

**TEMPORAL VARIATION IN FALL BIRD DENSITY AT HIGH
ELEVATION HABITATS IN SOUTHERN BRITISH COLUMBIA:
AN ANALYSIS USING DISTANCE SAMPLING**



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August 2001

Available at: <http://www.forestry.ubc.ca/alpine/research/papers.html>

Summary

A survey of birds using line transect sampling was conducted across an alpine-subalpine-montane habitat gradient in ten mountain sites in Southern British Columbia, over a period of three years from 1998 to 2000. Overall mean bird density and mean densities of various taxonomic bird groups were calculated for each habitat in each study site for the three years using the distance sampling software, DISTANCE (version 3.5). Mean bird density was significantly lower in 1999, relative to 1998. Mean bird density patterns across habitats in 1999 also differed with 1998 and 2000, with an observed sharp decline in alpine bird density in 1999. This may be attributed to colder weather conditions in fall in 1999. Recovery of bird densities varied across the taxonomic bird groups. The larks and pipits, chickadees, kinglets and wrens, woodpeckers, and thrushes showed signs of recovery in 2000, whereas densities for the warblers and sparrows were even lower than that of 1999. The finches and corvids appeared to be least affected, with erratic density patterns across the years. The line transect sampling was also evaluated in terms of its ability to correct for variation in bird detectability in different habitats and its sensitivity to observer bias. The results suggest that bird detectability has been corrected, but that observer variation in the estimating of distances was prevalent. The latter was however controlled by the study design. The significance of weather perturbations in the regulation of bird densities at higher elevation habitats is discussed. The importance of high elevation habitats, especially the subalpine habitat, is further highlighted.

Introduction

Several hypotheses pertaining to the determination of species composition and densities of bird communities in high elevational habitats have been tested over the years. Resource availability in terms of foraging substrates and food has been approximated through measures of vegetation structure and floristics, and has been shown to influence niche partitioning and the differential use of high elevational habitats by various species (Sabo 1980; Sabo and Holmes 1983; Airola and Barrett 1985; Finch 1989). Competition amongst bird species under the condition of limited food resources has been commonly cited as the main process that is driving this observed pattern of niche partitioning and differential resource use amongst bird species in high elevational habitats (Noon 1981; Hutto 1985). While competition may be important, the ability of bird species to thermoregulate under cold conditions may limit its use of high elevation habitats. For example, the Blackpoll Warbler was found to be the dominant warbler species in high elevational krummholz in the White Mountains of New Hampshire. This could be attributed to its larger body mass relative to other warbler species, thereby conferring it thermoregulatory advantage (Sabo 1980).

However, it is becoming clear that weather could be an overriding factor in determining patterns of bird species composition and densities in high elevational habitats. Ehrlich et al. (1972) had suggested that sudden weather perturbations could be an important driving force in the regulation of animal population density in high elevation habitats, bringing about local declines and extinction. It is well-known that mountain weather is capricious and can disrupt the reproductive cycle of bird species, thereby adversely affecting recruitment and population densities. In a long-term study of

White-crowned Sparrow in the Sierra Nevada Mountains in California, Morton (1978) showed that the variation in snowpack across years can affect the arrival and occupancy schedules of the sparrows. In years of high snowfall and deep snowpack, breeding was delayed until late summer where habitat patches free of snow were available. This reduced the number of breeding pairs in the area and the overall breeding success and productivity of the population. In another long-term study of hummingbirds in the subalpine zone of the Salmon-Trinity Alps in northwest California, Gass and Lertzman (1980) showed that after a violent summer hailstorm, the number of fall migrant rufous hummingbirds holding territories was dramatically reduced due to the decimation of a large proportion of flowers in the meadows. Adverse conditions of cold and wind, such as those experienced in high elevational habitats, would not only disrupt reproductive cycles, but could potentially affect the foraging efficiency of birds (Grubb 1975, 1978). The importance of weather in regulating bird densities in high elevational habitats has led to suggestions that bird populations inhabiting high elevation habitats may exhibit a source-sink structure. Source populations would tend to occur at optimal elevations for each species and dispersing individuals, especially young, may move up or down this gradient depending on environmental conditions (DeSante 1990). More recently, Martin et al. (2000) emphasized the importance of the dispersal of young and external population recruitment in ensuring the persistence of bird populations inhabiting high elevational habitats.

Most studies that investigate the influence of weather on bird density patterns in high elevation habitats were conducted during the breeding season. Consequently, there is very little information about the role of weather in influencing bird density patterns and

high elevation habitat use outside the breeding season. In North America, high elevation habitats are used extensively by migrating bird species in fall due to the openness and permeability of these habitats, as well as the greater availability of food relative to other lower elevation habitats at this time (Pattie and Verbeek 1966; Antor 1995; Berthold 1993; Korner 1999). In British Columbia, subalpine and alpine habitats are used by large number of songbird species on their southward migration in fall (Cannings and Cannings 1996; Martin and Ogle 1998, 2000, 2001).

A study was conducted by K. Martin over three years (from 1998 to 2000) in ten mountain sites in south and central British Columbia to obtain information on temporal and spatial patterns of bird density in high elevation habitats during fall (Figure 1). Bird surveys using line transects were conducted across an elevation gradient ranging from 800m to 2200m in these sites. Habitats surveyed across this gradient include the alpine tundra (rock, grassland, tundra and krummholz, usually at elevations greater than 1650m), subalpine parkland (meadows and parkland) and montane forest (contiguous canopy with openings) (zonations of alpine, subalpine and montane habitats follow after Love 1970). Transect lengths varied between 200m to 1400m. Bird surveys were conducted between early August and mid-October, with three to four visits in each year. A total of seven observers were used over the three years (Billie Gowans (BG), Patricia Collins (PC), Pam Ronalds (PR) and Steve Ogle (SO) in 1998; Catherine Conroy (CC) and SO in 1999; Marty Mossop (MDM) and Yolanda Moreby (YM) in 2000). Bird densities were estimated for each habitat type in each site with distance sampling (Buckland et al. 1993). Line transects were used in this study because they were considered to be the most effective in sampling across environmental gradients.

Compared to the point count technique, it is also more efficient in that it is possible to obtain density estimates of migrating bird species (Wilson 2000). More importantly, when used in combination with distance sampling (hereinafter referred to as line transect sampling), it corrects for the differences in detectability of birds in alpine, subalpine and montane habitats (Burnham et al. 1980; Buckland et al. 1993). This allows bird density estimates to be comparable across the habitats. This is unlike the use of fixed-width transects, which does not account for variation in bird detectability (Bell and Ferrier 1985; Harden et al. 1986; Er et al. 1995). Further details of the study design can be obtained from Martin and Ogle (2000, 2001).

Using bird density data obtained from this study, I first determined if line transect sampling had corrected for differences in bird detectability in the three habitats and that the patterns are not manifested by the use of several observers in the study in different years. I then proceeded to test the hypothesis that bird density in high elevation habitats in fall is affected by sudden weather perturbations. If this were true, bird density would decline in years of poor weather conditions, relative to years with good weather conditions. To test this hypothesis, I compared bird densities across years and related these differences (if any) to weather data of the study area. I further investigated if responses to weather perturbations vary from one taxonomic bird group to another. Of interest would be the question of whether birds show shift in habitat use under the conditions of poor weather conditions. This report summarizes the results of this preliminary analysis.

Method of Analysis

Theoretical aspect of line transect sampling

The theoretical aspect of line transect sampling has been developed and described in Buckland et al. (1993). It is summarized here.

In fixed-width strip transect sampling, bird density is usually calculated as the number of birds detected per unit area. This is as follows:

$$\hat{D} = \frac{n}{2wL} \quad (\text{Eq 1}),$$

where n is the number of birds detected, w is the width and L is the length of the transect. This assumes that all birds in the population or community are detected within the survey area and have similar detectability. Both assumptions are often incorrect, especially for a community level study.

In line transect sampling, the assumption is that all birds along the transect are detected and that the number of birds detected is a proportion of the true population in the survey area. If we know the proportion of birds that have been detected in the survey area, \hat{P}_a , we can correct the density estimate as follows:

$$\hat{D} = \frac{n}{2wL\hat{P}_a} \quad (\text{Eq 2}).$$

As bird detection can be assumed to decline with distance from the transect, the proportion of birds detected within the survey area can be defined as such:

$$\hat{P}_a = \frac{\int_0^w g(x)dx}{w} \quad (\text{Eq 3}),$$

where $\int_0^w g(x)dx$ is the integral of the detection function which is the probability of

detecting an object with distance from the transect¹ and w is the width of the transect (Figure 2). Substituting \hat{P}_a into equation 2, the estimate of bird density can be re-written as such:

$$\hat{D} = \frac{n}{2L \int_0^w g(x) dx} \quad (\text{Eq 4}).$$

Hence, the ability to obtain the detection function by modelling the frequency of bird occurrences with distance from the transect is central to the use of line transect sampling. In this analysis, the modelling is done using the software DISTANCE (version 3.5) (Thomas et al. 1998).

Data organisation in DISTANCE

Bird observation data from line transect surveys in each of the study sites for each year were imported into DISTANCE (version 3.5). The data included bird species, bird numbers, radial distance and angles of bird detection from the transect, total length of the transect (i.e. length of transect multiplied by the number of times the transect was surveyed) and habitat type (i.e. alpine or subalpine or montane). The bird species were also grouped into various taxonomic bird groups as follows: larks and pipits (LAP) (comprised of the Horned Lark and American Pipit), chickadees, kinglets and wrens (CHK) (dominated by the Mountain Chickadee, Golden-crowned Kinglet and Ruby-crowned Kinglet), warblers (WAR) (dominated by the Yellow-rumped Warbler, the Wilson Warbler and Townsend's Warbler), sparrows (SPA) (dominated by the Savannah Sparrow, White-crowned Sparrow and Dark-eyed Junco), woodpeckers, nuthatches and

¹ The detection function is obtained by modelling the probability of bird detection with distance from the transect. The probability of detection at a given distance from the transect is calculated as the number of bird detections at that distance as a proportion of the total number of bird detections.

creepers (WOD) (dominated by the Red-breasted nuthatches, Red-shafted Flickers and Red-breasted sapsuckers), corvids (COR) (dominated by the Stellar Jay, Clark's Nutcrackers, Gray Jays and Common Ravens), finches (FIN) (dominated by the Pine Siskin and Red Crossbill) and thrushes (THR) (dominated by American Robin, Varied Thrush, Hermit Thrush, Townsend's Solitaires and Cedar Waxwing). Bird detections were treated as clusters in DISTANCE as birds occurred mainly in flocks during the study.

Estimating effective strip widths

To determine if line transect sampling had corrected for variation in the detectability of birds in different habitats, the effective strip width was estimated by DISTANCE for each habitat in each study site for each year. A mean effective strip width for each habitat in each year was then obtained by averaging across all study sites in that year. The effective strip width is defined as half-width of the strip extending either side of a transect such that as many birds are detected outside the strip as remain undetected within it (Buckland et al. 1993).

Generating mean detection distances obtained by different observers

The effects of observer could influence apparent patterns of bird densities, if the observers in this study vary significantly in their estimation of distances in different habitats. A mean detection distance in each habitat was calculated for each observer in that year after pooling all available records of bird detections within each year.

Estimating bird density, cluster density and cluster size

DISTANCE was used to estimate the bird density (i.e. number of birds per ha), cluster density (i.e. number of clusters per ha) and cluster size of different habitats for each study site in each year. This was done by stratifying the data from each study site in each year by habitat. Data from each habitat were modelled by DISTANCE to produce a detection function. The half-normal, hazard rate, negative exponential and uniform models (with and without cosine series expansion) were fitted to the data. The “best” model was selected with the use of the Akaike’s Information Criterion (AIC) and a corresponding bird density for each habitat was estimated by DISTANCE. Estimates of cluster density and cluster size for each habitat were also provided by DISTANCE. Cluster density was corrected for size-biased sampling by the use of a regression model of cluster size against the distance from the line (i.e. larger clusters or flocks will be more detectable) (Buckland et al. 1993). The means of bird density, cluster density and cluster size for each habitat were obtained by averaging across all study sites within each year.

To further estimate the bird density for each taxonomic bird group for different habitats within each study site in each year, the data in the habitat stratum were further post-stratified by taxonomic bird groups. Data within each habitat were pooled according to the groups and the detection function for each group was modelled by DISTANCE using the four models described earlier. AIC was used to select the “best” model and a corresponding density estimate was estimated for each taxonomic bird group in each habitat. The mean bird density of each taxonomic bird group in each habitat was also obtained by averaging across the study sites within each year.

Weather Data

Weather data for Whistler and Kamloops were obtained from Environment Canada. These two weather stations are located in the vicinity of most of the study sites (around 100 km). Both weather stations are located at lower elevations than the study sites (Whistler weather station ~ 650 m; Kamloops weather station ~ 350 m), but the weather trends at lower elevations would be similar in pattern, albeit higher temperatures, to higher elevations. Weather information included monthly minimum temperature and the amount of precipitation (snowfall and rainfall) for the months of May to December in 1998, 1999 and 2000. Weather conditions for the three years were also obtained at a regional scale from Environment Canada (2001).

