their proportional use.

Results

Relative abundance. Differences in abundance were observed among forest types (Table 2). The likelihood ratio Chi square statistic indicated that the distribution of species differed significantly among forest types, and the binomial statistic indicated that overall woodpecker abundance differed significantly when forest types were compared in a pairwise manner. Although individual species showed different trends in their abundance, woodpeckers, in general, were most abundant in the unlogged forest, and least abundant in the 10 year logged forest.

Substrate preference. Although variation was notable in substrate use among species, some substrates, such as snags and live wood, were used frequently by most species. The most commonly used substrates were live wood, dead wood of various types (patches on live trees, snags, logs or fallen trees, and dead lianas), and arboreal ant and termite nests. Results from correspondence analysis revealed a changing pattern of substrate use with forest type (Fig. 1). For example, the substrates "*Macaranga*" and "bamboo" ordinated near the logged forest sites. Both of these plants are commonly found in disturbed areas and were absent in the unlogged forest. Woodpeckers were able to use such novel resources when available. Live wood oriented almost exactly in the middle of the three forest types, indicating it was used in even frequency at all sites. Some substrates, such as dead wood patches, were used frequently in 10 year logged forest and unlogged forest, whereas other substrates, such as snags, were used frequently in 5 year logged forest and unlogged forest. In general, a larger variety of substrates were used in the unlogged forest than in any other forest type.

Substrate availability. The raw data indicate that logs were much more abundant in the 5 year forest than in the other two forest types (Fig. 2). To increase resolution in the remaining data, the variable "log" was removed from Fig. 2. Consequently, the three variables "d. liana" (dead liana), "A/T" (ant and termite nest), and "patch" (dead wood patch) increase in abundance in older forest types (Figure 3). Snags, like most other resources, were highest in abundance in the unlogged forest. However, unlike the other substrates, snags were lowest in abundance in the 10 year old forest. If the pattern of woodpecker abundance correlates with the pattern of substrate availability, then one would expect snags to be highly preferred and thus account for the higher abundance of woodpeckers in the 5 year old forest compared to the 10 year old forest.

Use vs. availability. Use vs. availability profiles indicated that snags were a strongly preferred substrate in all forest types, whereas dead wood patches were least preferred (Fig. 4). Other substrates were generally used in similar proportion to their availability. The strong preference for snags in all forest types supports the suggestion that snags are important in determining the abundance of woodpeckers found in logged forest.

Discussion

In this study, significant changes in the woodpecker community associated with logging were documented. Overall abundance was highest in the unlogged forest or VJR, and this protected area appears to be effective at maintaining a diverse and abundant group of woodpeckers. The 10 year old forest had the lowest woodpecker abundance of the three sites. This result may seem surprising, but consideration of foraging preferences provided some clarification. Although woodpeckers were able to use novel resources that were available in the logged forest, a larger variety of substrates were abundant in the unlogged forest. Both logged sites had lower abundance of resources than the unlogged forest, and the main difference between the five and 10 year old logged forest was the abundance of dead wood. Because of the damage caused by tree felling and extraction, the five year old site had a relatively high abundance of logs and snags. As this residual of dead wood decayed, very few new snags or treefalls occurred, and the older logged stand was depauperate of these important resources. This conclusion is not based solely on

Table 2. Relative abundance of woodpeckers in 5 and 10 year logged forest and unlogged forest at Sungai Lalang Forest Reserve. The last three columns are p values for binomial comparisons of each forest type to another forest type. Significant (< 0.05) p values are represented in boldface.

SPECIES	ENGLISH NAME	L5	L10	Unig	5/10	10/Un	Un/5
Sasia abnormis	Rufous Piculet	5	*	4	**0.03**	0.06	0.25
Hemicircus concretus	Grey-and-Buff Woodpecker	1	2	8	0.38	**0.04**	**0.02**
Meiglyptes tristis	Buff-rumped Woodpecker	11	5	4	0.07	0.25	**0.04**
Meiglyptes tukki	Buff-necked Woodpecker	3	12	16	0.31	**< 0.001**	**0.002**
Celeus brachyurus	Rufous Woodpecker	14	*	7	**< 0.001**	**0.008**	**0.002**
Picus puniceus	Crimson-winged Woodpecker	11	3	14	**0.02**	**0.005**	0.13
Picus mentalis	Checker-throated Woodpecker	4	14	21	**0.01**	0.07	**0.004**
Picus miniaceus	Banded Woodpecker	6	0	1	**0.02**	0.50	0.05
Blythipicus rubiginosus	Maroon Woodpecker	14	13	8	0.15	0.10	0.80
Dinopium rafflesii	Olive-backed Woodpecker	1	*	*	NA	NA	NA
Reinwardtipicus validus	Orange-backed Woodpecker	4	13	13	**0.02**	0.15	**0.02**
Dryocopus javensis	White-bellied Woodpecker	12	0	14	**< 0.001**	**< 0.001**	0.14
Mulleripicus pulverulentus	Great Slaty Woodpecker	8	0	5	**0.004**	**0.03**	0.16
TOTAL **$G^2 = 35.0$ (df = 10)** **$P < 0.001$**		**94**	**54**	**115**	**< 0.001**	**< 0.001**	**0.02**

this study at three sites, but is supported by other studies (JOHNS 1989, 1992, STYRING & ICKES 2001). Other resources such as ant and termite nests, dead wood patches, and certain understory vegetation were more abundant in the 10 year old logged stand, but these resources appeared to be less important than snags in determining the abundance of a majority of species. Resource use vs. availability profiles indicated that snags are the most in demand foraging resource for woodpeckers in these forests. Thus, snags are likely to be very important in determining the abundance and diversity of woodpeckers in logged forest.

These results are not surprising to many woodpecker biologists. In temperate regions, where woodpeckers are more intensely studied, and where viewed as important

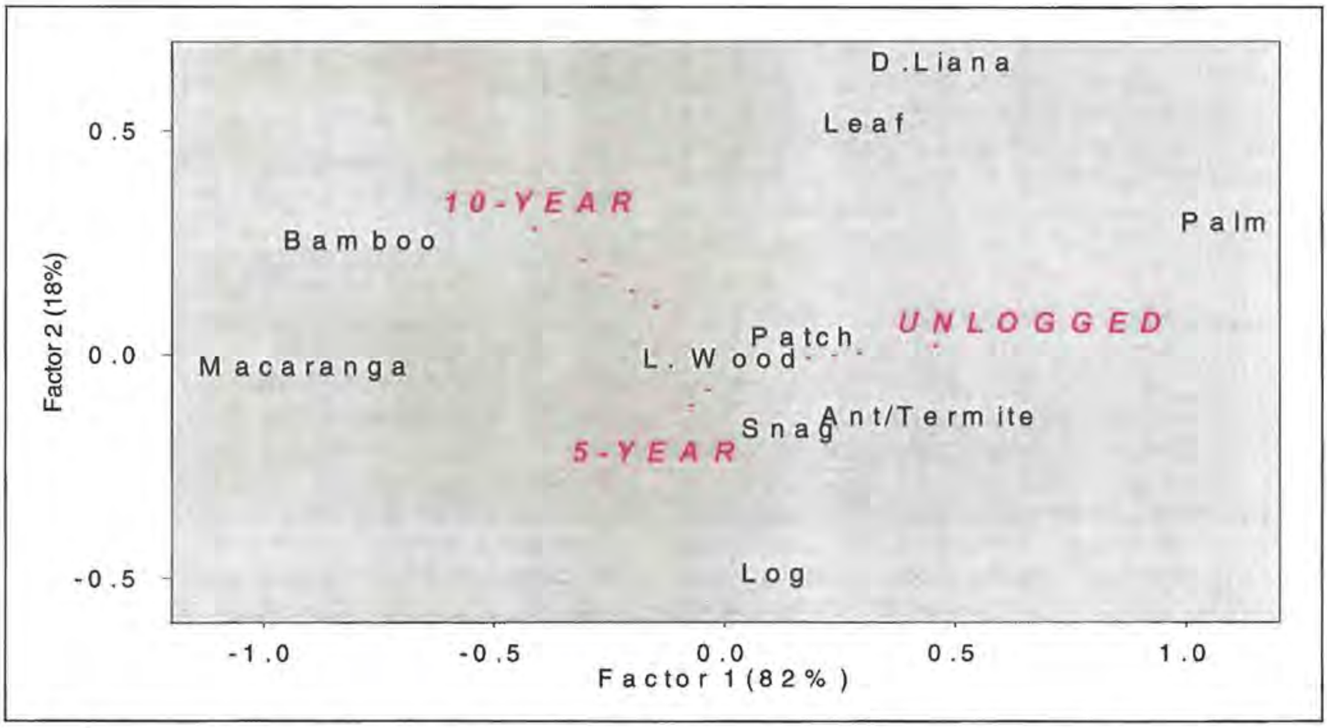

Fig. 1. Correspondence analysis of substrate use by forest type. Substrates (in black) orient closely to the forest type in which they were most frequently used. Percentages on each axis represent the percentage of variation explained by each dimension. Log = down dead tree, Patch = dead wood patch, A/T = ant or termite nest, D.liana = dead liana, Snag = standing dead tree.

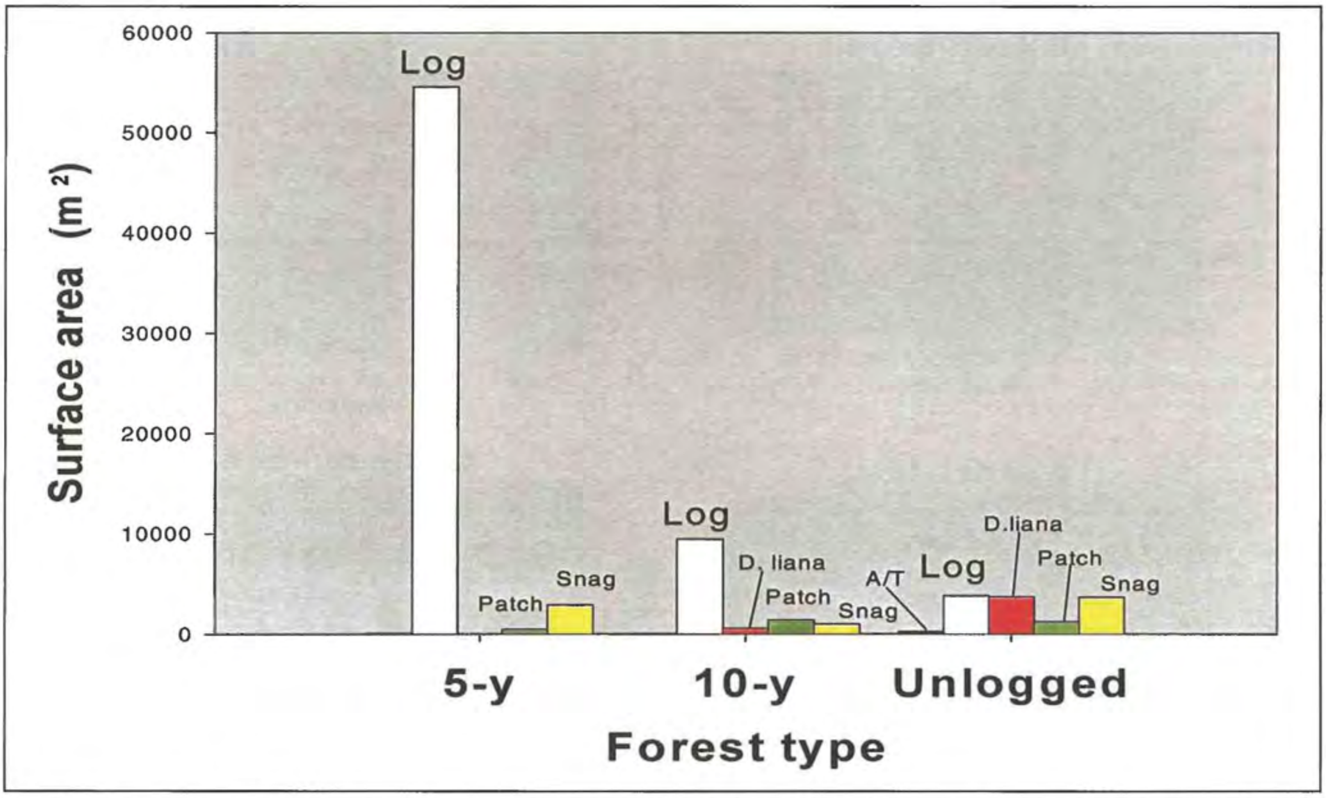

Fig. 2. Raw abundance of five substrates across forest types (1,000 m^2 of 10,000m^2 sampled). Log = down dead tree, Patch = dead wood patch, A/T = ant or termite nest, D.liana = dead liana, Snag = standing dead tree.

