

# **BIOLOGY AND CONSERVATION OF FOREST BIRDS**

**Proceedings of the Society of Canadian Ornithologists  
Special Science Symposium, Fredericton, New Brunswick  
23-25 August 1996**

**Edited by**

**A.W. Diamond and D.N. Nettleship**



**Society of Canadian Ornithologists  
Special Publication No. 1  
Fredericton, New Brunswick**

**1999**

# **Society of Canadian Ornithologists**

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Edited by

A.W. Diamond<sup>1</sup> and D.N. Nettleship<sup>2</sup>

<sup>1</sup> Atlantic Cooperative Wildlife Ecology Research Network  
University of New Brunswick, P.O. Box 45111  
Fredericton, New Brunswick, Canada E3B 6E1

<sup>2</sup> Canadian Wildlife Service, Environment Canada  
45 Alderney Drive, Dartmouth, Nova Scotia, Canada B2Y 2N6  
and  
Lundy Environmental Consulting  
25 Tidewater Lane, Head St. Margaret's Bay  
Tantallon, Nova Scotia, Canada B0J 3J0

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*Cover illustration:*

Downy Woodpecker (*Picoides pubescens*) nest building  
in summer forest habitat by Karen L. Allaben-Confer.

**This SCO Special Publication Number 1  
is dedicated to the memory of**

**Henri R. Ouellet**

**(1938-1999)**

**cherished friend and colleague  
who made outstanding contributions to  
Canadian ornithology and provided great leadership  
to the Society of Canadian Ornithology as President (1994-95)  
including the push towards the establishment of an SCO  
science journal focused on the biology, conservation  
and management of Canadian birds.**

# BIOLOGY AND CONSERVATION OF FOREST BIRDS

Society of Canadian Ornithologists  
Special Publication No. 1  
December 1999

Edited by  
A.W. Diamond and D.N. Nettleship

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## PREFACE

I am extremely excited about the launch of this new Special Publication Series of the Society of Canadian Ornithologists (SCO), introduced with this first issue entitled "*Biology and Conservation of Forest Birds*". The purpose of the series is to allow topics of immense importance to the birds of Canada to be addressed and reported upon to the avian science community at large. The hope is to develop a publication process within the Society that will meet the communication needs of Canadian ornithologists, a form that more properly reflects our avian research and conservation mandate, as well as providing an integrated platform for the transfer and exchange of important and stimulating information on birds and their habitats. The special publication series, to be issued irregularly as special projects on specific topics or avian groups are generated and completed, is but one route of achieving our communication and information dispersion goal. Others will follow, including a new avian journal in response to the many requests from members for a more regular science publication by the Society on the biology, conservation and management needs of Canadian birds. Our success in this new communication function will ultimately be measured by our members and readers, through their use of the material delivered and participation as authors. We can only hope that this broader vision of our Society reflects the future of the avian sciences in Canada.

This project of communication began at the outset of the Society's establishment in 1982. The need to provide a mechanism for the transfer and exchange of information important to professional ornithologists and serious amateurs in Canada was fundamental to its formation. During the past 17 years of growth, the Society has moved from the production of a mimeographed general newsletter and an annual 1-2 hour business meeting — usually held in association with a meeting of another ornithological society outside Canada — for information exchange to a multi-day annual science meeting in Canada and a high-end glossy printed news bulletin, *Picoides*. The science meetings have allowed avian scientists and their students to assemble, trade ideas, and exchange findings of new researches to the benefit of all. It has also permitted us to focus on special subjects and satisfy the need to synthesize and supplement existing information, with the hope to provide direction for future research and management. Part of this process has revealed the clear opportunity to publish the proceedings of special science symposia following peer-review and to ultimately establish a Canadian journal of avian biology. The appearance of this Special Publication No. 1 of the Society of Canadian Ornithology "*Biology and Conservation of Forest Birds*" represents the successful attainment of the first phase of this endeavour. I hope that, with this issue, we can prove that our Society and its members are ready to put out useful and significant science publications.

What more can I say? Only that I hope that our record of moving forward from a simple newsletter to a more sophisticated and noteworthy bulletin, on to the external publication of the mini-symposium held by SCO in conjunction with the Wilson Ornithological Society in 1993 — "*Monitoring bird populations: the Canadian Experience*" (Canadian Wildlife Service Occasional Paper No. 95, 1997) — and now to our own Special Publication Number 1, demonstrates real and steady progress towards our original communication mission, an effort worthy of your continued

interest and support. We welcome your reaction, response, and input in making our special publications series a grand success over both the short- and long-terms. Your comments and suggestions are key in shaping this special publication series.

And finally, now let me admit that I'm biased. When you launch a new initiative such as a publication series, you expect plenty of comments, some ferocious, and hopefully some complimentary and admiring. But I hope you share my view, and that of my predecessor — Henri Ouellet, who set up a formal publications committee during his presidency (1994-95) to assess the feasibility of an SCO science journal — and past vice-president (1996-97) and current president, Tony Diamond, that it is imperative for us as a national ornithological society to provide an effective publication system for information on Canadian birds. I'm convinced (see my original mission message in *Picoides* 9, No. 1: 1-4, 1996) that our collective opinion — and that expressed by the membership at large when polled in 1996 — is correct. I figure the first work of any published series is the most difficult, breaking new ground, and that those to follow will be much easier.

I leave it to Tony Diamond, co-convener and organizer of our first stand-alone science meeting, to explain the germination and rationale of the special symposium on forest birds, the highlight of the conference proceedings and its Canadian orientation (see Introduction). This symposium gave rise to this volume: Special Publication Number 1 of the Society of Canadian Ornithologists. In conclusion, let me wish everyone good reading and learning, and continued success in the attainment of the broader communication vision of the future of our Society.

David Nettleship  
SCO President, 1996-97

October 1999



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In the preparation of "*Biology and Conservation of Forest Birds*" we have benefited enormously from the advice and suggestions of many avian biologists, both inside and outside of the Society of Canadian Ornithologists. We would like to thank especially Fred Cooke, Spencer Sealy, Keith Hobson and Jean-Pierre Savard for their continuing interest in and support of the publication.

All the papers contributed to this volume have been reviewed by one or two peers. Our special thanks go to the following people, who reviewed manuscripts and offered valuable criticism and advice to the authors and editors: Robert Askins, David Bird, Marcel Darveau, Tony Erskine, Graham Forbes, John Hagan, Susan Hannon, Dick Holmes, David Kirk, Kathy Martin, Peter McKinley, Gerry Parker, Bruce Peterjohn, C.J. Ralph, Greg Robertson, Raleigh Robertson, Jean-Pierre Savard, Jim Schieck, and Marc-André Villard. We thank Jean-Pierre Savard and Karel Allard for translating the abstracts into our other official language.

For helping to make the meeting and this special publication a reality, we warmly thank Dr. Tom Sterner, Director Forest Health, Canadian Forest Service, Natural Resources Canada, Atlantic Forestry Centre, Fredericton, New Brunswick; and Dr. George Finney, Director of the Canadian Wildlife Service and Environmental Conservation Branch, Environment Canada, Atlantic Region, Sackville, New Brunswick, who helped finance the publication of the conference proceedings. The joint support by these two federal departments bodes well for the future collaboration between foresters and ornithologists called for in this publication. Their patient support through to completion is greatly appreciated.

We would also like to thank the contributors for their patience and understanding through the lengthy process of preparation for publication. We also thank family, students and colleagues for the neglect they have endured through this process. Thanks are extended to Graham Forbes for the use of facilities at the Sir James Dunn Wildlife Research Centre, Fredericton, New Brunswick.

A.W. Diamond and D.N. Nettleship

## LIST OF CONTRIBUTORS

**Bortolotti, G.R.,**  
Department of Biology, University of Saskatchewan, 112 Science  
Place, Saskatoon, Saskatchewan, Canada S7N 5E2

**Boulanger, J.,**  
Integrated Ecological Research, 801 Victoria Street, Nelson,  
British Columbia, Canada V1L 4L4

**Collins, B.T.,**  
National Wildlife Research Centre, Canadian Wildlife Service,  
100 Gamelin Blvd., Hull, Québec, Canada K1A 0H3

**Cooke, F.,**  
Department of Biological Sciences, Simon Fraser University,  
Burnaby, British Columbia, Canada V5A 1S6

**Dawson, R.D.,**  
Department of Biology, University of Saskatchewan, 112 Science  
Place, Saskatoon, Saskatchewan, Canada S7N 5E2

**Deroccher, A.E.,**  
British Columbia Ministry of Forests, 21 Labieux Road, Nanaimo,  
British Columbia, Canada V9T 6E9 [Current address: Norwegian  
Polar Institute, Storgt. 25, Box 399, N-9001 Tromsø, Norway]

**Desrochers, A.,**  
Département des Sciences du bois et de la forêt, Pavillon Abitibi  
Pressé, Université Laval, Ste-Foy, Québec, Canada G1K 7P4

**Diamond, A.W.,**  
Atlantic Cooperative Wildlife Ecology Research Network,  
University of New Brunswick, P.O. Box 45111, Fredericton,  
New Brunswick, Canada E3B 6E1

**Doucette, D.,**  
552 rue Breaux, Dieppe, New Brunswick, Canada E1A 5N8

**Downes, C.M.,**  
National Wildlife Research Centre, Canadian Wildlife Service,  
100 Gamelin Blvd., Hull, Québec, Canada K1A 0H3

**Doyon, F.,**  
Groupe de Recherche en Écologie Forestière, Université du  
Québec à Montréal, C.P. 888, Succ. Centre-ville, Montréal,  
Québec, Canada H3C 3P8 [Current address: Institut Québécois  
d'Aménagement de la Forêt Feuillue, 88 rue Principale, St-André-  
Avellan, Québec, Canada J0V 1W0]

**Falardeau, G.,**  
Service Canadien de la Faune, 1141 route de l'Église, C.P. 10100,  
Ste-Foy, Québec, Canada G1V 4H5

**Freedman, B.,**  
Department of Biology, Dalhousie University, Halifax, Nova  
Scotia, Canada B3H 4J1

**Gagnon, D.,**  
Groupe de Recherche en Écologie Forestière, Université du  
Québec à Montréal, C.P. 888, Succ. Centre-ville, Montréal,  
Québec, Canada H3C 3P8

**Giroux, J.-F.,**  
Groupe de Recherche en Écologie Forestière, Université du  
Québec à Montréal, C.P. 888, Succ. Centre-ville, Montréal,  
Québec, Canada H3C 3P8

**Haché, D.,**  
Gros Morne National Park, P.O. Box 136, Rocky Harbour,  
Newfoundland, Canada A0K 4N0

**Hobson, K.A.,**  
Prairie and Northern Wildlife Research Centre, Canadian Wildlife  
Service, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada  
S7N 0X4

**Johnson, C.,**  
Department of Biology, Dalhousie University, Halifax, Nova  
Scotia, Canada B3H 4J1

**Kaiser, G.,**  
Canadian Wildlife Service, 5421 Robertson Road RR1, Delta,  
British Columbia, Canada V4K 3N2

**Kingsley, A.,**  
Watershed Ecosystems Graduate Program and Biology  
Department, Trent University, Peterborough, Ontario, Canada K9J  
7B8 [Current address: 4605 Highway 12, RR 2, Kentville, Nova  
Scotia, Canada B4N 3V8]

**Martin, K.,**  
Centre for Applied Conservation Biology, Faculty of Forestry,  
University of British Columbia, Vancouver, British Columbia,  
Canada V6T 1Z4 [and Canadian Wildlife Service, 5421  
Robertson Road RR1, Delta, British Columbia, Canada V4K 3N2]

**Nettleship, D.N.,**  
Canadian Wildlife Service, Environment Canada, 45 Alderney  
Drive, Dartmouth, Nova Scotia, Canada B2Y 2N6 [and Lundy  
Environmental Consulting, 25 Tidewater Lane, Head St.  
Margaret's Bay, Tantallon, Nova Scotia, Canada B0J 3J0]

**Nel, E.,**  
Watershed Ecosystems Graduate Program and Biology  
Department, Trent University, Peterborough, Ontario, Canada  
K9J 7B8

**Parker, G.R.,**  
Canadian Wildlife Service, Box 6227, Sackville, New Brunswick,  
Canada E4L 1G6

**Savard, J.-P.L.,**  
Service Canadien de la Faune, 1141 route de l'Église, C.P. 10100,  
Ste-Foy, Québec, Canada G1V 4H5

**BIOLOGY AND CONSERVATION  
OF FOREST BIRDS**

**Society of Canadian Ornithologists  
Special Publication No. 1**

# Introduction to Biology and Conservation of Forest Birds

**A.W. Diamond**

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## Abstract

Events leading to the recent increase in research activity on forest birds are reviewed briefly, in the context of their influence on the decision of the Society of Canadian Ornithologists to hold its first stand-alone scientific meeting on this topic. I distinguish between 'landscape' effects on the ecology of forest birds, in which populations are distributed among small patches in a hostile (non-forested) matrix and are probably influenced as much by what happens to the land around the forest than within it; and effects of forestry practices on birds within generally forested landscapes, which was the focus of the meeting and of this volume. The extent to which landscape effects are important in the demographics of birds in landscapes still dominated by forest, is unclear, but is receiving increased interest among researchers. A brief glossary of terms commonly used by foresters, which ornithologists need to understand if they are to understand how the birds' habitats will respond, is included to facilitate understanding and interpretation of the papers that follow.

## Résumé

Une révision des événements menant à l'augmentation de l'effort de recherche sur les oiseaux forestiers est présentée dans le contexte de l'influence de ces recherches sur la décision prise par la Société des Ornithologues du Canada d'organiser une première réunion autonome traitant ce sujet. Je fais la différence entre les effets du paysage et les effets de méthodes d'exploitation forestières sur les oiseaux se trouvant à l'intérieur des régions forestières sur l'écologie des oiseaux forestiers. Les populations de ceux-ci sont distribuées parmi de petites parcelles à l'intérieur d'une matrice d'habitat hostile (non-recouverte d'arbres) et sont probablement tout autant influencées par ce qui arrive dans la région avoisinante qu'à l'intérieur-même de la forêt. Les effets de méthodes d'exploitation forestières ont été le sujet de la réunion sus-mentionnée et sont discutés à l'intérieur du présent document. Le degré de l'importance des effets des différents paysages sur la démographie des oiseaux qui s'y trouvent est incertain, surtout en ce qui concerne les paysages toujours dominés par la forêt. Cette matière suscite présentement l'intérêt grandissant des jeunes chercheurs. Un bref glossaire de la terminologie est compris à l'intérieur du document afin de faciliter la compréhension et l'interprétation des articles qui suivent. Les ornithologues doivent se familiariser avec le langage des forestiers si ils ont pour but de comprendre comment l'habitat des oiseaux forestiers réagira face à l'exploitation forestière.

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A.W. Diamond, Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick, Canada E3B 6E1. ([diamond@unb.ca](mailto:diamond@unb.ca))

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The Society of Canadian Ornithologists' first stand-alone meeting focused on forest bird issues for a number of reasons. For many years there has been widespread concern both at the rate at which forestry is expanding the area of forest cut each year, and at mounting evidence that populations of forest birds are

declining. These trends lead inevitably to the recognition that the future of forest birds lies largely in the hands of those who manage their habitat, i.e., professional foresters. Until recently there was relatively little research or monitoring directed towards these issues, especially among government agencies.

Related anxiety about the prospects for neotropical migrants - many of which are also forest species - had attracted considerable attention in North America as a whole (e.g., Keast and Morton 1980; Hagan and Johnston 1992), particularly in the United States (e.g., Martin and Finch 1995), but also increasingly in Canada (Diamond 1991; Kuhnke 1993; Kirk et al. 1996, 1997).

Several events in the early 1990s reflected an increased sense of urgency to address these issues. The Canadian government's Green Plan enhanced the forest ecology and non-game bird programs of the Canadian Wildlife Service (Burnett 1999:154-155), and in 1994 the Network of Centres of Excellence program of Industry Canada awarded significant funds to bird research within the Sustainable Forest Management (SFM) Network (Adamowicz 1999). The Partners in Flight initiative in the United States was beginning to stimulate attention to these issues in Canada, including development of a national Landbird Conservation Strategy for Canada (Dunn 1997). As a result of these and other changes there has been a significant increase in both research and conservation activities directed towards forest birds in Canada, which the Council of the Society of Canadian Ornithologists (SCO) felt should be recognised and discussed at the Society's inaugural Scientific Meeting.

The meeting was held on the campus of the University of New Brunswick in Fredericton and was sponsored by the regional offices of the Canadian Forest Service and Canadian Wildlife Service. Not all of the speakers provided manuscripts for publication, and some contributions were invited subsequently to improve the balance of the publication, which consequently is based on the meeting rather than being strictly a record of its proceedings. The opening speaker, Dr. John Hagan of Manomet Observatory in Massachusetts, set the stage with an absorbing overview of some of his work in the industrial forests of northern Maine. This work, which is being published elsewhere (e.g., Hagan et al. 1996, 1997) provides a model of collaboration between researchers, industry and foundations to provide information of direct interest to forest managers.

The papers in the present publication are arranged in three groups. Since most of the literature on population trends of North American birds refers either to the United States or to the continent as a whole, we felt it was important to provide an analysis specifically of Canadian populations. Thus, the first paper (Downes and Collins) reviews current knowledge of population trends in forest birds in Canada, setting the

conservation context for the following material. The next three papers (Hobson, Cooke, and Boulanger et al.) focus on important methods for exploring some of the research issues relevant to forest birds. Hobson provides an authoritative account of exciting recent developments in stable-isotope technology, ranging widely beyond strictly forest birds to expose some of the potential applications of this technology to birds in general. Cooke, and Boulanger et al., describe some of the innovative and creative approaches being developed to tackle some extremely difficult problems in studying a threatened species normally thought of as a seabird but dependent on forest for nesting habitat. Their papers describe innovative field and modeling approaches to providing the best possible science to a situation where forest management and bird conservation are frequently in conflict.

The remaining papers address the effects on birds of specific forest practices, either as reviews of a range of existing work (Freedman and Johnson) or as results of original research not published elsewhere (Parker et al.; Kingsley and Nol; Doyon et al.; Falardeau et al.). Dawson and Bortolotti describe the impacts of a large burn on boreal forest; their paper is not only an example of creatively seizing upon an experiment offered by nature, but is also important in the context of the long-standing debate between foresters and biologists over the extent to which clearcutting 'mimics' the effects of natural fires.

Current research on forest bird ecology and conservation (in Canada and elsewhere) falls into two distinct categories. The first, which is the focus of this publication, addresses the impact on forest birds of specific forestry practices (clearcutting, various forms of selective harvesting, etc.). This work offers guidelines for silvicultural practices (total volume cut, extent of thinning, spacing, rotation age, etc.) at the spatial level of the forest stand. This is the frame of reference within which we are used to thinking about habitat use by birds (and other wildlife).

The other category concerns what are now widely referred to as landscape effects, i.e., effects of the size and spacing of forest patches separated by non-forested habitat. Much forest bird research in the last decade has focused on these larger-scale effects. It is perhaps paradoxical that these features of forest bird ecology - which have dominated research in the last few years - apply most obviously when forestry is no longer the dominant land use. They apply most clearly when forestry has given way to agriculture (or urbanization) as the dominant land use, to the extent that suitable habitat for forest species is distributed as an

arrangement of patches embedded in a matrix of unsuitable (i.e., non-forested) habitat. Commercial forestry is rarely economic when this is the case, so the problems of dispersal between patches (which probably dominate the demographics of species in this situation) are in that sense due to not too much forestry, but too little. Consequently, solutions to the problems identified in these situations lie more in the realm of land-use policy than of silvicultural practices.

Research on effects of landscape structure on forest birds began sufficiently recently in Canada that results are only recently beginning to be published (e.g., Villard et al. 1995, 1999; Schmiegelow et al. 1997; Drolet et al. 1999; Friesen et al. 1999; Potvin et al. 1999). The extent to which such effects are important to birds living in landscapes still dominated by forest cover - especially by comparison with effects of stand-level silvicultural practices - is still unclear. Andr  n (1994) suggested that landscape effects become important when forest cover drops below about 30% of the landscape, but the application of this figure to Canadian forest birds needs to be assessed (for a recent discussion see Drolet et al. 1999). In the interests of maintaining a clear focus on interactions between birds and forest management, we do not address landscape issues directly in this volume.

This publication includes material from across the country, but for various reasons does not reflect the full range of forest bird research being carried out in Canada. Part of the reason lies in the very fact of the recent dramatic increase in activity; some very exciting projects, including those under the umbrella of the SFM Network, were still in progress when this project was conceived and are being published elsewhere or still in progress. For short accounts or previews of much of this work see particularly papers by Hannon, Darveau, B  langer, Drapeau, Villard, and McKinley, in Veeman et al. (1999).

One of the less recognised, but I believe very significant, problems that arises when biologists and foresters try to communicate, is the difference in the technical vocabularies they use. In the interests of trying to improve this situation, and of helping readers of this volume to make the most of the information it offers, I provide below a short glossary of some of the more common terms used by foresters, especially those most relevant to habitat issues.

## Terminology

The following papers use a number of terms familiar to foresters, but unfamiliar to (and often misunderstood by) many ornithologists. In compiling this glossary, I

have drawn heavily on Smith (1986), Thompson et al. (1995), and especially Seymour and Hunter (1999). Not all the terms discussed here necessarily appear in the papers that follow, but they are included in the interests of completeness.

## Stands, forests, and landscapes

**Stands** are 'patches of forest that are reasonably homogeneous in terms of species composition, age and density' (Seymour and Hunter 1999); or 'contiguous groups of trees sufficiently uniform in species composition and structure to serve as a management unit' (Thompson et al. 1995). They correspond generally to the polygons drawn by photo-interpreters on the forest cover-type maps that foresters commonly use to illustrate harvest plans.

Commercial forests are managed at a larger spatial scale incorporating 'a collection of stands administered as an integrated unit' (Smith 1986), often referred to as a **Forest Management Area (FMA)**, but usually subdivided into smaller spatial units (**compartments**) comprising groups of stands (Thompson et al. 1995). The ecological equivalent of this larger spatial scale is the **landscape**, the 'arrays of forest stands, grasslands, wetlands, and so on that form heterogeneous mosaics across the land' (Forman 1995).

## Harvesting methods - clearcuts, shelterwoods, and partial cuts

**Silviculture** refers to the suite of activities carried out in a stand to control establishment, composition, structure and growth of the trees. These activities, often referred to generally as **interventions**, comprise a silvicultural system or program of management for the entire rotation of a stand, where **rotation** refers to the time between successive harvests. The **silvicultural system** defines how and when trees are cut, how new trees are grown, and whether the resulting stand will be even-aged or uneven-aged.

In **even-aged** stands (of which the most familiar example is a plantation), there are only one or two age-classes in the stand, whereas **uneven-aged** stands contain three or more age-classes. Even-aged forests are created or maintained by **clearcutting** (in which all or most trees are removed at the same time, sometimes leaving a few 'seed trees' to help regenerate the stand), or by the **shelterwood** method in which trees are removed in a series of **partial cuts** (or **passes**) separated by several years, allowing seedlings to regenerate under the protection of a partial overstory before the final cut (see the paper by Kingsley and Nol for an example in Ontario). There are several variants

on these methods, including **patch cutting** which is clearcutting on a very small spatial scale (i.e., a hectare or so), compared with the tens, hundreds or (rarely nowadays) thousands of hectares of a clearcut; and **strip cutting**, in which partial cuts are arranged in linear strips.

Uneven-aged forests (normally preferred by birds, or at least by ornithologists) are maintained by **selection** harvesting of some sort; **single-tree selection**, in which individual trees are removed, or **group selection** in which they are removed in small groups. Early exploitation of forests in Canada (by men and horses rather than machines) usually involved selection of individual trees of high market value, and is often referred to derogatively as '**high-grading**'. Biologists tend to regard this form of forestry as ecologically benign, but because it was highly selective of both size and species it had effects which are often subtle but may be very significant. For example, the selective removal of red spruce *Picea rubens* from Acadian forests in the northeastern United States and Maritime Canada has helped to convert a mixed forest of spruce and long-lived hardwoods into one dominated by short-lived balsam fir *Abies balsamea*, red maple *Acer rubrum* and aspens *Populus* spp. (Scymour and Hunter 1999). The process of **conversion** of one type of forest into another, which is one of the most ecologically significant effects of forest harvesting, is widespread, but insidious because it takes place over time scales long enough to escape notice by all but the longest-lived observers.

## Natural disturbances

The term '**natural disturbance**' recognises that most forests, far from remaining undisturbed until human beings appeared (as some biologists seem still to believe), owe their characteristics to natural 'disasters' such as fire, disease, defoliation by insect pests, ice-storms or wind storms, which have visited all Canadian forests since the glaciers retreated, at intervals which vary by geography, soils, climate and forest type. Boreal forest, for example, is widely recognised as a fire-induced ecosystem (Hunter 1993). Current forestry not only imposes its own 'un-natural' disturbance patterns on the forest, but strives to suppress the natural disturbance patterns; these efforts are, at the national level, generally unsuccessful, since in most years the volume of forest in Canada burnt or defoliated by insects reaches about 70% of the volume harvested (Canadian Council of Forest Ministers 1994).

Landscapes subject to even-aged management

comprise forest stands with an age-class distribution that usually differs from that of unharvested forests, or those subject to uneven-aged management. The distribution of age-classes, and the frequency of cutting, both depend on the rotation length; in a 100-year rotation, for example, about 10% of the area would be in 'regenerating' age-classes (stands 1-10 years old). This proportion will differ from that of the unmanaged forest to the extent that the rotation age differs from the frequency of natural disturbances; if, for example, the forest is historically swept by fire or insect pests every 100 years, the age-class distribution would be similar in the two forests.

In most Canadian forests, rotation ages are much shorter than the periodicity of natural disturbances, so not only are the age-class distributions different in managed forests, but probably much more important, stands older than rotation age disappear from the managed portion of the landscape. This explains the demand by biologists for old forests to be set aside as protected areas, or for forests to be managed to more closely emulate natural disturbance patterns (Adamowicz 1999; Scymour and Hunter 1999: 29-32). It is salutary that 80-90% of forest harvesting in Canada is still implemented by clearcutting and 'old growth is still the favoured target of harvest operations' (Hebert 1999).

Two different types of natural disturbance are generally recognised, differing in the spatial scale over which they operate and therefore in the nature of their effects on the forest. **Stand-replacing** disturbances, such as fire and windthrow, kill all or most of the overstory (the tallest trees) and affect whole stands or groups of stands at one, whereas **gap-replacing** disturbances usually involve the death of individual trees (Woodley and Forbes 1997). The prevalence of each disturbance pattern determines to a large extent the type of forest, and, under the 'natural disturbance paradigm' (Adamowicz 1999) of forest management, should also drive the silvicultural system (Hunter 1993).

## Silvicultural practices

Silvicultural practices (as distinct from silvicultural systems, above) are the interventions undertaken to speed regeneration of the desired tree species (e.g., planting, site-preparation including slash-removal, burning, and scarification [mechanical removal or mixing of the organic matter with the mineral soil]); and those carried out to increase tree growth by freeing them from competition (**release cutting** or **thinning**). Thinning is often referred to as '**pre-commercial**' or

'commercial' according to whether or not the saplings removed can be sold.

## Forest types

Finally, the distinction is often made between *tolerant* and *intolerant* tree species or forest types. The 'tolerance' referred to in these terms is the tolerance of the regenerating sapling to shade; tolerant species grow in shade, i.e. beneath a forest canopy (and so will not grow in clearcuts), whereas intolerant species (such as paper birch *Betula papyrifera*, aspens, etc.) will regenerate in unshaded conditions and are consequently the first to recolonise clearcuts.

These notes are offered in the hope that a common understanding of terminology should clarify issues and allow better appreciation of the interpretation and intent of the papers that follow.

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# **Population trends of woodland and scrubland birds from the Canadian Breeding Bird Survey, 1966-94**

**C.M. Downes and B.T. Collins**

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## **Abstract**

Data from the North American Breeding Bird Survey (BBS) can be used to determine long-term population trends in terrestrial birds at regional, national and continental scales. In this paper, data from the Canadian Breeding Bird Survey are used to examine population trends in woodland and scrub/successional birds. Population trend estimates are calculated for Canada overall, and for each of 7 biogeographical regions over the periods 1966-94, 1966-79, 1980-94 and 1993-94. The proportion of individual species increasing or decreasing was also calculated. Long-term trends (1966-1994) for Canada indicate that woodland birds as a group are not declining, although annual indices showed high year-to-year variation. Several individual species showed long-term declines, yet 60% of the species showed increasing population trends in Canada during the period 1966-1994. There is evidence of more decreases in total woodland bird numbers after 1980. Declines in scrub/successional species were detected between 1966 and 1994 in Canada overall, and in the Atlantic Maritime and Boreal Shield regions. Trends for both woodland and scrub/successional birds vary widely among biogeographic regions. These results can be compared with trends in the United States to determine the relative status of breeding birds in Canada.

## **Résumé**

Les données du relevé des oiseaux nicheurs de l'Amérique du Nord (RON) peuvent être utilisées pour déterminer les tendances à long terme des populations d'oiseaux terrestres aux échelles régionale, nationale et continentale. Dans ce papier, les données du RON sont utilisées pour examiner les tendances des populations d'oiseaux forestiers et buissonniers (de forêts de succession). Les tendances sont calculées pour le Canada entier, et pour chacune des 7 régions biogéographiques pour les périodes 1966-94, 1966-79, 1980-94 et 1993-94. La proportion d'espèces avec des tendances positives ou négatives a été calculée. Les tendances à long terme (1966-94) pour le Canada indiquent que les oiseaux forestiers comme groupe ne sont pas en déclin quoique les indices annuels révèlent de fortes variations d'année en année. Quoique plusieurs espèces aient décliné depuis les années 60, 60% des espèces ont augmenté durant la même période (1966-94) au Canada. Certaines évidences indiquent un déclin pour plusieurs espèces forestières après 1980. Des déclin dans les espèces buissonnières/de succession furent détectées entre 1966 et 1994 à l'échelle du Canada de même que dans les régions des Maritimes et du bouclier boréal. Les tendances pour les espèces forestières et buissonnières variaient beaucoup entre les régions biogéographiques. Ces résultats peuvent être comparés avec les tendances aux États-Unis pour déterminer le statut relatif des espèces nichant au Canada.

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C.M. Downes and B.T. Collins, National Wildlife Research Centre, Canadian Wildlife Service, 100 Gamelin Blvd., Hull, Québec, Canada K1A 0H3. ([connie.downes@ec.gc.ca](mailto:connie.downes@ec.gc.ca))

## Introduction

The North American Breeding Bird Survey (BBS) provides data on population changes in terrestrial birds at regional, national and continental scales (Peterjohn and Sauer 1994). The BBS began in 1966 in the eastern United States and maritime Canada and has since expanded throughout the United States and Canada including Alaska, Yukon and a few surveys in the Northwest Territories. For most landbirds, the BBS is the only source of long-term data on population change that extends throughout the continent. The BBS is jointly co-ordinated by the U.S. Geological Survey, Patuxent Wildlife Research Center and the National Wildlife Research Centre, Canadian Wildlife Service (CWS).

Several authors have examined trends among habitat or migratory groups and time periods for landbirds and analyses have been conducted using data from the North American Breeding Bird Survey for physiographic regions and the continent (e.g., Robbins et al. 1989; Johnston and Hagan 1992; Askins 1993; Böhning-Gaese et al. 1993; Peterjohn and Sauer 1994; Peterjohn et al. 1994, 1996; Sauer et al. 1996). These papers have generated much concern and discussion about the status of landbirds in North America and the causes of population change.

Robbins et al. (1989) examined populations of neotropical migrants in the eastern United States, many of which are woodland birds, and found more declines between 1978 and 1987 as compared with 1966-78. More recent analyses of BBS data across the continent (Peterjohn et al. 1994, 1996) indicate that although fewer species were increasing than decreasing over the course of the BBS in the Eastern and Central regions of the continent, more Neotropical migrant species increased during the 1990s than the long-term trends (1966-95) in those regions. Long-term trends (1966-95) for Neotropical migrants in the Western region of the continent showed more species increasing than decreasing (Peterjohn et al. 1996). Peterjohn et al. (1996) suggest these recent results are more positive for Neotropical migrants than the declines reported in the late 1980s (Robbins et al. 1989), but do not yet indicate a long-term reversal of these declines.

Population trends have also been examined for birds grouped by habitat type (i.e., woodland, scrubland/successional) as well as migratory habits. Sauer and Droege (1992) reported that while populations of Neotropical migrants generally increased over the long-term of the BBS survey (between 1966 and 1988), they showed declines after

1978, especially for eastern forest and central scrub/successional species. Peterjohn and Sauer (1994) found a similar increase in the proportion of decreasing woodland species between 1982 and 1991. More woodland species were increasing than decreasing over the long-term (1966-95) in the eastern and western regions of North America and across the continent (Peterjohn et al. 1996). Recent short-term trends for woodland birds during the 1990s were variable among regions (Peterjohn et al. 1994, 1996). Peterjohn et al. (1995) also examined BBS trends in woodland birds between 1966-79 and 1980-91. During the early period more woodland birds increased than decreased in the eastern North America and continent-wide analyses. In the later period, decreasing species outnumbered increasing species in the Eastern region and no other region had significantly more increasing species. In comparison to other habitat groups there was a higher proportion of woodland birds showing increasing trends than in the grassland or scrub/successional groups (Peterjohn and Sauer 1994) over 30 years of the BBS (1966 to 1995).

Long-term trends (1966-95) for scrub/successional birds showed more species decreasing than increasing in eastern and central regions of North America and across the continent as a whole. Recent short-term trends for scrubland birds in the 1990s were variable from year to year (Peterjohn et al. 1994, 1996). During the early years of the BBS (1966-79), more scrub/successional birds were increasing than decreasing in eastern and western North America and continent-wide regions. In the later years (1980-91), more species were increasing in western North America while other regions showed no significant differences (Peterjohn et al. 1995). Other authors have shown declines in various individual species of scrub/successional birds. Using data from the BBS, banding and migration counts from eastern North America, Askins (1993) reported that the majority of scrub/successional species were showing declining populations between 1960s and 1980s. Hagan (1993) showed consistent, long-term declines (8-10% per year) in eastern United States populations of Rufous-sided Towhees (see Appendix 1 for scientific names).

The causes for these changes in population trends are still uncertain but include habitat loss and fragmentation (Whitcomb et al. 1981; Askins and Philbrick 1987; Wilcove 1985; Terborgh 1989), parasitism (Brittingham and Temple 1983) and predation (Wilcove 1985; Böhning-Gaese et al. 1993). Some authors have suggested that forest birds may be

exhibiting cyclic changes in populations, rather than long-term declines (Askins 1993), that may be associated with spruce budworm outbreaks and cold winters (Hussell et al. 1992). Sauer et al. (1996) found that weather influenced populations of short-distance migrants during the mid-1970s. Declining eastern populations of shrubland birds may be responding to habitat loss through the reversion of early-successional to more forested habitat and more intensive agricultural practices that reduce old-field habitat (Askins 1993; Hagan 1993).

In this paper we use data from the Canadian BBS to examine regional and national population trends for woodland and scrubland birds between 1966 and 1994. These results for Canada and Canadian ecozones illustrate the variation in trends among regions and can be compared with United States results to determine the relative status of breeding birds in Canada.

Broad-scale monitoring of bird populations, such as the BBS, will help in the detection of environmental changes not observable at smaller geographical scales. Trends in species characteristic of particular habitats may be used to assess those habitat types. We hope such information will be useful in establishing national and regional conservation objectives for birds.

## Methods

The BBS is run each year during the peak of the breeding season. In Canada, volunteers are encouraged to carry out their surveys after 1 June (or for the boreal regions after 5 June) and before 7 July. Surveys are made along designated "routes" located on all-weather, secondary roads. The starting point and starting direction of routes are selected randomly in order to sample a range of habitats representative of the region. Participants are encouraged to run their routes for as many consecutive years as possible in order to reduce the effects of observer variability on data analysis (Collins and Wendt 1989; Sauer et al. 1994).

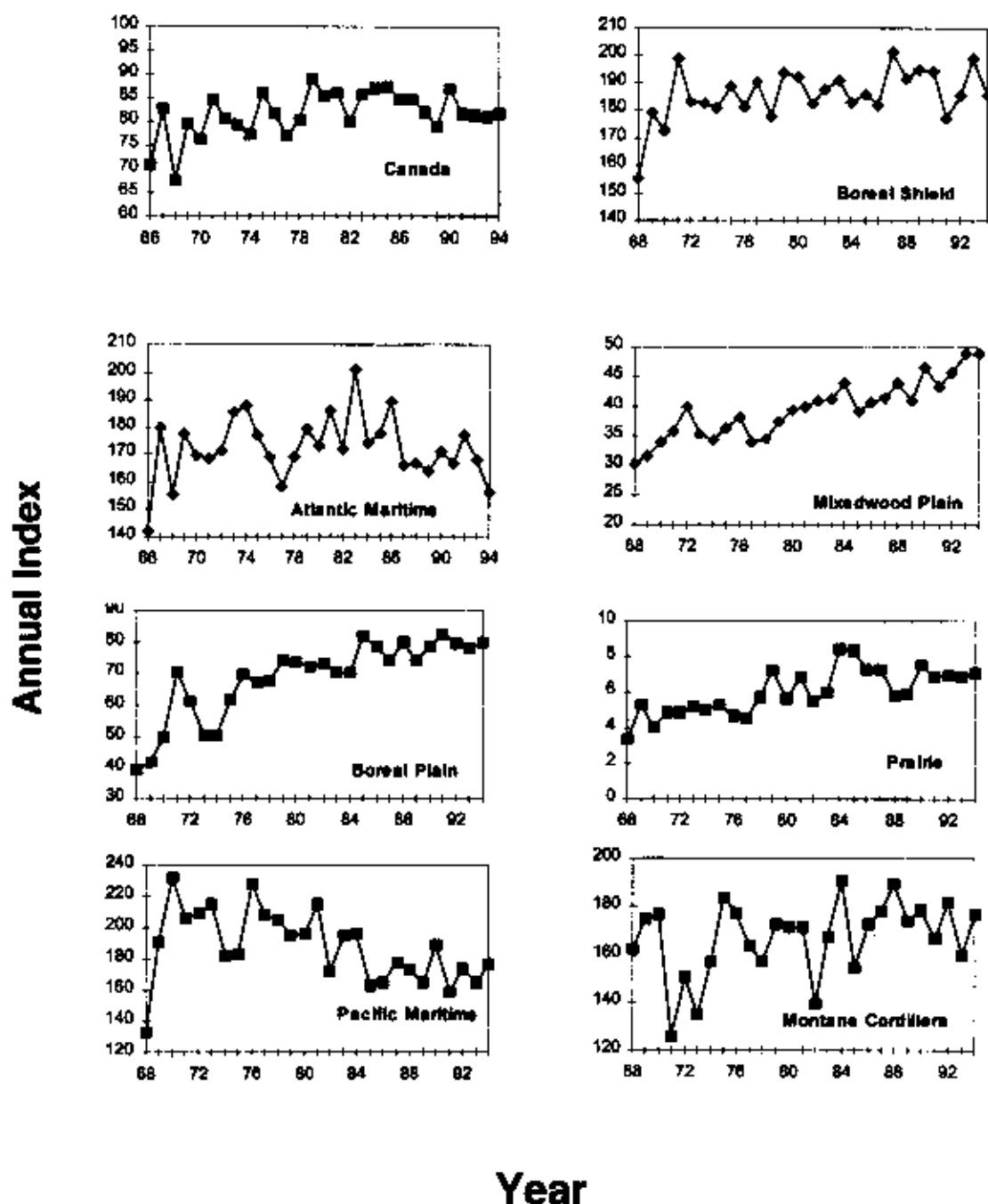
Routes consist of 50 stops spaced 0.8 km apart along a 39.4-km stretch of secondary roads. Participants run their route once a year starting a half hour before dawn. The total number of individual birds heard or seen within 0.4 km of each stop during a 3-minute observation period is recorded by participants. Data on starting and finishing time, and weather conditions, are also recorded. Canadian volunteers submit data forms to the National Wildlife Research Centre, Canadian Wildlife Service, where data are checked for errors, trends are analysed, and the Canadian BBS database is maintained. Canadian data

are also forwarded to the U.S. Geological Survey, Patuxent Wildlife Research Center for inclusion in the North American BBS database.

Birds were classified into two habitat groups, woodland and scrubland / successional, according to Peterjohn et al. (1994) (see Appendix 1). Group trends were estimated for species designated as forest and scrubland / successional birds using a linear route-regression method described by Geissler and Noon (1981), but with some modifications (Downes and Collins 1996). Analyses for each group were based on the total number of individuals of all birds within the two habitat groups recorded along each route.

For a more detailed description of BBS methodology and statistical analyses, see Downes and Collins (1996). Annual indices of population trend are an estimate of the mean count of individuals that would be recorded on a route if all routes were run each year under comparable conditions. Annual indices were calculated as the sum of the predicted count under average conditions and the average annual residual. These indices allow an examination of the annual variability within the long-term trend for a group. The proportion of species increasing and decreasing in each habitat type was also calculated. In contrast to the calculation for group population trends, the proportion of species increasing or decreasing was calculated using the individual species trends for all species within each habitat group. Individual species trends were estimated only for those species for which there was considered sufficient data to calculate a population trend (Downes and Collins 1996). Therefore, the number of species with individual trends used in the calculation of proportions is smaller than that used in the group analyses of population trend. Species with trend equal to zero are rare and were excluded from the analysis.

Here we calculate short- and long-term trends for seven biogeographical areas or "ecozones" (Ecological Stratification Working Group 1996): Boreal Shield, Atlantic Maritime, Mixed Wood Plain, Boreal Plain, Montane Cordillera, Pacific Maritime and Prairie, and for Canada overall (see Figure 1). Trends are reported for 4 time periods: beginning of survey to 1994, beginning of survey to 1979, 1980-94, and 1993-94. The first year of the analyses was determined by the availability of data for that ecozone. Although there are approximately 15 active BBS routes in the Boreal Cordillera, those routes were not run consistently until the early 1980s and trends are not reported for that ecozone.

**Figure 1.** Annual indices of woodland bird abundance in Canada.

## Results and Discussion

In 1994, 377 BBS routes were run in Canada by approximately 292 volunteers. Coverage is highest in the southern part of Canada close to areas of high human population and a good road network. In the northern parts of the provinces, the territories and Newfoundland, coverage is less regular or non-existent. In particular, in the Boreal Shield ecozone the majority of routes are located in the southern part of boreal Ontario and Quebec, and trends may therefore not reflect the entire ecozone. Coverage is also sparse in the northern section of the Pacific Maritime ecozone.

The division of trends into time periods in this paper is arbitrary and is intended to allow an examination of the persistence of trends over the entire period of the survey. The route-regression technique assumes a linear change in population (Table 1). The graphs of annual indices (Figure 1) illustrate the non-linear, year-by-year changes in direction of the trends over the survey period. When comparing trends among regions it should be noted that species composition and abundance varies (i.e., not all members of each habitat group will be present or in the same numbers in all regions). The number of species in each group in each ecozone and in Canada is listed in Table 1 (1966-1994). These sample sizes do not vary widely among regions. However, the number of individual records for each species in a particular habitat group will vary among regions and may be another source of variation in the trends.

Because there are many ways in which species can be grouped and because group analyses mask changes at the individual species level, examining population changes for species groupings should be viewed as only a first step in understanding how bird populations are changing. Although this paper does not examine individual species trends, we present the proportion of species showing increasing and decreasing population trends (Table 2) within each habitat type in Canada. We also include the group trend as an indication of whether the average annual trend estimate (Table 1) for the group is driven by a small number of species or whether it reflects the majority of species within the group. However, trends for individual species have also been calculated (Peterjohn et al. 1994; Downes and Collins 1996) and should be taken into account when assessing the need for conservation action.

## Woodland

Over the entire period of the survey (1966-94),

woodland birds as a group showed few statistically significant trends (Table 1). Only the Prairie ecozone showed a significant increase in total woodland bird numbers ( $p=0.024$ ); the Mixed Wood Plain had a positive trend approaching significance ( $p=0.061$ ). During the early part of the survey (pre-1980) increasing trends ( $p<0.05$ ) were detected in 4 ecozones and for Canada as a whole. These increases contrast with the 1980-94 period in which no significant positive trends were detected. During this latter period, 4 ecozones had negative population trends although only the Atlantic Maritime trend approached statistical significance ( $p=0.051$ ).

For the woodland group, the proportion of increasing species was significantly higher than the proportion of decreasing species in Canada overall over the period 1966-94 (Figure 1). However, the percentage of decreasing species rose from 32% nationally to 56% between 1966-79 and 1980-94. The annual indices for the woodland group in Canada overall are variable from year-to-year, but the general pattern does not indicate a large change between the 1960s and the 1990s. Annual indices for the Mixed Wood Plain, Boreal Plain and, less so, in the Prairie show increasing populations in the 1980s. The strongest pattern of decrease occurred in the Pacific Maritime from the late 1970s onwards; a less pronounced pattern of decline is indicated in the Atlantic Maritime from the mid-1980s onwards. Annual indices for the Boreal Shield were relatively stable or slightly increasing. In the Montane Cordillera the indices are highly variable, but show little change in the overall population over the course of the survey. The larger fluctuations during the first few years of the survey in many of the regions are likely attributable to small sample sizes in those years. (In 1966 and 1967, 34 and 66 routes were run, respectively, and all were located in eastern Canada as compared with the 387 routes run in 1994 and located throughout Canada in all provinces and territories.)

Our results show that, over the course of the survey, woodland birds as a group are not declining. However, there is evidence of more decreases in total woodland bird numbers after 1980. Trends for individual woodland species varied (Downes and Collins 1996). Several woodland species showed long-term declines in population throughout much of their range in Canada (e.g., Ruffed Grouse, Black-billed Cuckoo, Boreal Chickadee, Eastern Wood-Pewee, Olive-sided Flycatcher, Purple Finch) while others declined in one or more regions (e.g., Northern Flicker, Mixed Wood Plain; Pine Siskin, Pacific

**Table 1.** Summary of trends from the Canadian Breeding Bird Survey for woodland and scrubland/successional birds during 3 time periods. "ns" indicates  $p > 0.05$ . "N" indicates the number of species in each group for the 1966(68)-94 period.

Guild		1966(68)-94*			1966(68)-79*		1980-94	
	Area	Trend	P	N	Trend	P	Trend	P
Woodland								
	Canada	0.2	ns	103	2	0	-0.02	ns
	Boreal Shield	0.2	ns	75	1.4	ns	0	ns
	Atlantic Maritime	0	ns	68	1.8	0.016	-1.2	0.051
	Mixedwood Plain	1.4	0.061	73	0.3	ns	2	ns
	Boreal Plain	1.6	ns	81	7.6	0.01	-0.2	ns
	Prairie	1.9	0.024	52	4.9	<0.001	0.1	ns
	Pacific Maritime	-0.9	ns	61	4	0.042	-0.9	ns
	Montane Cordillera	0.3	ns	75	0.6	ns	0.3	ns
Scrubland/successional								
	Canada	-0.5	0.029	44	-0.4	ns	0.2	ns
	Boreal Shield	-0.7	0.067	27	-0.4	ns	-0.3	ns
	Atlantic Maritime	-1.3	0.013	21	-1.1	0.01	-1.1	ns
	Mixedwood Plain	0.3	ns	27	-2.2	0.043	0	ns
	Boreal Plain	-0.3	ns	27	0.7	ns	0.1	ns
	Prairie	0.5	0.089	25	0.5	ns	1.5	0
	Pacific Maritime	-1.1	Ns	21	1.3	ns	-0.3	ns
	Montane Cordillera	1.7	0	25	0.4	ns	2.4	<0.001

\* In 1966 BBS routes were run only in the Atlantic Maritimes; by 1968 routes were run in all provinces.

**Table 2.** Proportion of species showing increasing and decreasing population trends in Canada, grouped by habitat. Proportions are listed for all species for which trends could be calculated and for those species with trends significant at  $p < 0.15$ . \* indicates a significant difference from a 50:50 ratio.

Habitat Group	% Increasing		% Decreasing		N	
Time Period	All Trends	Significant Trends	All Trends	Significant Trends	All Trends	Significant Trends
Woodland						
1966-94	59%	50%	41%	50%	66	22
1966-79	68% *	61%	32%	29%	63	24
1980-94	44%	29%	56%	61%	66	23
Scrub/Successional						
1966-94	50%	50%	50%	50%	30	10
1966-79	62%	66%	38%	33%	29	6
1980-94	53%	70%	47%	30%	30	10

Maritime) (Downes and Collins 1996). Other species (e.g., Hairy Woodpecker, Black-capped Chickadee and American Robin) showed increases throughout much of their range and several species increased in one or more regions (e.g., Downy Woodpecker, Boreal Shield; Hairy Woodpecker, Boreal Plain; Least Flycatcher, Prairie).

### Scrubland/Successional

Statistically significant ( $p < 0.05$ ) declines in scrub/successional species as a group were detected between 1966 and 1994 in Canada overall and the Atlantic Maritime, while the Boreal Shield approached a significant decline ( $p = 0.067$ ) (Table 1). An increase occurred in total scrubland bird numbers in the Montane Cordillera and in the Prairie during that period. During the early part of the survey (pre-1980) only the Mixed Wood Plain and Atlantic Maritime showed statistically significant ( $p < 0.05$ ) decreases in total scrubland birds. No regions showed increasing trends during the pre-1980 period, although increasing trends were detected in both the Prairie and the Montane Cordillera ( $p < 0.05$ ) between 1980 and 1994. Over the entire survey period the scrub/successional group had equal proportions of increasing and decreasing species in Canada overall (Table 2), although the percentage of decreasing species rose between the years 1966-79 (38%) and 1980-94 (47%). Annual indices of population abundance for Canada suggest a general decline in total scrubland bird numbers that appears to taper off after the early 1990s (Figure 2). Annual indices for the Boreal Shield, Atlantic Maritime and Pacific Maritime ecozones reflect a similar decline; the Prairie and Montane Cordillera show marginal increases during the latter part of the survey. The Mixed Wood Plain and Boreal Plain are highly variable, but show a generally stable population over the course of the survey.

Similar to the forest birds, the trends for scrubland birds vary widely among ecozones. However, the general trend for Canada shows a long-term decrease that appears to be more pronounced during the early years of the survey. These results are consistent with other studies of population change (e.g., Askins 1993). Individual species showing long-term declines throughout much of their range include the Gray Catbird, Brown Thrasher, White-throated Sparrow and Song Sparrow. Other species that are increasing throughout much of their range include the Yellow Warbler and House Wren (Downes and Collins 1996).

The many factors influencing bird numbers vary in type and intensity over their range, which results in

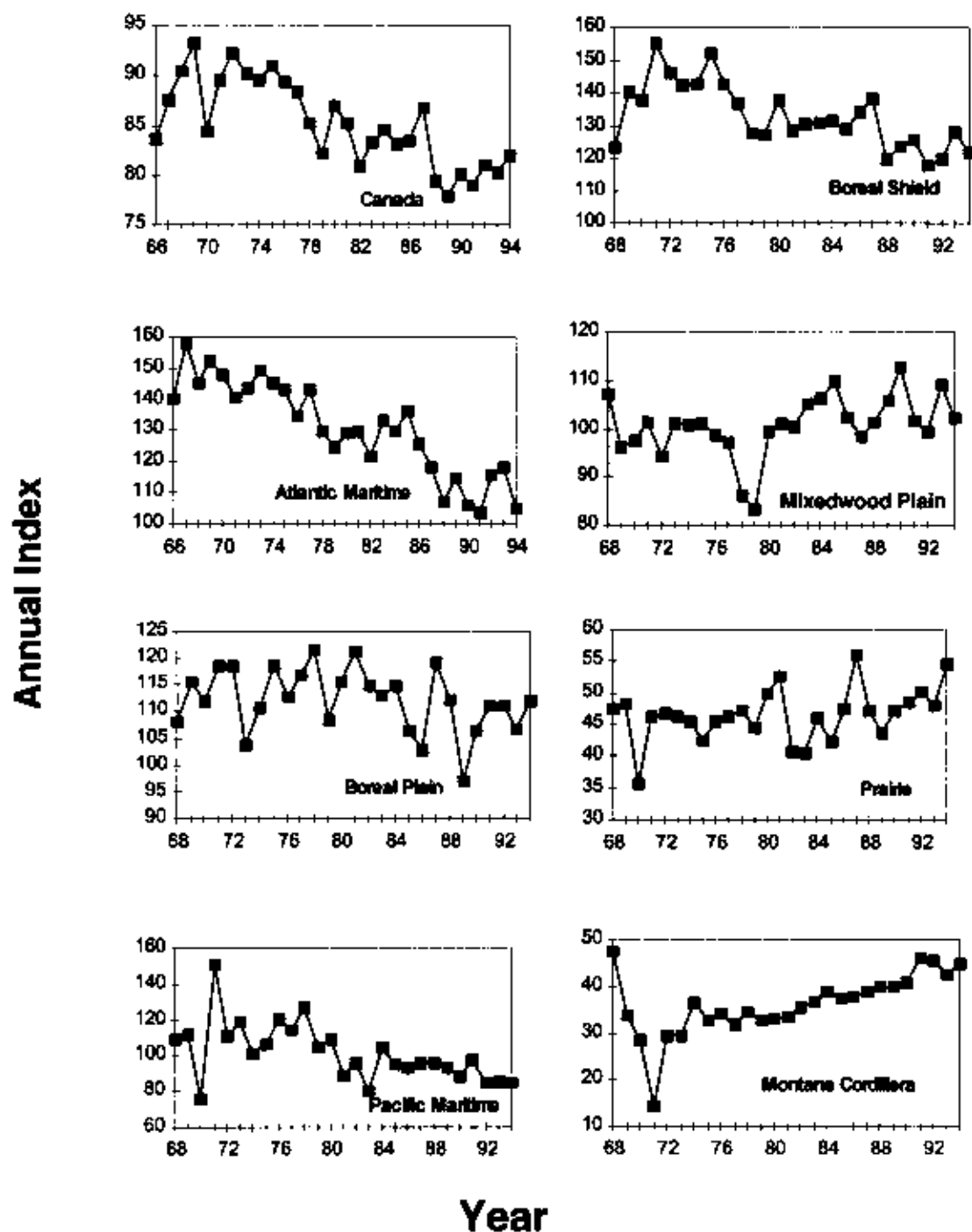
population changes that vary both regionally and temporally. However, some general patterns emerge. Woodland birds as a group showed relatively stable population trends in most ecozones and in Canada overall, and a higher number of species increased than decreased in Canada over the course of the survey. This pattern of population change is generally in agreement with similar studies in the literature (Peterjohn and Sauer 1994; Peterjohn et al. 1996). There was much variation in the trends of individual woodland species with some species showing long-term declines (Downes and Collins 1996; Peterjohn et al. 1996). Several species with long-term declines continentally (Peterjohn and Sauer 1994) also declined in Canada over the long term (e.g., Olive-sided Flycatcher, Veery, Wood Thrush, Eastern Wood-pewee). The fact that these reports and our study indicate the number of negative population trends increased in the late 1980s and 1990s suggests some cause for concern. Askins (1993) emphasized that concern for woodland species is warranted in light of continued habitat fragmentation and loss.

