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Wildlife Modeling and Biomonitoring

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Wildlife Modeling and Biomonitoring

SFM Network Project: Large Scale Issues in Sustainable Forestry

by

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ABSTRACT

As one project within the Boreal Ecology and Economics Synthesis Team, this research contributed to the development of an integrated suite of models for use in management scenario evaluations and policy analysis. The work focussed on the identifcation, measurement and modeling of wildlife indicators, and had three major components, each of which applied sophisticated statistical approaches to existing data sets. Fine-scale bird habitat models were developed from localised point count data and spatially explicit forest inventory data. Poisson regression models, describing relationships between species abundance and distribution and forest composition and configuration within local (3 ha) and neighbourhood (81 ha) areas, were derived for over 20 forest bird species. Coarse-scale bird habitat models were developed from more geographically extensive bird atlas data and aspatial forest inventory data. Multivariate logistic regression models were derived for 29 species, at 100 km^2 resolution. At this scale, bird species response to habitat amount and configuration was senstive to the definition of habitat (e.g., all forest, older forest, older deciduous forest), was species-specific, and characteristics of the forest matrix were also important predictors of species occurrence. An analysis of cost-effective bird monitoring utilised both fine- and coarse-scale bird data to derive estimates of variance parameters for use in simulations that estimated power of several potential sampling designs. A cost model evaluated the relative expense of various sample effort components. Integration of power and cost estimates was used to identify cost-effective sampling strategies, which varied with the variance characteristics of the monitoring target. A final stage involved incorporation of the habitat-based bird models into landscape simulation frameworks to faciltate scenario evaluations.

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INTRODUCTION

A broad goal of the SFM Network is to synthesize information from various research sources into appropriate practices for sustainable management of the boreal forest. The Boreal Ecology and Economics Synthesis Team (BEEST), established in 1997, is an integrated, multi-disciplinary research group addressing sustainable forest management issues. In conjunction with other BEEST members and projects, the goal of this project was to contribute to the development of an integrated suite of models of natural forest dynamics and forest management that facilitate the evaluation of various management scenarios.

Strategies for sustainable forest management require knowledge about the economic and ecological outcomes of policy decisions and management actions across a variety of planning scales: from allocation of land tenures over very large areas, to tenure-level harvest scheduling of townships, through township-level cutblock layout, and cutblock-level harvest and regeneration treatments. Commensurate ecological data are rarely, if ever, available for such purposes. At the level of forest tenures, one approach to alleviating the need for such data advocates using natural disturbances regimes as a guide to forest management. The underlying assumption of the natural disturbance paradigm is that by maintaining a range of stand ages and tree species compositions within the range of natural variability, system structure and function, and hence biological diversity, will be conserved.

To apply such a strategy in the boreal mixedwood forest of Alberta, quantification of natural variability, and management planning, must largely be based on forest inventory information. However, the ability of forest inventory data to predict wildlife habitat quality is not known, and specific associations from detailed, but geographically limited ecological studies may not be representative of broader-scale patterns. There is also a need to understand how spatial aspects of habitat distribution, such as patch size, shape and juxtaposition, affect suitability. Furthermore, it is necessary to identify measurable parameters to check whether the biodiversity objectives encapsulated in a landscape management approach are, in fact, being realised.

The specific objectives of this project were to (1) develop fine-scale statistical models of bird species occurrence and abundance in relation to forest composition and configuration, (2) develop coarse-scale statistical models of bird species distribution in relation to forest composition and configuration, (3) identify candidate species, and develop methodologies for design and analysis of monitoring data, and (4) incorporate models of select species into landscape simulation frameworks to predict patterns in distribution and abundance over large areas through time, under a variety of management scenarios. Objective 1 proceeded collaboratively with the project of Bunnell, Walters and Schmiegelow, results from which are available in Vernier et al. (in press). Objective 2 relied heavily on preliminary modeling of forest inventory data under the projects of Bunnell, Walters and Schmiegelow, and Beck, Schmiegelow and Adamowicz (see Vernier and Cumming 1998). Objective 3 was the thesis project of Matthew Carlson (Carlson 2000), and proceeded in collaboration with the Alberta Forest Biomonitoring Program. Objective 4 is an ongoing initiative that involves many BEEST members.

STUDY AREAS

We used three study areas: one to develop fine-scale bird habitat models (Objective 2) and to derive some of the parameter estimates necessary for design of a monitoring program (Objective 3), a second to generate coarse-scale bird habitat models (Objective 3), and a third to derive the remaining parameter estimates necessary for monitoring program design and evaluation. Our fine-scale study area encompassed ≈140 km^2 of boreal mixedwood forest near Calling Lake, in north-central Alberta, Canada (55° N, 113° W; indicated by the star symbol in Figure 1). Our coarse-scale study area comprises about 7,500,000 ha of boreal mixedwood forest (Rowe 1972), in northeast Alberta, Canada (approx. 56° N, 113° W; Figure 1). The largest study area contained the closed boreal forest physiographic region of Alberta (USGS Patuxtent Wildlife Research Center 2000).

The boreal mixedwood region is transitional between colder, conifer-dominated forests to the north and warmer, drier aspen parklands to the south (now largely farmland). Mean summer (early June through mid-August) precipitation in the region is ≈320 mm, accounting for >70% of the total yearly precipitation; July is generally the wettest month. The mean summer temperature is 12.0°C, and the mean frost-free period is 85 days (Strong and Leggat 1981). The most abundant tree species are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), black spruce (*Picea mariana* (Mill) B. S. P.), jack pine (*Pinus banskiana* Lamb), and white spruce (*Picea glauca* (Moench) Voss). The dominant understory shrubs are alder species (*Alnus tenufolia, A. crispa*) with lesser amounts of willow (*Salix* spp.). Various fruiting shrubs (*Rubus, Rosa* spp.), sarsaparilla (*Aralia nudicaulis*), and other herbaceous plants dominate the lower strata. Wetland areas are abundant in the mixedwood, and cover about 50% of the shaded region in Figure 1. The region has generally low relief, with limited variation in landforms and topography. Historically, stand-replacing fires and insect outbreaks have been the dominant disturbance agents.