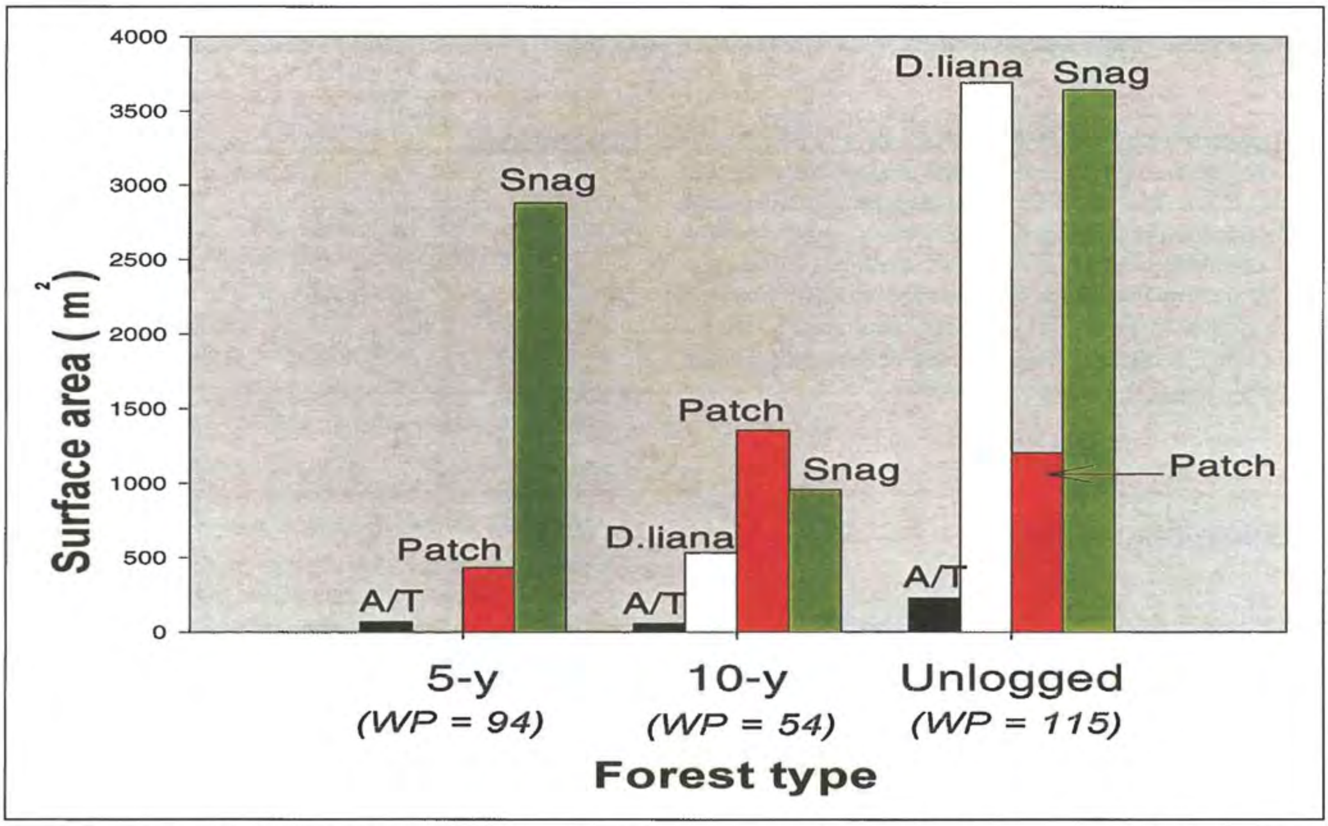

Fig. 3. Abundance of four substrate variables (the variable "log" removed) (1,000 m^2 of 10,000 m^2 sampled). ANOVA of individual substrates yield p values < 0.05. Patch = dead wood patch, A/T = ant or termite nest, D.liana = dead liana, Snag = standing dead tree.

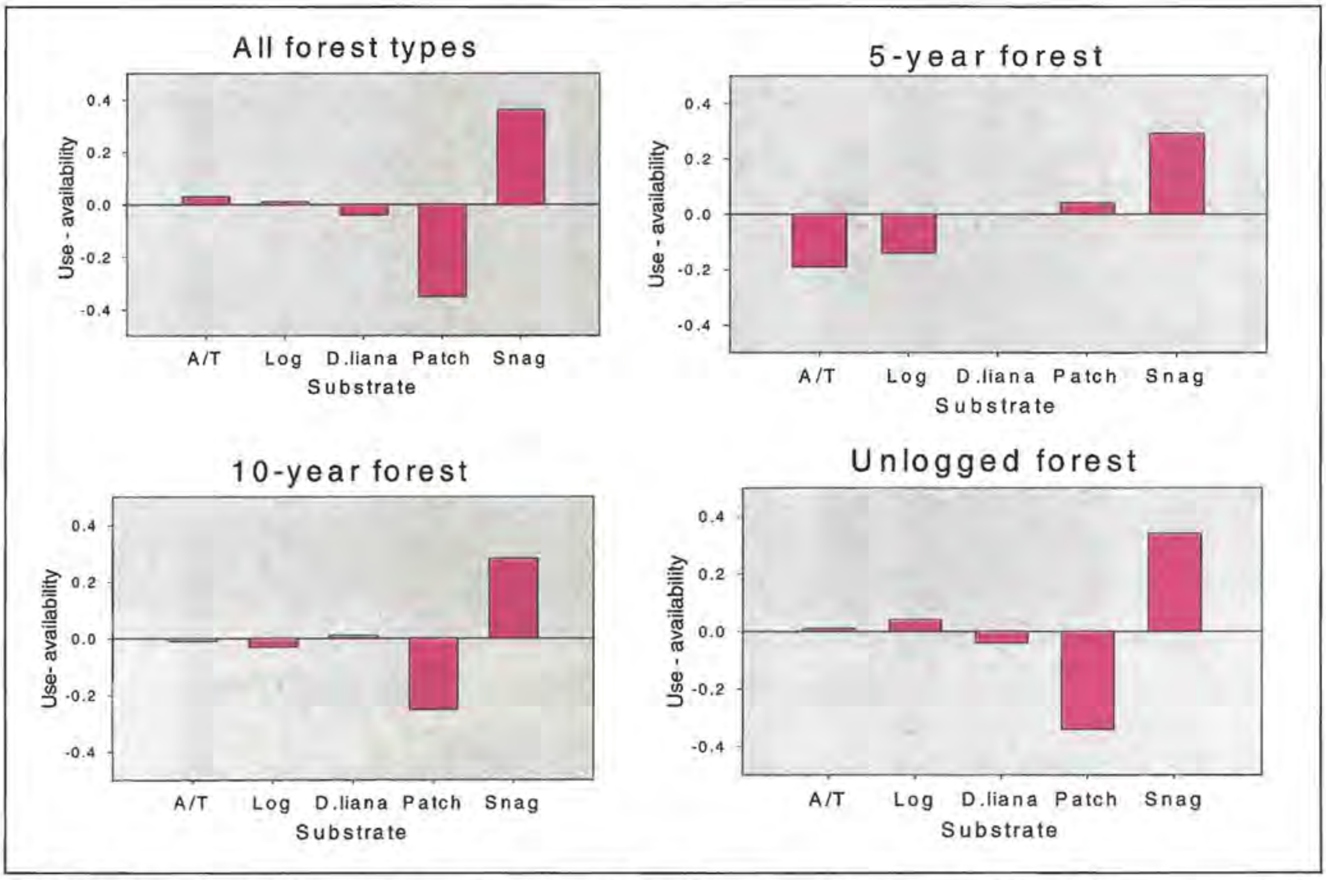

Fig. 4. Proportional substrate use minus proportional availability. Bars above the line are substrates that were used more frequently than expected given their abundance, and bars below the line are substrates used less frequently than expected given their abundance. Patch = dead wood patch, A/T = ant or termite nest, D.liana = dead liana, Snag = standing dead tree.

indicators or keystone species, the link between woodpeckers and snags is undisputed. Snags are a central focus when it comes to management of temperate forests for woodpeckers and secondary cavity nesters. It is comforting to know that the strong link between snags and woodpeckers exists in these forests and that logic similar to that used in temperate forest management likely applies for management of the most diverse woodpecker community in the world.

Acknowledgments

I would like to thank Dr. Mohamed Zakaria and the wildlife group at University Putra Malaysia for allowing me to collaborate with them on their forest recovery project, and for making my stay in Malaysia enjoyable and enlightening. J.V. Remsen, Jr. made helpful comments on this manuscript. Field research was supported by the Tropical Bird Fund of the Louisiana State University Museum of Natural Science. Finally, I would like to thank the Bavarian Ministry of Environment for supporting my travel to the 2001 symposium.

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Division of parental labour in the Great Spotted Woodpecker

Unterschiede in der elterlichen Investition bei der Aufzucht des Buntspechts

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Abstract

Reports of the breeding behavior of the Great Spotted Woodpecker *Picoides major* are numerous, but there is a lack of precise, quantitative data obtained from observations of a large number of nesting pairs. In this study, 27 woodpeckers pairs were observed (9 of them bred in already existing holes) in two breeding seasons (1997-–1998), from the initiation of hole excavation to the fledging of the young. It was the males that largely contributed to hole excavation and nest sanitation. All the other breeding activities – daytime incubation and brooding, and nestling feeding efforts – were shared equally by both sexes. During incubation, the birds changed over after 55 ± 28 min. The birds spent some of the incubation period outside the holes – females 16 %, males 22 %. An average brooding shift lasted ca 10 min. The young were fed on average 8.5 times per 45-min observation period. The feeding intensity increased with the number of nestlings and their age. The division of labour between the sexes was unrelated to the number of nestlings. However, significant variations in the division of labour between the sexes were found in nearly all phases of the breeding cycles, but especially after the young birds had hatched.

Informationen zum Brutverhalten beim Buntspecht gibt es zahlreich, aber es fehlt an genauen, quantitativen Daten von einer größeren Anzahl der Brutpaare. In der vorliegenden Untersuchung wurden 27 Spechtpaare (neun davon brüteten in bereits existierenden Höhlen) zwischen der Zeit des Höhlenbaus bis zum Ausfliegen der Jungen in zwei Brutperioden (1997-1998) beobachtet. Vor allem die Männchen bauten die Höhlen und trugen den Kot aus. Bei den anderen Aktivitäten – tagsüber Bebrütung der Eier und Hudern sowie Fütterungen – beteili-gten sich die beiden Geschlechter gleichmäßig. Wäh-rend der Bebrütung lösten sich die Tiere nach 55 ± 28 min ab. Es wurde beobachtet, dass die brütenden Vögel regelmäßig für einige Zeit ihre Gelegen verließen. Die Tiere verbrachten dabei 16–22% der Brutzeit außerhalb der Höhlen (Weibchen, Männchen entsprechend). Die durchschnittliche Dauer beim Hudern war ca. 10 min. Die Jungen wurden im Durchschnitt 8,5 mal innerhalb von 45 min gefüttert. Die Intensität des Fütterns erhöhte sich mit der Anzahl der Nestlinge und ihrem Alter. Dagegen war die Aufteilung der Aufgaben zwischen den Geschlechtern unabhängig von der Anzahl der Nestlinge. Allerdings konnten signifikante Unterschiede bei der Arbeitsaufteilung zwischen den Geschlechtern in fast allen Phasen des Brutzyklus beobachtet werden, besonders wenn auch die Jungen geschlüpft sind.