Statistical Analysis

To determine if line transect sampling had corrected for variation in the detectability of birds in different habitats, mean effective strip width was first analyzed across years with one-way ANOVA (data pooled from habitats of all study sites in the three years, $n = 58$). Where there was a significant difference, paired student's t-test was used to identify years that were significantly different from one another. To further determine if mean effective strip width varies significantly across habitats, one-way ANOVA was then performed by either pooling the data from all three years or separately in different years (subject to whether mean effective strip width differed significantly across years).

To determine if the mean detection distance of birds estimated by different observers vary significantly in each habitat, statistical analysis was done for each habitat in each year. One-way ANOVA was used in 1998 where there were four observers and

the student's t-test was used in 1999 and 2000 where there were two observers in each year. The paired student's t-test was also used to identify pairs of observers that were significantly different in 1998.

A one-way analysis of variance (ANOVA) was used to determine if mean bird density, mean cluster density, mean cluster size and the mean bird densities of each taxonomic bird group differed across years (data pooled from habitats of all study sites in the three years, $n = 58$). A significant result would warrant further analysis with paired student's t-test to identify pairs of years that were significantly different. This relied on a means comparison method that tested if the actual difference in the means of a pair (known as the absolute difference, Abs. Dif.) was greater than the difference that would result in a significant t-statistic ($\alpha = 0.05$) (known as the least significant difference, LSD). Positive difference suggests significant difference in a pair (i.e. $\text{Abs. Dif} - \text{LSD} > 0$) (SAS Institute 2001). Further analysis of each of these variables with habitat was then performed using one-way ANOVA by either pooling the data from all three years or separately in different years (subject to whether the variables differed significantly across years). Paired student's t-test was used to identify pairs of habitats that were significantly different. The results of this analysis were then discussed in relation to the weather data.

To ensure normality, logarithm transformation (i.e. $\text{Log}(x)$ and $\text{Log}(x+1)^2$) of the data was applied to all dependent variables, except mean effective strip width (Zar 1984). All statistical analysis was performed with SAS JMP version 4 (SAS Institute 2001).

² The transformation $\log(x+1)$ is often recommended when dealing with data with small values and zeros (Zar 1984, pp. 238), as is the case with mean bird densities of the various taxonomic bird groups.

Results

Validating the methodology

Annual habitat variation in effective strip width

Mean effective strip width differed significantly across years ($F = 2.80$, $p = 0.07$, $n = 58$). This difference was highly significant between 1998 and 1999, and between 1998 and 2000. No significant difference was detected between 1999 and 2000 (Table 1; Figure 3). One-way ANOVA of mean effective strip width across habitats was performed separately for 1998, and 1999 and 2000. The results showed that mean effective strip width differed significantly across habitats only in 1999 and 2000, but not in 1998 (1999/2000: $F = 3.60$, $p = 0.04$, $n = 30$) (Figure 3). In 1999 and 2000 combined, mean effective strip width was greatest for the alpine habitat (45.4 m), followed by the subalpine habitat (34.9 m) and montane habitat (31.8 m, Table 1). In 1998, the mean effective strip width for the alpine habitat (29.1 m) was relatively similar to that in the subalpine habitat (30.5 m), although they were still greater than that in the montane habitat (25.7 m). On average, the mean effective strip width was greater in the more open alpine and subalpine habitats than the forested montane habitat (40 m in the alpine habitat, compared to 33.6 m in the subalpine habitat and 29.8 m in the montane habitat over three years).

The effective strip width is dependent not only on the openness of the habitat and hence the extent at which birds could be detected, but also on the proportion of birds detected close to the transect (i.e. higher proportion of birds detected nearer to the transect would result in a smaller effective strip width). Examination of the detections pertaining to the alpine habitat across the three years showed that 25% of the detections

were less than 17.5 m from the transect in 1998. In comparison, 25% of the detections were less than 25 m from the transect in 1999 and less than 20 m from the transect in 2000. Hence, a greater proportion of birds were detected closer to the transect in the alpine habitat in 1998, thereby resulting a smaller mean effective strip width.

Variation in distances obtained by different observers

To determine if observer bias was prevalent, I tested if there was a significant difference in the mean detection distance of birds estimated by different observers in each habitat. This was done in separate years. In 1998, four observers were working in teams of two (PC and PR; PC and BG; occasionally PC and SO, and BG and SO). The one-way ANOVA revealed that differences in mean detection distance of birds amongst observers in 1998 were significant in alpine, subalpine and montane habitats (alpine: $F = 9.53$, $p < 0.0001$, $n = 584$; subalpine: $F = 26.55$, $p < 0.0001$, $n = 1123$; montane: $F = 12.98$, $p < 0.0001$, $n = 925$). Further analysis with paired student's t-test between observers showed that the variation in mean detection distance was restricted to differences between PC and SO, and PC and BG in all three habitats; PR and SO, and PR and BG in the alpine and subalpine habitats; BG and SO, and PC and PR in the montane habitat only (Table 2; Figure 4).

In 1999 and 2000, two observers were used in each year (CC and SO in 1999; MDM and YM in 2000). In 1999, the difference in the mean detection distance between the two observers was only significant for the subalpine habitat ($t = -4.49$, $p < 0.0001$, $n = 384$). SO was detecting birds at a mean distance much greater than CC (SO = 54 m, CC = 33 m) (Figure 5). Similarly in 2000, a significant difference in the mean detection distance was found only in the montane habitat where MDM detected birds over a wider

range than YM so that a significant result was obtained despite the mean detection distance being similar (standard deviation of distances for MDM = 49.2 m, compared to 16.9 m for YM; $t = -2.26$, $p = 0.03$, $n = 441$; Figure 6).

Observer variation in detection was more prevalent in 1998 where there were more observers. Furthermore, observer variation in detection seemed to interact with habitat, i.e. the montane and subalpine habitats being more prone to observer variation than the alpine habitat.

Variation of bird density in high elevation habitats with weather conditions

Variation in weather conditions

Comparing across the years of 1998, 1999 and 2000, temperatures were lowest in 1999 for the period of peak fall migration in September and October. The minimum temperature for the Whistler weather station was 4.5°C for the month of September in 1999, as compared to 7.1°C in 1998 and 6.2°C in 2000; and 0.6°C for the month of October in 1999, as compared to 2.7°C in 1998 and 1.1°C in 2000 (Figure 7). Similar annual trends in the minimum temperature for the months of September and October can also be seen from the Kamloops weather station records (Figure 8).

Although there was no significant trend in the total precipitation of the Whistler and Kamloops weather stations for September and October across the three years (Figures 9 and 10), the relatively sharp drop in minimum temperature for September/October 1999 brought about early snowfall in Whistler. This is evident by the presence of snowfall in October 1999, but not in October 1998 (Figure 11). It is unfortunate that snowfall data for the Whistler weather station was not available for the months of October in year 2000. However, on the basis that the minimum temperature for

October was similar for 1998 and 2000, there was likely no or very little snowfall in October 2000.

It is reasonable to conclude that 1999 was much colder than 1998 or 2000 for the period of peak fall migration in September and October. When projected upwards in terms of elevation, weather conditions in the high elevation study sites would be expected to be much colder in 1999, than in 1998 or 2000. This is consistent with observations of the field workers in this study, which suggest that 1999 was not only colder and windier, but had also protracted snowstorms in the months of September and October (K. Martin pers. comm.; S. Ogle pers. comm.).

On a regional scale, it is important to note that the winter of 1998 was the fifth warmest winter ever experienced in southern British Columbia over a 54 year period, with a departure of mean temperature 3.0°C above average (Environment Canada 2001). This would also suggest that temperature in fall is higher than usual.

Variation in overall bird density, cluster density and cluster size

Overall, mean bird density differed significantly across years ($F = 11.45$, $p < 0.0001$, $n = 58$), with mean bird density in 1998 (9.8 birds/ha) being significantly higher than in 1999 (2.9 birds/ha) or 2000 (4.1 birds/ha). Mean bird density did not differ significantly between 1999 and 2000 (Table 3, Figure 12). Separate analysis of mean bird density across habitats in 1998, and in 1999 and 2000 showed that mean bird density did not differ significantly across habitats. However, an interesting trend was observed. In 1998 and 2000, mean bird density was highest in the alpine habitat (1998 – 10.4 birds/ha; 2000 – 6.6 birds/ha), followed by the montane habitat (1998 – 9.8 birds/ha; 2000 – 3.4 birds/ha) and subalpine habitat (1998 – 9.4 birds/ha; 2000 – 2.2 birds/ha). This pattern

was most distinct in 2000, while a slight variation could only be detected in 1998. In 1999, the trends were reversed, with mean bird density being highest in the montane habitat (3.6 birds/ha), followed by the subalpine habitat (2.8 birds/ha) and alpine habitat (2.3 birds/ha) (Figure 12).

One-way ANOVA of mean cluster density across years yielded the same results as mean bird density ($F = 14.59$, $p < 0.0001$, $n = 58$, Table 3, Figure 13). When analyzed within 1998, mean cluster density did not differ significantly across habitats. But, a significant difference in mean cluster density across habitats was found when data from 1999 and 2000 were pooled ($F = 15.57$, $p < 0.0001$, $n = 30$). Mean cluster density in the alpine habitat (0.7 clusters/ha) was significantly lower than that in the subalpine habitat (1.5 clusters/ha) and montane habitat (2.4 clusters/ha). Mean cluster density did not differ significantly between the subalpine and montane habitats (Table 3, Figure 13). The trends in mean cluster density across the three habitats remained similar in all three years, with the montane habitat having the highest mean cluster density, followed by the subalpine and alpine habitats (Figure 13).

As expected, mean cluster size did not differ significantly across years ($F = 1.01$, $p = 0.37$, $n = 58$), but differed significantly across habitats for all years combined ($F = 10.52$, $p = 0.0001$, $n = 58$) (Figure 14). Mean cluster size was largest in the alpine habitat (4.4 birds/cluster), followed by the subalpine habitat (1.8 birds/cluster) and montane habitat (1.5 birds/cluster) (Table 3, Figure 14). Hence, relative to the subalpine and montane habitats, the mean number of bird detections (i.e. mean cluster density) in the alpine habitat was lower, but the number of individuals per detection (i.e. mean cluster size) was on average higher.

Bird density is a measure of the number of individuals and is a function of cluster density or the number of detections, cluster size and effective strip width (Figures 15, 16 and 17), i.e. $\text{Log}(\text{mean bird density}) = 0.989 \text{ Log}(\text{cluster density}) + 0.995 \text{ Log}(\text{cluster size}) - 0.018 \text{ Log}(\text{mean effective strip width}) + 0.070$, $F = 11385.58$, $p < 0.0001$, $R^2 = 0.998$, $n = 58$ ³. Although the overall pattern in mean cluster density and mean cluster size by habitat was similar across the years, there were substantial variations within each habitat across years. In 1998 and 2000, changes in mean cluster density were offset by changes in mean cluster size in the alpine habitat so that overall mean bird density remained high in the alpine habitat for those years. In contrast, both mean cluster density and mean cluster size were depressed in the alpine habitat in 1999 so that overall mean bird density was lower in that year, as compared to 1998 and 2000 (Figures 12 to 14).

Variation in the density of various taxonomic bird groups

Analysis of mean bird density for the various taxonomic bird groups across all years showed that bird density was significantly different only for SPA ($F = 14.89$, $p < 0.0001$, $n = 58$) and THR ($F = 4.06$, $p = 0.02$, $n = 58$). Nevertheless, the trends clearly showed that for all bird groups, mean density in 1998 was higher than in 1999 (Table 4 and Figures 18 to 25). The mean density for 2000 was variable amongst different bird groups. Some bird groups seemed to be recovering or have recovered from the effects of the harsher fall weather conditions in 1999. This is evident from the densities of the LAP, CHK, WOD, and THR, which were higher in 2000 than 1999, but still below the levels

³ Individual F-tests on the independent variables showed that mean cluster density ($F = 15821.86$, $p < 0.0001$) and mean cluster size ($F = 6465.28$, $p < 0.0001$) were significant at $\alpha = 0.05$. Mean effective strip width was not highly significant ($F = 1.35$, $p = 0.25$). This suggests that mean effective strip width did not contribute significantly to the model in the presence of the other two variables. It does not suggest that mean effective strip width is not an important explanatory variable of mean bird density. On its own, it is able to explain 51% of the variation in mean bird density (Figure 13). As such, it was retained in the model.

attained in 1998. At least for the FIN, bird density in 2000 was relatively similar to that in 1998. On the other hand, the WAR, SPA and COR did not seem to have recovered, given that their densities in 2000 were even lower than that in 1999 (Table 4, Figures 18 to 25).

Across the three years, mean density patterns across the habitats were similar for the LAP, CHK, WOD, WAR, SPA and THR (Table 4, Figures 18 to 22 and 25). Further statistical analysis of these trends in mean densities across the habitats was done by pooling data from all three years for the LAP, CHK, WOD and WAR, and by treating the data from 1998 and 1999/2000 separately for the SPA and THR. Differences in the mean densities across habitats were significant only for the LAP, CHK, WOD and WAR (LAP: $F = 7.30$, $p = 0.0015$, $n = 58$; CHK: $F = 16.91$, $p < 0.0001$, $n = 58$; WOD: $F = 13.00$, $p < 0.0001$, $n = 58$; WAR: $F = 3.33$, $p = 0.04$, $n = 58$). Overall, mean density of the LAP was significantly higher in the alpine habitat, while mean densities of the CHK and WOD were significantly higher in the montane habitat (Tables 4 and 5; Figures 18, 19 and 22). The mean density of the WAR was significantly higher in the subalpine habitat (Tables 4 and 5; Figure 20). Mean bird densities of the SPA and THR were spread more across all three habitats so that they did not differ significantly across habitats. Nevertheless, higher mean bird densities were maintained in the subalpine habitat for the SPA and in the montane habitat for the THR (Figures 21 and 25). These results suggest that the LAP, CHK, WOD and WAR express greater obligatoriness in habitat selection during fall, relative to the SPA and THR.

