

## Migratory Strategy and Seasonal Patterns of Bird Diversity in Relation to Forest Habitat

**ABSTRACT.**—Aspen stands and riparian areas are important to breeding birds in the southwestern U.S. because they provide resources such as food and shelter. We investigated how this importance varies throughout the year for both resident and migratory birds. We sampled birds in 96 sites, half in small isolated aspen stands and half in the ponderosa pine forest in northern Arizona during the summer of 1996, and a subset of those plots during fall of 1996 and the spring of 1997. Bird species richness and abundance varied seasonally. During the summer there were more birds and more bird species in aspen stands. This relationship appears to be driven by an affiliation between Neotropical migrants and aspen trees. During fall, residents were associated with riparian areas. We demonstrate the importance of small inclusions of aspen to Neotropical migrants in the Southwest during the breeding season and we show that preference for habitat types among migratory groups can vary seasonally.

### INTRODUCTION

Resources vary throughout space and time and we should expect birds to vary in their use of these resources based on life history requirements. Within a season, birds that use the same strategies for migration might be expected to choose similar habitat types based on timing and availability of resources in relation to their migration. For instance, migrants may select breeding sites based on cues different from those used by residents because they are able to exploit highly seasonal resources (Rabenold, 1993) and they may be dependent on highly specialized breeding sites to maintain reproduction (Sherry and Holmes, 1995). Residents are on, or near, the breeding sites longer and might be less dependent on seasonal flushes in production. Between breeding and non breeding seasons we may see the same migratory guild selecting components of the habitat differently; for example, home ranges and habitat breadth tend to expand during non breeding seasons due to decreased resource concentration (Rolando, 1998; Wiktander *et al.*, 2001). Additionally, resource requirements can change based on season; for example, species that are typically granivores or frugivores during the winter often consume insects during the breeding season to obtain protein for nestlings.

In a pilot study, we examined bird abundance and species richness of resident, short distance migrant and Neotropical migrant species during different seasons in small aspen (*Populus tremuloides*) stands and compared these measures to those in the ponderosa pine (*Pinus ponderosa*) forest matrix in northern Arizona. Additionally, we examined the abundance and species richness of residents and short distance migrants between the summer breeding season and the following fall and spring. We examined correlations between bird abundance and diversity and environmental variables during these periods.

### METHODS

#### STUDY SITE

We studied bird communities in small quaking aspen stands and the surrounding forest matrix in the Coconino National Forest of northern Arizona during the summer of 1996 (June–July), fall of 1996 (September) and spring of 1997 (April). The forest matrix was primarily ponderosa pine and ponderosa pine-Gambel oak (*Quercus gambelii*). Elevation of our study sites ranged from about 2060 to 2480 m. We selected aspen stands >0.1 ha and that were surrounded by forest matrix on at least two-thirds of the stand's edge. Aspen stands were small, averaging 13 ha (median 4 ha), and comprised a very small percentage of the landscape at elevations between 1900 and 2600 m. These stands are described in greater detail by Griffis-Kyle and Beier (2003).

#### SAMPLING

We placed one plot in each aspen stand and a second plot in the ponderosa pine forest 275 m to 950 m straight line distance away from the edge of each aspen stand. Plots within the aspen stands were located randomly; whereas each pine plot was located to match the paired aspen plot in elevation, slope, aspect and topographic setting. In the study area, aspen occurs in two topographic settings: riparian areas (including drainage bottoms, canyon slopes and springs) and north facing hillsides. During 1996

we sampled 52 riparian and 44 hill plots during breeding season 1996, 36 riparian and 32 hill plots during fall. During spring 1997, 26 riparian and 30 hill were sampled. All plots sampled during the fall and spring also were sampled during the summer. Some of the points were inaccessible during the fall and spring; therefore, only 14 riparian and 18 hill plots were sampled during all three seasons. We use the term *overstory vegetation* to distinguish between aspen and pine plots, the term *topographic setting* to distinguish between riparian and hill plots and the term *plot type* to refer to one of four combinations of tree species and topographic setting, namely aspen-riparian, pine-riparian, aspen-hill and pine-hill.