Introduction

The activities relating to nest site-selection, building, defence and sanitation, the laying and incubation of eggs, the care of nestlings (brooding and feeding), and fledging are all part of the parental investment in the reproduction and rearing of young birds. The division of parental duties between males and females is specific to particular families or species of birds (KENDEIGH 1952). In breeding activities mates may compensate their efforts: for example, one bird makes a greater con-

Great Spotted Woodpecker (Photo: Peter Pechacek)

tribution to nest defence or sanitation, while the other works harder feeding the nestlings (GRUNDEL 1987, BUITRON 1988, LOMBARDO 1991). In woodpeckers *Picidae* males probably play a greater part than females in rearing the young – they excavate and guard breeding holes, incubate and brood at night, and sometimes feed the nestlings more frequently than the females do (SHORT 1982, WINKLER et al. 1995).

The Great Spotted Woodpecker *Picoides major* is the most numerous woodpecker species in Europe (HAGEMEIJER & BLAIR 1997). Existing records suggest that males are more actively involved in breeding activities (CRAMP 1985); if a female is lost, the male is capable of rearing his young to fledging alone (BLUME 1977). However, there are only a few papers describing parental care in this species, and they are based on observations of a small number of single holes. This paucity of observations may lead to misconceptions about the general way in which breeding activities are divided between the sexes. For instance, this species frequently reuses old holes for nesting (BLUME 1977), so many birds invest the energy otherwise required for excavating holes in other activities, such as feeding nestlings.

The aim of this study was to describe the general pattern of the division of parental labour in a Great Spotted Woodpecker population on the basis of precise quantitative data collected from a considerable number of nests.

Study Area, Methods, Material

The study was carried out in the Kabacki Forest nature reserve on the outskirts of Warsaw, Poland (52°07'N, 21°03'E). A detailed description of the study area and the woodpeckers' nest sites can be found elsewhere (MAZGAJSKI 1998). The study was conducted in two breeding seasons 1997–1998 in mostly deciduous stands of the forest, where birds excavating nest holes were searched for. Already existing holes were also monitored. The pairs of woodpeckers chosen for careful observation bred relatively low down (no higher than about 7 m), so visual inspections of the nests were possible. The contents of the holes were monitored using a ladder, lights and a mirror every 3–5 days and the number of eggs or nestlings counted.

To avoid disturbing the woodpeckers, all observations of their behavior were carried out from sites well away from the nest-holes (10–15 m). During the various phases of breeding period different methods were used. When freshly excavated holes were found, 30-min observations were carried out – these began even when there were no birds actually working at the hole. During the observation period, the exact time of excavation, and the sex of the birds was recorded. For further analysis, only data from freshly excavated holes used for breeding during the same season were used. Observations classified later as nest guarding (a bird spent some time in the hole, but no drumming was heard, and the bird did not remove wood chips) were excluded from the analysis. A total of 19 observations were used (9.5 h).

During the processing of incubation data, it was assumed that woodpeckers start incubating after the last egg has been laid (PYNNÖNEN 1939). The incubation period was divided into two parts: day 1 to day 5, and from day 6 to hatching. The time between two changeovers of incubating birds was calculated as the length of an incubation shift. The time the birds spent outside the nest during the incubation shift was also recorded. In all 43 incubation shifts in 14 nests were observed between 10:00 and 16:00. The brooding time was determined to up to day 12 of a nestling's life (BLUME 1977): 174 brooding shifts of 15 nesting pairs were observed.

Parental feeding efforts and nest sanitation were observed in the mornings (06:30–12:00) and afternoons/evenings (14:00–20:30). During each 45-minute observation period, the number of feeding trips, the sex of the birds feeding the young, and the number of faecal sac removals were recorded. The fledging period was divided into three roughly equal phases (after CISAKOWSKI 1992): early – from hatching to the end of the first week of a nestling's life, when adult birds brood frequently (data recorded during brooding shift observations were recalculated to 45-min observation time); intermediate – from the start of the second week of a nestling's life to the beginning of feeding at the hole entrance (approx. 14–16 days old), when nestlings are brooded less frequently; terminal – the phase when the young are fed at the hole entrance – from approx. 14–16 days old to fledging.

A total of 268 45-min observation periods of feeding at 27 nests (33 % of them in old holes), and 89 45-min observation periods of nest sanitation at 20 nests were carried out.

During the data processing the efforts of males and females were compared in successive phases of the breeding cycle. Data from 2 nests were excluded from the analysis because only the breeding efforts of the males were observed. In a few nests, young birds died or were killed by predators, but observations made prior to such events were included in the data processing. In the χ^2 test it was assumed that males and females make equal contributions. Average shift lengths during incubation and brooding are given in h:min:sec.

Results are shown as mean ± SD, and for all statistical comparisons, the significance level was $p < 0.05$.

Results

Hole excavation

On average 62 % of the observation time (9.5 h) involved birds excavating holes. 97 % of these observations related to males. Males excavating nesting holes worked an average of 20:07 ± 6:50 min during a 30-min observation period. Only once was a female seen to be altering the shape of the nest chamber. However, females were involved in guarding nest holes.

Incubation and brooding

The average length of a shift during the incubation period was 0:54:59 ± 0:28:23 ($N = 43$). During the first and second period of incubation, the duration of shifts was similar (1st period – 0:53:15 ± 0:25:32, $N = 20$; 2nd period – 0:52:09 ± 0:32:16, $N = 18$; Mann-Whitney U-test: $Z = 0.44$, ns). There were no differences in the average duration of incubation shifts between particular pairs in this population of Great Spotted Woodpecker (ANOVA $F_{11,29} = 1.12$, ns).

No differences were recorded in the average length of shifts between males and females in the 1st and 2nd periods during daytime incubation (Mann-Whitney U-test: $Z = 0.49$, ns; $Z = -1.06$, ns respectively) (Table 1). Thus, males and females spend their incubation periods in a similar way (Mann-Whitney U-test $Z = 1.03$, ns) (Table 1).

During incubation females spent 15.8 % and males 21.6 % of the shift period outside the nest holes, but these differences were not statistically significant ($\chi^2 = 0.58$, ns).

After the young had hatched, both parents were involved in brooding. The average shift length was 0:10:37 ± 0:09:49 and was similar for males and females (Mann-Whitney U test $Z = 0.62$, ns) (Table 1). There were differences between particular woodpecker pairs as regards the length of shifts in daytime brooding ($F_{14,159} = 2.87$, $p < 0.05$). During brooding shifts, birds also left the nest for some time. Females spent 26 % and males 39 % of the shift outside the hole, but this difference was not statistically significant ($\chi^2 = 0.03$, ns).

Feeding efforts

Both parents were engaged in feeding the nestlings. Differences in the numbers of feeding trips between the three phases of the fledging period were found (Kruskal-Wallis ANOVA $H = 11.88$, $p < 0.003$). However, in all three phases the proportion of the parental provisioning effort between males and females was similar (Table 2). It was found that the number of feeding trips differed between the three phases in males (Kruskal-Wallis ANOVA $H = 6.68$, $p < 0.05$) but not in females (Kruskal-Wallis ANOVA $H = 4.51$, ns) (Table 2). Woodpeckers breeding in old holes shared their provisioning efforts in the same way as birds nesting in holes freshly excavated before breeding ($\chi^2 = 3.78$, ns).

Table 2. Average number of feeding trips by males and females during 45-min observation periods in the three fledging phases.

Phases	males	females	U test
early	2.86 ± 1.49	2.71 ± 1.22	$Z = 0.47$ ns
intermediate	3.68 ± 1.98	4.00 ± 1.97	$Z = -0.5$ ns
terminal	4.70 ± 1.88	4.49 ± 2.31	$Z = 0.49$ ns

Different numbers of nestlings led to differences in the number of feeding trips (Kruskal-Wallis ANOVA $H = 17.13$, $p < 0.005$). In broods with two young, females made significantly more feeding trips than males ($\chi^2 = 7.6$, $p < 0.01$); in broods with 3, 4 and 5 young the share of the parental effort was divided uniformly ($\chi^2 = 3.44$; $\chi^2 = 0.83$; $\chi^2 = 3.3$ respectively, all cases ns).

Nest sanitation

Both parents removed faecal sacs 2 ± 1.5 times during one 45-min observation, roughly after every fourth feeding. The males removed 69 % of faeces (average 1.4 ± 1.3 per observation), the females only 31 % (average 0.6 ± 0.9). This result differs significantly from that to be expected if parental efforts were equally shared ($\chi^2 = 27.5$, $p < 0.005$).

Males from broods with 2, 3 and 4 nestlings did significantly more as regards nest sanitation ($\chi^2 = 18.7$, p <

Table 1. Average length (± SD) of shifts in males and females of Great Spotted Woodpecker during daytime incubation and brooding. *N* = number of observed shifts. Results are shown as h:min:sec.

		males	females
incubation		0:58:50 ± 33:11 ($N = 22$) range 0:08:06–1:53:40	0:50:58 ± 0:22:23 ($N = 21$) range 0:20:11–1:49:45
	first part	1:02:13 ± 0:30:51 ($N = 11$)	0:42:17 ± 0:10:39 ($N = 9$)
	second part	0:45:37 ± 0:36:25 ($N = 8$)	0:57:22 ± 0:29:27 ($N = 10$)
brooding		0:10:23 ± 0:09:58 ($N = 46$) range 0:00:30–0:43:52	0:10:51 ± 0:09:46 ($N = 49$) range 0:00:15–0:55:50

0.005; $\chi^2 = 4.8$, $p < 0.05$; $\chi^2 = 11.7$ $p < 0.001$ respectively), but in nests with 5 young, females worked just as hard as their mates ($\chi^2 = 0.35$; ns).

It was found that the nest hole history influenced the way faecal sac removal was shared. In pairs breeding in freshly excavated holes, males did the most of this work ($\chi^2 = 32.4$, $p < 0.0005$). However, in birds nesting in old holes males and females shared the nest sanitation efforts equally ($\chi^2 = 0.64$, ns).

Discussion

In many ornithological handbooks it is emphasized that male woodpeckers invest more in nest hole excavation and brood care (WINKLER et al. 1995). This paper is an attempt to verify existing information about the division of parental care between the sexes in the Great Spotted Woodpecker. The only assumptions made on the basis of the literature were that males incubate and brood at night (SHORT 1982, CRAMP 1985) .

Both published data – Sielmann after BLUME (1977), CISAKOWSKI (1992), MICHALEK (1998) and the observations of this study confirm that males make a greater contribution to nest hole excavation. However, it is easier to observe birds excavating the nesting chamber, and the earlier stages of excavation may well be carried out by the female as part of the nest site selection process. A similar pattern has been observed in the Middle Spotted Woodpecker *Picoides medius* – males did more actual hole excavation, but females contributed to these efforts, especially at the start of nest-building (PETTERSSON 1984). In many other woodpecker species, males contribute more than females to nest building, but there are strong variations between particular pairs (SHORT 1982, CRAMP 1985, WINKLER et al. 1995). In our study only 5 pairs were observed excavating holes, but this could lead to a false conclusion, because females intensively working on nest building had been observed in the study area in previous years. Other factors, such as the age of the birds and the hardness of the tree species may also affect the division of labour in hole construction. On the other hand, males of the Great Spotted Woodpecker have longer and stronger bills than females – HOGSTAD (1978), and this may explain why females play a smaller part in nest excavation.

