

# Songbird Use of Four Floodplain Vegetation Types in the Revelstoke Reach, Upper Arrow Reservoir, British Columbia, Canada

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*Photo courtesy of Wendy Beauchamp*

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Evaluation of the Ancillary Benefits of Upper Arrow Reservoir Drawdown Zone Revegetation Project

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## **Abstract**

We surveyed the bird use of 4 terrestrial vegetation types within the flooding zone of the Upper Arrow Reservoir during a year of little or no flooding. Fifty-meter fixed distance point counts were conducted at sampling sites stratified by vegetation type during 5 periods between 16 May and 31 July, 2001. Simultaneous sound recordings during the counts allowed later verification of observer results. Seventy-four species of birds were recorded <50 m and 12 additional species were seen within the floodplain but not within any 50 m point count. In terms of species richness, species diversity, and bird abundance, cottonwood and willow habitats received more use than planted Fall Rye or native grass habitats. Cumulative bird lists for each habitat included: 54 species in cottonwood habitat; 47 species in willow habitat; 35 species in native grasses habitat; and, 32 species in planted Fall Rye habitat. Analysis results suggest that cottonwood and willow habitat types had the highest number of species occurring during surveys when compared to native grass and planted rye. In addition, cottonwood and willow habitat types had the highest density of birds, and highest species diversity of habitat types surveyed. Little is known of the complex interplay between water levels, soil erosion, natural vegetation colonization, and vegetation management in this system. While it is apparent that birds use these vegetation types both during migration and the breeding season, the demographic consequences for any species are unknown. Previous studies have documented use of the area by waterbirds throughout the year (Jarvis and Woods 2002) and by land birds during autumn migration (Anonymous 1998, 1999, Jarvis and Woods 2000, Jarvis 2001). This project was the first major survey of bird use of the draw down zone at Revelstoke during the breeding season. Several species of rare birds were observed during this study including the first Short-eared Owl breeding evidence at Revelstoke in June and a probable migrant Loggerhead Shrike in May.

## 1. Introduction

The Upper Arrow Reservoir immediately downstream from Revelstoke, British Columbia, Canada is unique within the reservoir system along the main stem of the former Columbia River (Figure 1). In most areas of these reservoirs, long-periods of inundation and steep shoreline gradients have resulted in very little persistent vegetation below the high-water level (Bonar 1979). However, in the Revelstoke Reach wetlands (Revelstoke to Shelter Bay), a relatively flat floodplain at the highest elevations of the reservoir supports a riparian vegetation and marshland complex. In turn, this wetland complex attracts considerable use by waterbirds (Bonar 1979, Tremblay 1993, Jarvis and Woods 2002) and landbirds (Anonymous 1998, 1999, Jarvis and Woods 2000, Jarvis 2001).

As part of BC Hydro's dust control programme, large areas of bare sand/mud (Figure 2) are seasonally planted with annual Fall Rye to stabilize the soil and reduce blowing dust. This planting programme combined with natural re-vegetation of the higher elevations of the floodplain has resulted in a complex of riparian vegetation types (Figure 3).

In this survey, we compare bird density and the estimated number of species present (species richness) for birds in 4 riparian habitats on this floodplain. In addition, we compare habitats using species diversity indices that consider both the abundance and richness of species to index the relative balance of species in a habitat. Further demographic analysis is undertaken to estimate the relative fidelity and rate of additions of species to habitat areas over the course of the survey.

We would like to thank the following organizations for assisting this project including: BC Hydro; the Friends of Mount Revelstoke and Glacier National Parks; Parks Canada; and the Canadian Wildlife Service. We also would like to thank the following individuals for their assistance: Marie Gallagher who designed the basic study protocol; Darcie Mattheissen who along with Janice Jarvis was a principal field observer; Wendy Beauchamp for GIS analysis, field GPS surveys, and mapping; Janis Hooge for making the initial selection of survey points; and Ed Hill who provided constant encouragement and enthusiasm.



**Figure 1. Songbird Survey Study Area and Point Count Locations in the Upper Arrow Reservoir Floodplain**

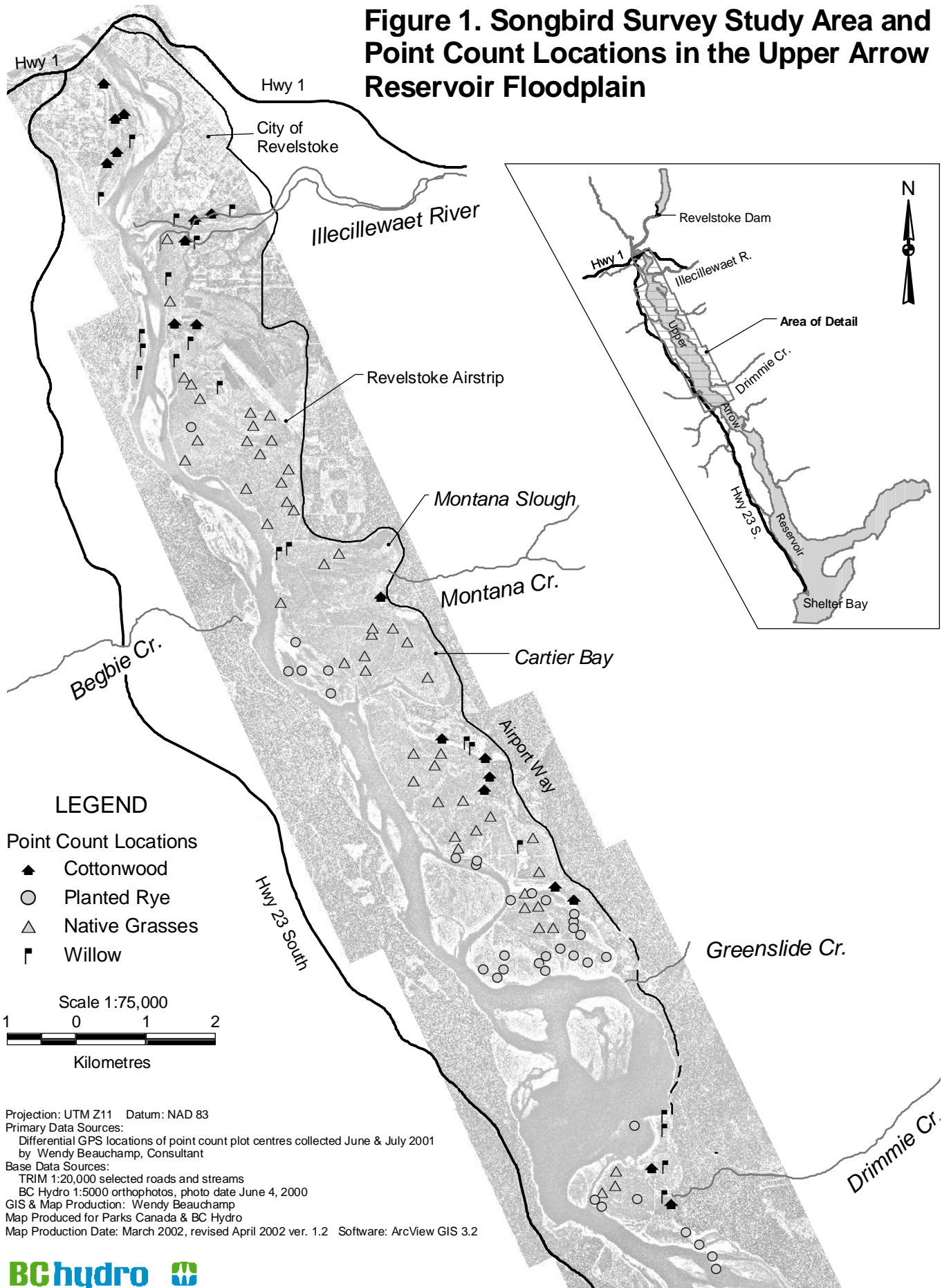




Figure 2. Arrow Reservoir near Drimmie Creek. Lower portions of the study area within the Revelstoke Reach cannot sustain vegetation cover due to prolonged flooding. Parks Canada: Michael Morris photograph, April 2001.