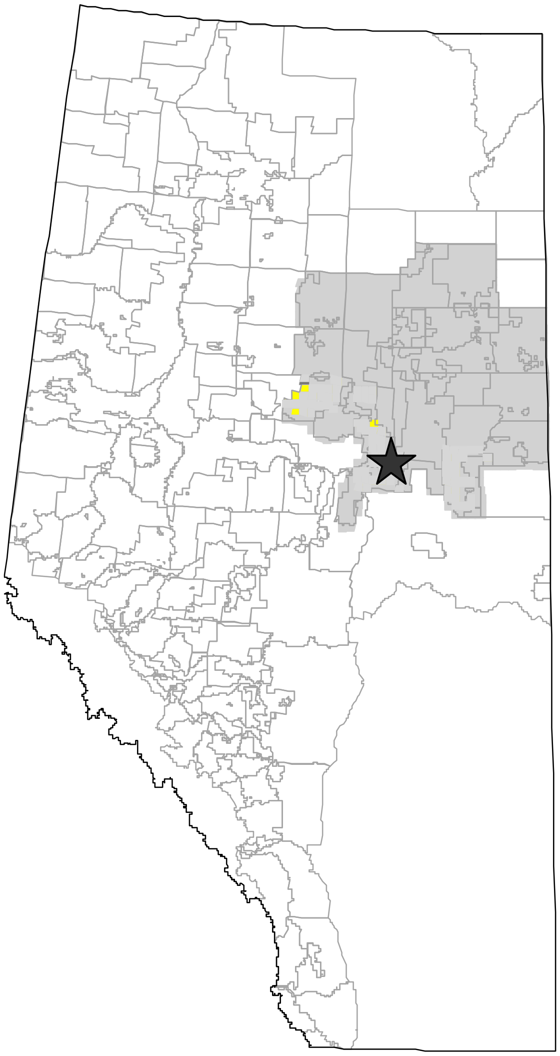

Figure 1. Study area location in northern Alberta. The light grey area represents Alberta Pacific Forest Industries Forest Management Area, from which is breeding bird atlas squares were selected. The location of the Calling Lake study area is indicated by the star. Irregular polygons represent forest management unit boundaries in Alberta.

OBJECTIVE 1: DEVELOPMENT OF FINE-SCALE BIRD MODELS

We used data from the boreal mixedwood forest in Alberta to develop statistical models relating bird abundance to habitat characteristics measured at local and neighbourhood scales. Bird abundances were estimated from 1-6 years of point count surveys, at 445 stations, associated with experimental and mensurative studies at Calling Lake (e.g., Schmiegelow et al. 1997; Schmiegelow and Hannon 1999). Habitat characteristics were derived from Alberta Vegetation Inventory (AVI) data. At the local scale (100 m radius = 3 ha) we measured patch attributes such as canopy height and crown closure. At the neighborhood scale (100-500 m radius = 74 ha), we characterised the forest composition and configuration. Poisson regression models were developed for over 20 bird species. To evaluate the relative influence of local and neighbourhood habitat variables on each species, we compared five alternate habitat models. Details of methods are presented in the final report of Bunnell, Walters and Schmiegelow, and in Vernier et al. (*in press*). Here, we present and discuss the results for five focal bird species.

The focal species (Table 1) were: Black-throated Green Warbler (BGNW; *Dendroica virens*), Red-breasted Nuthatch (RBNU; *Sitta canadensis*), White-throated Sparrow (WTSP; *Zonotrichia albicolis*), Yellow-rumped Warbler (YRWA; *D. coronata*), and Yellow Warbler (YWAR; *D. petechia*). This suite of species follows Schmiegelow and Hannon (1999), representing a range of observed abundances and expected responses to forest fragmentation. For each bird species, we calculated the mean detections per station per year (after Schmiegelow et al. 1997), and multiplied (weighted) this by the number of years a station was sampled (between 1 and 6 years). We used this aggregated count value as our response variable in subsequent statistical modelling.

TABLE 1. Focal species for fine-scale modelling. Species are listed from most common to least common based on the number of stations in which they were detected.

Code	**Common name**	**Scientific name**	**No. of stations**	**Mean detections**
WTSP	White-throated Sparrow	*Zonotrichia albicolis*	356	3.96
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	327	2.11
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	266	0.61
BGNW	Black-throated Green Warbler	*Dendroica virens*	224	0.92
YWAR	Yellow Warbler	*Dendroica petechia*	172	0.13

Results

For three species, the best models included both local and neighborhood habitat variables. These models explained between 54 and 73% of the variation in abundances of the Black-throated Green Warbler, Yellow-rumped Warbler and White-throated Sparrow. For the Red-breasted Nuthatch and Yellow Warbler, the best models included only local habitat variables, and explained only 43 and 37% of the variation in bird abundance, respectively (Table 2).

TABLE 2. Summary statistics for each bird species' best model (i.e. lowest Akaike Information Criteria (AIC; Akaike 1974) indicating the number of local and neighbourhood variables selected, degrees of freedom, the null model deviance (assuming only a mean effect), the residual deviance unaccounted for by the model, the percent deviance explained, and AIC values.

Summary statistic	**BGNW**	**RBNU**	**WTSP**	**YRWA**	**YWAR**
Local variables	1	2	3	4	2
Neighbourhood variables	5	0	4	2	0
Degrees of freedom	399	403	398	399	403
Null model deviance	582.73	252.08	984.60	520.65	122.15
Residual deviance	266.43	143.29	267.69	220.91	77.45
% Deviance explained	54.28	43.16	72.81	57.57	36.59
AIC	751.49	619.35	1364.67	1105.30	248.90

Black-throated Green Warbler abundance was positively related to one local and four neighbourhood variables High abundances of this species were associated with areas of older, structurally diverse, deciduous dominated forest, containing at least some white spruce. The White-throated Sparrow was positively related to two local and two neighbourhood variables, and negatively related to one local and two neighbourhood variables. This species was most abundant in clearcuts adjacent to deciduous forest, with a low proportion of mid seral forest in the surrounding area. The Yellow-rumped Warbler was negatively associated with four local variables and positively associated with two neighbourhood variables. The presence of both clearcuts and old deciduous forest were the most important predictors at the local level, while the proportion of mid and late seral forest were influential at the neighbourhood level. Stations located in either clearcuts or old deciduous forests had the lowest abundance of YRWA whereas stations with a high proportion of young and mature forest had the highest abundance.

Both the Red-breasted Nuthatch and Yellow Warbler were best predicted by models consisting of only two local habitat variables. RBNU was associated with tall coniferous or coniferous dominated stands; YWAR was associated with old, relatively open patches of deciduous forest. Neither species was sensitive to any of the neighbourhood variables we measured, after accounting for variability in local habitat characteristics.