Yearly patterns in mean bird density across habitats were erratic for the COR and the FIN. COR density was highest in the subalpine habitat, followed by the montane and alpine habitats in 1998. This differed from 1999 and 2000 where the highest COR density

was recorded in the montane habitat, followed by the subalpine and alpine habitats (Table 4; Figure 23). For the FIN, mean density was highest in the subalpine, followed by the alpine and montane habitats in 1998 and 2000. This also differed from 1999 where the montane habitat had a higher FIN density than the subalpine habitat, and there were no records for the alpine habitat (Table 4; Figure 24). Overall, mean density for the COR and FIN did not differ significantly across habitats, data pooled from all three years. Their mean densities also did not differ significantly across years. This suggests that COR and FIN may move between habitats from one year to another, depending on weather conditions. Hence, COR and FIN seem to be more facultative than obligatory in habitat selection during fall.

Overall, bird densities in all taxonomic bird groups were higher for 1998 in the subalpine habitat, relative to 1999 and 2000. This suggests perhaps increased use of the subalpine habitat by all bird groups during fall, where weather conditions are good (Figures 18 to 25).

Discussion

Evaluation of line transect sampling and observer variation

Earlier use of transects in censusing birds were mainly associated with the use of fixed widths, which did not correct for differences in the detectability of bird species with habitats (Bell and Ferrier 1985; Harden et al. 1986). In this study, line transect sampling was used as it was felt that detectability would vary across the alpine, subalpine and montane habitats. Results of this analysis showed that on average mean effective strip width varied across the habitats such that the alpine habitat had the greatest strip width,

followed by the subalpine and montane habitats. It is interesting to note that effective strip widths can differ temporally. As such, even if the use of a fixed width was validated for a particular habitat (as in the case of Er et al. 1995), it may not be the most optimal over time. In this study, it is quite evident that the effects of varied bird detectability in the different habitats have been corrected for by the use of line transect sampling.

While line transect sampling is advantageous in that it accounts for the differences in bird detectability, it requires that distances be accurately and precisely estimated. This can be a potential problem if more than one observer is used. Scott et al. (1981) found significant variability in precision among observers in estimating distances and angles. Similarly in this study, the use of four observers in 1998 brought about greater variation in the estimates of detection distance, as compared to the use of only two observers in 1999 and 2000. Furthermore, the use of multiple observers can bring about variation in bird identification and estimation of numbers (Faanes and Bystrak 1981; Kavanagh and Recher 1983; Cunningham et al. 1999). This was not tested in this analysis. However, it is noteworthy that mean cluster size did not differ across all three years. Given that birds tend to be in flocks during fall and that flock size rarely change temporally (Morrison et al. 1987), this would suggest that any variation in the estimation of bird numbers was probably minimal. Although observer variation was evident in this study, this was controlled in the study design as follows: (1) observers were in teams of two; (2) where there were two teams in 1998, all teams visited all study sites and all habitats within each study site; (3) each transect was also surveyed more than once by each team, with counts being made by alternating members. It is unlikely that the observed patterns of bird density across years and habitats in this study is an artefact of observer variation.

Importance of weather perturbations

The temporal patterns of mean bird density in this study offer some evidence that bird density in high elevation habitats in fall is affected by sudden weather perturbations. Mean bird density was significantly lower in 1999, relative to 1998. Mean bird density patterns across habitats in 1999 also differed with 1998 and 2000, with an observed sharp decline in alpine bird density in 1999. This may be attributed to colder weather conditions in fall in 1999.

The weather in 1999 was much colder than in 1998 or 2000, with earlier snowfall and protracted snowstorms. The earlier snowfall in 1999 would have covered the plants, reducing the availability of seeds and fruits left over from summer. This would also bring about a reduction in the population of insects that are supported by these plants. Overall, there would be a reduction of important food resources for birds. This could potentially bring about increased mortality of young and adult birds or/and shifts in bird population to more sheltered habitats (i.e. alpine and subalpine to montane habitats). The decline in overall bird density and the density patterns of almost all taxonomic bird groups across all habitats in 1999 suggest that mortality rather than shifts in densities across a habitat gradient was predominant (with the exception of the FIN and COR, which seemed to show shifts in densities across the habitats from one year to another). Similar reduction in animal populations through increased mortality as a result of protracted snowstorms at other high elevation locations in summer have been documented by Ehrlich et al. (1972), Morton and Sherman (1978), and Gass and Lertzman (1980). Notwithstanding this, long term data at low elevation sites in England and high elevation sites in Colorado, United States showed that with warmer spring temperatures, arrival dates of migratory birds

have been earlier (Crick et al. 1997; Crick and Sparks 1999; Inouye et al. 2000). In a similar vein, it is possible that with earlier and lower minimum temperatures in late summer and early fall of 1999, birds could have migrated to the lower elevation habitats earlier (i.e. late July). This would then bring about lower bird densities during the period of survey in 1999 (early August to late September). However, this could not be confirmed in the current analysis.

Responses of birds to sudden weather perturbations are complex. This is evident from this study as different taxonomic bird groups exhibited different recovery responses in 2000. If one assumes that bird populations were significantly reduced through increased mortality in young and adult birds in the summer or fall of 1999, then with new recruitment in these populations in the summer of 2000, an appreciable increase in bird density would follow. This was the case with the LAP, CHK, WOD, and THR, but not with the WAR and SPA. With the FIN and COR, trends were erratic. Bird density for the FIN was down in 1999 from 1998, but returned to the same levels as 1998 in 2000. Bird density for the COR in 1999 was relatively similar to 1998 (with appreciable shifts across habitats), but declined in 2000. The bird density patterns manifested in the high elevation habitats could also be the result of changes in populations in the wintering grounds, especially since large proportion of the birds at these habitats are altitudinal and latitudinal migrants (Terborgh 1989; Rappole and MacDonald 1994). Hence, the low bird density in fall of 2000 for the WAR and the SPA may have been the combined result of the impact of colder weather conditions on the bird populations in fall 1999 and changes in populations at lower elevation and latitude wintering grounds in winter 1999. Unless conditions and population densities at wintering grounds are also known, the real impact

of weather perturbations on bird populations in the high elevation habitats cannot be fully ascertained.

Importance of the subalpine habitat

An important result from this analysis is that the subalpine habitat may be more important than previously thought for some bird species during fall. Based on the observed pattern of bird density trends of various taxonomic bird groups across habitats, this appears to be especially so for the WAR. The mean bird density of the WAR was significantly higher in the more open subalpine habitat than in the forested montane habitat. This is interesting because the WAR are essentially insectivorous forest species and would have been expected to occur in higher densities in the forested montane habitat, as with other bird groups dominated by insectivorous forest species (e.g. the CHK and WOD). The important difference is that the WAR is dominated by long-distance forest migrants such as the Yellow-rumped Warbler, Townsend's Warbler and Wilson's Warbler, whereas the CHK and WOD are made up mainly of resident or partial migrant species such as the Golden-crowned Kinglet, Ruby-crowned Kinglet, Mountain Chickadee, the Red-breasted nuthatches, Red-shafted Flickers and Red-breasted sapsuckers. As long-distance migrants, the warblers do not hold onto any territories and may not be able to compete for resources with the resident or partial resident species in the forested montane habitats upon their return in the breeding season. As such, they are restricted to the less optimal subalpine habitats and continue to do so even in fall. This observation is consistent with that found in other studies on subalpine bird communities. In a detailed study of subalpine bird community patterns in the White Mountains of New Hampshire in the United States during summer, Sabo (1980) showed that the foraging

range in five warbler species (i.e. American Redstart, Yellow-rumped Warbler, Blackpoll Warbler, Canada Warbler and Black-throated Green Warbler) was centred upon the subalpine krummholz habitat, rather than the insect-rich hardwood woodlands. In another study, Hutto (1985) suggested that shifts in the density of transient insectivorous species from lower elevation to higher elevation habitats in spring is greatly mediated by competition between the species for food resources at the lower elevation habitats so that species unable to compete would move to higher elevations.

The importance of the subalpine habitat is further emphasized during years of good weather conditions. There appears to be increased use of the subalpine habitat during fall by almost all taxonomic bird groups in 1998, where weather conditions were mild relative to 1999 and 2000. Subalpine habitats may serve as a buffer for birds in high elevation habitats during fall, akin to the idea of a “sink” as suggested by DeSante (1990) for breeding bird populations. In other words, birds in the montane and the alpine habitats may spill over to the less optimal subalpine habitat in favourable years where population densities are high and optimum density packing is prevalent in the montane and alpine habitats. Some support of this hypothesis can also be inferred from the observation that bird species in the subalpine habitat tends to have more variable densities and greater niche overlap than lower elevation species-rich forests along the same elevation gradient (Sabo and Holmes 1983). In this respect, the subalpine habitat plays an important role in the persistence of bird populations at high elevations.

References

Airola, D.A. and R.H. Barrett. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. *Condor* **87**: 205-216.

- Antor, R.J. 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *Journal of Avian Biology* **26**: 81-84.
- Bell, H.L. and S. Ferrier. 1985. The reliability of estimates of density from transect counts. *Corella* **9**: 3-13.
- Berthold, P. 1993. *Bird Migration. A General Survey*. Oxford University Press, Oxford, United Kingdom.
- Buckland, S.T., D.R. Anderson, K.P. Burnham and J.L. Laake. 1993. *Distance Sampling. Estimating Abundance of Biological Populations*. Chapman & Hall, London, United Kingdom.
- Burnham, K.P., D.R. Anderson and J.L. Laake, J.L. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monograph*. **72**: 10-55.
- Cannings, R.J. and S.G. Cannings. 1996. *British Columbia, A Natural History*. Douglas and McIntyre, Vancouver, Canada.
- Crick, H.Q.P. and T.H. Sparks. 1999. Climate change related to egg-laying trends. *Nature* **399**, 423.
- Crick, H.Q.P., C. Dudley, D.E. Glue and D.L. Thomson. 1997. UK birds are laying eggs earlier. *Nature* **388**, 526.
- Cunningham, R.B., D.B. Lindenmayer, H.A. Nix and B.D. Lindenmayer. 1999. Quantifying observer heterogeneity in bird counts. *Australian Journal of Ecology* **24**: 270-277.
- DeSante, D.F. 1990. The role of recruitment in the dynamics of a Sierran Subalpine bird community. *American Naturalist* **136**: 429-445.

- Ehrlich, P.R., D.E. Breedlove, D.E., P.F. Brussard, M.A. Sharp. 1972. Weather and the “regulation” of subalpine populations. *Ecology* **52**: 243-247.
- Environment Canada 2001. *Winter regional temperature departures ranked from warmest to coolest, for the period 1948- 2001.* (www.msc-smc.ec.gc.ca/ccrm/bulletin/winter00.html)
- Er, K.B.H., A.P. Robinson and C.R. Tidemann 1995. Importance of censusing duration and strip width in the use of the fixed-width strip transect for the censusing of birds in Yellow Box woodland. *Corella* **19**, 109-114.
- Faanes, C.A. and D. Bystrak. 1981. The role of observer bias in the North American Breeding Bird Survey. *Studies in Avian Biology* **6**: 353-359.
- Finch, D.M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology* **70**: 866-880.
- Gass, C.L. and K.P. Lertzman. 1980. Capricious mountain weather: a driving variable in hummingbird territorial dynamics. *Canadian Journal of Zoology* **58**: 1964-1968.
- Grubb, T.C., Jr. 1975. Weather-dependent foraging behaviour of some birds wintering in a deciduous woodland. *Condor* **77**: 175-182.
- Grubb, T.C., Jr. 1978. Weather-dependent foraging rates of wintering woodland birds. *Auk* **95**: 370-376.
- Harden, R.H., R.J. Muir and D.R. Milledge. 1986. An evaluation of the strip transect for sampling bird communities in forests. *Australian Wildlife Research* **13**: 203-211.
- Hutto, R.L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* **102**: 120-132.

- Inouye, D.W., B. Barr, K.B. Armitage and B.D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Science of the United States* **97**: 1630-1633.
- Kavanagh, R. and H.F. Recher. 1983. Effects of observer variability on the census of birds. *Corella* **7**: 93-100.
- Korner, C. 1999. *Alpine Plant Life: Functional Plant Ecology in the High Mountain Ecosystems*. Springer-Verlag, Heidelberg, Germany.
- Love, D. 1970. Subarctic and subalpine: where and what? *Arctic and Alpine Research* **2**: 63-73.
- Martin, K. and S. Ogle. 1998. *The Use of Alpine Habitats by Fall Migrating Birds on Vancouver Island (1996-97)*. Report ALPMIG-1, Department of Forest Sciences, UBC and Canadian Wildlife Service, Pacific and Yukon Region, Delta, British Columbia (www.forestry.ubc.ca/alpine/research/papers.html)
- Martin, K. and S. Ogle. 2000. *The Use of Alpine Habitats by Migratory Birds in B.C. Parks 1998 Summary*. Report ALPMIG-2, Department of Forest Sciences, UBC and Canadian Wildlife Service, Pacific and Yukon Region, Delta, British Columbia (www.forestry.ubc.ca/alpine/research/papers.html)
- Martin, K. and S. Ogle. 2001. *The importance of alpine habitats to migratory birds in south-central British Columbia*. Unpublished Draft Technical Report.
- Martin, K. P.B. Stacey and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured White-tailed Ptarmigan populations. *Condor* **102**: 503-516.