Consistent with other studies (Peterjohn et al. 1996), our results indicate that scrubland birds are declining more rapidly than woodland birds. Losses in scrubland birds have been attributed to the loss of successional habitat as abandoned farmland matured and intensive agricultural practices diminished remnant patches of successional habitat (Askins 1993). Peterjohn et al. (1996) found greater numbers of scrubland/successional species decreasing in the east as compared to central or western North America. This pattern was evident in the population trends for the Atlantic Maritime region of Canada, but was less pronounced in the Mixed Wood Plain ecozone encompassing southern Ontario and Quebec.

Declines in both scrubland and woodland birds in our study and others were considerably less than those shown in the grassland bird group (Askins 1993; Peterjohn et al. 1996; C.M. Downes unpubl.). Since it is often difficult to distinguish actual change in bird populations from short-term fluctuations, long-term data are required that allow an examination of population patterns. The BBS is the only nation-wide long-term survey of songbirds. However, not all species and habitats are covered equally. Crepuscular, rare and secretive species are not covered or are poorly covered, as are some habitats such as marshes and high-altitude areas. Because the BBS is run along all-weather roads the large expanses of roadless areas in the boreal forest, taiga and tundra regions of Canada are not covered. The interiors of



Figure 2. Annual indices of scrubland / successional bird abundance in Canada.



large, unbroken tracts of forest or grassland in other areas may not be well covered. Despite these limitations, the BBS provides a system to monitor over 200 species in Canada and gives an early warning of those species and species groups showing signs of population change. Results from the BBS are now being used to establish regional and national priorities for conservation action and to encourage and focus research efforts in Canada (Dunn 1998).

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**Appendix 1.** Species groups used in analyses.

Common name	Scientific name	Common name	Scientific name
<b>Woodland Species</b>			
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Warbling Vireo	<i>V. gilvus</i>
Cooper's Hawk	<i>A. cooperii</i>	Philadelphia Vireo	<i>V. philadelphicus</i>
Northern Goshawk	<i>A. gentilis</i>	Red-eyed Vireo	<i>V. olivaceus</i>
Red-shouldered Hawk	<i>Buteo lineatus</i>	Gray Jay	<i>Perisoreus canadensis</i>
Broad-winged Hawk	<i>B. platypterus</i>	Steller's Jay	<i>Cyanocitta stelleri</i>
Merlin	<i>Falco columbarius</i>	Clark's Nutcracker	<i>Nucifraga columbiana</i>
Ruffed Grouse	<i>Bonasa umbellus</i>	Black-capped Chickadee	<i>Parus atricapillus</i>
Spruce Grouse	<i>Falcapennis canadensis</i>	Mountain Chickadee	<i>P. gambeli</i>
Blue Grouse	<i>Dendragapus obscurus</i>	Chestnut-backed Chickadee	<i>P. rufescens</i>
Wild Turkey	<i>Meleagris gallopavo</i>	Boreal Chickadee	<i>P. hudsonicus</i>
Band-tailed Pigeon	<i>Columba fasciata</i>	Tufted Titmouse	<i>Parus bicolor</i>
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	Red-breasted Nuthatch	<i>Sitta canadensis</i>
	<i>C. americanus</i>	White-breasted Nuthatch	<i>S. carolinensis</i>
Yellow-billed Cuckoo	<i>Otus kennicottii</i>	Pygmy Nuthatch	<i>S. pygmaea</i>
Western Screech-Owl	<i>O. asio</i>	Brown Creeper	<i>Certhia americana</i>
Eastern Screech-Owl	<i>Glaucidium gnoma</i>	Winter Wren	<i>Troglodytes troglodytes</i>
Northern Pygmy-Owl	<i>Strix varia</i>	Golden-crowned Kinglet	<i>Regulus satrapa</i>
Barred Owl	<i>Asio otus</i>	Ruby-crowned Kinglet	<i>R. calendula</i>
Long-eared Owl	<i>Aegolius acadicus</i>	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>
Northern Saw-whet Owl	<i>Caprimulgus vociferus</i>	Western Bluebird	<i>Sialia mexicana</i>
Whip-poor-will	<i>Chaetura vauxi</i>	Townsend's Solitaire	<i>Myadestes townsendi</i>
Vaux's Swift	<i>Archilochus colubris</i>	Veery	<i>Catharus fuscescens</i>
Ruby-throated Hummingbird	<i>A. alexandri</i>	Gray-cheeked Thrush	<i>C. minimus</i>
Black-chinned Hummingbird	<i>Stellula calliope</i>	Swainson's Thrush	<i>C. ustulatus</i>
Calliope Hummingbird	<i>Selasphorus rufus</i>	Hermit Thrush	<i>C. guttatus</i>
Rufous Hummingbird	<i>Melanerpes carolinus</i>	Wood Thrush	<i>Hylocichla mustelina</i>
Red-bellied Woodpecker	<i>Sphyrapicus thyroideus</i>	Varied Thrush	<i>Ixoreus naevius</i>
Williamson's Sapsucker	<i>Picoides pubescens</i>	Bohemian Waxwing	<i>Bombicilla garrulus</i>
	<i>P. villosus</i>	Tennessee Warbler	<i>Vermivora peregrina</i>
Downy Woodpecker	<i>P. tridactylus</i>	Northern Parula	<i>Parula americana</i>
Hairy Woodpecker	<i>P. arcticus</i>	Magnolia Warbler	<i>Dendroica magnolia</i>
Three-toed Woodpecker	<i>Dryocopus pileatus</i>	Cape May Warbler	<i>D. tigrina</i>
Black-backed Woodpecker	<i>Contopus cooperi</i>	Black-throated Blue Warbler	<i>D. caerulescens</i>
Pileated Woodpecker	<i>C. sordidulus</i>	Yellow-rumped Warbler	<i>D. coronata</i>
Olive-sided Flycatcher	<i>C. virens</i>	Black-throated Green W.	<i>D. virens</i>
Western Wood-Pewee	<i>Empidonax flaviventris</i>	Townsend's Warbler	<i>D. townsendi</i>
Eastern Wood-Pewee	<i>E. virescens</i>	Blackburnian Warbler	<i>D. fusca</i>
Yellow-bellied Flycatcher	<i>E. minimus</i>	Pine Warbler	<i>D. pinus</i>
Acadian Flycatcher	<i>E. hammondi</i>	Bay-breasted Warbler	<i>D. castanea</i>
Least Flycatcher	<i>E. oberholseri</i>	Blackpoll Warbler	<i>D. striata</i>
Hammond's Flycatcher	<i>Myiarchus crinitus</i>	Cerulean Warbler	<i>D. cerulea</i>
Dusky Flycatcher	<i>Vireo flavifrons</i>	Black-and-white Warbler	<i>Mniotilta varia</i>
Great Crested Flycatcher	<i>V. solitarius</i>	American Redstart	<i>Setophaga ruticilla</i>
Yellow-throated Vireo	<i>V. huttoni</i>	Ovenbird	<i>Seiurus aurocapillus</i>
Solitary Vireo			
Hutton's Vireo			

## Appendix 1 (continued)

Common name	Scientific name	Common name	Scientific name
Northern Waterthrush	<i>S. noveboracensis</i>	Black-headed Grosbeak	<i>P. melanocephalus</i>
Louisiana Waterthrush	<i>S. motacilla</i>	Pine Grosbeak	<i>Pinicola enucleator</i>
Hooded Warbler	<i>Wilsonia citrina</i>	Purple Finch	<i>Carpodacus purpureus</i>
Canada Warbler	<i>W. canadensis</i>	Cassin's Finch	<i>C. cassinii</i>
Scarlet Tanager	<i>Piranga olivacea</i>	Red Crossbill	<i>Loxia curvirostra</i>
Western Tanager	<i>P. ludoviciana</i>	White-winged Crossbill	<i>L. leucoptera</i>
Dark-eyed Junco	<i>Junco hyemalis</i>	Pine Siskin	<i>Carduelis pinus</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	Evening Grosbeak	<i>Coccothraustes vespertinus</i>
<b>Scrubland/Successional Species</b>			
Sage Grouse	<i>Centrocercus urophasianus</i>	Prairie Warbler	<i>D. discolor</i>
California Quail	<i>Callipepla californica</i>	Palm Warbler	<i>D. palmarum</i>
Northern Bobwhite	<i>Colinus virginianus</i>	Connecticut Warbler	<i>Oporornis agilis</i>
American Woodcock	<i>Scolopax minor</i>	Mourning Warbler	<i>O. philadelphia</i>
Common Poorwill	<i>Phalaenoptilus nuttallii</i>	MacGillivray's Warbler	<i>O. tolmiei</i>
Gray Flycatcher	<i>Empidonax wrightii</i>	Common Yellowthroat	<i>Geothlypis trichas</i>
White-eyed Vireo	<i>Vireo griseus</i>	Wilson's Warbler	<i>Wilsonia pusilla</i>
Bushtit	<i>Psaltiriparus minimus</i>	Yellow-breasted Chat	<i>Icteria virens</i>
Carolina Wren	<i>Thryothorus ludovicianus</i>	Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>
Bewick's Wren	<i>Thryomanes bewickii</i>	Clay-colored Sparrow	<i>Spizella pallida</i>
House Wren	<i>Troglodytes aedon</i>	Brewer's Sparrow	<i>S. breweri</i>
Gray Catbird	<i>Dumetella carolinensis</i>	Field Sparrow	<i>S. pusilla</i>
Sage Thrasher	<i>Oreoscoptes montanus</i>	Lark Sparrow	<i>Chondestes grammacus</i>
Brown Thrasher	<i>Toxostoma rufum</i>	Fox Sparrow	<i>Passerella iliaca</i>
Blue-winged Warbler	<i>Vermivora pinus</i>	Song Sparrow	<i>Melospiza melodia</i>
Golden-winged Warbler	<i>V. chrysoptera</i>	Lincoln's Sparrow	<i>M. lincolnii</i>
Orange-crowned Warbler	<i>V. celata</i>	White-throated Sparrow	<i>Zonotrichia albicollis</i>
Nashville Warbler	<i>V. ruficapilla</i>	White-crowned Sparrow	<i>Z. leucophrys</i>
Yellow Warbler	<i>Dendroica petechia</i>	Golden-crowned Sparrow	<i>Z. atricapilla</i>
Chestnut-sided Warbler	<i>D. pensylvanica</i>	Northern Cardinal	<i>Cardinalis cardinalis</i>
Black-throated Gray Warbler	<i>D. nigrescens</i>	Lazuli Bunting	<i>Passerina amoena</i>
		Indigo Bunting	<i>P. cyanea</i>
		American Goldfinch	<i>Carduelis tristis</i>

# Tracing diets and origins of migratory birds using stable isotope techniques

Keith A. Hobson

## Abstract

Measurements of naturally occurring stable isotopes of several elements found in foodwebs are being used increasingly to address a number of ecological questions, particularly those involving nutrient flow and foodweb structure. However, only during the last decade has the potential of this technique been realized by avian ecologists, and there exists a multitude of potential applications in this field. In this paper, the uses of stable isotope applications to avian ecological studies are reviewed. In particular, emphasis is given to the use of  $\delta^{15}\text{N}$  ( $^{15}\text{N}/^{14}\text{N}$ ) measurements to delineate trophic position in marine systems and  $\delta^{13}\text{C}$  ( $^{13}\text{C}/^{12}\text{C}$ ) and  $\delta^{34}\text{S}$  ( $^{34}\text{S}/^{32}\text{S}$ ) measurements to establish sources of nutrients in avian diets. Recent applications of the measurement of deuterium isotope ratios  $\delta\text{D}$  (D/H) in feathers to trace origins of migratory songbirds is also presented. When combined with DNA analyses, the stable isotope approach holds great promise for linking breeding and wintering areas of neotropical migrant birds and other migratory organisms.

## Résumé

Les mesures de fréquences naturelles d'isotopes stables de plusieurs éléments que l'on retrouve dans les chaînes alimentaires sont de plus en plus utilisées pour répondre à plusieurs questions écologiques, tout particulièrement celles impliquant les flux de nutriments et la structure des chaînes alimentaires. Cependant, ce n'est qu'au cours de la dernière décennie que le potentiel de cette technique a été apprécié par les écologistes aviens. Dans cet article, l'utilisation de la technique des isotopes stables pour les études d'écologie avienne sont résumées. En particulier, l'emphasis est mise sur l'utilisation des mesures de  $\delta^{15}\text{N}$  ( $^{15}\text{N}/^{14}\text{N}$ ) pour déterminer les positions trophiques dans les systèmes marins et de  $\delta^{13}\text{C}$  ( $^{13}\text{C}/^{12}\text{C}$ ) et  $\delta^{34}\text{S}$  ( $^{34}\text{S}/^{32}\text{S}$ ) pour déterminer les sources de nutriments dans le régime alimentaire des oiseaux. Des applications récentes des mesures de ratios d'isotope de Deutérium  $\delta\text{D}$  (D/H) dans les plumes pour retracer l'origine des oiseaux migrateurs sont aussi présentées. L'approche des isotopes stables, lorsque combinée avec des analyses d'ADN montre de grands potentiels pour relier les aires de nidification et d'hivernage des oiseaux migrateurs néotropicaux, et autres organismes migrateurs.

Keith A. Hobson, Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada S7N 0X4. ([keith.hobson@ec.gc.ca](mailto:keith.hobson@ec.gc.ca))

## Introduction

Conventional approaches to avian dietary studies have involved gut contents analysis, either by collecting birds, stomach flushing or the use of emetics (e.g., Laursen 1978; Harrison 1984; Duffy and Jackson 1986; Major 1990; Poulin et al. 1994), direct observation of foraging adults or, more typically, the prey they deliver to young, or the analysis of prey

remains in the form of regurgitations, pellets, or faeces found at nest or roost sites (Davies 1977; Loisele and Blake 1990). Dietary inferences have also been made from analyses of contaminant or radioactive tracers in foodwebs (Smith et al. 1979; Beviss-Challinor and Field 1982; Macko and Ostrom 1994). Each of these approaches may adequately describe diet, particularly over the short term. However, they all have

considerable drawbacks, at least when applied in isolation. Gut content analysis involves destructive sampling and typically provides information only for the individual's last few meals. More importantly, this technique may be biased against soft-bodied prey or those materials that are more readily digested (Duffy and Jackson 1986). While being non-destructive, similar drawbacks are apparent with stomach flushing or the use of emetics and the analysis of prey remains or regurgitated pellets or faeces. Moreover, these approaches at best provide only a picture of what was ingested and not what was assimilated into the bird's tissues. So, unless details of assimilation efficiency and how foods enter nutritional pathways are known, frequency of occurrence or biomass of prey remains in stomachs may often provide misleading information (Duffy and Jackson 1986). Finally, analysis of prey remains is a tedious technique that requires researchers to have a good taxonomic knowledge of organisms available to birds.

The problems outlined above with respect to the analysis of individual diets are compounded further when one attempts to consider dietary relationships among several taxa within a foodweb. The difficulties inherent in systems or foodweb studies have undoubtedly resulted in the lag in empirical evidence for foodweb theory (Paine 1988). Stable isotope analysis is based on the measurement of naturally occurring stable isotopes of several elements that occur in foodwebs. This technique offers a number of advantages over conventional dietary approaches. In particular, dietary information is based on: (1) nutrients assimilated into consumers, not just those ingested; and (2) a dietary integration over various temporal scales ranging from a few days to the lifetime of the individual depending on the tissue analyzed. In addition, the collection technique is simple and straightforward and the analysis relatively inexpensive.

Stable isotope applications to avian dietary studies fall into four general categories: (1) the determination of trophic level of individuals and trophic relationships within complex systems, including correlations between trophic level and bioaccumulation or depuration of contaminants; (2) the determination of nutrient source or location of feeding; (3) the evaluation of endogenous vs exogenous reserves to reproduction; and (4) the tracking of migration and the linkage of breeding and wintering grounds in migratory species. All of these applications rely on the simple fact that stable-isotope signatures present in foodwebs can act as natural markers to trace dietary origins of birds and other

consumers. Such tracing can involve the delineation of feeding relationships at a local scale or at the scale of thousands of kilometres in the case investigations of migration. Following a brief background on the theory and measurement of stable isotopes, each of the above broad applications will be described and discussed. It is not the intention of this paper to provide an exhaustive review of the field of ecological applications of stable isotopes since excellent reviews are provided elsewhere (e.g., Peterson and Fry 1987; Rundel et al. 1988; Lajtha and Michener 1994). Rather, an emphasis will be placed on existing and potential applications to avian ecological studies.

## Stable isotope background

In nature, elements exist in both stable and nonstable (i.e., radioactive) forms. Elements common to biological systems typically occur in more than one stable form and these are referred to as stable isotopes of that element. Isotopes differ in the mass of the nucleus and depend on the number of neutrons present. Characteristically, the heavier isotopes of an element occur more rarely in nature than the lighter isotope. Those elements in nature of most interest in terms of stable isotope applications are carbon, nitrogen, oxygen, sulphur and hydrogen, with the overwhelming majority of work being focused on carbon and nitrogen (see Table 1).

**Table 1.** Average terrestrial abundances of the stable isotopes of elements of primary interest in avian dietary and tracing studies (from Ehleringer and Rundel 1988).

Element	Isotope	Abundance (%)
Carbon	$^{12}\text{C}$	98.89
	$^{13}\text{C}$	1.11
Hydrogen	$^1\text{H}$	99.985
	$^2\text{H}$	0.015
Nitrogen	$^{14}\text{N}$	99.63
	$^{15}\text{N}$	0.37
Oxygen	$^{16}\text{O}$	99.759
	$^{17}\text{O}$	0.037
	$^{18}\text{O}$	0.204
Sulfur	$^{32}\text{S}$	95.00
	$^{33}\text{S}$	0.76
	$^{34}\text{S}$	4.22
	$^{36}\text{S}$	0.014

Isotopes behave differently in biogeochemical processes due to thermodynamic and kinetic

considerations. In general, differences in physical and chemical properties of isotopes are proportional to differences in their masses (Broecker and Oversley 1976). The net difference in isotope abundance resulting from these processes is known as isotopic fractionation. In nature, isotopic fractionation processes discriminate for or against an isotope of a particular element in the order of a few percent. Analytically, it is most convenient to measure these small absolute differences in isotopic composition by measuring isotopic differences between a sample and a known standard. Isotopic composition of a sample is usually expressed in delta ( $\delta$ ) notation as follows:

$$\delta X_{\text{std}} = (R_{\text{sample}}/R_{\text{std}} - 1) \times 1000$$

where  $\delta X_{\text{std}}$  is the isotope ratio in delta units relative to a standard, and  $R_{\text{sample}}$  and  $R_{\text{std}}$  are the absolute isotope ratios of the sample and standard, respectively. Delta values are expressed as parts per thousand (‰) or on a "per mil" basis. Currently, there are four international standards for the five principal light isotopes of interest in this paper. The Pee Dee belemnite (PDB) standard is used for carbon, atmospheric air (AIR) for nitrogen, the Canyon Diablo meteorite (CD) for sulfur and the standard mean ocean water (SMOW) for hydrogen and oxygen. The arbitrary choice of these standards results in  $^{13}\text{C}$  samples typically being negative (i.e. the standard is usually enriched in  $^{13}\text{C}$  compared to the unknown) and  $^{15}\text{N}$  samples being positive (atmospheric air is typically depleted in  $^{15}\text{N}$  relative to the unknown). Stable hydrogen and oxygen isotope values are typically negative and stable sulfur isotope values can be both positive and negative. Below, I provide a brief background on each element of interest. Information on oxygen is not presented because, despite its potential use in avian ecological investigations, few researchers have conducted studies using this element (but see Schaffner and Swart 1991). In addition, hydrogen isotope analysis can often provide similar types of information in studies involving tracing of water.

## Carbon

Carbon occurs in two stable forms as  $^{12}\text{C}$  and  $^{13}\text{C}$ . Carbon isotopic compositions of animals reflect those of the diet within about 1‰ (DeNiro and Epstein 1978; Peterson and Fry 1987). For this reason, stable-carbon isotope analysis is an ideal tool for tracing origins of nutrients in foodwebs since carbon may enter the base of foodwebs with characteristic isotopic signatures due to a variety of biogeochemical

processes and these change little throughout the foodweb. The two main processes of interest in this paper are those resulting in differences in  $\delta^{13}\text{C}$  values of terrestrial versus marine foodwebs and  $\delta^{13}\text{C}$  values of plants with C-3 vs C-4 photosynthetic pathways.

Carbon in the atmosphere is depleted in  $^{13}\text{C}$  relative to dissolved carbonate in the oceans by about 7‰ (Craig 1953; Chisholm et al. 1982). This difference arises from the fact that dissolved inorganic carbon in the oceans is derived ultimately from the atmosphere. Effectively, heavier carbon dioxide enters into bicarbonate ion exchange at the ocean/atmosphere interface more readily than does lighter carbon dioxide. In general then, marine foodwebs tend to be enriched in  $^{13}\text{C}$  compared with terrestrial C-3 foodwebs (see below) and this difference has been used to trace the relative contributions of terrestrial versus marine protein in the diets of contemporary (e.g., Hobson 1986, 1990) and prehistoric consumers (e.g., Chisholm et al. 1982; Hobson and Collier 1984).

The stable-carbon isotope composition of terrestrial plants is influenced in part by photosynthetic pathway and much of the earlier work on stable carbon isotopes in nature was concerned with linking isotopic fractionation with plant metabolism (reviewed by Ehleringer and Rundel 1988). In temperate areas, most plants have a so-called C-3 photosynthetic pathway resulting in  $\delta^{13}\text{C}$  values close to -27‰. Plants with a C-4 photosynthetic pathway, often growing in more xeric conditions, have more enriched  $\delta^{13}\text{C}$  values ranging between -9 to -14‰. The relative contributions of C-3 versus C-4 plants to foodwebs have been investigated using stable-carbon isotope measurements. In particular, the introduction of corn, a C-4 plant, to an otherwise C-3 based foodweb has been traced in prehistoric agricultural systems (e.g., Vogel and van der Merwe 1977; Bender et al. 1981).

## Nitrogen

There are two stable forms of nitrogen,  $^{14}\text{N}$  and  $^{15}\text{N}$ . In terrestrial systems, nitrogen enters foodwebs through symbiotic fixation or through direct conversion of atmospheric nitrogen within plants (reviewed by Nadelhoffer and Fry 1994). These processes typically lead to different isotopic signatures of plants adopting these strategies. In marine systems, inorganic nitrogen occurs as molecular nitrogen, ammonia, nitrate, nitrite and nitrous oxide. Relatively little is known about the isotopic fractionation effects occurring between these nitrogen pools and phytoplankton (Owens 1987; but see Wada and Hattori 1978).



As was found for stable-carbon isotopes, the stable nitrogen isotopic composition of animals is related ultimately to the isotopic compositions of their diets (DeNiro and Epstein 1981; Macko 1981; Minagawa and Wada 1984). Through processes associated primarily with differential excretion of  $^{14}\text{N}$ , animals incorporate dietary  $^{15}\text{N}$  into their tissues preferentially, an effect due to discrimination against the lighter isotope during protein amination and deamination (Gaebler et al. 1966; Macko et al. 1982; Minagawa and Wada 1984). A broad survey of field and laboratory data confirms that there is a significant linear relationship between  $\delta^{15}\text{N}$  values of an organism and its diet (DeNiro and Epstein 1981; Owens 1987). This phenomenon forms the basis of using  $\delta^{15}\text{N}$  measurements to infer trophic level.

## Sulfur

Sulfur occurs in nature in four stable forms,  $^{32}\text{S}$ ,  $^{33}\text{S}$ ,  $^{34}\text{S}$  and  $^{36}\text{S}$ . Of most interest in biological systems is the relative abundance of  $^{32}\text{S}$  and  $^{34}\text{S}$  (depicted as  $\delta^{34}\text{S}$ ). The large variability (of the order of 150‰) in sulfur isotope ratios in natural materials from light sulfides to heavy sulfates and the apparent lack of a trophic enrichment effect (see Krouse 1988; Hesslein et al. 1993) has led to the primary use of stable sulfur isotopes as natural tracers in foodweb studies. In particular, differences in  $\delta^{34}\text{S}$  between terrestrial and marine biota makes this isotope extremely useful in tracing relative contributions of terrestrial and marine-derived nutrients. Compared with other elements, it was previously relatively difficult to perform routine sulfur isotope measurements on biological material. However, with the advent of continuous flow isotope ratio mass spectrometry (IRMS), sulfur isotope measurements have become more routine. The first application to avian studies was by Trust (1993).

## Hydrogen

Hydrogen occurs in two stable forms,  $^1\text{H}$  (usually denoted as H) and  $^2\text{H}$  or deuterium (D). Isotopic fractionation effects tend to be far more pronounced in hydrogen because the relative mass difference between H and D is greater than other isotopic elements. Ecological studies using stable hydrogen isotopes are often related to the deuterium content of local water. Once water leaves the ocean, climate and geography influence the large-scale pattern of the D isotope. Important geological and climatic factors affecting natural distributions of D/H ratios in precipitation include latitude, altitude, season, and distance inland (Dansgaard 1964; White 1989). At low latitudes where

seasonality is not pronounced, and at mid-latitudes in summer, the amount of rainfall becomes important in determining  $\delta\text{D}$  of precipitation (Dansgaard 1964). Generally,  $\delta\text{D}$  in precipitation decreases in a north-westerly direction across North America (Cormie et al. 1994; Hobson and Wassenaar 1997; Figure 1).  $\delta\text{D}$  also decreases with increasing altitude, is higher in summer and lowest in winter at latitudes above  $30^\circ$  (Ziegler 1989) and decreases with heavy versus sparse precipitation (Dansgaard 1964).

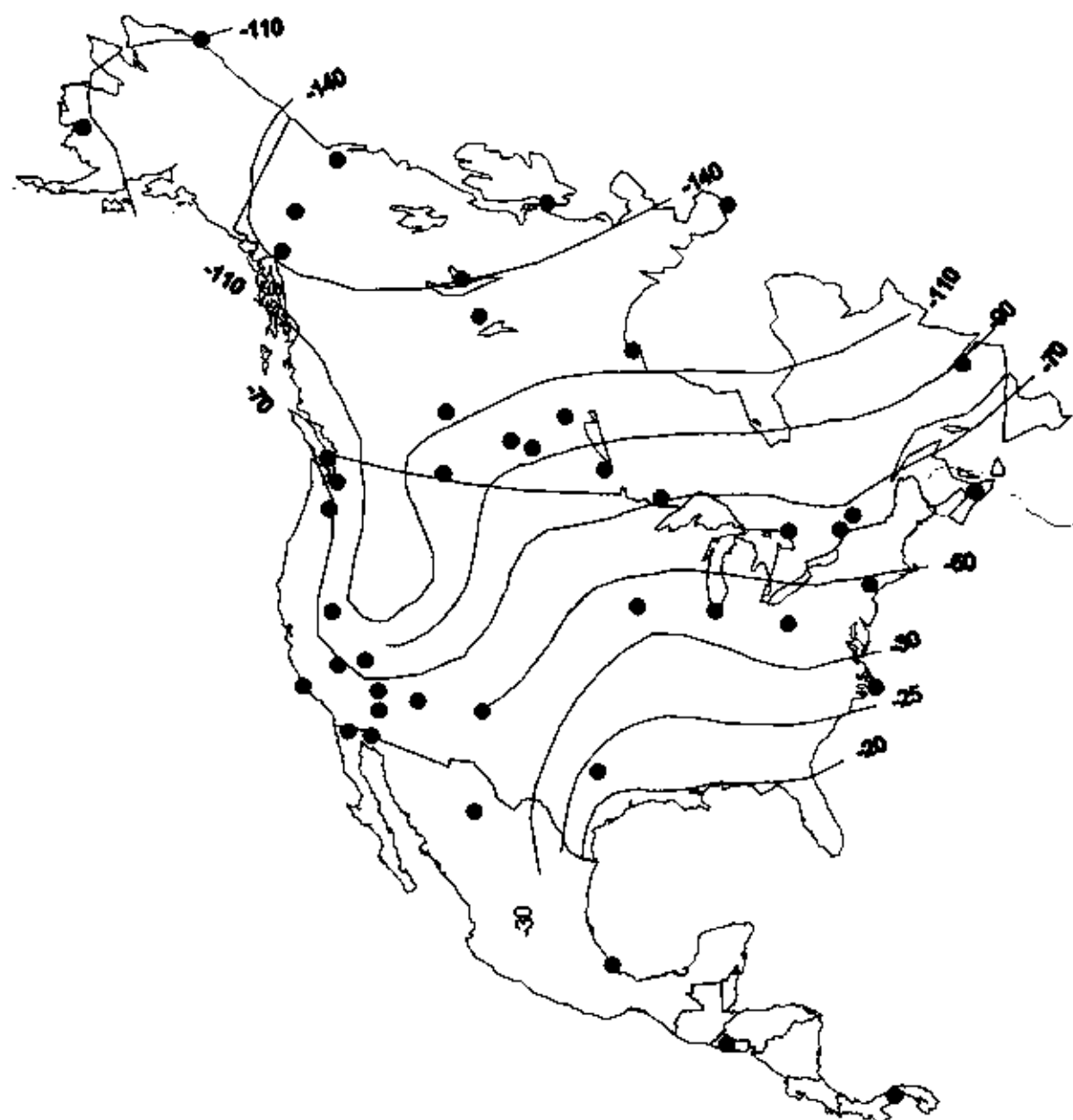
As with stable-carbon isotopes, most work on isotopes of hydrogen in biological systems has been restricted to investigations of isotopic measurements of plants (e.g., Smith and Epstein 1970; Estep and Hoering 1980; Ziegler 1989). Schimmelmann and DeNiro (1986) investigated trophic enrichment of deuterium in an aquatic food chain, but isotopic investigations of higher-trophic level organisms are generally lacking. Recently, Cormie et al. (1994) found high correlation of bone collagen  $\delta\text{D}$  with growing season rain  $\delta\text{D}$  in modern deer bone. This study provided the inspiration for investigations by Hobson and Wassenaar (1997) to use  $\delta\text{D}$  measurements of feathers grown on breeding grounds to link breeding and wintering grounds of neotropical migratory birds (see below).

## Captive studies

Until relatively recently, there were two major limitations to the application of stable isotope analyses in avian dietary studies. First, it was not well understood how stable isotopes fractionate or change once they are incorporated into tissues. Tieszen et al. (1983) conducted controlled laboratory studies on gerbils (*Meriones unguiculatus*), but it was not known to what extent their findings were applicable to studies of birds, especially since birds produce different nitrogenous waste products compared with mammals. Mizutani et al. (1991a) opportunistically examined the tissues and diet of a single cormorant (*Phalacrocorax carbo*) raised on a constant diet of mackerel (*Pneumatophorus japonicus*) and provided the first published estimates of carbon and nitrogen isotopic fractionation between diet and bird tissues. However, the investigation of a single piscivorous bird did not allow extrapolation to birds in general, particularly to non-piscivores.

A second limitation to the application of stable isotope analysis to avian studies was that precise turnover rates of isotopes in tissues of wild birds were poorly known. Although Tieszen et al. (1983) had investigated stable isotopic turnover rates in gerbils by

**Figure 1.** Patterns of  $D_w$  for North America. Circles indicate precipitation sites (updated from Hobson and Wassenaar 1997).



switching isotopic compositions of diets of laboratory animals under controlled conditions, again, it was not clear how reliably their results might apply to birds.

### Isotopic turnover and fractionation of body tissues

The period over which tissue isotopic abundance will reflect the isotopic signature of a particular diet will

depend, in part, on the isotopic turnover rate in that tissue. This rate is not to be confused with decay rates associated with radioisotopes. Rather, I refer here to elemental turnover in tissues, a process directly linked to the metabolic rate of that tissue. Tissues with rapid isotopic or elemental turnover will reflect recent diet whereas those with slow turnover will reflect longer-term dietary averages. The choice of tissue will

**Table 2.** Summary of diet-tissue fractionation values derived from captive studies of Hobson and Clark (1992b) and others. Sample sizes and food type in parentheses.

Tissue	Diet-tissue fractionation factor (‰)						
	Chicken (8) (TS) <sup>1</sup>	Quail (5) (TS)	Gull (14) (Perch)	Falcon (6) (Quail)	Crow (7) (Perch)	Piscivorous Birds (6 spp.) <sup>2</sup>	Cormorant (1) (Mackerel) <sup>3</sup>
<b>Carbon</b>							
Blood		1.2 ± 0.6	-0.3 ± 0.8	+0.2 ± 0.01			
Liver	+0.4 ± 0.2	+0.2 ± 0.6	-0.4 ± 1.0		3.7 ± 1.6		+1.3
Muscle	+0.3 ± 0.3	+1.1 ± 0.5	+0.3 ± 0.4		1.1 ± 1.0		+2.1
Collagen	+0.8 ± 1.2	+2.7 ± 0.4	+2.6 ± 1.1				+2.5
Feather	-0.4 ± 0.02	+1.4 ± 0.6	+0.2 ± 1.3	+2.1 ± 0.08		+2.9 to +3.8	+3.6
<b>Nitrogen</b>							
Blood		+2.2 ± 0.2	+3.1 ± 0.2	+3.3 ± 0.4			
Liver	+1.7 ± 0.1	+2.3 ± 0.2	+2.7 ± 0.1		2.9 ± 0.7		+2.3
Muscle	+0.2 ± 0.2	+1.0 ± 0.1	+1.4 ± 0.1		1.7 ± 1.0		+2.4
Collagen	+1.5 ± 0.1	+2.5 ± 0.4	+3.1 ± 0.2				+3.9
Feather	+1.1 ± 0.1	+1.6 ± 0.1	+3.0 ± 0.2	+2.7 ± 0.5		+3.7 to +5.3	+3.6

<sup>1</sup> TS refers to Turkey Starter commercial food mix.

<sup>2</sup> Mizutani et al. (1992).

<sup>3</sup> Mizutani et al. (1990).

depend, then, on the ecological question of interest; Tieszen et al. (1983) suggested that, by analyzing combinations of tissues, greater information concerning an animal's diet could be obtained. As a first step in establishing isotopic turnover rates applicable to birds, and isotopic fractionation factors between diet and a variety of avian tissues, Hobson and Clark (1992a,b) conducted several experiments using captive birds raised on isotopically known diets. They determined  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  diet-tissue fractionation factors for blood, liver, muscle, bone collagen and feathers of domestic chickens (*Gallus gallus*), Japanese Quail (*Coturnix japonica*) and Ring-billed Gulls (*Larus delawarensis*) and blood and feather samples of adult Peregrine Falcons (*Falco peregrinus*) raised on known isotopic diets (see Table 2).

Turnover rates of  $^{13}\text{C}$  in tissues of fully grown Japanese Quail were established by switching the diet of an experimental group from a wheat-based (i.e. C-3) diet to a corn-based (i.e. C-4) diet and sampling tissues periodically for 212 days. An exponential model described patterns of isotopic turnover in all tissues. Turnover rates for quail tissues were ranked liver>blood>muscle>bone collagen (Table 3). Hobson

and Clark (1993) later expanded these results to include the potential isotopic assay of materials involving non-destructive sampling by determining the isotopic turnover rates of the cellular and plasma fractions of blood. By switching the diets of captive crows from C-3 to C-4 composition and sampling blood over a 45-day period, they demonstrated that cellular and plasma fractions had half-lives of 29.8 and 2.9 days, respectively. This suggests that where birds can be captured alive, the isotopic analysis of blood fractions can provide the same dietary information as that based on muscle and liver.

**Table 3.** Elemental carbon turnover rates in tissues of captive-raised Japanese Quail.

Tissue	Half-Life (d)	Source
Blood - whole	11.4	Hobson and Clark (1992)
Blood - cellular	29.8	Hobson and Clark (1993)
Blood - plasma	2.9	Hobson and Clark (1993)
Muscle	12.4	Hobson and Clark (1992)
Liver	2.6	Hobson and Clark (1992)
Bone Collagen	173.3	Hobson and Clark (1992)

### Isotopic turnover and fractionation related to egg production

Bird eggs are another potential source of material for isotopic investigation of avian diets because they are formed from nutrients that are derived ultimately from the diet of the laying female. Eggs are also usually readily available, either from the wild or through archived collections, and so are a convenient source of material for isotopic analysis. Another motivation for the isotopic investigation of eggs is that it can provide information on how quickly nutrients from the diet are incorporated into various egg components and the extent to which endogenous reserves are used in egg formation (Krapu 1981; Austin and Fredrickson 1987; Afton and Ankney 1991). If yolk is formed rapidly from dietary sources then the contribution of the new diet to the isotopic signal in the yolk should be proportional to the additional mass of yolk formed using the new diet.

Previous studies have shown that stable-carbon and oxygen isotope analysis of the organic matrix (C) or carbonate (C and O) component of eggshells can reveal dietary information from both archaeological and contemporary specimens (von Schirnding et al. 1982; Schaffner and Swart 1991). However, prior to Hobson (1995), only Trust (1993) had used other components of eggs such as the yolk and albumen fractions and virtually no information existed on how isotopic signatures change or fractionate between diet and the various components of the avian egg (but see von Schirnding et al. 1982; Schaffner and Swart 1991). Hobson (1995) investigated isotopic signatures of eggs laid by captive Japanese Quail and wild-strain Mallards (*Anas platyrhynchos*) raised on grain-based diets, and three species of falcon raised on quail, to determine possible influences of diet. That study of bird eggs indicated fairly uniform patterns of isotopic fractionation between diet and yolk, albumen, yolk lipid, shell membranes and shell carbonate. However, the magnitude of fractionation differed substantially between egg components, reflecting differences in the biochemical and metabolic processes involved in tissue synthesis (Tieszen and Bouton 1988; Nakamura et al. 1982; Krueger and Sullivan 1984). The magnitude of nitrogen isotope fractionation between diet and albumen, yolk and shell membrane were similar, being close to +3.4‰. This value is in agreement with the 3–5‰  $^{15}\text{N}$  trophic enrichment seen in terrestrial and marine food webs (Schoeninger and DeNiro 1984; Fry 1988; Hobson et al. 1994). Nitrogen in yolk, albumen and membranes occurs primarily as protein, and  $^{15}\text{N}$  fractionation between diet and protein

generally occurs during processes of amino acid amination and transamination (Macko et al. 1982). As such, protein synthesis and its corresponding isotopic fractionation in egg components is similar to the synthesis of other proteins in the adult bird.

Shell carbonate is highly enriched in  $^{13}\text{C}$  compared to diet for all species examined (von Schirnding et al. 1982; Schaffner and Swart 1991; Hobson 1995). Animal shell carbonates are typically enriched over substrates (Fritz and Poplawski 1974; Fry and Wainright 1991) and, in the case of birds, it is likely that major carbon isotopic fractionation occurs during the formation of carbonate ions by carbonic anhydrase of oviduct fluids (Simkiss and Tyler 1958; von Schirnding et al. 1982). However, falcons showed a consistently lower carbonate enrichment factor compared with quail and mallard fed plant-based diets. In their isotopic study of seabird eggshells, Schaffner and Swart (1991) also reported smaller differences between eggshell carbonate and diet for protein versus carbohydrate feeders. Similar differences in carbon isotopic fractionation have also been recorded between herbivore and carnivore bone apatite and collagen (Krueger and Sullivan 1984) and, in this sense, carbonates in bone apatite are analogous to carbonates in the eggshell matrix.

In general, herbivore diets consist of relatively more carbohydrates and fewer proteins and lipids than carnivore diets. Carbohydrates in herbivore diets are allocated primarily to energy metabolism whereas protein is allocated mainly to growth and maintenance of tissues such as collagen. Bone apatite (and shell carbonate) is derived from blood bicarbonate which is in turn generated from the metabolism of energy substrates (DeNiro and Epstein 1978). Carnivores depend relatively more on lipids than on carbohydrates for their energy metabolism and since lipids are depleted in  $^{13}\text{C}$  relative to proteins and carbohydrates, the carbon available for bone and shell formation in carnivores should be, on average, more depleted relative to diet than for herbivores. More recently, Ambrose and Norr (1993) and Tieszen and Fagre (1993) investigated the relationships of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate by manipulating the isotope composition of macronutrients in the diets of laboratory rats and mice. Both studies demonstrated that carbonates in bone apatite are derived from whole diet whereas bone collagen is derived primarily from dietary protein (see also Ambrose 1993). Dietary protein not used in tissue maintenance and growth is apparently used in energy metabolism. The above

discussion emphasizes that, in addition to analyzing whole diet, it is important to consider also fractionation patterns associated with dietary macromolecules such as carbohydrates, lipids, proteins and even individual amino acids (Tieszen and Boutton 1988; Macko et al. 1982).

### Isotopic enrichment due to fasting or nutritional stress

During their study of isotopic fractionation between diet and tissues of various captive birds, Hobson and Clark (1992b) determined that American Crows (*Corvus brachyrhynchos*) raised on a plant-based diet did not grow as well and had tissues enriched in  $^{15}\text{N}$  relative to diet, compared with birds raised on a high protein diet of perch. While it appeared as though nutritional stress caused differential enrichment in  $^{15}\text{N}$ , interpretation of these results was confounded by the different diets. For this reason, Hobson et al. (1993) conducted another set of experiments on captive quail raised on a single diet (one batch of Turkey Starter) but subjected a treatment group to a ration that maintained their body mass while allowing the control group ad libitum access to food that supported normal growth. They found that the treatment group had enriched  $^{15}\text{N}$  values of muscle, liver, bone collagen, feather and blood compared with the control group. This provided the first evidence that nutritional stress could cause isotopic enrichment in consumers' tissues.

To evaluate whether or not such enrichment occurs in nature, Hobson et al. (1993) also measured  $^{15}\text{N}$  values in tissues of nesting Ross' Geese (*Chen rossii*) before and after their fast during incubation on their high arctic breeding grounds. As predicted, post incubation geese showed enriched tissue  $^{15}\text{N}$  values compared with pre-incubating birds. Thus, substantial evidence of  $^{15}\text{N}$  enrichment due to nutritional stress was established. However, the precise mechanisms for this enrichment effect are poorly understood.

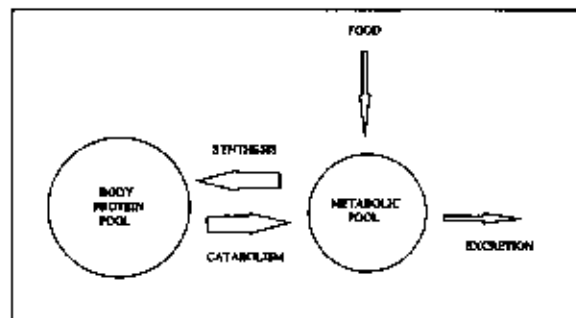
Ambrose and DeNiro (1986) similarly observed that  $^{15}\text{N}$  values of the bone collagen of drought-tolerant herbivores were higher than those of water-dependent species in East Africa and related this effect to physiological processes relating to mechanisms of water conservation. These authors noted that herbivorous mammals on diets high in protein have the capacity to excrete highly concentrated urine under conditions of heat and water stress and that this is accompanied by often spectacular increases in urea output. Urea is the major form of excreted nitrogen in mammals and is significantly depleted in  $^{15}\text{N}$  relative to the diet (Steele and Daniel 1978). The excretion of

a more concentrated urine with a quantitative increase in the excretion of  $^{15}\text{N}$ -depleted urea in water stressed mammals would result in higher  $^{15}\text{N}/^{14}\text{N}$  ratios in the unexcreted nitrogen. Subsequent  $^{15}\text{N}$  enrichment of the remaining body nitrogen incorporated into tissues is expected from considerations of isotopic mass balance (see also Ambrose and DeNiro 1987). Hobson et al. (1993) proposed an analogous mechanism to account for apparent enrichment of  $^{15}\text{N}$  observed in fasting birds.

Nitrogen available for the synthesis of body proteins can be recycled from metabolic amino acid pools with inputs from assimilated foods and through protein breakdown or catabolism. A primary source of nitrogen isotopic fractionation is believed to occur during processes of deamination and transamination of amino acids (Gaebler et al. 1966; Macko et al. 1982; Minagawa and Wada 1984). In this way metabolized amino acids are enriched during anabolism (i.e. tissue synthesis), and nitrogenous waste products depleted in  $^{15}\text{N}$  relative to diet (e.g., Steele and Daniel 1978). Under conditions of fasting and nutritional stress, a greater proportion of nitrogenous compounds available for protein synthesis are derived from catabolism (i.e. tissue breakdown) and, since this source of nitrogen has already been enriched in  $^{15}\text{N}$  relative to diet, additional enrichment in the metabolic nitrogen pool must occur. One consequence of this process would be the eventual enrichment in  $^{15}\text{N}$  of all body tissues relative to periods without stress (see also Swick and Benevenga 1977; Figure 2). The extent of  $\delta^{15}\text{N}$  enrichment in tissues due to fasting and nutritional stress should be influenced by the isotopic turnover rates in those tissues. Metabolically active tissues (e.g., liver) are expected to show the effects of enrichment due to stress more readily than tissues with slower isotopic turnover (e.g., bone collagen in adult birds, Tieszen et al. 1983). Consistent with this suggestion, Hobson et al. (1993) found that adult female Ross' Geese showed a greater enrichment in liver  $\delta^{15}\text{N}$  values compared with those of muscle. Experimental quail showed high  $\delta^{15}\text{N}$  enrichment in both liver and bone collagen but these birds were still growing and bone isotope values were more dynamic than that expected for adult birds.

Stable isotope analysis of the tissues of wild animals and their prey to delineate diet or trophic relationships within communities offers numerous advantages over conventional approaches (e.g., Ambrose and DeNiro 1986; Peterson and Fry 1987). However, the reliability of the isotope approach depends directly on our understanding of processes

**Figure 2.** Hypothetical depiction of nitrogen enrichment due to nutritional stress. In situations where food intake diminishes and catabolism increases, the total body protein pool is expected to become enriched (providing excretion still occurs).



contributing to the abundance of stable isotopes in consumer tissues. Studies using  $^{15}\text{N}$  analysis to infer diet or trophic position must take account of the nutritional history of the individuals whose tissues are being examined.

The effect of  $^{15}\text{N}$  enrichment associated with changes in body composition is particularly relevant to isotopic studies of birds, especially the many species which lose body mass during egg-laying and incubation. Among waterfowl, for example, it was previously felt that most of this mass loss reflected gonadal regression and depletion of fat reserves (e.g., Hanson 1962; Harris 1970). However, breast, leg and gizzard muscles are important protein reserves during incubation in arctic-nesting Lesser Snow (*Chen caerulescens*) and Ross' Geese (Ankney and MacInnis 1978). As noted by Ankney (1977), even in species in which the incubating female does not fast, considerable mass loss occurs (Weller 1957; Oring 1969; Anderson 1972). Penguins also fast during egg-laying (Richdale 1947) and several species of seabirds may undergo periods of food stress due to competition near colonies or crashes in prey stocks (e.g., Hunt et al. 1986; Erikstad 1990). In addition, nestling seabirds may experience protracted periods of reduced growth due to intermittent food provisioning (e.g., Ricklefs et al. 1980). Although there is tremendous potential for the application of stable-isotope analysis to avian dietary studies, researchers should consider possible  $^{15}\text{N}$  enrichment of tissues in some individuals or species due to physiological effects rather than diet per se.

### Foodweb source studies

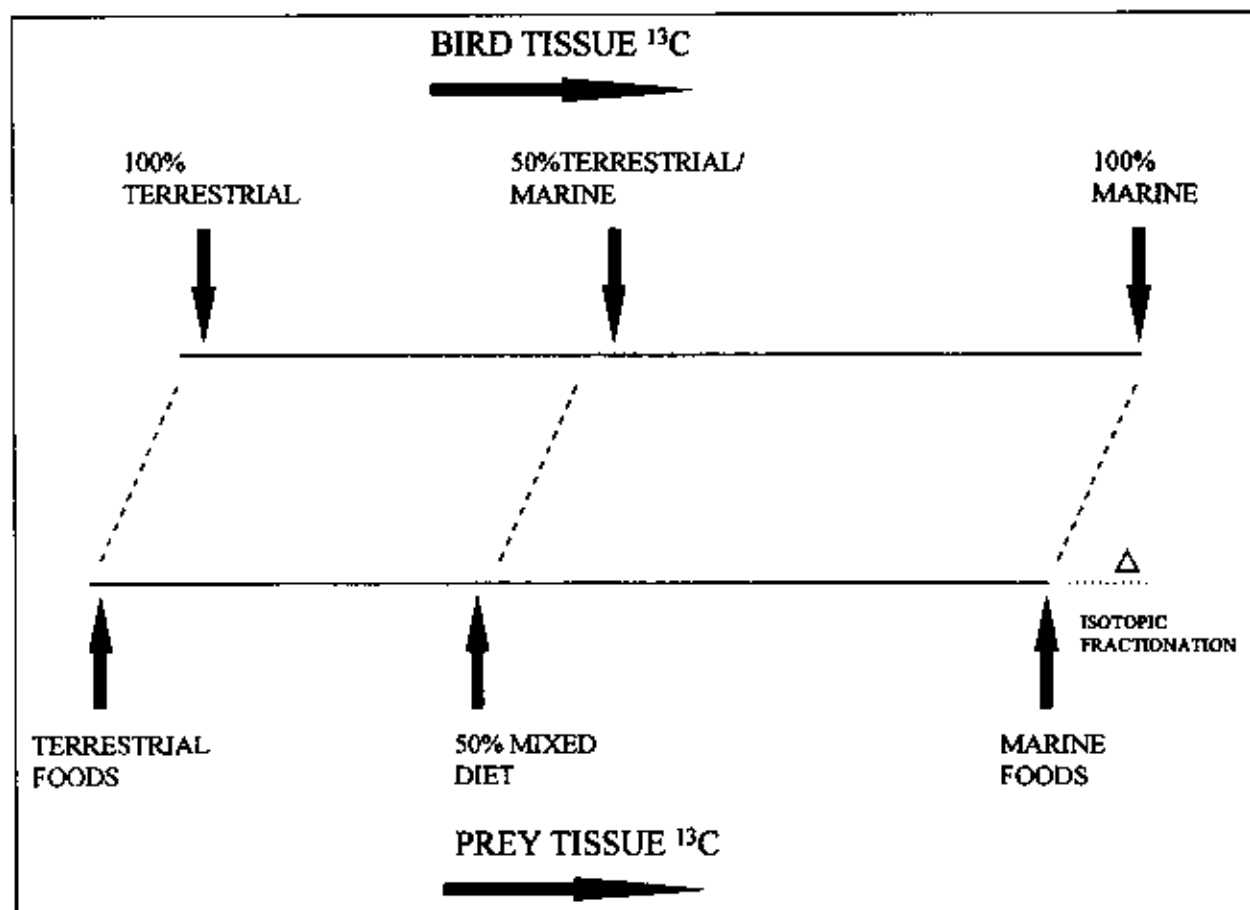
The first applications of stable isotope analysis to

avian studies was to determine source of feeding. This approach is based on the fact that isotope ratios in consumers reflect those in their prey and, where two isotopically distinct sources of food are available, a simple linear mixing model can be constructed to predict the relative nutritional inputs from each source (Figure 3). The measurement of several stable isotopes in consumer and diet can allow better resolution of dietary contributions and may also allow the approximation of inputs from more than two isotopically distinct sources (e.g., Mariotti et al. 1984; Hobson et al. 1997).

Tietje and Teer (1988) examined the reliance of Northern Shovelers (*Anas clypeata*) on freshwater and saline habitats using  $\delta^{13}\text{C}$  analyses of pectoral muscle tissues and concluded that these birds did not move between habitats during the midwinter period. Another, more recent, tracer application to waterfowl studies involved the analysis of stable carbon and sulfur isotopes in muscle, eggs, and prey tissues of Redhead Ducks (*Aythya americana*) on breeding and wintering grounds (Trust 1993). That study revealed differential dietary sources for carbon and sulfur on wintering grounds and generally alluded to birds reflecting the isotope ratios of foods available to them. Using stable carbon isotope analysis of bone collagen, Hobson (1986) provided a minimum estimate of the importance of terrestrial C-3 based garbage in the diets of Glaucous-winged Gulls (*Larus glaucescens*) wintering near Vancouver, British Columbia. While that study represented an advance over previous conventional dietary studies, it was complicated by the fact that terrestrial and marine isotopic endpoints were not well understood. Mizutani et al. (1990) later analyzed  $\delta^{13}\text{C}$  values in feathers of Great Cormorants and delineated freshwater and marine protein inputs to the diets of birds having access to freshwater and marine biomes during the period of feather growth.

The first isotopic analysis of more than one tissue type to determine dietary inputs to birds over different time periods was provided by Hobson (1990) who used stable-carbon and nitrogen isotope analyses of muscle and bone collagen from Marbled Murrelets (*Brachyramphus marmoratus*) that had been collected in marine coastal areas and at a freshwater lake in British Columbia. The impetus behind that study was to determine if murrelets occurring on the lake actually foraged there to any significant extent. By creating a model depicting isotopic values expected from birds feeding exclusively in a freshwater C-3 biome compared with a coastal marine biome, Hobson (1990) was able to determine that individuals collected

**Figure 3.** Depiction of a simple linear mixing model for a bird feeding (a) exclusively at a marine dietary endpoint, (b) exclusively at a terrestrial dietary endpoint, and (c) at 50% marine and 50% terrestrial position.



on the lake had short-term (i.e., based on muscle tissue) freshwater-derived protein inputs to their diets ranging from 50 to 100%, but had little evidence of long-term (i.e., based on bone collagen) reliance on freshwater for feeding. Hobson and Sealy (1991) conducted a similar isotopic study on Northern Saw-whet Owls (*Aegolius acadicus*) from the Queen Charlotte Islands, British Columbia, after observing that stomachs of several road-killed owls contained intertidal invertebrates. These authors wondered to what extent the *brooksi* subspecies of owls on the Queen Charlottes depended on this marine food source throughout the year. By conducting isotopic analyses of owl and terrestrial and marine prey tissues from the Queen Charlottes, and Northern Saw-whet and Boreal Owl (*A. funereus*) tissues from mainland populations with no access to marine foods, these authors were able to construct a two-source dietary input model for both muscle and collagen tissues of owls. The model based on muscle provided dietary estimates for a

period of about a month (see above) and revealed a dependence on marine amphipods ranging from zero to complete. However, the analysis of collagen from the same individuals showed no long-term dependence on amphipods. Thus, it was concluded that the owls that foraged intertidally on amphipods were either opportunistic or depended upon this food source only for short periods during the nonbreeding season.