Figure 3. Study area looking south at low water, Revelstoke Reach, Arrow Reservoir. Bright green areas are under water at high pond. Parks Canada: Michael Morris photograph, June 2001.

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## 2. Methods

### 2.1. Field methods

Terrestrial vegetation within the flooded zone was stratified into 4 classes: planted Fall Rye, native grasses, willow shrub, and cottonwood (Figures 4-7). These four vegetation classes roughly correlated with elevation. Fall Rye was planted annually in the lowest zones (with the most persistent flooding). Native grasses included a complex of grasses, sedges, and horsetails with no shrubs that naturally invaded the floodplain and were typically found between the Fall Rye and the Willow Shrub. The Willow Shrub class had variable shrub density of 1+ stems and typically was located between the Native Grasses class and the Cottonwood class. The Cottonwood class had a variable density of 1+ cottonwood stems and was at the highest elevation below the maximum reservoir elevation.

This study area included that portion of the floodplain on the east side of the reservoir from the Trans-Canada Highway bridge at Revelstoke to Drimmie Creek and the west side of the reservoir from the Trans-Canada Highway bridge to Tonkawatla Creek. Using orthophotographs taken at low water levels, a set of randomly selected survey points was generated for each vegetation class. Although an attempt was made to have equal numbers of survey sites in each vegetation stratum, this was not possible because of unequal availability. One hundred and thirty-two sample sites were identified.

Each site was visited at 15-day intervals from May 16 to July 31, 2001 (5 samples per site maximum) within 4 hours after astronomical sunrise. Time of visit was not consistent between samples. During each site visit an observer would conduct a 5 minute point count by actively scanning by sight and sound for any species identifiable from the site. Species were recorded as within or outside of 50 m and notes made on numbers and activity (e.g., flying, singing). In addition, the observer made a sound recording of the entire 5-minute sample using minidisc recorders and an external microphone. These recordings were then reviewed by an independent observer to verify species identity.

During each point count, the observer also noted birds detected outside the 50 m plot, but within the floodplain. Sampling was discontinued during periods of heavy rain or fog.

Field notes were then transcribed into an Access database.





a.

b.

Figure 4. Planted rye vegetation type. a. ) shortly after planting (April 2001) b) in mid summer (July 2001). a. ) Parks Canada: Michael Morris photograph b) BC Hydro: Janice Jarvis photograph



Figure 5. Native grasses vegetation type. Parks Canada: J. Woods photograph.



Figure 6. Willow vegetation type. Parks Canada: J. Woods photograph.



Figure 7. Cottonwood habitat type. Parks Canada: J. Woods photograph.



Figure 8. Primary field observers, D. Mattheissen (L) and J. Jarvis (R). Note sound recording device mounted on the tripod. Typically observers would work independently. Parks Canada: J. Woods photograph.



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## 2.2. Analysis methods

Bird community indices included species abundance, species richness, species diversity, and species evenness (Krebs 1998) (Table 1).

### 2.2.1. Species Richness

Species richness was estimated using mark-recapture methods that account for differences in the sightability of songbird species. The procedure for this analysis was as follows. First presence or absence of species was tabulated for each period of the survey for each habitat type. Second, this data set was constructed as a mark-recapture x-matrix with each row being the presence or absence particular species for each survey period. Mixture model heterogeneity estimators (Pledger 2000) as incorporated in program MARK (White and Burnham 1999) were then used to estimate species richness (Boulinier et al. 1998). The heterogeneity estimators allow each species to have its own unique probability of sighting. This is done by letting capture probabilities come from more than one capture probability distribution. There are three parameters with the 2 distribution mixture model. The parameters are the probability that a given capture probability will come from the first distribution ( $\pi$ ), the mean capture probability of the first distribution ( $p_1$ ), and the mean capture probability of the second distribution ( $p_2$ ). The probability that the capture probability comes from the second distribution is  $1 - \pi$  (Pledger 2000).

The heterogeneity models were contrasted with models that assume equal sighting probabilities for the mixture model analysis in program MARK to assess the assumption of unequal sighting probabilities of bird species. In addition, the influence of varying numbers of point counts for each habitat type was also examined using program MARK. It is possible that habitat types in which more point count circles were sampled would record more species as an artifact of increased effort or area surveyed (Krebs 1998). Effort (as indexed by the mean number of point count circles visited for each sample period) was entered in the mixture model analysis as a covariate of the  $p_1$  and  $p_2$  sighting probability parameters to determine the influence of effort, and potentially account for this potential issue.

Model fit was assessed using AICc or QAICc model selection methods. Models with the lowest AICc or QAICc scores were considered most supported by the data. Delta AICc ( $\Delta$ AICc) values were also used to evaluate the fit of models when their AICc scores were close. In general, any model with a  $\Delta$ AICc score of less than 2 was most supported by the data. Given the sparseness of data, model averaging of estimates using AICc weights was used to confront model selection uncertainty (Burnham and Anderson 1998). Model averaging allows the estimates of all the models used in the analysis to be considered and therefore provides a more robust estimate than traditional estimates based on single models. In addition, evaluation of estimates and associated error provides a more

realistic evaluation of parameter estimates than traditional hypothesis tests (Burnham and Anderson 1998).

It could be argued that increasing effort will result in both an increase in detection rates of species (as accounted for in the MARK analysis by introduction of effort as a covariate) and the total number of species sighted. Therefore, use of effort as a covariate may not completely account for increased numbers of species sighted in habitat types that received greater effort. Therefore, a rarefaction method was used to estimate species richness that accounts for different degrees of effort for each area surveyed. Rarefaction estimates standardize the count of species for a given number of individual birds sighted. Or in other words, rarefaction answers the question “How many species would have been sighted if  $n$  individual birds were sighted in each habitat type?”. This standardized number ( $n$ ) was set at 200 birds for each habitat type and data from all survey periods was pooled for the analysis for each habitat type. The rarefaction estimates can only be used for comparison between habitats since rarefaction estimates are not robust to heterogeneity, and they are standardized at a number of individual birds which is less than the total number of individuals sighted in any community (Krebs 1998). The ecological methodology programs of Krebs (1998) were used for estimates.