After the males have finished excavating holes, the nests are guarded by both parents, but males spend more time in this work (MICHALEK 1998). Incubation starts after ca. 2 days before or after clutch completion (STEINFATT 1937, PYNNÖNEN 1939). However, it should be borne in mind that few data describing incubation in the Great Spotted Woodpecker are available (STEINFATT 1937, PYNNÖNEN 1939, DURANGO 1945). In fragmentary observations it has been found that at the beginning of incubation the birds change over very frequently, on average every 11 min, but later at less frequent intervals – approx. every 40–50 min. Males incubate more than females, and also spend the night in the nests. The longest recorded daytime shift of a male is 121 min, in females – 55 min (SHORT 1982, CRAMP 1985). The results of the present study bring greater precision to those data. We found that there were no differences in shift duration at the beginnings and ends of incubation. Moreover, during daytime incubation, both sexes worked in a similar way (Table 1) (see also MICHALEK 1998). The longest shift of a male – 114 min – was similar to that recorded earlier, but the longest shift of a female was twice as long (approx. 110 min). Thus, it is possible that the parents compensate their efforts in this phase of reproduction. At the start of incubation, when females were rebuilding their energy reserves after egg laying, males incubated for longer periods, but later this pattern was reversed (Table 1); however, the results were not statistically significant.

Interestingly, the birds spent some time outside the nest during their incubation shifts, but it is hard to find a possible explanation for this behavior. Probably it is very warm inside the hole and the birds avoid overheating the eggs or themselves; alternatively, a short inspection of the neighbourhood of the nest hole may be connected with anti-predator tactics.

It was found that both parents take an equal share of brooding. The average length of a brooding shift (approx. 10–11 min) was similar to that found earlier (CRAMP 1985, MICHALEK 1998).

Much data is available describing the feeding pattern in the Great Spotted Woodpecker, but in most cases this information is based on observations of a single nest for a few hours or for one day (PYNNÖNEN 1939, STAHLBAUM 1959, BREJNIAK 1990). As many different factors might affect the observed division of labour between sexes, the results presented in those papers varied considerably. It is generally accepted that males make a greater contribution to feeding the nestlings. Sometimes, differences in the division of labour between mates are related to the phase of the fledging period – especially at the end of it, females may stop feeding the nestlings (SHORT 1982, CRAMP 1985). Similar behavioral patterns have also been observed in the other *Picoides* species (HOGSTAD & STENBERG 1997, WIKTANDER et al. 2000). However, in our study we found that the feeding efforts of both parents were similar throughout the fledging period (Table 2). Similar data were obtained by MICHALEK (1998). We assumed that a large number of observations from many nests, more or less equally distributed during the day and during the three phases of the fledging period, would be sufficient to describe the general nestling feeding pattern in this species.

The great variation in the earlier data might have been caused by differences in the numbers of nestlings or their ages in the nests observed. In this and other detailed studies of European woodpecker species, it has been found that the number of young and the age of nestlings do influence the number of parental feeding trips (PETTERSSON 1984, HOGSTAD & STENBERG 1997, WIKTANDER et al. 2000).

At the start of the present study it was assumed that males which bred in existing holes and did not expend any energy in excavating holes should contribute more to the feeding of young birds. However, our results do not confirm this. The division of parental provisioning efforts was similar in all pairs, regardless of whether they nested in old or freshly excavated holes.

This study confirmed the observation of STAHLBAUM (1959), who found that woodpeckers removed faeces after the fourth feeding. During 10 h of observation Stahlbaum saw only males occupied with nest sanitation. In our study, however, we found that while females do assist males in removing faeces, they do significantly less of the work. However, in broods containing 5 young, the females worked as hard as the males, probably because the males would not have been able to cope alone with removing faeces from so many nestlings. An interesting finding of this study are the relations between the nest sanitation efforts of male birds and nest hole history. Where males had expended much energy in excavating fresh holes, they too maintained the cleanliness of the holes. This may be because the bright colour of the fresh wood on the walls and bottom of the nesting cavity stimulates them to keep it clean. In old holes, by contrast, where the nesting chamber is rather dark, males were not so interested in nest sanitation, and females played a more active part in removing faeces.

It was found that the division of parental labour differs between the pairs of woodpeckers studied in many aspects of breeding activities, especially after the young hatch. The experience and age of birds, the number and age of nestlings are probably the main reasons for such variations. Therefore, generalizations drawn from anecdotal data may lead to misconceptions regarding the distribution of parental duties in this species. The general pattern of the division of parental labour in the Great Spotted Woodpecker seems to be as follows: males work harder at nest building, guarding and sanitation, females necessarily invest their energy in egg laying, while both sexes take an equal share of daytime incubation and brooding, and nestling feeding.

Acknowledgements:

The authors wish to thank Jerzy Mazgajski for all the logistic support, and Piotr Czechyra for field assistance. The English version was kindly verified by Peter Senn. Tomasz D. Mazgajski is very grateful to the Deutsche Forschungsgemeinschaft (DFG) for the financial support which enabled him to participate in the International Woodpecker Symposium.

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Woodpeckers as indicators for sustainable forestry? First results of a study from Lower Saxony

Spechte als Indikatoren einer nachhaltigen Forstwirtschaft? Erste Ergebnisse einer Studie aus Niedersachsen

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Abstract

In the process of developing a monitoring system for sustainable forestry in Europe, we assess the suitability of woodpeckers as indicator species. In this context, we raise questions concerning requirements for a sustainable forestry from a conservation point of view. We suggest that maintaining biodiversity in forests is crucial for sustainability, and that it requires that viable populations be maintained for all naturally occurring species. Within the framework of the EU-LIFE-Project "Demonstration of Methods to Monitor Sustainable Forestry" a census of six woodpecker species was carried out in the "Lüneburger Heide" and in the "Solling", two forest regions in Lower Saxony different in structure and history, on each approximately 1800 hectares of woodland. The results emphasize the significance of old forest stands, and especially old deciduous trees, for the abundance and diversity of woodpeckers. We conclude that woodpeckers as a group are good indicator species, although further research is needed to specify what habitat characteristics the different woodpecker species can indicate, and how closely the occurrence of other taxa of forest organisms is related to the presence of woodpeckers. Woodpeckers can be part of a monitoring system of sustainability in forests, but other indicator species are also required (e.g., mosses, lichens, and fungi).

Im Rahmen des sogenannten „Rio-Prozesses" wird in Europa zur Zeit an einem Monitoring-System für nachhaltige Forstwirtschaft gearbeitet. In der vorliegenden Arbeit wird die Eignung der Spechte als mögliche Indikatoren in einem solchen Monitoring-System bewertet. Dazu muss zunächst definiert werden, was eine ökologisch nachhaltige Forstwirtschaft im einzelnen bedeutet, welche Anforderungen also die Forstwirtschaft erfüllen muss, um den Erhalt der Biodiversität in Wäldern garantieren zu können. Es wird auf einige in diesem Zusammenhang wichtige, noch offene Fragen hingewiesen. Im Rahmen des EU-LIFE-Projektes „Demonstration of Methods to Monitor Sustainable Forestry" wurde in der Lüneburger Heide und im Solling eine Spechterfassung auf jeweils etwa 1800 ha Wald durchgeführt. Die Ergebnisse wurden mit den vorliegenden Daten der Forsteinrichtung in Beziehung gesetzt. Die Bedeutung hohen Bestandesalters und besonders alter Laubbäume für die Siedlungsdichte und Artenvielfalt der Spechte wurden bestätigt. Spechte sind sicherlich als Indikatoren für eine nachhaltige Forstwirtschaft geeignet, wenngleich die Indikationsleistung der verschiedenen Arten noch genauerer Untersuchungen bedarf. Für ein sinnvolles Monitoringsystem nachhaltiger Forstwirtschaft werden jedoch unbedingt weitere Indikatoren aus anderen Organismengruppen benötigt.

Introduction

During the conferences in Helsinki 1993 and Lisbon 1998, the European Ministers of Forestry agreed on common European criteria for sustainable forest-management. These include the preservation of biological diversity of forests (BARTHOD 1998, MERKER & SPELLMANN 2000). In order to be able to check whether the forests in Europe are actually under sustainable use, and to assess the future development of forest management, a monitoring system is required (HUGHES 1996, ANGELSTAM 1998, McLAREN et al. 1998, SEYMOUR & HUNTER 1999, MROSEK & BALSILLIE 2001).

In the process of developing a monitoring system, the EU-LIFE-Project "Demonstration of Methods to Monitor Sustainable Forestry." is situated. Countries involved in this project are France, Denmark, Sweden, Finland, and Germany. The Lower Saxony forest administration participates as the German partner. One small part of the German investigation was to consider whether or not woodpeckers can serve as an indicator group for "ecological" sustainability of forest management, and how a monitoring system for this purpose could be designed. This was carried out by the "Alfred Toepfer Akademie für Naturschutz", Schneverdingen, in cooperation with the "Staatliche Vogelschutzwarte" at the Lower Saxony "Landesamt für Ökologie" (NLÖ) as technical supervisor.

To check what recommendations could be made for a reliable and large-scale monitoring system for woodpeckers that is supposed to be carried out over large areas, we censused six woodpecker species in two study areas in Lower Saxony. To assess if an ongoing evaluation of an indicator system could be based on the forest data provided by the forestry commission, the woodpecker data were related to forest data drawn from the current forest inventory.

In this paper, first we will discuss what is necessary for a sustainable management of European forests while maintaining biodiversity in forest ecosystems, and if woodpeckers are suitable indicators to monitor such a sustainable management. We will address these questions by reviewing the relevant literature. Next we will suggest a census method for woodpeckers that could be used for a reliable and large-scale monitoring system, and we will present some results of the woodpecker census and some conclusions concerning habitat use of woodpeckers in the two study areas as they relate to the forest inventory data.

Maintaining biodiversity in European forests – requirements for a sustainable forest management from a conservation point of view

It is widely accepted that a sustainable use of the environment has to include not only resource sustainability, but also social and socio-economic aspects and the maintenance of biodiversity (AMMER et al. 1995, BARTHOD 1998, MROSEK & BALSILLIE 2001). The conference of European Ministers of Forestry in Lisbon (in June 1998) created a system of criteria and indicators for a sustainable management of European Forests (Table 1). The Center for International Forest Research (CIFOR) has developed a similar system for temperate forests in general (MROSEK & BALSILLIE 2001).

Every subcriterion in Table 1 is specified by qualitative and quantitative indicators. For example, for subcriterion 4.2 (representative, rare and vulnerable forest ecosystems), the quantitative indicators are: area of natural forest types (virgin forests), area of old semi-natural forest types, strongly protected areas, and areas with a specific conservation management. For subcriterion 4.4 (biodiversity in managed forests), the quantitative indicators are: areas for seed production, areas for generesources, proportion of mixed stands with at least two or three tree species, and annual natural regeneration in relation to total regeneration. For these quantitative indicators, standards and threshold values have to be established. The process of defining requirements for sustainable forest management is still in progress, and there has been much discussion about this over the last years.

Indicator species are sensible only for the ecological aspect of sustainability, so in the following we concentrate exclusively on the maintenance of biodiversity as one important aim for sustainable forestry (criterion four in Table 1).

If indicator species for a sustainable forest management are to be selected, we must first clearly define the detailed characteristics of such management. The existing systems of criteria and indicators are too general for this purpose. Forest certifications as the FSC (Forest Stewardship Council) and the PEFC (Pan-European Forest Certification) have developed more detailed guidelines, but these show clear differences in some crucial aspects (FSC Arbeitsgruppe Deutschland 1999, 2001, DFZR 2000, MOLLER 2000a).