Discussion

In general, our quantitative models were consistent with qualitative accounts of habitat requirements for the selected species (e.g., Semenchuck 1992; Kaufman 1996; Fisher and Acorn 1998), and we do not dwell on specific interpretations of variables here. An interesting outcome of our analyses was the variation in the inclusion of local and neighborhood habitat descriptors in species models. We quantified habitat composition and configuration at two scales, in order to test whether the spatial context of habitat patches affected habitat selection at the level of territories. Our results suggest that, for some species, habitat quality at the level of territories (as approximated by long-term mean species abundances) is mediated by characteristics of the surrounding area. In other cases, only local characteristics explained variation in abundances. In the latter cases, explained deviance of our models was lower than for species models including habitat descriptors at multiple scales. We present 2 contrasting interpretations of these results.

First, species responding only to local habitat characteristics may have selected specific features, regardless of their spatial context, and these features were not well described by relatively coarse-scale habitat data. Second, such species represent generalists; relatively insensitive to both habitat composition and configuration, regardless of scale. We are testing hypotheses arising from the first interpretation with extensive, detailed vegetation data collected from the same study area over the same time period during which birds were sampled. The second interpretation is testable in the analytical framework we developed, with a larger suite of species. Regardless, we emphasise that the species models containing only local habitat descriptors, although poorer than those containing both local and neighborhood variables, were still able to account for ca. 40% of the variation in abundance using, in each case, only 2 habitat variables derived from forest inventory data.

A fundamental criticism of habitat-based models is that they are rarely validated. As a first step, we employed a statistical cross-validation approach (see Vernier et al. *in press)* However, because we are ultimately interested in testing hypotheses about landscape dynamics and wildlife response, our predictive models must be validated across a range of spatial scales and geographic locations. We plan to use spatially-referenced bird data from other localised studies in the boreal mixedwood for geographic validation. At a coarser scale, survey data from the Alberta Breeding

Bird Atlas permit us to test whether our finer-scale models can be generalized, i.e. whether the spatial scale of response to habitat varies. Steps towards this are described under Objective 2 (this report).

Another criticism of habitat-based abundance models is that abundance in a given habitat is not necessarily indicative of quality, as measured by reproductive success (van Horne 1983). If occupation of sink habitats (those where expected reproduction is below replacement) is limited by immigration from nearby source habitats (e.g., Pulliam 1988), then projections of population abundance may fail to predict actual population persistence. In the absence of productivity measures, we use long-term mean abundance as a proxy for habitat quality (see also arguments in Boyce and McDonald 1999). We assume that the system is dynamic and unsaturated, and that optimal habitat will be most frequently occupied, subject to variation imposed by environmental stochasticity, individual mortality and dispersal limitation, i.e. an ideal free distribution (Fretwell and Lucas 1969).

Occupancy of suboptimal habitats will also be a function of their density. In regions where suboptimal habitats make up a large portion of the landscape, surplus production from the rare nearby source habitats is unlikely to provide colonists to occupy sink habitats with frequency sufficient to permit estimation of their relative suitability. In such areas, observed abundances in areas of relatively low predicted quality should be less than expected, given our models. Thus, our models can be used to design extensive sampling efforts to test metapopulation models and identify sink habitats. In such an application, source habitats would be identified as areas of both high predicted quality and high observed abundances.

This again points to the need for model validation across multiple sites and scales, as source habitat detection is dependent on predicted habitat quality. In the landscape from which the present models were derived, the contrast in continuous variables (at local and neighborhood scales) was nearly as high as possible, given the overall composition of the study area, but this area is dominated by older forest. We are now using our existing models (from both Objectives 1 and 2, i.e. fine- and coarse-scale models) to locate new sampling sites in areas with high contrast in independent variables that are highly significant in existing models, or where uncertainty (prediction variance) is high. In addition, future sampling sites will target areas with contrast in independent variables that are anticipated to change most as industrial development in the region proceeds (e.g., the density of anthropogenic edges).

Conclusions

In Alberta, forest management planning is largely based on forest inventory information, but the ability of such information to predict species abundances has not previously been evaluated. We attempted such an evaluation, using Poisson regression analysis to model the relationship between bird species abundances observed in the field and habitat characteristics derived from forest inventory data. We demonstrated that relatively fine-scale predictive models of bird abundance could be generated from forest inventory data, permitting evaluation of activities at a resolution and extent commensurate with tactical-level forest management planning. The models presented here are a subset of those we have developed, representing species with a range of observed abundances and expected responses to forest fragmentation. Our final selection of species to model for scenario evaluations requires identification of species most at risk from land-use practices (primarily forestry and energy sector development) that are resulting in widespread habitat modification in Alberta's boreal forests. This will proceed in conjunction with the coarse-scale bird habitat modeling described under our second objective.

OBJECTIVE 2: DEVELOPMENT OF COARSE-SCALE BIRD MODELS

Because we are interested in assessing ecological response to land-use practices at multiple spatial scales, and varying resolutions, it was necessary to develop indicator models commensurate with these scales. We also wanted to develop models using more geographically extensive data sets than available at the time for our fine-scale modeling efforts. Such data were available from the Federation of Alberta Naturalists, based on the Alberta Breeding Bird Atlas (Semenchuck 1992). From these data, we developed multiple logistic regression models for a suite of forest bird species within a 74,000 km^2 study area in northeastern Alberta. Full details of this study are available as an SFMN Working Paper (Cumming and Schmiegelow 2001).

Atlas data were collected betwwen 1987 and 1991, by volunteers coordinated by the Federation of Alberta Naturalists. Sampling was organised to 10 x 10 km units of the UTM grid system. Some UTM units were visited several times during the sampling period. On each visit, or "survey", the observer(s) recorded all bird species detected, ranked by evidence of breeding. For most surveys, sampling effort (in hours) was recorded. We restricted our analyses to surveys recording at least 9 species of forest birds. Data coverage is sparse, as much of the area was inaccessible by road. Of over 700 UTM units covering the study area, only 97 were actually sampled, of which 50 passed our selection criteria. Seventy-four surveys were conducted in these units.

We selected 24 passerine species for modeling (Table 3), all of which have been found to be relatively abundant in older, aspen dominated mixedwood forests (Schmiegelow et al., 1997). We also selected 10 species of woodpecker, hawks and owls, for which more than four observations were recorded in the 74 surveys. The surveys recorded 873 positive observations of the 34 species: 12% were simple detections, 55% were observations made in "suitable breeding habitat", 21% recorded territorial displays, nest building or similar evidence of breeding, and so were considered as probable breeding observations, and 12% were classed as "confirmed" based on behavioral evidence or direct observations of eggs or fledglings. We excluded the simple detections from our analysis, and used the presence or absence of these species as our dependent variable.