We surveyed birds using point counts, recording all birds detected within a 75 m radius of plot center. After arriving at the site we waited 2 min before starting the 8 min survey so that the observer's ear could attune to the ambient acoustics and birds could acclimate to the observer's presence. All surveys were conducted within 3 h after sunrise. We did not sample during sustained rain or wind. We excluded birds flying overhead if they did not land in the plot. We surveyed each plot twice per season at least 2 wk apart in the summer and 1.5 wk apart in the fall and spring, rotating observers among plots and the order of visitation with respect to time of day to control observer and temporal biases. We only included residents and short distance migrants (Philips *et al.*, 1964; National Geographic Society, 1987) in the analyses for fall and spring and comparisons between all seasons, because long distance migrants for the most part had left in the fall and were just beginning to arrive in the spring. As an index of each species' abundance, we used the maximum of the two counts in each season. Bird species richness was the number of species detected at a given plot during two point counts within a season.

#### STATISTICAL ANALYSIS

We used general linear models (GLM), for each season ( $\alpha = 0.05$ ), to determine if bird abundance or species richness by migratory strategy varied with overstory vegetation and topographic setting (Neter *et al.*, 1996; SPSS Inc., 1997a). We used a Bonferroni correction for multiple comparisons. We then used forward stepwise multiple regression ( $P = 0.10$  to enter,  $P = 0.13$  to remove) to identify habitat factors (Appendix 1) affecting avian species richness and abundance within each season (Neter *et al.*, 1996; SPSS Inc., 1997b). Additionally, within each season, we examined bivariate correlations of bird abundance and species richness with area and isolation of aspen stands using Spearman's correlation coefficient ( $\alpha = 0.05$ ).

### RESULTS

#### TREE SPECIES AND TOPOGRAPHIC SETTING

During June and July 1996 we detected a total of 622 residents (17 species), 332 short distance migrants (15 species) and 397 Neotropical migrants (18 species). During September 1996 we detected a total of 406 residents (14 species) and 71 short distance migrants (11 species). During April 1997 we detected 144 residents (8 species) and 106 short distance migrants (12 species). Additionally, the abundance of residents declined markedly between fall and spring, while the abundance of short distance migrants increased.

*Summer.*—During the summer there were more birds and bird species per plot, regardless of migratory strategy, in aspen stands than in pine areas (abundance  $F = 23.4$ ,  $P < 0.001$ ; species richness  $F = 24.2$ ,  $P < 0.001$ ), regardless of topographic setting (abundance  $F = 4.4$ ,  $P = 0.07$ ; species richness  $F = 2.8$ ,  $P = 0.2$ ) (Fig. 1). This relationship held for both Neotropical migrants and short distance migrants, with more individual species in aspen stands regardless of topographic setting (overstory tree species  $6.4 < F < 39.9$ ,  $0.02 < P < 0.0005$ ; topographic setting  $0.4 < F < 0.8$ ,  $0.3 < P < 0.5$ ) (Fig. 2). In comparison, for residents there was no detectable relationship between numbers of individuals or species and overstory tree species ( $0.5 < F < 1.2$ ,  $0.3 < P < 0.5$ ) or topographic setting ( $F = 3.6$ ,  $P = 0.06$ ) (Fig. 2).

*Fall.*—During the fall there were more individuals of short-distance migrants and residents and more species of residents in riparian plots than on hillsides ( $4.1 < F < 8.0$ ,  $0.01 < P < 0.05$ ). However, short distance migrant richness was not significantly related to either overstory tree species or topographic setting ( $0.2 < F < 2.7$ ,  $0.1 < P < 0.7$ ) (Fig. 3).

*Spring.*—During spring there was no detectable relationship between bird abundance or diversity and plot type for residents or short distance migrants ( $0.2 < F < 2.6$ ,  $0.1 < P < 0.7$ ). However, we did detect a non significant trends for more resident detections in aspen riparian plots than in any other habitat associations, and more short distance migrants on hillsides than in riparian areas (Fig. 4).