Table 1. Criteria and subcriteria for a sustainable forestry in Europe (resolution L2, 3rd Conference of Ministers for the protection of forests in Europe, 02–04 June 1998, Lisbon).

Criterion 1: Forest Resources	Criterion 2: Health and Vitality	Criterion 3: Production	Criterion 4: Biodiversity	Criterion 5: Conservation functions	Criterion 6: Socio-economic functions
1.1 general legal validity		3.1 wood production	4.1 general conditions	5.1 general conservation	6.1 Importance for national economy
1.2 land use and forest area		3.2 other products	4.2 representative, rare and vulnerable forest ecosystems	5.2 soil erosion	6.2 recreation function
1.3 stock/wood reserves			4.3 endangered species	5.3 water balance in forests	6.3 employment function
1.4 carbon balance			4.4 biodiversity in managed forests		6.4 research and training
					6.5 public relations work
					6.6 participation
					6.7 cultural values

Many authors agree that maintaining biodiversity requires that viable populations should be maintained of all naturally occurring species (ANGELSTAM 1999, SEYMOUR & HUNTER 1999, REIF 1999/2000). Although this might be regarded as completely self-evident, it is a very ambitious goal and a difficult forestry management task (ANGELSTAM 1999). If the goal is accepted, some important questions arise concerning ecological aspects of forest management:

- To what extent are unmanaged reference areas important to maintain biodiversity, and what proportion of unmanaged forests is necessary (AMMER et al. 1995, SCHERZINGER 1996, NORTON 1999, SEYMOUR & HUNTER 1999, Sachverständigenrat für Umweltfragen 2000)? The importance of unmanaged forests as reference areas has to be considered, as natural successional cycles of European forest ecosystems are insufficiently known (LEIBUNDGUT 1993, RAUH 1993, KORPEL 1997, ANGELSTAM 1999, OHLSON & TRYTERUD 1999, ZUKRIGL 1999). Additionally, unmanaged control areas may be important as benchmarks in order to separate forestry effects on population trends of animal and plant species from the effects of factors unrelated to management measures such as long-term climate changes (McLAREN et al. 1998, NORTON 1999, SCHULZE 1999).

- Should forest management in general be closely orientated towards natural forest dynamics (SCHERZINGER 1996, ANGELSTAM 1998, OHLSON & TRYTERUD 1999, SEYMOUR & HUNTER 1999)? To what extent is it necessary (and possible) to allow and include successional processes in managed forests (STURM 1993, SCHERZINGER 1997, MOLLER 2000b)?

- In what way and to what extent does tree species composition (and the use of exotic tree species) affect biodiversity in forests (SCHERZINGER 1996, PALIK & ENGSTROM 1999, REIF 1999/2000, BURGER-ARNDT 2000)?

- What amount of dead wood and "biotope trees" is required in managed forests to offer enough habitat for dead-wood specialists (ANGELSTAM 1990, RAUH & SCHMITT 1991, KLEINEVOSS et al. 1996, HAASE et al. 1998, McCOMB & LINDENMAYER 1999, KOHLER 2000)?

- Do we have enough old forests stands to keep all the species that are dependent on old and very old trees (many mosses, lichens, fungi, xylobiontic invertebrates, but also several vertebrate species; SCHERZINGER 1996, KOST 1989, ULICZKA & ANGELSTAM 1999, HANSTEIN 2000, MOLLER 2000)?

Woodpeckers as indicators for a sustainable forestry

The suitability of woodpeckers as indicators for biodiversity in forests (and in the following for a sustainable forestry) has been discussed intensively in recent years (SCHERZINGER 1982, ANGELSTAM 1990, SHORT & HORNE 1990, RAUH 1993, ANGELSTAM & MIKUSIŃSKI 1994, FERNANDEZ & AZKONA 1996, JEDICKE 1997, MIKUSIŃSKI 1997, SCHERZINGER 1998). Of course, woodpeckers or other indicator species cannot indicate a certain type of management, but only habitat characteristics that derive from management measures. To assess the suitability of different woodpecker species as indicators and to specify what habitat characteristics they can indicate, the "fundamental niches" of each species must be sufficiently known. Although the ecology of European woodpeckers is relatively well understood compared to the situation for other vertebrate or even invertebrate species, in some aspects there is still a lack of information even for the very well-known and widespread Great Spotted Woodpecker *Picoides major* (e.g. the importance of migration patterns and seasonal differences in feeding ecology in different forest types).

Generally, woodpeckers appear to be a good choice indicator species for biodiversity in forests (SCHERZINGER 1982, MIKUSIŃSKI & ANGELSTAM 1997, McLAREN et al. 1998). Following the criteria for indicator species for sustainable forestry used by McLAREN et al. (1998), woodpeckers as a group meet the most important criteria:

- Many woodpeckers are "keystone species": the cavities excavated by woodpeckers are an important, sometimes indispensable habitat resource for many other species of birds, mammals, and invertebrates.
- Most woodpeckers are resident species, and as such they are more reliable indicators than migrants, whose populations are affected not only by conditions on their breeding grounds, but also by habitat changes in their migration and wintering areas.
- Woodpeckers are directly affected by forest management measures.
- The different woodpecker species are dependent on properties of naturally dynamic forests as well as properties of naturally dynamic forest landscapes, so they can indicate habitat changes at different scales.
- They use different strata of vegetation from the ground and lying dead wood to the trunk region and the canopy of forests.
- They show a great variety of feeding strategies from the omnivorous Great Spotted Woodpecker to the very specialized, ant-eating Green Woodpecker *Picus viridis*.
- Census techniques for woodpeckers are available, even though more evidence from field research is necessary to assess the reliability and effectiveness of these methods.

Of course there is one more crucial requirement for indicator species: patterns of distribution and abundance of indicator species must reflect those of other taxa (MIKUSIŃSKI 1997). So far, this has been proven for woodpeckers only in a relatively limited context. For example, species richness of saproxylic beetles (Coleoptera) in Karelia (north-east Europe) was considerably higher in habitats occupied by the White-backed Woodpecker *Picoides leucotos* (MARTIKAINEN et al. 1998). JANSSON (1998) found that when the Lesser Spotted Woodpecker *Picoides minor* was present in a patch of deciduous forest, the probability of the presence of long-tailed tit *Aegithalos caudatus*, marsh tit *Parus palustris* and blue tit *Parus caeruleus* was very high.

However, we have good indications that similar relationships exist between woodpeckers and the occurrence of many other species. Generally, European woodpecker species are adapted to habitat structures of old forests: a patchy stand structure with gaps, dead wood (especially standing dead wood of bigger dimensions), and old trees with broken boughs and treetops (SCHERZINGER 1996). The same habitat structures are very important for a lot of other species, for example cavity-breeding birds, some raptors, owls, bats, xylobiontic insects, fungi, mosses and lichens (WESOLOWSKI 1989, ANGELSTAM 1990, RAUH & SCHMITT 1991, KLEINEVOSS et al. 1996, HOHLFELDT 1997, BORRMANN 1996, SCHER-ZINGER 1996, HAASE et al. 1998, McCOMB & LINDENMAYER 1999, HANSTEIN 2000, KOHLER 2000). MIKUSIŃSKI & ANGELSTAM (1998) used the completeness of the woodpecker guild as an indicator for forest biodiversity in Central Europe. On the other hand, they suggest that the relative abundance of the omnivorous Great Spotted Woodpecker might be a good predictor of the level of anthropogenic change in forest ecosystems.

Materials and Methods

In 2000, a census of six woodpecker species was carried out in two study areas in Lower Saxony: the "Lüneburger Heide" (53°11'N, 09°53'E), a region in the lowland strongly affected by deforestation and characterized by large areas of heath vegetation in the past, then reforestated since the 1850s; and the "Solling" (51°45'N, 09°31'E), a low mountain range in the south of Lower Saxony with a longer history of forestry. In each study area, 12 census plots (each between 50 and 230 hectares) were selected, thus including a total of about 1800 ha in each region.

In the "Lüneburger Heide", the census plots are dominated by pine *Pinus sylvestris* forest (32 %) and mixed pine and spruce *Picea abies* forest (25 %). Stands of beech *Fagus sylvaticus* and oak *Quercus robur/petraea* add to almost 12 %. Other important tree species are birch *Betula pendula* and *B. pubescens*, larch *Larix decidua* and *L. kaempferi* and douglas fir *Pseudotsuga menziesii*. About 30 % of the stands are more than 100 years old.

The "Solling" is dominated by beech (25 %), spruce (25 %), or mixed beech and spruce stands (22 %). Stands of oak and oak mixed with beech or hornbeam *Carpinus betulus* take about 15 %. Other important tree species are birch and larch. The stands are on average older than in the "Lüneburger Heide", 52 % are older than 100 years.

The census method used was a modified type of territory mapping (cf. BIBBY et al. 1995), specially adapted for censusing woodpeckers. We propose this method for use in monitoring woodpeckers in European forests.

Important requirements for the method were a clear standardization, compatibility for different forest types in Europe, and efficiency, including cost effectiveness. The census should be carried out on a yearly basis, until natural population dynamics (depending on severe winters, for example, or supply of pine and spruce cones in the case of the Great Spotted Woodpecker) are sufficiently understood. After that a census every three or five years should be enough.

We recommend the following protocols.

- The census should take place in spring, when calling and drumming activity of woodpeckers is highest (in north Germany in March and April).
- Each census plot should be visited three times at intervals of 10 to 14 days.
- Single census plots should have a size of about 150 ha.
- The route through a census plot (or, if possible, linear transects) should not be more than 150 meters away from any point of the area – so the distance between two linear transects should be 300 m at maximum.
- We recommend use of existing pathways where available, because this is easier and produces less noise; furthermore, one can concentrate on the birds instead of the thorny undergrowth.
- The fieldworker should move at a rate of 1.5 to 2 km per hour, so that a census plot can be mapped in about four to five hours during one morning.
- A scale of 1:10,000 is sufficient for the map.
- No mapping should take place in bad weather conditions (wind of more than four Beaufort or heavy rain).
- Every woodpecker sighting should be noted on the map and additionally on a prepared data paper, where the sighting number, time, species, and record type (optical or acoustical record, type of vocalization, drumming or other instrumental sounds) and, if possible, sex, behavior, tree species and stratum (ground, trunk, lower canopy, upper canopy) should be recorded.
- For the Grey-headed and the Middle Spotted Woodpecker, the use of playback (tape recorder) is recommended, especially in areas with low densities of these species.