Alexander et al. (1996) recently applied  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses of tissues and prey of Long-billed Dowitchers (*Limnodromus scolopaceus*), Silt Sandpipers (*Calidris himantopus*), and Hudsonian (*Limosa haemastica*) and Marbled Godwits (*L. fedoa*) at an inland migratory stopover in Saskatchewan. Alexander et al. (1996) noted the broad isotopic range of dietary samples including highly enriched  $\delta^{13}\text{C}$  values for sago pondweed tubers (*Potamogeton pectinatus*) and were able to demonstrate that godwits relied primarily on tubers, whereas the other species fed mostly on invertebrates. By analyzing a time series

of liver samples in birds throughout the stopover period, they were able to monitor dietary change through time for each species. However, the authors cautioned that researchers using stable isotopes to assess migratory shorebird diets should be aware of possible complications arising from isotopic variability within prey types, even over small geographic ranges. High isotopic variability at inland agro-wetland complexes may preclude reliable isotopic assessment of shorebird diets due to fertilizer input, ammonification (i.e., the enrichment of soil  $^{15}\text{N}$  due to a loss of isotopically lighter ammonia through evaporation) and often pronounced chemical differences between wetlands.

### Using stable isotopes to trace nutrients to reproduction

Other elements with stable-isotope values that are typically enriched in marine versus terrestrial foodwebs include sulfur, hydrogen and nitrogen (Fry and Sherr 1988; Michener and Schell 1994). The occurrence of isotopically distinct inputs to various systems also forms the basis for using stable-isotope measurements to trace sources of pollutants in foodwebs (reviewed by Macko and Ostrom 1994).

Dietary shifts in birds from terrestrial or freshwater C-3 to marine ecosystems (and vice versa) influence isotopic signatures in a variety of tissues (Hobson 1986, 1990; Mizutani et al. 1990; Thompson and Furness 1995). Bird eggs are particularly amenable to this type of analysis since nutrients required for egg production are derived ultimately from the diet of the laying female (von Schimding et al. 1982; Schaffner and Swart 1991; Hobson 1995; Jarman et al. 1996). In their recent examination of seabird eggs and marine prey, Jarman et al. (1996) suggested that the combined use of contaminant and stable-isotope analyses of egg proteins and lipids might provide information on the allocation of endogenous versus exogenous lipid reserves to eggs. This, together with the isotopic investigations of Hobson (1995) using captive-raised birds, clearly suggests that stable isotopic analyses of various egg components can provide information on the source of nutrients in egg production.

Although birds might be expected typically to synthesize egg proteins directly from diet, systematic declines in somatic protein in response to protein demands during egg production have been demonstrated in wild waterfowl (reviewed by Alisauskas and Ankney 1992; see also Houston et al. 1995; Williams 1996). In such cases, the occurrence of

carbon or sulfur from proteins originating in body reserves that were in turn derived from areas separate from the breeding grounds is possible. Lipid nutrient storage prior to reproduction has been demonstrated in waterfowl (Alisauskas and Ankney 1992; but see Perrins 1996) and it was this component of eggs that we assumed would have the greatest likelihood of providing isotopic evidence for transfer between marine and freshwater systems by migrating birds.

Hobson et al. (1997) performed  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  analyses on eggs of two migratory species of fish-eating birds, Caspian Terns (*Sterna caspia*) and Double-crested Cormorants (*Phalacrocorax auritus*) from Lake Ontario, Canada, to examine the extent to which nutrient reserves acquired on marine wintering grounds are transferred to eggs laid on freshwater breeding grounds. In order to establish isotopic patterns typical of eggs of birds using marine and freshwater C-3 biomes, eggs of Herring Gulls (*Larus argentatus*), a year-round resident on the Great Lakes, and those of Caspian Terns and Herring Gulls, breeding respectively in the Gulf Coast of Texas and Atlantic coast of Canada, were analyzed isotopically. Individual egg components showed distinct isotope values that were similar for both migratory and non-migratory birds breeding on Lake Ontario and were significantly lighter than those from species breeding in a marine biome. Hence, there appears to be little evidence for significant nutrient transfer between the two biomes. The intermediate isotope values shown for egg components of Herring Gulls breeding on the Atlantic coast suggest nutrient input from terrestrial as well as marine sources. These results indicated the utility of stable-isotope analysis for tracing endogenous and exogenous contributions to reproduction in birds and further validated the use of migratory birds as indicators of breeding area contaminant levels and their effects on the Great Lakes.

### Trophic relationships

Numerous studies have demonstrated a step-wise trophic enrichment of  $^{15}\text{N}$  in marine foodwebs (reviewed by Michener and Schell 1994). However, it has only been relatively recently that this approach has been applied to studies of seabirds. Hobson (1990) who measured archived tissues of Marbled Murrelets from coastal British Columbia. This study provided the impetus to expand isotopic investigations to whole seabird communities and Hobson and Welch (1992) then investigated stable-carbon and nitrogen isotope ratios in the high arctic foodweb of Lancaster Sound. That study, based on an analysis of particulate organic



matter (POM) through polar bears (*Ursus maritimus*), showed an overall trophic enrichment of 3.8‰ for  $^{15}\text{N}$  and little or no trophic effect for  $^{13}\text{C}$ . Within marine birds, Dovekie (*Alle alle*) and Common Eider (*Somateria mollissima*) were shown to occupy lower trophic levels than the more piscivorous Thick-billed Murre (*Uria lomvia*) and Black Guillemot (*Cepphus grylle*). The highest trophic level was determined for Glaucous Gull (*Larus hyperboreus*) that in turn fed to some degree on murre chicks. Hobson (1993) extended this work by modelling short-, intermediate-, and long-term trophic positions of the Lancaster Sound seabird community by considering isotope ratios of liver, muscle, and bone collagen, respectively. Importantly, Hobson (1993) refined these models by using tissue-dependent isotopic fractionation factors determined from studies of captive Ring-billed Gulls (Hobson and Clark 1992b).

Following the initial work in Lancaster Sound, Hobson et al. (1994) then applied a similar approach to delineating a more complex seabird community involving 22 species in the Gulf of Alaska. Both the Lancaster Sound and Gulf of Alaska studies revealed that lower trophic-level organisms were more important to several seabirds than was previously recognized. In addition, these studies also clearly demonstrated that inshore or benthic feeding species were more enriched in  $^{13}\text{C}$  than those species feeding offshore on more pelagic foodwebs (see also Hobson et al. 1995). The isotope approach proved valuable, then, in delineating both spatial and trophic aspects of seabird feeding relationships.

An interesting further application of trophic delineation of seabirds using stable-nitrogen isotope analyses was the isotopic investigation of the diet of the extinct Great Auk (*Pinguinus impennis*). Hobson and Montevecchi (1991) measured  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in bone collagen of adult and juvenile Great Auks excavated at Funk Island, Newfoundland, and determined that adult birds fed at a trophic continuum from crustaceans through piscivorous fish. The few juveniles measured occupied low trophic positions. These results led to the hypothesis that chicks may have been fed large quantities of euphausiids by regurgitation, suggesting further a greater evolutionary convergence between Great Auks and southern hemisphere penguins than was previously thought (Prince and Harris 1988).

Following the very clear demonstration of the value of an isotope approach to seabird studies (Hobson et al. 1994), other researchers have since applied this technique. Notably, Thompson et al.

(1995) investigated historical and contemporary diets of Northern Fulmars (*Fulmarus glacialis*) from two northeast Atlantic colonies by analyzing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in archived feathers. These authors provided isotopic evidence for a change in trophic level following the end of whaling when offal apparently became less available (see also Thompson and Furness 1995). Minami et al. (1995) investigated stable-carbon and nitrogen isotope ratios in pectoral muscle of Sooty (*Puffinus griseus*) and Short-tailed (*P. tenuirostris*) Shearwaters during their northward migration in the North Pacific Ocean and provided evidence for changes in dietary preference during this period. That work was continued by Minami and Ogi (1997) who also used  $\delta^{15}\text{N}$  values in Sooty Shearwaters to infer migratory pathway used by individuals to reach the North Pacific. Recently, Gould et al. (1997) investigated trophic relationships of albatrosses associated with squid driftnet fisheries in the North Pacific Ocean and provided evidence for differences in diet among species. Although not trophic determination studies *per se*, a few researchers have also used stable nitrogen isotope ratios of soils in order to delineate locations of historical seabird rookeries (Mizutani et al. 1986, 1991b,c; Mizutani and Wada 1988).

### Tracking migratory birds

Most songbirds that breed in temperate forests of North America migrate annually to wintering sites in the southern United States or neotropics (Hagan and Johnston 1992; Finch and Stangel 1993). However, virtually no information exists on links between discrete breeding and wintering areas. This lack of information is of particular concern because neotropical migrant songbirds have shown dramatic declines in recent decades (Robbins et al. 1989; Hagan et al. 1992; Robbins et al. 1993; Askins et al. 1990; Sherry and Holmes 1993; Rappole and MacDonald 1994). Essential to the conservation of these songbirds is an ability to link breeding and wintering populations (Myers et al. 1987; Sherry and Holmes 1995; Chamberlain et al. 1997), especially since many species are philopatric to wintering as well as breeding sites (Greenwood and Harvey 1982; Rappole et al. 1983, 1992; Holmes and Sherry 1992). Such information would contribute to understanding factors influencing population regulation in these species and would be a powerful tool in their protection since conservation efforts could be matched at both ends of migration routes and at intermediate migratory stopover sites (Moore and Simons 1992). To date, it

has been difficult to trace migratory paths of neotropical songbird populations by marking with bands or transmitters, through the use of molecular techniques (Moore and Simmons 1992; Wenink et al. 1994) or through behavioural characters (e.g., DeWolfe and Baptista 1995). However, the recent measurement of naturally-occurring stable isotopes in animal tissues has been used to delineate geographically-distinct populations (van der Merwe et al. 1990; Vogel et al. 1990; Alisauskas and Hobson 1993) and this approach may also be suitable for the study of migrant songbirds (Chamberlain et al. 1997; Kelly and Finch 1998).

Stable-hydrogen isotope ratios ( $\delta D$ ) in precipitation show continent-wide patterns (Sheppard et al. 1969; Taylor 1974) with a general trend of decreasing  $\delta D$  in precipitation from the Gulf of Mexico across the North American continent to higher latitudes in a northwesterly direction (reviewed by Cormie et al. 1994; Figure 1). Previous studies have shown that  $\delta D$  signatures in rainfall during the growing season are translated to plant biomass and higher trophic-level consumers (Shiegl and Vogel 1970; Estep and Dabrowski 1980; Yapp and Epstein 1982; Cormie et al. 1994). For birds, the non-exchangeable isotopic composition of feathers (i.e. the signature that remains fixed following feather formation) reflect diet only during the period of feather growth (e.g., Hobson and Clark 1992a). Since many species of migrant songbirds grow feathers on or close to their breeding grounds before migration, the  $\delta D$  values of the non-exchangeable hydrogen fraction of their feathers should be correlated with  $\delta D$  values for local growing season precipitation ( $\delta D_w$ ). Preliminary evidence for the use of  $\delta D$  analysis of bird feathers to discern the origin of feather growth was provided by Chamberlain et al. (1997) in their study of Black-throated Blue Warblers (*Dendroica caerulescens*) breeding along a north-south gradient of the eastern seaboard of the United States. These authors demonstrated that deuterium values in whole feathers, including exchangeable and non-exchangeable components ( $\delta D_f$ ), were correlated with those they expected from rainfall in areas where birds were sampled.

Hobson and Wassenaar (1997) expanded on these findings by investigating  $\delta D$  patterns in songbird feathers on a continental scale. Moreover, because there have been no experimental studies investigating relationships between  $\delta D_f$  and  $\delta D$  in diets of birds under controlled conditions, they conducted studies on captive birds to investigate patterns of isotopic

fractionation in  $\delta D$  between whole diet and feathers. Hobson and Wassenaar (1997) examined the relationship between  $\delta D_f$  in wild passerines and  $\delta D_w$  from their breeding locations across North America in order to see if the hydrogen isotope technique could be applied broadly and across species of similar trophic level. At a wintering site in Guatemala, they also tested this technique by examining  $\delta D_f$  of wintering songbirds having both broad and narrow breeding distributions in North America. A strong positive correlation between  $\delta D_f$  and  $\delta D_w$  ( $r^2=0.83$ ) was found. This indicates that songbird  $\delta D_f$  reflects  $\delta D_w$  in areas where feathers were grown and that the technique is largely independent of species occupying a particular trophic level. Hobson and Wassenaar (1997) observed also that  $\delta D_f$  for hatch-year Least Flycatchers (*Empidonax minimus*) were significantly lower than those of adults (i.e.  $-102.6 \pm 2.4$  versus  $-66.1 \pm 5.4$ ,  $n=7,8$ ,  $t=5.81$ ,  $p<0.001$ ). This observation was consistent with the fact that adults of this species moult and grow new flight feathers after their migration to Central America where  $\delta D_w$  is heavier than at Canadian breeding sites. The results of  $\delta D_f$  analyses of wintering neotropical migrants in Guatemala illustrated the utility of this approach for linking breeding and wintering grounds.

A potential limitation to the general application of  $\delta D$  measurements to food web studies is the exchange of hydrogen between ambient environment and non-carbon bonded (e.g., O-H and N-H) hydrogen in organic matter (DeNiro and Epstein 1981; Schimmelmann 1991; Schimmelmann et al. 1993; Cormie et al. 1994). In various organic materials, hydrogen bound to oxygen and nitrogen is known to exchange with hydrogen in local water vapor, thereby presenting problems of interpretation and analysis. In the study of Hobson and Wassenaar (1997) and that of Chamberlain et al. (1997),  $\delta D_f$  measurements were made without correcting for possible isotopic exchange between feather samples and local water vapor. However, both studies demonstrate a strong relationship between  $\delta D_f$  and  $\delta D_w$  where feathers were grown and not where they were analyzed. Of the 40% of hydrogen occurring in keratin that is potentially exchangeable (i.e. that bonded to oxygen or nitrogen) only 15% or less appears to exchange with ambient water vapor, a process taking approximately 2 weeks (Chamberlain et al. 1997). Nonetheless, it will be necessary to address this issue, particularly in cases where bird feathers are retrieved from the wintering grounds for those species known to migrate between areas encompassing a broad gradient in  $\delta D_w$ . In such

cases, it will be necessary to equilibrate all feathers with water of known isotopic composition or extract only the non-exchangeable fraction of keratin prior to isotopic analysis (e.g., Schimmelmann et al. 1993; Cormie et al. 1994; Chamberlain et al. 1997). Such procedures would also allow comparison of hydrogen isotope data for feathers between laboratories.

The utility of using  $\delta D_f$  measurements to link breeding and wintering sites of neotropical migrants will vary according to individual species' ecology and distribution, and the use of additional stable isotopes may also better segregate individuals or populations (van der Merwe et al. 1990; Vogel et al. 1990; Alisauskas and Hobson 1993; Chamberlain et al. 1997). In addition, refinements to our knowledge of the distribution of stable hydrogen isotope ratios in rainfall and how these relate to local foodwebs involving migratory birds, will allow corresponding improvements in our ability to link breeding and wintering sites. However, despite the need for further refinements, the large hydrogen isotopic gradient in rain across North America currently allows the ready discrimination of distinct breeding populations of songbirds and other organisms. This phenomenon provides a new means of associating birds on their wintering grounds to general areas in North America where their feathers were grown.

## Future directions

The measurement of naturally-occurring stable isotopes of several elements to elucidate the ecology of individual species or communities of birds has undergone tremendous growth during the last decade and cover a broad spectrum of applications (Table 4). However, there are areas of isotopic research that should be encouraged in order for the field to progress. One area of immediate interest is the continuation of studies using captive birds raised on controlled diets in order to improve our understanding of isotopic

fractionation factors between diet and several tissues (see also Gannes et al. 1997). The earlier studies of Hobson and Clark (1992a,b) and Mizutani et al. (1990, 1992) must be considered preliminary. A better understanding of how fractionation factors are affected by diet is also required, and the hypotheses of Hobson (1995) regarding the influence of carnivory and herbivory on isotope fractionation involved in the synthesis of egg components need to be confirmed. Captive studies could also be used to better understand the behavior of hydrogen and sulfur isotopes in foodwebs involving birds. Both of these isotopes are currently much underused and our knowledge of factors influencing their fractionation and abundance in nature is rudimentary. Future applications of stable isotope analyses will also provide a direct means of quantifying the role of endogenous and exogenous reserves to reproduction in a wide variety of species and will likely put to rest a number of outstanding questions and controversies in this area of avian reproductive physiology and ecology.

To date, the vast majority of isotopic applications to foodweb studies have focused on bulk tissues such as muscle, liver, blood and feathers. However, with changing technology it is now possible to look at isotopic signatures of individual amino acids and fatty acids (e.g., Macko et al. 1983; Abrajano et al. 1994). Analysis of these components may allow a more refined means of tracing source of feeding in birds since it allows the tracing of those essential materials that are necessarily derived only from diet and not synthesized within the animal.

The recent development of the use of stable hydrogen isotope analysis to track migratory birds and other wildlife represents an extremely exciting area of research, particularly when integrated with other marker or tracer techniques such as DNA and trace element analysis. This approach may provide the only viable means of linking breeding and wintering areas

**Table 4.** Summary of the typical applications of stable isotope analyses to avian ecological studies.

Application	Typical Tissues	Isotope(s)	Approximate Cost/sample (1998\$)
Source of feeding:			
$C_3$ versus $C_4$ , CAM	muscle, blood, feather, eggs	$^{13}C$	\$10-15
marine versus terrestrial/freshwater	muscle, blood, feather, eggs	$^{13}C$ , $^{34}S$ , $^{15}N$ , $^{87}Sr$ , $^{18}O$	\$10-60
inshore versus offshore	muscle, blood, feather, eggs	$^{13}C$ , $^{34}S$	\$10-60
Trophic level:	muscle, blood, feather, eggs	$^{15}N$ , $^{13}C$	\$10-20
Natal origin and migration route:	keratin (feather, nail, bill)	$D$ , $^{18}O$ ?, $^{87}Sr$ , $^{13}C$	\$100

for small migratory songbirds. An important avenue of research in this regard will be the development of more accurate isotopic maps of North America and an understanding of the scope of variability in patterns of D/H in rainfall between years.

Finally, while I have espoused the virtues of using stable isotope analyses in ecological investigations involving birds, it is important to realize that this approach cannot, nor should it, replace more traditional methods. Instead, it is very clear that, for dietary studies, stable isotope analyses will rather *augment* those methods that provide more taxonomic information (see Sydeman et al. 1997). Nonetheless, the renewed interest in how birds fit into larger ecosystems and their possible roles as ecological indicators (e.g., Furness and Greenwood 1993), suggests that the stable isotope approach will provide new information that could not be obtained using any other techniques.

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# Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia

Fred Cooke

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## Abstract

We describe a novel approach to the study of a population of forest nesting seabirds (Marbled Murrelets *Brachyramphus marmoratus*) which are thought to be declining as a result of various potential threats to their environment. This is the first research on this species which makes wide use of individually marked birds. It was made possible through the development of two capture techniques; (1) a floating mist net system which can be used in narrow coastal inlets close to where the birds breed and (2) using dip nets at night. These techniques not only led to the marking of more than 1000 birds for a population based study, but allowed the collection of blood samples for physiological examination of breeding status in the absence of a large sample of birds at nests. We provide the first evidence of breeding area philopatry in this species. We also document the first longevity record for the species. Using a newly developed sexing technique based on DNA technology, which could have wide application for other seabird studies, we found a large excess of males in our marked population. This probably reflects a differential tendency of males to be captured, and may reflect a greater tendency of males to fly into the woods.

## Résumé

Nous décrivons une nouvelle approche pour l'étude d'une population d'oiseaux de mer (Aloue marbré, *Brachyramphus marmoratus*) nichant en forêt et que l'on croit en déclin, à cause de plusieurs menaces potentielles sur leur environnement. C'est la première étude sur cette espèce qui utilise des oiseaux marqués individuellement. Ceci fut rendu possible grâce au développement de deux techniques de capture ; (1) un système de filets japonais flottants qui peut être utilisé dans les fjords étroits près des sites de nidification et (2) la capture nocturne sur l'eau à l'aide d'épuisettes. Ces techniques ont permis non seulement de marquer plus de 1,000 oiseaux pour une étude de population, mais ont aussi permis la récolte d'échantillons sanguins pour des études physiologiques du statut de nidification étant donné l'absence d'échantillons d'oiseaux au nid. Nous présentons la première évidence de philopatrie aux sites de nidification chez cette espèce. Nous documentons aussi le premier record de longévité pour l'espèce. Nous avons démontré un excès de mâles dans notre population marquée en utilisant une technique nouvellement développée, basée sur les analyses d'ADN, technique qui pourrait avoir une application plus large pour l'étude d'autres populations d'oiseaux de mer. Ce biais en faveur des mâles reflète probablement un taux de capture plus élevé pour les mâles et peut aussi refléter une tendance plus forte des mâles à fréquenter la forêt.

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Fred Cooke, Chair of Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6. (fcooke@sfu.ca)

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## Introduction

Much avian research associated with Canadian forests has emphasized a multi-species approach. By contrast, the work which we describe focuses on a single species, the Marbled Murrelet (*Brachyramphus marmoratus*), that is thought to be vulnerable to the

changes in forest ecosystems which result from forestry practices. The research program was planned as a cooperative one among several agencies, the Canadian Wildlife Service/National Science and Engineering Research Council Chair of Wildlife Ecology at Simon Fraser University, the British

Columbia Ministry of Forests (MOF) and the Canadian Wildlife Service (CWS). The work has been directed by Andrew Derocher and Louise Waterhouse (MOF), Gary Kaiser, Sean Boyd and Kathy Martin (CWS), and Tony Williams and Fred Cooke of the CWS/NSERC Chair of Wildlife Ecology at Simon Fraser University. Many graduate and summer students have been involved in the data collection and this paper represents an overview of the work.

The Marbled Murrelet is a small alcid which is widely distributed along the Pacific coast of North America, and in British Columbia has been found nesting only in coastal old-growth forests. There are several reasons for concern for the conservation of these birds. Firstly, they are unique among alcids in that they nest solitarily or in loose associations in large trees, usually within 60 kilometers of the sea (Hamer and Nelson 1995a). These areas are susceptible to logging and development. Secondly, they have an apparent dependence for nest sites located atop large side branches of old-growth coniferous trees (Hamer and Nelson 1995a). Trees are usually at least 100 years old before such side branches develop which are large enough to accommodate a nest and these trees are in great demand by the lumber industry. Thirdly, throughout the year they require marine habitat for their food supply, mainly small fishes such as Sand Lance (*Ammodytes hexapterus*) and tend to be found close to the shore (Carter and Sealy 1990). This habitat is increasingly used by human populations on the Pacific coast. Potential threats include gill-netting, oyster leases, oil spills, increased recreational usage and urban development with its production of toxic waste (Fry 1995). Fourthly, the murrelet is a species with low fecundity (Nelson and Hamer 1995) and is suspected of having a late age of sexual maturity (Sealy 1995), as are other members of the Alcidae (Nettleship 1996). It lays only one egg per clutch, and there is no evidence of more than one nesting attempt per year. It is assumed to be long lived but there is no evidence on this point. In such species increases in adult mortality could affect population viability. Fifthly, fragmentation of forests may make their nests more vulnerable to predation, particularly by Common Ravens (*Corvus corax*), Northern Flying Squirrels (*Glaucomys sabrinus*) and Steller's Jay (*Cyanocitta stelleri*). Low nest success has been recorded in areas where there has already been much destruction of old growth forests (Nelson and Hamer 1995).

Research on the Marbled Murrelet in British Columbia is a major challenge to biologists and conservationists because of its secretive habits. The

first active nest in the province was found only in 1993 (Jones 1993). The species is classified as threatened or endangered by the U.S. Fish and Wildlife Service in Washington, Oregon and California, as well as by the State of California and is red-listed in the Province of British Columbia. In Canada, it is a nationally threatened species and there is a Marbled Murrelet Recovery Team, chaired by Anne Harfenist of the Canadian Wildlife Service. There is a widespread public belief that the population is under threat from logging practices, but very little solid information exists about either population changes or the requirements needed to maintain healthy populations. Provincial government guidelines through the British Columbia Forest Practices Code are planned to provide provisions for setting aside areas where old growth forest will be maintained when there is evidence of activity (preferably nesting) of this species. These guidelines arose partly as a result of concern for habitat protection and the Marbled Murrelet came to represent a symbol in some quarters of the need for protection of biodiversity. The areas which may be set aside represent large reductions in the profitability of the forests to the logging companies, and so naturally there is concern that the right areas are chosen from the perspective of the needs of the species. From the point of view of both the public and the companies, it was important to be sure that this protection of this species is based on solid science and that the measures taken will in fact help the species.

Much research to date has concentrated on determining standardized methods for assessing numbers of birds both in the marine and forest habitats with a view to monitoring distribution, population changes and habitat requirements. Although recent work has concentrated on studying the demographic processes necessary to understand the population dynamics of the species, the elusiveness of the nesting behaviour and lack of marked populations has made progress slow. A population model of the species by Beissinger (1995) had to rely on limited data for some of the parameters and inference from other species of alcids for others.

We adopted a demographic approach in our studies which concentrates on two questions: (1) Is there evidence for declines in the British Columbia populations? and (2) If so, what are the important components of the life cycle which are responsible for these changes?

Trends in murrelet populations are not easy to detect and often depend on reports from naturalists.

Perhaps the best evidence of decline comes from historical data from California, where the only locations where birds can still be found at sea are those areas adjacent to residual areas of old growth Redwood (*Sequoia sempervirens*) in the northern and central parts of the State (Ralph 1994).

Most information on population levels is based on two sorts of counts (i.e. at sea and in the forest) and for both, teams of biologists have established standard protocols (Ralph et al. 1994; Paton, 1995; Strong et al. 1995). These are, however, subject to considerable sampling variance and environmentally induced fluctuations and have been of limited utility to date in documenting long-term trends (Becker et al. 1997). Moreover given the presumed high annual survival rates of this species, even if there had been marked changes in demographic patterns of fecundity, it might be difficult to detect declines from counting. Another approach involves finding and observing nests (Hamer and Nelson 1995b), but sample sizes are still extremely small despite much effort. This tells us something of the breeding biology, but little about demographic changes or evidence for anthropogenic effects on the population.

We felt that a new approach was necessary, beyond counts and nest observations. To carry out a demographic study, it is essential, first, to catch and individually mark a large population, and second, to follow the breeding success of individuals within and between seasons. Even though this is a daunting task for a species as difficult to study as Marbled Murrelets, because of the potential conservation threats, we thought it to be of sufficient importance to try.

This seemingly impossible task for Marbled Murrelets may seem a foolhardy research project except for three recent innovations: (1) Development of a capture method. We use a floating mist-net technique (Kaiser et al. 1995) which allowed us to catch large numbers in the Desolation Sound Area, where many birds occur during the breeding season. More recently we have used a dip-netting technique whereby birds are collected from the open water at night using small boats. (2) In addition to studying the breeding biology by finding nests, we decided to concentrate on monitoring the physiological state of the birds in the nesting area during the breeding season by catching them in the inlets. Physiological and morphological changes would give us some indications of nesting phenology and should also enable us to determine breeding versus non-breeding status in the population. (We do not report on the

physiological aspects of the work here). (3) Recent developments in molecular methods for sexing birds from blood samples (Griffiths et al. 1996) allowed us to sex individuals, since in common with all seabirds, it is almost impossible to do this by morphological methods alone. The ability to know the sex of the individual birds allows many more demographic questions to be asked.

The objectives of this paper are to: (1) describe the approach we have taken to establish a demographic study of the Marbled Murrelet in British Columbia; (2) report on some of our early findings; and (3) to place these findings within the context of the many other research studies on this species.

## Methods

We chose the Desolation Sound area located in the Northern part of the Strait of Georgia, British Columbia, as the major study site because large numbers of Marbled Murrelets were known to be in the area during the breeding season and because of a history of studies on this species in this area (Kaiser et al. 1991; Mahon et al. 1992). Theodosia Inlet (50° 05' N, 124° 40' W) was chosen as our banding site because large numbers fly through this narrow (<200m) inlet during the dawn and dusk periods. We also chose an area of potential nesting habitat in the Bunster Range (within 30 km of the banding site) for a detailed nesting area study.

We used a series of floating mist nets comprising up to two arrays of three 18 m nets, which could be strung out across a large part of the inlet. The poles are inserted into a flotation device which is attached by rope to the shore and to an anchored buoy located beyond the nets from the shore line. A pulley system between the shore and the buoy allows the nets to be put in place from the shoreline. Nets are attended using small boats. This system is described in more detail in Kaiser et al. (1995). Nets were in place most evenings from 2100h to about 2315h (PDT) and most mornings from 0400h to 0630h from late May until mid August. In addition to processing all birds caught, we make a count of those birds seen flying over and around the nets, and record direction of flight of all birds.

Birds caught were weighed and measured for tarsus, culmen and wing chord. The presence or absence, and condition of a brood patch were recorded. Some birds received supplemental markers such as nasal disks, wing-tags and radios (Cooke et al. 1998). A small blood sample was taken for two major reasons. It provided samples of: (a) DNA to determine the sex of the birds using a modification of

the method described by Griffiths et al. (1996); and (b) blood proteins, enzymes and hormones, which might be useful in assisting us in determining the stage in the breeding cycle of the birds.

Nest finding was an essential, though not dominant focus of the research; it was required to provide a temporal framework for interpreting the information gathered from the birds in the inlet. We used two approaches for finding nests: (1) by attaching radio transmitters to birds caught on the inlet, we hoped to follow them to nest sites, thus not biasing the sample of nesting birds to locations and habitats where we suspected breeding; (2) by placing a field crew in the Bunster Range during and after the nesting period, we located birds as they visited specific nesting trees, which we later climbed to find actual nest sites.

The study began in 1994, though exploratory banding was carried out in 1991 and 1993. We document our findings from the banding data for the years 1994 through 1997. Other results are in the process of being reported elsewhere.

## Results

### Surveys

The only published documentation of population changes in British Columbia comes from at-sea surveys repeated several years apart (Kelson et al. 1995). They documented a decrease in numbers during the period. We have carried out at-sea surveys in the Desolation Sound area using standard techniques, but

**Table 1.** Comparisons of average numbers of all waterbirds ('All') and Marbled Murrelet ('MAMU') counts at Boundary Bay, British Columbia, 1980-81 (Savard 1988) and 1994-95 (Cooke 1996).

Month	1980/81		1994/95	
	All	MAMU	All	MAMU
Nov	6355	4	4010	0
Dec	5401	2	3142	0
Jan	3255	2	3354	0
Feb	2173	0	1370	0
May	675	11	2430	0
Jun	702	42	417	0
July	899	3	725	1
Aug	751	2	644	1
<b>Total</b>	<b>20211</b>	<b>66</b>	<b>16092</b>	<b>2</b>

have not yet enough years of data for useful comparisons. Thus our only evidence for population change comes from a different British Columbia population in the Strait of Georgia, that in Boundary Bay. Casual observations in this area showed Marbled Murrelet as a common bird in the region particularly during the summer.

We compared a published survey (Savard 1988), which documents all waterbirds seen along a 6 km stretch of shoreline between Crescent Beach and White Rock, British Columbia, in the winter of 1980-81, with a survey using similar methods carried out by volunteers from the White Rock and Surrey Naturalists in 1994-95 (Cooke 1996). Table 1 documents the average number of Marbled Murrelets relative to other water birds in the months when surveys were made in the respective years. There has been a highly significant decline in murrelets numbers between 1980 and 1995 relative to other waterbird species numbers in this region ( $\chi^2 = 78.9$ ;  $p < 0.001$ ). Subsequent counts in 1996 and 1997 showed that Marbled Murrelets continued to be very rare throughout the year in this area; in fact, no birds of this species were seen in either year. These findings are consistent with more casual observations made by naturalists in the area.

### Captures and recaptures

Table 2 documents the number of birds caught and recaptured in mist nets for each season up to 1997. Within season recaptures are not included. Years 1991 and 1993 were essentially experimental seasons when we developed the banding and capture techniques. Since 1994, we have been operating the station throughout the summer season, from late May until early August, coinciding with the period when Marbled Murrelets flew along the inlet. A full banding crew was present during this time and nets were operating whenever tide and weather permitted. Both evening and early morning banding sessions were carried out where possible. Roughly equal numbers were caught in each time period (Derocher et al. 1996). Of the birds caught, 84% (416 / 494) were captured as they flew out of the inlet in both morning and evening banding sessions; the rest were flying into the inlet. A slightly higher proportion of birds (90%, 2454/2852) detected by radar in 1996 and 1997 were flying out of the inlet. This difference is significant ( $\chi^2 = 10.06$ ,  $p < 0.01$ ). All birds caught were adults and all had brood patches, although late in the season most birds were showing signs of re-feathering.

**Table 2.** Numbers of Marbled Murrelets banded and recaptured by mist net in Theodosia Inlet, British Columbia, 1991-97. Within-year recaptures excluded.

Year banded	Number banded	Year recaptured					No. and (%) of cohort recaptured
		1993	1994	1995	1996	1997	
1991	21	0	0	1	0	2	3 (14)
1993	15		1	1	0	0	2 (13)
1994	173			7	4	9	20 (13)
1995	189				6	22	30 (15)
1996	95					5	5 (6)
1997	172						
<b>Total</b>	<b>665</b>		<b>1</b>	<b>9</b>	<b>10</b>	<b>38</b>	<b>58 (12)*</b>

\* Percentage excludes birds first banded in 1997.

### Sex ratios

One of the surprising features of the study was the finding of a highly skewed sex ratio among the birds which we caught (Table 3). There was no significant variation in this ratio throughout the banding period, nor any difference in the ratios in the morning and evening sessions (Vanderkist et al. 1999).

**Table 3.** Numbers of Marbled Murrelets of each sex in the samples of birds caught in mist nets at Theodosia Inlet, British Columbia, 1994-1997.

Year	Males	Females	Total	Sex ratio
1994	48	19	67	2.5:1
1995	80	42	122	1.9:1
1996	66	38	105	1.7:1
1997	121	69	190	1.8:1
<b>Total</b>	<b>275</b>	<b>153</b>	<b>428</b>	<b>1.8:1</b>

### Nests

One nest tree was found in 1994, 8 in 1995, 23 in 1996 and 30 in 1997, for a total of 62 nest trees, mostly in our main study area in the Bunster Range. Only the nest found in 1994 was located by attaching radio transmitters to the birds, although in 1998 we had great success with this approach. The others were found by visual detection during the season or by tree climbing later. Of these, 25% of the trees contained more than one nest, which suggests that they had been used for more than one breeding attempt, though not

necessarily in the same breeding season (Manley 1999).

### Discussion

This paper presents a few highlights of a systematic long-term study of a seabird species that has proven difficult for biologists to study. Our documentation of population declines in the Strait of Georgia is the only quantitative data available to our knowledge and emphasizes the conservation concern which has been expressed for this species. Although this count was made a considerable distance from the study site, it may be symptomatic of the Strait of Georgia as a whole. A bird banded at Desolation Sound in June 1995 was recaptured alive in the southern Georgia Basin in September 1996 (Beauchamp et al. 1999).

The development of a reliable capture technique has allowed us to examine a live sample of nesting birds. During the course of the study, 774 individuals have been captured and banded through the 1997 breeding season. Most of these ( $n=655$ ) were in mist nets but 109 birds were caught by dip netting. This demonstrates that we are able to sample large numbers of murrelets for study purposes without resorting to the collection of dead specimens, a procedure formerly used widely (e.g., Sealy 1974) but no longer acceptable considering the threatened status of the species.

Assuming brood patches are an indication of breeding status (Sealy 1974), then all the birds caught were breeders. It seems unlikely that all the birds occurring in a region during the summer would be breeding birds, given the fact that all known species of

Alcidae have delayed sexual maturity (Nettleship 1996) and Sealy (1974) reported non-breeders in his sample. Since our nets intercept mainly birds flying between forest and inlet, this strongly suggests that only breeding birds enter and leave the forests during the summer. Most birds were caught while leaving the forest rather than entering it, since most were caught flying in a seaward direction. Since as many birds must enter the forest as leave it, this would again suggest that we are catching birds non-randomly. Birds detected flying over and around the nets, either by sound, sight or radar showed a similar strong bias towards flying in a seaward direction, which suggests that different routes may be used on the inward and outward trips. An alternative suggestion is that birds fly at different heights in the two directions. The dynamics of flight may cause the birds entering the forest to fly at a higher flight altitude than those leaving. A lower altitude would allow greater opportunity for us to catch them. This explanation however is inconsistent with our finding that a significantly higher proportion of birds in our radar sample, which includes many birds which flew over the net, were flying out of the inlet compared to our mist net sample.

Around 12% of the Marbled Murrelets caught in the years 1994 through 1997 were birds banded in a previous year. This demonstrates for the first time that known individuals use the same area of inlet over a period of years. Although capture-mark-recapture (CMR) methods are typically the means used to determine patterns of fidelity to specific sites, difficulties associated with catching Marbled Murrelets and locating their nests have hitherto precluded using this approach. This fidelity to the region of Theodosia Inlet supports the idea that Marbled Murrelets are philopatric to their breeding areas and the high local survival estimate calculated (see below) also supports that. Divoky and Horton (1995) summarized what is known about breeding philopatry (i.e. the return of individual birds to locations used in a previous season) in Marbled Murrelets. Evidence came solely from the occasional re-use of nest sites in subsequent years. However, identities of the individuals were not ascertained and although re-use suggests that the same birds are using their nest sites of a previous year, there was no direct evidence. Indeed, if nest sites are limiting, as several authors have argued (e.g., Burger 1995; Hamer and Nelson 1995), perhaps prime nest sites are always in demand and are likely to be re-occupied not necessarily by the same birds as in previous seasons.

Despite the lack of direct evidence, Divoky and Horton (1995) argued that nest-site tenacity may be lower in Marbled Murrelets than in most other alcids. The habit of nesting in trees would liberate this species from the need to have high nest-site fidelity (in contrast to other alcids) unless the number of suitable trees and platforms becomes very limited, as likely has happened in some parts of its range.

The frequency of recaptured birds is high enough to calculate at least a preliminary local survival rate. A value of 85% was calculated (Cooke et al. 1998; S. Loughheed, unpublished data), but there are wide confidence limits on this value. Nevertheless it is close to that assumed by Beissinger (1995) based solely on a comparison with the body masses of other alcids. More years of data are necessary before more reliable survival estimates can be calculated.

The recapture data also provide us with a longevity record for Marbled Murrelets of at least 7 years. Two birds caught in 1991 as adults were recaptured in 1997. If we assume delayed breeding in this species, then these birds must be at least 8 years old. As banding continues it is likely that these records will soon be broken.

Despite the presence of recaptured birds in our banding samples of 1994-1997, the number of recaptures is relatively low, about 12% of those banded prior to 1997. We can think of at least two possible non-exclusive explanations for this. We may be sampling from a relatively large population; or birds may learn to avoid the area where the mist-netting occurs if they have some long-term memory of the initial capture (trap shyness). At present it is impossible to differentiate between these possibilities.

The almost 2:1 sex ratio in favour of males was a complete surprise to us. It seems unlikely that the population sex ratio would be so heavily skewed towards males, but this cannot be ruled out. We have every confidence in the method for assigning sex so it seems more realistic to imagine that some form of capture bias explains the unusual result. The pattern was the same in all four seasons and there was no evidence of changes in sex ratio at different parts of the breeding sequence. Nets were placed across the inlet only in late May, at a time which coincided with the first observations of murrelets flying into the inlets. This also coincides with the onset of the nestling stage of the life cycle (Hamer and Nelson 1995b), and so we assume that most of the birds caught are actively feeding young at the nest. Several birds were carrying fish on capture. One possible explanation for the sex ratio bias is that males feed the chicks more than the



females. Observations at the nest (Nelson and Harner 1995) show that birds differ individually in plumage, but there has been no indication as to the sex of the visiting birds. There is also no evidence that one parent feeds more than another. At present this finding is a puzzle for which we have no explanation. We are continuing to examine this question, using other methods of sampling.

The information on the nesting birds was presented elsewhere (Manley 1999) but is included here briefly to provide an overview of all aspects of the project. Ultimately, we need to relate our knowledge of birds in the forests to what we can discover from their behaviour at sea. By piecing together information on different aspects of the behaviour of the birds during the summer months, we can slowly learn more about this elusive species.

## Overview and future directions

The above findings show the value of long term studies of individually marked birds. Such studies provide the essential framework for detailed demographic data collection. This is fundamental to an understanding of the demographic and environmental causes of population changes, and is the most effective way of pointing to conservation solutions. There are still many gaps in our knowledge however. Most of the birds caught in the mist nets are well advanced in their nesting cycle. Incubation probably begins in British Columbia in April, and we do not catch birds until late in May. The recently developed technique of dip-netting birds can be carried out at all times of year and will allow a more thorough understanding of the egg-laying and incubation period. It will also allow the capture of juvenile birds which could then provide insight into the crucial recruitment stage of the life cycle. Radio telemetry provides an additional tool for tracking incubating birds back to the nest locations, and any nests found in this way will not be subject to the biases due to expectations of where the observer thinks the nests ought to be. Radios will also allow juvenile birds to be followed after first arrival on the inlets from the nests, and will allow a more reliable estimate of nesting success. To date, one of the problems in estimating fledging success is that late fledging juveniles are easily confused with adults which undergo their pre-alternate body moult soon after nesting is finished.

Physiological approaches are valuable additions to the standard ecological approaches to studying the breeding biology. The use of blood sampling to

measure hormonal state and the existence of egg proteins should be useful not only to discover the timing of nesting events from birds captured away from the nesting sites, but also may give an indication of the frequency of non-breeding and the age of first breeding. These demographic parameters are currently unknown in Marbled Murrelets and indeed in most alcids.

A long-term, capture-mark-recapture (CMR) data set is essential for determining survival, longevity and recruitment. The data we have collected to date provides a solid beginning for the calculation of these, but more years are needed before we can obtain reasonably precise measures of these fundamental life history parameters as well as provide evidence for their annual variation. Only with many more years of data can we hope to understand the factors which influence the murrelets, information which is necessary for wise conservation action.

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# Evaluating uncertainty in estimating population trends of Marbled Murrelets

John Boulanger, Kathy Martin, Gary Kaiser,  
Andrew E. Derocher

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## Abstract

We used a mathematical matrix model to explore life history strategies and evaluate conservation measures for the Marbled Murrelet (*Brachyramphus marmoratus*), a threatened seabird species. Demographic parameter estimates for Marbled Murrelets are crude, but existing data and allometric comparisons with other seabirds suggest that both productivity and adult survival are low. This combination of low parameter values is not possible if populations are to maintain stability. As a result, we examine two possible alternative life history scenarios (high survival and high productivity) which represent the extremes of plausible murrelet parameter values. For both life history scenarios we used a matrix model to conduct sensitivity analyses of life history parameters. We found that regardless of life history scenario, murrelet populations are very sensitive to changes in adult survival, and less sensitive to juvenile survival and productivity. This leads us to conclude that reduction in adult survival may constitute the most immediate threat to murrelet populations even if habitat loss is the most significant long-term factor affecting conservation. Our power analyses show that only large reductions (20% reduction in adult survival, > 50% reduction in productivity) in individual parameters would be detected in 10 years by current monitoring techniques. Results of recent field studies document lower power of most census monitoring methods. We suggest that more emphasis be placed on obtaining estimates of adult survival and easily obtained measures of productivity such as juvenile/adult ratios using recently refined field techniques. Given low power to detect population changes using current methods, managers and policy-makers must implement active conservation strategies before researchers can detect population declines statistically and fully document the causes.

## Résumé

Nous avons utilisé un modèle mathématique matriciel pour explorer les stratégies d'histoire naturelle et évaluer les mesures de conservation de l'Alque marbré (*Brachyramphus marmoratus*), une espèce d'oiseau de mer menacée. Les estimés des paramètres démographiques de l'Alque marbré sont grossiers. Cependant, les données disponibles et les comparaisons allométriques avec les autres espèces d'oiseaux de mer suggèrent que la productivité et la survie des adultes sont faibles. Cette combinaison de faible productivité et survie n'est pas possible si une population doit demeurer stable. C'est pourquoi nous examinons deux scénarios alternatifs (survie élevée et productivité élevée) qui représentent les extrêmes plausibles des paramètres démographiques de l'Alque marbré. Pour ces deux scénarios, nous utilisons un modèle matriciel pour conduire des analyses de robustesse des paramètres démographiques. Nous avons démontré que, indépendamment du scénario d'histoire naturelle, les populations d'Alques sont très sensibles aux variations dans le taux de survie des adultes, et moins sensibles au taux de survie des juvéniles et au taux de productivité. Ceci nous amène à conclure que la réduction dans le taux de survie des adultes pourrait constituer la menace la plus immédiate aux populations d'Alques, même si la perte d'habitats est le facteur le plus significatif affectant la conservation à long terme. Notre analyse de puissance démontre que seules des réductions importantes (20% dans le taux de survie, >50% dans la productivité) dans les paramètres démographiques pourraient être détectées en 10 ans avec nos techniques actuelles de suivi. Les résultats d'études de terrain récentes documentent une puissance même plus réduite pour la plupart des méthodes de suivi. Nous suggérons que plus d'emphasis devrait être mise à obtenir des estimés de taux de survie des adultes de même que des mesures simples de productivité telles que les ratios juvéniles/adultes en utilisant quelques techniques de terrain récemment développées. Vu la faible puissance des méthodes actuelles à détecter des changements

de population, les gestionnaires doivent implanter des stratégies proactives de conservation bien avant que les chercheurs ne puissent détecter statistiquement des déclins et en documenter les causes.

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**John Boulanger**, Integrated Ecological Research, 924 Innes Street, Nelson, British Columbia, Canada V1L 5T2 ([boulange@ecological.bc.ca](mailto:boulange@ecological.bc.ca)); **Kathy Martin**, Centre for Applied Conservation Biology, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4, and Canadian Wildlife Service, 5421 Robertson Road RR1, Delta, British Columbia, Canada V4K 3N2; **Gary Kaiser**, Canadian Wildlife Service, 5421 Robertson Road RR1, Delta, British Columbia, Canada V4K 3N2; **Andrew E. Derocher**, British Columbia Ministry of Forests, 2100 Labieux Road, Nanaimo, British Columbia, Canada V9T 6E9 (Current address: Norwegian Polar Institute, Storgt. 25, Box 399, N-9001, Tromsø, Norway).

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## Introduction

Uncertainty about population size and life history attributes of rare or cryptic species is a common problem in conservation biology. Failure to confront uncertainty regarding population dynamics, and the low power of monitoring strategies to detect changes in population trends, have been used to forestall management decisions, sometimes leading to disastrous population declines of cryptic species (Ludwig et al. 1993). Evaluation of conservation strategies using theoretical methods such as matrix models and power analysis have been restricted mainly to species for which solid data exist as a result of large investments in field research (Crouse et al. 1987; Lande 1988; Caswell 1989; Taylor and Gerrodette 1993). However, for many cryptic species there are insufficient data to allow precise parameter estimates, and as a result little effort has been directed at understanding population dynamics using the rigorous framework of a population model. Furthermore, little attempt has been made to determine the ability of monitoring methods to detect declines (but see Thomas and Martin 1996).

This study focuses on the Marbled Murrelet (*Brachyramphus marmoratus*), a Pacific seabird (Alcidae) that nests in coastal old-growth temperate forests from California to Alaska. Populations of Marbled Murrelets face negative impacts from the extensive loss and fragmentation of old-growth forests as well as oil spills, fishing mortality, and other anthropogenic disturbances. Because of these and related concerns, the Marbled Murrelet was designated as a threatened species in Canada (Rodway 1990; Rodway et al. 1992) and in California, Oregon, and Washington in the United States (Carter and Morrison 1992; Nelson and Hamer 1995; Ralph et al. 1995). The world population size of Marbled Murrelets has

been estimated at about 287,000 - 300,000 individuals, with most (approximately 220,900) in Alaska (Ralph et al. 1995). A significant number of the remaining Marbled Murrelets breed in British Columbia.

Despite the Marbled Murrelet being a high priority species for conservation, many basic life history details required for effective management are poorly known. Because Marbled Murrelets nest high in the inner branches (next to the tree trunk) of coastal conifers (except in some northern Alaska populations), their nests are very difficult to locate. Summaries of breeding information and suspected nesting activities for British Columbia were given by Sealy (1974). The first active nest for British Columbia was located in 1993 (Jones 1993). Thus, estimation of productivity parameters has been very difficult. High spatial variability in at-sea distributions has also hampered estimation of survival rates and related population parameters (Ralph et al. 1995). Improved statistical techniques for estimating productivity from juvenile/adult ratios, and advances in techniques in mist-netting and radio telemetry (Kaiser et al. 1995; Becker et al. 1997; Kuletz and Kendall 1998; Cooke 1999) offer new insights into murrelet life history. However, it appears unlikely that sufficient information will be collected to estimate precisely murrelet population status before substantial declines have occurred in most of the southern part of its distribution (Rodway et al. 1992; Ralph et al. 1995).

Adult and juvenile survival of Marbled Murrelets are unknown. Features of their breeding biology such as crepuscular nest attendance, cryptic plumage, and open nests high in trees suggests that murrelets have low survival and attempt to avoid high predation risks (Nelson and Hamer 1995). Marbled Murrelets have low potential productivity (1 egg per clutch, no evidence of reneesting) and apparently high loss of

young during incubation and after fledging (DeSanto and Nelson 1995; Nelson and Hamer 1995). Low observed juvenile/adult ratios of Marbled Murrelets at sea also suggest low productivity (Beissinger 1995). In contrast, other seabird species of similar body mass (guillemot *Cepphus*) and other murrelet species (*Synthliboramphus* sp.) produce two eggs per clutch and nest on islands or in colonies that are less vulnerable to predators. Larger alcid species such as murres (*Uria*) and Razorbill (*Alca torda*) produce one egg, but appear to compensate for low fecundity with effective breeding strategies and unusually high annual adult survival (Hudson 1985). Overall, allometric comparisons of Marbled Murrelets with other piscivorous seabirds suggest that Marbled Murrelets show lower productivity and possibly lower survival rates when compared to similar sized alcids (DeSanto and Nelson 1995).

The apparently unlikely combination of low fecundity and low adult survival has caused some authors to argue that murrelets must have higher survival than similar-sized alcids to maintain stable populations (Rodway et al. 1992; Ralph et al. 1995). Alternatively, murrelets may have higher productivity than estimated by juvenile/adult ratios or direct estimates of nesting success (DeSanto and Nelson 1995; Ralph et al. 1995). In a demographic analysis of Marbled Murrelet populations, Beissinger (1995) compiled data from a research compendium (Ralph et al. 1995) to provide likely population parameter estimates. Using a matrix model, he concluded that murrelets were declining annually by 2-12 percent. However, he did not discuss the limitations on detecting population trends given the uncertainty about the input values available and the difficulty of making inferences without power analyses when using data from available monitoring methods.

In this paper we use a mathematical matrix model coupled with statistical power analysis to evaluate current monitoring strategies used for Marbled Murrelets. We conduct sensitivity analysis of several life history parameters to compare the relative effects of individual parameter change on population trajectories. We simulate hypothetical population declines, and test the power of current methods to detect these declines. Each analysis is conducted for two opposing life history scenarios which represent the extremes of plausible life history parameter values. Using this approach we determine the robustness of sensitivity and power analyses across a full range of plausible parameter values. Unlike the demographic study of Marbled Murrelets by Beissinger (1995), we

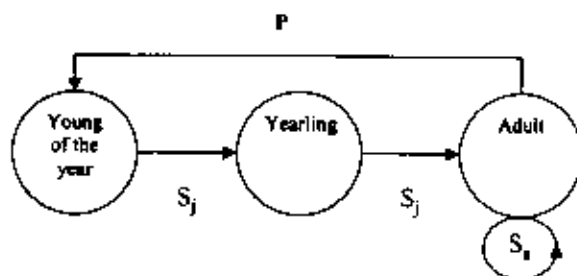
do not attempt to predict actual population trends. Instead, we focus on determining optimal strategies for future research and monitoring programs.

## Methods

### Population model and sensitivity analyses

To aid in the conceptual process of exploring murrelet population dynamics we constructed a stage-based matrix model (Caswell 1989). The parameters of the matrix model and the life cycle model of Marbled Murrelets are shown in Figure 1 and a mathematical description of the model is given in Appendix 1. By calculating the dominant eigenvalue ( $\lambda$ ) from the matrix we can determine the future population trajectory for a set of population parameters. If the population is stable,  $\lambda$  equals one over time (if decreasing,  $\lambda < 1$  and if increasing,  $\lambda > 1$ ; Caswell 1989). We used sensitivity analysis to investigate the relative importance of each life history parameter in maintaining murrelet populations. In each analysis we started with parameter combinations that maintained a stable population ( $\lambda = 1$ ), then decreased a given parameter by percentage increments while holding the others constant, and recorded the response of  $\lambda$ . To evaluate the sensitivity of juvenile/adult ratios to changes in population and life history parameters, we simulated population declines and calculated corresponding juvenile/adult ratios from the model (Appendix 1).

Figure 1. A life cycle diagram for the Marbled Murrelet for age of first breeding at 2 yrs. Note that this life history diagram pertains to a population in which a post-breeding census is conducted.  $S_j$ =survival from first fall census to 2 years of age.  $S_a$ =adult survival,  $P$ =productivity.



Some assumptions apply to this matrix model. First, the model considers only females, and assumes an even sex ratio and that breeding age females always find mates (Sealy 1975). Second, the population is

censused in the fall after breeding. Third, the population is at equilibrium, i.e. always has a stable age structure. Fourth, the model is linear with no density-dependent effects. Finally, we assume there is no senescence.

### Marbled Murrelet life history parameters

We define adult survival as the annual probability that an individual murrelet (aged  $\geq 2$  years) will survive to the next age class. Most inference about murrelet survival has been through allometric comparison with other alcid species. Adult survival was estimated at 0.845 (95% CI: 0.81-0.88) by Beissinger (1995) and at 0.83 by DeSanto and Nelson (1995). Recently, a mark-recapture study in Desolation Sound, British Columbia, produced an adult survival rate estimate of 0.85 (95% confidence interval: 0.47 to 0.97; Loughheed et al. 1998).

We define juvenile survival as the annual probability that a fledgling will survive its first two years of life. Beissinger (1995) estimated that Marbled Murrelets survive at 70% of adult survival in their first year of life and at 88% in their second. To keep our model simple, we compressed pre-breeding survival into one parameter by taking the geometric mean of 0.88 and 0.70. Juvenile survival was then calculated by multiplying this value (0.78) by the adult survival for each simulation.

We define productivity as the proportion of breeding age females that produce one female offspring that survives to the census period. Estimates of murrelet productivity have been derived from two sources: observed nesting success and juvenile/adult ratios of murrelets observed at sea.