- Morrison, M.L., K.A. With, I.C. Timossi and K.A. Milne. 1987. Composition and temporal variation in flocks in the Sierra Nevada. *Condor* **89**: 739-745.
- Morton, M.L. 1978. Snow conditions and the onset of breeding in the mountain White-crowned Sparrow. *Condor* **80**: 285-289.
- Morton, M.L. and P. Sherman 1978. Effects of a spring snowstorm on behaviour, reproduction, and survival on Belding's ground squirrels. *Canadian Journal of Zoology* **56**: 2578-2590.
- Noon, B.R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. *Ecological Monographs* **51**: 105-124.
- Pattie, D.L. and N.A.M. Verbeek. 1966. Alpine birds of the Beartooth Mountains. *Condor* **68**: 167-176.
- Rappole, J.H. and M.V. MacDonald. 1994. Cause and effect in population declines of migratory birds. *Auk* **111**: 652-660.
- Sabo, S.R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. *Ecological Monographs* **50**: 241-259.
- Sabo, S.R. and R.T. Holmes. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. *Condor* **85**: 121-138.
- SAS Institute 2001. *A Guide to Statistics and Data Analysis Using JMP and JMP IN Software*. Duxbury, Pacific Grove, California, United States.
- Scott, M.L., F.L. Ramsey and C.B. Kepler. 1981. Distance estimation as a variable in estimating bird numbers. *Studies in Avian Biology* **6**: 334-340.

- Terborgh, J. 1989. *Where Have the Birds Gone?* Princeton University Press, Princeton, New Jersey, United States.
- Thomas, L., J.L. Laake, J.F. Derry, S.T. Buckland, D.L. Borchers, D.R. Anderson, K.P. Burnham, S. Strindberg, S.L. Hedley, M.L. Burt, F. Marques, J.H. Pollard and R.M. Fewster. 1998. *Distance 3.5*. Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom.
- Wilson, R.R., D.J. Twedt, A.B. Elliott. 2000. Comparison of line transects and point counts for monitoring spring migration in forested wetlands. *Journal of Field Ornithology* **71**: 345-355.
- Zar, J.H. 1984. *Biostatistical Analysis, 2nd Edition*. Prentice Hall, Englewood Cliffs, New Jersey, United States.

Table 1. Paired student's t-test of mean effective strip width between years and habitats.

***Positive difference between Abs. Dif. and LSD suggests significant difference in a pair (highlighted in italic) ($\alpha = 0.05$) (SAS Institute 2001).**

Mean effective strip width between years.

Pairwise comparison	Abs(Dif) – LSD*
1998 vs 1999	<i>0.305</i>
1998 vs 2000	-0.897
1999 vs 2000	-8.203

Mean detection distance between habitats in 1999 and 2000 combined

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	-0.226
Alpine vs Montane	<i>2.916</i>
Subalpine vs Montane	-6.693

Table 2. Paired student's t-test of mean detection distance between observers in each habitat for 1998. *Positive difference between Abs. Dif. and LSD suggests significant difference in a pair (highlighted in italic) ($\alpha = 0.05$) (SAS Institute 2001). Mean detection distance was logarithmic transformed to ensure normality, i.e. Log (x). BG – Billie Gowans; PC – Patricia Collins; PR – Pam Ronalds; SO – Steve Ogle.

Mean detection distance between observers in alpine habitat for 1998

Pairwise comparison	Abs(Dif) – LSD*
BG vs PC	<i>0.032</i>
BG vs PR	<i>0.166</i>
BG vs SO	-0.135
PC vs PR	-0.104
SO vs PC	<i>0.197</i>
SO vs PR	<i>0.326</i>

Mean detection distance between observers in subalpine habitat for 1998

Pairwise comparison	Abs(Dif) – LSD*
BG vs PC	<i>0.134</i>
BG vs PR	<i>0.252</i>
BG vs SO	-0.001
PC vs PR	-0.054
SO vs PC	<i>0.342</i>
SO vs PR	<i>0.456</i>

Mean detection distance between observers in montane habitat for 1998

Pairwise comparison	Abs(Dif) – LSD*
BG vs PC	<i>0.169</i>
BG vs PR	-0.123
BG vs SO	<i>0.004</i>
PC vs PR	<i>0.191</i>
SO vs PC	<i>0.316</i>
SO vs PR	-0.075

Table 3. Paired student's t-test of mean bird density, mean cluster density and mean cluster size between years and habitats. *Positive difference between Abs. Dif. and LSD suggests significant difference in a pair (highlighted in italic) ($\alpha = 0.05$) (SAS Institute 2001). Mean bird density, mean cluster density and mean cluster size were logarithmic transformed to ensure normality, i.e. Log (x).

Mean bird density between years

Pairwise comparison	Abs(Dif) – LSD*
1998 vs 1999	<i>0.549</i>
1998 vs 2000	<i>0.478</i>
1999 vs 2000	-0.517

Mean cluster density between years

Pairwise comparison	Abs(Dif) – LSD*
1998 vs 1999	<i>0.553</i>
1998 vs 2000	<i>0.693</i>
1999 vs 2000	-0.478

Mean cluster density between habitats (data pooled from 1999 and 2000)

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	<i>0.414</i>
Alpine vs Montane	<i>0.876</i>
Subalpine vs Montane	-0.010

Mean cluster size between habitats (data pooled from 1998, 1999 and 2000)

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	<i>0.178</i>
Alpine vs Montane	<i>0.342</i>
Subalpine vs Montane	-0.092

Table 4. Summary trends of mean bird density of various taxonomic bird groups across years and habitats. * statistically significant at $\alpha = 0.05$. LAP – larks and pipits; CHK – chickadees, kinglets and wrens; WAR – warblers; SPA – sparrows; WOD – woodpeckers, nuthatches and creepers; COR – corvids; FIN – finches; THR – thrushes and waxwings.

<i>Bird group</i>	Mean annual bird density	Mean bird density across habitats
LAP	1998>2000>1999	Alpine>Subalpine>Montane*
CHK	1998>2000>1999	Montane>Subalpine>Alpine*
WAR	1998>1999>2000	Subalpine>Montane>Alpine*
SPA	1998>1999>2000*	Subalpine>Montane>Alpine
WOD	1998>2000>1999	Montane>Subalpine>Alpine*
COR	1998>1999>2000	1998: Subalpine>Montane>Alpine 1999: Montane>Subalpine>Alpine 2000: Montane>Subalpine>Alpine
FIN	1998~2000>1999	1998/2000: Subalpine>Alpine>Montane 1999: Montane>Subalpine>Alpine
THR	1998>2000>1999*	Montane>Subalpine>Alpine

Table 5. Paired student's t-test of mean bird density of different taxonomic bird groups between years and habitats (pooled across years, 1998-2000). *Positive difference between Abs. Dif. and LSD suggests significant difference in a pair (highlighted in italic) ($\alpha = 0.05$) (SAS Institute 2001). Mean bird density was logarithmic transformed to ensure normality, i.e. $\text{Log}(x+1)$. LAP – larks and pipits; CHK – chickadees, kinglets and wrens; WAR – warblers; SPA – sparrows; WOD – woodpeckers, nuthatches and creepers; COR – corvids; FIN – finches; THR – thrushes and waxwings.

Mean annual density of SPA

Pairwise comparison	Abs(Dif) – LSD*
1998 vs 1999	<i>0.284</i>
1998 vs 2000	<i>0.528</i>
1999 vs 2000	-0.170

Mean annual density of THR

Pairwise comparison	Abs(Dif) – LSD*
1998 vs 1999	<i>0.069</i>
1998 vs 2000	<i>0.027</i>
1999 vs 2000	-0.277

Mean density of LAP between habitats

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	<i>0.094</i>
Alpine vs Montane	<i>0.496</i>
Subalpine vs Montane	-0.108

Mean density of CHK between habitats

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	<i>0.071</i>
Alpine vs Montane	<i>0.708</i>
Subalpine vs Montane	<i>0.281</i>

Mean density of WOD between habitats

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	-0.047
Alpine vs Montane	0.146
Subalpine vs Montane	0.093

Mean density of WAR between habitats

Pairwise comparison	Abs(Dif) – LSD*
Alpine vs Subalpine	0.071
Alpine vs Montane	-0.184
Subalpine vs Montane	-0.028

Figure 1. Study sites in southern British Columbia (from Martin and Ogle 2000).

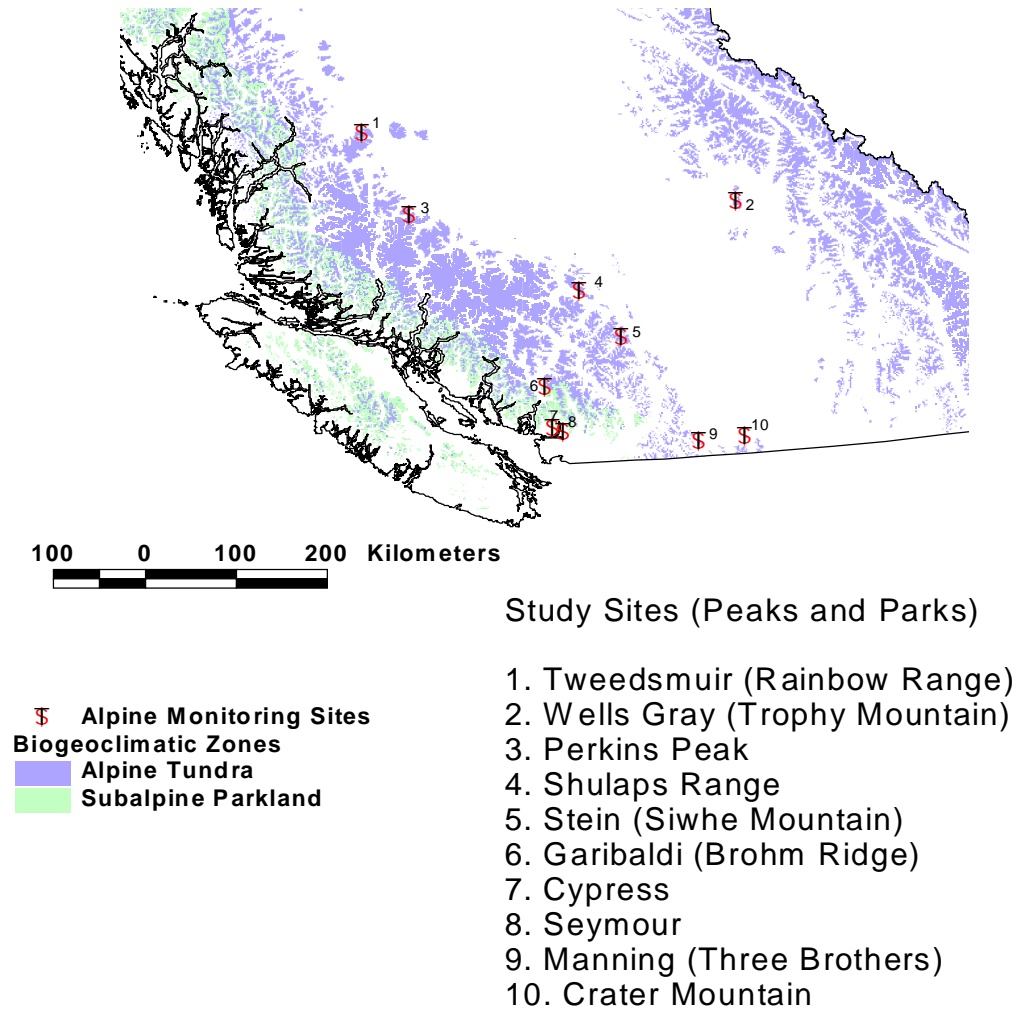


Figure 2. Probability of bird detection with distance from the transect. The area under the detection curve (i.e. the integral of the detection function) as a proportion of the total area (i.e. $1 \times w$) represents an estimation of the proportion of birds detected within the survey, given the assumption that the detection function is a half-normal distribution (adapted from Buckland et al. 1993).