#### 2.2.2. Species richness demographics

Changes in species composition due to migration and the nesting season potentially inflated species richness estimates. If species composition was changing during surveys then the species richness estimates represent the cumulative count of species visiting habitat types rather than a point estimate of species richness (similar to closure bias in tradition mark-recapture surveys (Kendall 1999)). The Pradel (1996) model in program MARK was used to investigate whether time-specific trends of bird species fidelity to habitat types, or rates of additions to specific habitat types was occurring. The Pradel (1996) model estimates fidelity ( $\phi$ ) of bird species to particular habitat types, or the probability that a bird species observed in a given habitat type will be observed again in the same habitat type. In addition, the Pradel (1996) model estimates rate of additions of bird species ( $f$ ) to a habitat type, or the proportion of new species present in a habitat type in a given period compared to species in a previous period (Cam et al. 2000). As with the species richness analysis, the effect of effort was considered on sightability of bird species.

#### 2.2.3. Species Diversity

Species diversity indices consider both the abundance and richness of species in an area. An area that has a higher density of dominant species but with few unique species will exhibit a lower species diversity index than an area that has abundance spread over many species. Species diversity was estimated using the Shannon Weiner  $H'$  function (Krebs 1998). The Shannon Weiner  $H'$  function was transformed to a  $N1$  index which

represented the number of equally common species which would produce a similar  $H'$  value (MacArthur 1965). The higher the  $N1$  value, the more diverse the community.

The data from all plots sampled for each vegetation type for each sampling period was pooled to estimate species diversity. Low sample sizes precluded estimation of species diversity on a plot specific basis.

The statistical analysis was conducted by using a generalized linear regression model which assumed a normal distribution for  $H'$  values (McCullough and Nelder 1989). Type 3 analyses were used to determine the significance of predictor variables (SAS Institute 2000). Habitat type was entered as the main factor in the analysis. As with other community indices, the estimated species diversity was potentially affected by changes in bird species abundance due to migration and the nesting season. Therefore, trends in species diversity were tested for by entering sampling period in the analysis as a covariate. In addition, the number of plots surveyed for each habitat type and period was entered as a covariate to determine if effort affected species diversity estimates.

#### 2.2.4. Number of bird counted and species density

Replicated counts of the number of birds (species pooled) counted in each point count circle are a potential index of relative abundance of birds in each habitat type. The counts for each habitat types and period were tabulated to investigate differences in relative abundance under the assumption that detectability of birds is similar in each habitat type.

The replicated count data was analyzed using Poisson regression (McCullough and Nelder 1989) with a log link function. The Poisson distribution is based upon counts and can accommodate data with zero counts. In addition assumptions regarding mean counts and variances can be accommodated through the estimation of a dispersion parameter which adjusts variances for mean counts (McCullough and Nelder 1989). The dispersion parameter was estimated by the Pearson chi-square of the model divided by its associated degrees of freedom (McCullough and Nelder 1989). All analysis was done in PROC GENMOD in SAS statistical package (SAS Institute 1997). Type 3 analyses were used to determine significance of predictor variables. Profile likelihood intervals were generated for each of the regression model parameters.

Habitat type was entered as the main factor in the Poisson analysis. The periods of survey included the migration period and the breeding season. One concern was that the density and richness of birds measured would be inflated during the migration period. Survey period was therefore also entered to determine if large trends in species counts existed throughout the survey period.

Species counts were used for statistical analysis but species density was used for results summaries to facilitate interpretation of results. Species density was estimated from species counts in each point count circle by dividing the number of species counted in each 50 m. point count circle by the area of the point count circle ( $157 \text{ m}^2$ ). An



assumption of this method is that all birds were detected within the 50-m point count circle.

An overview of the methods is presented in Table 1.

**Table 1. Indices used to assess bird communities**

Indicator	Statistic	Comments
Species richness	Heterogeneity mark-recapture estimators	Estimates species observed
	Pradel model	Explores demographics
Species diversity	Shannon-Wiener function	Considers abundance of each species, and the total number of each species
Species density	Mean densities of all bird species	A general index of species abundance

### 3. Results

The number of point counts sampled varied with vegetation type and with sampling period. Total sites and samples for each vegetation type included: planted rye, 41 sites, 201 samples; natural grassland, 50 sites, 243 samples; shrub-willow, 21 sites, 98 samples; cottonwood, 20 sites, 99 samples. The cottonwood and willow vegetation types received less point counts presumably due to the smaller area of these types when compared with native grasses and planted rye (Table 2).

**Table 2: Number of point counts per vegetation type per period**

Number	Dates	Vegetation type			
		Cottonwood	Native Grasses	Planted Rye	Willow
1	May 16-31	22	53	39	23
2	June 1-15	19	48	37	20
3	June 16-30	19	50	40	20
4	July 1-15	20	49	48	21
5	July 16-31	19	43	37	14

As mentioned earlier, the number of plots was entered as a covariate in the species richness and species diversity analyses to account for potential differences in species counted due to unequal effort between habitat types. The density and abundance estimates were based upon mean individual point counts and therefore were relatively robust to unequal effort.

Only birds that were not flying are considered in the statistical analyses in this paper. Other flying birds were not considered to be using the habitat types and were not considered but are presented in Appendix 1. Overall, 42, 22, 23, and 35 species were sighted in the cottonwood, native grass, planted rye, and willow habitat respectively over the course of the survey. There were 605, 422, 232, and 502 individual birds sighted in the cottonwood, native grass, planted rye, and willow habitats respectively over the course of the survey

### 3.1. Species richness

The results of the AIC model analysis suggested that the degree of effort (as indexed by the number of sites visited) did influence the sighting probabilities of birds when data from each period was pooled (Table 3). The most supported model suggested that the degree of heterogeneity (as indexed by  $\pi$ ) was different for each habitat types, however, differences in sighting probabilities could be explained by different degrees of effort in terms of the number of plots sampled. Models that simplified sighting probabilities of species to differ between open grass habitats (native grasses and planted rye) and wood habitat (willow and cottonwood) were less supported by the data. In general these results suggest that there was strong heterogeneity in species sightability with the heterogeneity models ( $M_{h2}$ ) showing the greatest degree of support when compared to non-heterogeneity models ( $M_o$ ,  $M_t$ ).