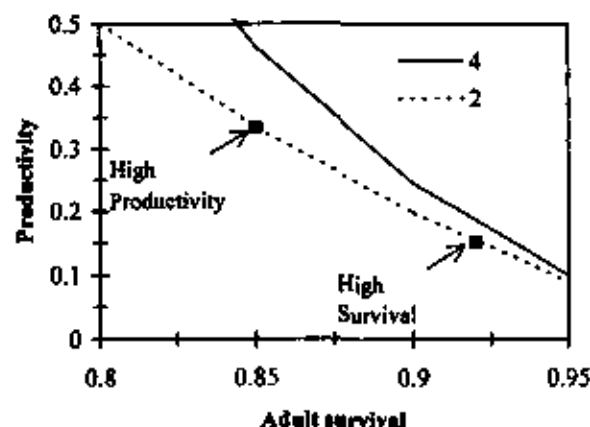
Murrelet productivity can be estimated by the percent of murrelet nests that fledge young. Nelson and Hamer (1995) calculate that 28% of 32 murrelet nests produced young. Since their analysis, 83 nests have been found in British Columbia, which will allow a better productivity estimate. For the matrix model, this yields an estimated productivity of 0.17 if half of the fledglings are female, but this value does not account for mortality during the actual fledging event or in the subsequent winter.

Beissinger (1995) used cumulative sightings of juvenile/adult ratios at sea to obtain a post-breeding season estimate of productivity. By averaging juvenile/adult ratios from different studies in the United States, productivity was estimated at 5%, with some estimates as high as 10%. Assuming an equal sex ratio, this estimate of productivity describes the

percentage of breeding females that produced one female offspring at the end of a breeding season.

Productivity is also influenced by age of first breeding. In alcids this ranges from 2-15 years (Hudson 1985; Gaston 1992; Harris et al. 1994). Given the low productivity, and possible low annual survival of Marbled Murrelets (as estimated from body mass), it seems plausible they have an early age of first breeding. Therefore, we set age of first breeding at 2 years. Later ages of first breeding (e.g., 4 years) require higher survival and/or productivity parameter values to maintain population stability (Figure 2).

**Figure 2.** Combinations of adult survival and productivity resulting in a stable population conducted for ages of first breeding of 2 (solid line) and 4 years (dashed line). Labeled points are the parameter values in which we conducted our analysis. The survival and productivity values proposed by Beissinger (1995) are displayed in the labeled box.



### Marbled Murrelet life history scenarios

We focus our analysis on two alternative life history scenarios with parameter values that maintain a stable population (Figure 2). In the first "high productivity" scenario we consider that productivity could be higher than estimated by juvenile/adult ratios or nest success (DeSanto and Nelson 1995; Ralph et al. 1995). With this scenario, adult survival falls within the range suggested for other alcid species. In the second "high survival" scenario, adults have higher survival than suggested by their body size (Beissinger 1995; Ralph et al. 1995). This scenario is most plausible if current juvenile/adult ratios and estimated nesting success reflect true productivity. With this scenario adult

survival is similar to other longer-lived alcid species such as the razorbill which also have low fecundity (DeSanto and Nelson 1995).

### Evaluation of at-sea surveys using power analysis

The main method for evaluating overall population status of murrelets is at-sea surveys or line transect counts (Strong et al. 1995). The power analysis we used is for regression analysis of population trends. The parameters for this model are: the number of annual surveys conducted, coefficient of variation (CV) of yearly surveys, the level, and true rate of change of population each year (Gerrodette 1987; Taylor and Gerrodette 1993). We considered a power level of 0.8 to be adequate to detect a population decline (Cohen 1988) and used an level (probability of Type I error) of 0.05 for our analysis.

Gerrodette's power calculation makes some restrictive assumptions. First, the population being monitored follows an exponential model of population decrease. Second, line transect or similar sighting per unit effort technique is used for population monitoring. Third, the CV input parameter takes into account variation due to demographic stochasticity as well as sampling variance. The model used for the power analysis accounts for change in coefficient of variation with decreasing abundance of animals being surveyed so that only an initial coefficient of variation is needed for the analysis. Coefficient of variations were calculated from 7 replicated strip transects at sea along the coast of Oregon during 1992 and 1993 (Strong et al. 1995). Data were used from transects that were replicated at least 4 times and as many as 13 times for coefficient of variation calculation. The mean coefficient of variation from these transects was 0.57 (range: 0.31-0.84).

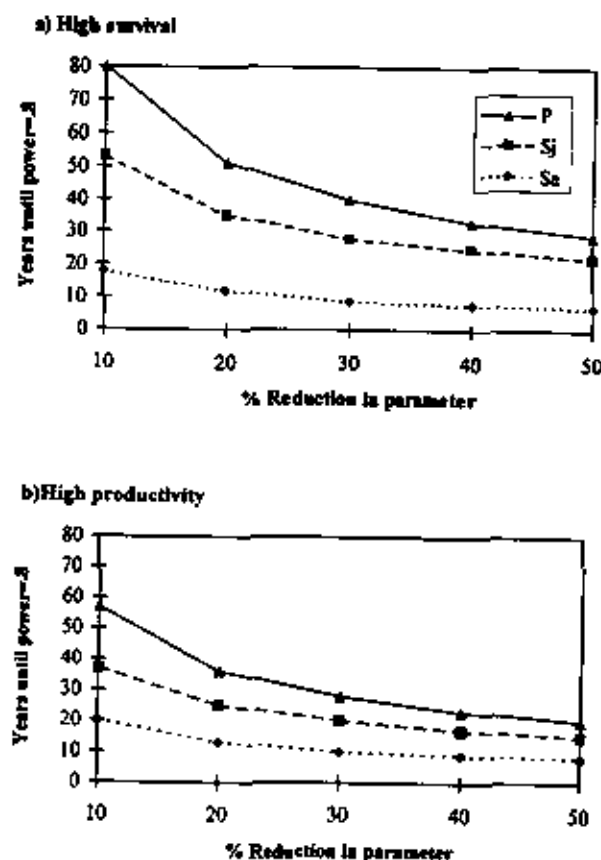
We feel this simplistic power model is the most parsimonious approach given the requirements for data of more complicated simulation methods. Gerrodette's power estimate ignores the statistical problems created by non-independence of points when linear regression is used to analyze time series data and as a result power will always be overestimated using this routine (Gerrodette 1987; Gerrodette 1991; Link and Hatfield 1990; Taylor and Gerrodette 1993). Therefore, the results of this analysis are an estimate of relative rather than absolute statistical power.

## Results and Discussion

### Sensitivity analysis

Sensitivity analysis suggests that regardless of life history scenario, murrelet populations are most influenced by changes in adult survival, followed by juvenile survival and productivity (Figure 3).

Figure 3. Results of sensitivity analysis of high survival(a) and high productivity (b) scenarios.  $\blacktriangle$  Productivity (P),  $\blacksquare$  Juvenile survival ( $S_j$ ),  $\blacklozenge$  Adult Survival ( $S_a$ ).



### Adult Survival

High model sensitivity to adult survival is of great conservation concern given the potential impacts of gill-net fishing by-catch and oil spills on murrelets (Carter and Kuletz 1995; Carter et al. 1995). Marbled Murrelets have the highest oil vulnerability index of birds in the Alaska region (King and Sanger 1979). Carter and Sealy (1984) estimated that 7.8% of the fall population of murrelets were killed in 1980 in Barkley Sound in fishing nets. If this type of mortality reduces



adult survival even slightly, it will result in a rapid population decline. A mark-recapture study in Desolation Sound which uses newly-developed mist-net and dip-net capture techniques recently produced an adult survival rate estimate of 0.845 (95% confidence intervals 0.47 to 0.94; Kaiser et al. 1995, Loughheed et al. 1998, F. Cooke submitted). This estimate is based on four sampling sessions (conducted yearly from 1994-1997) and therefore precision is low due to low numbers of recaptures. Future estimates from this project should provide critical information regarding survival rates as the sample size of marked birds and corresponding precision of estimates increases (Loughheed et al. 1998).

### Juvenile survival

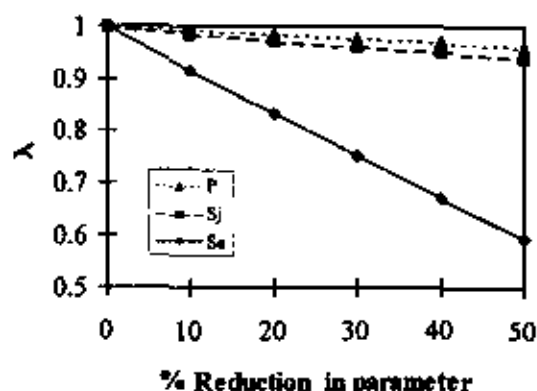
In both life history scenarios, the model showed relatively low sensitivity to juvenile survival (Figure 3). However, this might be an artifact of the assumption that juvenile survival is directly proportional to adult survival. This assumption may be valid if adults and juveniles congregate in similar areas and are vulnerable to the same mortality sources and experience mortality factors similar to other alcids. Hudson (1985) commented that juvenile survival could represent a "bottleneck" in population dynamics and affect population trends more than shown by sensitivity analysis.

### Productivity

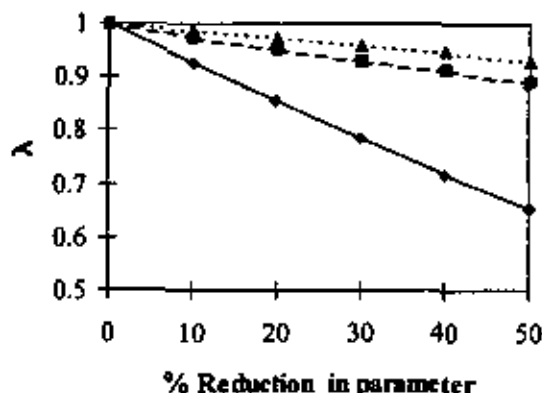
Productivity is of great interest in Marbled Murrelet population dynamics given the wide scale removal of old-growth forests. Low model sensitivity to productivity may suggest that murrelet populations are adapted to a breeding strategy dependent on yearly food resources where high variation in productivity might have minimal population effects. Murrelet populations therefore may not show immediate detectable effects of reduction in productivity given that the natural variation in this parameter will minimize power to determine any type of downward trend. Possibly murrelets, like other seabirds, exhibit high temporal variation in productivity. For instance, in a 12-year period Common Murre pairs produced an average of 0.86 young per season, but this value varied from 0.10 to 0.96 (Boekelheide et al. 1990). Current estimates of murrelet productivity could be negatively biased because the data were collected in El Niño years (Ralph et al. 1995) in which other alcids had low reproductive success (Boekelheide et al. 1990).

**Figure 4.** Results of power analysis, based on line transect surveys documented by Strong et al. (1995), for high survival (a) and high productivity (b) scenarios. The y-axis represents the number of years it would take to statistically detect a population decrease resulting from a percentage reduction in a given parameter.  $\blacktriangle$  Productivity (P),  $\blacksquare$  Juvenile survival ( $S_j$ ),  $\blacklozenge$  Adult Survival ( $S_a$ ).

#### a) High survival



#### b) High productivity



### Evaluation of monitoring methods

#### Power analysis of population surveys

Power analysis of at-sea survey data reflects the difficulty in detecting statistically significant declines in populations based upon current monitoring methods (Figure 4). With high productivity, it took less time to detect decreases in population due to productivity as opposed to the high survival scenario. However, even with the high productivity scenario it still took six times as long to detect the decline in population based

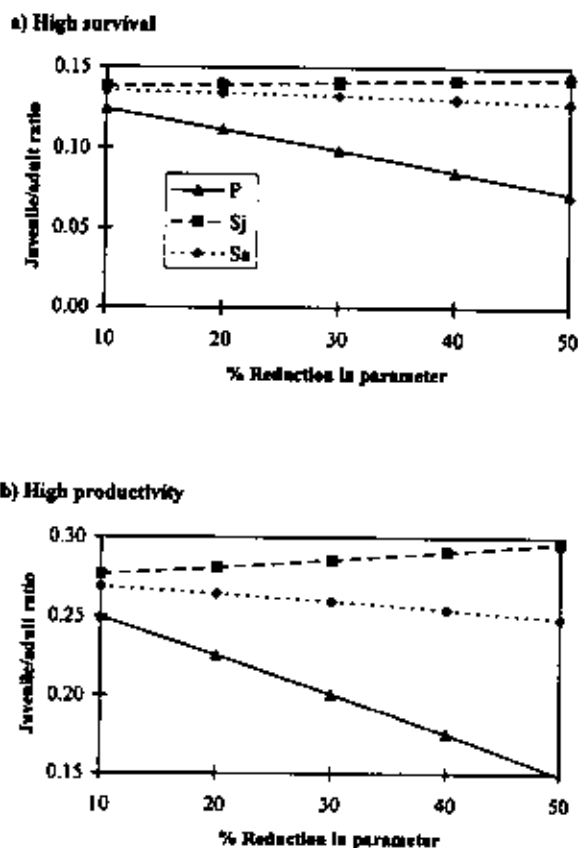
on a productivity decline of 10%. This finding suggests that only comparatively large changes in productivity might be detectable with present survey methods. With high productivity and high survival scenarios, the population decreased by an average of 68% and 72%, respectively, before the power to detect the decline reached 0.8 when parameters were individually reduced by 10%. Results from power analysis suggest that only the most rigorous, replicated surveys will be able to detect population declines. To increase power of detection researchers can increase the number of yearly surveys (increase precision) or increase the level in the analysis. We found that with surveys that had a CV of 0.2, it would take ten years to detect a population decline caused by a 10% decrease in adult survival.

The observed CV from strip transect surveys of Strong et al. (1995) used in this exercise was 0.57 (range: 0.31-0.84) which reflects the current range of survey values. A recent study by Becker et al. (1997) tested the power of line transect methods (Buckland et al. 1993) used in at-sea surveys to detect population declines. Using data from line transect surveys Becker et al. (1997) found they could detect annual population declines of 9% over 10 years with an estimated power of 0.8 ( $\approx 0.1$ ) if areas were sampled at least 5 times per year using line transects. Note that a 9% annual decline would compound to a 57% total population decline over a 10-year period. Becker et al. (1997) did not publish CV estimates for line transect results; they used a Monte Carlo simulation based power analysis method (Gibbs 1995) which is more conservative than the power analysis method of Gerrodette (1987) used in this study (Link et al. 1990). The study of Becker et al. (1997) was conducted on a relatively straight section of coastline in California and it is questionable whether similar levels of precision could be attained in the more complex fjords and inlets in British Columbia and further north. We conclude that given present monitoring techniques, populations will be reduced significantly before a statistically significant decline is detected.

### Monitoring of productivity

The sensitivity of detecting a population decline using juvenile/adult ratios was responsive only to changes in productivity (Figure 5). Juvenile/adult ratio was stable or increased slightly during simulations of population decline caused by reduced adult or juvenile survival. When less substantial decreases in population size were simulated (lower sensitivity of the model to

**Figure 5.** Changes in juvenile/adult ratios resulting from reductions in individual parameter values for the high survival (a) and high productivity (b) scenarios.  $\blacktriangle$  Productivity (P),  $\blacksquare$  Juvenile survival ( $S_j$ ),  $\blacklozenge$  Adult Survival ( $S_a$ ).



productivity), juvenile/adult ratio declined by 0.08.

Monitoring of annual variation in productivity could provide valuable insight into whether murrelets show a typical alcid pattern of high variation in productivity (Boekelheide et al. 1990). Results from a recent study in Alaska by Kuletz and Kendall (1998) suggest that juvenile density estimates with lowered coefficients of variation (mean CV=0.42, range 0.17-0.86) can be obtained by identification of core survey periods in which juvenile densities are highest. Kuletz and Kendall conducted power analysis using the same methods of Gerrodette (1987) that were used in this study. Using the lower estimated CV range of 0.17 to 0.42, they could detect total declines of 24% and 50%, respectively, in juvenile abundance in 10 years with an estimated power of 0.8 (at  $\approx 0.1$ ) when 5 surveys were conducted each year. This level of power is higher than that documented by Becker et al. (1997);

however, this may be due partly to potential positive biases with the Gerrodette (1987) method of power calculation as discussed previously in this paper (Link et al. 1990). Using these data Kuletz and Kendall (1998) developed an index of regional productivity based on the slope of paired juvenile and adult abundance estimates. The study of Kuletz and Kendall (1998) was conducted in fjords and inlets and therefore this technique may be more easily applied than the methods of Becker et al. (1997) to Marbled Murrelet populations in British Columbia and farther north. We conclude that monitoring juvenile/adult ratios or monitoring of juvenile density using methods similar to Kuletz and Kendall (1998) may be the best way to monitor and evaluate temporal and spatial variation in productivity.

### Effect of uncertainty regarding life history strategies

It is important that researchers conducting demographic analyses account for the effects of uncertainty in parameters on calculation of population trajectories. In his demographic analysis of Marbled Murrelets, Beissinger (1995) used an adult survival value (estimated from other alcids) of 0.85 (confidence limits 0.81-0.88) for his demographic analysis to conclude that murrelet populations were declining from between 2 and 12 percent. Given high sensitivity of the model to adult survival values, even a small change in adult survival, well within the confidence limits estimated for this parameter, would drastically affect the calculated population change. It is our opinion that estimation of population decline rates based on models will be valid for murrelets only when more information is known about adult survival values.

### Optimal Management and Research Strategies

We suggest that matrix modeling and power analysis can be used as design tools even in situations where data are sparse for the species in question. Power analysis computer software packages are now available to facilitate this process (Thomas and Krebs 1997). From our study we conclude that regardless of life history parameter assumptions, adult survival will most significantly affect the overall population trajectory and may influence detection of changes in other parameters. Low model sensitivity, and evidence from seabird species that are suspected to have similar life histories, suggest that Marbled Murrelets may show high temporal variability in productivity. Given

this constraint, and the low power of monitoring methods, it will be difficult to document statistically immediate declines in population size based on small decreases in this parameter.

We suggest that future work be focused on estimation of survival parameters such as is currently being conducted in British Columbia (Lougheed et al. 1998, Cooke 1999). More effort should also be directed at documenting the variability in productivity by developing better statistical methods to detect changes in populations using available and improved monitoring programs (Thomas 1996; Becker et al. 1997; Kuletz and Kendall 1998). Most importantly, the wider effort to confront uncertainty should include caution in management integrated with a diverse conservation program that considers a number of promising research directions and efforts to improve existing monitoring programs.

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## APPENDIX 1

The matrix model we used is described mathematically by the population vector:

$N_0$  - number of fledged young during a breeding season

$N_1$  - number of murrelets from the  $N_0$  cohort that survive to the  $N_1$  cohort

$N_2$  - number of murrelets in the  $N_2$  and above cohort

The form of the model for a population in which a post-breeding census is conducted (with an age of first breeding of 2 years) in matrix form is:

$$\begin{bmatrix} N_0 \\ N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & P \\ S_j & 0 & 0 \\ 0 & S_j & S_a \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \end{bmatrix}_t$$

This type of population matrix model is defined as a stage matrix. It differs from the fundamental Leslie matrix (Leslie 1945) in that each "stage" may represent an age class, or a general class (such as  $N_2$  which represents adult birds). Because this matrix is primitive,  $\lambda$  can be found by raising the matrix to successive powers and calculating the ratio of  $N_{t+1}/N_t$  (to the point of convergence) to determine  $\lambda$ . Also at the point of convergence the ratios of stage classes in the population vector that form a stable age distribution can be determined. The juvenile/adult ratio was calculated as:

$$J/A \text{ ratio} = \frac{N_0}{N_1 + N_2}$$

The stage-based matrix model method is documented in Caswell (1989) and Crouse et al. (1987).

# Selected studies of forestry and bird communities in Nova Scotia and New Brunswick

**Bill Freedman and Greg Johnson**

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## Abstract

Forestry practices can cause intense disturbances, which result in dramatic changes in the habitats available to support all elements of biodiversity, including birds. Many species of birds require mature and older forests as habitat for breeding, migratory movements, or wintering; some also use habitats occurring during earlier stages of forest succession, including those created through such forestry activities as clearcutting. We summarise results of several research projects which have examined the effects of various harvesting systems, plantation establishment, and silvicultural herbicide spraying in Nova Scotia and New Brunswick.

## Résumé

Les pratiques forestières peuvent causer de grandes perturbations qui résultent en des changements dramatiques dans la disponibilité des habitats nécessaires pour supporter tous les éléments de la biodiversité, incluant les oiseaux. Plusieurs espèces d'oiseaux ont besoin de forêts matures et anciennes comme habitat de nidification, d'hivernage et de déplacements migratoires; certaines espèces utilisent les habitats reliés aux stades de succession de la forêt, incluant les habitats créés à l'aide de pratiques forestières telles que la coupe à blanc. Nous résumons plusieurs projets de recherche qui ont examiné les effets de divers systèmes d'exploitation forestière, d'établissement de plantations et d'application d'herbicides en Nouvelle-Écosse et au Nouveau-Brunswick.

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**Bill Freedman and Greg Johnson**, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1. ([billfree@is.dal.ca](mailto:billfree@is.dal.ca))

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## Introduction

Intense disturbances of forests are associated with clearcutting and other forestry practices. These result in dramatic changes in the habitats available to support all elements of biodiversity. Some species, guilds, and communities benefit from habitat changes caused by forestry, but others suffer severe harm (Freedman 1989, 1995; Hunter 1990; DeGraaf et al. 1992; Freedman et al. 1994, 1996).

In particular, many species of birds require mature and older forests as habitat for breeding, migrating, or wintering. Many others, however, use habitats occurring during earlier stages of forest succession,

including those created through such forestry activities as clearcutting. In general, disturbances associated with forest harvesting and site management have indirect effects on bird species, guilds and communities, acting through changes in the physical structure and plant species composition of the available habitats. In addition, spraying of forestry pesticides can have direct effects on birds, occurring because of poisoning caused by exposure to toxic chemicals (particularly insecticides).

We describe here the results of studies on effects of forestry practices on birds in Nova Scotia and New Brunswick. The research summarized here examined

the effects of various harvesting systems, plantation establishment, and silvicultural herbicide spraying. The component studies were conducted between 1980 and 1996.

## Methods

All studies involved comparisons of stands that had been modified by forestry, with reference (that is, non-affected) stands in the immediate vicinity (often adjacent to an affected stand). This research design assumes that the habitat of the reference stands was similar in quality to that occurring in the modified stands prior to harvesting or herbicide application.

The research involved use of the spot-map technique to census bird populations. Wherever possible, plot sizes were 10 hectares or more in area. In some cases, however, they were smaller than this, being constrained by the stand-level scale of the operational forestry being practised. However, in each of the studies summarized here, the reference and treatment plots were of a similar size. The perimeter of each plot was marked at 50m intervals, as were 1 or 2 internal transects along the longer axis of the plot. These points were the listening stations where observations of song and other avian behaviour were made. Each census plot was surveyed 10 times (8 morning and 2 evening censuses), beginning in the first week of June and extending as late as mid-July. The locations of singing males were marked on maps of the sites, with particular attention paid to simultaneous registrations of more than one male of the same species. Territories were assigned on the basis of clusters of observations, which were interpreted to represent the activities of individual male birds.

Detailed investigations were also made of habitat structure. The abundance of plant species and foliage cover were measured in three strata: ground vegetation, shrubs, and trees, including snags and coarse woody debris. These habitat data are not reported here, but are available in the original publications that describe the research.

Common and scientific names of all bird species mentioned are given in Appendix 1.

## Component Studies

The following studies are summarized here:

### 1. Harvesting hardwood forest

Fieldwork was conducted during 1980 in central Nova Scotia, in an area of mature hardwood forest dominated by red and sugar maple (*Acer rubrum* and *A. saccharum*) and white and yellow birch (*Betula*

*papyrifera* and *B. alleghaniensis*) (Freedman et al. 1981). Comparisons were made of avian communities in three 3-year-old clearcuts, two 4-year-old strip-cuts (one had 20-m wide strips and the census plot comprised 45% harvested and 55% forest habitat; the other plot had 30m wide strips and was 38% cut and 62% forested), a shelterwood cut (45% residual basal area of non-harvested trees), and three reference stands of non-harvested, mature forest. The reference forest was about 75 years old, and had originated from a natural wildfire. All of the harvested stands were regenerating naturally.

### 2. Avian succession after clearcutting hardwood forest

Fieldwork was conducted during 1980 and 1981 in a region of mature maple-birch forest in central Nova Scotia (Morgan and Freedman 1986). Successional patterns were inferred using data from a chronosequence of 23 stands. There were 13 stands of various ages after clearcutting (up to 20 years), plus 10 reference stands aged 30 to 75 years after a wildfire. All harvested stands were regenerating naturally.

### 3. Intensively-managed conifer plantations

Fieldwork was conducted during 1992 and 1993 in southeastern New Brunswick, in and near Fundy National Park (G. Johnson and B. Freedman, unpub.) The study area is dominated by mature, mixed-species forest dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), red maple, and white birch. This natural forest has been, and is being, extensively clearcut and converted into intensively-managed plantations of black spruce (*Picea mariana*), which were planted as seedlings. The initial stages of plantation development (up to age 21 years) were examined using a chronosequence of 11 stands of about 10 ha, and these were compared with 5 reference stands of unharvested, natural forest.

### 4. Effects of silvicultural herbicide spraying

Fieldwork was conducted from 1986 to 1990 in central Nova Scotia (MacKinnon and Freedman 1993). The pre-spray avifauna of five census plots in 3-year-old spruce plantations was surveyed initially in 1986. Four of the plots were then operationally treated with glyphosate herbicide in August, 1986 at 2.3 kg/ha, while one plot was left unsprayed as a reference comparison. Post-spray changes in the avifauna were monitored during the first, second, and fourth years after herbicide treatment.

## Results and Discussion

### 1. Harvesting hardwood forest

This study found no substantial differences in the total



abundance, species richness, or species diversity of breeding birds among stands of mature maple-birch forest, or young clearcuts, strip-cuts, or a shelterwood cut of that forest (Table 1). However, the bird species using the mature forest and the recently disturbed habitats were almost completely different. Species prominent in mature stands included Least Flycatcher, Hermit Thrush, Red-eyed Vireo, Black-throated Green Warbler, Ovenbird, and American Redstart. In contrast, species prominent in the young clearcuts included Chestnut-sided Warbler, Mourning Warbler, Common Yellowthroat, Dark-eyed Junco, White-throated Sparrow, and Song Sparrow.

Strip-cuts included both mature-forest and clearcut habitats, and the bird species segregated among these habitat elements within the strip-cut area. The shelterwood cut had about one-third the tree

density, basal area, and canopy cover of the mature forest, with abundant shrub and ground vegetation. These intermediate habitat conditions supported some bird species of mature forest and some of clearcuts, particularly Least Flycatcher, Red-eyed Vireo, Chestnut-sided Warbler, Mourning Warbler, Common Yellowthroat, American Redstart, and White-throated Sparrow.

## 2. Avian succession after clearcutting hardwood forest

The chronosequence of 23 stands of clearcuts and natural hardwood forest showed that once the clearcuts had regenerated for at least three years, there was no substantial difference in bird community variables (such as total density, species richness, and species diversity) among stands of different age, in spite of

**Table 1.** Density of breeding birds of 3 stands of mature hardwood forest, 3 clearcuts, a shelterwood cut, and two strip-cuts in Nova Scotia. The mature forest was dominated by maple and birch; all harvests were 3-5 years old. The shelterwood and strip-cuts had a habitat structure intermediate to the forest and clearcuts. Data are in pairs/10 ha., averaged within each of the habitat types. Uncommon species are not included. Modified from Freedman et al. (1981).

Species	Mature forest	Clearcut	Shelterwood	Strip-cut
Common Snipe	0.0	0.8	0.0	0.0
Ruby-throated Hummingbird	0.0	2.3	0.0	0.0
Least Flycatcher	13.7	0.0	14.0	8.0
Hermit Thrush	4.3	0.0	0.0	0.8
Veery	2.0	0.8	0.0	0.8
Solitary Vireo	3.0	0.0	0.0	0.8
Red-eyed Vireo	5.3	0.0	8.0	5.0
Black-and-white Warbler	3.5	0.0	0.0	4.3
Northern Parula	2.8	0.0	0.0	2.5
Black-throated Green	3.7	0.0	0.0	0.8
Chestnut-sided Warbler	0.0	11.0	11.0	6.0
Ovenbird	15.7	0.0	0.0	8.0
Mourning Warbler	0.0	3.0	8.0	1.0
Common Yellowthroat	0.0	15.2	8.0	2.5
American Redstart	6.5	0.0	3.0	9.0
Rose-breasted Grosbeak	0.8	0.0	0.0	0.0
Dark-eyed Junco	1.7	5.0	0.0	2.3
White-throated Sparrow	0.7	12.7	3.0	0.0
Song Sparrow	0.0	5.3	0.0	0.0
<b>Total density</b>	<b>66.3</b>	<b>58.8</b>	<b>55.0</b>	<b>52.5</b>
<b>Species richness</b>	<b>12</b>	<b>8</b>	<b>7</b>	<b>13</b>
<b>Species diversity (<math>H'</math>)</b>	<b>2.1</b>	<b>1.8</b>	<b>1.8</b>	<b>2.2</b>

great differences in habitat (Figure 1). Only the 1- and 2-year-old clearcuts had smaller bird populations than uncut stands; the range of total avian density of clearcuts 3 to 10 years old fell within the range of variation of density for mature stands. As in the previous study (1, above), a distinct suite of bird species occurred relatively early in the post-clearcutting succession, and these were later replaced by another group as clearcuts matured into hardwood forest.

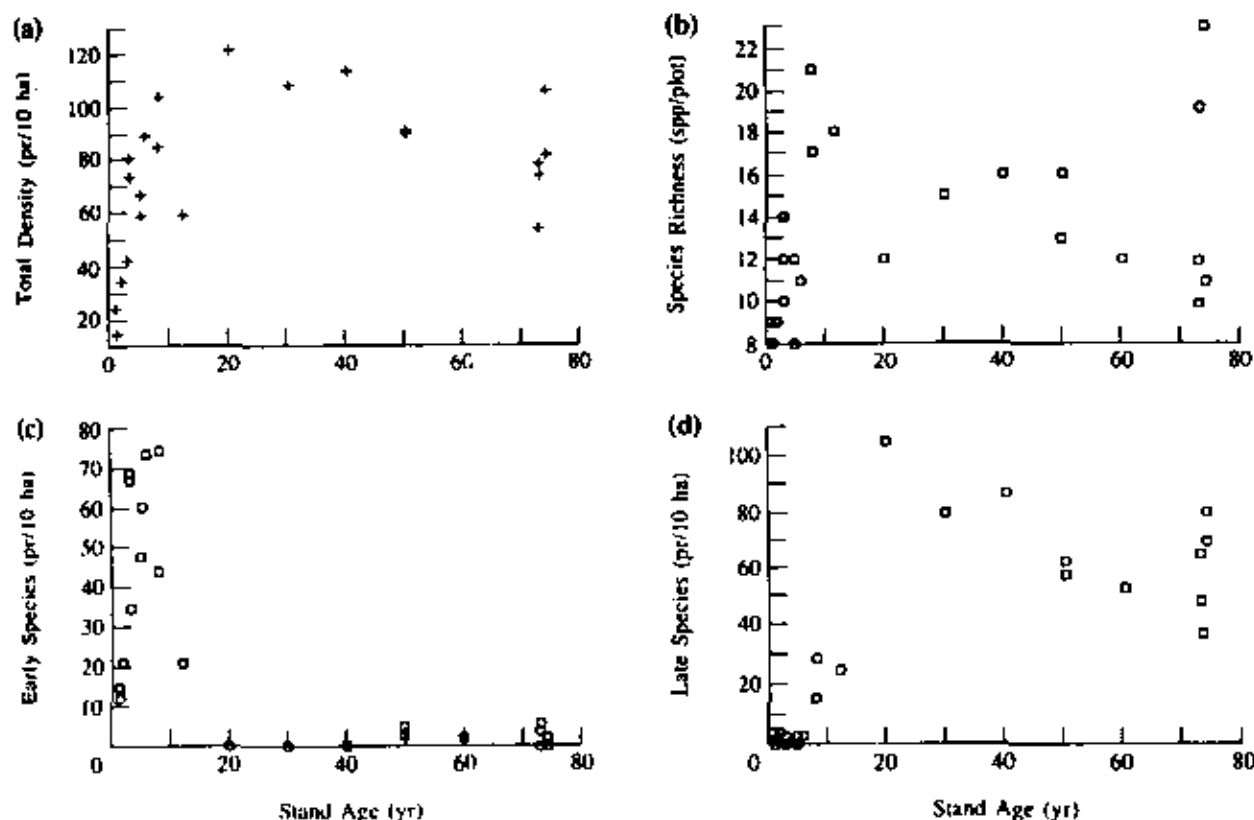
The transition between these avian communities occurred largely in stands 12-20 years old (Morgan and Freedman 1986). During this period hardwood stump sprouts and saplings had thinned to relatively few stems with a canopy at about 8-12 m. At the same time the shrub and ground-vegetation strata were declining in prominence because of shading exerted by

the overhead canopy of trees. This habitat maturation allowed the progressive invasion of the stand by bird species characteristic of mature forest. The distinctness of the "early" and "late" avian communities was demonstrated by a cluster analysis of the data matrix of bird species abundance versus stand age. This multivariate procedure separated the avian communities of stands 1-12 years old from those of stands 20-74 years old. Clusters of stands within these two age groups were much weaker, indicating that their avian communities were rather similar (Morgan and Freedman 1986).

### 3. Intensively-managed conifer plantations

Avian density reached pre-cutting levels within 5 years of plantation establishment, and peaked at about 15

**Figure 1.** Avian community parameters in a chronosequence of 23 stands in an area of hardwood forest in Nova Scotia. Stands older than 20 years were part of a post-fire landscape mosaic, while younger stands originated with clearcutting. (a) total density of breeding species; (b) number of breeding species; (c) species prominent in younger stands (i.e., Alder Flycatcher, Chestnut-sided Warbler, Common Yellowthroat, Dark-eyed Junco, White-throated Sparrow, Song Sparrow); (d) species prominent in mature stands (i.e., Least Flycatcher, Hermit Thrush, Veery, Red-eyed Vireo, Black-throated Green Warbler, American Redstart, Ovenbird). Modified from Morgan and Freedman (1986), and Freedman (1995).



years (Table 2). The avian community of younger plantations was dominated by ground-nesting species, particularly Common Yellowthroat, Lincoln's Sparrow, Song Sparrow, and White-throated Sparrow. The density of these species increased quickly, and then generally decreased to lower levels in the oldest plantations and reference stands of mature mixed-species forest. The density of canopy-nesting species (Yellow-bellied Flycatcher, Ruby-crowned Kinglet, Magnolia Warbler, and Yellow-rumped Warbler) was very low until tree-sized plants became established, after a plantation age of about 13 years. Plantations aged 13 to 15 years maintained relatively high populations of both ground- and canopy-nesting birds.

Notably absent or sparse in conifer plantations were cavity-nesting birds such as woodpeckers, chickadees, and nuthatches. (The only exceptions were single pairs of Eastern Bluebird and Northern Flicker in a 5-year-old plantation, nesting in the only two snags in the census plot.) Owing to the intensive management system used to develop the plantations examined, the quantities of coarse woody debris, snags, and cavity trees were very small compared with natural reference forests (Table 3). Consequently, few or no opportunities were provided for species of birds that require these elements as essential components of their habitat (Freedman et al. 1996).

A total of 16 species that bred in natural forest

Table 2. Breeding birds in 16 stands of natural, conifer-dominated forest and spruce plantations near Fundy National Park, New Brunswick. Only relatively abundant birds are listed. Bird numbers in pairs/10 ha; stand age in years; X = <0.5 territories per plot; V = visitor (included in species richness) (G. Johnson and B. Freedman, unpublished data).

Species	Plantation (age in yr.)									Forest		
	3	4	5	6	7	8	13	15	21	M	M	M
Common Snipe	1.3		1.0	1.0	1.0		1.0					
Common Nighthawk	V	1.0	V		V	1.0						
Yellow-bellied Flycatcher							18.0	6.9	13.0	4.7	1.0	4.5
Alder Flycatcher				5.3		6.0	V	13.4				
Black-capped Chickadee								X	X	X	3.0	2.0
Red-breasted Nuthatch							X	V	V	3.4	3.0	2.0
Brown Creeper										1.7		1.5
Winter Wren										2.1		0.5
Golden-crowned Kinglet								2.0	8.0	4.2	2.0	6.0
Ruby-crowned Kinglet				V			4.5	5.0	7.5	1.3		0.5
Swainson's Thrush								0.5	3.0	4.7	2.5	3.0
Hermit Thrush	V					0.5	0.5	2.0	2.0	2.5	2.0	
American Robin	V	X	X	V	0.5		0.5	X	2.5	0.4		
Solitary Vireo							V	V		0.4	3.0	1.0
Nashville Warbler	V						V	3.5	3.0	0.8		
Northern Parula								V		1.3		0.5
Magnolia Warbler				1.9		0.5	9.0	13.4	8.5	10.6		7.0
Black-throated Blue Warbler										3.8	3.5	1.5
Yellow-rumped Warbler							5.5	5.4	7.0	2.5	4.5	7.5
Black-throated Green Warbler							V	V	4.5	2.5	5.0	7.5
Blackburnian Warbler									6.5	5.1	9.5	5.0
Palm Warbler				V	4.0	5.5	9.0	9.5	1.0			
Bay-breasted Warbler									4.5	2.1	0.5	6.0
American Redstart				V			V	1.5		V		1.0
Ovenbird										1.7	8.0	5.0
Common Yellowthroat	0.9	2.0	3.0	15.0	4.0	11.0	10.0	15.3				
Song Sparrow	4.8	8.0	18.5	4.4	21.0	9.5						
Lincoln's Sparrow	4.3	15.5	16.0	10.2	21.5	11.0	6.0	5.9				
White-throated Sparrow	X	3.5	3.0	12.6	4.0	9.5	18.0	8.4	9.5	1.7		X
Northern Junco	3.5	X	X	1.0		0.5	2.0	2.5	4.0	2.5	2.0	4.0
Purple Finch							V	V		0.8	2.0	X
Total bird density	16.5	30.6	43.4	54.3	56.2	55.4	84.6	104.6	86.0	68.3	54.0	70.3
Species richness	17	11	12	18	12	15	27	36	24	41	25	32
Species diversity (H')	1.8	1.3	1.4	1.9	1.4	2.0	2.2	2.7	2.6	3.1	2.6	2.9

**Table 3.** Snags (dead trees), coarse woody debris (CWD), and living trees in stands of natural forest and conifer plantations in vicinity of Fundy National Park, New Brunswick. Data are for snags, CWD and trees with diameter  $\geq 5$  cm. Snags and live trees in basal area ( $\text{m}^2/\text{ha}$ ); CWD volume in  $\text{m}^3/\text{ha}$ . (T. Fleming and B. Freedman, unpubl. data).

	Snags	CWD	Live tree
<b>Mature, natural forest</b>			
Hardwood	3.5	18.7	29.3
Mixedwood	3.6	19.9	29.1
Mixedwood	5.4	13.0	28.0
Mixedwood	4.1	32.7	33.1
Conifer	11.4	41.6	25.4
Conifer	19.5	45.4	30.5
Conifer	12.7	56.5	27.7
<b>Plantation forest</b>			
21-yr.-old spruce	0.03	0.6	15.1
15-yr.-old spruce	0.0	8.9	10.8
15-yr.-old pine	0.1	0.0	28.8
13-yr.-old spruce	0.2	14.1	5.6
8-yr.-old spruce	0.2	28.0	5.1
7-yr.-old spruce	0.0	21.4	0.0
7-yr.-old spruce	0.0	23.9	0.5
6-yr.-old larch	0.0	32.1	0.3
5-yr.-old spruce	0.0	23.7	0.0
5-yr.-old spruce	1.8	55.3	0.0
4-yr.-old spruce	0.0	52.2	0.0
3-yr.-old spruce	0.0	48.1	0.0
3-yr.-old spruce	0.0	81.2	0.0

plots in the present study were not found in the plantations, including three species of cavity nesters and five species that prefer or require forest with a significant component of angiosperm trees. However, clearcutting and subsequent plantation establishment did provide temporary site opportunities for many open-canopy species of birds, and later on, species of conifer-dominated forest. If plantations were adjacent to natural forest, they were also used by some forest species for foraging. In general, our results are similar to those of Parker et al. (1994) for plantations elsewhere in New Brunswick. The effects on avifauna that we observed are, however, less severe than have been reported in studies of intensively managed

conifer plantations in Europe and the southeastern United States (Moss 1978; Reppening and Labisky 1985).

#### 4. Effects of silvicultural herbicide spraying

Only small changes in the abundance and species richness of breeding birds occurred on clearcuts treated with glyphosate herbicide (Table 4). Avian abundance decreased between the pre-spray and first post-spray years. However, this change occurred on both the sprayed and reference plots, which suggests it may have been caused by factors unrelated to the herbicide treatment (such as bad weather during the breeding, migrating, or wintering seasons). In the second year after spraying, the abundance of birds on the sprayed plots remained similar to that during the first post-spray year, while that of the unsprayed plot increased to about the pre-spray value. In the fourth post-spray year the treatments differed little in avian density.

The most common species on the clearcuts were White-throated Sparrow and Common Yellowthroat. These had a somewhat lower abundance on the spray plots up to the second post-spray year, and then recovered by the fourth post-spray year. On the reference plot, Song Sparrow and Lincoln's Sparrow declined in abundance during the course of the study, but on the sprayed plots these species were most abundant in the second and fourth years after spraying. As succession proceeded the reference plot became colonized by some new species in low densities, including Black-and-white Warbler, Red-eyed Vireo, Ruby-throated Hummingbird, and Palm Warbler. These species did not invade the sprayed plots, because the herbicide treatment had caused the habitat to revert to a younger successional stage, which was less favourable to these birds.

The effects of a herbicide treatment on animals using regenerating clearcuts as habitat can be caused by two types of influences: (1) direct toxicity of the herbicide, and (2) changes in the character of the habitat. Compared with many insecticides, herbicides used in forestry (particularly 2,4,5-T, 2,4-D, glyphosate, hexazinone, and triclopyr) are not very toxic to animals (Freedman 1995). At exposures encountered during typical forestry uses, the direct toxicological risks of these chemicals appear to be small and unimportant. This is particularly true of glyphosate, the most commonly used herbicide in forestry in Canada.

Glyphosate use does, however, cause large

**Table 4.** Range of abundance of breeding birds among five clearcut plots treated with glyphosate herbicide, and one reference plot. Only abundant species are listed; data are pairs/ha, determined by spot-map census, prior to spraying and in the first, second and fourth subsequent years. Data for sprayed treatment are ranges among five separate plots. Modified from MacKinnon and Freedman (1993).

Species	Reference plot (years)				Spray plots (years)			
	Pre-spray	1	2	4	Pre-spray	1	2	3
Common Yellowthroat	12	11	12	16	13-19	10-16	7-12	7-18
White-throated Sparrow	14	7	9	16	18-24	10-14	8-11	13-18
Dark-eyed Junco	3	4	6	10	3-7	5-8	4-8	5-8
Song Sparrow	4	2	1	1	3-5	1-4	5-7	6-14
American Goldfinch	6	4	2	2	3-8	2-3	0-3	0-3
<b>Total bird density</b>	<b>54</b>	<b>40</b>	<b>53</b>	<b>84</b>	<b>53-81</b>	<b>38-53</b>	<b>38-52</b>	<b>60-92</b>
<b>Species richness</b>	<b>12</b>	<b>15</b>	<b>15</b>	<b>12</b>	<b>10-14</b>	<b>10-15</b>	<b>12-15</b>	<b>12-13</b>

changes in habitat, by affecting the productivity and biomass of plants, and consequently changing the availability of berries and other plant foods. These changes indirectly result in smaller populations of insects and spiders, which are important foods for most birds, particularly during the breeding season (Freedman 1995; Woodcock et al. 1997). In our study, however, these potential, indirect effects of herbicide spraying resulted in only small changes in the populations of breeding birds.

## Summary

Our studies in Nova Scotia and New Brunswick found that forestry-related disturbances result in large changes in the habitat available for breeding birds. Many bird species occupying natural, mature forests found these habitat changes to be unsuitable. However, areas disturbed by forestry provided breeding habitat for indigenous, early-successional species. In terms of abundance, species richness, and species diversity, the overall changes in avian communities were not large, at least once clearcuts or plantations reached several years of age.

In general, intensively-managed plantations had greater effects on bird habitat than naturally regenerating sites. One of the most important differences in this regard involves critical habitat for bird species dependent on snags, cavity trees, and coarse woody debris.

Many of the effects of forestry on avian communities can be avoided if forest managers ensure that adequate areas of closed-canopy, mixed-wood and

angiosperm-dominated forest always remain available on the landscape. In addition, areas converted to plantations should be allowed to retain or regenerate a substantial component of deciduous trees, and actions should be undertaken to ensure the availability of snags, cavity trees, and coarse woody debris as critical habitat for dependent species.

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## Appendix 1. Common and scientific names of bird species mentioned in this paper.

Common name	Scientific name	Common name	Scientific name
Common Snipe	<i>Capella gallinago</i>	Northern Parula	<i>Parula americana</i>
Common Nighthawk	<i>Chordeiles minor</i>	Magnolia Warbler	<i>Dendroica magnolia</i>
Northern Flicker	<i>Colaptes auratus</i>	Black-throated Blue W.	<i>D. caerulescens</i>
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Yellow-rumped Warbler	<i>D. coronata</i>
Least Flycatcher	<i>Empidonax minimus</i>	Black-throated Green W.	<i>D. virens</i>
Alder Flycatcher	<i>E. alnorum</i>	Chestnut-sided Warbler	<i>D. pensylvanica</i>
Yellow-bellied Flycatcher	<i>E. flaviventris</i>	Bay-breasted Warbler	<i>D. palmarum</i>
Black-capped Chickadee	<i>Poecile atricapillus</i>	Palm Warbler	<i>D. palmarum</i>
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Blackburnian Warbler	<i>D. fusca</i>
Brown Creeper	<i>Certhia familiaris</i>	American Redstart	<i>Setophaga ruticilla</i>
Winter Wren	<i>Troglodytes troglodytes</i>	Ovenbird	<i>Seturus auricapillus</i>
Ruby-crowned Kinglet	<i>Regulus calendula</i>	Nashville Warbler	<i>Vermivora ruficapilla</i>
Golden-crowned Kinglet	<i>R. satrapa</i>	Mourning Warbler	<i>Oporornis philadelphia</i>
Eastern Bluebird	<i>Sialia sialis</i>	Common Yellowthroat	<i>Geothlypis trichas</i>
American Robin	<i>Turdus migratorius</i>	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Swainson's Thrush	<i>Catharus ustulatus</i>	Purple Finch	<i>Carpodacus purpureus</i>
Hermit Thrush	<i>C. guttatus</i>	Dark-eyed Junco	<i>Junco hyemalis</i>
Veery	<i>C. fuscescens</i>	White-throated Sparrow	<i>Zonotrichia albicollis</i>
Solitary Vireo	<i>Vireo solitarius</i>	Song Sparrow	<i>Melospiza melodia</i>
Red-eyed Vireo	<i>V. olivaceus</i>	Lincoln's Sparrow	<i>M. lincolni</i>
Black-and-white Warbler	<i>Mniotilta varia</i>		

# Breeding bird population studies at Hayward Brook, Fundy Model Forest

Gerry R. Parker, Denis Doucette and Denis Haché

## Abstract

A 5-year research project at Hayward Brook, a small second order stream within the Fundy Model Forest, began in 1993 to study the ecological implications of retaining forested buffer zones along water courses during forest harvest operations. This study combined control and experimental plots to compare responses of selected components of the terrestrial and aquatic ecosystems to buffer zones of different widths and treatments. Pre-treatment (before cutting) data were collected in 1993 and 1994. Cutting, and establishment of stream buffers, occurred in 1995, while the ecological responses to those treatments were measured in 1996 and 1997. This paper describes the general study designs and preliminary results of two of those studies, much of the information coming from the initial two years of pre-treatment resource calibration. One study examines the distribution of songbird territories in relation to stream proximity and stand type; the other compares use of tree species as nesting substrates by cavity-nesters.

## Résumé

Un projet de recherche de 5 ans a été initié en 1993 à Hayward Brook, un cours d'eau de second ordre à l'intérieur de la forêt modèle de Fundy, pour étudier les implications écologiques reliées au maintien d'une bande d'arbres tampon le long des cours d'eau lors des opérations forestières. Cette étude combine des places échantillons contrôles et expérimentales afin de comparer les réponses de certaines composantes des écosystèmes terrestres et aquatiques à la rétention de zones tampon (bandes riveraines) de diverses largeurs et de diverses interventions. Les données d'avant traitement furent récoltées en 1993 et 1994. La coupe et l'établissement des bandes riveraines eurent lieu en 1995 alors que les réponses écologiques aux traitements furent mesurées en 1996 et 1997. Cet article décrit le plan d'étude général et présente les résultats préliminaires de deux de ces études avec la plupart des données provenant des deux années d'avant traitement. Une des études examine la répartition des territoires d'oiseaux en relation avec la proximité du cours d'eau et avec le type de peuplement; l'autre compare l'utilisation des espèces d'arbres comme substrat de nid pour les espèces nichant dans les cavités d'arbres.

Gerry R. Parker, Canadian Wildlife Service, Box 6227, Sackville, New Brunswick, Canada E4L 1G6 (gerry.parker@ec.gc.ca); Denis Doucette, 552 rue Breau, Dieppe, New Brunswick, Canada E1A 5N8; Denis Haché, Gros Morne National Park, P.O. Box 136, Rocky Harbour, Newfoundland, Canada A0K 4N0.

## Introduction

One of the prime objectives of the Fundy Model Forest (FMF) is to improve knowledge of ecosystem function, to better understand the responses of the system to forest disturbance, and from that knowledge to improve our ability to develop a multiple resource management plan within the concept of sustained, or enhanced environmental quality. There is an initial

need to expand and complete certain data bases for resources within the FMF, and to measure the responses of wildlife resources to specific forest interventions and silviculture practices.

Research must concentrate on establishing cause/effect relationships and with those results develop improved forest ecosystem management strategies. If sustaining healthy and diverse forest

ecosystems is to be a goal of forest management, then applied systems of harvest and silviculture must consider ecological processes beyond those which directly affect establishment of seedlings and the growth of future crop trees. Forest management guidelines must also be tested and refined based on data generated from specifically designed and scientifically rigorous experimentation. This requires cooperation and coordination among biological disciplines and between the scientific and industrial communities.

The concept of the forested stream buffer study was developed by the Greater Fundy Ecosystem Research Group (GFERG), a committee of scientists and managers concerned by the fragmentation of forests by timber harvesting in southern New Brunswick, especially as it increasingly isolates Fundy National Park. Among the concerns over the changing landscape was that of forestry practices near water courses, and the ability of forested stream buffers to ensure the ecological integrity of aquatic and terrestrial systems. Canadian Wildlife Service, Environment Canada, was asked to develop a research study to address that concern, especially as it might affect breeding birds.

This paper outlines the methods and approaches of this study and presents some preliminary results from the pre-treatment phase. The study was designed as a 5-year cause-effect experimental research project. The first challenge was to find a watershed within FME which would lend itself to this experimental approach. The landscape within FME has a long history of forest harvesting, and complete unaltered watersheds would be unusual. However, through consultations with the landowner (J. D. Irving Ltd.), the Hayward Brook area was identified as one of the few which might lend itself to such a cause-effect experiment. The 30 km<sup>2</sup> area was accessible, wholly owned by J. D. Irving Ltd., and the proposed timber harvest operations would need only slight modifications to accommodate the proposed treatments.

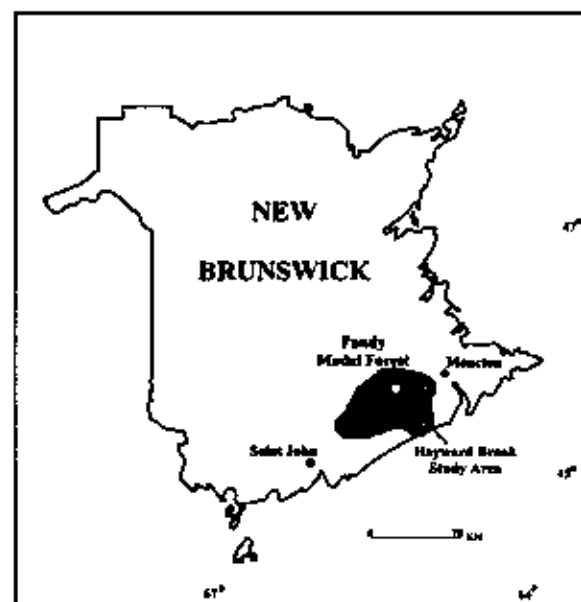
The Hayward Brook Study Group (HBSG) included personnel and/or resources from Environment Canada, Natural Resources Canada, University of New Brunswick, Université de Moncton, and J.D. Irving, Ltd. Sources of funding included those from the principal partners as well as from the FME.

## Study Design

The study area consists of approximately 30 km<sup>2</sup> near-mature (~80 yr) mixed forest at Hayward Brook near

the town of Petitcodiac in Westmorland County, New Brunswick. It lies within the upper reaches of the Hayward and Holmes Brooks watersheds which drain westerly into the Anagance and Petitcodiac Rivers and is located within the northeast portion of the Fundy Model Forest in southeastern New Brunswick (Figure 1). The basic design is a 5-year cause-effect experimental study with pre-treatment, treatment and post-treatment phases. The original objectives of the overall study were to measure changes to the physical qualities of the water and stream flow and breeding bird populations from cutting and retention of forested stream course buffers of different widths. The value of this experimental approach became obvious and other researchers joined the project to study additional components of the aquatic and terrestrial systems.

**Figure 1.** Location of the Hayward Brook study area within the Fundy Model Forest in southeastern New Brunswick

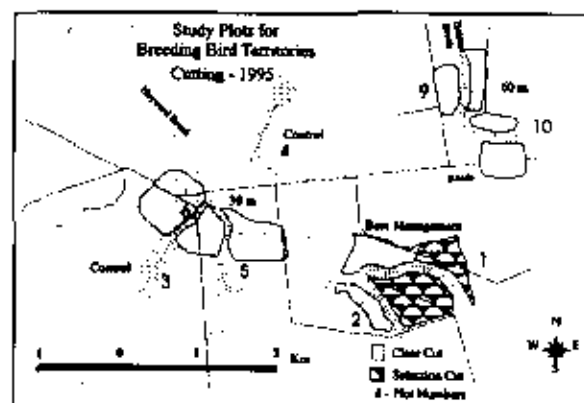


There were 2 replicates of the following 4 treatments: (1) clearcutting with 30 m buffers; (2) clearcutting with 60 m buffers; (3) "best management practices", i.e., clearcutting and selection cutting; and (4) control (no cutting). The 5-year study called for two years of pre-disturbance resource calibration (1993, 1994), one year of timber harvest (1995) followed by two years of post-disturbance response measurement (1996, 1997). The main study plot at each site extended 150 m perpendicular to each side of the stream, and followed the water course for distances which varied at individual sites from 650 to 1000 m



(20 - 30 ha). The study design was intended to accommodate an assessment of cutting and forested buffers on the richness, density and diversity of breeding birds and the spatial distributions of their territories. The distribution of macroplots and the harvest treatments within the Hayward and Holmes Brooks drainages is shown in Figure 2.