We included sampling effort in our analyses, as the number of observer hours varied by two orders of magnitude among surveys. We fit a non-linear model to the data (species count versus observer effort), and included this as an independent variable, along with various habitat descriptors. Previous treatments of bird atlas data from other regions, with similar variation in sampling effort (e.g., Trzcinski 1999), have not accounted for this.

We used Alberta Phase 3 forest inventory (Alberta Forest Service 1985) to measure the abundance and configuration of habitat, and the forest matrix, within the UTM units. Although the Phase 3 data are aspatial, previous work within our group (Vernier and Cumming 1998) has demonstrated strong relations between sets of habitat configuration indices and simple measures of total habitat area and patch size distributions, which can be computed directly from the inventory data. Our resultant index of configuration was essentially a linear combination of three different aspects of fragmentation, corrected for the constraints imposed by habitat abundance. In addition to effort and habitat configuration, 7 compositional variables, 6 matrix variables, and a measure of habitat abundance (Cover) were also used in multivariate logistic modeling (Table 4). An interaction term (Inter = Cover x Config) was also included.

TABLE 3: List of common names, scientific names, migratory type and four-letter codes for all species modeled. n is the number and p_i the proportion of surveys where the species was observed. Species are listed from least to most commonly detected, within passerine, woodpecker and hawk and owl groupings. Migratory types are neotropical migrants (NTM), short distance migrants (SD) and residents (RES), following Schmiegelow et al. (1997).

Common Name	Scientific Name	Type	Code	n	p_i
Blackpoll Warbler	*Dendroica striata*	NTM	BPWA	4	0.05
Evening Grosbeak	*Coccothraustes vespertinus*	SD	EVGR	6	0.08
Black-throated Green Warbler	*Dendroica virens*	NTM	BGNW	7	0.09
Golden-crowned Kinglet	*Regulus satrapa*	SD	GCKI	7	0.09
Yellow-bellied Flycatcher	*Empidonax flaviventris*	NTM	YBFL	8	0.11
Winter Wren	*Trolodytes troglodytes*	SD	WIWR	10	0.14
Philadelphia Vireo	*Vireo philapdelphicus*	NTM	PHVI	10	0.14
Canada Warbler	*Wilsonia canadensis*	NTM	CAWA	11	0.15
White-winged Crossbill	*Loxia leucoptera*	SD	WWCR	12	0.16
Pine Siskin	*Carduelis pinus*	SD	PISI	18	0.24
American Redstart	*Setophaga ruticilla*	NTM	AMRE	19	0.26
Magnolia Warbler	*Dendroica magnolia*	NTM	MNWA	20	0.27
Boreal Chickadee	*Parus hudsonicus*	RES	BOCH	21	0.28
Northern Waterthrush	*Seiurus novaboracensis*	NTM	NOWA	23	0.31
Red-breasted Nuthatch	*Sitta canadensis*	RES	RBNU	25	0.34
Ovenbird	*Seiurus aurocapillus*	NTM	OVEN	33	0.45
Western Tanager	*Piranga ludoviciana*	NTM	WETA	33	0.45
Yellow Warbler	*Dendroica petechia*	SD	YEWB	36	0.49
Swainson’s Thrush	*Catharus ustulatus*	NTM	SWTH	37	0.50
Yellow-rumped Warbler	*Dendroica coronata*	SD	YRWA	39	0.53
Least Flycatcher	*Empidonax minimus*	NTM	LEFL	41	0.55
Black-capped Chickadee	*Parus atricapillus*	RES	BCCH	42	0.57
Red-eyed Vireo	*Vireo olivaceus*	NTM	REVI	48	0.65
White-throated Sparrow	*Zonotrichia albicolis*	SD	WTSP	52	0.70
Black-backed Woodpecker	*Picoides arcticus*	RES	BBWO	5	0.07
Three-toed Woodpecker	*Picoides tridactylus*	RES	TTWO	11	0.15
Downy Woodpecker	*Picoides pubescens*	RES	DOWO	14	0.19
Pileated Woodpecker	*Dryocopus pileatus*	RES	PIWO	22	0.30
Hairy Woodpecker	*Picoides villosus*	RES	HAWO	29	0.39
Yellow-bellied Sapsucker	*Saphyrapicus varius*	SD	YBSA	38	0.51
Northern Flicker	*Colaptes auratus*	SD	NOFL	49	0.66
Sharp-shinned Hawk	*Accipiter striatus*	SD	SSHA	9	0.12
Red-tailed Hawk	*Buteo jamaicensis*	NTM	RTHA	20	0.27
Great Horned Owl	*Bubo virginianus*	RES	GHOW	9	0.12

TABLE 4. Summary of variables used in multivariate logistic regression modelling. The seven compositional variables are proportional areas and sum to 1.0 for each atlas square. The six matrix variables were obtained by log-ratio transformation, and the proportional habitat variable Cover was arcsin √ transformed. Details in text and Cumming and Schmiegelow (2001).

Type	**Name**	**Definition**
Compositional	Deciduous (x_1)	Deciduous $\geq$ 70%
	Mixed (x_2)	Mixtures of deciduous and white spruce
	Black Spruce (x_3)	Black soruce dominant
	Pine (x_4)	Pine dominant, or deciduous/pine mixtures
	Muskeg (x_5)	Muskeg and other wetlands
	Disturbed (x_6)	Burns and clearcuts $\leq$ 20 years old
	Water (x_7)	Ponds and lakes
Matrix	Aw	$\log(x_1/x_5)$
	Sw	$\log(x_2/x_5)$
	Sb	$\log(x_3/x_5)$
	Pj	$\log(x_4/x_5)$
	Dist	$\log(x_6/x_5)$
	Wa	$\log(x_7/x_5)$
Habitat	Cover	Proportional area of habitat
Configuration	Config	Configuration index
	Inter	Cover x Config
Other	E	Sampling effort

We evaluated a hierarchy of models, using different sets of potential explanatory variables and/or definition of habitat. At Levels 0 and 1, we defined habitat to be all mesic stands, which were considered to be embedded in an unsuitable matrix comprised of unforested patches and patches of non-mesic pine and black spruce. At level 0, we evaluated only the variables Cover, Config and Inter. At level 1, and all higher levels, we included the sampling effort term E. Level 2 defined habitat to be mesic patches > 90 years old, and included the six matrix variables. Level 3 defined habitat to be only deciduous stands over 90 years old, and also included the matrix variables.