**Table 3: Species Richness mixture model selection**

Model	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
$M_{h2}$ : $\pi$ (habitat) $p1 \& p2$ (effort)	144.11	0.00	0.39	11	144.24
$M_{h2}$ : $\pi(.^A)$ $p1 \& p2$ (.)	144.49	0.38	0.32	7	152.88
$M_{h2}$ : $\pi(.)$ $p1$ (effort) $p2$ (effort)	144.77	0.67	0.28	8	151.11
$M_{h2}$ : $\pi$ (habitat) $p1$ (habitat) $p2$ (habitat)	152.47	8.37	0.01	16	142.11
$M_{h2}$ : $\pi(.)$ $p1$ (grass) $p2$ (grass)	159.51	15.40	0.00	9	163.78
$M_{h2}$ : $\pi$ (grass) $p1$ (grass)	162.90	18.79	0.00	9	167.17
$M_o$ ; $p$ (habitat)}	223.22	79.11	0.00	8	229.56
$M_t$	228.96	84.86	0.00	9	233.24
$M_o$	229.77	85.66	0.00	5	242.25
$M_t$ $p$ (habitat)}	232.46	88.35	0.00	36	178.23

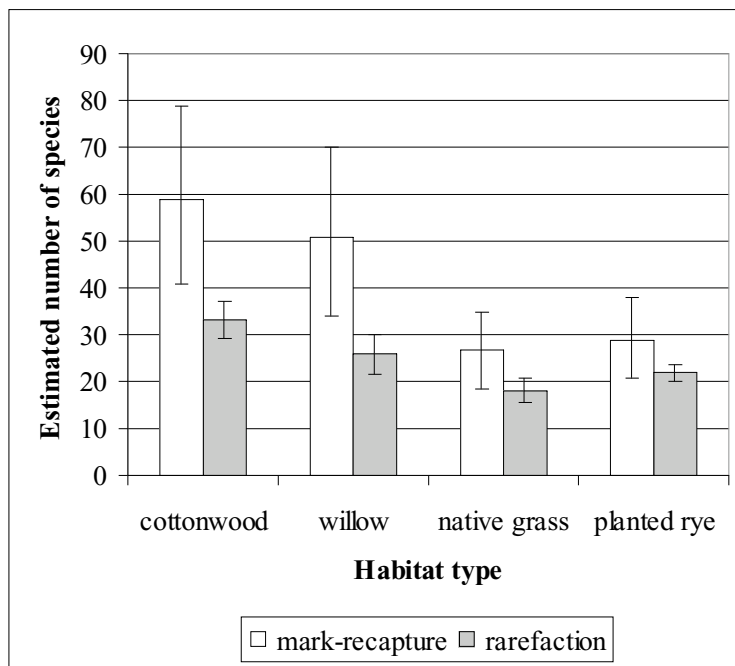
<sup>A</sup>Parameter was constant

Model averaged estimates of species richness suggested that cottonwood and willow habitat types had much greater species richness than native grass and planted rye. Observation of mixture probabilities suggest that the greatest heterogeneity in probabilities of detection for species existed in the cottonwood, willow, native grass, and planted rye (in order of magnitude).

Rarefaction estimates (standardized for 200 individual birds sighted per habitat type) are also presented for comparative purposes. It is stressed that the number of individuals (200) used for standardization is much lower than the number sighted in all habitat types and therefore the rarefaction estimates can only be used for comparison. It can be seen that similar trends are present however the cottonwood and willow habitat types show comparatively lower numbers of species. However, this is most likely due to heterogeneity of species detectability in the cottonwood and willow habitat types. Higher heterogeneity will result in negatively biased estimates of species richness using the rarefaction method.

The mark-recapture estimates could potentially be inflated if new birds arrived during the course of the survey. Therefore these results should be interpreted in unison with the demographic analysis presented next.

A comparison of mark-recapture and rarefaction method results is presented in Figure 9.



**Figure 9: Estimates of species richness from mixture models**

### 3.2. Pradel demographic analysis

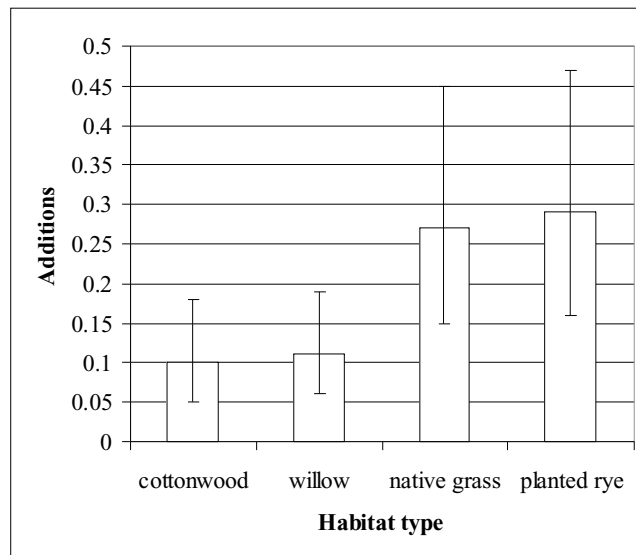
Results from the Pradel demographic analysis also suggested that the number of plots sampled also affected the probability of sighting a species (Table 4). In addition it was suggested that the rate of additions for the grass habitats (native grass, planted rye) was different than the willow and cottonwood habitat types. Fidelity ( $\phi$ ) was similar for all habitat types.



**Table 4: Pradel demographic analysis model selection results**

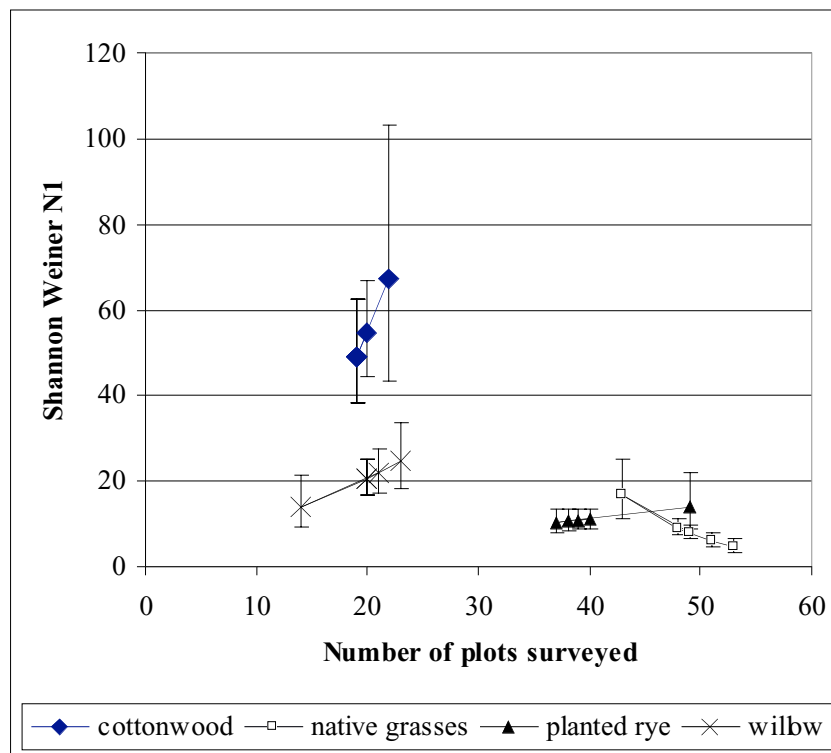
Model	AICc	$\Delta$ AICc	AICc Weights	Num. Par	Deviance
$\phi (.) p(.) f(\text{grass})$	739.08	0.00	0.26	4	468.60
$\phi (.) p(\text{effort}) f(\text{grass})$	739.75	0.67	0.18	5	467.20
$\phi (.) p(\text{grass}) f(\text{grass})$	739.89	0.81	0.17	5	467.34
$\phi (\text{grass}) p(.) f(\text{grass})$	741.15	2.07	0.09	5	468.60
$\phi (\text{grass}) p(\text{effort}) f(\text{grass})$	741.65	2.57	0.07	6	467.01
$\phi (\text{grass}) p(\text{grass}) f(\text{grass})$	741.77	2.69	0.07	6	467.13
$\phi (.) p(.) f(\text{habitat})$	742.51	3.43	0.05	6	467.87
$\phi (.) p(\text{effort}) f(\text{habitat})$	743.13	4.05	0.03	7	466.38
$\phi (\text{habitat}) p(.) f(\text{habitat})$	744.68	5.60	0.02	9	463.68
$\phi (.) p(\text{effort}) f(.)$	745.00	5.91	0.01	4	474.52
$\phi (.) p(.) f(.)$	746.06	6.98	0.01	3	477.64
$\phi (\text{habitat}) p(\text{habitat}) f(\text{habitat})$	748.02	8.94	0.00	12	460.50