**Figure 2.** Distribution of control and experimental plots within the Hayward Brook study area and the treatments (timber harvest operations) which were applied in late summer and fall 1995.



A second component of avifaunal studies at Hayward Brook examined nest tree selection and habitat use by cavity-nesting species of birds. Existing snag-management guidelines for New Brunswick, and for Acadian Forests in general, are based on inadequate knowledge of the habitat requirements and use by these important forest birds. For example, there are no specifications concerning species, sizes, conditions or emplacement of snags to be retained during commercial harvesting operations.

Breeding birds that make extensive use of tree cavities are divided into two groups: primary cavity-nesters and secondary cavity-nesters. Both groups use cavities in trees for nesting and roosting. Primary cavity-nesters, such as woodpeckers, excavate the cavities they use. Secondary cavity-nesters, such as nuthatches or chickadees, use naturally occurring cavities or abandoned cavities excavated by primary cavity-nesters, although they will on occasion excavate their own cavities in very decayed wood. This 2-year research project concentrated on the nesting microhabitats of the cavity-nesters found in the Hayward and Holmes Brooks drainage basins and attempted to characterize primary and secondary cavity-nesting microhabitat.

The study of cavity-nester habitat is not new,

although its importance has increased with the recognized role of snags in forest ecosystems. Many research projects have dealt with various aspects of cavity-nesting bird ecology. Nesting habitat requirements (Conner et al. 1975; Conner and Adkisson 1977; Li and Martin 1991), foraging habitat selection (Kilham 1970; Conner and Crawford 1974; Conner 1981), and effects of habitat modification (Galli et al. 1976; Zarnowitz and Manuwal 1985; Stribling et al. 1990) are but some of the aspects of cavity-nesters that have been and are currently being studied. Most research in North America has been in the United States, although surprisingly little from the northeastern part of the continent. Very few studies of cavity-nesters have been conducted in Atlantic Canada. Cavity-nesters are believed to have different nesting habitat search images depending on forest type and composition, as well as geographical location (Lundquist and Mariani 1991). Nesting habitat requirements for cavity-nesters in southern New Brunswick, for instance, may differ greatly from those of similar birds located elsewhere on the continent. It is thus of prime importance to quantify the use of nesting habitat by cavity-nesters in New Brunswick to ensure the proper management of these birds in the Acadian forest.

The 8 study plots were established as sites for specific interventions. Their placements were chosen so that individual site treatments would not affect the resources of any of the others. As the widths of all plots were standardized at 300 m, the area of each depended upon the distance of the stream it included. Plot length was influenced by property boundaries and stream length and flow, so individual plot sizes varied from 20-30 ha.

Each plot was flagged at 50 m intercepts to aid in the breeding bird surveys. Most transects were further subdivided and marked by flagging to ensure that field personnel knew their precise location at all times. This master grid was maintained throughout the study and was used in the selection of vegetation and small mammal sample sites. The grid was also convenient when sampling for feeding and nesting sites of woodpeckers. The tree cover on all plots was predominantly second-growth mixed forest (Table 1). The age of most mature trees, as determined from core samples of 4 randomly selected trees at each vegetation sampling site, was approximately 80 years. A few red and white pines were aged at slightly over 100 years.

Red spruce, red maple, balsam fir, trembling aspen, white pine and white birch (in decreasing order

**Table 1.** The stand composition of all plots expressed as number of hectares of each stand type in the Hayward Brook study area.

Plot #	Stand Type										
	THIH	IHTH	INHW	IHSP	SPIH	THSP	SPTH	SPBF	BFSP	PINE	NP
1					7.9			0.5		20.8	
2		5		2.5	8.1					3.9	
3		0.9	5.4	7		0.4	7.2				
4	9.1	2.1		11.5	5.4		1.4				0.5
5		0.2	8.7	14.3			6.6				
6			0.2	3.7		4.3	1	12			
7	0.8	12.8				1.2	8.4				
8		5.8		0.9	2.1			2.9	7.8		
9		3.3		2.2			5.7	5.2			3
10			2.1	3.9			4	6.6		2.5	0.1

THIH = 50-75% tolerant hardwoods, 25-50% intolerant hardwoods; IHTH = 50-75% intolerant hardwoods, 25-50% tolerant hardwoods; INHW = >70% intolerant hardwoods; IHSP = 50-75% intolerant hardwoods, 25-50% spruce; SPIH = 50-75% spruce, 25-50% intolerant hardwoods; THSP = 50-75% tolerant hardwoods, 25-50% spruce; SPTH = 50-75% spruce, 25-50% tolerant hardwoods; SPBF = 50-75% spruce, 25-50% balsam fir; BFSP = 50-75% balsam fir, 25-50% spruce; PINE = >50% white and/or red pine; NP = strip of alders over stream, classed as non-productive. Tolerant hardwoods include American beech, yellow birch, red and sugar maple; intolerant hardwoods include trembling and largetooth aspen, and white and grey birch.

of basal area) were the dominant tree species in the study area. Speckled alder, characteristic of riparian sites, was also common. Most sections of stream on all plots were bordered by a closed band of alders from 10m to 30 m wide. As buffer zones began at the stream edge, these alders fell within the area protected from cutting. Forest canopy closure over streams was inversely related to the width of riparian alder cover. Coniferous tree species predominated on Plots 1, 2, 9 and 10 while the remaining plots supported a more mixed forest. White birch and trembling aspen were dominant on Plots 3 and 4, respectively, while red maple and red spruce were sub-dominants on both. Red spruce, red maple, trembling aspen and balsam fir dominated on Plots 5 through 8, while black spruce was common on Plots 9 and 10. Roads were established in the autumn of 1994, and timber harvesting (treatments) began in the summer of 1995 and continued into the winter of 1995/96.

## Methods

### Bird Territories

The standard territory mapping method was used to

sample the bird communities on all plots (International Bird Census Committee 1970). As song is the principal means by which males both defend a territory and attract unmated females (Welty and Baptista 1988), individual bird territories can be mapped by repeat surveys of singing males on a defined tract of forested habitat. One observer walked slowly along transect lines and recorded the exact position of all birds observed and/or heard on a map (scale = 1:2,000). The principle data for each observation included species and sex of bird, use of song and use of calls. Additional information might include displays of courtship behaviour, aggressive interactions, nest building, nest use and food carrying.

Each plot was surveyed 6-7 times through the breeding season. Visits were evenly distributed between 26 May and 10 June 1993, and between 28 May and 4 July 1994. Surveys were usually conducted between 0600h and 1100 h (AST). Each observer (3 in 1993, and 4 in 1994) conducted an equal number of surveys on each plot to minimize potential bias from variable levels of skill to detect and identify bird species. As surveys extended over a period of

several hours, starting and finishing locations within plots were varied to avoid potential bias due to diurnal variation in bird activity. As heavy rains and strong winds also reduce bird activity and observer efficiency, surveys were not conducted during inclement weather. Speed of survey remained constant among surveyors.

Observations for each visit to a plot were recorded on separate maps. At the end of the bird surveys all observations for each species were tabulated on a final species map. Species maps show which species were present, where and when they were observed, and occasionally some of their behaviour. Species maps revealed the number and the spatial arrangement of territories from clusters of bird registrations. Most registrations are locations of male birds singing. Territories are, therefore, defined by an area used by a singing male. Three registrations were the minimum number required before a cluster was accepted as a territory.

Bird observations extended to 50 m outside plot boundaries. These registrations helped to determine the position of territories that extended beyond the defined survey plot. Edge territories were counted as half of a territory (Bibby et al. 1992). Due to a change in the harvest plans by the land owner, the bird community on Plot 8 was sampled during the first year only (1993), while Plots 9 and 10 on Holmes Brook were added in the second year (1994) to provide replicates of 60 m buffers.

Vegetation was sampled using the circular plot method described by Noon (1981). These 22.6 m<sup>2</sup> (0.04 ha) diameter plots were centred at randomly selected 50 m intercepts on the transect grids used for surveying breeding birds. One-quarter of these points in each plot were selected for vegetation sampling with a table of random numbers. This sampling scheme included approximately five percent of the total bird census plot area. A total of 293 vegetation samples were distributed throughout the 10 plots and were measured after the bird breeding season. Circular sample plots were delimited by setting out two 22.6 m ropes in the cardinal directions so that their centers crossed at grid intercept points. Within the circular plot, all trees with stems greater than 3 cm in diameter at breast height (dbh) were tallied by species and placed in one of seven dbh size classes. Snags (dead and partially dead trees) taller than 1.4 m with dbh greater than 3 cm were tallied using the same dbh classes.

Understory vegetation was sampled by two procedures: (1) saplings with a dbh of 3 to 8 cm were

counted along with trees and placed in the first size class; and (2) shrub stems of a diameter less than 3 cm and taller than 1 m were counted in two 2 m wide belt transects oriented along the cardinal directions within the circular plot. Coniferous and deciduous stems were tallied separately. Stumps between 10 cm and 1.4 m in height were also counted within the 0.04 ha plot. Coniferous and deciduous stumps were recorded separately.

Foliage profiles estimate the density of vertical vegetation strata of the forest. Foliage profile was measured at 20 points along 2 axes oriented in the cardinal directions within the circular plot. Foliage profiles were measured by sighting through an ocular tube, made from a piece of plastic tubing with cross hairs at one end. At each of the 20 locations, the presence or absence of green vegetation at the intersection point of the cross hairs was recorded for each of the following vertical layers: (1) 0 - 0.5 m; (2) 0.5 - 3.0 m; (3) 3.0 - 10.0 m; and (4) more than 10.0 m. The first stratum (ground layer) was estimated by sighting downwards directly over each of the 20 locations, while the others were observed by sighting upwards. The height of each layer was estimated visually. Observer estimation was aided by other measures of canopy height obtained with a clinometer that were not included with these analyses.

An important modification of this method was how the data were recorded. Rather than simply noting presence "+" or absence "-" of vegetation, the presence of vegetation was recorded as either deciduous (D), coniferous (C), or as ground layer vegetation (H - represented a species that would not grow out of the ground cover and was used only in the 0 - 0.5 m layer). Absence of vegetation was noted as "0".

Simple indices of species richness, density and diversity were calculated to describe the bird community of each plot. Species richness is the number of breeding species present; diversity was expressed by the Shannon/Weiner diversity index  $H'$ , derived from the formula

$$H' = - \sum_{i=1}^s p_i \log_e p_i$$

where  $s$  = the number of species, and  $p_i$  = the proportion of the  $i^{\text{th}}$  species in the community.

A geographic information system (GIS) using the Arc/Info software program was used to analyze and describe the spatial distribution of bird territories (see

Shaw and Atkinson 1990). The study plots and bird territories were digitized into the Fundy Model Forest GIS database. Study plots were divided into zones located at 5 distances from the stream. The density of bird territories was then compared between the different zones. Zone 1 was centered on the stream and had a width of 60 m. The 4 other zones consisted of the area on both sides of the stream within the following ranges of distance: 30 - 60 m, 60 - 90 m, 90 - 120 m, and 120 - 150 m.

The frequency of overlap between species' territories and stand types was also examined to determine whether forest stand availability was proportional to use (degree of forest stand selectivity) by each species. Ten stand types were identified in the study area (Table 1). Bird territories were related to the vegetation measurements of plots located randomly within the boundaries of respective territories. When several vegetation plots fell within the same bird territory, the means for vegetation measurements from those plots were used. Mean number of vegetation sample plots per bird territory mapped in 1993 and 1994 were 2.43 ( $\pm 1.47$ ) and 2.41 ( $\pm 1.37$ ), respectively. Of 1430 bird territories, only 10 and 16 contained no vegetation sample plots during 1993 and 1994, respectively. These territories, and bird species with less than 8 territories identified during one breeding season, were not used in these analyses.

The habitat variables were summarized into three different data sets. Distribution of birds was analyzed in relation to (1) variables representing the amount of basal area per tree species for all trees larger than 3 cm dbh, (2) variables of stem densities of snags, coniferous and deciduous trees of different size classes, and (3) variables representing the foliage profile. Thus, the ordination of bird habitat selection relative to two data sets that describe the habitat in a structural fashion was calculated as well as one data set that provides a description of the floristic composition of the habitat. In a graph from a correspondence analysis, the proximity of the points and their direction indicate their similarity (see Greenacre 1984).

### Cavity-Nesters

A preliminary season of cavity searching was conducted during the 1993 field season. Active cavity nests (*i.e.*, cavities used for nesting during that reproductive season) were located during breeding bird surveys. Active cavity-nests were identified with flagging tape and mapped for future reference. The first season of extensive cavity searching began in

1994. Cavity searches began on 11 May and were concluded on 4 July, by which time most young were fledged. Cavity searching was interrupted from 28 May to 4 July while field personnel were occupied with breeding bird censuses; during this period cavity searches were mostly confined to the breeding bird survey plots. Cavity searches were conducted from approximately 0600 until 1100h ADT. The forest habitat adjacent to the breeding bird survey plots was also searched for evidence of cavity-nester breeding behaviour (*i.e.* courtship rituals, drumming, conflicts, excavation, etc.). Piles of wood chips or coarse sawdust at the bottom of some trees also helped to identify fresh excavations. Cavity searches were not carried out during rainy or exceptionally windy days. Regular visits to trees with active cavities were conducted at 4 to 5 day intervals to determine general breeding chronology and presence of predation. Cavity locations in 1993 were also examined to determine degree of cavity and cavity-tree re-use. Cavity searches in 1995 began on 2 May and concluded on 6 July. They were briefly interrupted for two days during the first week by a storm that left 5 to 10 cm of snow on the study area. This snow persisted for almost two weeks and seemed to lessen our search efficiency.

The vegetation near nest-trees was sampled as described for the bird-territory study except that the 0.4 ha plots were centred on the cavity trees, and all trees and snags with stems larger than 8 cm dbh (considered minimum diameter for potential cavity nest trees) were measured and mapped to record their spatial distribution within each sample plot. Trees were identified to species, while snags were identified to type (coniferous or deciduous) and by decomposition stage (see Hunter 1990 for decomposition stage classification). All nest-tree measurements and microhabitat sampling were performed after fledging so not to interfere with reproductive activities.

An equal number of potential cavity-trees was selected randomly on each study site. Descriptions and measurements of these randomly selected trees and their surrounding microhabitat were made to search for differences between selected nest sites and apparently potential nest sites that were not selected. Random sites were chosen using a dot grid over a forest cover map (scale = 1 : 12,500). One tree on each of these sites was chosen randomly to match an actual cavity-tree found during cavity searches. Random trees matched to live trees had to be of the same genus (for aspen) or species (for all other tree species) and of similar dbh ( $\pm 5$  cm when possible). Random trees

matched to dead or further decayed trees (snags) had to be of the same decomposition stage and dbh ( $\pm 5$  cm when possible). Some of the very large trees and snags used as cavity substrate were difficult to match because of their rarity, causing selection of smaller random trees and snags. Principal Component Analysis was used to quantify the nesting habitat of cavity-nesters found within the Hayward and Holmes Brooks drainage basins. Exact choices of statistical tests and database formats are being resolved at the present time. The Arc/Info GIS will also be used to help analyze the data. Nesting-cavity locations will be digitized into the FMP GIS and matched to the existing forest stand classification.

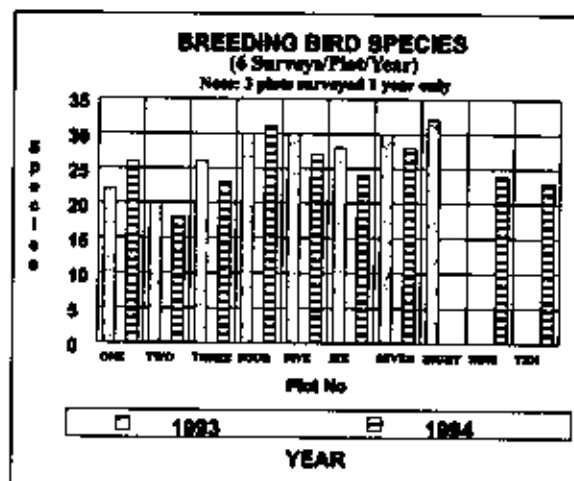
## Results

### Bird Territories

Sixty-six species of birds were observed during the breeding bird censuses in 1993 and 1994. Forty-two of those species were breeders with at least one territory within the study plots during one of the seasons. The 24 other species were either visitors from other habitats (e.g., Common Nighthawk, Tree Swallow, Chimney Swift, American Crow, Cedar Waxwing, Chestnut-sided Warbler and Brown-headed Cowbird), or forest birds that were not breeding, breeding outside of the study plots, inconspicuous due to low density, nocturnal, of discreet behaviour, or had an extremely large home range (American Woodcock, Ruffed Grouse, Broad-winged Hawk, Barred Owl, Ruby-throated Hummingbird, Pileated Woodpecker, Least Flycatcher, Common Raven, Grey Jay, Boreal Chickadee, Northern Waterthrush, Red Crossbill and American Goldfinch). Many are species not targeted by the census technique used.

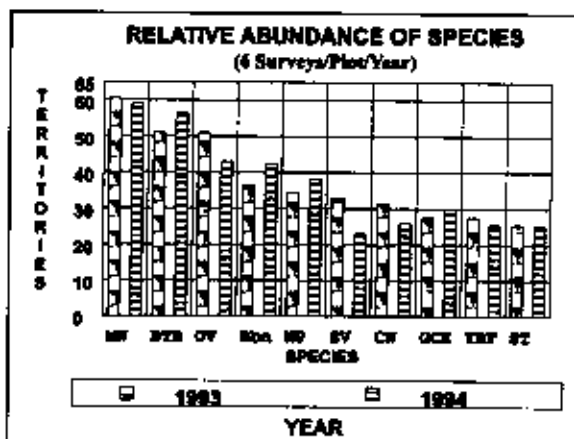
Seven hundred and thirty-five territorial individuals were counted in 1993 and 695 in 1994. The total numbers of territories used, however, were reduced to 684 and 621 because edge territories were counted as one-half (Bibby et al. 1992). The number of bird species found to be breeding on individual plots averaged near 25 both years (Figure 3). The most common breeding species on the study area were Magnolia Warbler, Black-throated Blue Warbler and Ovenbird, the total territories for each averaging 45-60 per year (Figure 4). The breeding avian community was dominated by parulid warblers; fifteen species of warbler accounted for more than one-half of the territories mapped: 373 (54.5%) in 1993 and 367 (59.1%) in 1994. The most common warblers were Magnolia Warbler, Black-throated Blue Warbler, Ovenbird, Blackburnian Warbler, Northern Parula,

Figure 3. Number of bird species breeding on the study plots in 1993 and 1994.

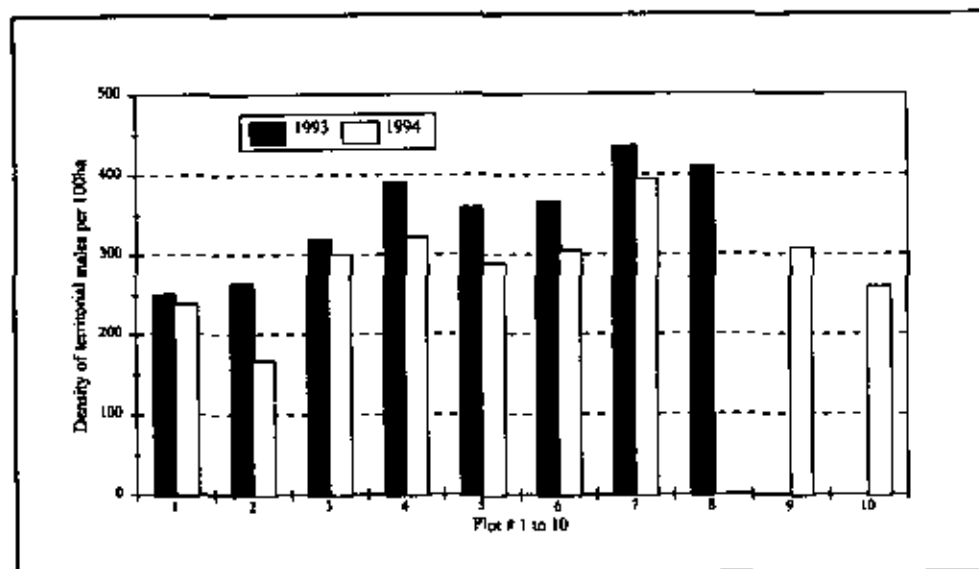


Bay-breasted Warbler and Canada Warbler. Other important families were (number and proportion of total territories in 1993 and 1994): Turdinae - 55 (8.0%) and 50 (8.1%); Vireonidae - 53 (7.7%) and 33 (5.3%); Sylviinae - 36 (5.3%) and 35.5 (5.7%); Tyrannidae - 31 (4.5%) and 32.5 (5.2%) and Picidae - 31 (4.5%) and 23 (3.7%).

Figure 4. The most abundant species breeding on the study plots in 1993 and 1994. MW = Magnolia Warbler, BTB = Black-throated Blue Warbler, OV = Ovenbird, Bbn = Blackburnian Warbler, NP = Northern Parula, SV = Solitary Vireo, CW = Canada Warbler, GCK = Golden-crowned Kinglet, YBF = Yellow-bellied Flycatcher, ST = Swainson's Thrush.



Territory densities ranged from 2.50/ha to 4.35/ha in 1993 and from 1.67/ha to 3.94/ha in 1994. An average decline of 15.8% in territory density was observed between 1993 and 1994 on plots surveyed

**Figure 5.** Densities (pairs/100 ha) of breeding bird territories on plots surveyed at Hayward Brook in 1993 and 1994.

both years (Figure 5). A gradient of density related to altitude seemed to be apparent when ranks of bird densities were examined for the plots on Hayward Brook (Plots 1 through 8). Densities were at their lowest on Plots 1 and 2 in the upper reaches of the watershed. Densities increased down stream and were highest on Plots 7 and 8. Species richness was also lower in 1994 with the exception of Plots 1 and 4. Species diversity was generally lower in 1994 (Table 2).

In 1993, mean densities of bird territories within zones 1 to 4 (zones were 30m wide strata parallel to each side of the stream) ranged between 3.29/ha and 3.52/ha and were not significantly different from one another (Table 3). The mean density of zone 5, the most distant from the stream, was not significantly different from zone 1, the closest to the stream, but was lower than the others (Tukey's pairwise comparisons of means). Although mean densities were lower during the second year, pairwise comparisons were similar. Mean densities within zones 1 to 4 ranged from 2.82/ha to 2.99/ha and were not significantly different from one another; however, mean density in zone 5 (2.15/ha) was less than in the others. Distance from stream had a significant effect on the variation in density of 18 individual bird species. Tukey's test for non-additivity indicated that 12 of these contained a significant interaction between factors of distance and census plot. In five cases (Yellow-bellied Sapsucker, American Robin, and Ovenbird in 1993; Black-capped Chickadee and

**Table 2.** Number of species (richness, R), density of territories (T) per ha, and Shannon-Weiner Index of Diversity (D) of birds breeding on plots surveyed at Hayward Brook in 1993 (1<sup>st</sup> row) and 1994 (2<sup>nd</sup> row). (\* = plot not surveyed).

Plot #	Area (ha)	R	T	D
1	30	22	2.5	1.22
		26	2.38	1.3
2	19.75	20	2.63	1.2
		18	1.67	1.17
3	21	26	3.19	1.32
		23	3	1.27
4	30	30	3.9	1.38
		31	3.22	1.39
5	30.5	30	3.59	1.36
		27	2.89	1.3
6	21	28	3.67	1.36
		24	3.05	1.27
7	24	30	4.35	1.37
		28	3.94	1.36
8	20	32	4.1	1.43
		---	---	---
9	19.5	---	---	---
		24	3.08	1.27
10	19.5	---	---	---
		23	2.59	1.3

Table 3. Results of analysis of variance of mean territory density per hectare of individual species and of all species together within 5 zones of increasing distance from the stream. Species presented are those whose mean densities were significantly affected by distance as detected by two-way analysis of variance without replication. Critical values for comparison (CVC) as well as degrees of freedom (DF) for Tukey's pairwise comparisons of means are presented. Total number of territories (NT) and number of plots (NP) where the species was present are also shown. Zone 1 was a 60 m wide strip centred on the stream and zones 2 to 5 consist of the area on both sides of the stream within the following ranges: 30 - 60 m; 60 - 90 m; 90 - 120 m, and 120 - 150 m.

SPECIES	ZONE					CVC	DF	NP	NT
	1	2	3	4	5				
1993									
Yellow-bellied Sapsucker *	0.1135 <sup>a</sup>	0.1038 <sup>ab</sup>	0.0970 <sup>ab</sup>	0.0883 <sup>b</sup>	0.0599 <sup>c</sup>	0.0207	28	8	21.0
Yellow-bellied Flycatcher *	0.2097 <sup>a</sup>	0.1864 <sup>a</sup>	0.1399 <sup>ab</sup>	0.0885 <sup>bc</sup>	0.0403 <sup>c</sup>	0.0942	28	8	27.5
Winter Wren *	0.1309 <sup>a</sup>	0.1091 <sup>ab</sup>	0.0765 <sup>abc</sup>	0.0464 <sup>cd</sup>	0.0286 <sup>d</sup>	0.0777	24	7	13.5
American Robin *	0.1587 <sup>a</sup>	0.1282 <sup>ab</sup>	0.1034 <sup>abc</sup>	0.0704 <sup>cd</sup>	0.0368 <sup>d</sup>	0.0745	16	5	13.5
Bay-breasted Warbler	0.2462 <sup>a</sup>	0.1795 <sup>ab</sup>	0.1382 <sup>b</sup>	0.1344 <sup>b</sup>	0.1176 <sup>b</sup>	0.0713	20	6	24.5
Blackburnian Warbler	0.2004 <sup>a</sup>	0.2041 <sup>a</sup>	0.1989 <sup>a</sup>	0.1696 <sup>ab</sup>	0.1177 <sup>b</sup>	0.0767	28	8	36.5
Ovenbird *	0.0596 <sup>a</sup>	0.1563 <sup>b</sup>	0.2778 <sup>c</sup>	0.3641 <sup>d</sup>	0.3479 <sup>cd</sup>	0.0846	28	8	51.0
All Species	3.2878 <sup>ab</sup>	3.4897 <sup>a</sup>	3.5182 <sup>a</sup>	3.4144 <sup>a</sup>	2.6871 <sup>b</sup>	0.7017	28	8	684.0
1994									
Yellow-bellied Flycatcher	0.1659 <sup>a</sup>	0.1414 <sup>ab</sup>	0.1208 <sup>ab</sup>	0.0988 <sup>ab</sup>	0.0704 <sup>b</sup>	0.0813	32	9	25.5
Black-capped Chickadee *	0.1195 <sup>ab</sup>	0.1213 <sup>ab</sup>	0.1258 <sup>a</sup>	0.1041 <sup>ab</sup>	0.0762 <sup>b</sup>	0.0470	24	7	20.0
Red-breasted Nuthatch *	0.0607 <sup>ab</sup>	0.0774 <sup>a</sup>	0.0740 <sup>a</sup>	0.0593 <sup>ab</sup>	0.0320 <sup>b</sup>	0.0340	32	9	14.0
American Robin	0.1090 <sup>a</sup>	0.1013 <sup>a</sup>	0.0895 <sup>ab</sup>	0.0612 <sup>ab</sup>	0.0394 <sup>b</sup>	0.0527	20	6	11.5
Veery *	0.0908 <sup>a</sup>	0.0831 <sup>a</sup>	0.0638 <sup>ab</sup>	0.0461 <sup>ab</sup>	0.0244 <sup>b</sup>	0.0564	16	5	8.0
Solitary Vireo	0.1520 <sup>a</sup>	0.1363 <sup>ab</sup>	0.1057 <sup>bc</sup>	0.0702 <sup>cd</sup>	0.0471 <sup>d</sup>	0.0440	32	9	23.0
Black-throated Blue Warbler **	0.1003 <sup>a</sup>	0.2001 <sup>ab</sup>	0.2900 <sup>b</sup>	0.3082 <sup>b</sup>	0.2469 <sup>b</sup>	-----	32	9	56.5
Yellow-rumped Warbler *	0.0323 <sup>a</sup>	0.0446 <sup>ab</sup>	0.0728 <sup>ab</sup>	0.0936 <sup>b</sup>	0.0603 <sup>ab</sup>	0.0560	32	9	13.0
Canada Warbler *	0.2067 <sup>a</sup>	0.1539 <sup>ab</sup>	0.1068 <sup>ab</sup>	0.0942 <sup>a</sup>	0.0779 <sup>b</sup>	0.1012	28	8	26.0
Bay-breasted Warbler	0.2534 <sup>a</sup>	0.2102 <sup>ab</sup>	0.1600 <sup>bc</sup>	0.1161 <sup>cd</sup>	0.0831 <sup>d</sup>	0.0736	32	9	37.5
Ovenbird **	0.0564 <sup>a</sup>	0.1362 <sup>b</sup>	0.2123 <sup>bc</sup>	0.2514 <sup>c</sup>	0.2459 <sup>cd</sup>	-----	32	9	43.0
All Species **	2.8196 <sup>a</sup>	2.9268 <sup>a</sup>	2.9856 <sup>a</sup>	2.8360 <sup>a</sup>	2.1533 <sup>b</sup>	-----	32	9	621.0

\* interaction between factors of distance and sampling plot could not be eliminated.

\*\* interaction between factors was eliminated by transformation to natural logarithm  $\ln(x)$ .

<sup>ab,cd</sup> within each row, letters in superscript identify groups of mean densities that are not significantly different from one another based on Tukey's pairwise comparisons.

Canada Warbler in 1994), transformation of data could not eliminate the interaction.

A gradient of decreasing territory densities with increasing distance from the stream was apparent in many species for which distance had a significant effect (Yellow-bellied Sapsucker, Yellow-bellied Flycatcher, Winter Wren and American Robin in 1993; Solitary Vireo and Bay-breasted Warbler in 1994). The opposite effect was apparent with the Black-throated Blue Warbler and Ovenbird - densities of both increased with distance from stream. Although distinct trends were not as evident for other species, densities were generally higher within the first two to three zones from the stream (from 0 to 60-90 m).

Frequencies of occurrence of breeding bird

territories within different forest stand types allowed a measurement of stand preference, if any, for each species. The results of these analyses are not yet completed. However, with few exceptions, it appears that the overall proportionate use of different stand types by all species remained constant over the two years. Frequency of occurrence of territories within stand type classes obtained in 1993, in 1994, and for both years combined showed that the breeding bird territories were unevenly distributed among the different forest stands, i.e. birds were selective for specific habitats used for breeding. In general, stands of intolerant and tolerant hardwoods and mature mixed woods were selected for, while stands of intolerant hardwoods and pine were selected against.

Stands of conifer (spruce [species lumped] and balsam fir) were used in proportion to availability.

### Cavity-Nesters

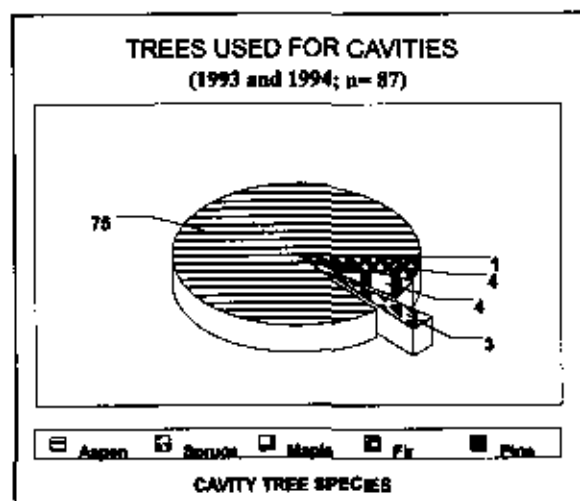
In 1995, active cavities were located by criss-crossing the breeding bird sample plots and, to a greater extent than in 1994, the forest adjacent to these plots. Fewer nests were found in 1995 ( $n = 34$ ) than in 1994 ( $n = 57$ ), due most likely to fewer persons searching and a shortened season due to the beginning of forest harvest operations in June 1995. Breeding chronologies were conducted in both years for some of the more accessible nest sites. In 1995, harvesting operations began before some birds could successfully fledge their young. Trees and snags used as cavity-nesting substrate in 1993 and in 1994 were revisited throughout the summer of 1995 to determine degree of re-use; only 9 of these trees and snags were re-used from the preceding nesting seasons. All nest site and random site coordinates have been georeferenced using GPS devices and digitized into the Fundy Model Forest GIS at Sussex, and GIS analyses are currently underway with help from the ARC/VIEW program.

**Table 4.** Number of nests of each species of cavity-nesting bird from 1993 to 1995.

Species	1993	1994	1995	Total
Black-capped Chickadee	0	2	2	4
Downy Woodpecker	0	6	0	6
Hairy Woodpecker	4	5	3	12
Northern Flicker	0	4	2	6
Pileated Woodpecker	0	3	1	4
Red-breasted Nuthatch	6	9	7	22
Yellow-bellied Sapsucker	20	28	19	67

A total of 121 active cavities from 7 cavity-nesting species were found over the three field seasons (Table 4). Yellow-bellied Sapsucker was the most common species with a total of 67 nests. Of all tree species used as cavity trees, trembling aspen was by far the favoured species, accounting for 79.3% of all nesting cavities found from 1993 to 1995 (Figure 6), although, in basal area, aspen varied from 24% to as low as 5% in plots sampled. Red spruce was the most common species, followed by red maple and balsam fir. Yellow-bellied Sapsuckers have been shown to nest frequently in trembling aspen in the northeastern United States (Kilham 1971). Since much of the study area contains rather large aspen trees (25 to 45 cm dbh), it appears that the Hayward Brook Study Area

**Figure 6.** Distribution of active nests ( $n=87$ ) among tree species used by primary and secondary cavity-nesting species of bird in 1993 and 1994.



offers suitable habitat for most species of woodpecker. Although further analyses of the data will allow greater comment on that assumption, the importance of trembling aspen as a nesting substrate is apparent.

### Discussion

Indices of breeding bird species richness and density estimates are similar to results of breeding bird surveys of 1992 in nearby Fundy National Park (Christie 1993). In that study, densities of 2.75 to 3.89 pairs/ha and species richness of 15 to 22 were found in predominantly coniferous forests of the park. This compares well with predominantly coniferous sites at Hayward and Holmes Brooks (plots 1, 9 and 10) where densities ranged from 2.38 to 3.08 territories/ha and species richness ranged from 22 to 26. Mixed coniferous-deciduous sites in Fundy Park had densities of 2.31 to 3.89 pairs/ha and species richness of 17 to 22. Mixed sites at Hayward Brook (Plots 2, 3, 4, 5, 6, 7 and 8) had densities between 1.67 and 4.35 territories/ha and species richness of 18 to 32.

### Riparian habitats

Many studies have shown that certain riparian habitats support higher bird densities and/or a more diverse breeding community than forested upland habitats (Stauffer and Best 1980; Tubbs 1980; Swift et al. 1984). However, most of those studies were situated in areas where the contrast between riparian and upland habitats was obvious. The riparian zone at Hayward Brook was very narrow and differed little from the adjacent forested habitat. Mean density of bird



territories was not significantly different among the first four 30 metre zones from the stream (0 to 120 m). However, the mean density of breeding birds in zone 5 (120-150 m) was significantly less than in the others. The apparent lower densities in the outer zone may be due to the influence of edge. The boundaries of bird territories are more difficult to determine at the edge of a plot than within (Bibby et al. 1992). Also, the zones created at different distances from streams with the "buffer" function of the Arc/Info program may have extended partially beyond the edge of coverage of the census plots. The subsequent enlarged area of zone 5 would contribute to reduced density estimates for that outside zone. We conclude, therefore, that overall densities of breeding birds did not vary by distance from stream, which supports a similar study of second order streams in the Blue Ridge Mountain range of Virginia (Murray and Stauffer 1995).

It has been suggested that the width of riparian habitats may limit species richness of riparian avian communities (Manuwal 1986). Although distance from stream did have a significant effect on the densities of several species, no species was exclusively restricted to, or dependent upon the riparian area (i.e., the strip of alders and/or the opening of the canopy over the stream). Mean density of some species, such as Yellow-bellied Sapsucker and Winter Wren in 1993, Solitary Vireo in 1994 and Yellow-bellied Flycatcher, American Robin and Bay-breasted Warbler in both years, showed significant decreases with increasing distance from stream. The effect was most pronounced for the American Robin whose mean density was 431% higher near streams than at edges of census plots during 1993 and 277% higher in 1994. This species is known to be a forest edge dweller (Elliott 1987) and probably reacted to the canopy opening over streams similar to forest edge.

### Stand characteristics

Stand-type (for description of stands see Table 1) selection was examined for 23 species of breeding birds for 1993 and 1994 combined. Seventeen of 23 species were found to have a distribution that was significantly different from that expected (Table 5). Yellow-bellied Flycatcher, Red-breasted Nuthatch, Brown Creeper, Golden-crowned Kinglet, Swainson's Thrush and Yellow-rumped Warbler were the six species for which the hypothesis that their territories were evenly distributed among the different classes of stands sampled could not be rejected.

There was general agreement between analyses of breeding birds with forest stands and with basal area.

Surprisingly, no birds were related to densities of coniferous and deciduous stems taller than 1 m and less than 3 cm in diameter (the smallest stem classes measured). Studies elsewhere have found these variables significantly related to distributions of some breeding birds (Whitmore 1975; Anderson 1979; Niemi and Pfannmuller 1979). However, results from this study suggest that this level of forest classification may not be necessary for describing availability of avian habitat in the Acadian forest. Such measurements of habitat may be most applicable in mature stands where birds often use habitats above the shrub layers. The presence of lower vegetation would be most important in regenerating forest stands, i.e. where the overstory is reduced or absent. The densities of saplings (stems of 3 to 8 cm dbh) were related to the distribution of several birds, such as the American Robin, Veery, Black-and-white Warbler and Canada Warbler, all of which showed preference for coniferous saplings. The American Robin often nests within saplings (Godfrey 1986) while the other three species often nest at the base of shrubs or saplings. The Nashville Warbler and Ovenbird were most common where densities of deciduous saplings were highest.

Associations between many breeding birds and densities of large stems suggests selection for a mature forest structure. Birds such as the Red-eyed Vireo, Black-throated Blue Warbler, Canada Warbler, Ovenbird, Northern Parula, Bay-breasted Warbler, American Redstart and Black-capped Chickadee were all related to high densities of large deciduous stems. The Yellow-bellied Flycatcher, Red-breasted Nuthatch, Brown Creeper, Golden-crowned Kinglet, Yellow-rumped Warbler and Blackburnian Warbler were all related to high densities of large coniferous stems. By themselves, foliage profiles were not particularly suitable for describing bird habitat selection.

In summary, none of the 42 species of birds breeding at Hayward Brook were exclusively associated with riparian habitat. However, a few species, such as the Yellow-bellied Sapsucker and Winter Wren in 1993, Solitary Vireo in 1994, and Yellow-bellied Flycatcher, American Robin and Bay-breasted Warbler in both years, did have significantly higher densities near streams. Two species, the Black-throated Blue Warbler and the Ovenbird, had significantly lower densities near streams, similar to their avoidance of forest edge. The responses of established breeding bird populations, as defined during the first and second years of this study (1993, 1994) to timber harvesting and retention of forested stream buffers will be measured in 1996 and 1997.

It may be possible to predict the avifaunal communities over a defined landscape by knowing the forest stand composition of that landscape. More research is needed, however, to better describe bird/habitat relationships and to refine population predictions in other areas of the Fundy Model Forest. Although this study did estimate availability of avian habitat over a prescribed landscape, many questions remain unanswered. We know very little of the impact of forest fragmentation on distribution, abundance and reproductive rates of forest breeding birds. The impact of minimum area of breeding habitat is most evident and measurable in areas where fragmentation has resulted from agriculture and urbanization, but is less apparent where forested habitat is a patchwork of regenerating blocks of different ages following

disturbance, as demonstrated by Sabine et al. (1996) for Ovenbirds in New Brunswick. These questions are important when developing a forest-wildlife habitat management plan.

### Cavity-nesters

The relative abundances of the 7 dominant species of cavity-nesting birds illustrate the importance of the Yellow-bellied Sapsucker to that particular avifaunal guild. This one species occupied more than one-half of the total active nests located at Hayward Brook. Perhaps of greater significance to forest management strategies, was the high dependency by all cavity nesters on aspen trees, especially small-toothed aspen. Earlier studies of tree selection by cavity nesters in northern New Brunswick also found the Yellow-

**Table 5.** Relative difference (%) between observed and expected frequencies of occurrence of breeding territories within particular forest stand types in 1993 and 1994 combined (portions less than 5% of territory area were ignored). Expected frequencies based on proportion of total area covered by each stand type. Chi-square analyses of frequencies indicate whether or not species' territories were distributed evenly among stand types. See Table 1 for stand type definitions.

		STAND TYPES							No. of obs.	$\chi^2$	p
SPECIES	Area (ha) Area (%)	INTH/ THIH	INHW	IHSP	SPIH	SPTH/ THSP	SPBF/ BFSP	Pine			
		60.7 15.1	40.7 10.1	85.1 21.2	45.1 11.2	70.9 17.6	47.4 11.8	51.9 12.9			
Yellow-bellied Sapsucker		37	-15	6	-54	52	10	-73	116	20.1	0.003
Yellow-bellied Flycatcher		15	-69	-7	-23	29	20	10	127	10.1	0.120
Black-capped Chickadee		64	-21	-4	-45	40	-17	-52	113	17.7	0.007
Red-breasted Nuthatch		30	-3	-11	11	16	-32	-17	112	4.3	0.635
Brown Creeper		-11	-40	-25	-2	-17	34	79	82	10.8	0.095
Winter Wren		65	-67	10	-11	4	55	-87	60	14.9	0.021
Golden-crowned Kinglet		-26	-27	-6	-1	5	19	37	135	5.6	0.468
American Robin		130	-57	-11	-74	64	-14	-100	69	38.5	<0.001
Swainson's Thrush		27	-27	8	-54	26	7	-20	135	9.5	0.148
Veery		189	-82	-14	-100	86	-69	-100	55	57.1	<0.001
Red-eyed Vireo		86	73	16	-22	-20	-55	-86	57	18	0.006
Solitary Vireo		44	56	17	-46	-10	-30	-42	133	16.9	0.010
Northern Parula		8	55	-9	-41	40	-8	-49	166	18.5	0.005
Black-throated Green Warbler		4	66	8	-57	64	-49	-63	83	19.4	0.003
Black-and-white Warbler		115	-36	-14	-77	62	-23	-80	77	33.8	<0.001
Black-throated Blue Warbler		12	40	8	-19	16	-30	-36	254	14.1	0.028
Magnolia Warbler		56	29	-4	-43	38	-3	-48	280	36.8	<0.001
Yellow-rumped Warbler		-23	-23	-8	4	18	-12	41	77	3.3	0.766
Canada Warbler		113	-58	-16	-43	30	-9	-56	140	43.1	<0.001
Bay-breasted Warbler		84	-18	2	-50	14	0	-62	144	27.6	<0.001
Blackburnian Warbler		-37	-27	-13	8	17	3	51	189	13.5	0.036
American Redstart		148	39	33	-72	-29	-74	-88	64	38.8	<0.001
Ovenbird		25	64	4	-36	4	-54	-10	223	22.7	0.001
All species		39	-6	-2	-32	21	-9	-31	3189	178	<0.001

bellied Sapsucker to be most common, but there beech replaced aspen as the tree species most often selected for nesting (G. R. Parker, unpubl.).

This apparent selection of certain trees for nesting may be greatly influenced by tree availability. In the northern New Brunswick study area aspen were not common. Rather, large beech trees were an important component of the deciduous-dominated stands. In contrast, at Hayward Brook, beech was insignificant as a large-diameter tree, but aspen was very common, and trees in these 80-year-old mixed stands reached large diameters. If left undisturbed, much of the early- to mid-successional aspen component in these mixed stands would soon be replaced by spruce, pine, maple and yellow birch. It is uncertain whether following such forest successional change at Hayward Brook, cavity-nesting species would revert to other trees for nesting, such as maple and birch, or move to areas where aspen remained common and available. As few nests were found in other species of deciduous trees, we anticipate that populations of cavity nesters would change according to changes in the availability of aspen trees suitable for nesting.

The more common and abundant species of cavity nesters provide the most reliable information on the importance of certain species of trees, as well as the importance of microhabitats around those trees, to preferred nesting habitats and substrates. However, it is probable that the less common species, those more vulnerable to habitat change, deserve more immediate attention. At Hayward Brook, several of those species were the Pileated, Downy and Black-backed Woodpeckers, and the Northern Flicker.

Measurements of trees used by primary cavity nesters also showed that many were not dead or decadent snags. Rather, most (70%) were apparently fully or partially alive. Primary cavity nesters most likely "test" certain trees with tapping or initial short excavations in search of those most favourable for cavity nest construction, including a degree of early centre rot which would aid in cavity excavation. Such tree conditions may not be obvious from simple external visual examination, such as that given during most site examinations by foresters or biologists. At Hayward Brook 24% of trees (in 1993 and 1994) used by cavity nesters showed no indication of decay, and 70% showed only very early signs, such as one or several upper branches without leaves. Further comment may be possible following analyses of habitat measurements around trees used for nesting.

Studies at Hayward Brook raise serious questions relative to the effects of certain forestry management

practices on species of cavity nesting birds. For instance, leaving a few large, mature and often dying white pine or yellow birch trees in the middle of clearcuts to serve as nesting substrate for cavity nesters is of little value to most species. A few secondary cavity nesters, such as American Kestrels and Northern Flickers, which also prefer fragmented or open landscapes, may benefit from such trees, and although they may serve as foraging and roosting sites for others, their limited use should be recognized. It is most likely that potentially suitable cavity nest trees, such as large-diameter aspen, must be left in treed islands, or within corridors between contiguous forests, to serve any real value to most birds.

We encourage further experimental studies to measure the responses of many components of forest ecosystems to current and proposed timber harvest practices and forest management strategies. We do not believe that the extraction of wood fibre products should be the exclusive goal of sustainable forest management policies and strategies. Rather, the limits of forestry, which is the business of deriving economic gain from a single forest resource, i.e. timber, must be dependent upon the ability of a defined forested landscape subjected to forestry operations to maintain acceptable levels of ecological integrity. Research must obtain answers to ecological questions, and from this knowledge base provide resource managers, and the public, with management options. This, we suggest, is the challenge of integrated forest ecosystem management.

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## Appendix 1. Common and scientific names of birds mentioned in text.

Common name	Scientific name	Common name	Scientific name
Broad-winged Hawk	<i>Buteo platypterus</i>	Winter Wren	<i>Troglodytes troglodytes</i>
Ruffed Grouse	<i>Bonasa umbellus</i>	Golden-crowned Kinglet	<i>Regulus satrapa</i>
Barred Owl	<i>Strix varia</i>	American Robin	<i>Turdus migratorius</i>
American Woodcock	<i>Scolopax minor</i>	Veery	<i>Catharus fuscescens</i>
Common Nighthawk	<i>Chordeiles minor</i>	Swainson's Thrush	<i>C. ustulatus</i>
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Northern Parula	<i>Parula americana</i>
Chimney Swift	<i>Chaetura pelagica</i>	Nashville Warbler	<i>Vermivora ruficapilla</i>
Northern Flicker	<i>Colaptes auratus</i>	Canada Warbler	<i>Wilsonia canadensis</i>
Downy Woodpecker	<i>Picoides pubescens</i>	Magnolia Warbler	<i>Dendroica magnolia</i>
Black-backed Woodpecker	<i>P. arcticus</i>	Chestnut-sided Warbler	<i>D. pensylvanica</i>
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Black-throated Blue W.	<i>D. caerulescens</i>
Tree swallow	<i>Tachycineta bicolor</i>	Yellow-rumped Warbler	<i>D. coronata</i>
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Blackburnian Warbler	<i>D. fusca</i>
Least Flycatcher	<i>E. minimus</i>	Bay-breasted Warbler	<i>D. castanea</i>
Solitary Vireo	<i>Vireo solitarius</i>	Black-and-white W.	<i>Mniotilta varia</i>
Red-eyed Vireo	<i>V. olivaceus</i>	American Redstart	<i>Setophaga ruticilla</i>
American Crow	<i>Corvus brachyrhynchos</i>	Ovenbird	<i>Seiurus aurocapillus</i>
Common Raven	<i>C. corax</i>	Northern Waterthrush	<i>S. noveboracensis</i>
Gray Jay	<i>Perisoreus canadensis</i>	Red Crossbill	<i>Loxia curvirostris</i>
Black-capped Chickadee	<i>Poecile atricapillus</i>	American Goldfinch	<i>Carduelis tristis</i>
Boreal Chickadee	<i>P. hudsonicus</i>	Cedar Waxwing	<i>Bombycilla cedrorum</i>
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Brown-headed Cowbird	<i>Molothrus ater</i>
Brown Creeper	<i>Certhia americana</i>		

# Bird responses to the first cut of the uniform shelterwood silvicultural system in white pine forest

Andrea Kingsley and Erica Nol

## Abstract

The response of birds to the first cut of the white pine uniform shelterwood silvicultural system was examined in Algonquin Provincial Park, Ontario, in 1995 and 1996. Bird abundances and vegetation cover were compared between stands logged 2 to 18 years previously and mature stands with no recorded logging history. Of 61 bird species recorded, six varied significantly in relative abundance among treatments. Ruffed Grouse, White-throated Sparrows, Chestnut-sided Warblers, and Mourning Warblers were most abundant in recently cut stands, whereas Black-capped Chickadees were most abundant in stands with no recorded logging history. Ovenbirds were least common in stands cut 10 to 18 years previously and more common in both recently cut stands and those with no recorded logging history. Bird species richness was greatest in unlogged stands and in stands logged 10 to 18 years previously. Closed canopy and cavity-nesting species had the highest relative abundance in stands with no recorded logging history, whereas open-nesting species had the highest relative abundance in the recently cut stands. Bird communities in stands with similar logging history were similar, although there were some recently cut stands with similar communities to old cut stands. Percent cover of deciduous canopy and sub-canopy trees, and density of understory vegetation, explained significant variation in relative abundance of open shrub-nesting species. A longer rotation period would ensure higher numbers of canopy species and greater species richness in the landscape, although this method of timber harvesting is relatively benign in its impact on avian communities.

## Résumé

Nous avons étudié la réponse des oiseaux à la première récolte du système sylvicole de coupe progressive d'ensemencement uniforme en forêt de pins blancs dans le parc provincial Algonquin, Ontario en 1995 et 1996. L'abondance des oiseaux et le couvert végétatif furent comparés entre des parcelles coupées il y a 2 à 18 ans et des parcelles de forêt mature sans histoire de coupe. L'abondance de seulement 6 des 61 espèces observées variait de façon significative entre les traitements. La Gélinoite huppée, le Bruant à Gorge blanche, la Paruline à flancs marrons et la Paruline triste étaient plus abondantes dans les peuplements coupés récemment alors que la Mésange à tête noire était plus abondante dans les peuplements matures sans histoire de coupe. La richesse en espèces était plus élevée dans les peuplements intacts de même que dans ceux exploités il y a 10 à 18 ans auparavant. Les espèces de canopée fermée et les espèces nichant dans les cavités d'arbres étaient les plus abondantes dans les peuplements intacts alors que les espèces de milieux ouverts étaient plus abondantes dans les peuplements récemment coupés. Les variations dans l'abondance des espèces de milieux ouverts associées aux buissons étaient expliquées en grande partie par le pourcentage de couvert de la canopée décidue et des arbres de la sous canopée. Quoique cette pratique sylvicole ait relativement peu d'effets sur les communautés aviennes, une période de rotation plus longue assurerait la persistance d'un plus grand nombre d'espèces associées à la canopée de même qu'une plus grande richesse d'espèce dans le paysage.

Andrea Kingsley<sup>1</sup> and Erica Nol (corresponding author, [enol@trentu.ca](mailto:enol@trentu.ca)), Watershed Ecosystems Graduate Program and Biology Department, Trent University, Peterborough, Ontario, Canada K9J 7B8.

<sup>1</sup> (Current address: 4605 Highway 12, RR 2, Kentville, Nova Scotia, Canada B4N 3V8.)

## Introduction

White pine (*Pinus strobus*) is an economically and ecologically important species in Canada's mixed and southern boreal forests, especially in the Great Lakes-St. Lawrence Forest Region (Lowe 1994; Naylor et al. 1994). The management of these forests has recently been the focus of debate, as it is estimated that 80% of Central Ontario's forest-inhabiting wildlife use forests that contain red (*Pinus rugosa*) or white pine (Naylor et al. 1994).

Recent declines in neotropical migrant bird populations have been a cause for concern in both their breeding and wintering grounds, and habitat change is implicated as one possible explanation for the decline (Robbins et al. 1989; Thompson et al. 1995). Changes in breeding and wintering habitats may be due to logging and silvicultural practices, and may significantly affect avian populations at both the landscape and stand level (Franzreb and Ohmart 1978; Thompson et al. 1995). Information on how birds respond to clearcut logging is plentiful (Steffen 1985; Thompson et al. 1992; Welsh and Healy 1993; King et al. 1996; Norton and Hannon 1997), but there is less information on the effects of other silvicultural systems on bird communities (Franzreb and Ohmart 1978; Freedman et al. 1981; Thompson and Capen 1988; Thompson 1993; Thompson et al. 1995; Annand and Thompson 1997).

The uniform shelterwood silvicultural system results in gradual removal of the original forest rather than removing all or most trees in an initial cut, as is the case in a clearcut. A series of four cuts (preparation, regeneration, first removal, and final removal; Chapeskie et al. 1989), performed at twenty year intervals, removes the original stand while regeneration becomes established under the existing stand's canopy (Corbett 1994; Algonquin Forestry Authority (AFA) 1995; Thompson et al. 1995). The entire process is repeated after the passing of a further 40 years when the regeneration is 80 years old (AFA 1995). In Algonquin Park, Ontario, this silvicultural method has been used since the 1970's, at which time it was in an experimental stage. By the 1980's the system had been improved and deemed successful in promoting white pine regeneration (Chapeskie et al. 1989). Our purpose was to determine the effects of the first cutting of the uniform shelterwood silvicultural system on the abundance and richness of breeding birds, and on the vegetation structure of the white pine forests of Algonquin Provincial Park, Ontario. We predicted a loss of canopy species from the most recently cut stands, and a corresponding

increase in shrub-nesting species, because the canopy is thinned to 50% canopy cover after the initial cut (Chapeskie et al. 1989). We also predicted that logging, in general, would increase the total number of bird species in the Algonquin landscape, through the creation of a diversity of forest age classes (Welsh and Healy 1993). We examine the relationship between vegetation features and birds to determine which vegetation characteristics best predicted relative abundance of forest birds. We also use similarity coefficients to determine the similarity of the bird communities in stands at different stages of regeneration after the initial cut.