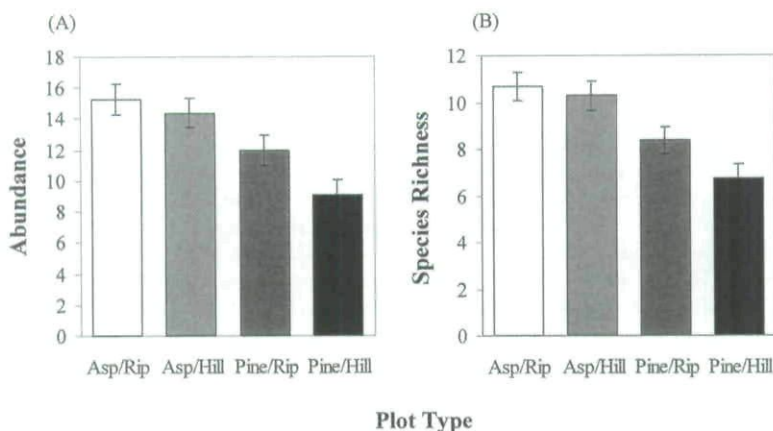
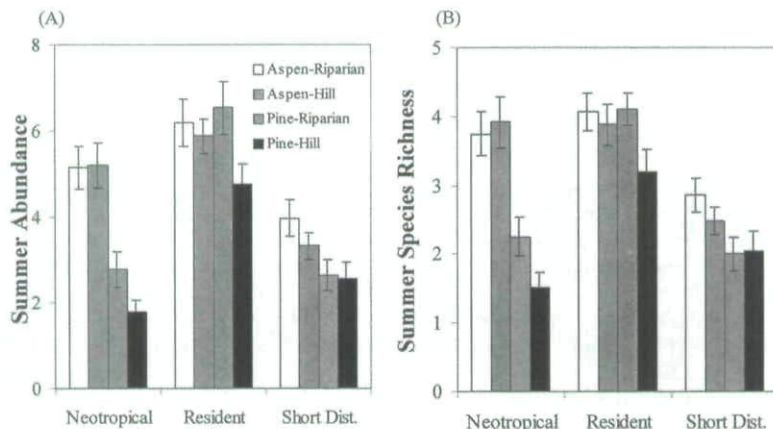


FIG. 1.—Average and standard error for (A) bird abundance and (B) species richness for birds detected on four plot types during point counts on the Coconino National Forest, summer 1996

#### HABITAT PREDICTORS

During the summer the number of large aspen greater than 30.5 cm dbh and the slope of the area were significant predictors of the total avian species richness ( $R^2 = 0.12$ ,  $P = 0.003$ ); large aspen was positively related to richness and slope was negatively related to richness. The number of large aspen was positively related and the number of ponderosa pine was negatively linked to bird abundance ( $R^2 = 0.15$ ,  $P = 0.001$ ). When Neotropical migrants were excluded from the analysis, both avian diversity and abundance were negatively correlated with slope (abundance,  $R^2 = 0.05$ ,  $P = 0.02$ ; richness,  $R^2 = 0.05$ ,  $P = 0.03$ ) (Fig. 5). In all cases the  $R^2$  values are very small signifying a small amount of explanatory power. Figure 5 demonstrates the large degree of variation in short distance migrants and resident bird diversity and abundance in plots with less slope and an overall decline in richness and abundance as slope increases.



#### Migratory Strategy

FIG. 2.—Average and standard error for (A) bird abundance and (B) species richness for Neotropical migrants, short distance migrants and residents detected on four plot types during point counts on the Coconino National Forest, summer 1996