Only models meeting goodness of fit critieria beyond simple classification accuracy (Fielding and Bell 1997) were accepted, to eliminate trivial results. In short, the method we used estimated the probability that a random selection from the positive group (correct classification of species presence = true positives) will have a score greater than a random selection from the negative group (false positives). This is represented by an AUC value (area under the curve, where curve refers to the receiver operating characteristic = ROC curve). A value of 0.5 indicates a model with no predictive power; we accepted any models with an AUC ≥ 0.75.

Results and Discussion

The explanatory power of multiple logistic regression models of the bird atlas data increased as sampling effort (Levels 0 and 1) and forest matrix variables (Levels 2 and 3) were added. Failure to account for variability in observer effort (E) would alter the interpretation with respect to the importance of habitat abundance and configuration for many species. As well, the relative importance of habitat abundance and configuration changes as the definition of breeding habitat becomes increasingly refined (Table 5).

TABLE 5. Frequency with which different classes of variables enter into acceptable models at Levels 0, 1, 2 and 3.

Level	Cover	Config	Inter	C/I[1]	Matrix[2]	Effort
0	1	2	2	2	0	0
1	10	15	10	15	0	17
2	5	10	8	14	27	27
3	5	13	12	17	25	27

[1] Config or Inter

[2] One or more of the 6 matrix variables

In all models above Level 0, configuration variables (Config and/or Inter) entered more frequently then Cover. For Level 0 models, the two variables were of equal importance. However, the apparent significance of habitat configuration for individual species varied markedly as the definition of habitat was refined. In many cases Config was significant at one level and not others. At Level 3, acceptable models were found for 29 of the 34 species we attempted to model (Table 6). In these models, where cover and configuration described the abundance and distribution of older, deciduous forest, configuration was included 2.6 times more often than cover.

TABLE 6. Level 3 atlas-based bird habitat models, where suitable habitat is defined as near pure deciduous stands over 90 years, and descriptors of the forest matrix were included as candidate variables. Four-letter species codes are provided in Table 3. Models are only shown for those species where variables other than E entered.

Species	Linear Predictor
BPWA	-156.39 + 17.12 Aw + 4.69 Dist – 23.63 Wa + 39.30 E
GCKI	-23.41 + 0.86 Pj + 0.81 Dist – 3.17 Wa + 9.88 E
PHVI	-2.64 + 0.54 Pj + 2.53 E
WETA	1.52 – 0.89 Aw + 0.60 Sw + 0.37 Pj – 0.45 Sb + 0.57 Wa + 2.62 E
OVEN	-3.68 + 0.82 Aw – 0.44 Sw – 0.33 Sb + 4.07 E
WTSP	1.77 + 0.72 Wa + 5.09 E
WIWR	-14.11 + 1.04 Sw – 1.66 Wa + 2.88 Config – 12.48 Inter + 5.70 E
CAWA	-16.61 + 1.04 Aw – 0.84 Pj + 8.93 Inter + 15.24 E
WWCR	-7.04 + 2.05 Aw + 0.85 Pj + 1.25 Dist – 1.94 Wa + 4.17 Config – 11.96 Inter
AMRE	0.90 + 0.78 Aw – 0.52 Sw + 0.27 Dist + 0.56 Wa + 2.10 E
MNWA	0.11 + 0.37 Sb + 0.79 Dist – 1.36 Config + 11.50 Inter + 3.02 E
BOCH	-4.45 + 0.71 Sw + 0.79 Config + 5.87 E
NOWA	3.01 + 0.73 Sw + 0.66 Wa – 8.03 Cover + 2.52 E
PISI	-7.13 + 0.47 Pj + 0.36 Dist – 0.95 Wa + 0.74 Config + 4.41 E
RBNU	-2.16 + 0.34 Dist – 3.94 Cover + 0.97 Config + 4.65 E
YRWA	-2.11 + 0.59 Sw – 0.89 Pj + 0.86 Sb + 0.41 Dist – 8.05 Cover – 1.96 Config + 10.04 Inter + 7.91 E
LEFL	1.21 + 0.65 Wa + 0.57 Config + 3.94 E
YEWB	1.29 + 0.88 Aw _ 0.69 Sb + 0.65 Wa – 3.85 Inter + 2.95E
REVI	-0.01 + 0.38 Aw + 0.22 Dist + 4.31 Inter + 2.95 E
BCCH	-2.12 + 0.40 Aw + 0.56 Config + 4.17 E
BBWO	-7.34 – 0.57 Sw + 4.96 E
TTWO	-9.12 + 8.04 Cover + 2.96 Config – 10.67 Inter + 7.30 E
DOWO	-11.89 – 1.14 Wa + 10.35 Cover + 3.63 E
PIWO	-4.07 + 1.60 Config – 6.35 Inter + 4.50 E
HAWO	-3.58 + 2.04 Config – 6.01 Inter + 4.61 E
NOFL	-0.31 + 0.48 Sb + 0.27 Dist + 5.22 Inter + 5.06 E
SSHA	-1.73 – 0.50 Sb + 10.33 Wa + 7.21 E
RTHA	-2.77 + 2.28 Aw – 1.13 Sw – 0.29 Pj + 0.41 Dist – 0.79 Config + 2.16 E
GHOW	-10.36 – 0.66 Sw – 2.74 Config + 20.61 Inter + 8.65 E

Our results show that habitat must be explicitly defined in analyses of configuration effects in forested landscapes. The appropriate definition of habitat must be species specific. However, our results do not support the hypothesis that the amount of habitat alone determines the distribution of species in heterogeneous forest regions. We also found significant interactions between cover and configuration for roughly 25% of all species, which may support the hypothesis that habitat configuration becomes more important at low levels of habitat abundance (Andrén 1994).

Matrix variables were important for most species at Levels 2 and 3, with a number of species responding only to variation in the matrix. This may reflect several factors. Some species may specialize on habitat types not targeted in our analysis. For example, the Winter Wren is associated with dense pure conifer forests (Semenchuk 1992). The Level 2 model for this species is consistent with these reports: similarly, at Level 2, the Pine Siskin is associated with the abundance of pine forest and correlates (little open water relative to muskeg). In both cases, the inclusion of configuration or interaction variables at Level 3 probably represents a correlation between the spatial distribution of old deciduous stands and the abundance or configuration of the habitat type actually used by these species. In heterogeneous natural landscapes, the matrix for one species will contain habitat for others.