Table 2. Abundance of woodpeckers in 24 study plots. GSWO: Great Spotted woodpecker *Picoides major*; MSWO: Middle Spotted Woodpecker *Picoides medius*; LSWO: Lesser Spotted Woodpecker *Picoides minor*; GWO: Green Woodpecker *Picus viridis*; GHWO: Grey-headed Woodpecker *Picus canus*; BWO: Black Woodpecker *Dryocopus martius*; all WO: all woodpecker species.

study area / census plot	**elevation** m above s.l.	**area** ha	**GSWO** terr./10 ha	**MSWO** terr./10 ha	**LSWO** terr./10 ha	**GWO** terr./100 ha	**GHWO** terr./100 ha	**BWO** terr./100 ha	**all WO** terr../10 ha
Lüneburger Heide (NW German Lowlands)									
Ki-Wald N Bullenberge	60–65	121.3	0.49	-	-	-	-	0.82	0.58
Bullenberge	65–75	152.1	1.12	-	-	–	-	1.31	1.25
Erhorner Dünen	70–80	84.2	1.19	-	-	1.19	-	1.19	1.43
Karck-Berg u. Altes Feld	80–120	134.3	1.19	-	-	-	-	0.74	1.27
An der alten Wümme	70–75	125.3	1.12	-	-	-	-	0.80	1.20
Meninger Holz	80–105	139.9	1.14	-	-	-	-	1.43	1.29
Hainköpen	100–125	54.0	1.85	-	-	1.85	-	1.85	2.22
Oberhaverbecker Holz	95–125	141.1	0.99	-	0.07	0.71	-	2.13	1.35
Wald bei Volkwardingen	80–95	141.1	0.57	-	-	-	-	0.71	0.64
Toppenstedter Wald	80–100	162.1	0.80	-	-	0.62	-	1.23	0.99
Heimbucher Heide	60–100	186.2	0.43	-	-	-	-	0.54	0.48
Döhler Fuhren	65–95	142.9	0.84	-	-	-	-	0.70	0.91
Auf dem Töps	70–110	240.1	0.46	-	-	-	-		0.46
sum/average		1824.6	0.85	-	0.01	0.22	-	0.93	0.97
Solling (mountain area)									
Wolfskopf	380–440	157.7	0.25	-	-	-	0.06	0.06	0.38
Friedrichshäuser Bruch	440–510	136.5	0.07	-	-	-	-	0.07	0.15
Kleines Bruch	350–400	114.5	0.17	-	-	-	-	0.09	0.26
Limker Strang	400–440	168.7	0.18	0.06	-	-	0.06	-	0.30
Am Wildpark	320–450	118.9	0.50	0.34	-	-	0.08	0.08	1.01
Buchenwald bei Boffzen	200–350	101.7	0.29	-	-	-	-	0.10	0.39
Hainbuchensohl	360–420	113.0	0.44	-	-	-	0.09	0.09	0.62
Reiherbachtal	200–280	172.8	0.41	0.35	0.06	-	-	0.06	0.87
Uhlenbruch	460–490	127.9	0.16	-	-	-	-	0.08	0.23
Langer Grund	380–460	142.5	0.28	-	-	-	-	0.07	0.35
Winterlieth	380–490	227.3	0.09	-	-	-	0.04	-	0.13
Gr. Kuhlenberg. Weserst.	120–330	204.0	0.34	0.10	0.10	-	0.05	0.05	0.64
sum/average		1785.5	0.26	0.07	0.02	-	0.03	0.06	0.44

Table 3. Correlations between abundance of Great Spotted Woodpecker (GSWO) resp. all woodpecker species (all WO) as well as number of woodpecker species and the forest parameters: elevation (average elevation above sea level of a census plot), >80/>100/>120 (proportion of stands more than 80/100/120 years old), decid./conif. >80/>120 (proportion of deciduous/coniferous stands more than 80/120 years old). Spearman-Rank-Correlation (correlation coefficients Rs); $^{*}p < 0{,}05$; $^{**}p < 0{,}01$; $^{***}p < 0{,}00$.

		elevation	**> 80**	**> 100**	**> 120**
Abundance GSWO	**LGH**	0.234	0.631*	0.530*	0.097
	Solling	−0.705**	0.538*	0.643*	0.538*
Abundance all WO	**LGH**	0.474	0.804**	0.748**	0.517*
	Solling	−0.771**	0.692**	0.748**	0.587*
Number of species	**LGH**	0.577*	0.694**	0.670*	0.670*
	Solling	−0.486	0.769**	0.857***	0.829***

		decid. > 80	**decid. > 120**	**conif. > 80**	**conif. > 120**
Abundance GSWO	**LGH**	0.456	0.259	0.698**	0.080
	Solling	0.601*	0.476	−0.224	0.250
Abundance all WO	**LGH**	0.706**	0.614*	0.503*	0.448
	Solling	0.699**	0.531*	−0.259	0.142
Number of species	**LGH**	0.806**	0.767**	0.124	0.484
	Solling	0.738**	0.797**	−0.084	0.142

Analyses of the woodpecker data were carried out on two spatial levels: On the stand level, the "density" of woodpecker sightings (sightings/ha) was determined, while on the census plot level the abundance (territories/ha) of woodpecker species was compared. Data analyses were carried out using the Geographical Information System program ArcView 3.2.

The forest parameters, mainly the age and species composition of the stands, were taken from the current forest inventory. In this paper, we concentrate on the importance of stand age and elevation of the census plot above sea level. In the forest inventory in Lower Saxony, stands are divided into nine age classes based on the age of the main tree species in the stand or the one the management measures are aligned with. Each age class covers 20 years, so age class one includes trees of one to 20 years, age class two 21 to 40 years, and so on. Age class nine consists of all stands older than 160 years. Stands with "legacy trees" ("Überhälter"; trees of the previous tree generation that were not cut when the stand was harvested), occurring in age classes 1 to 3, were excluded from the analysis, because a few old trees on a stand can be of much more ecological importance than all the young trees that define the age class.

Results

In the "Lüneburger Heide", four woodpecker species were found: Great Spotted Woodpecker, Lesser Spotted Woodpecker, Green Woodpecker and Black Woodpecker *Dryocopus martius*. The Wryneck *Jynx torquilla* is quite frequent in the region, but this species was not included in the study because it is rather a bird of the open and half-open landscape. In the "Solling" 6 woodpecker species were recorded: Great Spotted Woodpecker, Middle Spotted Woodpecker *Picoides medius*, Lesser Spotted Woodpecker, Grey-headed Woodpecker *Picus canus* and Black Woodpecker.

In both regions, the Lesser Spotted Woodpecker was so rare that a quantitative analysis of the data was not possible. Table 2 shows the abundance of woodpeckers in the 24 study plots.

On the stand level, the "sighting density" for all woodpecker species increases with the stand age (Fig. 1, Fig. 2) in both study areas. Especially in the "Lüneburger Heide", the Great Spotted Woodpecker was regularly recorded in stands of age class two, three and four (though much more frequent on older stands), while all

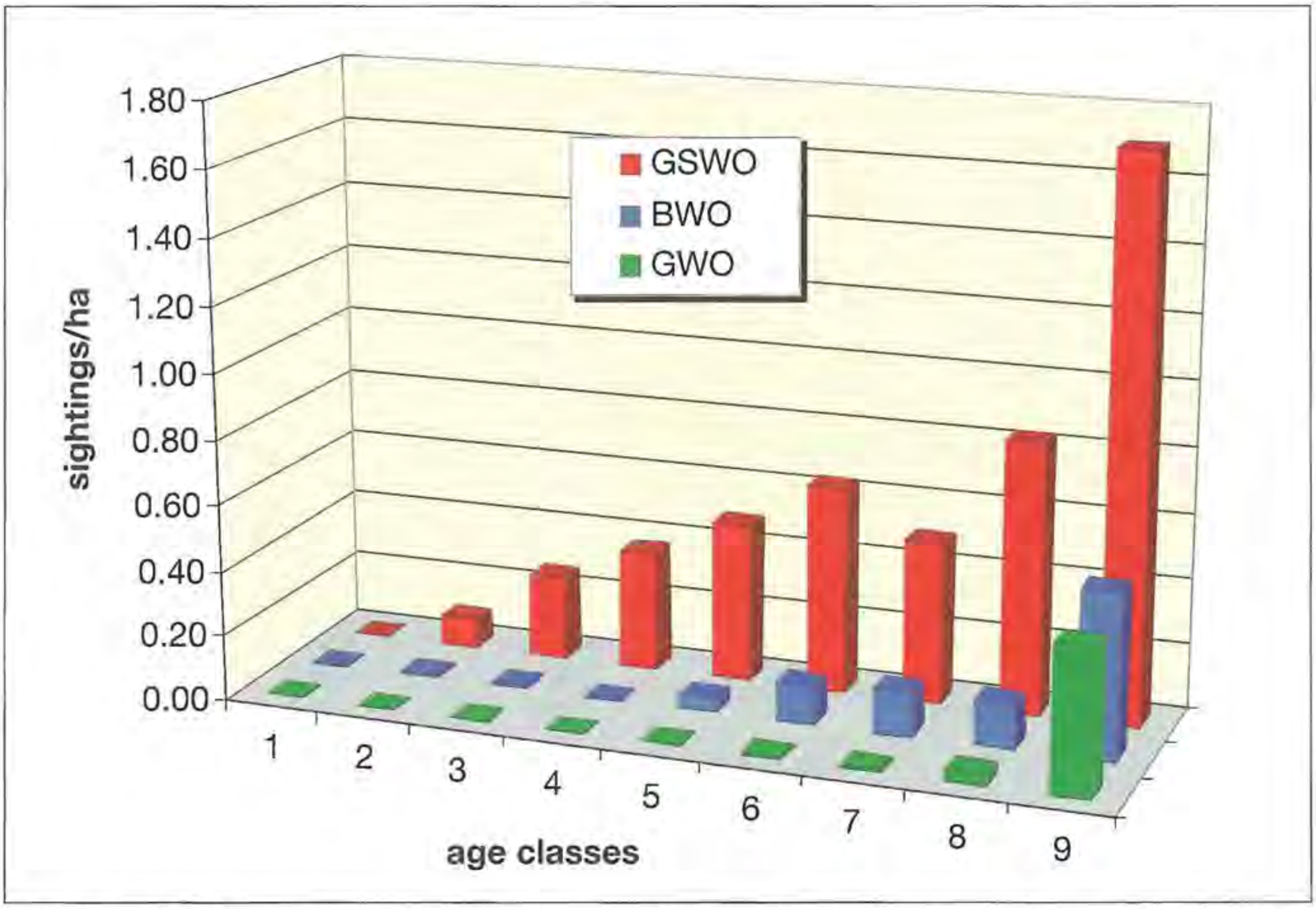

Fig. 1. Distribution of woodpecker sightings of three species (GSWO: Great Spotted Woodpecker *Picoides major*; BWO: Black Woodpecker *Dryocopus martius*; GWO: Green Woodpecker *Picus viridis*) on age classes of forest stands (stands with "legacy trees" excluded) in the "Lüneburger Heide" (sightings per ha).

