

Concluding remarks: content versus context in forest bird research

A.W. Diamond

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.

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)

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.

References

- Andr n, H. 1994. Effects of habitat fragmentation on birds and mammals on landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Bamford, R. 1986. Broadleaved edges within conifer forest: the importance to bird life. *Quarterly Journal of Forestry* 80: 115-121.
- Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitat using resource selection functions. *Trends in Ecology and Evolution* 14: 268-272.
- Burgess, R. and D.M. Sharpe (eds.). 1981. *Forest island dynamics in man-dominated landscapes*. Springer, New York.
- Cot , M.-A. 1999. Possible impact of forest product certification on the worldwide forest environment. *Forestry Chronicle* 75: 208-212.
- Diamond, J.M. and R.M. May. 1981. Island biogeography and the design of nature reserves. Pages 228-252 in *Theoretical ecology: principles and applications* (R.M. May, ed.). Blackwell, Oxford, England.
- Drolet, B., Desrochers, A. and Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *The Condor* 101: 699-704.
- Erskine, A.J. 1977. Birds in boreal Canada. *Canadian Wildlife Service report series No. 41*: 1-73.
- Faaborg, J., M. Brittingham, T. Donovan and J. Blake. 1993. Habitat fragmentation in the temperate zone: a perspective for managers. Pages 331-338 in *Status and management of neotropical migratory birds* (D.W. Finch and P.W. Stangel, eds.). U.S. Department of Agriculture Forest Service Rocky Mountain Forest Range Experimental Station, General Technical Report RM-229. Fort Collins, Colorado.
- Freemark, K. and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443-454 in *Ecology and conservation of Neotropical migrant landbirds* (J.M. Hagan III and D.W. Johnston, eds.). Smithsonian Institution Press, Washington, D.C.
- Fretwell, S.D. and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 14: 16-36.
- Hanski, I. and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal Of Linnean Society* 42: 3-16.
- Hawrot, R.Y. and G.J. Niemi. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. *Auk* 113: 596-598.
- Hutto, R. 1998. Using landbirds as an indicator species group. Pages 75-92 in *Avian conservation: research and management* (J.M. Marzluff and R. Sallabanks, eds.). Island Press, Washington, D.C.
- Kirk, D.A., A.W. Diamond, A.J. Erskine, A.R. Smith, G. Holland and P. Chytky. 1997. Population changes in boreal forest birds in Saskatchewan and Manitoba. *Wilson Bulletin* 109: 1-27.
- Kirk, D.A., A.W. Diamond, K.A. Hobson and A.R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest. *Canadian Journal of Zoology* 74: 1749-1770.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358: 493-495.
- Komdeur, J. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* 385: 522-525.
- MacArthur, R.H. and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Newton, I. 1995. The contribution of some recent research on birds to ecological understanding. *Journal of Animal Ecology* 64: 675-696.
- Robinson, S. K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Schmiegelow, F.K.A., C.S. Machtans and S.L. Hannon. 1997. Are boreal birds resilient to forest fragmentation? an experimental study of short-

- term community responses. *Ecology* 78: 1914-1932.
- Sutherland, W.J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford, England.
- van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.
- Villard, M.A., K. Freemark and G. Merriam. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an empirical investigation. Pages 474-482 in *Ecology and conservation of Neotropical migrant landbirds* (J.M. Hagan III and D.W. Johnston, eds.). Smithsonian Institution Press, Washington, D.C.
- Walters, J.R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. Pages 181-192 in *Avian conservation: research and management* (J.M. Marzluff and R. Sallabanks, eds.). Island Press, Washington, D.C.
- Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125: 879-887.