Wiens (1997) highlights the limitations of approaches to understanding spatial patterning of landscapes which treat habitat patches as discrete and static entities embedded in a featureless background matrix. An emergent emphasis is the need to consider context, in particular aspects of spatial heterogeneity of the environment, and recognition of the role that this patterning plays in mediating patch dynamics. Characteristics of the matrix influence movement rates, and determine the relative isolation of patches of breeding habitat. Responses will be species-specific, and are likely to be closely tied to habitat requirements (Hannon and Schmiegelow, unpubl. data).

Management Applications

Since 1990, most of western Canada's ~ 485,00 km^2 boreal mixedwood forest has been allocated to industrial forestry (Anonymous 2000). In combination with other large-scale activities, notably the exploration for and extraction of fossil fuels, substantial changes in the age structure, species composition and spatial pattern of the forest will occur over the next century. Species of forest birds associated with older merchantable forest, the habitats considered in our Level 2 and 3 models, will be especially vulnerable to these changes. As the economic rotation age for deciduous species in the region is roughly 70 years, little 90+ year old deciduous forest will remain unless it specifically managed for (Cumming et al. 1994). As might be expected, preliminary spatial simulations (our unpublished analysis) show that patches of older deciduous and mixed forest will become much smaller and more isolated than at present. The history of comparable forests in Fennoscandia suggest that significant declines in biodiversity will result (Helle and Jarvinen 1986; Angelstam and Mikusinski 1994).

Predictive models of the effects of these changes on boreal fauna are needed, most importantly to assess which amongst the feasible set of management alternatives are most likely to maintain populations of indigenous species—a goal to which many governmental and industrial agents are committed, either by international treaty or explicit administrative undertakings. Modeling the relative effects of habitat abundance and fragmentation will become increasingly important as land-use changes continue and management options become more constrained. For a given rate of harvest, fragmentation indices are likely to be more readily manipulated by managers than the total amount of habitat. For example, about 4.5% of merchantable forest in the study area is presently committed to linear buffers around streams and lakes (S. Cumming, unpubl. data). This area could be redistributed into large, contiguous reserves at little cost, given a change in policy. However, current regulations will tend to maximize the fragmentation of remaining old forest.

Conclusions

Our models are best regarded as hypotheses to be tested. The gold standard for model validation is an independent data set, or prospective sampling (Fielding and Haworth 1995; Fielding and Bell 1997). The question is, how to effectively select new sampling areas that are in some sense optimal. We propose that this should be done using the information in the existing models. For example, new sample units which yield large expected change in log-likelihood of the fitted models could be selected as being potentially the most informative. Or, those sites which produce the largest expected changes in the standard error of a specific parameter estimate might be selected, as being most likely to decrease (or increase) the confidence intervals of some parameter having management implications. Prospective new sample sites can be evaluated by re-estimating models for each species using imputed positive and negative observation at the new site, and applying various model-fitting tests (Dobson 1991) to evaluate the effect of the imputed observation. Expectations of the resultant statistics are calculated using the existing model. Although somewhat computationally intensive, such exercises are perfectly feasible. We have constructed prototype “information maps” for 20+ species over our study area, and intend to develop these methods more fully, to guide extensive sampling efforts now being planned for our study region.

OBJECTIVE 3: COST-EFFECTIVE METHODS FOR MONITORING

Ecological monitoring is the repeated measurement of an ecosystem component over time and space, with the intent of detecting change. It facilitates adaptive management by providing an information feedback loop to assess the effects of management on ecosystems. Here, we discuss the design of a broad-scale monitoring program for birds. Empirical parameter estimates were used in simulations that estimated power of different sampling designs to detect trend in species' populations and community metrics. This study comprised the graduate work of Matthew Carlson, and full details can be found in his thesis (Carlson 2000).

Variability in monitoring data has two sources: natural variation and sampling variation. Natural variation is due to spatial and temporal heterogeneity in the distribution of individuals. Eight bird species and three community metrics were selected as subjects for this study based on their variance characteristics. Estimates of within-site temporal variation and mean initial abundance were derived from data collected over a six-year period (1993-98) as part of the Calling Lake Fragmentation Study (Schmiegelow et al. 1997). Between-site variation in initial abundance and trend were estimated using Breeding Bird Survey data from the closed boreal forest region of Alberta, collected between 1989 and 1998 (USGS Patuxent Wildlife Research Center 2000). All variance parameters were estimated as coefficients of determination (dimensionless measures of variability), to make them suitable for use in simulation studies.

Results

Using a plot of within-site temporal and between-site spatial variance (Figure 2), species representing four variance categories were selected. For the ubiquitous category, the White-throated Sparrow and Yellow Warbler were selected. This category likely represents generalist species whose broad niches facilitate occupancy of a wide range of habitats. The Black-throated Green Warbler and Brown-headed Cowbird were selected as examples of spatially patchy species. Species in this category are likely spatially variable because their narrow niches allow occupancy of only a subset of available habitat. Occupancy within this subset of habitats, however, is consistent across years. As examples of temporally fluctuating species, the Black-capped Chickadee and Gray Jay were selected. These species may depend upon resources that vary temporally over large spatial scales. This category may also contain generalist species associated with high sample error, causing inflation of within-site temporal variance. To represent irruptive species, the Pileated Woodpecker and White-breasted Nuthatch were selected. The quality of habitat for these species may be variable, such as is the case with cone crops and insect outbreaks. In addition, sampling issues may contribute to the high variance of species belonging to this category. For example, the Pileated Woodpecker is not an irruptive species per se, but its large home range relative to the scale of point count stations results in variable counts, even in the presence of a stable population. In addition, species in this category are rare, causing them to be associated with high sample error, which inflates within-site temporal variance.