The model averaged estimates of rates of addition are shown in Figure 10 which suggests that more species arrived in the grass habitats over the course of the study as compared to the willow and cottonwood habitats. This may have been due to green up of the grass habitats in later periods as well as the onset of the nesting season. Fidelity was approximately 0.85 for all habitat types which, means that the probability of resighting a species in any given habitat from one period to the next was 0.85.

**Figure 10: Estimates of rate of additions to habitat types.**

### 3.3. Species diversity estimates

The effects of trend, habitat type, effort, and the interaction of trend and habitat type and trend and effort were explored in the generalized linear model analysis. Of these, habitat type ( $\chi^2=17.85$ ,  $df=3$ ,  $p=0.0005$ ) and the interaction of habitat type and effort ( $\chi^2=23.54$ ,  $df=4$ ,  $p<0.0001$ ) were significant suggesting that species diversity was affected by both habitat type and effort or the number of plots surveyed (Figure 11). Observation of species diversity estimates as a function of effort shows an increase in species diversity with increasing survey effort for all habitat types except native grasses where species diversity declines with increasing effort. One reason for this might be that the number of plots surveyed declined for native grasses (Table 1) during the course of the project while the number of species sighted increased (as indicated by the Pradel demographic analysis results). Therefore, the decrease in species diversity may be an artifact of increasing species richness over the course of the survey. In general, the diversity of the cottonwood and willow is higher than the native grass and planted rye habitat types despite the fact that less plots were surveyed. However, it could be speculated that the comparative diversity of the cottonwood and willow habitat could have been potentially higher if more plots were surveyed (as discussed later).

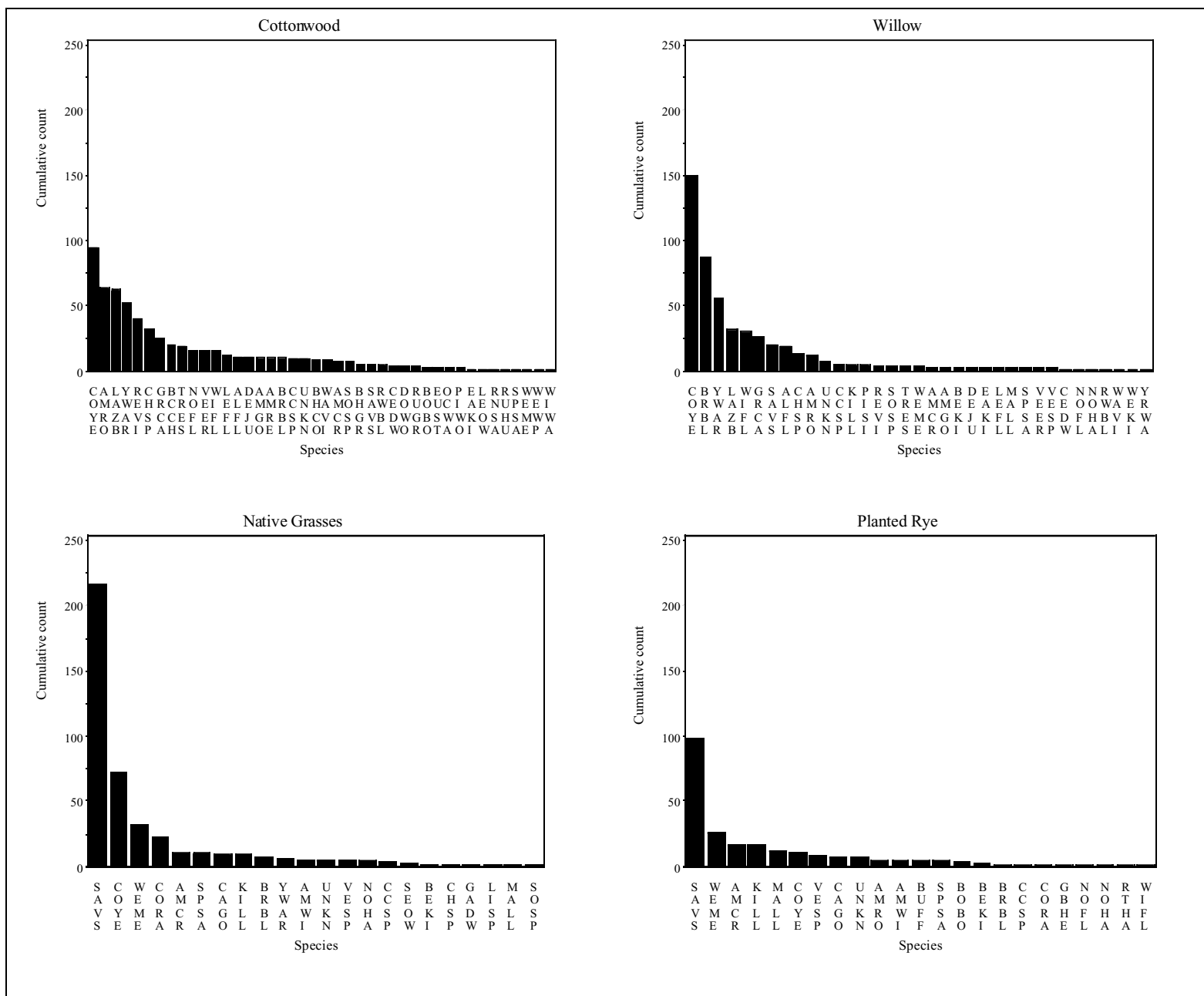


**Figure 11: Species diversity indices for habitat types**

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A more intuitive display of species diversity is a plot of the cumulative count of species sighted in each habitat type ranked by their abundance (Krebs 1998) (Figure 13). From these plots it can be seen that the native grass communities have relatively few species and are dominated by one or two species (i.e. SAVS-savannah sparrow and WEMA-western meadowlark) as indicated by high abundances of dominant species. In contrast, the cottonwood and willow have lower abundances of dominant species but more overall species. This attribute is what resulted in a higher Shannon-Weiner species diversity index value for these habitat types





**Figure 13: Cumulative count of species for each habitat type surveyed**

### 3.4. Species counts and density

The Poisson regression analysis explored the effects of habitat type, sample period, and the interaction of habitat type and trend in estimating the number of birds counted at a point count circle (Figure 14). Of these factors, habitat and trend (sample period) were significant (habitat;  $\chi^2=168.05$ ,  $df=3$ ,  $p<0.001$ , sample period;  $\chi^2=53.12$ ,  $df=1$ ,  $p<0.001$ ) predictors of bird abundance. This result suggests that different numbers of birds were observed in each habitat type and the number of bird changed in a similar fashion for each habitat type during the course of the survey.