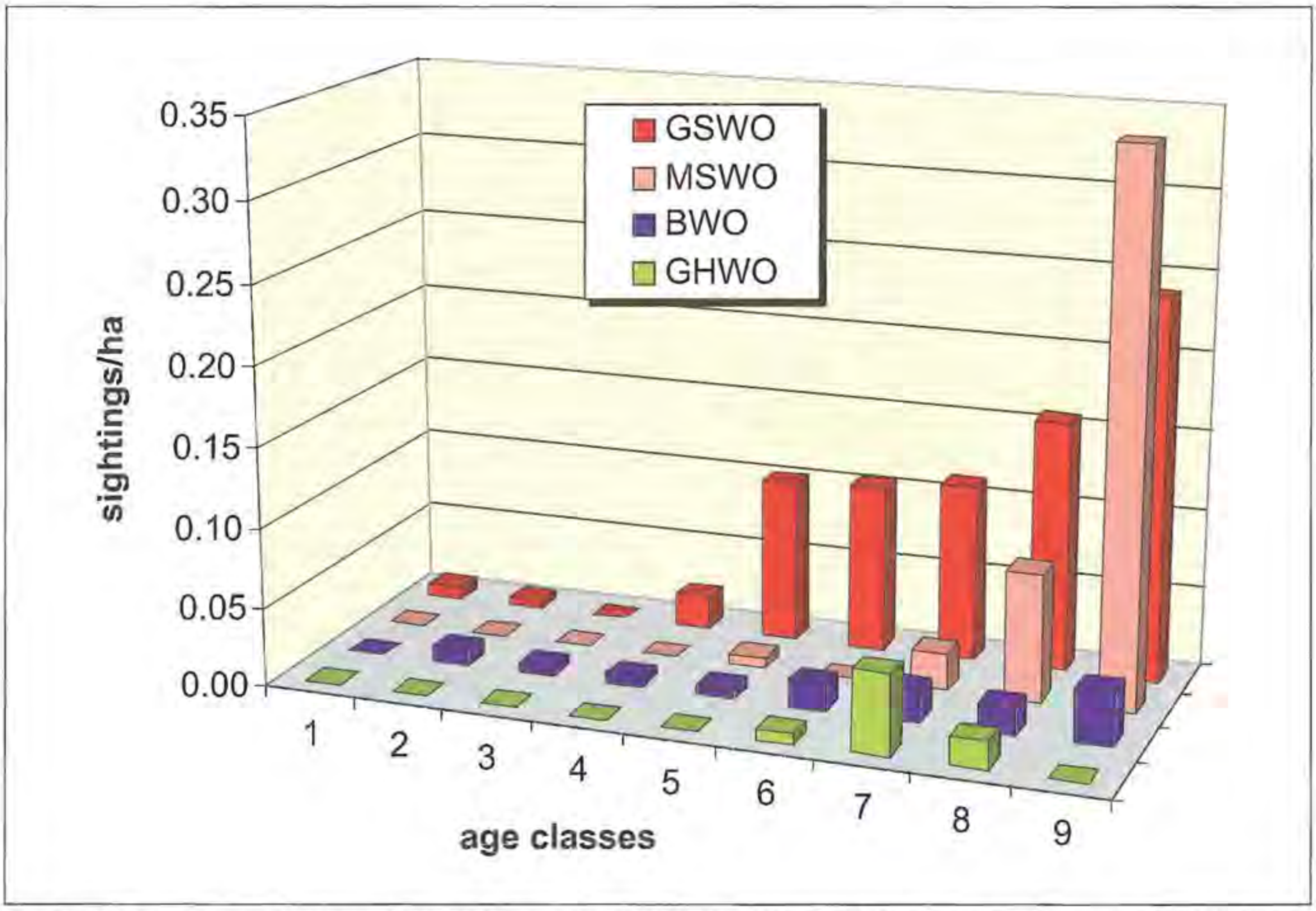

Fig. 2. Distribution of woodpecker sightings of four species (GSWO: Great Spotted Woodpecker *Picoides major*; MSWO: Middle Spotted Woodpecker *Picoides medius*; BWO: Black Woodpecker *Dryocopus martius*; GHWO: Grey-headed Woodpecker *Picus canus*) on age classes of forest stands (stands with „legacy trees" excluded) in the Solling low mountain range (sightings per ha).

other species seemed to avoid stands younger than 100 years. Of all recorded species, the Middle Spotted Woodpecker seemed to have the strongest affinity to old trees (Fig. 2). Fig. 3 shows the "sighting density" of all woodpeckers on stands of the different age classes compared to the average.

On the census plot level, the results are similar. A comparison of the 12 census plots in each area ("Lüneburger Heide" and "Solling") suggests that the total woodpecker abundance is positively correlated with the proportion of trees older than 80 years in a census plot (Rs = 0,804 resp. Rs = 0,692; Table 3; Fig. 4). The same is true for the Great Spotted Woodpecker as the most numerous species (Table 3). The other species occurred only in a few census plots or their abundance was generally too low for a single species analysis.

In "Solling", where diversity of woodpecker species was a little higher than in the "Lüneburger Heide", the number of species in a census plot was also positively correlated with the proportion of trees older 80 years (Rs = 0,769; Fig. 5). Higher elevations of more than 400 m above sea level had a negative effect on both woodpecker abundance and diversity (Fig. 6).

Table 3 shows the correlation coefficients (Spearman Rank Correlation) for all tested age and elevation parameters in both study areas.

Discussion

The results emphasize the significance of old forest stands, and especially old deciduous trees, for the abundance and diversity of woodpeckers. The very old stands in this study (age class 9, more than 160 years old) are by far the most attractive areas for woodpeckers. Although data on the amount of dead wood in the different stands were not available, it can be assumed that in most cases the stands of age class nine are the ones richest in dead wood and snags. The amount of dead wood, lying and standing, increases considerably when a stand turns from the "optimum phase" (where harvesting normally takes place) to the early "climax phase" (in Germany sometimes called "plenter phase") in the forest development (LEIBUNDGUT 1993, SCHERZINGER 1996). The importance of dead wood, especially standing dead wood of large dimensions, for woodpeckers (for excavating cavities as well as for foraging) has been shown by many authors (e.g., SCHERZINGER 1982, NOEKE 1989, ANGELSTAM 1990, SHORT & HORNE 1990, UTSCHICK 1991, RAUH 1993, PECHACEK 1995, WESOLOWSKI & TOMIALOJC 1995, SMITH 1997, McCOMB & LINDENMAYER 1999).

Woodpecker abundance was considerably higher in the "Lüneburger Heide" than in the "Solling". Only two census plots in the "Solling", both with a high proportion of oaks, show total woodpecker abundances that reach the average of the "Lüneburger Heide" region. This might be due to the relatively high elevation of many

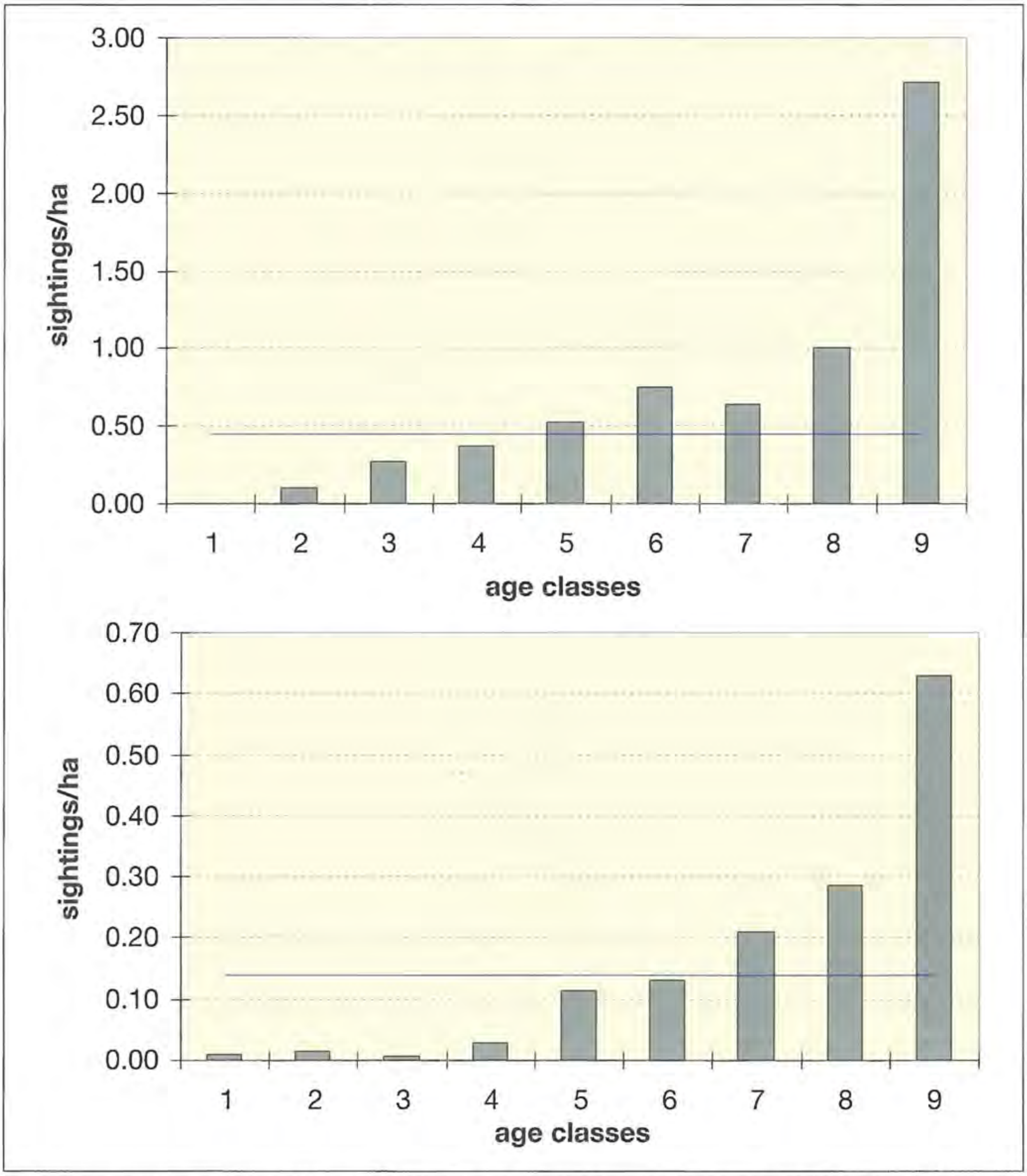

Fig. 3. Distribution of woodpecker sightings (all species) on age classes of forest stands (stands with "legacy trees" excluded) in the "Lüneburger Heide" (above) and in the "Solling" (below; sightings per ha), compared to the average of 0.45 resp. 0.14 sightings per ha (blue line).

census plots in the "Solling", together with the fact that the forest is often dominated by spruce stands, especially on higher elevations. These are unsuitable for most of the woodpeckers, and only marginal habitat for the Great Spotted and Black Woodpecker (GLUTZ VON BLOTZHEIM & BAUER 1980, SCHERZINGER 1982, WAGNER 2000). Compared to other forest regions in Germany, the abundance of Great Spotted and Black Woodpeckers in the "Lüneburger Heide" is relatively high (GLUTZ VON BLOTZHEIM & BAUER 1980, ZANG 1986, FLADE 1994, BLUME & TIEFENBACH 1997).

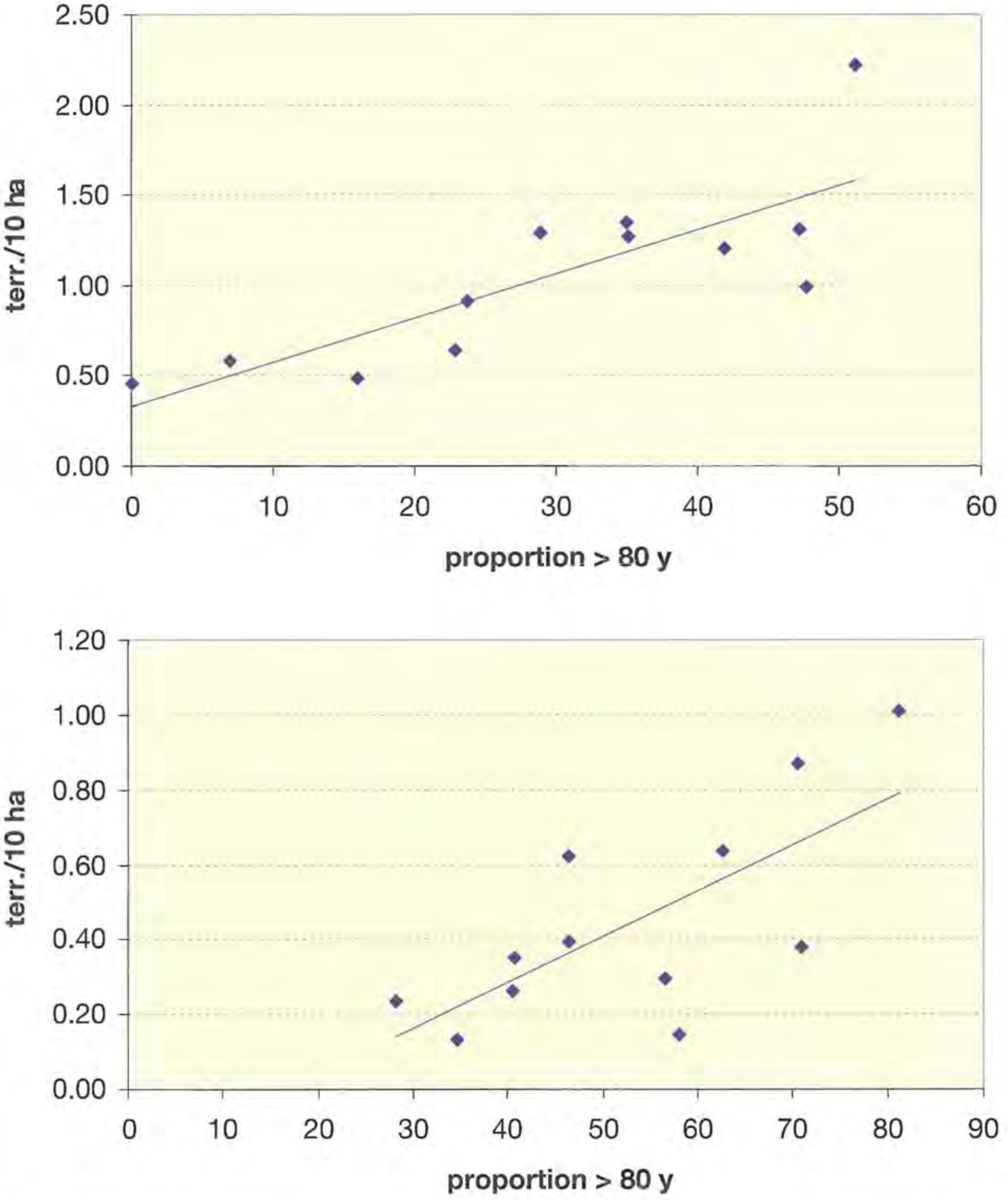

Fig. 4. Relation of total abundance of woodpeckers and the proportion of > 80-year-old trees in the 12 investigation areas in the "Lüneburger Heide" (above) and in the "Solling" low mountain range (below).