## Study sites and methods

The study was conducted on the east side of Algonquin Provincial Park, Ontario, Canada (44°10'N, 77°23'W). This area is dominated by white pine forests with trees that replaced the large white pine forests logged between 1850 and 1900 (Martin 1959). Existing white pine canopy trees were between 80 and 100 years in age and 25-30m in height (Naylor et al. 1994). The white pine forests in the study area are relatively continuous, separated only by logging roads and water bodies.

Forest stands with different logging histories were divided into three treatments: those logged between 1986 and 1994 (2-9 year cut), 1978 and 1986 (10-18 year cut); and stands without a written logging history (hereafter referred to as "old-cut"). Stands logged prior to 1978 were not included in this study because logging techniques other than the shelterwood system were used during those years, or the uniform shelterwood system was in an experimental stage (Kingsley 1998).

Stands were chosen using Forest Resource Inventory (FRI) maps, Ontario Ministry of Natural Resources (OMNR) and AFA logging history records. For a stand to be chosen it had to be accessible by road, have a minimum stand composition of 50% white pine, contain trees that were a minimum age of 70 years, fall into one of the three treatments, and be a minimum of 15 ha in size. Once stands were located, survey points for breeding birds were chosen within each stand (hereafter referred to as 'plot'). Points were placed at least 200 m from roads, water bodies or stand boundaries to minimize possible effects of edge habitat on bird and vegetation communities. The results from a total of 24 bird census plots from the spring of 1995 (old-cut [n=14]; 10-18 year cuts [n=10]); and 38 bird census plots from 1996 (old-cut [n=15]; 10-18 year cut [n=11]; 2-9 year cut [n=12]) are reported herein.

Most of the sites chosen in 1995 were recensused in 1996. Stands were never contiguous and were considered independent because they were separated by at least 500 m and usually over 1 km (up to 40 km).

### Vegetation survey

A total of 28 plots (nearly all of the plots used for bird census points in 1996), ten in the 2-9 year cuts, and nine in each of old-cut and 10-18 year cuts, were surveyed once in 1996, after the completion of the bird surveys (July). To determine the cover characteristics of each site, a square 400 m<sup>2</sup> quadrat was established within each of the plots, centred at the point count station used during the bird surveys and with the sides parallel to the four cardinal compass directions. Diameter at breast height (DBH) measurements were taken for all trees and snags greater than 10cm DBH in the quadrat. Percent cover estimates were also taken for six vertical forest layers (ground, 0 to 0.33 m in height; <2m, 0.33 to 2 m in height; 2-5 m; 5-10 m; subcanopy; and canopy). To measure percent cover of the two lowest layers, 10 quadrats of 1 m<sup>2</sup> were placed randomly (with the aid of a random number generator, and a grid system) within the 400 m<sup>2</sup> study quadrat. The percent cover of each species was estimated visually within each of the 1 m<sup>2</sup> quadrats. For species present in the higher layers, the percent cover was estimated within each of the four 100 m<sup>2</sup> quadrats of the 400 m<sup>2</sup> study quadrat. As percent cover was estimated for each species and many species overlapped in space, total cover could be greater than 100%. All plants were identified to species. Plant species were grouped into broad categories (e.g., ferns, herbaceous plants, shrubs, trees [coniferous or deciduous]).

### Surveys of forest breeding birds

In both years, breeding birds were monitored using a ten minute, unlimited distance point count (Ralph et al. 1993). Two counts were made at each point, between dawn and 09:30 EDT, during weather other than rain, hail or appreciable wind, all of which would affect the ability to hear birdsong. Counts included birds both seen and heard. To reduce problems associated with observer bias, only two comparably experienced observers performed surveys, and they were given approximately equal numbers of stands in each treatment to census, the same observer visiting the same set of plots for both of the two visits. The order in which the stands were surveyed was determined using a random number table. Totals of birds in the count circle were used as an index of relative

abundance for a stand.

To determine whether the two years' bird data differed significantly we compared relative abundances using a one-way ANOVA for each of the three treatments. Results differed between years only for Ovenbirds (Kingsley 1998); here we focus primarily on the 1996 results. One-way ANOVA was also used to determine if there were significant differences in the relative abundance of species among treatments, only for species that had occurred in a minimum of eight different plots in any of the treatments. We used the Least Significant Difference (LSD) Multiple Comparison test to determine where the difference(s) occurred. Where data on relative abundances were not normally distributed, we used the Kruskal-Wallis ANOVA. We used cluster analysis (UPGMA) with Euclidean distances on the relative abundance data to determine the pattern of clustering of the stands with different regeneration ages and a principal components analysis on the vegetation percent cover data to determine whether the data could be reduced to a smaller number of explanatory variables. We also used stepwise multiple regression to determine which principal components from the vegetation cover data explained variation in the relative abundance of bird species or selected habitat categories of birds.

Scientific names of all bird species mentioned in the text and tables are given in Appendix 1.

## Results

### Basal area, plant species richness and vegetation cover

As expected, average basal area of white pine, and of all species, was highest in the old-cut treatment, and lowest in the recently cut treatment (Table 1), although the basal area of snags did not vary significantly among treatments. The total number of stems of white pine, snags and all species was highest in the old cut treatment and lowest in the recently cut treatments. Plant species richness was highest in the 10-18 year cut treatment, because of the presence of species common to both open and closed canopies (Kingsley 1998).

We found few significant differences among treatments in the percent cover of different vegetative layers. Old-cut and 10-18 year cuts had significantly greater amounts of coniferous and total cover in the canopy than the 2-9 year cuts (Table 2), and percent cover of ferns in the <2m forest layer was significantly greater in the 2-9 year cuts than the remaining treatments (Kingsley 1998). Principal components



**Table 1.** Comparison of plant species richness, basal area and stem density of white pines, snags and all plant species, for each treatment. Basal areas in m<sup>2</sup>/ha, per plot; numbers in stems/ha.

Measure	Old cut	10-18 year cut	2-9 year cut
Mean basal area white pine *	24.7	22.8	10.7
Mean basal area of snags **	9.6	4.7	4.3
Mean basal area of all tree species **	40.8	35.1	18.8
Number white pine stems per ha	305.6	263.9	142.5
Number snag stems per ha	69.4	55.6	32.5
Total Number stems per ha	663.9	605.6	345
Total number plant species (unique species)	52 (6)	66 (9)	51 (3)

\*  $p < 0.05$ , \*\*  $p < 0.01$

analysis on the 13 variables describing percent cover of the vegetation layers resulted in four principal components (PC's) explaining 62% of the observed variance. The first PC (explaining 21.3% of the variance), contrasted stands with a high degree of deciduous cover in the canopy and subcanopy (positive values) and a large herbaceous layer (negative values, Table 3). Positive values of the second PC (20.3% variance explained) indicated stands with full coniferous sub-canopy and canopy layers and a sparse shrub layer, a situation typical of the old-cut stands (Tables 2 and 3). Recent cuts had high negative values, indicating a dense shrub layer and less coniferous canopy cover (Table 2). Positive values of PC4 (12.3% variance explained) indicated, by contrast, a high percent cover of the coniferous component in the 2 to 5, and 5 to 10 m heights (positive values), and a dense ground vegetation layer (negative values). Positive values of PC4 (8.7% of variance) appeared to describe stands with a well-developed herbaceous layer and a well developed coniferous sub-canopy, features seen primarily in the most recently cut stands (Table 2). The remaining principal components each explained less than 8% additional variance among vegetation variables.

**Table 2.** Percent cover of the 13 vegetation variables, and PC scores in each treatment from white pine forest stands in Algonquin Park in 1996.

Vegetation layer	Old cut	10-18 year cut	2-9 year cut
Tree seedlings	6.5	6.6	6.8
Ground layer	31.9	30.6	43.1
Herbaceous	31.7	40.6	46.8
Trees < 2 m	35.2	23.9	19.6
Shrubs < 2m	20.2	23.1	28.7
Deciduous shrubs 2-5m **	16.3	28.2	19.4
Coniferous shrubs 2-5m	34.8	33.3	13.4
Deciduous 5-10m	11.6	8.4	5.1
Coniferous 5-10m	16.5	16.2	14.6
Deciduous sub-canopy	10.1	5.8	1.9
Conifer sub-canopy	59.5	56.9	48.8
Deciduous canopy	4.7	3.4	0.7
Conifer canopy *	37.4	37.2	19.8
Sum	306.5	308.3	268.7
PC1	0.38	-0.13	-0.97
PC2	0.92	0.29	-0.32
PC3	0.08	0.10	-0.56
PC4	-0.44	0.09	0.14

\*  $p < 0.05$ , \*\*  $p < 0.01$

### Bird species richness and relative abundance

We recorded a total of 61 bird species in the two years of study. Of this total, the greatest number observed in any one treatment (all stands combined) during one year was 52, in 1995 in the old-cut treatment (Table 3, Appendix 1). Nineteen species were completely absent from all plots in one of the three treatments in the study period: eight of these were absent from the recent (2-9 year) cut stands (Downy Woodpecker, Olive-sided Flycatcher, Gray Jay, Ruby-crowned Kinglet, Swainson's Thrush, Cedar Waxwing, Common Yellowthroat, Pine Siskin) and present in the other treatments, two species were absent from the 10-18 year plots (Hairy Woodpecker, Eastern Woodpecker) and present in the other treatments, and one species (Yellow Warbler) was absent from the old-cut plots and present in the other treatments. Five species (Common Grackle, White-breasted Nuthatch, Cape May Warbler, Scarlet Tanager, Song Sparrow) occurred only once in one treatment and only one year.

**Table 3.** Eigenvectors for principal components (PC) 1-4 on percent cover vegetation data from Algonquin Park white pine stands.

Variable (% cover)	PC1	PC2	PC3	PC4
Tree seedlings	0.23	0.33	0.07	0.28
Ground shrubs	-0.28	0.22	-0.34	-0.34
Herbaceous layer	-0.30	-0.09	0.09	0.44
Trees < 2 m	0.20	0.42	0.12	-0.19
Shrubs < 2m	-0.15	-0.41	-0.06	-0.05
Deciduous trees 2-5 m	0.33	-0.32	0.04	0.16
Coniferous trees 2-5 m	-0.12	0.07	0.61	-0.33
Deciduous trees 5-10 m	0.47	-0.15	0.03	0.22
Coniferous trees 5-10 m	0.03	0.07	0.65	-0.009
Deciduous sub-canopy	0.45	0.03	-0.08	0.04
Coniferous sub-canopy	-0.17	0.39	0.01	0.43
Deciduous canopy	0.37	0.16	0.17	0.33
Coniferous canopy	-0.03	0.42	-0.16	0.18

Yellow-bellied Sapsuckers, Red-breasted Nuthatches, Nashville Warblers, Yellow-rumped Warblers, Blackburnian Warblers, and Ovenbirds occurred in at least 50% of the plots per treatment in both years, and were the most common species in the study area. Of these, Ovenbirds were the most ubiquitous species occurring in 61 of 62 point counts (98.3%, Appendix 1). Only a few species had a high frequency of occurrence in some treatments and substantially lower occurrence in another treatment: Blue Jay occurred in all recent cut plots and all 10-18 year cut plots in 1996, but only 40% of these plots in 1995; Black-capped

Chickadees occurred in over 90% of old-cut plots and fewer than 20% of recently-cut plots; White-throated sparrows occurred in over 70% of 10-18 year cut, and 2-9 year cuts but less than 60% of old-cut plots. Evening Grosbeak occurrence varied from 35.7% to 93.3% between plots within a treatment (Appendix 1). Most species occurred in a similar proportion of plots in 1995 and 1996, although Solitary Vireo and Evening Grosbeak occurred on many more plots in 1996 than in 1995, and Red-eyed Vireo occurred in over 90% of old-cut plots in 1995, but less than 35% of these plots in 1996.

When we examined average richness of the plots among treatments (number of species/plot), we found no significant differences in species richness among treatments (Table 4), in either 1995 ( $F = 0.66$ ,  $p = 0.42$ ) or 1996 ( $F = 0.38$ ,  $p = 0.68$ ). When we examined the proportion of species from different ecological guilds, among treatments, we also found no differences: in general species from each ecological community were present in each of the three treatments (Table 5). When comparing relative abundance among these categories, we found significantly greater numbers of individuals of open shrub nesting species in the recently cut treatments, and significantly greater numbers of closed canopy and cavity nesting species in the old-cut plots (Table 6). When we compared the number of individuals heard in the point counts among treatments we also found no significant difference (Table 6).

Cluster analysis using relative abundance of bird species from the different treatments indicated that, in general, old-cut stands clustered together, but some stands cut either recently or 10-18 years ago also clustered with old-cut stands (Figure 1). The old-cut

**Table 4.** Bird species richness data for three treatments from Algonquin Park, in 1995 and 1996.

Measure	Old-cut		10-18 year cut		2-9 year cut
	1995	1996	1995	1996	1996*
Mean ( $\pm$ SE) number of species/stand	17.8 (0.75)	20.7 (0.75)	16.8 (0.99)	21.2 (1.17)	20.1 (0.66)
Total number of species	52	46	44	51	46
Number of unique species	3		3		1
Total number of species in study period (% of 61)	55 (90.2)		55 (90.2)		46 (75.4)

\* The 2-9 year cuts were not sampled in 1995.

**Table 5.** Number of species in each treatment belonging to 12 different habitat associations in the three treatments. Some species belong to two groups (e.g., coniferous and canopy; see Appendix 1 for categorization).

Habitat	Old cut	10-18 year cut	2-9 year cut
Open (O)	6	6	7
Canopy	15	15	13
Coniferous (CO)	16	16	12
Generalists (G)	6	4	5
Mixed (MX)	5	5	4
White Pine (WP)	1	1	1
Deciduous (D)	8	5	6
Understory (U)	3	3	3
Spruce Budworm (SB)	1	3	1
Cavities (CV)	7	6	6
Edge (E)	1	2	1
Wetland (W)	1	1	0

stands were significantly more similar to each other, and hence more uniform in their bird communities, than the stands cut either 2-9 or 10-18 years ago (mean [SE] of Euclidean distances; old-cut to old-cut: 12.8 [0.17], 10-18 year cut to 10-18 year cut: 14.6 [0.23], 2-9 year cut to 2-9 year cut: 16.2 [0.43],  $F = 42.1$ ,  $p < 0.00001$ ). Across treatments, the greatest difference between treatments was between the bird communities in stands cut 10-18 years ago, and those cut 2-9 years previously (mean [SE] Euclidean distance = 15.6 [0.27]). The least difference was between old-cut stands and stands cut 10-18 years previously (14.18 [0.17]), whereas bird communities from old-cut stands

and those cut 2-9 years ago were intermediate in average similarity (14.7 [0.20], not significantly different than distance between old-cut and 10-18 years stands,  $p = 0.14$ , LSD multiple comparison test).

Of the 32 species that were present in at least 8 stands, only six varied significantly (or nearly so) in relative abundance among treatments (Table 7). In all cases but Ovenbird, both years showed similar trends (Kingsley 1998). Ruffed Grouse were in higher relative abundance (although not significantly so) in recently cut stands than in the other treatments. Old-cut stands contained significantly higher relative abundance of Black-capped Chickadees than the other stands. Chestnut-sided and Mourning Warblers were found seldom or not at all in old-cut stands and were common in recently cut stands. In 1995, there was no significant difference between treatments for Ovenbirds (ANOVA,  $F = 1.96$ ,  $p = 0.16$ ), but in 1996, there were significant differences among treatments with the 10-18 year cuts having significantly lower numbers of birds than the old-cut treatment (Table 7). White-throated Sparrows were significantly more abundant in the 2-9 year cuts than the old-cut stands.

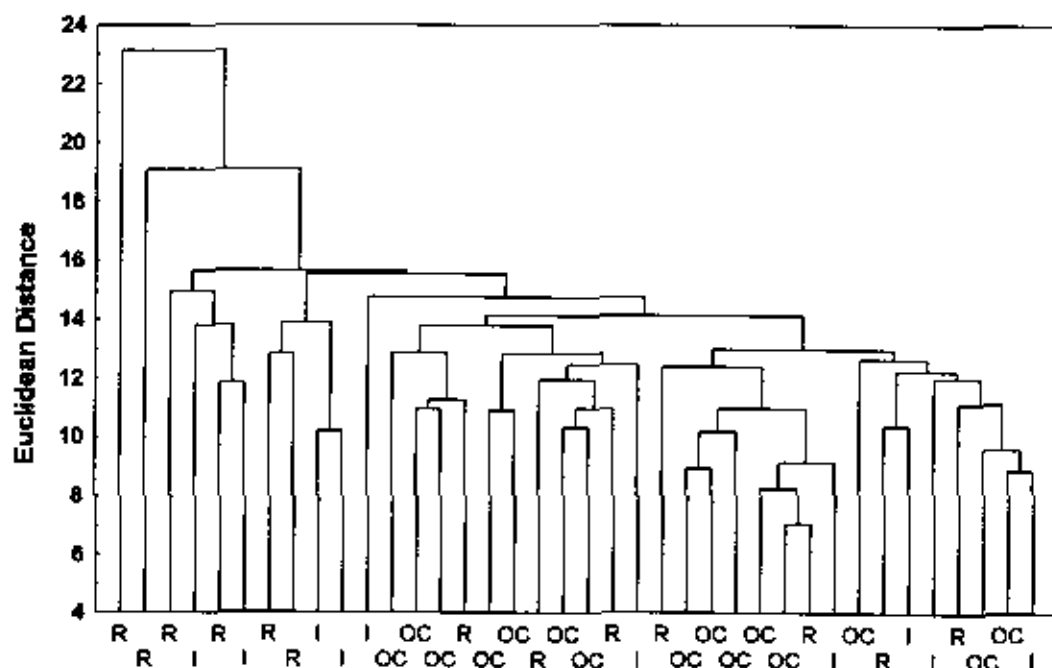
### **Vegetation and bird relationships**

The principal components of the vegetation data explained variation in relative abundance for only a small number of bird species, and not necessarily those that showed significant differences among treatments. Blue Jay relative abundance was higher in stands with low values of PC 1, the component indicating thick deciduous cover in the canopy and subcanopy (Table 8). Brown Creeper abundance was positively correlated with PC4 (greater herbaceous layer and coniferous subcanopy), Black-throated Blue Warblers were negatively associated with both PC1 and PC4 and

**Table 6.** Mean and (standard error) relative abundance of birds from seven habitat categories occurring in each of the three treatments in Algonquin Park.

Habitat preference	Old-cut	10-18 year cut	2-9 year cut	F	p
Cavities	5.8 (0.49)	3.7 (0.85)	3.5 (0.36)	5.2	0.01
Conifer	13.4 (1.27)	13.2 (1.89)	11.7 (2.08)	0.28	0.76
Closed Canopy	31.3 (1.34)	28.3 (1.85)	26.0 (0.70)	3.58	0.04
Open shrubs	4.1 (0.56)	7.5 (1.36)	14.8 (2.60)	11.45	0.0001
Understory	3.5 (0.51)	4.0 (0.86)	2.5 (0.61)	1.31	0.28
Ground vegetation	10.9 (0.78)	8.7 (0.68)	9.9 (0.94)	1.83	0.18
Generalists	14.3 (1.31)	14.2 (1.37)	15.8 (1.86)	0.35	0.70
Total individuals	57.5 (1.85)	59.6 (3.15)	61.0 (1.97)	0.29	0.74

Figure 1. Cluster diagram resulting from UPGMA on Euclidean distances of stands, based on relative abundance of bird species. OC = old-cut stands, R(ecent) = 2-9 year cuts, I(termediate) = 10-18 year cuts.



Black-throated Green Warblers were negatively associated with PC4. Veery abundance was higher in stands with high amounts of deciduous cover (PC1) and low amounts of coniferous cover (PC2). Mourning Warblers also were more abundant in stands with higher scores on PC4. White-throated Sparrow abundance was negatively related to PC1, the deciduous component of the forest. The relative abundance of no other species was related to these vegetative features. PC1 also explained a small, but

significant amount of variation in the relative abundance of all open shrub species (negative partial correlation, Table 8). The relative abundance of dense understory species was explained by PC2 (negative partial correlation). No principal component explained significant variation in the relative abundance of any other ecological group, although the total number of individuals was weakly (negatively) related to variation in PC2.

Table 7. Mean and (standard error) relative abundance of six species of birds in White Pine forests at different stages of cutting, in Algonquin Park.

Species	Old-cut	10-18 year	2-9 year	Statistic <sup>a</sup>	p
Ruffed Grouse	1.5 (.41)	1.3 (0.42)	2.7 (0.55)	3.20 <sup>a</sup>	0.053
Black-capped Chickadee	1.5 (0.34)	0.5 (0.40)	0.2 (0.10)	16.9 <sup>b</sup>	0.001
Chestnut-sided Warbler	0.5(0.24)	3.2(1.00)	5.5(1.54)	22.3 <sup>b</sup>	0.001
Mourning Warbler	0	0.3(0.23)	1.1(0.49)	13.1 <sup>b</sup>	0.005
Ovenbird	9.5(0.71)	6.6(0.85)	8.2(0.92)	3.93 <sup>a</sup>	0.029
White-throated Sparrow	2.1(0.61)	3.2(0.36)	4.5(1.17)	3.22 <sup>a</sup>	0.052

<sup>a</sup> Anova (F)

<sup>b</sup> Kruskal-Wallis  $\chi^2$

**Table 8.** The relationship between vegetative features and relative abundance for 6 species of birds and 3 ecological categories of birds found in White Pine forests in Algonquin Park, Ontario. Equations presented only when significant predictors of relative abundance were detected ( $p < 0.10$ ).

Species	Equation	$r^2$	p
Brown Creeper	$1.37+0.69PC$	20.8	0.02
Blue Jay	$2.15-0.38PC1$	24.8	0.01
Veery	$1.65+0.33PC$	13.6	0.063
Mourning Warbler	$0.24+0.35PC$	32.9	0.002
Black-throated Blue Warbler	4.66-	29.8	0.017
Black-throated Green	$4.75-0.60PC4$	12.7	0.075
Rose-breasted Grosbeak	$1.16+0.39PC$	13.2	0.068
White-throated Sparrow	3.16-	34.5	0.007
Open shrub species	$7.56-1.19PC1$	13.4	0.066
Dense understory species	$3.09-0.66PC2$	21.2	0.018
Number of individuals	$58.0-1.75PC2$	13.5	0.065

## Discussion

The uniform shelterwood logging system for white pine is an excellent system for pine regeneration on sandy soils characteristic of the region in the east side of Algonquin Park in central Ontario (Chapeskie et al. 1989). White pine regeneration in our study, judging by the stands cut 10-18 years ago, was good, with the basal area of white pine approaching that found in our old-cut stands. In other locations, where soils have greater organic content, white pine regeneration requires scarification through fire (Corbett 1994), a much more extreme disturbance to land bird communities, with large changes in both species composition and relative abundance of canopy dependent species (Dickson et al. 1983).

Our old-cut stands that had no record of cutting are presumably the closest in vegetation structure and bird communities to original old-growth white pine forests in central Ontario. The major impact of the timber harvesting appears to be a change in composition of a few bird species, with a slight reduction in the number of closed-canopy and coniferous associates, as predicted, and an increase of one open-shrub nesting species. Although the older cuts (both old-cut and 10-18 year cuts) contained almost 10 more species over the two years than the recently cut stands, there was substantial yearly variation in the total number of species found in one year in one treatment. Therefore, a second year of

surveying in the recently cut stands could possibly have resulted in similar species richness values in the 2-9 year cut and the detection of greater numbers of species (Smith et al. 1995). Unlike other studies where logging results in an increase in edge-related species, and an increase in overall species richness (Thompson and Capen 1988; Welsh and Healy 1993), the uniform shelterwood system, presumably because of the absence of intrusion of many edge species, resulted in no net change or possibly a slight reduction in richness across the landscape.

The relative abundance of birds from different ecological categories, and the relative abundance of particular species, were affected by this silvicultural method, particularly when comparing the bird communities in the recently cut stands with those from the old-cut stands. There was, as predicted, a decline in the relative abundance of species preferring closed canopy, and a substantial increase in the relative abundance of individuals from species preferring open shrubs for nesting. Unlike clearcutting, where both species composition and abundance are usually affected, we found that most of the closed-canopy species that occurred in the old cut stands were also present in the recently-cut stands, but in substantially smaller numbers. The loss of individuals of cavity-nesting species from both the intermediate aged stands and the recently cut stands is due primarily to the loss of Black-capped Chickadees, although the relative abundance of both Pileated Woodpeckers and Brown Creepers (the latter an occasional cavity user, Gauthier and Aubry 1996) was also lower in the recently cut stands.

Our intermediate treatment, where 10-18 years had elapsed for regeneration, demonstrates the relatively benign nature of this silvicultural technique, as most bird species that were not present in the more recent cut were present in this treatment, and the relative abundance of all species and ecological groups affected significantly by the cutting had approached that seen in the old-cut treatments. According to the silvicultural guidelines for the east side of Algonquin Park, the stands that were cut 18 years ago would undergo the next stage of cutting in two years (Chapeskie et al. 1989; N. Quinn pers. comm.), and these stands are predicted to lose canopy species and favour shrub-nesting species. Shrub-nesting species, in particular, Chestnut-sided Warblers, Mourning Warblers and White-throated Sparrows, generally respond positively to most silvicultural techniques (Titterton et al. 1979; Thompson and Capen 1988; Freedman et al. 1981; Falls and Kopachena 1994),

including the uniform shelterwood system. These species have healthy populations particularly outside of Algonquin Park (Cadman et al. 1988), where early successional stages predominate (Chapman and Putman 1984).

Our results indicated that the old-cut treatment had the highest degree of similarity among stands in bird communities, whereas the recently cut stands had the lowest degree of similarity. These results support the old idea that undisturbed ecological communities are more stable, or more predictable, than transitional communities (Horn 1975), despite the uniformity of the logging disturbance. The logged treatments would include, in some stands, both bird species from the undisturbed closed-canopy forest, as well as species that have newly colonized these stands. The underlying factors determining population colonization and extinction from forest patches is a research area that is relatively unexplored (Blake et al. 1994; Villard et al. 1995), but our data, showing very similar relative abundance of most species over two years of study, suggest relative stability of avian communities in successive breeding seasons across each treatment landscape.

Our measure of structural heterogeneity of the vegetation community, the sum of the vegetation layers, was not an important predictor of species richness at the stand level, a result contradictory to many other studies on bird communities (MacArthur et al. 1962; Karr and Roth 1971; James and Warner 1982; Niemi and Hanowski 1984; Steffen 1985; Thompson et al. 1995). The relative abundance of a small number of species was explained by particular features of the plant community; the most common explanatory variables were those that reflected the amount of deciduous and canopy cover and the extent of the herbaceous layer. These habitat variables explained the variation in relative abundance of Mourning Warblers and White-throated Sparrows. The gradual decrease in numbers of these species as the stand regenerated corresponded to the increase in canopy cover in the forest stands.

Some species, for which we found no significant vegetative feature that explained relative abundance, varied significantly in abundance among stands. The Black-capped Chickadee, a cavity-nester (primarily in small deciduous snags), was significantly more abundant in the old-cut treatments than in the other treatments. Unfortunately, we did not measure the density of small deciduous versus coniferous snags, and these were probably more common in the old-cut stands, as they would be lost through the logging

operations in the more recently cut stands. Chickadees prefer to excavate their nests in standing deciduous tree stumps with an average diameter of 10 to 18 cm at breast height (Peck and James 1987) and suitable nesting snags may limit population densities of this species (Smith 1993).

Several species had significant vegetative predictors but did not vary significantly among treatments, including Blue Jays and Brown Creepers. Presumably this result occurred because of the heterogeneity of vegetation features even within a single treatment. Blue Jays were negatively associated with habitats with a high degree of deciduous cover (PC1) in the subcanopy of the forest, features present to some degree in both the recent cuts and the 10-18 year cuts. Selective removal of this layer of the forest might result in vegetation characteristics that reduce the numbers of Blue Jays, a management technique that could be used to increase breeding success of some neotropical migrants that suffer extremely high rates of predation by this species (e.g., Red-eyed Vireo, Hanski et al. 1996; Burke 1998).

When analysed as ecological categories, the relative abundance of all open shrub species was explained by a negative partial correlation with the amount of deciduous cover, whereas relative abundance of dense understory species, like the Veery, was explained by principal components describing both deciduous and coniferous canopy cover. Although composition was affected, the relative abundance of conifer-associated species did not vary significantly among treatments, probably because most of these species were associated with conifers other than white pines (e.g., Golden-crowned Kinglets are associated with white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*); Gauthier and Aubry 1996). Generalists, as might be expected, were not affected by the silvicultural treatments, and their relative abundance was not related to any specific vegetation feature, indicating their very broad habitat preferences.

Point count data, although satisfactory for determining relative abundance (Ralph et al. 1993), do not provide an accurate assessment of the productivity of bird communities (Robinson et al. 1995). As Brown-headed Cowbirds (*Molothrus ater*) were never seen in the study area, cowbird parasitism is probably not an issue in the relatively continuous forest cover throughout Algonquin Park, a conclusion supported by other studies in eastern North America on bird communities in forested landscapes (Welsh and Healy 1993; Hanski et al. 1996; King et al. 1996; Sabine et

al. 1996). Relative abundance data from point counts can also overestimate productivity if predators respond positively to changes in vegetation structure as a result of timber harvesting (Welsh and Healy 1993; Hanski et al. 1996). Predators can greatly reduce the productivity of the habitat for breeding birds (Wilcove 1985; Andren and Angelström 1988; Rudnicki and Hunter 1993; Hanski et al. 1996). Although we do not have any information on mammalian predators, our data indicate that the egg predator, the Blue Jay, is not more common on the recently logged plots than in the old-cut plots, a result also similar to results from two other studies on timber harvesting and forest bird communities (Thompson et al. 1992; Welsh and Healy 1993).

Many species were not adversely affected by uniform shelterwood logging, including Winter Wrens and Ovenbirds, both species that use the forest floor for feeding and nesting, and most cavity-nesting species (e.g., woodpeckers, but not Black-capped Chickadees). This result is encouraging as woody debris, herbaceous plants, mosses, leaf litter and snags are often disrupted in clearcuts, and are important sources of food and nesting habitat for these groups of birds (Cadman et al. 1988; Van Horn and Donovan 1994; Naylor et al. 1996; Burke and Nol 1998). The provisions by the Algonquin Forest Authority for protecting these features in applying this method of timber management seem to be adequate for these species, although chickadee abundance suggests that smaller deciduous snags appear to have been reduced by logging.

## Management Recommendations

Owing to the loss of closed-canopy species, and lower densities of these species in the landscape, and the relative rarity of forested habitat in eastern Ontario outside of Algonquin Park (Chapman and Putman 1984), we recommend a longer rotation period (30-40 years for each cut, 120-160 year rotation) and the retention of 10% of remaining mature canopy trees in the final cuts in Algonquin Park. This will ensure that healthy populations of species that depend on a closed canopy will be maintained in these forests and in the region generally. Black-capped Chickadee populations in the east side of the park may be maintained by taking greater care, during timber harvesting, not to eliminate small deciduous snags. Continued use of this technique in Algonquin Park, with the above caveats, appears to be compatible with the goal of preserving avian biodiversity.

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**Appendix 1.** Percentage of plots observed (n) and habitat associations of bird species in the three treatments, in 1995 and 1996 in Algonquin Park.

Species	Old-cut		10-16 year cut		2-9 year cut
	1995	1996	1995	1996	
Ruffed Grouse <i>Bonasa umbellus</i> -G	0.286 (4)	0.467 (7)	-	0.272(3)	0.75(9)
Ruby-throated Hummingbird <i>Archilochus colubris</i> -G	0.071(1)	0.071(1)	-	-	-
Yellow-bellied Sapsucker <i>Sphyrapicus varius</i> -CV	0.642(9)	0.6(9)	0.6(6)	0.636(7)	0.917(11)
Downy Woodpecker <i>Picoides pubescens</i> -CV	0.214(3)	0.2(3)	-	0.182(2)	-
Hairy Woodpecker <i>P. villosus</i> -CV	0.071(1)	-	-	-	0.25(3)
Black-backed Woodpecker <i>P. arcticus</i> -CV	0.142(2)	-	-	0.091(1)	0.25(3)
Northern Flicker <i>Colaptes auratus</i> -CV	0.071(1)	0.267(4)	0.1(1)	0.454(5)	0.167(2)
Pileated Woodpecker <i>Dryocopus pileatus</i> -CV	0.142(2)	0.467(7)	0.1(1)	0.091(1)	0.25(3)
Olive-sided Flycatcher <i>Contopus borealis</i> -CO	0.071(1)	-	0.4(4)	0.091(1)	-
Eastern Wood-Pewee <i>C. virens</i> -D	0.071(1)	0.2(3)	-	-	0.25(3)
Least Flycatcher <i>Empidonax minimus</i> -D	-	0.071(1)	0.1(1)	0.364(4)	0.083(1)
Great Crested Flycatcher <i>Myiarchus cinerascens</i> -D	0.214(3)	-	0.3(3)	0.091(1)	0.083(1)
Gray Jay <i>Perisoreus canadensis</i> -CO	0.142(2)	0.2(3)	0.2(2)	0.091(1)	-
Blue Jay <i>Cyanocitta cristata</i> -G	0.643(9)	0.733(11)	0.4(4)	1.0(11)	1.0(12)
Common Grackle <i>Quiscalus quiscula</i> -CO	-	-	0.1(1)	-	-
Common Raven <i>C. corax</i> -CO	0.142(2)	0.33(5)	0.2(2)	0.273(3)	0.583(7)
Black-capped Chickadee <i>Parus atricapillus</i> -CV	0.929(13)	0.733(11)	0.8(8)	0.182(2)	0.167(2)
Brown Creeper <i>Certhia americana</i> -CO	0.357(5)	0.733(11)	0.3(3)	0.454(5)	0.417(5)
Red-breasted Nuthatch <i>Sitta canadensis</i> -CO	0.929(13)	0.867(13)	0.9(9)	0.727(8)	0.833(10)
White-breasted Nuthatch <i>S. carolinensis</i> -D	-	0.067(1)	-	-	-
Winter Wren <i>Troglodytes troglodytes</i> -CO	0.5(7)	0.467(7)	0.4(4)	0.727(8)	0.667(8)
Golden-crowned Kinglet <i>Regulus satrapa</i> -CO	0.357(5)	0.333(5)	0.5(5)	0.545(6)	0.167(2)
Ruby-crowned Kinglet <i>R. calendula</i> -CO	0.143(2)	0.133(2)	0.1(1)	0.273(3)	-
Veery <i>Catharus fuscescens</i> -US	0.571(8)	0.533(8)	0.6(6)	0.727(8)	0.333(4)
Swainson's Thrush <i>C. ustulatus</i> -CO	0.214(3)	-	0.1(1)	-	-
Hermit Thrush <i>C. guttatus</i> -MX	0.857(12)	0.8(12)	0.7(7)	0.454(5)	0.75(9)
Wood Thrush <i>Hylocichla mustelina</i> -D	0.071(1)	0.067(1)	-	-	-
American Robin <i>Turdus migratorius</i> -G	0.643(9)	0.467(7)	0.6(6)	0.273(3)	0.333(4)
Cedar Waxwing <i>Bombycilla cedrorum</i> -E	0.071(1)	-	0.3(3)	-	-
Solitary Vireo <i>Vireo solitarius</i> -CO	0.357(5)	0.933(14)	0.2(2)	0.636(7)	0.583(7)
Red-eyed Vireo <i>V. olivaceus</i> -D	0.929(13)	0.333(5)	0.9(9)	0.364(4)	0.333(4)
Tennessee Warbler <i>Vermivora peregrina</i> -SB	-	-	-	0.182(2)	-
Nashville Warbler <i>V. ruficapilla</i> -D	0.929 (13)	0.8(12)	0.8(8)	0.909(10)	0.917(11)
Chestnut-sided Warbler <i>D. pensylvanica</i> -O	0.286(4)	0.267(4)	0.9(9)	0.727(8)	0.833(10)
Magnolia Warbler <i>D. magnolia</i> -U	0.7(7)	0.667(10)	0.4(4)	0.545(6)	0.416(5)
Cape May Warbler <i>D. tigrina</i> -SB	-	-	-	0.091(1)	-
Black-throated Blue Warbler <i>D. caerulescens</i> -D	0.714(10)	0.733(11)	0.7(7)	0.818(9)	0.75(9)
Yellow-rumped Warbler <i>D. coronata</i> -MX	0.857(12)	1.0(15)	0.9(9)	1.0(11)	0.917(11)

## Appendix 1 (continued)

Species	Old-cut		10-16 year cut		2-9 year cut
	1995	1996	1995	1996	
Black-throated Green Warbler <i>D. virens</i> -CO	0.429(6)	0.533(8)	0.2(2)	0.454(5)	0.083(1)
Blackburnian Warbler <i>D. fusca</i> -CO	0.714(10)	1.0(15)	0.7(7)	0.818(9)	0.75(9)
Pine Warbler <i>D. pinus</i> -WP	0.429(6)	0.6(9)	0.5(5)	0.727(8)	0.583(7)
Bay-breasted Warbler <i>D. castanea</i> -SB		0.071(1)		0.182(2)	0.167(2)
Black-and-white Warbler <i>Mniotilta varia</i> -MX	0.5(7)	0.467(7)	0.3(3)	0.455(5)	0.167(2)
American Redstart <i>Setophaga ruticilla</i> -O	0.143(2)	-	-	0.182(2)	0.083(1)O
Ovenbird <i>Seiurus aurocapillus</i> -MX	1.0(14)	1.0(15)	0.9(9)	1.0(11)	1.0(12)
Northern Waterthrush <i>S. noveboracensis</i> -O	0.214(3)	0.2(3)	-	0.182(2)	0.083(1)
Mourning Warbler <i>Oporornis philadelphia</i> -O	0.071(1)	-	-	0.091(1)	0.416(5)
Common Yellowthroat <i>Geothlypis trichas</i> -W	0.071(1)	-	0.1(1)	0.273(3)	-
Canada Warbler <i>Wilsonia canadensis</i> -U	0.143(2)	0.2(3)	0.1(1)	0.182(2)	0.25(3)
Scarlet Tanager <i>Piranga olivacea</i> -O	-	-	0.1(1)	-	-
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i> -G	0.214(3)	0.467(7)	0.2(2)	0.455(5)	0.416(5)
Chipping Sparrow <i>Spizella passerina</i> -CO	0.285(4)	0.4(6)	0.3(3)	0.182(2)	0.333(4)
Song Sparrow <i>Melospiza melodia</i> -O	-	-	-	-	0.083(1)
White-throated Sparrow <i>Zonotrichia albicollis</i> -O	0.357(5)	0.533(8)	0.7(7)	0.833(10)	0.917(11)
Dark-eyed Junco <i>Junco hyemalis</i> -CO	0.071(1)	0.133(2)	-	0.273(3)	0.167(2)
Purple Finch <i>Carpodacus purpureus</i> -CO	0.286(4)	0.2(3)	0.4(4)	0.545(6)	0.5(6)
Red Crossbill <i>Loxia curvirostra</i> -CO	0.143(2)	0.2(3)	0.1(1)	0.091(1)	0.083(1)
Pine Siskin <i>Carduelis pinus</i> -CO	0.071(1)	0.067(1)	0.2(2)	0.091(1)	-
American Goldfinch <i>C. tristis</i> -G	0.143(2)	0.2(3)	0.1(1)	0.182(2)	0.167(2)
Evening Grosbeak <i>Coccothraustes vespertinus</i> -CO	0.357(5)	0.933(14)	0.5(5)	0.818(9)	0.75(9)

<sup>a</sup> Habitat Associations: O = open shrub, G = habitat generalists, CV = cavities, CO = coniferous (non-white pine), D = deciduous forest, MX = mixed woods, E = edge, US = understory, SB = spruce-budworm, WP = white pine, W = wetlands.

<sup>b</sup> No data.

# Snag characteristics and use as woodpecker drilling sites in harvested and non-harvested northern hardwood forests

**Frédéric Doyon, Jean-Pierre L. Savard, Daniel Gagnon  
and Jean-François Giroux**

## Abstract

Silvicultural practices can modify the availability and quality of essential habitat elements such as snags. In this study, we compared characteristics of snags and their use by woodpeckers (Picidae) as drilling forage in an extensive forest (~ 3600 ha) submitted to single-tree selection cutting and to strip cutting, while the last third was left non-harvested. A third of the 1312 snags (DBH  $\geq$  5 cm) sampled were used for foraging. Densities of snags (total and used) were 50% higher in the untreated area. Excavated snags had a larger DBH, and were shorter and more decayed than intact snags. Although snag characteristics (diameter, height and decay stage) did not differ among the three treatments, snags in the selection cut were used more often than expected while those in the strip cut were used less than expected. Tree species differed in their proportion of snags used for foraging. Since snag proportion (snags/live trees) also differed among tree species, attention should be given to shifts in composition in planning silvicultural practices if providing snags as good feeding sites for woodpeckers is a considered goal.

## Résumé

Les pratiques sylvicoles peuvent modifier la disponibilité et la qualité d'éléments de l'habitat forestier tels les arbres morts. Dans cette étude, nous comparons les caractéristiques des arbres morts et leur utilisation par les pics (Picidae) comme site d'alimentation dans une grande forêt (~ 3600 ha) soumise à une coupe sélective et à une coupe par bandes et où l'on a préservé un tiers de la forêt intacte. Un tiers des 1312 arbres morts (DHP  $\geq$  5 cm) échantillonnés étaient utilisés pour l'alimentation. Les densités d'arbres morts (totale et arbres utilisés seulement) étaient plus élevées dans le secteur intact. Les arbres morts utilisés avaient un DHP plus grand, étaient plus courts et plus décomposés que les arbres morts non-utilisés. Quoique les caractéristiques des arbres morts (diamètre, hauteur, stade de décomposition) ne différaient pas entre les trois traitements, les arbres morts dans la coupe sélective étaient utilisés plus fréquemment qu'espéré, alors que ceux de la coupe par bande étaient utilisés moins fréquemment qu'espéré. Toutes les espèces d'arbres morts n'étaient pas utilisées dans la même proportion par les pics. Puisque la proportion d'arbres morts (arbre mort/arbre vivant) différait aussi selon les espèces, on devrait se préoccuper des changements dans la composition spécifique des arbres en relation avec les pratiques sylvicoles, si l'on a pour but d'assurer des sites d'alimentation pour les pics.

F. Doyon<sup>1</sup>, Groupe de Recherche en Écologie Forestière, Université du Québec à Montréal, C.P. 8888, Succ. Centreville, Montréal, Québec, Canada H3C 3P8 ([fdoyon@iqaff.qc.ca](mailto:fdoyon@iqaff.qc.ca)); J.-P. L. Savard, Service Canadien de la Faune, 1141 route de l'Église, C.P. 10100, Ste-Foy, Québec, Canada G1V 4H5; D. Gagnon, Groupe de Recherche en Écologie Forestière, Université du Québec à Montréal, C.P. 8888, Succ. Centreville, Montréal, Québec, Canada H3C 3P8; J.-F. Giroux, Groupe de Recherche en Écologie Forestière, Université du Québec à Montréal, C.P. 8888, Succ. Centreville, Montréal, Québec, Canada H3C 3P8. <sup>1</sup> (Current address: Institut Québécois d'Aménagement de la Forêt Feuillue, 88 rue Principale, St-André-Avellin, Québec, Canada J0V 1W0.)

## Introduction

Snags have been recognized as a critical component of forest ecosystems (Hunter 1990). They are used for nesting, roosting, foraging, singing and hibernating by a variety of wildlife, especially woodpeckers (Conner et al. 1975; Scott 1978; Evans and Conner 1979; Miller and Miller 1980). Many studies have shown a negative impact of forest harvesting on snags. Managing forests for timber harvest can limit populations of cavity-nesting birds by changing either the distribution, abundance or characteristics of snags (Mannan et al. 1980; Dickson et al. 1983; Raphael and White 1984; Zarnowitz and Manuwal 1985; Schreiber and deCalesta 1992). However, few studies have addressed the impact of forest harvesting practices on the use of snags as feeding sites. In fact, several birds prefer snags as feeding sites (Evans and Conner 1979; Conner 1980), particularly those using drilling foraging techniques (Raphael and White 1984).

In hardwood forests of northeastern North America, single-tree selection cutting and strip cutting are both used to regenerate stands (Leak et al. 1987; Hornbeck and Leak 1992). During harvesting operations, many of the standing snags are felled for safety reasons or are knocked over by felling live trees. Consequently, in single-tree selection cutting, the dispersed harvesting of trees can destroy more snags than can local intensive strip cutting. Moreover, the retention of high quality trees associated with selection cutting eliminates defective stems and unhealthy trees which would eventually become snags (Stribling et al. 1990). Strip cutting, like all even-aged silvicultural systems, results in reduced snag size and density because the harvest rotation is shorter than the lifespan of most tree species (Conner and Crawford 1974). It also alters snag spatial distribution. Finally, the species composition of the snag community can also be altered by these forest practices. Selection cutting promotes regeneration of shade tolerant hardwoods, while shade intolerant hardwoods are more likely to become established in a strip cut.

We conducted this study in order to investigate the effect of two harvesting practices, single-tree selection cutting and strip cutting, when applied to an extensive forest landscape, on: (1) snag density, (2) snag characteristics, (3) proportion of snags per tree species, and (4) snag use by woodpeckers as drilling foraging sites.

## Study Area

Field work was conducted in southwestern Québec, 65

km north of Ottawa (45°45'N, 76°05'W), in the Gatineau Experimental Forest, a 36 km<sup>2</sup> forest, during summer 1993 and 1994. The landscape is characteristic of the Precambrian shield and elevations range from 675 to 1125 m. In this extensively (95%) forested region, the forest is composed of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), basswood (*Tilia americana*) and white ash (*Fraxinus americana*) with hemlock (*Tsuga canadensis*) on acid rock glacial tills. Mixedwood (*Abies balsamea* and *Picea glauca*) stands are found on fluvio-glacial deposits in the lowlands, and red oak (*Quercus rubra*) stands on the thin upland deposits. Early-succession stands are usually composed of red maple (*Acer rubrum*) associated with trembling (*Populus tremuloides*) and largetooth aspens (*Populus grandidentata*), and white birch (*Betula papyrifera*). Pileated Woodpeckers (*Dryocopus pileatus*) and Hairy Woodpeckers (*Picoides villosus*) are the main snag drillers in these forests, although Downy Woodpecker (*P. pubescens*) and Yellow-bellied Sapsucker (*Sphyrapicus varius*) occasionally excavate some snags for foraging.

At the beginning of the 20<sup>th</sup> Century, easily accessible, high quality timber trees might have been harvested by surrounding villagers who had the right at that time to harvest trees on crown lands for their personal use. Although the extent of this exploitation is not known, it was probably limited. During the same period, many fires occurred and approximately a third of the forest burned, mainly in the present day strip cut and untreated forest areas. After these fires, no major natural or artificial disturbance events occurred. In the early 1970s, the forest became the Gatineau Provincial Experimental Forest. This experimental forest has two parts: the Doyley Lake Forest (1100 ha) is about 8 km north of the Isabelle Lake Forest (2500 ha). Between 1982 and 1985, the Doyley Lake Forest was strip cut and about half of Isabelle Lake Forest was selection cut (single-tree). In the strip cut forest all stems with diameter at breast height (DBH, 1.3 m) 10 cm were to be removed in one of three strips every 30 years. At the time of our study, only one strip had been cut. Single-tree selection cutting varied in intensity between 15 and 30% of the basal area, removing trees from all merchantable (DBH 10 cm) diameter classes. Trees to be harvested were culled according to their ability to stay vigorous until the next entry (15-20 years later) and the quality of the stem, regardless of species. No specific guidelines for snag retention were given during either harvest operations. Although only a few snags were

**Table 1.** Proportion of sampling plots in the Gatineau Experimental Forest by habitat type, and availability of habitat types, prior to treatment.

Habitat types	Strip cutting	Selection cutting	Untreated	Total
	Plots % (availability %)	Plots % (availability %)	Plots % (availability %)	Plots % (availability %)
Shade-tolerant hardwood	54 (32)	74 (66)	64 (38)	64 (47)
Shade-intolerant hardwood	30 (45)	13 (12)	17 (22)	20 (25)
Mixedwood-conifer	16 (23)	13 (22)	19 (40)	16 (28)

deliberately cut for safety reasons, logging operations caused many to fall down (D. Joanisse, Québec Ministry of Natural Resources, pers. comm.).

## Methods

### Sampling

The forest was first stratified into shade tolerant hardwood, intolerant hardwood and mixedwood-conifer habitats, using forest cover maps (Gouvernement du Québec 1986; Majcen et al. 1986). Sampling plots were then randomly located across the treatment forests while trying to keep the habitat types balanced. However, proportion of habitat types differed between the three forests, mainly because the early century fires had increased the proportion of intolerant hardwood habitat in the strip cut and the untreated forests (Table 1). Because of that, and because the plots had to be 250 m apart and 100 m from any water body or wetland, the distribution of the plots is not totally balanced across the habitat types in the three treatments (Table 1), although not too far from it. We believe this sampling design ensures that differences will be attributed to the treatments instead of pre-treatment forest conditions.

We sampled 270 plots (91 in strip cut, 95 in selection cut, and 84 in untreated forest). Each plot consisted of five 80-m<sup>2</sup> circular micro-plots, located at the four corners and at the centre of a 60 m X 60 m square. Because of the random nature of the sampling design, some micro-plots in the two harvested forests were in cut areas, some were in uncut areas, and some straddled the two. In these micro-plots, we recorded the species and DBH of all living ( $\geq 10$  cm DBH) and dead trees ( $\geq 5$  cm DBH), with a caliper. Snag species were identified by their remaining bark and branching architecture. Using a clinometer, snag height was recorded by 3 m classes, except for the first 3 m which

was split into two classes (0-1.5, 1.5-3 m). We categorized snags in 5 decay classes according to the characteristics listed in Table 2.

**Table 2.** Snag characteristics used to assign decay classes.

Decay class	Snag characteristics
1	tree has recently died; bud, twigs, fine branches still apparent
2	bud, twigs, fine branches gone; bark deteriorating, loosening, beginning to slough off; sapwood still hard
3	only the limbs remain; tree top is broken; bark is extensively sloughed off; sapwood starting to soften and decay
4	only stubs of limbs remain; bark practically absent; most of sapwood is decayed; heartwood starting to soften; height significantly reduced
5	wood is completely rotten; vegetation has started to colonize snag; organic matter accumulated at base of snag

Evidence of foraging was noted according to three levels of feeding use: none (level of feeding = 0), few signs (0-3 signs, level of feeding = 1), abundant signs ( $>3$  signs, level of feeding = 2), using binoculars when needed. Signs of foraging by sapsuckers were not

included. Evidence of foraging was related to height areas (0-3 m, 3-9 m, 9-15 m, >15 m, top-3 m). The area use index (AUI) was then computed for each snag using the following equation [1]:

[1]  $AUI = \sum (\text{area height section} \times \text{level of feeding use of that section})$ .

The area of each section was obtained using the conic area formula, based on tree diameter and height. For snags with broken tops, previous height was estimated using a diameter-height regression from dendrometrical studies made in these forests (Majcen et al. 1984, 1985; Majcen and Richard 1989; Majcen et al. 1992). Total Area Use Index (TAUI) was obtained by adding all AUIs of each snag in the plot.

### Data Analysis

Snag characteristics per individual (DBH, height, decay stage and AUI) and per plot (density, basal area, TAUI) were compared among the three treatments and between used and unused snags using ANOVA (DBH, density, basal area, height classes, decay classes). Treatment effect on AUI and TAUI was tested with Kruskal-Wallis test. Comparisons among species were performed for diameter using ANOVA, and for height and decay using Kruskal-Wallis tests. When a significant effect was found, *a posteriori* tests were conducted to detect significant differences among levels (Bonferroni for ANOVA and SNK for Kruskal-Wallis). Snags used versus availability was compared with  $\chi^2$  using a confidence interval method (Neu et al. 1974) for each characteristic class (DBH, height, decay), in order to identify preference (Byers and Steinhorn 1984). Diameter classes used were 5-9.9 cm, 10-14.9 cm, 15-24.9 cm, 25-49.9 cm and  $\geq 50$  cm. We used the Spearman correlation coefficient to examine relationships among DBH, height and decay.

Snag proportion (snag versus living tree) and snag use (used versus unused snags) were compared among the three forest treatments using contingency analysis. In order to control for the tree species composition, snag proportion and snag use were modeled with a log-linear model (Agresti 1990), using tree species and forest treatments as independent variables. Infrequent tree species were removed until the contingency table had less than 20% of its cells with expected frequency < 5. Consequently, the tree species variable has 14 species categories for the snag proportion model and 12 for the snag use model. The model was fitted with the fewest number of parameters through backward hierarchical selection (SPSS Inc.

1988). Parameter estimates of the model were tested at the .05 level using their Z-value.

## Results

### Snag density

We measured 6708 live trees and 1312 snags representing 25 tree species. Snag density and basal area were higher in the untreated forest than in treated forests, for all and used snags only (Table 3). Although tree density was 10% lower in the strip cut and 21% lower in the selection cut forest areas, when compared to the untreated forest area, snag densities were as much as 24% and 38% lower in the strip cut and the selection cut respectively (Table 3). The selection cut forest had a significantly lower snag density than the untreated one for the first two diameter size classes (5-9.9 cm and 10-14.9 cm) while the inverse was true for the largest diameter class ( $\geq 25$  cm); the strip cut forest had significantly a lower density than the untreated. Density did not differ between the three forests for the 15-24.9 cm class. Of the only 8 snags  $\geq 50$  cm sampled, 5 were in the untreated, 2 in the selection cut, and 1 in the strip cut forest. TAUI differed among forest treatments (Table 3). However, even though the lowest snag density occurred in the selection cutting area, TAUI did not differ between the selection and the untreated forest.