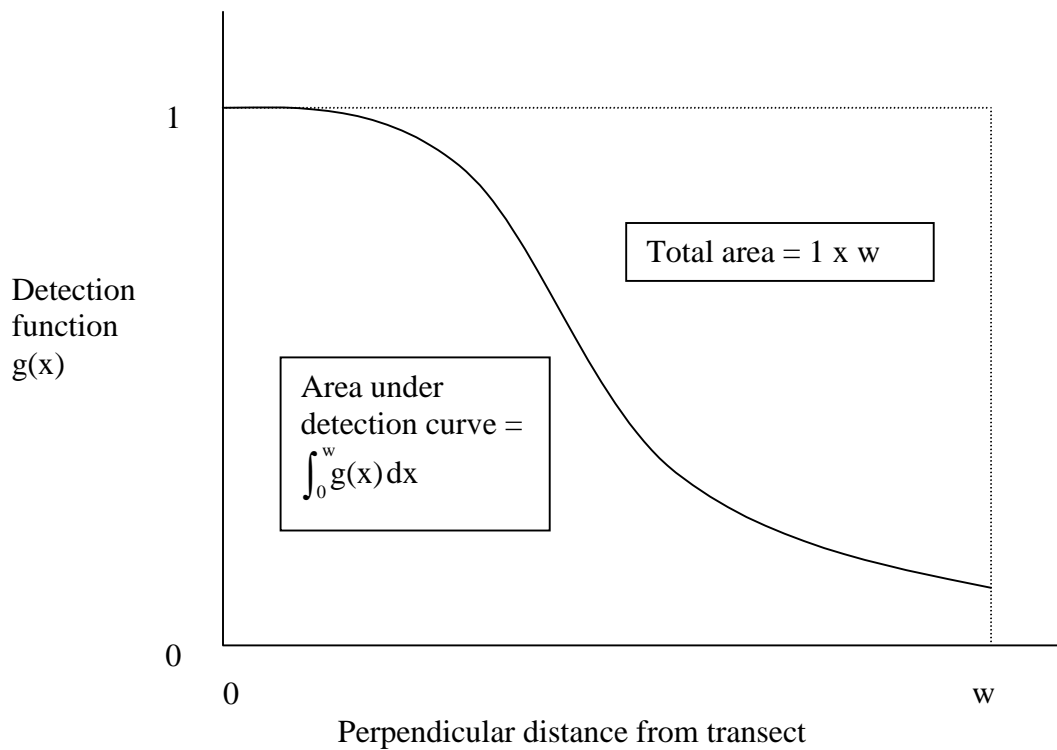


Figure 3. Variation in mean effective strip width (m) across habitats by year.

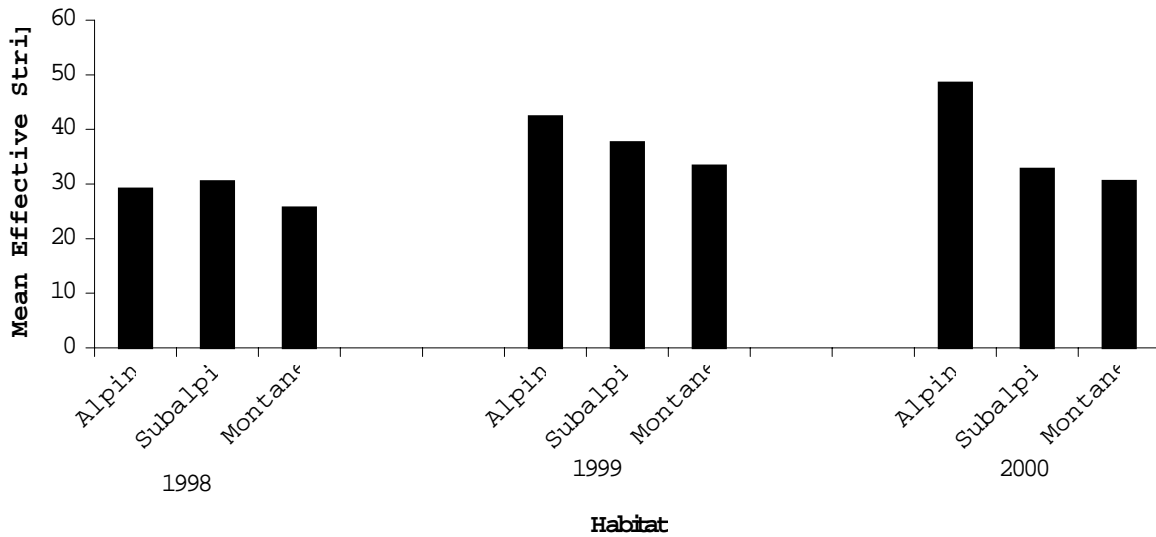


Figure 4. Variation in mean detection distance (m) across observers in 1998. BG – Billie Gowans; PC – Patricia Collins; PR – Pam Ronalds; SO – Steve Ogle.

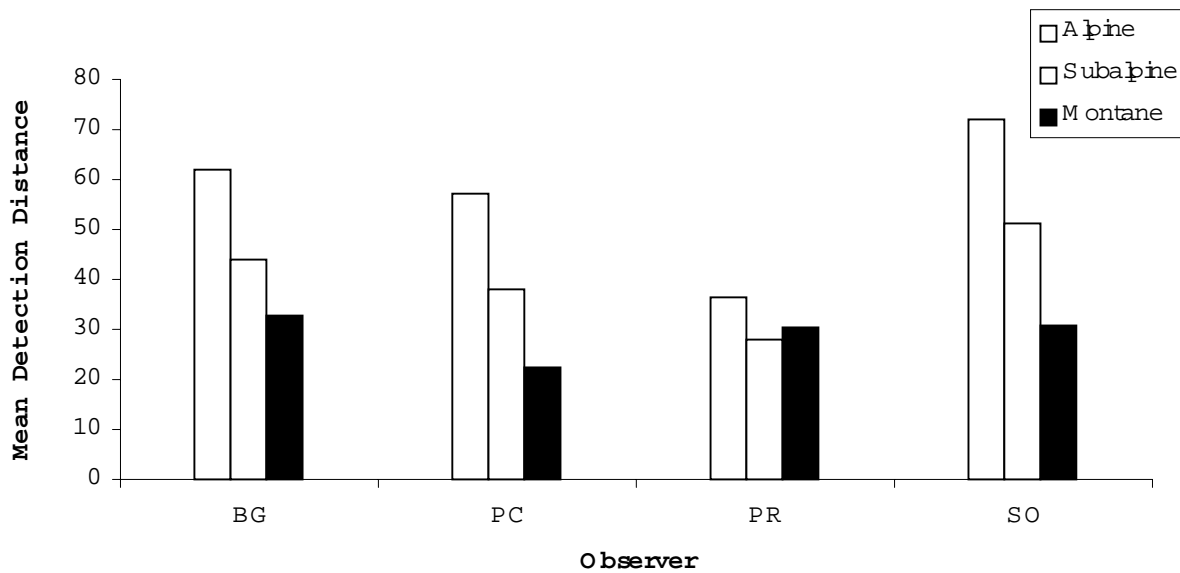


Figure 5. Variation in mean detection distance (m) across observers in 1999. CC – Catherine Conroy; SO – Steve Ogle.

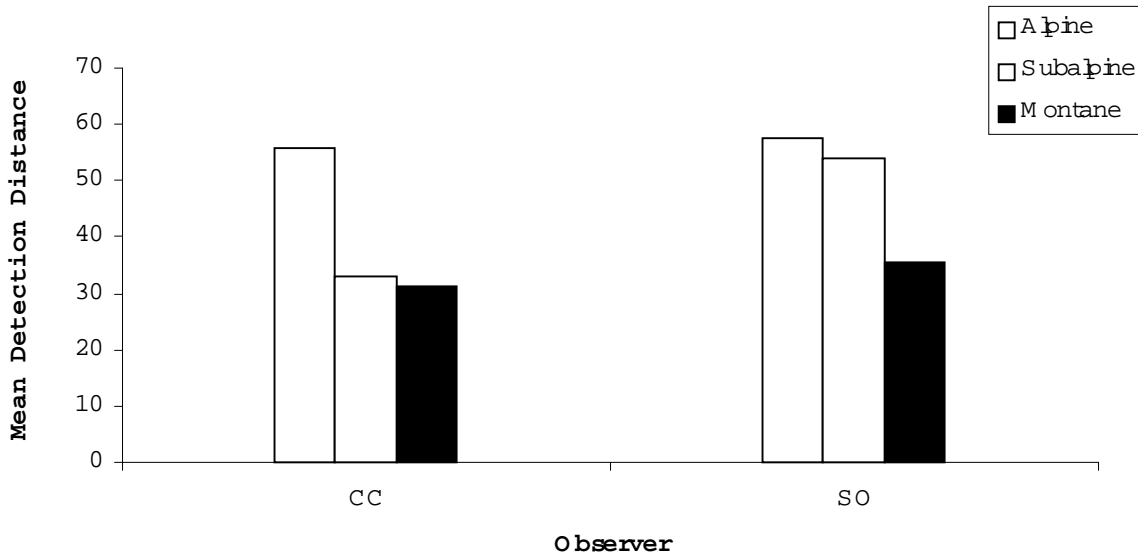


Figure 6. Variation in mean detection distance (m) across observers in 2000. MDM – Marty Mossop; YM – Yolanda Moreby.

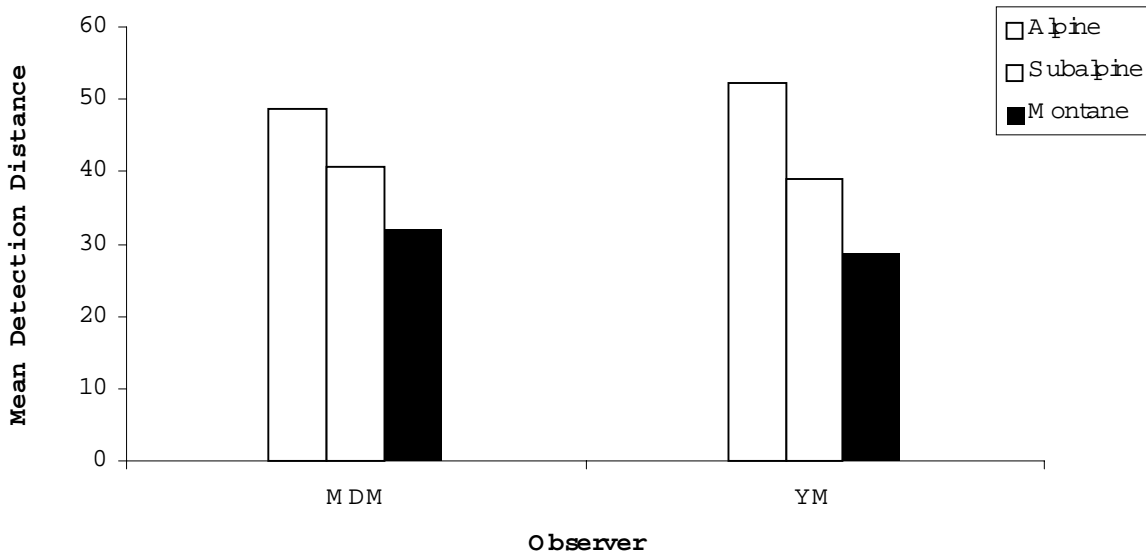


Figure 7. Monthly mean minimum temperature (°C) for the Whistler weather station (May to November 1998, 1999 and 2000).

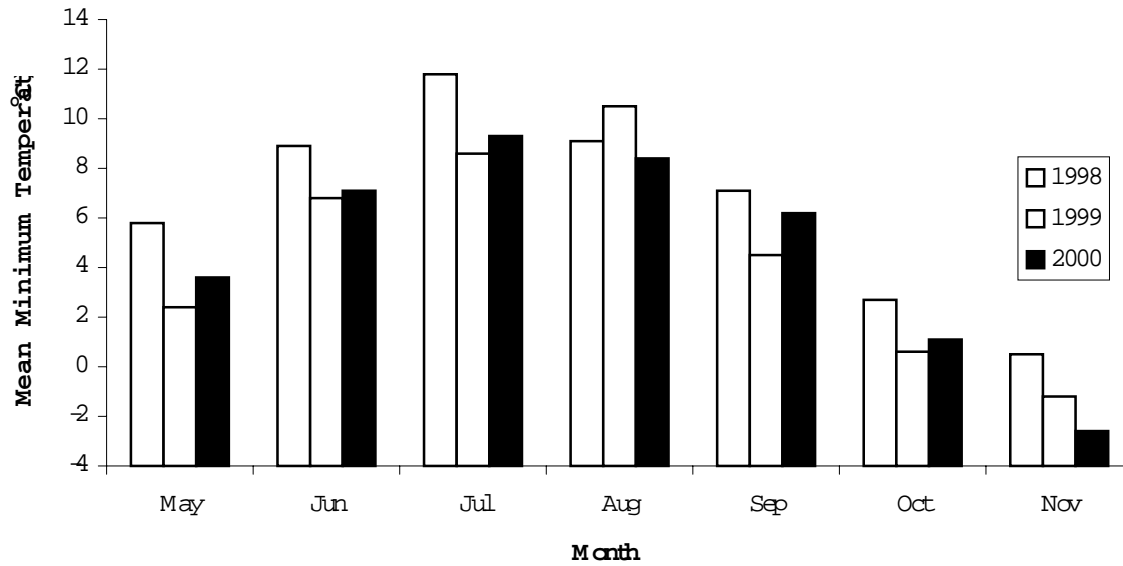


Figure 8. Monthly mean minimum temperature (°C) for the Kamloops weather station (May to November 1998, 1999 and 2000).