Observation of predicted density estimates suggests higher bird abundances in the willow and cottonwood habitat types, and also suggests an increase in density throughout the survey periods.

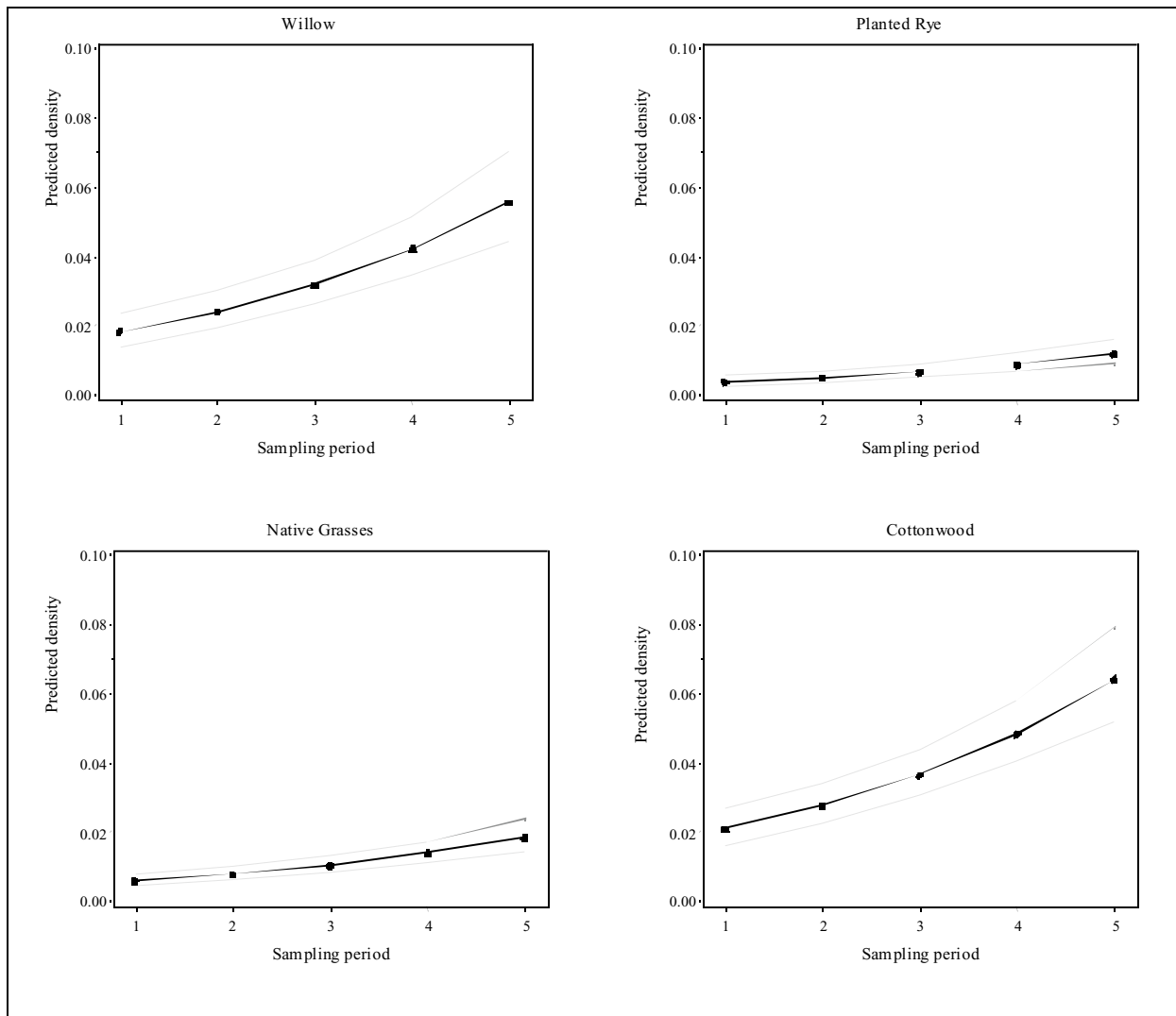


Figure 14: Density of birds sighted (species pooled) in birds per m<sup>2</sup> for each habitat type.

### 3.5. Rare species

During this project, J. Jarvis located an active Short-eared Owl nest (Figure 15). This is the first confirmed nesting of this species at Revelstoke within the wetlands.



Figure 15. Nesting habitat of Short-eared Owl located by J. Jarvis. Parks Canada: J. Woods photograph.

In May, J. Jarvis and J. Woods observed a single Loggerhead Shrike singing and perching within the willow habitat type near Drimmie Creek.

## 4. Discussion

The results of this analysis suggest that the greatest species diversity, species density, and species richness were found in the cottonwood and willow habitats when compared with the planted rye and native grasses habitat types. The grass communities have a few dominant species and a lower number of species overall when compared with the willow and cottonwood habitats.

In most cases the counts of individual birds and bird species increased during the course of surveys for all habitat types. The demographic analysis suggests that the greatest increase in new species occurred in the grass habitats as indicated by the higher rate of additions. One potential explanation for the higher increase in the grass communities was the later green-up of these areas when compared with the wooded areas. For example, it might be that the grass areas did not offer full cover and diverse food and sources of cover until the vegetation had reached a more mature stage, presumably in later June and July. This contrasts with the willow and cottonwood stands that have more permanent structure and therefore supported more species earlier on in the survey.

The mark-recapture estimates of species richness corresponds to a cumulative count of species in each habitat type due to the fact the actual count of species was changing throughout the survey. To obtain point estimates of species richness for each survey date an open mark-recapture model (Kendall 1999) would have to be used however this type of analysis is beyond the objectives of the comparative analysis presented in this paper.

Use of covariates to account for different effort or areas surveyed is an improvement over traditional analyses which assumed constant effort, or were less robust to heterogeneity of species sighting probabilities. The results of the mixture model analysis confirm the general conclusion of Boulinier et al. (1998) that species do show different sighting probabilities and therefore the use of more complex heterogeneity models to estimate species richness is warranted. One potential issue with the use of mark-recapture estimates is that unequal effort in terms of plots surveyed is not entirely accounted for. However, comparison with rarefaction estimates, which do account for unequal effort, does suggest that the general results are robust to unequal effort in the case of this study. The rarefaction method is not optimal in that it is biased by heterogeneity in species detection rates.

An assumption of the species density analysis is that all birds were observed within each point count circle. If this assumption is violated for certain cryptic species then density estimates will be negatively biased. If comparison of habitat types is the main objective, and the sightability of bird species is similar for each habitat type, then comparisons can still be made under the assumption that the degree of bias is similar for each habitat type. However, if sightability of birds differs for each habitat type then comparisons may be misleading. For example, birds that are further from the observers in brush habitat types may be less likely to be counted when compared to open grass habitats.