### Snag Characteristics

Characteristics of used and unused snags did not differ among the three forest treatments (Table 4). Used snags had larger diameter, smaller height, and were more decayed than unused snags. We observed a greater percentage of use as the diameter increased (Figure 1A). Snags with DBH < 10 cm were under-used while those between 15 and 50 cm were over-used ( $p(\chi^2) < 0.05$ , Bonferroni corrected). Indeed, nearly 70% of snags  $> 25$  cm DBH were used for foraging. Snags taller than 6 m, were under-used (~25%) whereas shorter ones were over-used (~50%) (Figure 1B). Snag diameter and height were not highly correlated ( $r_s=0.11$ ,  $p=0.001$ ). Finally, use increased with the degree of snag decay (Figure 1C). Use of snags increased when they reached the third decay class. Decay was negatively correlated with height ( $r_s = -0.58$ ,  $p < 0.001$ ) but very weakly with diameter ( $r_s = 0.12$ ,  $p < 0.001$ ).

### Snag Proportion

The proportion of snags over live trees differed among the three forest treatments (Strip=19%, Selection=18%, Untreated=22%;  $\chi^2=13.4$ ,  $df=2$ ,

**Table 3.** Tree density, snag density by DBH class, snag basal area, and Total Area Use Index (TAUI).

Treatment Sample size		Strip cut n = 91	Selection cut n = 95	Untreated n = 84	p
Tree density (no./ha)		626±25A*	548±21B	698±21C	0.0001
Snag density (no./ha)					
DBH class	5-9.9 cm	52±4.9AB	40±5.3A	6.7±6.1B	0.002
	10-14.9 cm	32±3.6AB	24±2.9A	40±4.3B	0.006
	15-24.9 cm	29±3.5	22±3.0	33±4.8	0.087
	≥ 25 cm	6±1.4A	9±1.9AB	15±2.4B	0.004
All		118±8.2A	94±8.8A	156±10.5B	0.001
Used		39±4.1A	36±3.8A	56±4.5B	0.001
Snag basal area (m <sup>2</sup> /ha)	All	2.0±0.3A	2.1±0.3A	3.3±0.3B	0.001
	Used	1.0±0.2A	1.1±0.2A	1.8±0.2B	0.014
TAUI <sup>b</sup> (m <sup>2</sup> /m <sup>2</sup> )		0.22±0.04A	0.28±0.04B	0.39±0.05B	0.022

\* Mean ± 1 standard error. Means followed by different letters within each row are significantly different ( $p < 0.05$ ).

<sup>b</sup> Total Area Use Index (level of use \* m<sup>2</sup>/m<sup>2</sup>).

$p=0.001$ ). It was lower than expected in the selection cut area and higher than expected in the untreated area ( $p(\chi^2) = 0.05$ , Bonferroni corrected). However, when the effect of tree composition was controlled, snag proportion differed among the three forest treatments for only four species (red maple, ironwood, trembling aspen and balsam fir) with a significant interaction term (Table 5). When looking at the species effect only, snags of balsam fir, red maple, white birch, large-

toothed aspen and trembling aspen were over-represented, when compared to their proportion as live trees, while species like beech, white spruce, basswood and eastern hemlock were under-represented (Table 5).

#### Snag Use

Approximately 37% of sampled snags had been used, at least slightly, as drilling forage by woodpeckers. Intensity of use per individual snag as expressed by the

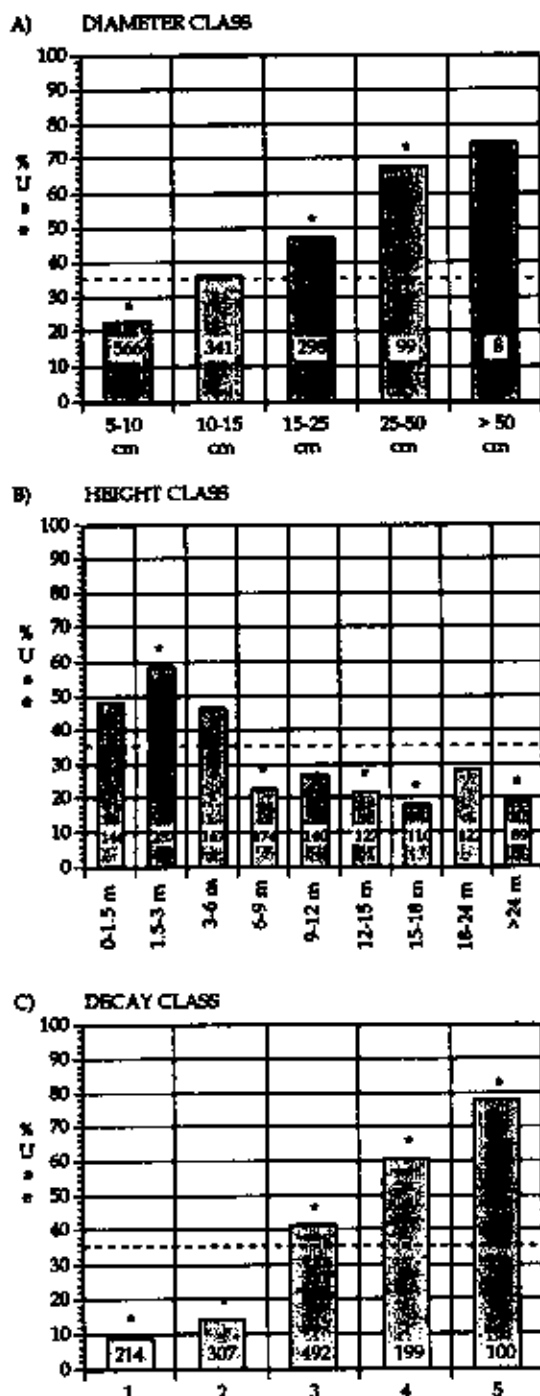
**Table 4.** Snag characteristics in a strip cutting, selection cutting, and untreated hardwood forest, southwestern Québec.

		Harvesting practice			Effects		
	Snag	Strip cutting	Selection cutting	Untreated	HP <sup>a</sup>	U <sup>b</sup>	HP × U
No. of snags	Unused	289	221	336			
	Used	142	136	188			
DBH (cm)	Unused	11.2±0.3A <sup>c</sup>	12.1±0.5A	11.9±0.4A	NS	0.001	NS
	Used	16.3±0.7B	16.9±0.9B	16.9±0.8B			
Height class	Unused	5.0±0.2A	5.4±0.2A	5.1±0.2A	NS	0.001	NS
	Used	3.4±0.2B	3.6±0.2B	4.0±0.2B			
Decay class	Unused	2.3±0.1B	2.3±0.1A	2.5±0.1A	NS	0.001	0.013
	Used	3.6±0.1B	3.3±0.1B	3.4±0.1B			
AUI <sup>d</sup>		2.3±0.3	3.1±0.3	2.8±0.3	NS		

<sup>a</sup> Harvesting practice; <sup>b</sup> Use; <sup>c</sup> Mean ± 1 standard error; means followed by different letters within each row and column for each parameter are significantly different ( $p < 0.05$ ); <sup>d</sup> Area Use Index (level of use \* m<sup>2</sup>).



Figure 1. Percentage of snag use by (A) diameter class, (B) height class, and (C) decay class (1 (least) to 5 (most) decayed). A star over the bar indicates over- or under-use ( $\chi^2$ ,  $p < 0.05$ , Bonferroni corrected), compared to the total percentage of use (dashed line). The number within each bar indicates the frequency of that class.



AUI did not differ among the three forest treatments ( $p=0.140$ , Table 3). Proportion of snags used did not differ among the three forest treatments (Strip = 33%, Selection = 38%, Untreated = 36%;  $\chi^2 = 2.3$ ,  $df = 2$ ,  $p = 0.32$ ). However, after controlling for the composition effect, snags were used less often in the strip cut area, and significantly more in the selection cut area, as expressed by the multiplicative coefficient (Table 5). Four species, beech, large-toothed aspen, trembling aspen and basswood, had foraging evidences more often than randomly expected while four species (balsam fir, red maple, sugar maple and ironwood) were less used (Table 5).

Snag characteristics differed among species. With the exception of the basswood, selected species usually had larger diameter and were more decayed (Table 6). Height was not as good in discriminating selected species and only differed between yellow birch and sugar maple, ironwood and balsam fir.

## Discussion

Forest cutting practices have considerably reduced snag abundance. In fact, snag density was proportionally more reduced than tree density in the two harvested forests, suggesting an accentuated detrimental effect of harvest on snags. However, this density reduction, although important (33%), might not have strongly affected the woodpecker community since snag densities ( $DBH \geq 10$  cm) in the untreated forests were actually higher than what has been observed in many other untreated hardwood forests in North America (McComb and Noble 1980; Carey 1983; McComb and Muller 1983; Chadwick et al. 1986; Sedgwick and Knopf 1986; Rosenberg et al. 1988). Indeed, even considering the lowest density observed among the three forests, snag availability was sufficient for maximum population density of small (Downy Woodpecker) and medium-sized woodpeckers (Hairy Woodpecker and Yellow-bellied Sapsucker) according to Evans and Conner (1979). However, nesting and foraging snag resources in treated forests might not be sufficient to support a healthy Pileated Woodpecker population which requires snags with  $DBH \geq 50$  cm, but our sampling method was not well designed to determine an accurate estimation of snag density of that size (Bull et al. 1990).

Globally, snag proportion (10.0%,  $DBH \geq 10$  cm, all three forests together) was within the range (4.5 - 10.2%) observed in other hardwood forests (McComb and Muller 1983; Chadwick et al. 1986; Conner et al. 1994). Like McComb and Muller (1983), we found that beech and red oak were poorly represented as

**Table 5.** Effects of tree species and harvesting practices on snag proportion and snag use proportion as expressed by the parameter coefficients of log-linear models.

Parameter (abbreviation)	Snag proportion <sup>a</sup>		Snag use <sup>b</sup>	
	Multiplicative Coefficient <sup>c</sup>	Z-value	Multiplicative Coefficient <sup>c</sup>	Z-value
Constant (K)	<u>0.1655</u>	-28.78	<u>0.6618</u>	-4.06
SPECIES EFFECT (SP)				
American beech (Fag)	<u>0.6610</u>	-3.01	<u>2.8344</u>	4.21
Balsam fir (Abb)	2.3101	7.56	<u>0.4299</u>	-4.25
Basswood (Tia)	<u>0.5265</u>	-2.5	<u>3.3489</u>	2.77
Eastern hemlock (Tsc)	<u>0.2667</u>	-2.79	0.3935	-1.76
Ironwood (Osv)	0.7176	-1.46	<u>0.1631</u>	-3.17
Large-toothed aspen (Pog)	<u>2.0431</u>	5.53	<u>2.3099</u>	4.32
Paper birch (Bep)	<u>1.7245</u>	3.58	1.3895	1.45
Red oak (Qur)	0.7917	-1.07	0.9280	-0.19
Red maple (Acr)	<u>1.3062</u>	2.71	<u>0.4961</u>	-3.85
Sugar maple (Acs)	1.0973	1.13	<u>0.6414</u>	-3.05
Trembling aspen (Pot)	<u>1.7417</u>	2.73	<u>2.5877</u>	2.87
White ash (Fra)	1.4623	1.21		
White spruce (Pig)	<u>0.4827</u>	-2.67		
Yellow birch (Bea)	1.3222	1.97	1.5556	1.79
HARVESTING PRACTICE EFFECT (HP)				
Strip cutting (SC)	0.8501	-1.67	<u>0.77</u>	-2.76
Selection cutting (SeC)	1.0116	0.13	<u>1.2913</u>	2.64
Untreated (UT)	1.1629	1.89	1.0058	0.07
INTERACTION EFFECT <sup>d</sup>				
Abb x SC	<u>0.6777</u>	-2.28		
Acr x SC	<u>1.6144</u>	3.51		
Acr x UT	<u>0.7007</u>	-2.67		
Osv x SeC	<u>2.1845</u>	2.85		
Pot x SeC	<u>2.2470</u>	2.63		

<sup>a</sup> Snag proportion log-linear model: Snag/living tree =  $K + Sp + HP + Sp*HP$ ,  $G = 0.000$ ,  $df = 0$ ,  $p = 1.000$ .

<sup>b</sup> Snag use selected log-linear model: Used/unused =  $K + Sp + HP$ ,  $G = 13.47$ ,  $df = 21$ ,  $p = 0.891$ .

<sup>c</sup> Estimates significantly different from 1 at  $p < 0.05$  are underlined.

<sup>d</sup> Only parameter coefficients significantly different from 1 are shown.

Table 6. Mean diameter (cm), height class and decay class of snags in southern Québec.

Species <sup>a</sup>	n	DBH		Height class		Decay class	
		Mean	SE	Mean	SE	Mean	SE
American beech +	75	18.6 A <sup>b</sup>	0.9	3.7 AB	0.3	3.0 AB	0.1
Balsam fir -	166	13.8 BCD	0.6	4.8 B	0.2	2.9 AD	0.1
Basswood +	21	13.5 ABCD	1.8	4.1 AB	0.6	3.1 ABCDE	0.2
Eastern hemlock	18	18.4 AB	1.9	4.6 AB	0.7	2.1 BCDE	0.3
Ironwood -	27	9.5 CD	1.6	5.5 B	0.5	2.2 DE	0.2
Large-toothed aspen +	131	18.2 A	0.7	4.2 AB	0.3	3.3 A	0.2
Paper birch	83	13.8 BCD	0.9	5.3 AB	0.3	2.9 ABCDE	0.1
Red maple -	210	11.0 D	0.6	4.7 AB	0.2	2.5 BCDE	0.1
Red oak	25	14.2 ABCD	1.6	5.4 AB	0.6	2.9 ABCDE	0.2
Sugar maple -	374	11.4 D	0.4	4.8 B	0.2	2.5 CE	0.1
Trembling aspen -	36	18.5 AB	1.4	3.9 AB	0.5	3.1 AC	0.2
White spruce	15	12.6 ABCD	2.1	4.6 AB	0.7	1.8 E	0.3
Yellow birch	67	15.5 ABC	1.0	3.7 A	0.4	3.5 A	0.1

\* + (more) or - (less) used than expected for foraging (Table 5).

<sup>b</sup> Numbers in a column sharing the same letter are not significantly different ( $p < 0.05$ ).

snags, when compared to live stems. On the other hand, unlike these authors, we found red maple snags were over-represented. Over- and under-representation result from species longevity, fate of dying stems (Tyrell and Crow 1994), snag durability (Morrison and Raphael 1993) and forest practices. For example, despite good snag durability resulting from high wood density, American beech's great longevity impedes snag formation. Inversely, many of the 10-15 cm balsam fir trees were attacked by *Scolytus* spp. (F. Doyon, pers. obs.), reducing their longevity and therefore promoting snag formation of small DBH (Table 6). However, we are aware that over-representation of species producing small DBH snags like balsam fir, paper birch and red maple could have also resulted from the fact that we have not sampled the live trees in the 5-9.9 cm class. Trembling aspen snag representation was affected by selection cutting practices as expressed by a strong positive interaction between trembling aspen and selection cutting (Table 5). Indeed, this species, based on the marking rules, was preferentially culled so as not to waste high quality stems between the last and the next entry. Residual unhealthy and poor quality live aspens were likely to become snags, whereas vigorous live trees had been considerably reduced by the harvest, leading to snag over-representation. Finally, long-lived and

easily uprooting species, like eastern hemlock (Tyrell and Crow 1994) and white spruce, are more likely to be under-represented in snags, as we observed.

Twelve years after treatment, forest harvesting practices did not alter snag population characteristics (diameter, height and decay). Only a few other studies have considered this aspect in response to forest practices. In their comparison between thinned and unthinned stands, Welsh et al. (1992) did not find a difference in snag diameter. However, in that case, thinning was executed with den and cavity tree retention guidelines. Hagan and Grove (1996) also did not see any difference in maximum snag DBH between a virgin hardwood forest and forests having been selection cut with different numbers of entries. In the strip cut forest, most of the snags were in the remaining intact green strips. Very few were observed in the strip cuts. Consequently, it is not surprising that the actual snag population still reflects the past distribution of the snag characteristics. In the selection cut, we expected that remaining snags, left after the selection cut, would be less decayed as a result of the application of tree felling security norms (Gouvernement du Québec 1981; Picher 1992) and the sanitation removal of some decayed snags, a practice generally included in the operations of this silvicultural system (Creha et al. 1987). Apparently,

snag felling indifferently occurred in all characteristic classes.

Larger snags were used to a greater degree. In our study, snags with a diameter over 20 cm were clearly selected, as reported in several other studies (Bull and Meslow 1977; Brawn et al. 1982; Raphael and White 1984; Rosenberg et al. 1988; Swallow et al. 1988). According to our results, this could not be attributed to a positive correlation between diameter and decay stage. One hypothesis is that larger snags offer more foraging area, more prey per tree and thus more food per unit area (Mannan et al. 1980; Raphael and White 1984) but our data did not allow us to test this hypothesis. It may be worthwhile to examine how the 20-cm threshold relates to prey density and optimal foraging bio-energetics.

Others attribute this relationship to a bias: large snags stand for a longer period of time than small ones, and evidence of foraging is more likely to occur on them (Cline et al. 1980; Dickson et al. 1983). This was probably also true in our study, however, most of the snags that had been excavated in the past usually still had fresh foraging signs, which suggests a positive feedback between excavating, wood decaying and prey density. Even if large diameter snags were selected for foraging, it does not dismiss small diameter snags as an important resource. We found that 23% of the snags in the 5-9.9 cm diameter class, which comprised 43% of all the snags, had foraging evidences. Rosenberg et al. (1988) had similar statistics.

Shorter snags were used more than expected and under-use significantly appeared for snags over 6 m high (Figure 1B). When a snag decays, it loses its branches and the top often breaks, reducing its height. The base and top of snags are used more often than any other height section (Conner et al. 1994). These two extremities are also more likely to be well-decayed, and therefore contain a higher arthropod biomass (Conner et al. 1994). Therefore, shorter snags should comprise a greater proportion of that high quality substrate, which requires less effort in order for woodpeckers to find prey. The large significant negative correlation between height and decay supports this explanation.

Foraging preference on oak (Conner 1980; Brawn et al. 1982; Conner et al. 1994) and elm snags (Swallow et al. 1988) has been observed, but never for beech, basswood, trembling aspen or large-toothed aspen, species that were significantly more used in our area. Under-use of red maple in foraging has also been noticed elsewhere (Conner 1980; Conner et al. 1994). Aspens have thin bark and low wood density (large-

toothed aspen and trembling aspen green wood specific gravity are 0.36 and 0.35, respectively (U.S. Forest Products Laboratory 1974)). These characteristics allow easy invasion by disease and decay organisms (Loehle 1988). Indeed, low wood density has been found to be inversely correlated with the number of foraging signs (Conner et al. 1994). Despite a high wood density (0.56), beech is frequently subject to beech bark disease (*Cryptococcus fagi/Nectria coccinea* var. *faginata*) and to frost split, causing the bark to crack. In addition to creating new microhabitats for insects, they expose sapwood to fungi invasion. In fact, snags of beech and aspens (trembling or large-toothed) were indeed more decayed than other species (Table 6). They were also larger, another feature of selected snags. Even if yellow birch was not selected more than expected at  $\alpha=0.05$  level (Table 5), it was not too far from it ( $p=0.073$ ). Since it has all the desired characteristics of forage snags (Table 6) and is one of the few that is long enough lived to provide very large (DBH  $\geq 50$  cm) snags, yellow birch should be considered an important snag-providing species. On the other hand, basswood snags, which were also more selected than randomly expected, were not larger or more decayed than other snags. Its very low wood density (0.32) probably gives it a softness similar to decayed denser wood.

## Conclusions

We have compared snag density, characteristics, and their use as forage sites by excavation by woodpeckers in two harvested forests and one left intact. Twelve years after a first entry, strip and selection cutting have had a strong impact on snag density but not on snag characteristics and tree species snag proportion. If the differences in snag density we observed after the first entry between the treated forests and the untreated one can be mainly attributed to harvest practices, as we believe, we are seriously concerned that such a reduction will bring snag density under some critical threshold after the next entry, if no retention guidelines are provided. Large diameter snags (DBH  $\geq 50$  cm), already rare, are likely to be extirpated, especially in the strip cut where recruitment will occur only in the last remaining green strip. We caution practitioners that a simple proportion calculation from tree density reduction to predicted residual snag density cannot be made. The felling of trees is critical in retention practices and recommendations should be given to woodcutters to maintain marked snags (Naylor et al. 1996). Our results suggest preferential retention of basswood, beech, aspen and yellow birch snags over 20

cm DBH, as favorable drilling forage for excavators. Greater consideration should be given to the dynamics of basswood and beech trees and snags, because these overused snags were proportionally poorly represented. Also, more quantitative information about foraging and nesting requirements for snag-dependent species is needed. Coupled with snag dynamics models (Morrison and Raphael 1993), snag density and quality could be managed through time in order to minimize the impact on snag-dependent species.

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# Strip-cutting: nest predation and breeding bird response to strip regrowth

Gilles Falardeau, Jean-Pierre L. Savard and  
André Desrochers

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## Abstract

We compared breeding bird abundance and nest predation rate in strip-cut stands of different age of cut and in clearcuts using the spot-mapping method. The forest was 50-70 years old and dominated by conifers. Timber harvesting created 20 m wide clearcut strips separated by 20 m interstrips of mature forest. Strip-cut plots had higher breeding bird densities and richness than clearcuts and final cuts (where the interstrip was cut). Strip-cut stands provided breeding opportunities for 28 forest-associated species not found in clearcuts or final cuts, whereas the latter habitats were used for nesting by 8 species not found in strip-cuts. Strip-cutting allowed the addition to the forest bird community of a few open country species such as Common Yellowthroat and Chestnut-sided Warbler. The abundance of these species decreased with forest regeneration. The regrowth dominated by deciduous trees and shrubs created suitable habitat for deciduous forest species such as Veery, Ovenbird, Canada Warbler and Rose-breasted Grosbeak. Predation rates on artificial nests did not differ between treatments or between strips and interstrips. Shrub nests, however, were more frequently preyed upon than ground nests, while well-concealed ground nests suffered the lowest predation. Bird communities were extremely dynamic, responding to changes in vegetation structure and composition. Strip-cuts permitted the retention of a large proportion of the forest bird community at least until the final cut. Thus, our results suggest that strip-cutting is an efficient compromise between forest harvesting and conservation, but only when interstrips are retained several years after the cut.

## Résumé

Nous comparons l'abondance des oiseaux nicheurs et le taux de prédation des nids dans des coupes par bandes d'âges différents et dans des coupes à blanc en utilisant la méthode des plans quadrillés. La forêt avait de 50 à 70 ans et était dominée par des conifères. La coupe forestière a créé des bandes de 20m de largeur séparées par des interbandes intactes de 20 m. Les parcelles dans les coupes par bandes avaient des densités et des richesses plus grandes d'oiseaux nicheurs que les coupes totales et les coupes finales (où l'interbande intacte a été coupée aussi). Les parcelles de coupe par bandes supportèrent 28 espèces d'oiseaux forestiers absentes des coupes totales et finales qui elles, ne supportèrent que 8 espèces absentes des parcelles de coupe par bandes. Les coupes par bandes ont permis l'addition de quelques espèces de milieux ouverts à la communauté d'oiseaux forestiers, par exemple, la Paruline masquée et la Paruline à flancs marrons. L'abondance de ces espèces a diminué avec la repousse de la végétation de la bande coupée. Cette repousse, dominée par des arbres et des buissons feuillus, a créé un habitat propice pour les espèces associées aux forêts feuillues telles que la Grive fauve, la Paruline couronnée, la Paruline du Canada et le Cardinal à poitrine rose. Le taux de prédation sur les nids artificiels ne différait pas entre les types de coupes ou entre les bandes et les interbandes. Cependant, les nids localisés dans les buissons ont été victimes de prédation plus fréquemment que les nids au sol. Les nids au sol bien cachés étaient aussi ceux ayant subi le moins de prédation. Les communautés d'oiseaux étaient très dynamiques, réagissant aux changements dans la composition et la structure de la végétation. Les coupes par bandes ont permis la rétention d'une grande proportion de la communauté des oiseaux forestiers, du moins jusqu'à la coupe finale. Alors, nos résultats suggèrent que la coupe par bandes est un compromis acceptable entre l'exploitation forestière et la conservation, mais seulement lorsque les interbandes sont préservées intactes pour plusieurs années.



Gilles Falardeau, Canadian Wildlife Service, 1141 Route de l'Église, P.O. Box 10100, Ste-Foy, Québec, Canada G1V 4H5; Jean-Pierre L. Savard (corresponding author), Canadian Wildlife Service, 1141 Route de l'Église, P.O. Box 10100, Ste-Foy, Québec, Canada G1V 4H5 ([jean-pierre.savard@ec.gc.ca](mailto:jean-pierre.savard@ec.gc.ca)); André Desrochers, Département des Sciences du bois et de la forêt, Pavillon Abitibi-Price, Université Laval, Ste-Foy, Québec, Canada G1K 7P4.

## Introduction

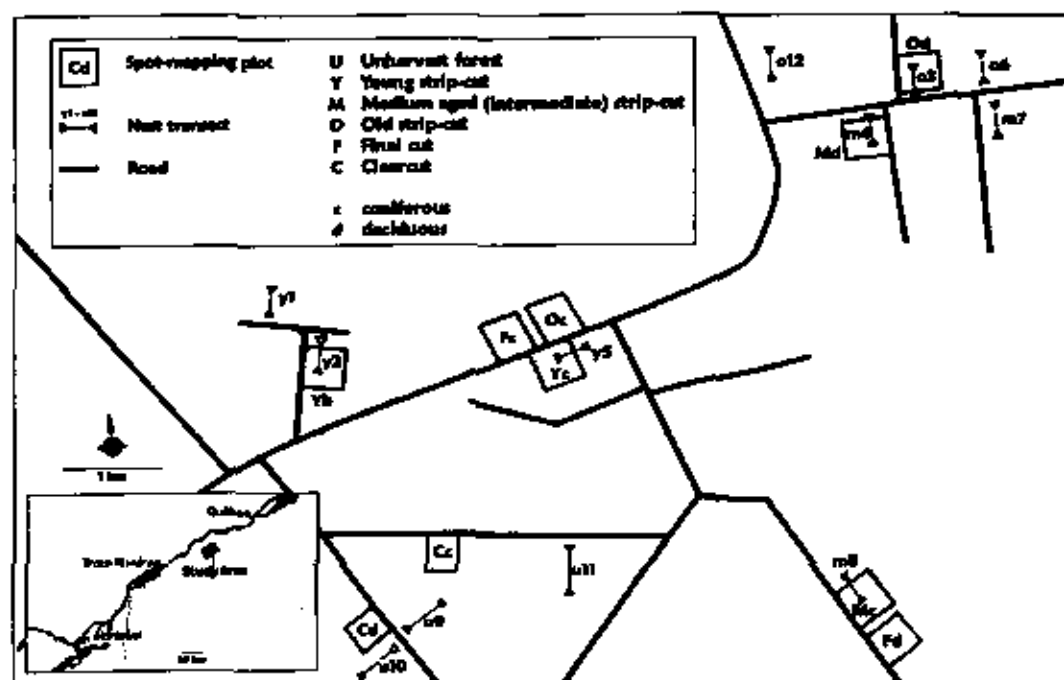
With Canada's ratification of the Convention on Biodiversity in 1992 the sustainable development of our forests has become a prominent issue (Biodiversity Science Assessment Team 1994). Sustainable forestry implies that harvesting activities are sustainable and do not permanently affect biodiversity in managed forest ecosystems (Hunter 1990; Salwasser 1990; Middleton 1994).

To achieve sustainable development of our forests and to be able to use harvesting practices as biodiversity management tools, it is essential to quantify the positive and negative impacts of each practice and regime of practices on biological diversity. The impact of forestry practices on birds is becoming increasingly quantified (Titterton et al. 1979; Crawford et al. 1981; Morgan and Freedman 1986; Welsh 1987; Hagan et al. 1997) and birds are

often used as umbrella species to protect other components of biodiversity (Welsh 1987; Savard 1994).

Strip cutting is most often used when a seed source needs to be preserved for natural regeneration, but is occasionally used as a compromise to clearcutting as a way of maintaining a temporary forest structure while extracting some wood. The impact of strip-cutting on birds is poorly known (Freedman et al. 1981; Doyon et al. 1994) and the response of birds to strip regrowth has yet to be studied. Little is known either of the impact of strip-cutting on breeding success of birds. Several studies have shown that in heavily fragmented agricultural or urban landscapes, nests located close to edges suffered higher probability of failure than nests located further away from edges (Gates and Gysel 1978; Andrén and Angerström 1988). However, studies in fragmented landscapes still

Figure 1. Sketch map of study area south-west of Québec City showing relative location of study plots and transects.



dominated by forest did not report similar trends (Yahner and Wright 1985; Rudnicki and Hunter 1993). Strip-cutting creates a large amount of edges. Such an increase in the proportion of habitat near edges could have significant impacts on the reproductive success of birds.

The goal of this study is threefold: (1) to document the changes in the composition of bird communities as harvested strips undergo succession; (2) to contrast bird communities of strip-cut areas with those of clearcuts and of final cuts, which are harvested areas whose interstrip has been removed several years after the initial cut; and (3) to compare nest predation in natural, strip-cut and clearcut forest stands.

## Study area

The study area, located about 60 km south-west of Québec city (Figure 1), was strip-logged from 1978 to 1990. Timber harvesting was done systematically with 20m wide harvested strips separated by 20m interstrips (Figure 2). The conifer forest was dominated by 50-70 year-old balsam fir and spruce trees ranging between 12 and 17 m in height. Located in the St. Lawrence lowlands, the area is rather flat and poorly drained due to a gleyed mineral soil (Dubé et al. 1993; Dubé et

Plamondon 1995). Temperatures average  $-13^{\circ}\text{C}$  in January and  $19^{\circ}\text{C}$  in July, with an average annual precipitation of 1228 mm (Environment Canada 1993).

## Methods

### Bird surveys

Breeding bird density was estimated using the spot-mapping technique (Williams 1936; Bibby et al. 1992). Ten spot-mapping plots of 10 to 14 ha each were surveyed in 1995. Two plots were located in five forest types: (1) recent strip-cuts (6 years old); (2) medium-aged or intermediate strip-cuts (10 years old); (3) old strip-cuts (14-15 years old); (4) final cuts (strip-cuts where the interstrip is cut after about 5-10 years of strip regrowth); and (5) clearcuts (3-5 years old). In each type, one spot-mapping plot sampled regeneration dominated by conifers and one by deciduous vegetation. Each plot was gridded at 40 m intervals to facilitate positioning of the birds except in clearcuts where a 50 m grid was laid. Plots were surveyed seven to eight times between 5 June and 4 July 1995. All censuses were conducted between sunrise and 1030h EDT, and observers were rotated between plots.

Figure 2. Aerial view of 20 m wide strip-cuts, also showing two final cut areas.



### **Vegetation surveys**

For each spot-mapping plot, except clearcut plots, vegetation cover was estimated visually at 80 points in the grid (40 in the strip, 40 in the interstrip). In clearcut plots 36 points positioned systematically throughout the plot were sampled. At each point we quantified regrowth in terms of proportion of conifer and deciduous species using five classes (conifer; conifer-deciduous; mixed; deciduous-conifer; deciduous). In the strip, we assigned a height class to the vegetation (<2 m, 2-5 m, >5 m) and evaluated the percent cover of the regrowth (<30%, 30-60%, >60%). At points located in interstrips, we estimated the percent cover of shrubs and trees <6 m (<10%, 10-40%, >40%). For trees taller than 6 m, we recorded only the coniferous-deciduous proportion because the overall tree cover was very uniform. Results were compiled using the number of stations classified visually in each height or cover categories.

### **Artificial nests**

We used artificial nests containing two Japanese Quail (*Coturnix coturnix japonica*) eggs to estimate predation in four forest types: uncut forest and three ages of strip-cut forest (young, intermediate, old). In each type we positioned three transects of 20 nests each oriented perpendicularly to the strips with nests located 20 m apart so that in strip-cut areas, 10 nests were located in strips and 10 in interstrips. Alternating nests were positioned in the following manner: 2 on the ground (1 in the strip, 1 in the interstrip), 2 at 1-2 m height (1 in the strip, 1 in the interstrip) and so on. Nests in shrubs were made of chicken wire and filled with mosses and leaves. Ground nests were depressions filled with dead leaves. We positioned a plastic chip under each ground nest to ensure relocation of depredated nests. Nests were visited at 7-, 14- and 21-day intervals. For each nest we recorded the number of eggs preyed upon. One observer classified each nest in three qualitative concealment categories: well, moderately and poorly hidden.

### **Data analysis**

The number of breeding pairs in each plot was estimated according to IBCC criteria (International Bird Census Committee 1970). Statistical analysis was limited due to small sample sizes. Species richness and breeding density were compared using a 2 factors ANOVA (forest type, regrowth type) with one observation per cell using the GLM procedure of the SAS software (SAS Institute, Inc. 1990a). As SAS cannot calculate the interaction between the two

factors when there is only one observation per cell, we used a test developed by Tukey (Montgomery 1984: 212-213). Homogeneity of variance was verified by plotting residuals against predicted values and normality of data was tested with the Shapiro-Wilk test of the UNIVARIATE procedure (SAS Institute, Inc. 1990b). We also used the number of detections during a census as a unit and averaged it over the seven or eight visits. This provided a relative abundance estimate for transient or non-territorial species (Appendix 1). To compare community structure among treatments, we used cluster analysis performed with the average linkage method (SAS Institute, Inc. 1990a). The similarity matrix obtained with Horn's index of similarity computed between each combination of plots was used as input data.

Artificial nest data were analysed with the SAS/INSIGHT unit of SAS, which allows adjustment of generalized linear models (SAS Institute Inc., 1993). Because the dependent variable was binary (1 = nest predation, 0 = no predation), we adjusted logistic regression models. The first model contained only strip-cut forest data with age of strip (young, intermediate, old), height of nest (ground or shrub), location (strip or interstrip) and concealment index (well, moderately, poorly hidden) as explanatory variables. The second model included data from both strip-cut and uncut forests with type of forest, height of nest and degree of concealment as explanatory variables. In both analyses interactions between explanatory variables were included in the model.

An adjustment was made to account for the over-dispersion of the data and Wald tests were used to determine if explanatory variables significantly improved the fit of the model.

## **Results**

### **Habitat features**

For a given age, the vegetation of the strip varied greatly according to whether the regrowth was predominantly coniferous or deciduous (Table 1). Conifer-dominated regrowth was more open and shorter than deciduous-dominated regrowth because of variation in rates of growth. The two intermediate (10 years old) strip-cuts were the most contrasting of the paired plots in term of vegetation structure and composition. In fact, from a structural perspective, the deciduous-dominated intermediate plot was quite similar to the conifer-dominated old-aged plot.

**Table 1.** Vegetation features of spot-mapping plots based upon 30-40 points within each plot (% of sampling points classified in the category). Vegetation types: Con = >60% conifer; Mixed = 40-90% deciduous; Dec = >90% deciduous.

Plot types: Y = young (6 yr old); M = medium (10 yr); O = old (14-15 yr); F = final cuts (interstrip removed); C = clearcut (3-5 yr old); c = conifer-dominated; d = deciduous-dominated.

Plot	Vegetation height in strip				Vegetation type in strip			Vegetation type in interstrip			>40% cover in interstrip
	<2m	2-5m	>5m	>60% cover	Con	Mixed	Dec	Con	Mixed	Dec	
Yc	55	55	-	3	-	63	37	93	7	-	80
Yd	42	58	-	70	-	2	98	63	22	15	97
Mc	100	-	-	5	-	85	15	100	-	-	68
Md	22	57	21	44	2	45	53	65	35	-	20
Oc	24	58	18	51	8	36	56	49	51	-	23
Od	15	85	-	75	-	7	93	58	40	2	93
Fc	84	16	-	0	11	81	8	21	72	7	-
Fd	57	43	-	7	-	90	10	13	87	-	-
Cc	81	19	-	19	-	78	22	-	-	-	-
Cd	47	53	-	56	-	14	86	-	-	-	-

### Breeding densities

The type of forest had an effect on breeding bird densities ( $F_{4,4} = 9.0$ ,  $p = 0.03$ ) and species richness ( $F_{4,4} = 37.2$ ,  $p = 0.002$ ). Strip-cut plots had higher breeding bird densities ( $\bar{x} = 51.2 \pm 3.1$  pairs / 10 ha,  $n=6$ ) than plots with no interstrips ( $\bar{x} = 37.1 \pm 2.5$ ,  $n=4$ ) (Table 2). Species richness was also higher in strip-cut plots ( $\bar{x} = 26.3 \pm 0.6$  species,  $n=6$ ) than in other plots ( $\bar{x} = 11.5 \pm 1.3$ ,  $n=4$ ). Species richness did not differ significantly between plots with conifer- and deciduous-dominated regrowth ( $F_{1,4} = 0.1$ ,  $p = 0.76$ ) but conifer-dominated plots tended to have higher breeding bird densities ( $F_{1,4} = 9.0$ ,  $p = 0.04$ ). However, differences were relatively small ( $< 7$  pairs) except for plots with 10 year old regrowth where the coniferous plot had 18 more breeding pairs. Two species accounted for that difference, the Common Yellowthroat (12.2 versus 2.6 pairs) and the White-throated Sparrow (8.4 versus 1.8 pairs). These two species still found suitable habitat in the shorter and more open coniferous regrowth but not in the higher and denser deciduous regrowth. Strip-cuts provided breeding opportunities for 28 forest-associated species not found breeding in final cuts and clearcuts. These latter habitats provided breeding habitat for eight species not found in strip-cuts. Final cuts supported more species than clearcuts.

Vegetation regrowth in strips reduced the density of species associated with open areas. Four species, abundant in final cuts and clearcuts, found adequate breeding habitat in newly-created strips but were much less abundant in older strips where vegetation regrowth formed a closed canopy. Those were the Chestnut-sided Warbler ( $\bar{x} = 6.9 \pm 0.6$  pairs / 10 ha,  $n=2$  in young strips vs  $2.3 \pm 1.1$ ,  $n=2$  in old strips), Mourning Warbler ( $1.0 \pm 0.2$  vs 0), Common Yellowthroat ( $8.9 \pm 0.2$  vs  $1.5 \pm 0.7$ ), and White-throated Sparrow ( $8.7 \pm 0.8$  vs  $5.1 \pm 1.9$ ). Three other species of open areas (Alder Flycatcher, Song Sparrow, Lincoln's Sparrow), although abundant in final cuts and clearcuts, did not use the open areas created by strip-cutting, likely requiring openings wider than 20 m. A few species responded positively to the increase in deciduous cover as the strip regrew, breeding at higher densities in the old deciduous strip-cut than in the young one (Veery, Nashville Warbler, Ovenbird, Canada Warbler, Magnolia Warbler, Black-and-white Warbler, Rose-breasted Grosbeak).

Vegetation structure and composition had a significant effect on bird communities. This is best illustrated by the intermediate strips which, although of similar age, were quite different in regrowth height ( $< 2$  m in MC and  $> 2$  m up to 5 m in MD) and composition (coniferous vs deciduous). The more

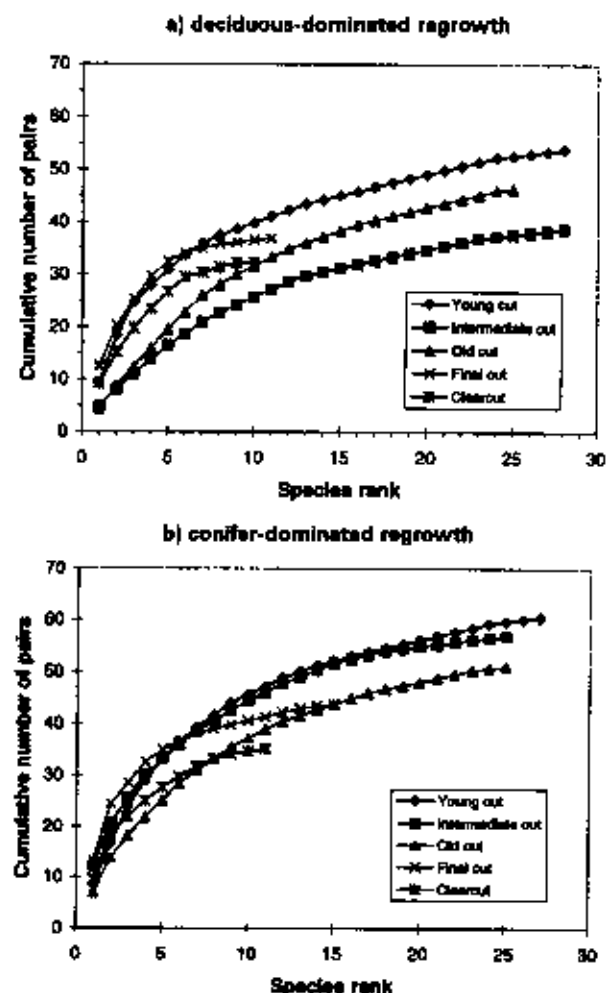
Table 2. Breeding bird densities (pairs / 10 ha) in various forest types.

Species	Strip-cut						Final cuts		Clearcuts	
	Young		Medium		Old		Con	Dec	Con	Dec
	Con (12.6 ha)	Dec (12.8 ha)	Con (11.9 ha)	Dec (13.6 ha)	Con (13.7 ha)	Dec (12.5 ha)	(12.3 ha)	(12.3 ha)	(9.8 ha)	(10.9 ha)
Ruffed Grouse		0.8			0.7	0.8				
Ruby-throated Hummingbird							0.8			
Yellow-bellied Sapsucker	0.8	0.8	1.7	0.7	1.1	0.8				
Hairy Woodpecker		0.4		0.7						
Black-backed Woodpecker	0.8									
Northern Flicker	0.8	0.4	0.4			0.4	0.8			
Pileated Woodpecker				0.4						
Eastern Wood-pewee	0.4	1.2								
Alder Flycatcher			0.4				4.1	4.5	2.0	2.8
Least Flycatcher		0.4								
Great Crested Flycatcher			0.4	0.4						
Tree Swallow										0.9
Blue Jay	0.8	0.8	0.8	0.7	0.7	0.8				
Black-capped Chickadee	2.4	0.8	1.3	0.7	1.1	1.2			0.5	
Red-breasted Nuthatch	0.8	0.8	0.8	0.4	0.7	0.8				
Brown Creeper				0.7						
Winter Wren	1.6	2.3	1.7	2.2	1.8	3.6				
Golden-crowned Kinglet	0.8		2.1			1.6				
Veery				0.7	3.3	1.2				
Hermit Thrush	2.8	0.8	1.7	1.5	2.6	2.0				
American Robin	0.4	0.8		0.7		0.8				
Cedar Waxwing	0.8	0.8	0.8	0.4	0.7	0.8	1.6	0.8	2.0	0.9
Solitary Vireo	1.2	1.2	2.9	0.7	0.4					
Red-eyed Vireo	0.8	1.6	0.4	2.9	1.1	1.2				
Nashville Warbler	1.2	1.2	2.1	3.3	3.6	3.2	0.8		1.5	
Chestnut-sided Warbler	7.3	6.3	2.9	4.8	3.3	1.2	4.1	4.9	1.0	
Magnolia Warbler	4.8	0.8	4.6	2.9	6.9	4.4	0.8			
Black-throated Blue Warbler	4.4	2.7	0.4	2.2	2.2	3.6				
Yellow-rumped Warbler	0.8	0.8	1.3	0.7	0.7					
Black-throated Green Warbler	1.6	3.1	2.5	1.5	1.5	4.4				
Blackburnian Warbler	2.4	3.1	3.0	0.4	1.1	0.8				
Palm Warbler							0.8	0.8		
Black-and-white Warbler	3.2		1.3	1.1	4.4	3.6	0.4			
American Redstart					0.7					
Ovenbird			0.4	1.5	1.1	2.0				
Blousing Warbler	0.8	1.2					1.6	0.4		
Common Yellowthroat	8.7	9.0	12.2	2.6	2.2	0.8	13.4	12.6	9.7	9.2
Canada Warbler					0.4	1.6				
Scarlet Tanager				0.7						
Rose-breasted Grosbeak	1.6	0.8	0.4	1.3	1.8	1.6				
Song Sparrow								2.8	3.6	4.6
Lincoln's Sparrow							2.4	1.6	3.1	3.2
Swamp Sparrow	0.4									
White-throated Sparrow	7.9	9.4	8.4	1.8	6.9	3.2	11.0	7.7	8.7	6.0
Dark-eyed Junco		0.4					0.4	0.4	2.6	3.7
Purple Finch								0.4		
American Goldfinch							0.8		0.5	0.9
Number of species	27	28	25	28	25	25	15	17	11	9
Number of pairs	60.3	53.5	57.1	39.0	51.1	46.4	43.9	37.0	35.2	32.1

open plot still had high breeding densities of Common Yellowthroat and White-throated Sparrow, whereas the more closed plot had higher breeding densities of Red-eyed Vireo, Chestnut-sided Warbler and Ovenbird, three species associated with deciduous vegetation. The breeding density of Magnolia Warbler increased from 0.8 pairs/10 ha in the deciduous-dominated young strip-cut to 4.4 pairs in the deciduous-dominated old strip. Conifer-dominated strip-cuts had high and similar breeding densities of Magnolia Warblers in young and intermediate strips (4.8 and 4.6 pairs), with the highest breeding density in the conifer-dominated old strip (6.9 pairs).

Bird community structure varied considerably between sampled forest types (Figure 3). The young strip-cut with deciduous regrowth had a bird community structure dominated by a few species, a situation similar to final cuts and clearcuts. The similarity in structure was due mainly to Common Yellowthroat and White-throated Sparrow, two species quite abundant in final cuts and clearcuts. Young strip-cuts, however, had twice as many species as final cuts or clearcuts. Bird communities of intermediate and old-aged strip-cuts, however, were less dominated by a few species. The importance of forest structure in defining bird communities is illustrated by the conifer-

Figure 3. Bird community structures in relation to forest types.



dominated plots (Figure 3) where open area species found adequate conditions in the short conifer regrowth of intermediate strip-cuts, which supported a bird community similar to young strip-cuts. This was not so in the taller deciduous regrowth.

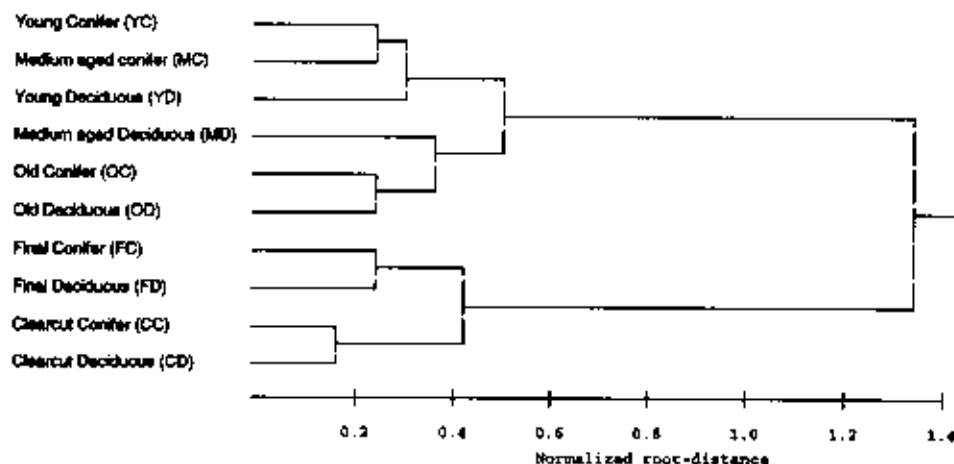
Bird communities of strip-cuts had a similar composition that differed as a whole from the communities of final cuts and clearcuts (Figure 4). They also differed more along their deciduous-conifer regrowth component than across ages. Intermediate plots with conifer regrowth, however, supported bird communities more similar to young strip-cuts than to older strip-cuts.

If we compute the number of individuals of each species seen during a spot-mapping survey and average this number over the total number of surveys, we obtain an estimate of relative abundance of species in the plot with an associated error estimate (Appendix 1). This is useful to obtain estimates for transient and non-territorial species. Generally these indices of relative abundance confirmed population trends observed from the breeding bird surveys, i.e. more species present in strip-cut plots ( $\bar{x} = 42.2 \pm 1.5$ ,  $n=6$ ) than in final and clearcut plots ( $\bar{x} = 28.0 \pm 2.0$ ,  $n=4$ ). Relative densities, however, were similar ( $\bar{x} = 52.5 \pm 2.7$  vs  $53.7 \pm 3.4$  birds). Results for individual species are quite variable but trends are similar to those observed using the number of territories (Appendix 1).

#### Predation rates of artificial nests

As expected, predation rates increased with exposure time but did not differ significantly between forest types in any of the exposure periods (Figure 5, Table 3). After 7 days of exposure, nests in shrubs suffered

Figure 4. Similarity of breeding bird communities (Horn index; average linkage clustering method).



the highest rates of predation, a pattern which persisted throughout the trials (Table 3). After 14 and 21 days of exposure, height and concealment interacted significantly to affect predation rates in the following manner; at first glance, it appears that ground nests were less frequently depredated than shrub nests (Figure 6) but a closer analysis taking into account nest concealment indicates that only well concealed ground nests experienced lower predation (three times less) than other nests (Table 4).

Because the number of nests in each concealment category varied greatly with nest height (more nests well concealed on the ground) and forest type, we adjusted predation rates by assuming a uniform distribution of nests in concealment categories among nest locations and forest types. Differences in predation rates between forest types that were not significant with unadjusted data differed even less after adjustments. However, shrub nests still suffered

**Table 3.** Logistic regression of predation rate in relation to forest type, nest height and degree of concealment for exposure times of 7, 14 and 21 days. df = degrees of freedom; significance (p) calculated using Wald test.

Source	df	$\chi^2$	p
<b>a) 7 days-exposure</b>			
Forest type	3	2.43	0.49
Nest height	1	5.12	0.024
Concealment	2	1.38	0.50
Type x height	3	2.05	0.56
Type x concealment	6	5.66	0.46
Height x concealment	2	4.29	0.12
<b>b) 14 days-exposure</b>			
Forest type	3	3.07	0.38
Nest height	1	10.13	0.002
Concealment	2	2.12	0.35
Type x height	3	4.03	0.26
Type x concealment	6	1.32	0.97
Height x concealment	2	6.72	0.034
<b>c) 21 days-exposure</b>			
Forest type	3	2.57	0.46
Nest height	1	7.33	0.007
Concealment	2	6.16	0.046
Type x height	3	6.30	0.098
Type x concealment	6	4.16	0.65
Height x concealment	2	6.40	0.041

higher predation rates than ground nests, although the difference is now smaller. No differences in predation rates were found between nests in strips and interstrips (1<sup>st</sup> week :  $\chi^2 = 0.19$ ,  $p = 0.66$  ; 2<sup>nd</sup> week :  $\chi^2 = 0.21$ ,  $p = 0.64$  ; 3<sup>rd</sup> week :  $\chi^2 = 0.52$ ,  $p = 0.47$ ).

**Table 4.** Relationships between predation rates, nest height and nest concealment.

Nest height	Concealment		
	Good	Average	Poor
Ground	0.21*	0.71	0.69
Shrub	0.71	0.63	0.83

\* predation rate

## Discussion

As expected, strip-cut areas retained several forest-species which continued to breed in the modified habitat. However, these species disappeared following the cut of the interstrip. Theoretically, the longer the removal of the interstrip is postponed the more vegetated the strip will become and the site might then attract and retain more forest-associated species than observed in this study. Strip-cutting permits the addition of open land species into the forest bird community. In this study, 20 m strips proved quite acceptable to Common Yellowthroat and Chestnut-sided Warbler, two species associated with open shrubby areas (Titterton et al. 1979, Morgan and Freedman 1986, Hagan et al. 1997) and which readily invade small openings (0.4 ha) in northern hardwood forests (Germaine et al. 1997).

The attraction of harvested strips to Common Yellowthroat may be due in part to the wet and humid soil conditions resulting from poor drainage. Some strips even had cattails growing in depressions created by machinery during harvesting. However, harvested strips proved too small for Song Sparrow, Lincoln Sparrow and Alder Flycatcher. Wider strips may be needed to attract these species. On the other hand, wider strips may reduce the use of strip-cuts by some forest species, as some species apparently included more than one interstrip in their territory. Rail et al. (1997) showed that the probability of crossing a gap larger than 20 m decreased rapidly for forest specialist

Figure 5. Predation rate in relation to forest type and exposure type.

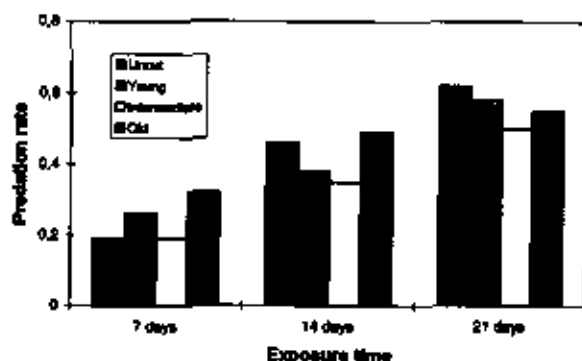
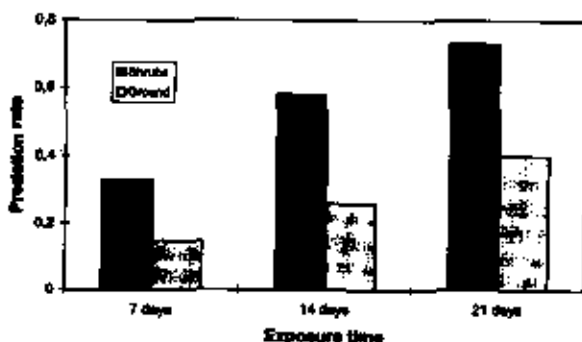


Figure 6. Predation rate in relation to nest height and exposure time.



birds. The slower growing conifer-dominated strips supported open area species longer than strips with more rapidly growing deciduous trees and shrubs.

Species associated with deciduous trees and shrubs (Rose-breasted Grosbeak, Ovenbird, Canada Warbler, Veery) invaded strip-cut areas with dense deciduous regeneration but not those with conifer-dominated regrowth. These species were rare in the uncut conifer-dominated forest (Falardeau and Savard 1999).

There have been few studies which have measured the impact of strip-cutting on breeding birds. Freedman et al. (1981) surveyed two small strip-cut plots (2.9 and 6.2 ha) in a hardwood forest of Nova Scotia, where breeding birds densities were 47.5 pairs and 57.5 pairs respectively, which is similar to our results. However, their species richness was much lower, only 13 and 10 species compared to 25-28 species in our study. This difference may reflect in part not only the smaller size of their plots but also the greater heterogeneity of our conifer-dominated mixed forest. Three species (Chestnut-sided Warbler,

Mourning Warbler, Common Yellowthroat), absent from their control hardwood forest, used strip-cut areas, as we also found. Song Sparrows did not use their strip-cut plots, but used clearcut plots, confirming their need for wider and more open areas (Freedman et al. 1981). Doyon et al. (1997) compared the relative abundance of birds in strip-cut and uncut hardwood forests in northwestern Québec. Their experimental design differed considerably from ours as they sampled strips 30, 60 and 90 m wide, separated by interstrips twice as wide as the strips and presented the data combined for these strip-cuts contrasting them with uncut forest. Four species (Chestnut-sided Warbler, American Redstart, Canada Warbler, Magnolia Warbler), were more abundant in strip-cut areas than in uncut forest. Interestingly, White-throated Sparrow and Common Yellowthroat were not abundant in their study area.