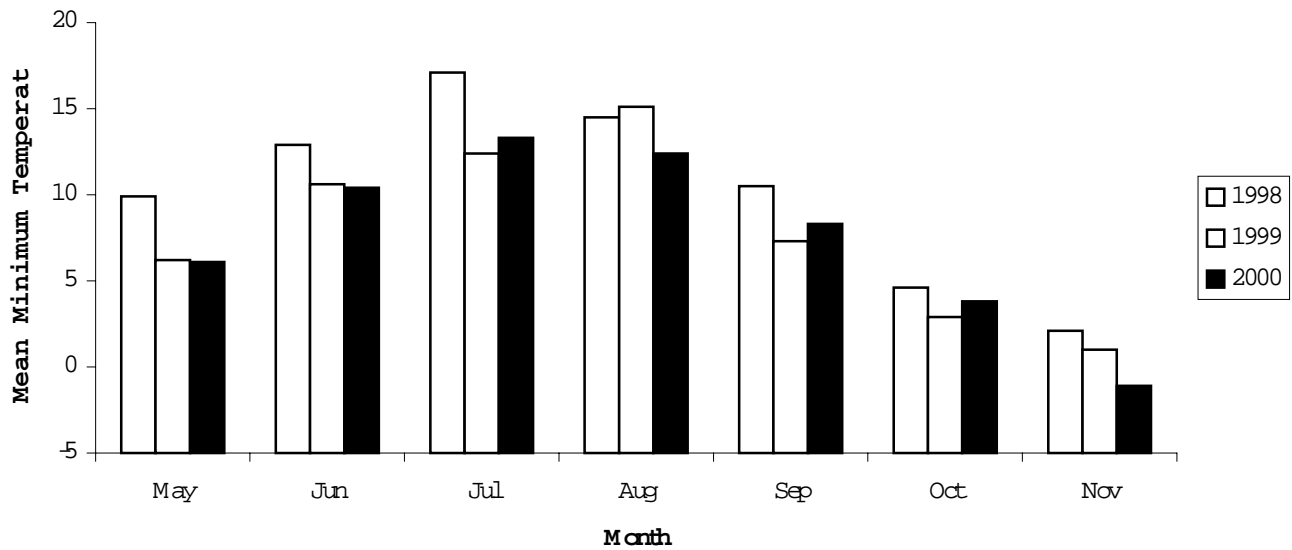


Figure 9. Monthly total precipitation (mm) for Whistler weather station (May to November 1998, 1999 and 2000).

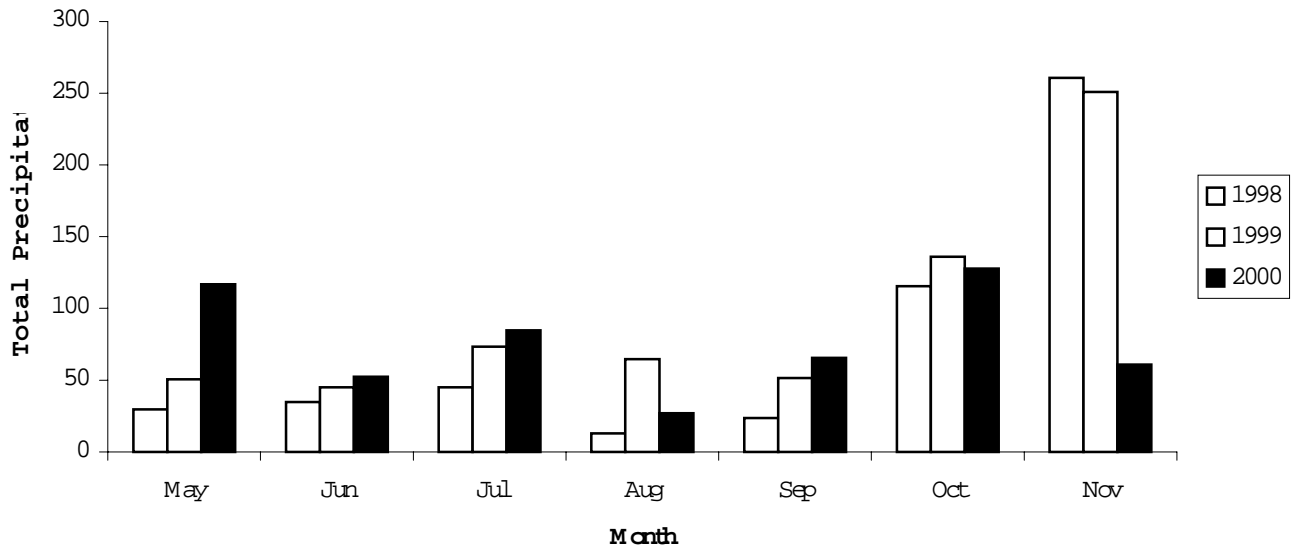


Figure 10. Monthly total precipitation (mm) for Kamloops weather station (May to November 1998, 1999 and 2000).

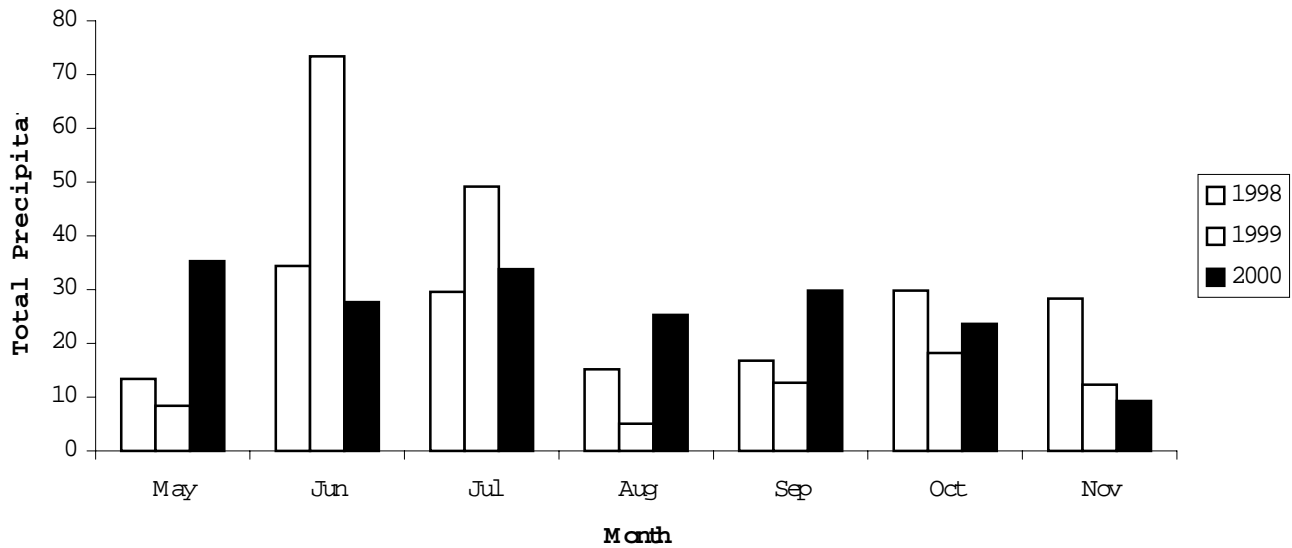


Figure 11. Total snowfall (cm) for Whistler weather station in October and November of 1998 and 1999.

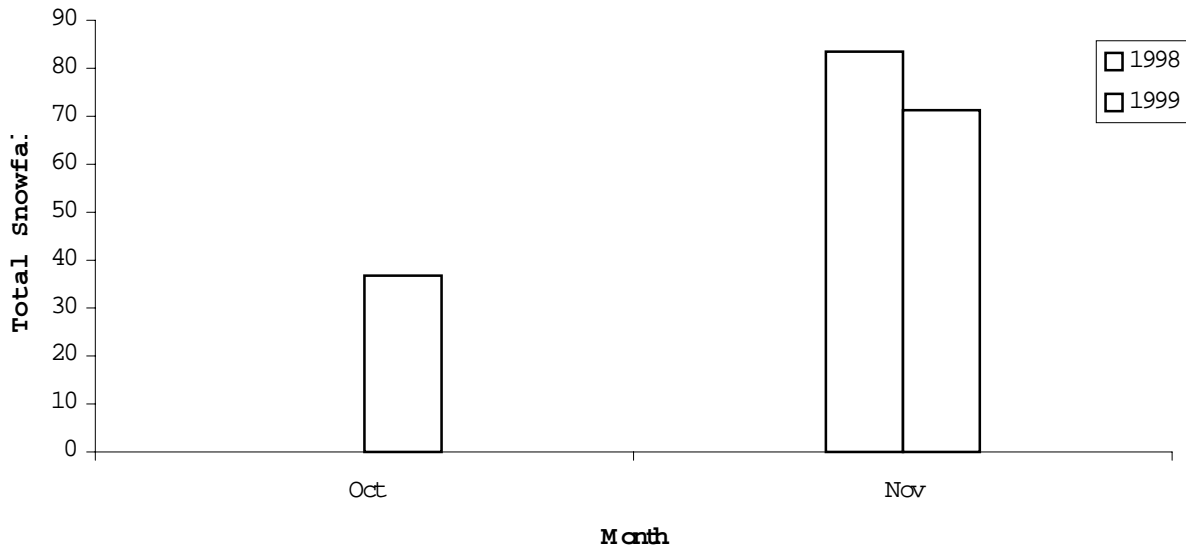


Figure 12. Variation in mean bird density (birds/ha) across habitats by year (1998-2000).

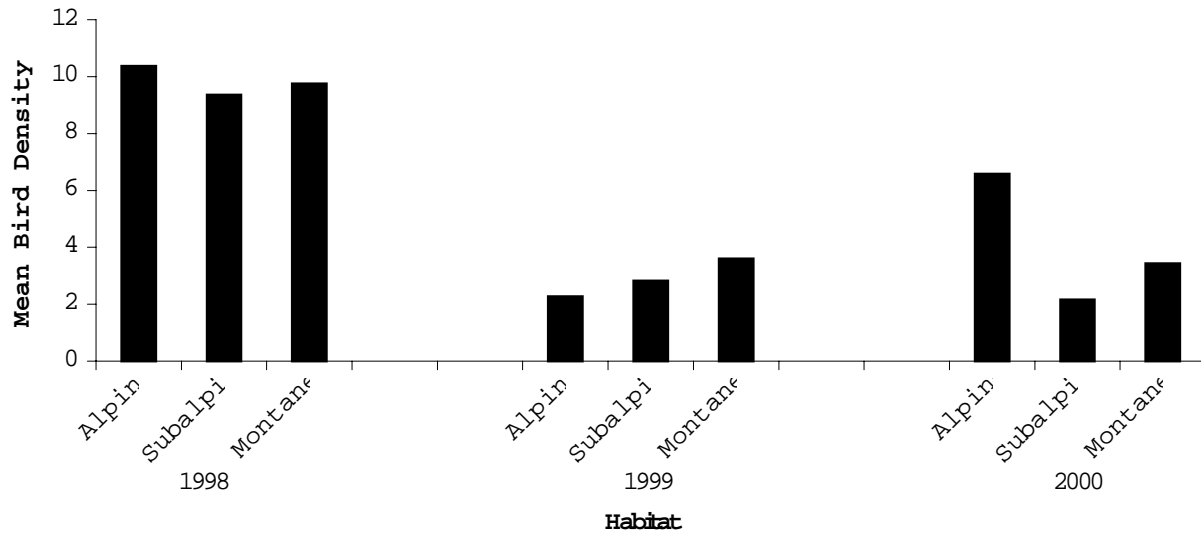


Figure 13. Variation in mean cluster density (clusters/ha) across habitats by year (1998-2000).

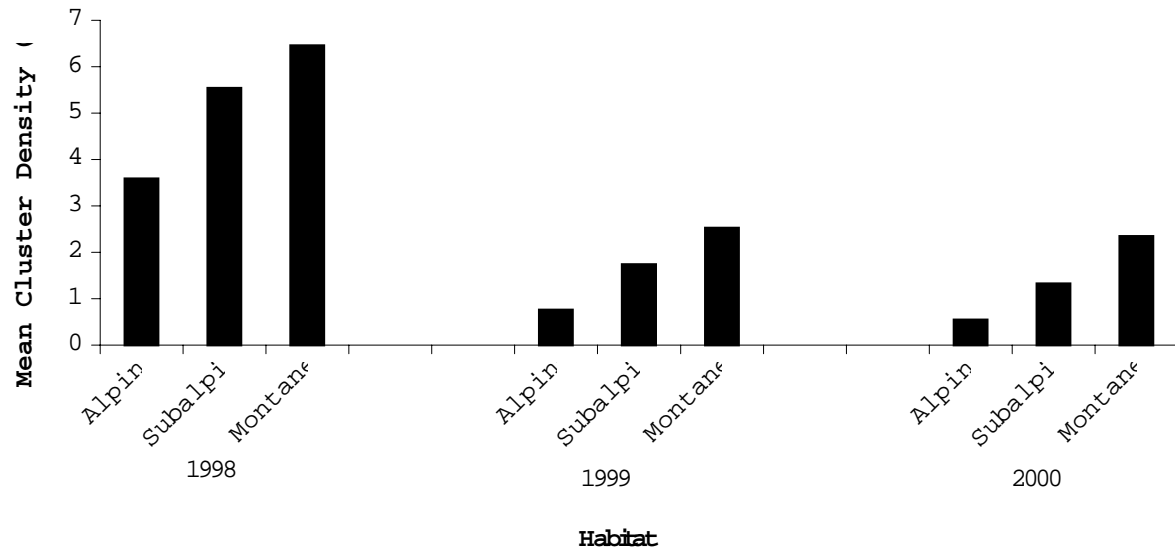


Figure 14. Variation in mean cluster size (birds/cluster) across habitats by year (1998-2000).