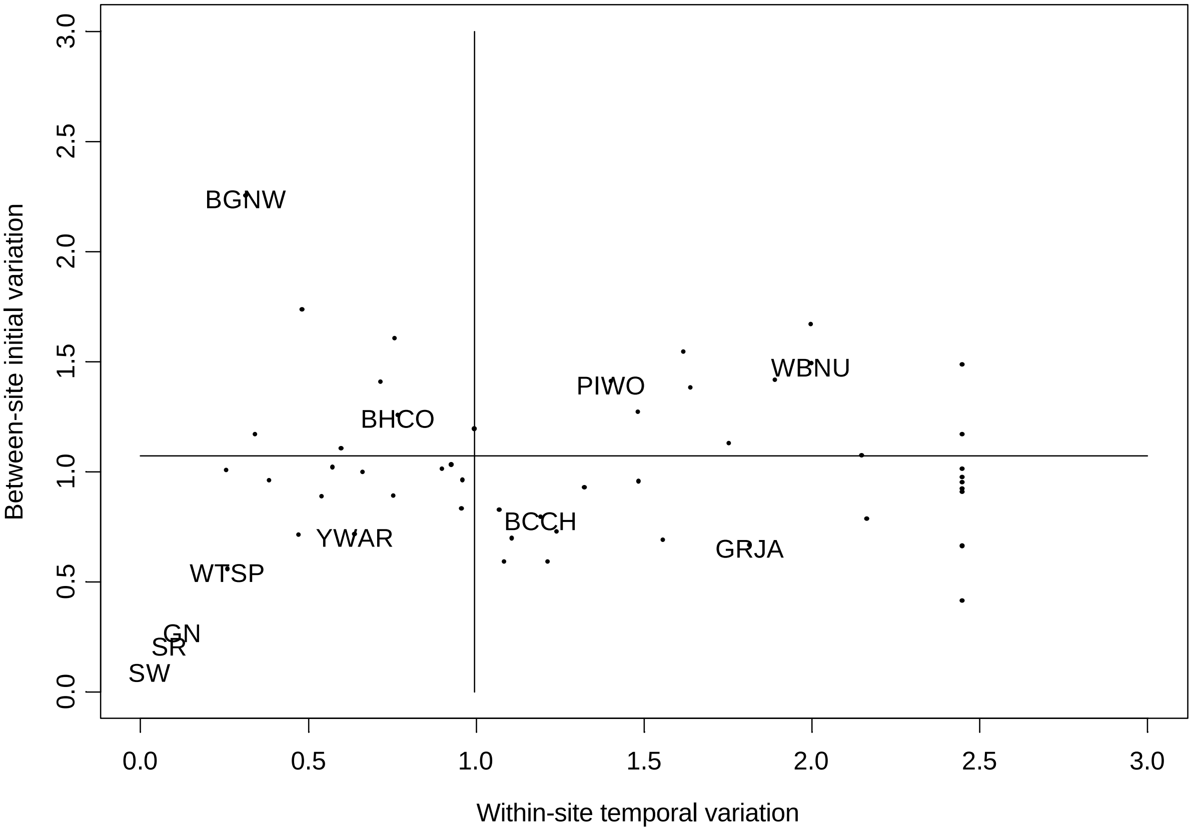

FIGURE 2. Temporal and spatial variability in bird species abundance and community metrics. The horizontal and vertical lines dissecting the plot represent mean between-site initial variation and median within-site temporal variation, respectively, across all species, excluding those with maximum within-site temporal variation (2.449). The four letter codes identify the eight species and three community metrics selected as targets for simulation studies (BCCH = Black-capped Chickadee, BGNW = Black-throated Green Warbler, BHCO = Brown-headed Cowbird, GRJA = Gray Jay, PIWO = Pileated Woodpecker, WBNU = White-breasted Nuthatch, WTSP = White-throated Sparrow, YWAR = Yellow Warbler, SR = species richness, GN = richness of the ground-nesting guild, SW = Shannon-Weiner index).

Parameter estimates for these species and community metrics were used to assess the effectiveness of a range of candidate sampling designs for bird monitoring. Design options were based on those being considered by the Alberta Forest Biomonitoring Program for a province-wide monitoring program. Monte Carlo simulations estimated statistical power for the various designs, given specified significance level and effect size. Estimation of relationships between sample effort components and power to detect trend involved three steps. Simulations were conducted to estimate the power of alternative sampling designs. Multiple regression was then used to model relationships between power and sample effort components. Finally, partial derivatives of these relationships with respect to each sample effort component were calculated to estimate the rate at which power changed with respect to each sample effort component. An example of the output from this analysis is provided in Figure 3.

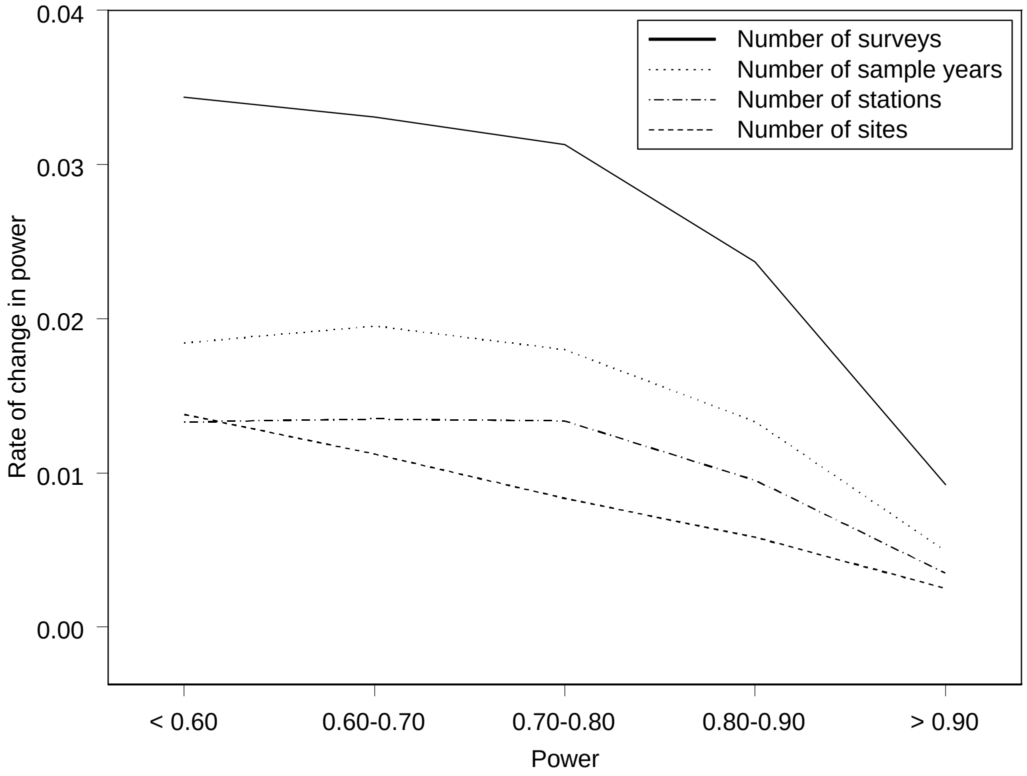

FIGURE 3. Rate of change in power to detect –3% trends in the Black-capped Chickadee over 20 years, with respect to four sample effort parameters, averaged across designs achieving one of four levels of power.