#### Nest predation rates

In contrast to predation studies conducted in agriculture and urban landscapes, studies in forest landscapes generally have not reported higher predation rates along edges. Some studies even recorded predation rates higher away from edges (Yahner and Wright 1985, Yahner and Cypher 1987, Rudnicki and Hunter 1993, Darveau et al. 1997). Our study supported those results, as we found no difference in rate of nest predation among and between strip-cut and uncut forests. This may in part be due to the recent origin of edges in forested landscapes compared to agricultural or urban areas where predator densities may be higher due to human sources of foods (Rudnicki and Hunter 1993).

The relatively narrow strips (20 m) we studied, may not create ecological edges as they are surrounded by 20 m strips of intact forest. Though questioned, the use of artificial nests still provides useful indications on predation risk (Major and Kendall 1996, Wilson et al. 1998). Our experiment did not reveal any major differences in nest predation rates between forest types or between strips and interstrips. Ground nests had lower probability of predation than shrub nests, which suggests that corvids and squirrels may be the most common predators in the type of forests we studied. However, caution is required in our conclusions as the fledging success of real broods in each forest type remains to be studied.

Clearly, more studies are needed to fully understand the dynamics of bird communities in relation to strip-cutting. Our study indicates that a substantial number of species can persist in a strip-



cutting regime, at least until the final cut. Of course the width of strips and interstrips will affect bird communities, with narrow strips favouring the retention of a greater part of the forest bird community and wider strips attracting more open land species. Bird communities were extremely dynamic, responding to changes in vegetation structure and composition. Strip-cuts where the interstrip is left uncut may prove to be effective in maintaining some forest-associated birds locally and to promote bird diversity. However, their value when the interstrip is removed will depend on the age of the regrowth at the time of removal. The younger the age, the more strip-cuts will approximate clearcuts, but older regrowth (greater than 20 years) may help retain some forest bird species.

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**Appendix 1.** Relative abundance of birds in the spot-mapping plots (mean [ $\pm$  S.E.] number of birds per 10 ha recorded during the spot-mapping survey). Vegetation types: Con = conifer; Dec = deciduous.

Strip age / type	Young strips		Medium strips		Old strips		Final cuts		Clearcuts	
	Con	Dec	Con	Dec	Con	Dec	Con	Dec	Con	Dec
Species	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.	n $\pm$ S.E.
American Bittern								0.23 $\pm$ 0.13		
Green Heron				0.11 $\pm$ 0.11						
Northern Harrier						0.10 $\pm$ 0.10			0.15 $\pm$ 0.15	0.15 $\pm$ 0.13
Northern Goshawk										0.15 $\pm$ 0.13
Broad-winged Hawk		0.10 $\pm$ 0.10						0.12 $\pm$ 0.12	0.29 $\pm$ 0.19	
American Kestrel				0.11 $\pm$ 0.11				0.12 $\pm$ 0.12	0.15 $\pm$ 0.15	0.26 $\pm$ 0.17
Ruffed Grouse		0.98 $\pm$ 0.87		0.11 $\pm$ 0.11	0.46 $\pm$ 0.27	1.10 $\pm$ 0.68				
Virginia Rail									0	0.15 $\pm$ 0.13
Mourning Dove	0.10 $\pm$ 0.10						0.23 $\pm$ 0.23			
Black-bellied Cuckoo				0.21 $\pm$ 0.21		0.26 $\pm$ 0.20				
Northern Saw-whet Owl						0.10 $\pm$ 0.10				
Chimney Swift			0.11 $\pm$ 0.11	0.74 $\pm$ 0.42	0.09 $\pm$ 0.09	0.60 $\pm$ 0.25				
Ruby-throated Hummingbird				0.11 $\pm$ 0.11	0.09 $\pm$ 0.09					
Belted Kingfisher				0.11 $\pm$ 0.11			0.35 $\pm$ 0.16	0.12 $\pm$ 0.12		
Yellow-bellied Sapsucker	0.89 $\pm$ 0.33	0.66 $\pm$ 0.23	1.79 $\pm$ 0.37	0.74 $\pm$ 0.28	0.73 $\pm$ 0.31	0.90 $\pm$ 0.49	0.23 $\pm$ 0.15			
Downy Woodpecker	0.10 $\pm$ 0.10				0.09 $\pm$ 0.09	0.20 $\pm$ 0.20				
Hairy Woodpecker	0.10 $\pm$ 0.10	0.29 $\pm$ 0.21		0.63 $\pm$ 0.23	0.09 $\pm$ 0.09	0.10 $\pm$ 0.10		0.12 $\pm$ 0.12		
Black-backed Woodpecker	0.30 $\pm$ 0.21	0.10 $\pm$ 0.10	0.11 $\pm$ 0.11						0	0.13 $\pm$ 0.13
Northern Flicker	0.39 $\pm$ 0.48	0.10 $\pm$ 0.10	0.53 $\pm$ 0.27	0.32 $\pm$ 0.22	0.09 $\pm$ 0.09	0.40 $\pm$ 0.21	0.70 $\pm$ 0.28	0.23 $\pm$ 0.15	0.15 $\pm$ 0.15	
Pileated Woodpecker	0.20 $\pm$ 0.13		0.11 $\pm$ 0.11	0.42 $\pm$ 0.22	0.09 $\pm$ 0.09	0.10 $\pm$ 0.10				
Olive-sided Flycatcher							0.23 $\pm$ 0.23		0.15 $\pm$ 0.15	
Eastern Wood-Pewee	0.40 $\pm$ 0.21	1.66 $\pm$ 0.38		0.21 $\pm$ 0.14						
Yellow-bellied Flycatcher		0.20 $\pm$ 0.13	0.21 $\pm$ 0.21		0.09 $\pm$ 0.09	0.20 $\pm$ 0.20				
Alder Flycatcher			0.52 $\pm$ 0.22	0.21 $\pm$ 0.14			4.07 $\pm$ 1.16	3.11 $\pm$ 1.00	2.04 $\pm$ 0.70	2.1 $\pm$ 0.79
Least Flycatcher		0.39 $\pm$ 0.21								
Eastern Phoebe				0.11 $\pm$ 0.11						
Great Crested Flycatcher	0.20 $\pm$ 0.13		0.32 $\pm$ 0.22	0.21 $\pm$ 0.14	0.18 $\pm$ 0.18	0.10 $\pm$ 0.10				
Tree Swallow								0.35 $\pm$ 0.35	0.29 $\pm$ 0.29	1.44 $\pm$ 0.19
Gray Jay			0.11 $\pm$ 0.11							
Blue Jay	1.19 $\pm$ 0.40	1.27 $\pm$ 0.44	0.84 $\pm$ 0.42	0.63 $\pm$ 0.19	1.37 $\pm$ 0.58	0.50 $\pm$ 0.21	0.23 $\pm$ 0.15	0.25 $\pm$ 0.25	0.15 $\pm$ 0.15	0.13 $\pm$ 0.13
American Crow			0.11 $\pm$ 0.11	0.11 $\pm$ 0.11						
Common Raven				0.11 $\pm$ 0.11	0.09 $\pm$ 0.09					
Black-capped Chickadee	2.98 $\pm$ 0.82	1.17 $\pm$ 0.47	1.26 $\pm$ 0.48	0.63 $\pm$ 0.23	1.37 $\pm$ 0.56	2.70 $\pm$ 1.09	0.81 $\pm$ 0.39	0.12 $\pm$ 0.12	0.58 $\pm$ 0.21	0.26 $\pm$ 0.17
Red-breasted Nuthatch	0.89 $\pm$ 0.28	0.58 $\pm$ 0.38	0.53 $\pm$ 0.13	0.84 $\pm$ 0.63	0.55 $\pm$ 0.30	0.80 $\pm$ 0.34				
Brown Creeper	0.10 $\pm$ 0.10	0.10 $\pm$ 0.10		0.63 $\pm$ 0.34		0.10 $\pm$ 0.10				
Winter Wren	1.69 $\pm$ 0.69	1.95 $\pm$ 0.64	1.89 $\pm$ 0.67	1.47 $\pm$ 0.52	2.28 $\pm$ 0.51	3.10 $\pm$ 0.51	0.35 $\pm$ 0.16	0.12 $\pm$ 0.12		
Golden-crowned Kinglet	0.60 $\pm$ 0.20		2.94 $\pm$ 0.94	0.11 $\pm$ 0.11	0.09 $\pm$ 0.09	1.00 $\pm$ 0.47				
Ruby-crowned Kinglet										0.15 $\pm$ 0.13
Veery	0.20 $\pm$ 0.13	0.20 $\pm$ 0.20		0.33 $\pm$ 0.31	2.46 $\pm$ 0.66	1.30 $\pm$ 0.48	0.46 $\pm$ 0.16			
Swainson's Thrush	0.20 $\pm$ 0.20					0.10 $\pm$ 0.10		0.58 $\pm$ 0.58		
Harris Thrush	2.18 $\pm$ 0.60	0.88 $\pm$ 0.40	2.31 $\pm$ 0.71	1.38 $\pm$ 0.37	3.01 $\pm$ 0.77	3.20 $\pm$ 0.62		0.23 $\pm$ 0.23		
American Robin	0.50 $\pm$ 0.40	0.59 $\pm$ 0.24		0.42 $\pm$ 0.15	0.27 $\pm$ 0.27	0.50 $\pm$ 0.21	0.35 $\pm$ 0.24	0.12 $\pm$ 0.12	0.44 $\pm$ 0.30	0.13 $\pm$ 0.13
Cedar Waxwing	1.49 $\pm$ 0.64	1.07 $\pm$ 0.86	1.28 $\pm$ 0.78	0.32 $\pm$ 0.22	1.28 $\pm$ 0.74	0.70 $\pm$ 0.38	3.02 $\pm$ 1.05	2.21 $\pm$ 0.46	3.25 $\pm$ 1.33	2.79 $\pm$ 1.33
Solitary Vireo	1.59 $\pm$ 0.56	1.95 $\pm$ 0.61	2.84 $\pm$ 0.45	0.63 $\pm$ 0.25	0.36 $\pm$ 0.2	0.30 $\pm$ 0.21			0.15 $\pm$ 0.15	
Red-eyed Vireo	0.50 $\pm$ 0.21	2.64 $\pm$ 0.61	0.63 $\pm$ 0.26	2.84 $\pm$ 0.25	1.64 $\pm$ 0.56	1.40 $\pm$ 0.52		0.70 $\pm$ 0.37		
Nashville Warbler	1.09 $\pm$ 0.33	0.88 $\pm$ 0.37	1.79 $\pm$ 0.40	2.75 $\pm$ 0.78	3.28 $\pm$ 1.20	2.40 $\pm$ 0.83	1.39 $\pm$ 0.39	0.35 $\pm$ 0.35	2.62 $\pm$ 0.86	
Northern Parula	0.10 $\pm$ 0.10	0.10 $\pm$ 0.10					0.12 $\pm$ 0.12			
Yellow Warbler							0	0.23 $\pm$ 0.23		
Chenopod Warbler	6.85 $\pm$ 1.97	6.45 $\pm$ 0.83	2.63 $\pm$ 0.51	4.75 $\pm$ 0.70	2.74 $\pm$ 0.86	2.30 $\pm$ 1.75	3.25 $\pm$ 0.81	3.11 $\pm$ 1.49	1.02 $\pm$ 0.39	
Magnolia Warbler	4.27 $\pm$ 1.13	0.49 $\pm$ 0.25	5.46 $\pm$ 1.39	2.42 $\pm$ 0.78	5.47 $\pm$ 1.18	3.30 $\pm$ 0.65	1.63 $\pm$ 0.39	0.12 $\pm$ 0.12	0.44 $\pm$ 0.30	
Black-throated Blue Warbler	4.07 $\pm$ 1.13	2.25 $\pm$ 0.43	0.42 $\pm$ 0.22	2.63 $\pm$ 0.88	1.64 $\pm$ 0.27	3.60 $\pm$ 0.60				0.13 $\pm$ 0.13
Yellow-rumped Warbler	0.69 $\pm$ 0.32	0.88 $\pm$ 0.40		0.63 $\pm$ 0.25	0.55 $\pm$ 0.30			0.12 $\pm$ 0.12		
Black-throated Green Warbler	1.79 $\pm$ 0.80	3.03 $\pm$ 0.93	2.73 $\pm$ 1.10	2.00 $\pm$ 0.55	1.28 $\pm$ 0.33	3.40 $\pm$ 0.81				
Blackburnian Warbler	2.08 $\pm$ 0.75	2.15 $\pm$ 0.82	2.94 $\pm$ 0.94	1.05 $\pm$ 0.93	1.09 $\pm$ 0.31	0.80 $\pm$ 0.26			0.15 $\pm$ 0.15	
Palm Warbler							0.58 $\pm$ 0.23	0.58 $\pm$ 0.23		
Black-and-white Warbler	3.67 $\pm$ 1.56	0.29 $\pm$ 0.21	1.16 $\pm$ 0.61	2.52 $\pm$ 0.60	4.47 $\pm$ 1.84	4.20 $\pm$ 1.55	1.51 $\pm$ 0.70	0.23 $\pm$ 0.23		
American Redstart		0.49 $\pm$ 0.33	0.11 $\pm$ 0.11		0.27 $\pm$ 0.19					
Ovenbird	0.10 $\pm$ 0.10	1.17 $\pm$ 0.42	0.21 $\pm$ 0.14	1.26 $\pm$ 0.31	0.73 $\pm$ 0.50	1.90 $\pm$ 0.21				0.13 $\pm$ 0.13
Mourning Warbler	0.50 $\pm$ 0.26	1.17 $\pm$ 0.55	0.21 $\pm$ 0.21	0.32 $\pm$ 0.22	0.18 $\pm$ 0.18		1.05 $\pm$ 0.34	0.35 $\pm$ 0.24		

## Appendix 1. (continued)

Strip age / type Species	Young strips		Medium strips		Old strips		Final cuts		Clearcuts	
	Can	Dec	Can	Dec	Can	Dec	Can	Dec	Can	Dec
Common Yellowthroat	9.95 ± 1.26	6.64 ± 1.24	9.24 ± 1.81	4.32 ± 1.37	3.28 ± 1.20	1.30 ± 0.43	20.91 ± 4.54	15.33 ± 3.11	13.70 ± 3.47	11.27 ± 2.24
Canada Warbler	0.10 ± 0.10			0.11 ± 0.11	0.27 ± 0.19	1.40 ± 0.47				
Summer Tanager			0.11 ± 0.11							
Scarlet Tanager	0.10 ± 0.10	0.10 ± 0.10		0.63 ± 0.25	0.18 ± 0.12					
Rose-breasted Grosbeak	2.08 ± 0.54	0.78 ± 0.50	0.32 ± 0.15	1.68 ± 0.26	2.01 ± 0.55	1.80 ± 0.60	0.23 ± 0.15			
Indigo Bunting		0.10 ± 0.10								
Seag Sparrow			0.11 ± 0.11				0.12 ± 0.12	2.79 ± 0.61	4.81 ± 0.99	6.03 ± 1.37
Lincoln's Sparrow							2.21 ± 0.42	1.97 ± 0.58	2.92 ± 0.75	6.03 ± 1.18
Swamp Sparrow	0.20 ± 0.13						0.12 ± 0.12		0.15 ± 0.15	0.13 ± 0.13
White-throated Sparrow	7.54 ± 0.92	6.15 ± 1.21	8.72 ± 1.50	3.36 ± 0.89	7.12 ± 1.22	3.00 ± 1.03	13.94 ± 1.52	8.01 ± 1.03	17.64 ± 1.99	7.86 ± 1.80
Dark-eyed Junco	0.10 ± 0.10	0.29 ± 0.14					0.58 ± 0.39	0.81 ± 0.40	3.35 ± 0.89	5.24 ± 1.11
Red-winged Blackbird							0.12 ± 0.12			
Common Grackle	0.10 ± 0.10					0.10 ± 0.10				0.13 ± 0.13
Brown-headed Cowbird	0.10 ± 0.10	0.29 ± 0.21				0.20 ± 0.20				
Purple Finch	0.30 ± 0.21	0.10 ± 0.10		0.11 ± 0.11			0.23 ± 0.15	0.35 ± 0.16		
White-winged Crossbill	2.78 ± 1.75		1.16 ± 0.85	0.21 ± 0.14					1.51 ± 1.31	
Pink Skink		0.10 ± 0.10	0.42 ± 0.42		0.09 ± 0.09		0.33 ± 0.24		0.58 ± 0.58	0.13 ± 0.13
American Goldfinch	0.10 ± 0.10	0.98 ± 0.98				0.10 ± 0.10	0.70 ± 0.28	0.29 ± 0.15	0.58 ± 0.30	3.47 ± 2.54
Evening Grosbeak	0.30 ± 0.30	0.30 ± 0.30			0.27 ± 0.27	0.10 ± 0.10		0.12 ± 0.12		0.28 ± 0.26
Number of species	46	43	37	46	40	41	31	32	25	24
Mean number of individuals	62.5	52.4	57.1	46.1	52.2	44.6	60.2	47.4	59.1	48.2

# Effect of a large burn in the boreal forest on reproduction of American Kestrels and other birds

Russell D. Dawson and Gary R. Bortolotti

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## Abstract

Little is known about the proximate effects of forest fires on the reproductive ecology of birds in the boreal forest. Such information is important, especially given the interest in having anthropogenic sources of disturbance in the forest, such as logging, mimic natural processes. In 1995, a 73,220 ha forest fire on our study area gave us the opportunity to assess the effects of fire on reproduction of American Kestrels (*Falco sparverius*). We compared reproductive variables on control and burn areas both before and after the fire in a "before-after-control-impact" design. Nest box occupancy, laying date, clutch size, egg size, number of offspring fledged, and condition of young at fledging were not affected by the fire. These results are not unexpected, given that the main prey of kestrels, small mammals, were also not affected by the fire. We conclude that large scale changes in the landscape have little impact on kestrels, provided their prey base remains intact. In addition, we comment on conspicuous changes in the abundance of several other bird species after the fire.

## Résumé

Peu de choses sont connues sur l'effet immédiat des feux de forêt sur l'écologie de reproduction des oiseaux de la forêt boréale. Des informations de ce type sont importantes surtout avec l'intérêt grandissant d'avoir des sources de perturbation anthropogéniques telles la coupe forestière qui ressembleraient de plus près aux processus naturels. En 1995, un feu de 73,220 ha sur notre aire d'étude nous a donné l'opportunité d'évaluer les effets du feu sur la reproduction de la Crécerelle d'Amérique (*Falco sparverius*). Nous avons comparé les paramètres de reproduction sur des parcelles contrôlées et des parcelles brûlées, avant et après feu, selon un protocole d'étude «avant-après-témoin- expérimental». Le degré d'occupation des nichoirs, la date de ponte, la taille de ponte, le nombre d'œufs, le nombre de jeunes à l'envol et leur condition à l'envol n'ont pas été affectés par le feu. Ces résultats ne sont pas surprenants, puisque les proies principales des crécerelles, les petits mammifères, n'ont pas été affectés par le feu. Nous concluons que les changements à grande échelle dans le paysage ont peu d'impacts sur les crécerelles, à condition que leur proies ne soient pas affectées. De plus, nous discutons plusieurs des changements importants dans l'abondance de plusieurs autres espèces d'oiseaux qui ont eu lieu suite au feu.

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Russell D. Dawson and Gary R. Bortolotti, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, Canada S7N 5E2. (bortolotti@sask.usask.ca)

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## Introduction

Despite the fact that fire is the primary ecological factor responsible for renewal in the boreal forest, its effects on wildlife populations have received little study (see Erskine 1977; Kelsall et al. 1977; Fox 1983; Whelan 1995). Although ultimately the fate of boreal forest bird communities is linked to fire history, little is known of the proximate response of birds to the changes in habitat brought about from a forest fire. Some studies have focused on changes in avian community structure (e.g., Fox 1983; Spires and Bendell 1983; Shutler 1987), but fewer have been able to address in detail how reproductive parameters might be affected. It is difficult to generalize about the effects of fire on birds because of variation in habitats studied, specific characteristics of the burns, as well as differences in methodologies and validity of controls (see Huff et al. 1985; Shutler 1987).

The need for information on the ecology of forest fires goes beyond academic concern, as there is increasing interest in having anthropogenic sources of disturbance in the forest, such as logging, mimic natural processes and natural landscape-level patterns of age structure and species composition (e.g., Bondrup-Nielsen 1995). This is a viable objective only if logging does in fact mimic the effects of forest fires, as is so often assumed to be the case (e.g., Kelsall et al. 1977). Some studies of birds have even combined logged and burned areas in their analyses (Bendell 1974; Fox 1983). Several research programmes are currently addressing the question of how forest fragmentation by logging affects birds, yet there are few data to compare these studies to natural forces of forest fragmentation. Our long-term (9 years) study of American Kestrels (*Falco sparverius*) has provided us with an exceptional opportunity to quantitatively investigate how birds and small mammals respond to fires. In addition, given a long-term database (29 years) on the avifauna of our study area (Gerrard et al. 1996; and G.R. Bortolotti, pers. obs.), we are able to comment, at least anecdotally, on the responses of some other species.

Many studies of the effects of fire on bird populations have lacked adequate controls (Bendell 1974; Shutler 1987). Our approach is to employ multiple comparisons in both space and time. As is commonly done, we compare burned versus unburned "control" areas in the year following the fire. However, unlike most studies we are also able to compare these areas in the years prior to the fire to ensure that the control is representative. In addition, we are able to compare post-burn results to data collected over a

period of years prior to the fire on the burned site. Our statistical design therefore corresponds to a "before-after-control-impact" design (Stewart-Oaten et al. 1986; Wiens and Parker 1995), and provides a powerful perspective on potential effects of fire.

## Materials and Methods

### Study area

Birds have been studied in the vicinity of Besnard Lake, north-central Saskatchewan (55N, 106W) since 1968, and an intensive research programme on kestrels began in 1988. This area is at the transition of the Northern Coniferous and Mixedwood sections of the Boreal Forest Region (Rowe 1972) and corresponds with the southern edge of the Precambrian Shield. Much of the mature jack pine (*Pinus banksiana*) forest was clearcut from the mid-1970s to the mid-1980s, although some cutting of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) continues today (Gerrard et al. 1996). Bortolotti (1994) and Gerrard et al. (1996) provide detailed descriptions of the physical and ecological attributes of the area. Our work has been focused on over 200 km of roads and logging trails accessible by truck (Figure 1).

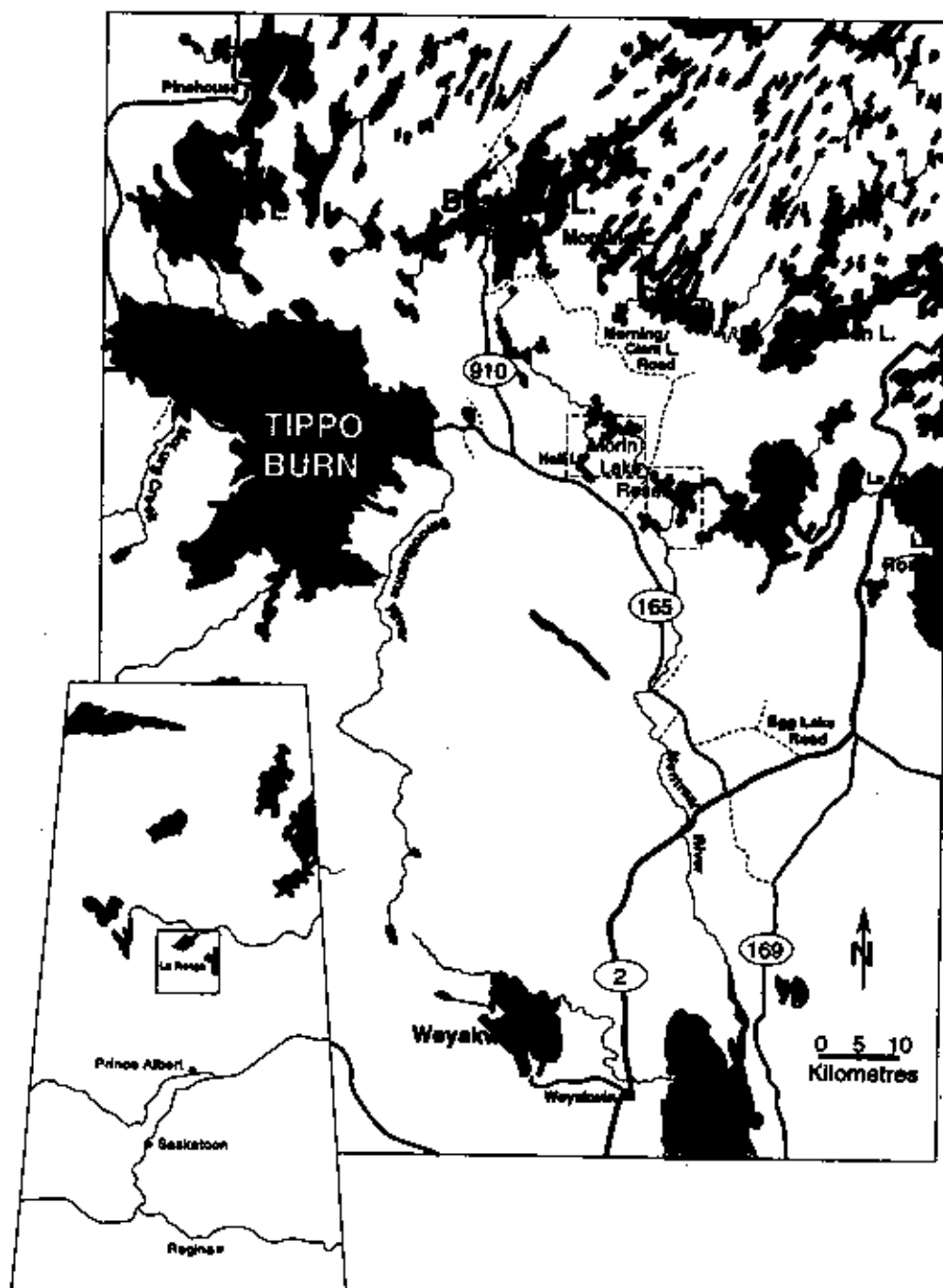
On 28 May 1995 lightning caused a fire in the westernmost portion of our study area. Despite considerable efforts by provincial forest fire-fighters, the "Tippo" fire burned continuously until it was extinguished by heavy rains on 10 July 1995. The total area of the burn was estimated to be 73,220 ha (Saskatchewan Forest Fire Management Branch, pers. comm.) (Figure 1). As is typical of fires in the boreal forest, some small patches remained partially unburned, but a considerable area was exposed to a hot fire and all trees were killed (but remained standing).

### Bird studies

Kestrels have been studied in the area since 1988. Although cavities abound in the area, most kestrels choose to nest in boxes (Bortolotti 1994). All boxes in this study were of uniform size (23.1 x 20.3 cm at the base, a 7.5 cm diameter entrance hole) and constructed of 15 mm exterior-grade plywood (for details see Bortolotti 1994). They were nailed to trees about 4 m above ground in a variety of habitats from continuous forests to clearcuts (see Bortolotti 1994, Gerrard et al. 1996).

As there were only 20 boxes in 1988 in the area that eventually burned, we limit most of our analyses to 1989-1996. In the year of the fire, 1995, there were 64 kestrel nest boxes in the area that burned and 307 boxes outside of it. The fire destroyed 19 of the 64

**Figure 1.** Map of entire study area. Data were collected on areas accessible from Highways 165 and 910, and adjoining logging roads (dashed lines). Dark shading indicates area consumed by "Tippo" fire in 1995. Inset map shows general location of study area.



boxes and so, in 1996, we erected replacements in the same locale, usually the same tree. We chose to include all boxes outside of the burn as a "control", rather than *post hoc* assess what might be the area most similar for comparison. In the years prior to the fire the number of

boxes in each area varied somewhat. From 1991 to 1996, the burned area had 60-64 boxes, while the control had 285-307. In 1989, there were 34 and 235, and in 1990 there were 38 and 270 in burn and control areas, respectively.

Almost all nest boxes have complete data for occupancy, laying date ( $\pm 1$  day) and clutch size given our rigorous schedule of checking nest boxes (e.g., see Bortolotti 1994; Dawson and Bortolotti 1997a). The few cases where data were imprecise have been deleted. Our data on egg size, nestling condition (see below) and brood size are from a subset of natural, unmanipulated nests because of limited availability or because there were experiments involving brood size.

Kestrels arrive on the study area in late-April and begin laying in mid-May. As the fire swept through the area during the incubation period, we were able to use the 1995 data on laying date and clutch size as the pre-fire period, and 1996 as the post-fire period. For analysis of egg size, brood size at fledging and nestling condition, we use 1994 as the pre-fire period.

For the analysis of egg size and nestling condition, it was inappropriate to treat individual measures as independent. Therefore, for egg size we used mean egg volume per clutch (see Wiebe and Bortolotti 1995). For an index of nestling condition, we used mass and tenth primary feather length of chicks measured when the first-hatched nestling of the brood was 24 days old (see Dawson and Bortolotti 1997b). We calculated means for mass and primary length of males and females separately for each nest. Subsequently, the sexes were analyzed separately rather than using sex as a factor, to avoid any one nest appearing repeatedly in any analysis.

We have also kept records on the distribution of other species of birds in the area for most of the summer months for 4 (RDD) and 16 (GRB) years. In addition to studies of kestrels, ornithologists have been working near-continuously in the area since 1968 and have provided an unusually thorough annotated list of the birds of the region (see Gerrard et al. 1996); however, we believe that we could detect only dramatic changes with reasonable certainty.

### Small mammal populations

As part of our work on kestrels, small mammals were snap-trapped each year since the project's inception to quantify prey abundance. Each trap line coincided with a kestrel territory. Our largest sample of lines for the pre-fire years was 1994, when 10 lines were trapped in the burn and 79 lines outside of the burn. In the post-fire year, 1996, we trapped at 20 lines in the burn and 34 outside of it. Each line was situated parallel to, and 10 m from, a road. At each line there were 10 stations spaced 30 m apart. At each station there were 2 snap traps baited with peanut butter. The traps were open for 3 consecutive days and any that

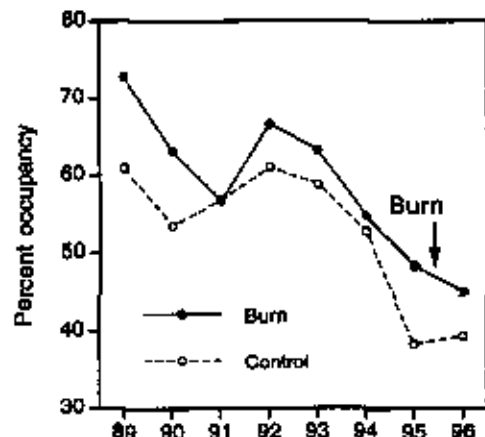
were triggered were reset each morning. At stations where both traps had been sprung, it was assumed that the traps were available for only half the time and so a corrected number of available traps was used. We present data on the mean number of all species of small mammals per 100 traps sampled in early July each year. We repeated the statistical analyses using only voles (almost all were red-backed voles *Clethrionomys gapperi*), but the results were the same so we present data only on total small mammals. Although this index would seem to be a coarse measure of food availability, it correlates well with kestrel reproduction (e.g., Bortolotti et al. 1991; Wiebe and Bortolotti 1992, 1994, 1995). Many predatory birds are dependent on small mammals and so these data are likely also relevant to predicting the response of other similar species of birds to fires.

## Results

### American Kestrels

Prior to the fire in 1995, 31 of 64 (48.4%) boxes were occupied on the burn and 117 of 307 (38.4%) were used on the control area. Occupancy after the fire in 1996 was 27 of 60 (45.0%) in the burn versus 115 of 297 (39.4%) in the control area. We used logistic regression with box occupancy as a binary dependent variable, and year and area as categorical explanatory variables. Occupancy of nest boxes was not different between years ( $\chi^2 = 0.08$ ,  $df = 1$ ,  $p = 0.78$ ), but the burn area had marginally higher occupancy than the control area ( $\chi^2 = 2.93$ ,  $df = 1$ ,  $p = 0.087$ ; Figure 2). There was no interaction between year and area ( $\chi^2 = 0.17$ ,  $df = 1$ ,  $p = 0.68$ ), suggesting the fire had little impact on nest box occupancy.

Figure 2. Nest box occupancy by American Kestrels in north-central Saskatchewan in burn and control areas. Arrow denotes onset of the fire.





**Table 1.** Reproductive parameters of American Kestrels breeding before (1994, 1995) and after (1996) the "Tipico" forest fire of 1995. Mean egg size was calculated using means of eggs in each nest.

Variable	Year	AREA					
		Burn			Control		
		Mean	S.D.	N	Mean	S.D.	N
Clutch size	1995	4.8	0.71	19	4.9	0.40	102
	1996	4.6	0.58	25	4.6	0.59	101
Laying date	1995	141.4	7.69	24	141.2	5.71	106
	1996	145.8	7.93	23	146.0	8.35	107
Egg volume (cm <sup>3</sup> )	1994	14.1	0.80	10	13.8	1.46	73
	1996	13.7	0.84	19	13.8	1.17	76
Brood size	1994	3.5	1.61	13	3.2	1.23	33
	1996	3.9	1.24	25	3.7	0.95	49

There was remarkable similarity between burn and control areas in all reproductive parameters that we measured both before and after the fire (Table 1). For laying date, a 2-way analysis of variance (ANOVA) of year (1995 versus 1996 corresponding to pre- and post-burn, respectively) and area (burn and control) showed a highly significant year effect ( $F_{[1,255]} = 14.88$ ,  $p < 0.001$ ). If the burn caused any effect on laying date, we predicted that there would be a significant interaction between year and area, but there was none ( $F_{[1,255]} = 0.02$ ,  $p = 0.88$ ). There was also no significant effect of area, suggesting that the control was representative ( $F_{[1,255]} = 0.001$ ,  $p = 0.98$ ).

Clutch size showed a pattern of variation similar to laying date. Mean clutch sizes were nearly identical for burn and control areas (Table 1). Most kestrels laid either 4 or 5 eggs, but we could not detect any difference in clutch size between the burn and control areas ( $F_{[1,243]} = 0.02$ ,  $p = 0.88$ ). The pre- versus post-fire comparison suggests a change in clutch size occurred between years ( $F_{[1,243]} = 7.86$ ,  $p = 0.005$ ), but this is clearly annual variation independent of area because the interaction between year and area was not significant ( $F_{[1,243]} = 0.45$ ,  $p = 0.50$ ; Table 1).

To examine the response of egg size to the burn we first investigated other potential sources of variation such as laying date and clutch size. We limited our analyses to the most common clutch sizes of 4 and 5 eggs. Only clutch size proved to be significant (see also Wiebe and Bortolotti 1995). We then performed a 3-way ANOVA including clutch size (4 and 5), year (1994 versus 1996, corresponding to

pre- and post-burn, respectively), and area (burn and control). Clutch size did not contribute to the model and so was dropped. The subsequent 2-way ANOVA of the potential effects of year and area showed no significant effects (area:  $F_{[1,174]} = 0.11$ ,  $p = 0.74$ , year:  $F_{[1,174]} = 0.57$ ,  $p = 0.45$ , area  $\times$  year:  $F_{[1,174]} = 0.98$ ,  $p = 0.32$ ).

Brood size at fledging was similar between the burn and control areas (Table 1;  $F_{[1,116]} = 0.87$ ,  $p = 0.35$ ), but there was a trend for brood size to be larger in 1996 than in 1994 ( $F_{[1,116]} = 2.99$ ,  $p = 0.09$ ). The year by area interaction was not significant ( $F_{[1,116]} = 0.001$ ,  $p = 0.99$ ).

There are several variables that may influence nestling condition. We therefore used an ANOVA model that incorporated not only area and year, but also hatching date and brood size as potential factors. The most important result would be an interaction between year (pre- versus post-burn) and area, but for neither males nor females was there any result approaching significance (all  $p > 0.12$ ) for mass or tenth primary length. Similarly, area was always nonsignificant ( $p > 0.60$ ) (see Table 2).

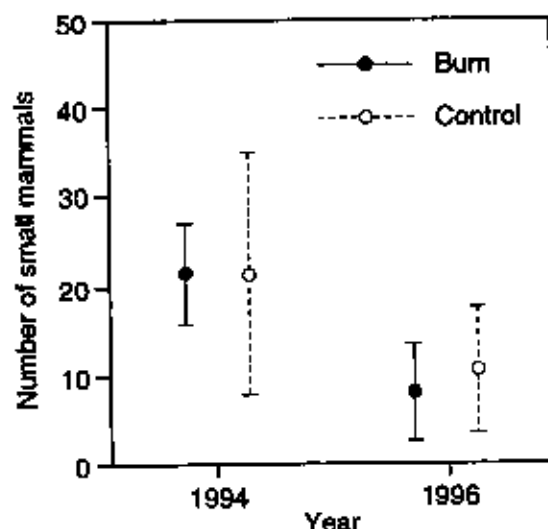
### Small Mammals

Similar to our results for kestrel reproduction, the number of small mammals did not appear to be affected by the burn (Figure 3). A 2-way ANOVA with year (1994 and 1996) and area as factors showed significant differences between years in the number of small mammals ( $F_{[1,139]} = 25.70$ ,  $p < 0.0001$ ); however, no area effects could be detected ( $F_{[1,139]} = 0.21$ ,  $p =$

Table 2. Mean weight (g) and tenth primary length (mm)  $\pm$  SD of male and female American Kestrels at 24-days old (minimum fledging age) from north-central Saskatchewan. 1994 represents the pre-burn year while 1996 is the post-burn year. Sample sizes refer to number of nests.

Variable	AREA											
	Burn						Control					
	1994			1996			1994			1996		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
Male weight	109	7.9	7	111	8.8	17	114	9	11	113	6.6	9
Female weight	119	5.3	7	121	11	17	123	8.6	10	123	8.4	9
Male 10 <sup>th</sup> primary	52.4	8.7	7	60.9	4.9	17	59	8.6	11	59	6.3	9
Female 10 <sup>th</sup> primary	56.3	4.1	7	62.3	5.6	17	60.4	9.8	10	62.5	6.3	9

Figure 3. Number of small mammals per 100 trap nights on kestrel territories before (1994) and after (1996) the 1995 forest fire. Error bars represent  $\pm 1$  standard deviation.



0.65), nor was there an interaction between area and year ( $F_{1,139} = 0.40$ ,  $p = 0.53$ ).

### Other birds

We did not systematically survey birds in the burn, but three species showed an apparent positive response to the burn. Northern Hawk-owls (*Surnia ulula*) were seen only 7 times in 27 years in the entire study area (Gerrard et al. 1996) prior to the fire. In both 1996 and

1997, it was possible to observe hawk-owls in the burn almost daily. In 1996, one bird was captured there with a bal-chatri trap (Berger and Mueller 1959); this bird possessed a brood patch, so it is reasonable to assume it was breeding. In 1997, two hawk-owls were captured in the same area.

Two species of passerines bred for the first time in our nest boxes in the year after the burn. In 1996, Tree Swallows (*Tachycineta bicolor*) laid eggs in 3 (5%) of the 60 kestrel boxes available in the burn that year. Two other partial nests were built that we attributed to Tree Swallows. Similarly, House Wrens (*Troglodytes aedon*) also laid in 3 (5%) boxes as well. None of the 297 control boxes in 1996, or any of the 2,541 previous years' boxes (summed 1988-1995) had ever been used by these two species.

### Discussion

The continued presence of kestrels after the fire was not unexpected, as they are an adaptable species and occur over a wide range of habitat types in our study area (from lakeshores with continuous mature forest, to muskeg, to clearcuts and road allowances) and across their North American range (forests, farmland, deserts). That there was no change in box occupancy rate or any other reproductive parameter was, however, surprising. Results for the burn and control areas were remarkably similar (Table 1). The few minor differences pre- and post-burn were clearly annual effects independent of area. So, despite a major change in the habitat, kestrels did not respond.

This lack of response may be less surprising when one considers the data on prey populations. Several reproductive parameters of American Kestrels in our area, including egg size (Wiebe and Bortolotti 1995) and nestling condition (e.g., Bortolotti et al. 1991; Wiebe and Bortolotti 1992), but not box occupancy rate (G.R. Bortolotti, unpubl. data), correlate with food supply. There did not appear to be any response of small mammals to the burn (Figure 3). Although the literature reports variable responses for small mammals, many studies show no effect of fire consistent with our results (see Bendell 1974; Kelsall et al. 1977; Whelan 1995). Even if population size of small mammals did not change, one would expect availability of prey to hunting kestrels to be greatly enhanced given the lack of post-fire cover. If such occurred, it did not translate into enhanced reproduction for the kestrels. We do not know what happened to populations of other common prey of kestrels such as frogs and dragonflies. However, whatever changes may have occurred in prey abundance or availability, kestrels appeared to have adapted well as they fledged the same number and quality of offspring on and off the burn (Tables 1 and 2). Little information on other raptors is available for comparison, but Yensen et al. (1992) reported that fires appear to have a negative effect on raptors of the Snake River Birds of Prey Area, Idaho, by creating an unstable prey base.

We do not have data on how large-scale logging might be comparable to the burn, but we suspect that results would differ. Although kestrels are abundant in the clearcuts we were working in, logging occurred 10 to 20 years ago in most of the area. The few kestrel territories where small-scale (<200 ha) logging has occurred have been abandoned immediately afterward, and generally we do not see kestrels in such areas for a few years after cutting. Again this may be expected if small mammal numbers are lower on recent clearcuts. As with fires, the effect of clearcutting is likely variable and site-dependent. Jones (1978) studied small mammal populations in the boreal mixedwood forest of Saskatchewan approximately 125 km south of our area. He found that populations of red-backed voles (by far the kestrels' main prey; G.R. Bortolotti, pers. obs.) were lower in the year following harvest on the clearcut compared to uncut adjacent forest. The same was true in clearcut jack pine stands in Manitoba (Simms and Buckner 1973). On the burn site, there was an immediate and lush regeneration of herbaceous growth. In contrast, it seems to take much longer for most cutovers we have seen to regenerate, and there is

always a proportion of the land that has little vegetation on it for years to come (e.g., landings, slash piles, compacted soil).

Other attributes of clearcuts are likely to make them even more inhospitable to kestrels than the depression in prey numbers. Current logging practices typically involve the complete removal of all trees. Previously in our area, only softwoods were removed and so clumps of aspen were left behind, thus providing hunting perches and potential nest sites. The standing timber left by fire has the same benefits.

It seems reasonable that the positive responses by Northern Hawk-owls, Tree Swallows and House Wrens were the result of fire and not merely the opening of the habitat as would be created by logging. While Tree Swallows have been reasonably common breeding birds in our study area, they never used our kestrel boxes except in the burn. In 1994, we erected 21 small nest boxes in clearcuts specifically for swallows. Only one of these appears to have been used that year (Gerrard et al. 1996), and 6 of these monitored in both 1995 and 1996 remained unused. Because we observed swallows in the area of these boxes we assume cavities were likely not limiting reproduction. It is unlikely that fewer absolute number of cavities existed in the burn after the fire, as most trees remained standing after being killed. However, the swallow population may have increased, resulting in a relative shortage of nest sites. The burn therefore may have been an attractive habitat for swallows. Smith (1996) includes "burnt lands" as the nesting habitat for tree swallows in Saskatchewan.

Both Northern Hawk-owls and House Wrens seemed to be absent as breeders in the area until after the fire. There were no records of House Wrens in the entire study area between 1968 and 1995 (Gerrard et al. 1996, and G.R. Bortolotti, pers. obs.); however, they have been seen in Beauval, approximately 60 km by air from our burn (Gerrard et al. 1996). There are three breeding records of Northern Hawk-owls in Saskatchewan, but they are believed to prefer burns and open bogs for nesting and foraging (Smith 1996). The breeding records of House Wrens reported here are more northern than any summarized in Smith (1996). Apparently, wrens in the boreal forest favour regenerating burns or other dry brushy sites (Smith 1996). While this species certainly responded to the burn in our area, they appear to be absent from brushy areas.

Although intuitively one expects bird populations to respond to major habitat alterations, such was not the case for American Kestrels. In contrast, it appears

that other species, like Northern Hawk-owls, House Wrens, and perhaps Tree Swallows, did respond positively to the fire. Clearly, generalizations must be made with caution and a clear statement of which species are evaluated. Our suggestion that logging and forest fires do not have comparable impacts on birds warrants further study, especially given the current interest in having anthropogenic sources of disturbance in the forest mimic natural processes.

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## **Concluding remarks: content versus context in forest bird research**

**A.W. Diamond**

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### **Abstract**

Research on the effects on birds of stand characteristics ('content') is contrasted with studies of effects of the landscape surrounding the stand ('context'). These approaches are currently converging, and the future direction of forest bird research will be shaped by the balance between them. This balance will likely vary regionally, depending on the extent of forest fragmentation. I argue for greater use of the opportunities offered by forestry - particularly the certification process - to conduct large-scale ecological experiments to test ecological theory and models. These opportunities offer exciting prospects for advancing our understanding of the habitat choices made by birds in the face of rapid changes. Ornithologists must recognise that the future of forest birds lies not in our hands, but in the hands of the foresters who manage the birds' habitat. We need to develop collaborative research and conservation programs with foresters if we are to improve the conservation prospects for forest birds. One realistic target to strive for is the incorporation of habitat needs for birds into foresters' cutting plans.

### **Résumé**

La recherche traitant les effets sur les oiseaux des caractéristiques des peuplements (contenu) est comparée aux études qui ont pour sujet l'effet du paysage entourant un peuplement (contexte). Dernièrement, ces approches convergent et la direction future des recherches portant sur les oiseaux forestiers sera orientée par l'équilibre entre celles-ci. Cet équilibre risque de varier selon les régions, dépendamment du degré de fragmentation des forêts. Je propose une utilisation plus extensive des opportunités présentées par la foresterie, particulièrement au niveau du processus de certification, afin d'entreprendre des recherches écologiques à grande échelle pour tester des modèles écologiques. Celles-ci offrent d'intéressantes possibilités d'avancer notre compréhension du choix d'habitat par les oiseaux face aux changements rapides. Les ornithologues doivent se rendre compte que l'avenir des oiseaux forestiers n'est pas entre leurs mains, mais plutôt dans celles des forestiers qui gèrent leur habitat. Nous devons développer des recherches collaboratives et des programmes de conservation avec les forestiers si nous sommes pour améliorer les perspectives de conservation des oiseaux forestiers. Un but à viser est l'incorporation des besoins en habitat des oiseaux à l'intérieur des plans de coupe des forestiers.

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A.W. Diamond, Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick, Canada E3B 6E1. ([diamond@unb.ca](mailto:diamond@unb.ca))

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## Contrasting the content and context of forest bird habitats

Most of the preceding papers address the influence of habitat *content* on forest birds: the effects of forestry on the species and structure of vegetation in the stand itself. As outlined in the Introduction, much current research also addresses the influence of the *context* in which that stand is set: the characteristics of the landscape surrounding the stand.

Most recent North American work on impacts of habitat change on wildlife focuses on habitat fragmentation, the process of partitioning formerly continuous habitat into smaller fragments (Robinson et al. 1995; Freemark and Collins 1992; Villard et al. 1992; Faaborg et al. 1993; Walters 1998). (Here I use 'habitat' to include both the stand and its landscape context). In forest this process occurs naturally through fire, pest outbreaks, and windfall; but the expansion and intensification of human land use is now the most significant cause of habitat fragmentation (Burgess and Sharpe 1981). The fragmentation process includes overall loss of original habitat, reduction in area of habitat patches, increasing area of edge habitat, and increasing isolation of patches, combining to reduce biological diversity in the original habitat (Wilcox and Murphy 1985) chiefly through increasing rates of local extinction combined with decreased probability of recolonisation influenced by patch size, isolation and edge effects. The conceptual frameworks of island biogeography (MacArthur and Wilson 1967; Diamond and May 1981) and metapopulation dynamics (Hanski and Gilpin 1991), which dominate fragmentation studies, both assume that habitat patches are isolated from each other by a matrix of unsuitable habitat in which species from the original habitat cannot persist. Forest patches in non-forested landscapes are indeed set in a hostile matrix; but in generally forested landscapes, patches are separated not by 'non-forest' but by *different* forest, differing in species composition, age structure, and patch size, where patch edges become subtle ('soft') rather than abrupt ('hard') (Bamford 1986; Hawrot and Niemi 1996). There is increasing recognition that at some point along the gradient from non-forested to forest-dominated landscapes, bird community dynamics switch from behaviour characteristic of fragments (influenced by patch-size, isolation and edge effects) to that characteristic of random samples of continuous forest (Andrén 1994). Andrén (1994) suggests that the threshold between random-sampling and fragmentation effects being the best predictors of

bird and mammal population persistence, is at around 30% forest cover in the landscape. This conclusion is derived from mainly European work, but North American birds may respond differently from European species (Newton 1995). For example, many North American bird species show area-dependence, whereas very few European forest birds do, probably because area-dependent species have been eliminated from European landscapes during several thousand years of intensive human land-use (Newton 1995).

Most recent research on forest birds (especially in Europe and the United States) has emphasized these landscape influences, to the neglect of effects at the stand level, and one challenge for the next phase of research will be to achieve an appropriate balance between these two approaches. This balance will differ between one ecological region and another. In southern Ontario and Quebec, for example, where most forest exists as remnants in a hostile matrix of agriculture or urban settlements, the landscape context is likely to dominate over the content of the site. In much of the boreal forest, where commercial harvesting is just beginning (e.g., northern Alberta) or of relatively recent origin, much of the landscape remains covered in forest, and stand content is likely to affect habitat quality more than the landscape context (see Drolet et al. 1999 for a recent discussion of the reasons for this). This probably also applies to Acadian forest in the Maritime Provinces, where forest still covers 80% or more of the landscape even though commercial forestry has operated for over 200 years in many places.

Andrén's (1994) figure of 30% forest cover as a threshold provides a useful rule-of-thumb to guide research in different landscapes. However, we do not know how well this figure might apply to landscapes where the matrix surrounding forest patches is forested rather than unforested; this question must surely be addressed urgently as large areas of boreal forest in Canada are transformed by industrial forestry. Comparison of population trends in continuous versus fragmented boreal forest has already provided surprising results (Kirk et al. 1997).

## Bird/habitat associations

We are still largely ignorant of many of the associations between individual species and characteristics of the forest. Erskine's (1977) ground-breaking work documented many such associations but without providing quantitative relationships between vegetation features and bird densities. Kirk et al. (1996) used modern multivariate statistics to

identify broad bird communities in western boreal forest, but this has still not been done elsewhere in the country. Hutto (1998) described a regional approach to documenting patterns of relative abundance among bird species in relation to forest cover types, and emphasized that we still do not know many of the basic species/habitat associations (even if we think we do). A more quantitative approach, particularly on a smaller geographic scale, is suggested by Boyce and McDonald (1999) who describe 'Resource Selection Functions' that essentially quantify the strength of habitat use versus availability ratios. These might be especially powerful in comparing habitat use by birds presented with different choices of available habitat, and allow us to better understand the continuing problem of 'selection' versus 'preference' shown by birds in different habitat contexts.

The study of forest birds — as distinct from that of birds in other habitats — offers unique opportunities for researchers to develop a stronger theoretical basis. We are gathering a good deal of high-quality data on bird populations and their habitat, but generally we are using this to assess impacts of forestry on birds rather than to test ecological theory. One of the most exciting recent developments in behavioural ecology is the application of 'individual-based' models (i.e., approaches based on the behaviour of individuals, rather than populations), to classical questions of habitat use, which we have traditionally addressed from a population perspective. Sutherland (1996) gives a number of examples that suggest that the real advances in understanding habitat use by birds, and the impacts of changes in habitat upon them, may come from the creative testing of realistic models in the field.

## Forestry as habitat experiments

Forestry offers us a potential experimental system in which foresters can manipulate habitat in ways which would test critical theories. By so doing we could simultaneously advance not only the prospects of improving habitat conditions for the birds in which we are interested, but also the broader scientific field (habitat ecology) which currently lacks a sound theoretical and empirical basis.

As one example, most researchers have accepted that 'density is a misleading indicator of habitat quality' (van Horne 1983), to the extent that the monitoring of survival and productivity is increasingly being incorporated into project designs; yet this conclusion is likely to apply in particular

situations, notably temporal unpredictability of resources, seasonal habitat differences, and patchiness of habitat. In more temporally predictable and spatially uniform situations we might expect birds to occupy habitat in patterns closer to the 'ideal free' distribution described by Fretwell and Lucas (1970); in such cases density is more likely to reflect habitat suitability. It would be very useful to know this, because we could then monitor density alone, and restrict the much more expensive and difficult task of monitoring demographic parameters to habitat situations where they are likely to be critical to interpreting population changes.

Are there situations in Canadian forests where bird population density can confidently be used to assess habitat quality? Does the increasing patchiness of forest habitats shift birds from an ideal free to a 'source-sink' distribution? If so, what are the thresholds for species of concern? Can they adapt to these changes, or is a species confined for eternity in its hereditary demographic straitjacket? Work by Komdeur (1992, 1997), for example, suggests that songbird demography may be much more plastic than we think. These questions are all important for ensuring the future of forest birds in Canada and obtaining clear answers will also contribute significantly to advancing ecological theory. Forest companies are often quite willing to amend cutting plans in order to provide experimental opportunities for biologists to test their theories, and some biologists are already exploiting these opportunities (Schmiegelow et al. (1997).

The business environment for industrial forestry is changing rapidly, as consumers (especially in Europe) begin to bring pressure on timber suppliers to show that they are managing their forests sustainably, for both commodity and non-commodity values. Recent developments in the field of forest certification (Côté 1999) provide an opportunity to ensure that the provision of adequate habitat for birds (as components of biodiversity) becomes a goal of management, rather than a constraint on timber supply as it has traditionally been regarded by foresters. Biologists need to seize on these opportunities to apply the best possible science to these critical issues and provide foresters with the information they need to manage their forests in ways that will sustain biodiversity (including bird populations).

The reality is that ornithologists (including professional wildlife managers) have very little direct influence on populations of forest birds. If we are



correct in believing that bird populations depend on habitat, then their future depends on those who control the habitat. Currently this means professional foresters, because our nation in its wisdom has delegated authority over forest lands to provincial governments who pass it on (for the most part) to forestry companies. Increasing collaborative research, and conservation planning, between ornithologists and foresters is essential for the future of forest birds in Canada. Only when birds' habitat needs are fully incorporated into foresters' annual cutting plans, will we have made measurable progress towards improving the conservation prospects for Canadian forest birds.

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