One potential method to confront differential sightability is the application of distance estimation to point count surveys as detailed in (Buckland et al. (1993) and the associated program DISTANCE (Thomas et al 1978) . For this methodology, the observer measures the distance (or distance category; i.e. 0-10m, 10-20, 20-50 etc) of the bird for each observation. This data is used to fit a sightability distribution based upon the frequencies of sightings in each distance category for each bird species. This method is best suited for target species analysis rather than community based analysis. For example, Setterington and Boulanger (2001) used distance methods to demonstrate that the differences in sightability of the dark-eyed junco between clearcut and natural stands produced misleading estimates using standard point counts. Distance methods requires larger sample sizes of birds however Setterington and Boulanger (2001) demonstrated that pooling of data from surveys in similar habitat types can partially mitigate sample size issues.

These results demonstrate that there is most songbird use in those reservoir floodplain habitats that most closely resemble natural riparian conditions (willow shrub, and cottonwood). The availability of these types of habitat within a working reservoir is a complex function of water-level management (depth and duration of flooding), topography, erosion, and active vegetation management (such as planting Fall Rye). Therefore, those management actions that promote the development of willow shrub and cottonwood habitat within the reservoir will likely promote more use by songbirds in terms of species richness, diversity, and abundance.

In a system such as this with widely fluctuating year-to-year conditions due to water levels (see Jarvis and Woods 2002), the origin of birds using these habitats and their reproductive output is of central interest. Birds using these habitats during the breeding season may have a widely variable reproductive output. During 2001, water levels were atypically low and very little of the

floodplain was inundated during the study. The inter-relationships between water levels, vegetation types, and food availability for songbirds (e.g., invertebrates) is unknown in this system.

Simultaneously recording bird songs during each observer-based point count proved to be very useful in allowing verification of species identification and facilitated observer learning. This system allows less experienced observers to make reliable contributions from the start of the sampling period.

## **5. Recommendations for future work**

1. Repeat these surveys during years with varying water conditions (e.g., “normal” years and “high” water years). The survey sites identified in 2001 could be used as base points for future sampling.
2. Investigate the relationship between water levels, vegetation types, and bird forage production.
3. For selected species, determine whether these reservoir habitats constitute “source” or “sink” populations.
4. Attempt to sample more cottonwood and willow plots. Use of different numbers of plots complicates the comparison of species richness and species diversity of different areas. Therefore, if possible, the sample size of plots for each habitat type should be made more even. Alternatively, there are potential randomization methods to further account for uneven sample sizes between plots when assessing species diversity measures.
5. Consider the use of distance methods if particular target species are of interest. Distance methods allow more robust estimation of species density. This method is much better suited for individual species rather than whole bird community analysis. The results of this study can be used to assess whether sample sizes are adequate to use distance methods for species of interest.
6. Consider the measurement of other covariates besides habitat type, which might affect species diversity and abundance. Other covariates such as water levels, elevation, the stage of vegetation (i.e. leaf cover), and potentially insect abundance may allow further explanation into differences between habitat types. The actual choice of covariates to measure should be based upon knowledge of factors that affect bird abundance.
7. Consider estimation of movement of species between habitat types. It is possible to further extend the Pradel demographic analysis to estimate movement rates of species between habitats as a function of water level or spring green up of habitat types. For example, if multiple surveys were conducted at various water levels then it would be possible to determine if bird species move to different habitat types as a function of water level. Or, it may be possible that species initially utilize the cottonwood and willow habitat types prior to

green-up of the grass stands. In this case there would be little movement of species until later periods in the survey. Using multi-strata models in program MARK (White and Burnham 1999) it is possible to estimate movement rates between habitat types to determine how the habitat types might relate to each other temporally in the migration and nesting seasons or as a function of water level. This analysis should be based upon a-priori hypothesis of movement, and was beyond the scope of the efforts presented in this manuscript.

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## Appendix 1: Cumulative species list for each habitat type

This table includes birds flying over habitat types as indicated by “Flying” in the behaviour category. The birds denoted by flying were not included in the statistical analysis.

Vegetation Type	Common_Name	Species Code	Behaviour
Cottonwood	Alder Flycatcher	ALFL	Not flying
Cottonwood	American Crow	AMCR	Not flying
Cottonwood	American Goldfinch	AMGO	Not flying
Cottonwood	American Redstart	AMRE	Not flying
Cottonwood	American Robin	AMRO	Not flying
Cottonwood	American Wigeon	AMWI	Flying
Cottonwood	Bank Swallow	BANS	Flying
Cottonwood	Black-capped Chickadee	BCCH	Not flying
Cottonwood	Brown-headed Cowbird	BHCO	Not flying
Cottonwood	Black-headed Grosbeak	BHGR	Not flying
Cottonwood	Bobolink	BOBO	Not flying
Cottonwood	Brewer's Blackbird	BRBL	Not flying
Cottonwood	Canada Goose	CAGO	Flying
Cottonwood	Clay-colored Sparrow	CCSP	Not flying
Cottonwood	Cedar Waxwing	CEDW	Not flying
Cottonwood	Chipping Sparrow	CHSP	Not flying
Cottonwood	Cliff Swallow	CLSW	Flying
Cottonwood	Common Raven	CORA	Flying
Cottonwood	Common Yellowthroat	COYE	Not flying
Cottonwood	Dark-eyed Junco	DEJU	Not flying
Cottonwood	Downy Woodpecker	DOWO	Not flying
Cottonwood	Eastern Kingbird	EAKI	Not flying
Cottonwood	European Starling	EUST	Not flying
Cottonwood	Great Blue Heron	GBHE	Flying
Cottonwood	Gray Catbird	GRCA	Not flying
Cottonwood	Lazuli Bunting	LAZB	Not flying
Cottonwood	Least Flycatcher	LEFL	Not flying
Cottonwood	Long-eared Owl	LEOW	Not flying
Cottonwood	Mallard	MALL	Flying
Cottonwood	Northern Flicker	NOFL	Not flying
Cottonwood	Orange-crowned Warbler	OCWA	Not flying
Cottonwood	Osprey	OSPR	Flying
Cottonwood	Pine Siskin	PISI	Flying
Cottonwood	Pileated Woodpecker	PIWO	Not flying
Cottonwood	Red-eyed Vireo	REVI	Not flying
Cottonwood	Red-naped Sapsucker	RNSA	Not flying
Cottonwood	Ruffed Grouse	RUGR	Not flying
Cottonwood	Rufous Hummingbird	RUHU	Not flying
Cottonwood	Red-winged Blackbird	RWBL	Not flying
Cottonwood	Savannah Sparrow	SAVS	Not flying
Cottonwood	Song Sparrow	SOSP	Not flying