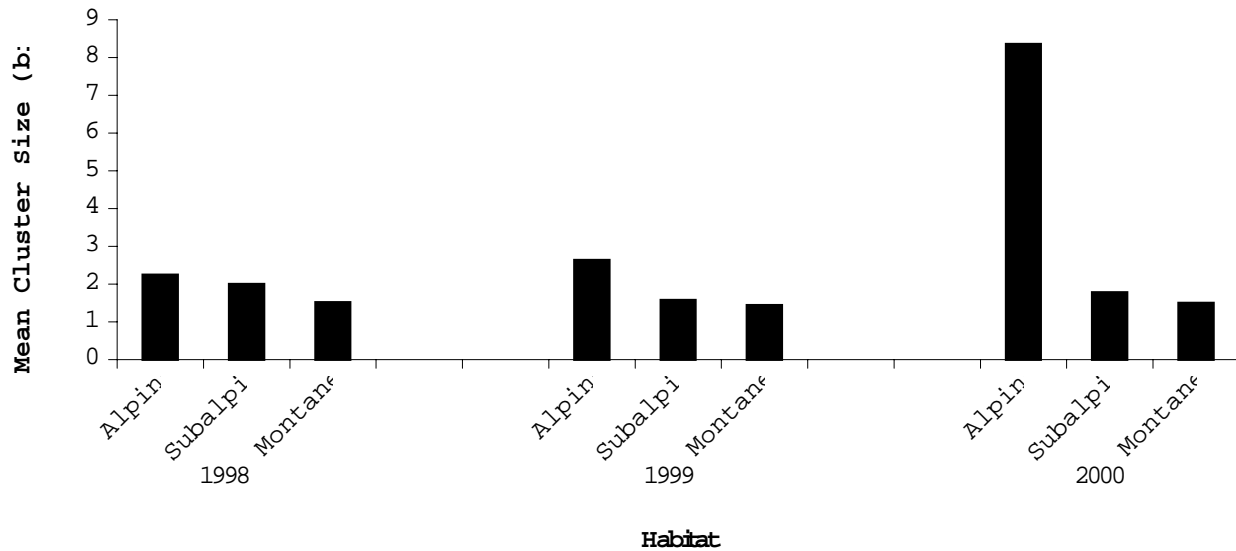


Figure 15. Relationship between mean bird density (birds/ha) and mean cluster density (clusters/ha) (data of all habitats from all study sites over 3 years). $\text{Log}(\text{Mean Bird Density}) = 0.869 \text{Log}(\text{Mean Cluster Density}) + 0.713$, $F = 190.8410$, $p < 0.0001$, $R^2 = 0.773$, $n = 58$.

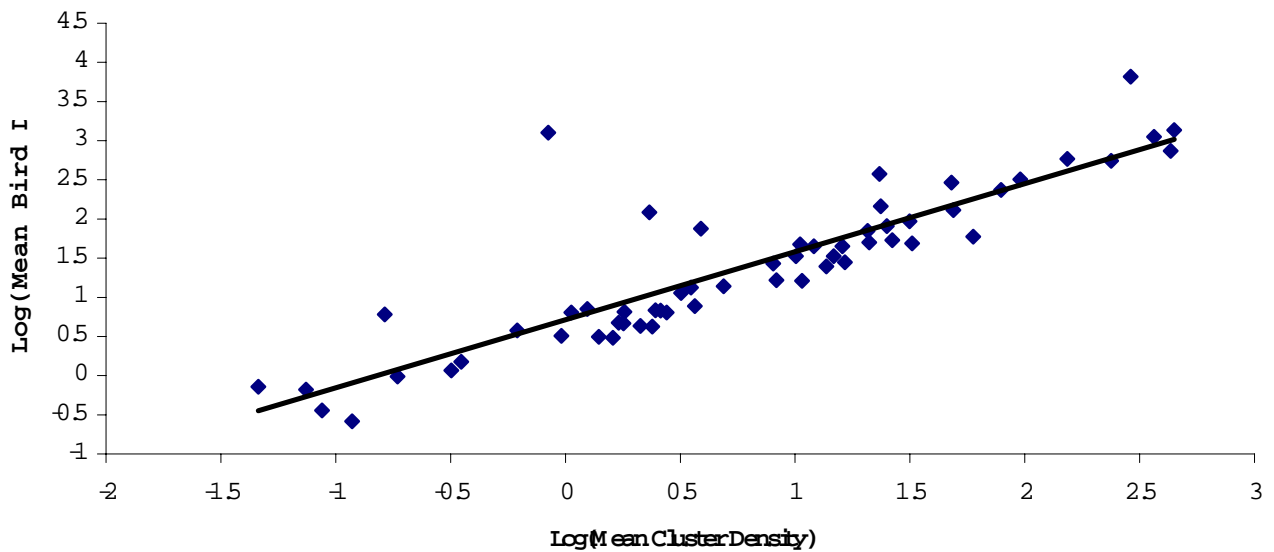


Figure 16. Relationship between mean bird density (birds/ha) and mean cluster size (birds/cluster) (data of all habitats from all study sites over 3 years). $\text{Log}(\text{Mean Bird Density}) = 0.467 \text{Log}(\text{Mean Cluster Size}) + 1.101$, $F = 3.110$, $p = 0.083$, $R^2 = 0.052$, $n = 58$.

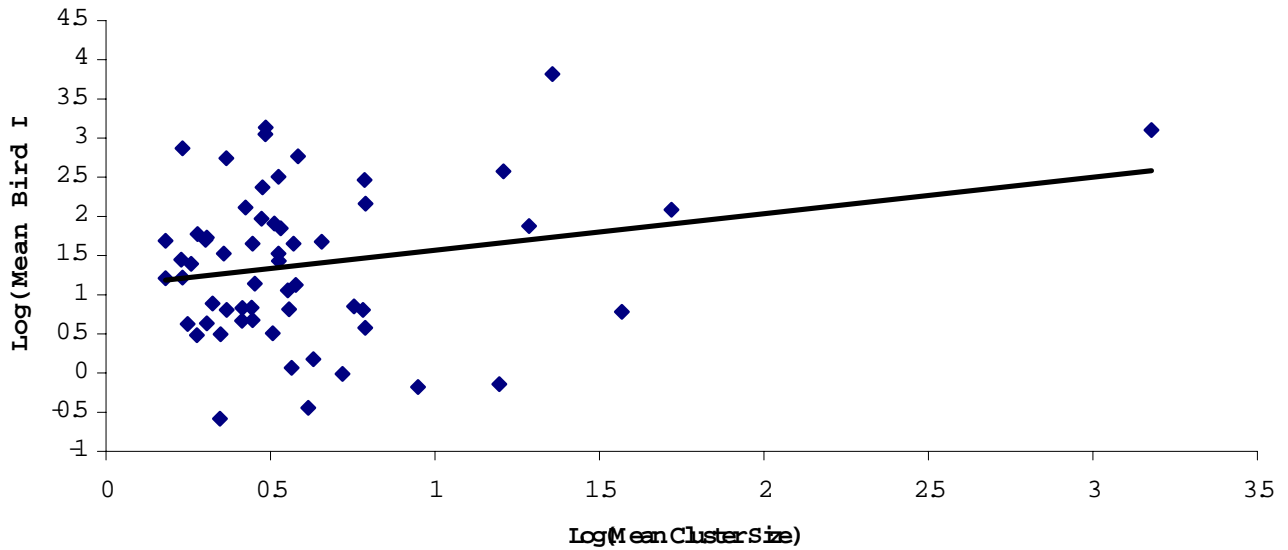


Figure 17. Relationship between mean bird density (birds/ha) and mean effective strip width (m) (data of all habitats from all study sites over 3 years). $\text{Log}(\text{Mean Bird Density}) = -1.423 \text{Log}(\text{Mean Effective Strip Width}) + 6.203$, $F = 59.283$, $p = 0.0001$, $R^2 = 0.514$, $n = 58$.

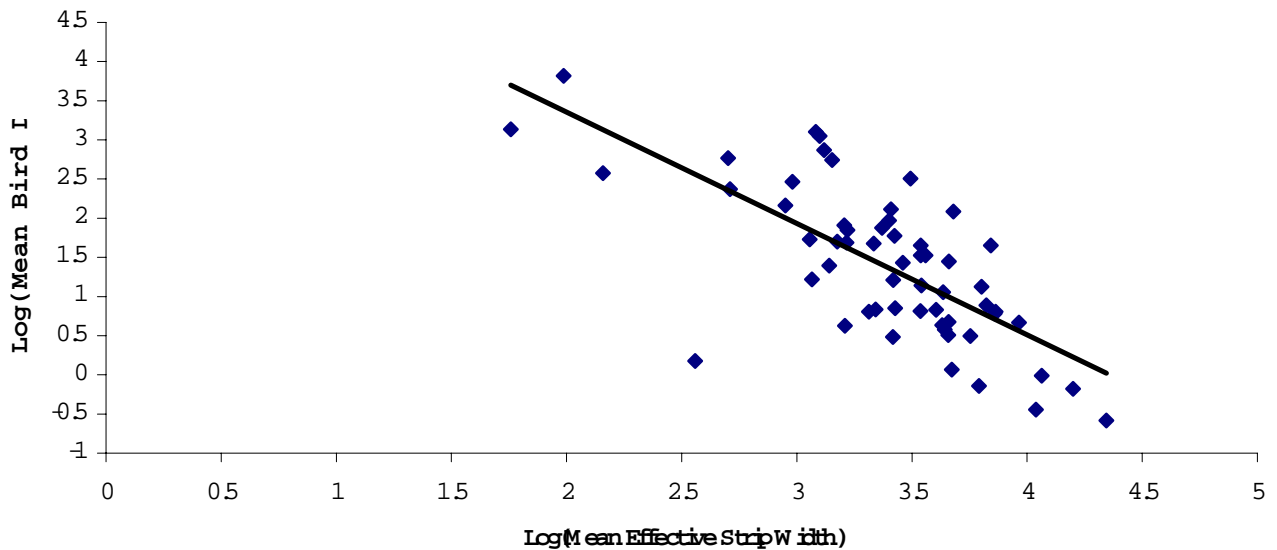


Figure 18. Variation in mean density of larks and pipits (LAP) across habitats by year (1998-2000).

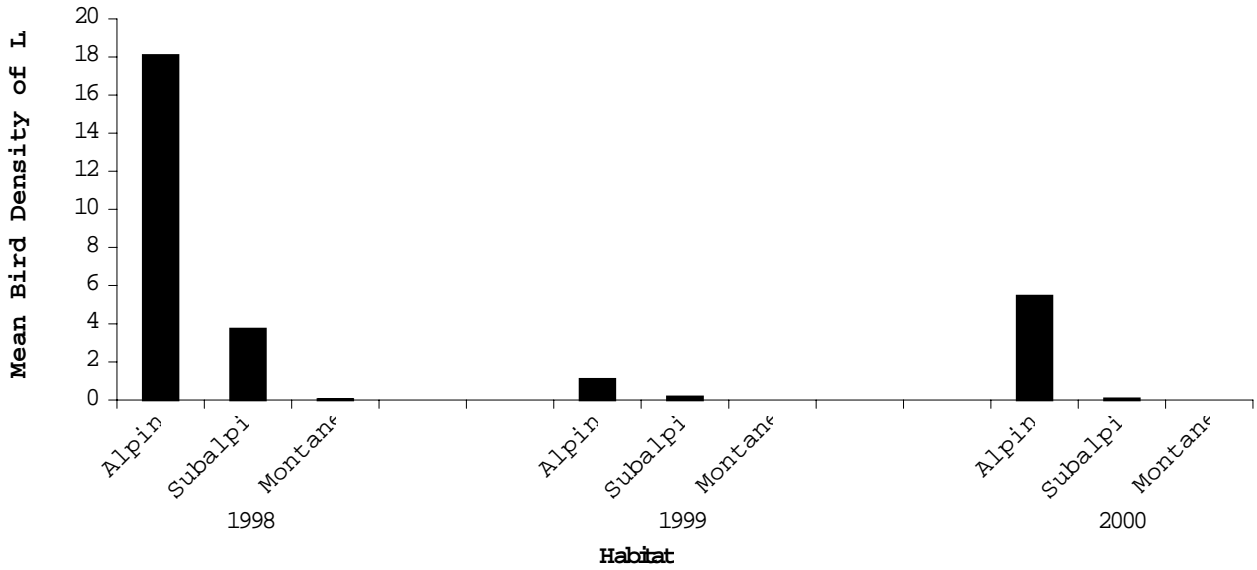


Figure 19. Variation in mean density of chickadees, kinglets and wrens (CHK) across habitats by year (1998-2000).