On the other hand, diversity of woodpeckers is higher in the "Solling" region. With Middle Spotted and Grey-headed Woodpecker as "additional" species compared to the "Lüneburger Heide", those census plots in the "Solling" rich in old deciduous trees are inhabited by three to five woodpecker species.

There are only a few records of Middle Spotted and Grey-headed Woodpeckers from the "Lüneburger Heide", mainly from the first half of the 20th century (LUTKEPOHL & PRUTER 2000, SCHMIDT 2001). Nevertheless, we suggest that before the almost complete deforestation of the north German lowlands, both species could have occurred in the formerly typical lowland deciduous forests (MIKUSIŃSKI & ANGELSTAM 1997, 1998). The same might be true for the White-backed Woodpecker; GLUTZ VON BLOTZHEIM & BAUER 1980). So the present absence of these species is possibly not due to natural geographic restrictions, but only to the complete change of the landscape by human activities (MIKUSIŃSKI & ANGELSTAM 1998).

Conclusion

The six woodpecker species differ in their suitability as indicator species. Further research for the "fundamental niche" of the species is needed to specify what habitat characteristics (on different spatial scales) the different species can indicate. Furthermore, there is a lack of studies that clearly relate occurrence of woodpeckers to other taxa (MIKUSIŃSKI 1997).

Despite these deficiencies, we conclude that woodpeckers in general seem to be good indicators for sustainable forestry. Of course, they can only be one part of a serious monitoring system of sustainability. Grouse (SCHERZINGER 1997, ANGELSTAM 1998), some species of owls and raptors (SCHERZINGER 1997, THOMPSON & ANGELSTAM 1999), flycatchers (PALEIT et al. 1998) and other birds also might be good indicators. Other groups of organisms must be considered, too. For example, xylobiontic insects are good indicators for the quality of dead wood habitats (RAUH & SCHMITT 1991, MOLLER 1993). While the diversity of vascular plants does not seem to be a suitable indicator at least for European forests (WESTPHAL in press), fungi (KOST 1989, SCHMIDT 1998, OHLSON & TRYTERUD 1999), lichens (LITTERSKI 1998, OHLSON & TRYTERUD 1999, OKOLOW 1999, ULICZKA & ANGELSTAM 2000), and mosses (OHLSON et al. 1997, BERG 1998), due to specific requirements towards the quality of forest ecosystems, are good indicator species.

Acknowledgments

We would like to thank the following persons and institutions for supporting this study: The fieldwork was financed by the "Niedersächsische Forstliche Versuchsanstalt" (NFV), an institution of the Lower Saxony forest administration. Data analysis carried out by the senior author was financed by the "Staatliche Vogelschutzwarte", Lower Saxony "Landesamt für Ökologie" (NLÖ). Man-

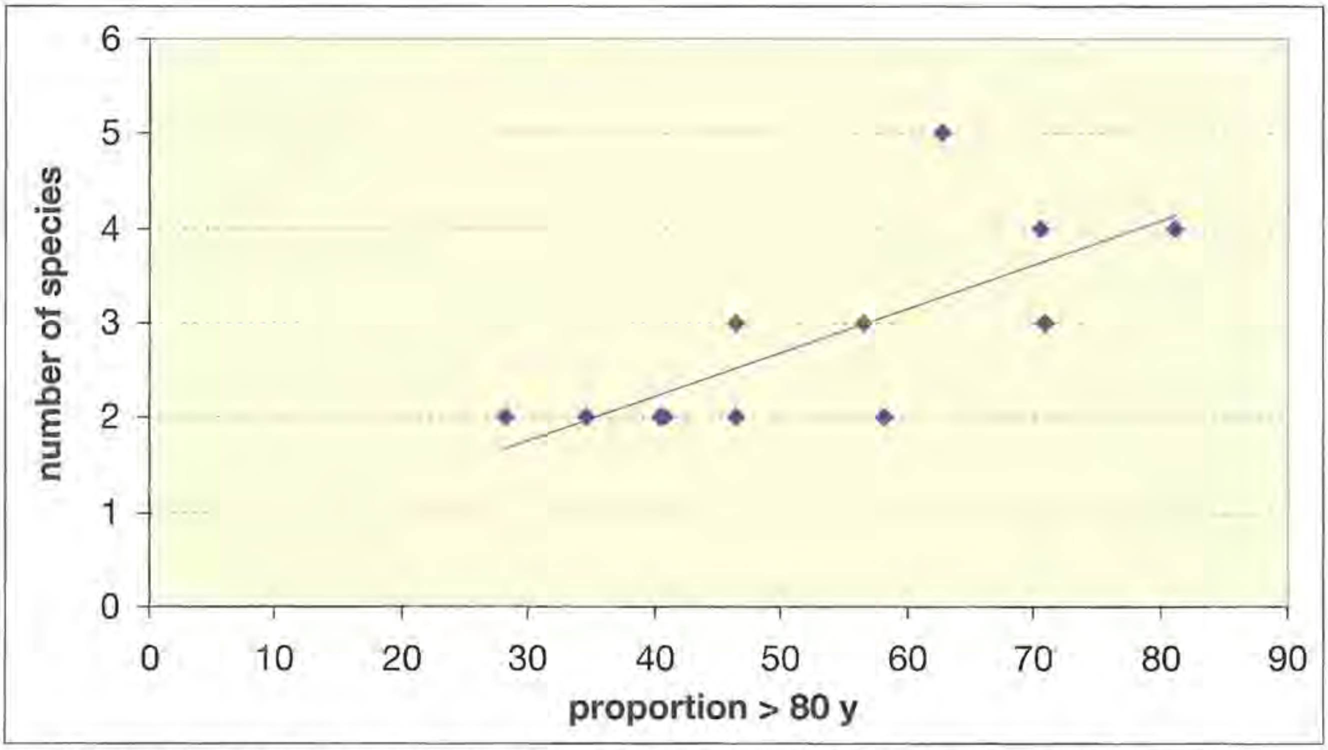

Fig. 5. Relation of woodpecker diversity (number of species) and the proportion of > 80-year-old trees in the "Solling".

fred Lütkepohl, Peter Martensen, Wolfgang Steinborn and Dietmar Zacharias selected the census plots. Field workers in the "Solling" were Gunnar Jacobs, Holger Sonnenburg and Rainer Babin. In the "Lüneburger Heide", Karsten Kohls took some of the census days. Johannes Prüter (Alfred Toepfer Akademie für Naturschutz) gave support and advice during the whole study. Jerome A. Jackson (Florida Gulf Coast University, Ft. Myers, Florida) made comments on the manuscript and improved the language.

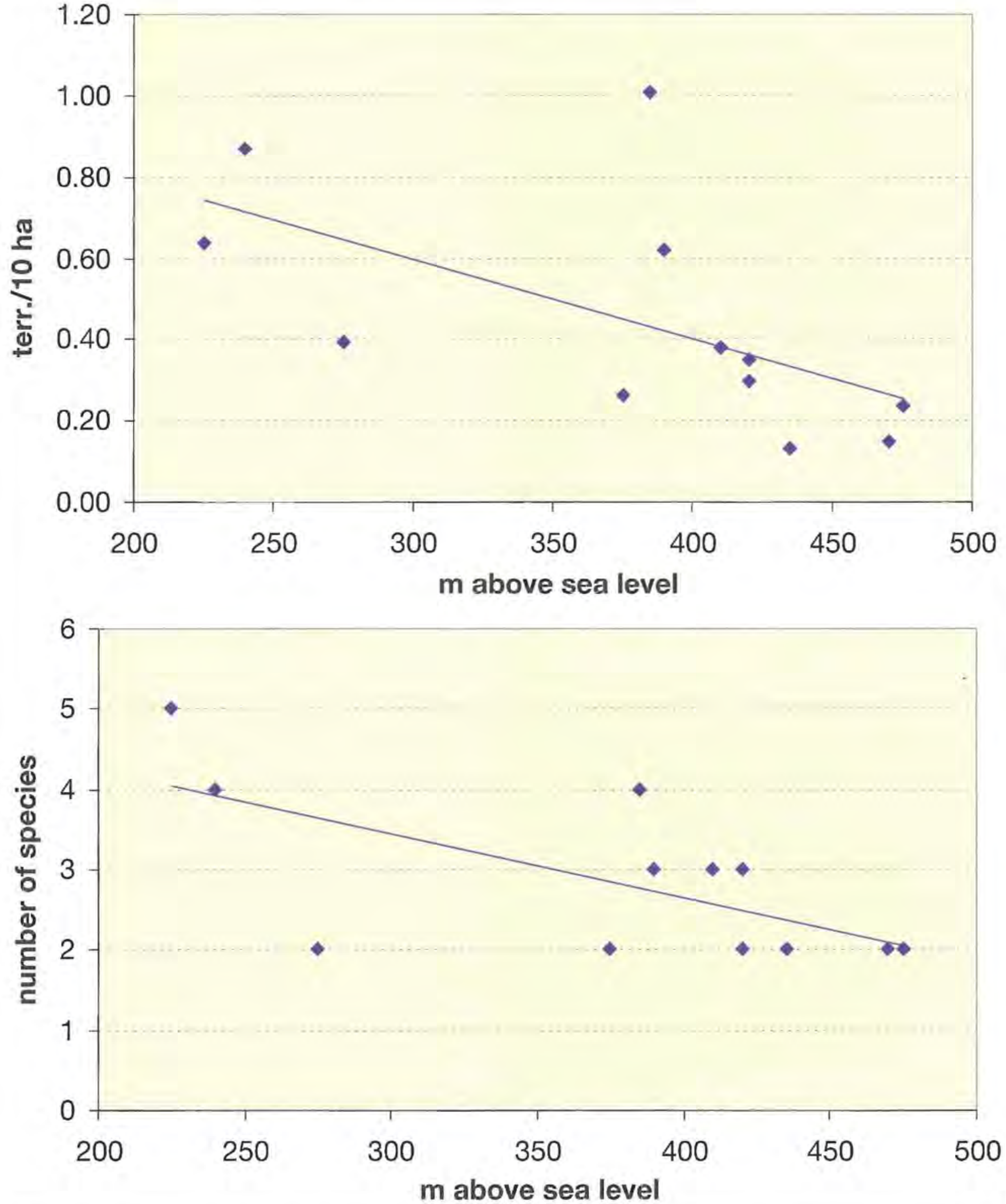

Fig. 6. Relation of total woodpecker abundance (above) resp. diversity (below) and elevation of investigated areas (below) in the Solling.

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