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Cottonwood	Spotted Sandpiper	SPSA	Not flying
Cottonwood	Tree Swallow	TRES	Not flying
Cottonwood	Vaux's Swift	VASW	Flying
Cottonwood	Veery	VEER	Not flying
Cottonwood	Violet-green Swallow	VGSW	Flying
Cottonwood	Warbling Vireo	WAVI	Not flying
Cottonwood	Western Meadowlark	WEME	Not flying
Cottonwood	Western Wood-Pewee	WEWP	Not flying
Cottonwood	Willow Flycatcher	WIFL	Not flying
Cottonwood	Wilson's Warbler	WIWA	Not flying
Cottonwood	Western Palm Warbler	WPAW	Flying
Cottonwood	Yellow Warbler	YWAR	Not flying
Native Grasses	American Crow	AMCR	Not flying
Native Grasses	American Pipit	AMPI	Flying
Native Grasses	American Wigeon	AMWI	Not flying
Native Grasses	Bald Eagle	BAEA	Flying
Native Grasses	Belted Kingfisher	BEKI	Not flying
Native Grasses	Black Swift	BLSW	Flying
Native Grasses	Brewer's Blackbird	BRBL	Not flying
Native Grasses	Blue-winged Teal	BWTE	Flying
Native Grasses	Canada Goose	CAGO	Not flying
Native Grasses	Clay-colored Sparrow	CCSP	Not flying
Native Grasses	Chipping Sparrow	CHSP	Not flying
Native Grasses	Common Merganser	COME	Flying
Native Grasses	Common Raven	CORA	Not flying
Native Grasses	Common Snipe	COSN	Flying
Native Grasses	Common Yellowthroat	COYE	Not flying
Native Grasses	Gadwall	GADW	Not flying
Native Grasses	Great Blue Heron	GBHE	Flying
Native Grasses	Killdeer	KILL	Not flying
Native Grasses	Lincoln's Sparrow	LISP	Not flying
Native Grasses	Mallard	MALL	Not flying
Native Grasses	Merlin	MERL	Flying
Native Grasses	Northern Harrier	NOHA	Not flying
Native Grasses	Northern Rough-winged Swallow	NRWS	Flying
Native Grasses	Osprey	OSPR	Flying
Native Grasses	Rufous Hummingbird	RUHU	Flying
Native Grasses	Savannah Sparrow	SAVS	Not flying
Native Grasses	Short-eared Owl	SEOW	Not flying
Native Grasses	Song Sparrow	SOSP	Not flying
Native Grasses	Spotted Sandpiper	SPSA	Not flying
Native Grasses	Tree Swallow	TRES	Flying
Native Grasses	Vaux's Swift	VASW	Flying
Native Grasses	Vesper Sparrow	VESP	Not flying
Native Grasses	Violet-green Swallow	VGSW	Flying
Native Grasses	Western Meadowlark	WEME	Not flying
Native Grasses	Yellow Warbler	YWAR	Not flying
Planted Rye	American Crow	AMCR	Not flying
Planted Rye	American Pipit	AMPI	Flying

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Planted Rye	American Robin	AMRO	Not flying
Planted Rye	American Wigeon	AMWI	Not flying
Planted Rye	Bank Swallow	BANS	Flying
Planted Rye	Belted Kingfisher	BEKI	Not flying
Planted Rye	Bobolink	BOBO	Not flying
Planted Rye	Brewer's Blackbird	BRBL	Not flying
Planted Rye	Bufflehead	BUFF	Not flying
Planted Rye	Canada Goose	CAGO	Not flying
Planted Rye	Clay-colored Sparrow	CCSP	Not flying
Planted Rye	Cliff Swallow	CLSW	Flying
Planted Rye	Common Raven	CORA	Not flying
Planted Rye	Common Yellowthroat	COYE	Not flying
Planted Rye	Great Blue Heron	GBHE	Not flying
Planted Rye	Killdeer	KILL	Not flying
Planted Rye	Mallard	MALL	Not flying
Planted Rye	Northern Flicker	NOFL	Not flying
Planted Rye	Northern Harrier	NOHA	Not flying
Planted Rye	Northern Rough-winged Swallow	NRWS	Flying
Planted Rye	Northern Shoveler	NSHO	Flying
Planted Rye	Osprey	OSPR	Flying
Planted Rye	Red-tailed Hawk	RTHA	Not flying
Planted Rye	Rufous Hummingbird	RUHU	Flying
Planted Rye	Savannah Sparrow	SAVS	Not flying
Planted Rye	Short-eared Owl	SEOW	Flying
Planted Rye	Spotted Sandpiper	SPSA	Not flying
Planted Rye	Tree Swallow	TRES	Flying
Planted Rye	Vaux's Swift	VASW	Flying
Planted Rye	Vesper Sparrow	VESP	Not flying
Planted Rye	Western Meadowlark	WEME	Not flying
Planted Rye	Willow Flycatcher	WIFL	Not flying
Willow	Alder Flycatcher	ALFL	Not flying
Willow	American Crow	AMCR	Not flying
Willow	American Goldfinch	AMGO	Not flying
Willow	American Pipit	AMPI	Flying
Willow	American Robin	AMRO	Not flying
Willow	American Wigeon	AMWI	Flying
Willow	Belted Kingfisher	BEKI	Not flying
Willow	Brown-headed Cowbird	BHCO	Flying
Willow	Brewer's Blackbird	BRBL	Not flying
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Willow	Common Raven	CORA	Flying
Willow	Common Yellowthroat	COYE	Not flying
Willow	Dark-eyed Junco	DEJU	Not flying
Willow	Eastern Kingbird	EAKI	Not flying
Willow	Great Blue Heron	GBHE	Flying
Willow	Gray Catbird	GRCA	Not flying

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Willow	Killdeer	KILL	Not flying
Willow	Lazuli Bunting	LAZB	Not flying
Willow	Least Flycatcher	LEFL	Not flying
Willow	Mallard	MALL	Not flying
Willow	Northern Flicker	NOFL	Not flying
Willow	Northern Harrier	NOHA	Not flying
Willow	Northern Rough-winged Swallow	NRWS	Flying
Willow	Osprey	OSPR	Flying
Willow	Pine Siskin	PISI	Not flying
Willow	Pileated Woodpecker	PIWO	Flying
Willow	Red-eyed Vireo	REVI	Not flying
Willow	Rufous Hummingbird	RUHU	Flying
Willow	Red-winged Blackbird	RWBL	Not flying
Willow	Savannah Sparrow	SAVS	Not flying
Willow	Song Sparrow	SOSP	Not flying
Willow	Spotted Sandpiper	SPSA	Not flying
Willow	Tree Swallow	TRES	Not flying
Willow	Vaux's Swift	VASW	Flying
Willow	Veery	VEER	Not flying
Willow	Vesper Sparrow	VESP	Not flying
Willow	Violet-green Swallow	VGSW	Flying
Willow	Warbling Vireo	WAVI	Not flying
Willow	Western Kingbird	WEKI	Not flying
Willow	Western Meadowlark	WEME	Not flying
Willow	Willow Flycatcher	WIFL	Not flying
Willow	Wood Duck	WODU	Flying
Willow	Yellow-rumped Warbler	YRWA	Not flying
Willow	Yellow Warbler	YWAR	Not flying

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