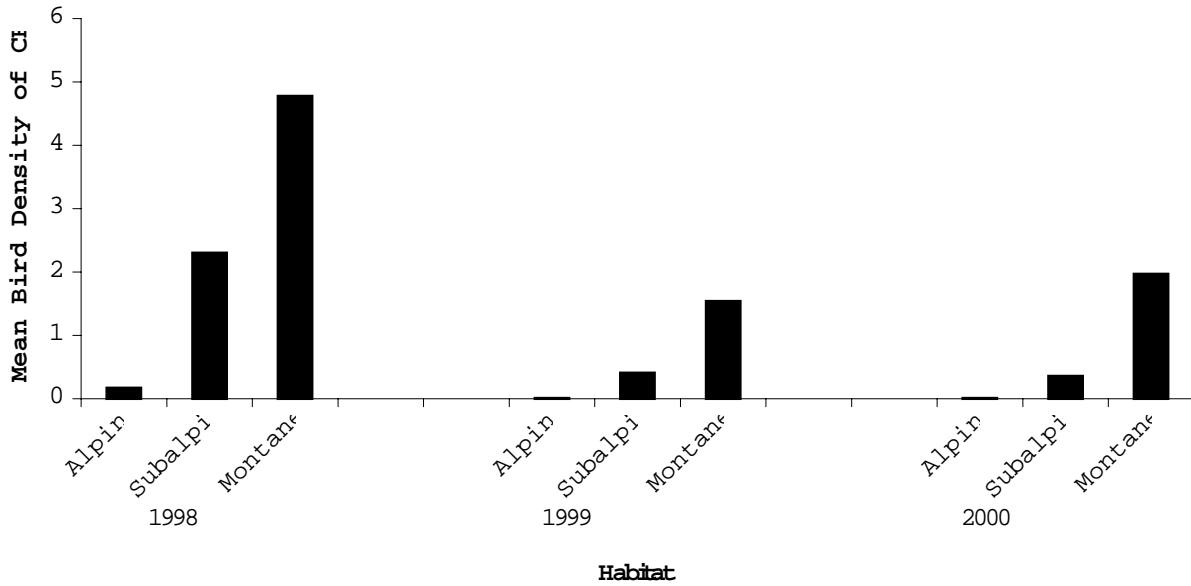


Figure 20. Variation in mean density of warblers (WAR) across habitats by year (1998-2000).

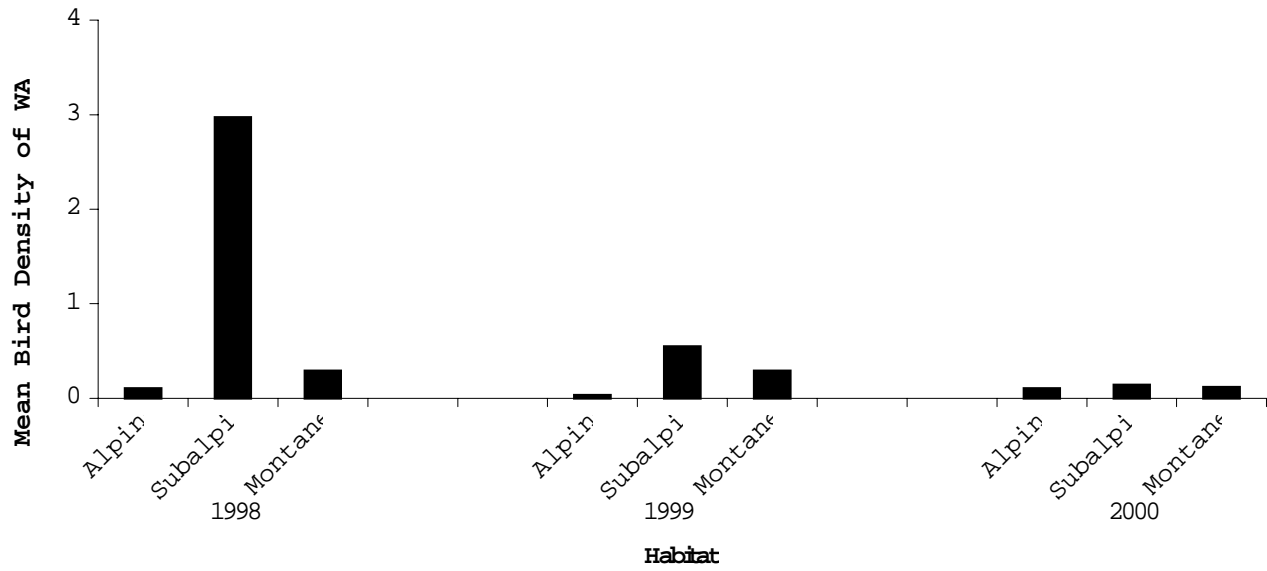


Figure 21. Variation of mean density of sparrows (SPA) across habitats by year (1998-2000).

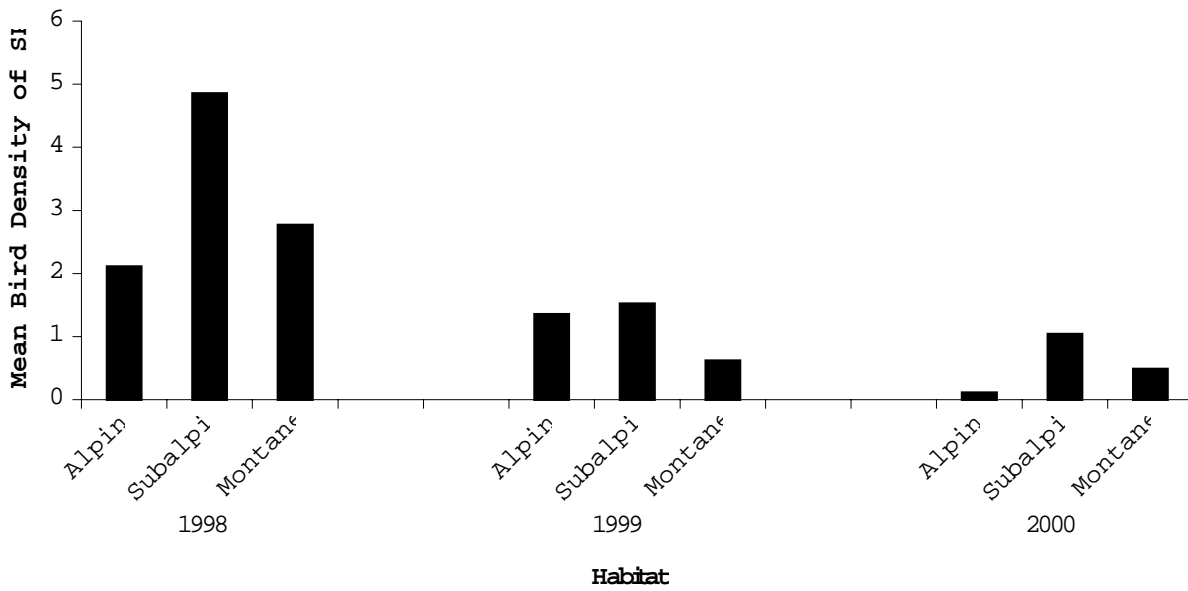


Figure 22. Variation in mean density of woodpeckers (WOD) across habitats by year (1998-2000).

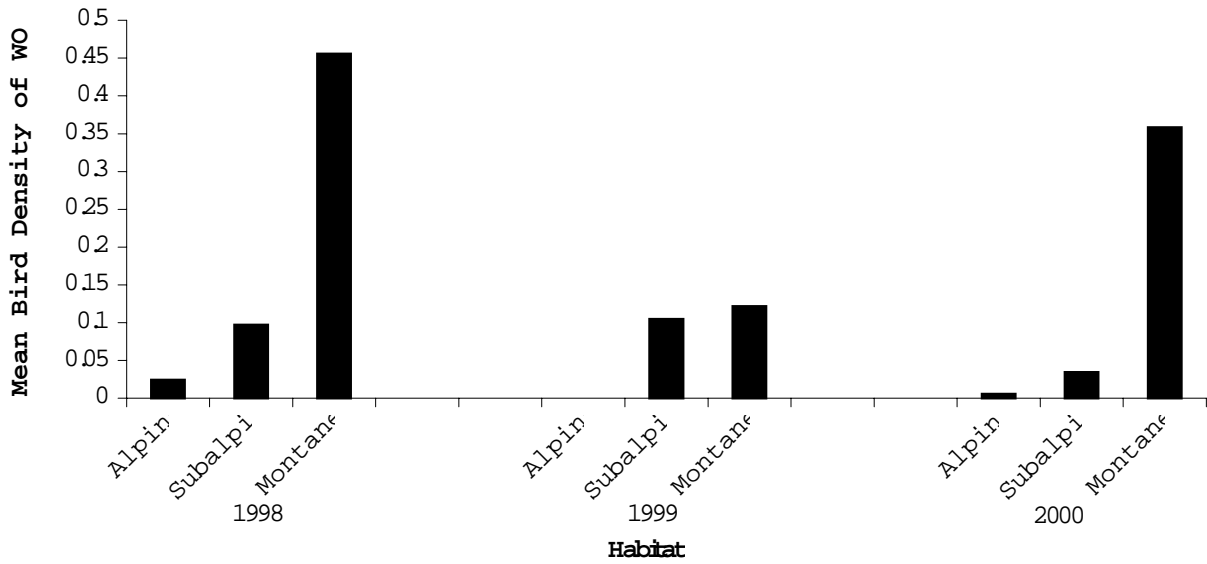
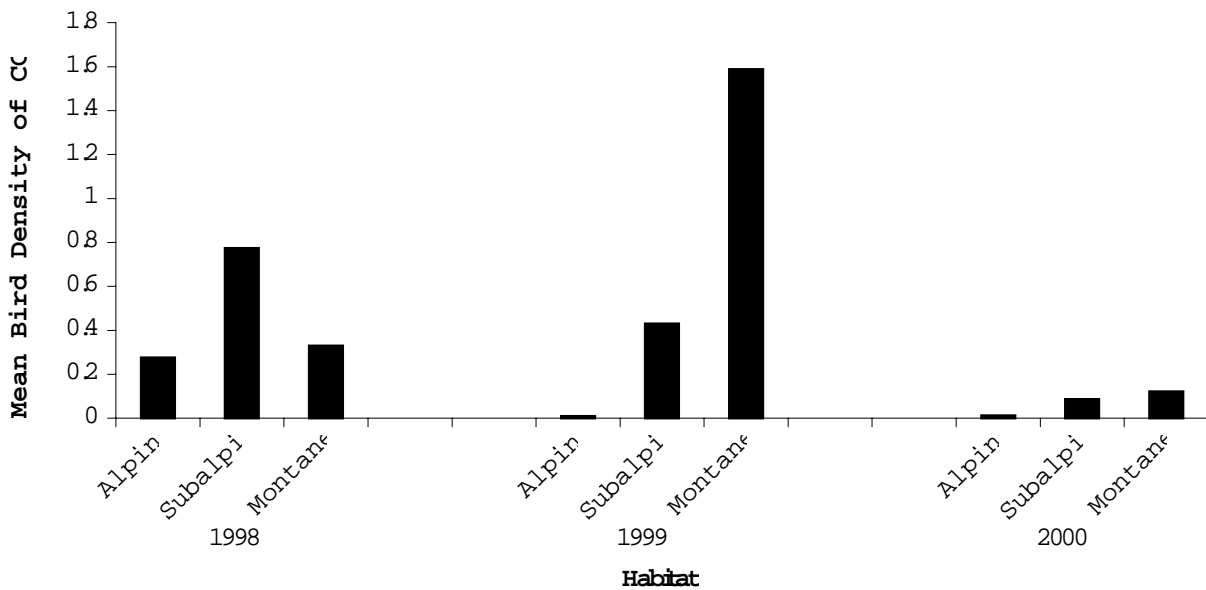


Figure 23. Variation in mean density of corvids (COR) across habitats by year



(1998-2000).

Figure 24. Variation in mean density of finches (FIN) across habitats by year (1998-2000).

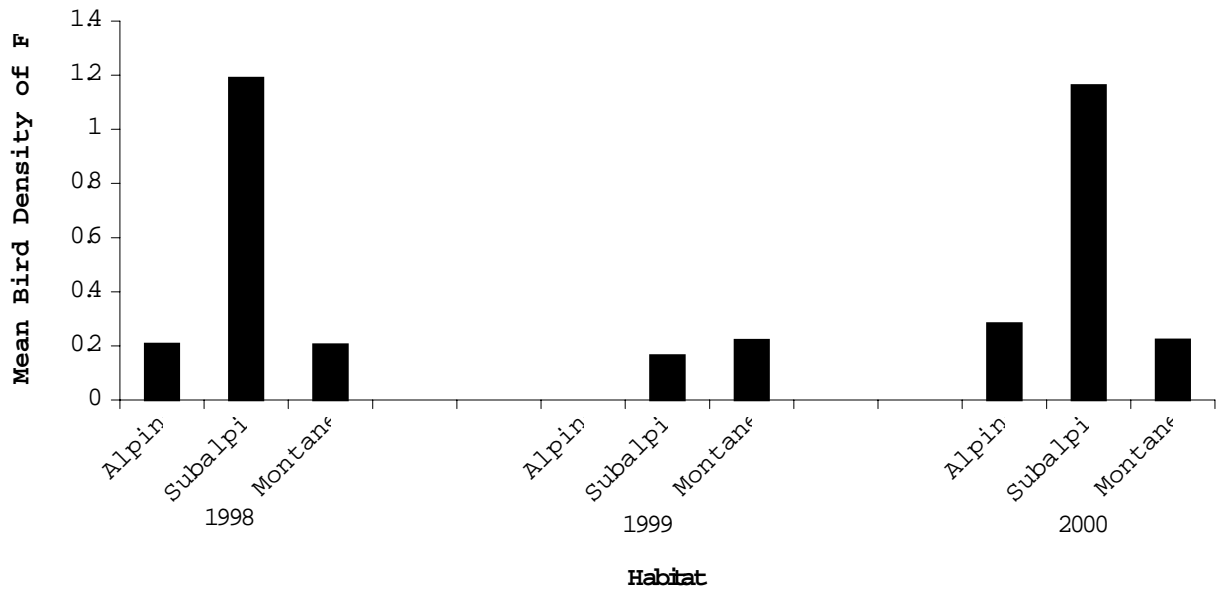


Figure 25. Variation of mean density of thrushes (THR) across habitats by year (1998-2000).