Power varied across species, with variable species being associated with lower power. Because variable species, which also tend to be rare, are likely to be of monitoring interest, population monitoring programs may require high levels of effort to achieve adequate power. Detection of trend in community metrics, on the other hand, was much more powerful. Comparison of power to detect trend over 10 and 20 year periods indicated detection of trend over relatively shorter time periods will require dramatically more sample effort. To evaluate the effect of individual sample effort parameters on power, the relationship between power estimates and sample effort parameters was modeled using nonlinear multiple regression. Calculation of the models' partial derivatives facilitated estimation of the rates at which power increased with increases in each effort parameter.

Evaluation of the efficiency of sample effort allocation involved two steps. First, costs of the alternative sampling designs were calculated according to a cost model. Second, estimates of sampling design cost were integrated with estimates of sampling design power. This involved determining the least expensive sampling design achieving 90% power for each species and community metric of interest, and comparing rates of increase in cost to rates of increase in power across sample effort components. As expected, power to detect trends increased as the cost of monitoring programs increased. The relationship was highly non-linear, however, which resulted in a large range of costs associated with sampling designs achieving 90% power or greater (Figure 4).

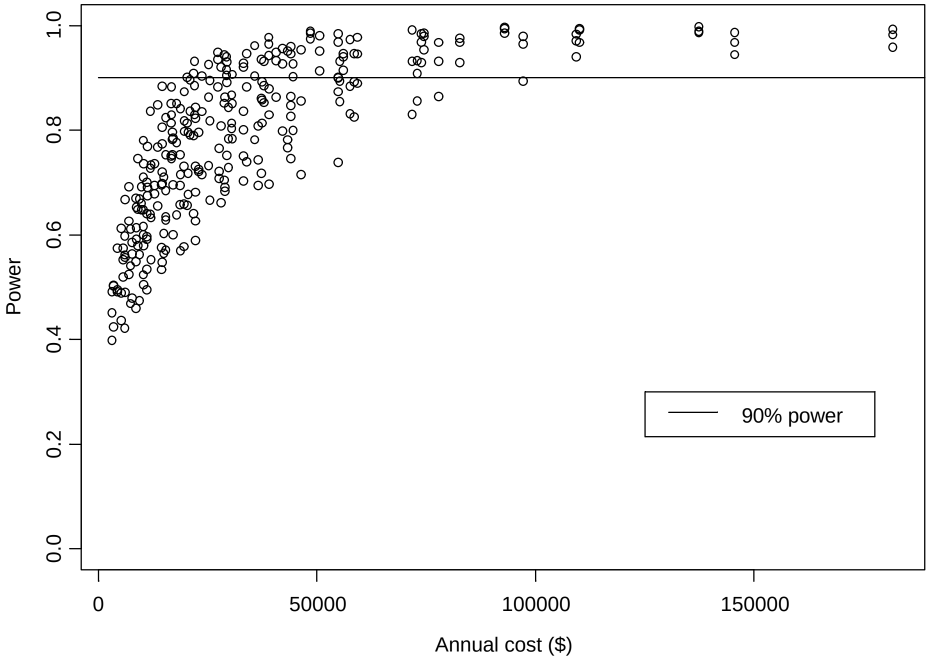

FIGURE 4. Power to detect –3% per year exponential trends in Black-capped Chickadee abundance over 20 years versus annual cost of monitoring program.

Conclusions

Generally, rare species tended to exhibit greater variability and, as exhibited by power analysis, this translated into increased sampling requirements. Due to the steep gradient in sampling requirements across species, population monitoring programs should be designed to achieve effective data for the most variable species of interest. Because of the increased sample effort required, effective sampling designs were expensive for rare species, compared to common species. Rare species are often sensitive to environmental disturbance and are usually of conservation concern. Therefore, inclusion of rare species in population monitoring will often be desired. If the expense associated with monitoring rare species is prohibitive, careful selection of target species that are sensitive to disturbance, yet exhibit low variability, is an alternative. Species in the spatially variable category (i.e. Black-throated Green Warbler) may be examples of such targets, due to their habitat specificity but temporal stability.

Monitoring of community metrics may be another viable alternative. Three community metrics were included in the analysis: total species richness, species richness of the ground-nesting guild, and the Shannon-Weiner diversity index. All metrics exhibited less variance than even the most common species, which translated into low sampling requirements and low program expense. Two issues must be resolved before monitoring of community metrics can be unequivocally recommended, however. First, the sensitivity of community metrics to disturbance must be resolved. Community metrics are almost certainly less sensitive to disturbance than populations, and a smaller magnitude was used in community metric power analyses to account for this reduction. The magnitude of the reduction was entirely subjective, however, and may not have adequately accounted for the relative stability of community metrics. Second, it is not at all clear which community metric, or combination of metrics, should be monitored to provide meaningful information on the status of the bird community. In addition, interpretation of metrics is difficult. For example, the implications of a 10% reduction in the Shannon-Weiner diversity index are unclear.

Effective monitoring programs must provide reliable estimates of change. As illustrated by the power analyses presented here, reliable trend estimates are not a guaranteed product, but instead are dependent on the sampling design used and the monitoring target. *A priori* evaluation of the feasibility of meeting monitoring targets is essential. Equally important, however, is program cost. Programs spanning a wide-range of costs achieved reliable trend estimates, indicating great potential for sampling design efficiencies. Comparison of cost and power gains associated with sample effort parameters revealed general strategies for achieving cost-effective data. To ensure limited resources are not wasted, *a priori* evaluation of efficient monitoring strategies is also essential.

OBJECTIVE 4: SCENARIO EVALUATIONS

Both our fine- and coarse-scale statistical habitat models (Objectives 1 and 2) were designed for, and have been incorporated into FEENIX and TARDIS, landscape simulation frameworks utlised by the Boreal Ecology and Economics Synthesis Team (BEEST). FEENIX, a spatially-explicit, grid-based model adapted from foundational work by Carl Walters (UBC), has been parameterised for investigation of white spruce, wildfire, and habitat dynamics in the boreal mixedwood forest using process and statistical models developed within BEEST. This modeling platform is well-suited to examination of interactions between natural processes and human activities, and their effects on a variety of forest attributes. However, FEENIX operates at a moderate spatial resolution (3 ha rasters), making analysis of areas beyond 1 000 000 ha or so in extent prohibitive in terms of computer time. TARDIS, a simulation modeling platform developed by S. Cumming, uses a much coarser resolution (~10 000 ha rasters) that permits rapid analysis of similar questions over very large areas, at the cost of some spatial detail. This integrated approach allows us to explore the effects of alternative management scenarios on forest bird communities over a variety of spatial and temporal scales. Some preliminary simulations have been run and more are planned for the near future.

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