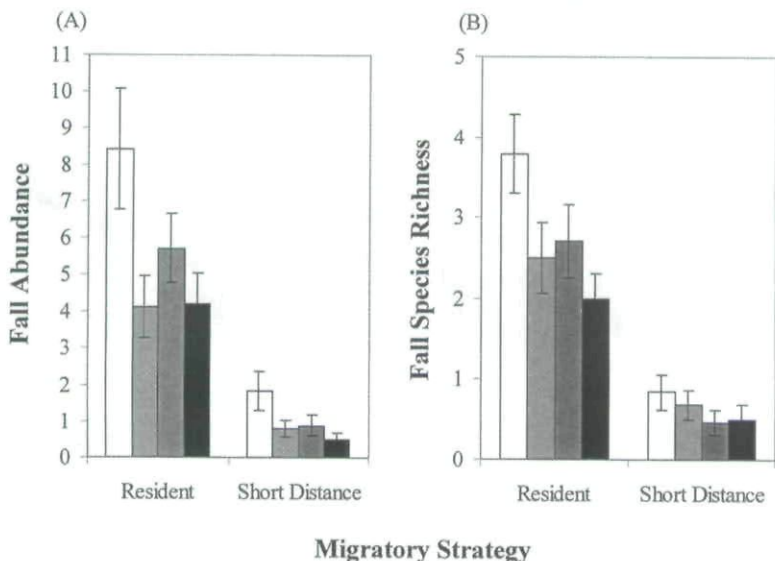


FIG. 3.—Average and standard error for (A) bird abundance and (B) species richness for short distance migrants and residents detected on four plot types during point counts on the Coconino National Forest, September 1996

During fall and spring slope continued to be a determinant of bird abundance and species richness. In fall slope was a significant predictor of the abundance of residents and short distance migrants combined (abundance,  $R^2 = 0.09$ ,  $P = 0.01$ ; richness,  $R^2 = 0.06$ ,  $P = 0.05$ ), with more individuals detected on gentler slopes, although the relationship in spring was marginal ( $R^2 = 0.06$ ,  $P = 0.06$ ). In all cases the  $R^2$  values are very small signifying a small amount of explanatory power.

In all seasons bird abundance and species richness were not explained by the number of shrubs, trees (other than large aspen) or snags, or the aspect of the stand (in all cases,  $P > 0.141$ ). Additionally, we did not detect a relationship between the size or isolation of aspen stands and the avian abundance or species richness detected (in all cases,  $P > 0.223$ ) and scatterplots failed to reveal any non linear trends between these variables.

#### DISCUSSION

Bird numbers varied between seasons and habitat in southwestern ponderosa pine forests with patchily distributed aspen stands. There was a strong positive relationship between the number of birds and bird species and the presence of aspen during the breeding season (more details in Griffis-Kyle and Beier, 2003), but not during the fall or the spring when individuals are moving throughout the forest. Overall, fewer birds were detected during the fall and spring, which likely was related to the departure of Neotropical migrants and the beginning of migration for short distance migrants (Yahner, 1986; Strong and Bock, 1990; Westworth and Telfer, 1993). Even so, resident birds were also found at lower densities than during the breeding season, perhaps due to seasonal changes in prey availability and resident habitat use (Rice *et al.*, 1980; Morrison *et al.*, 1985; Wiktander *et al.*, 2001).

The number of residents and short distance migrants declined from the breeding season into the fall, and residents continued to decline into the spring while short distance migrants increased. The initial declines from the breeding season into the fall are probably due to expansions in bird home ranges and travel in foraging groups caused by changing requirements and patchy resources (Winternitz, 1980; Wiktander *et al.*, 2001; Hurlbert and Haskell, 2003) as well as seasonal elevational migrations for the short distance migrants. The divergent pattern in the spring with residents declining and short distance

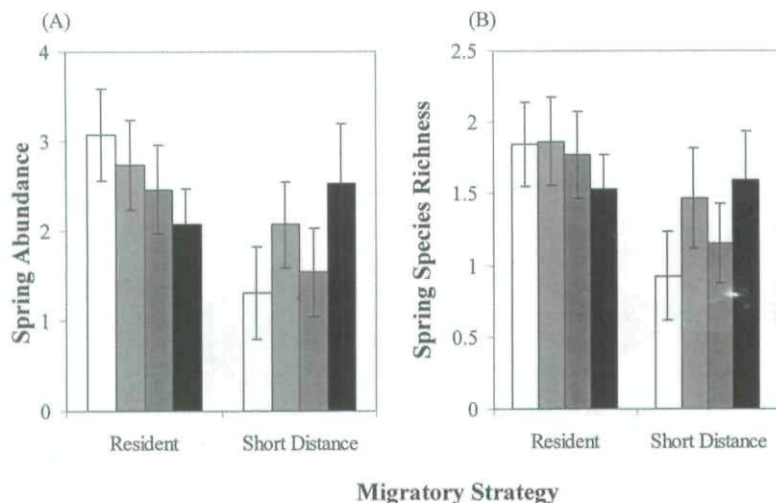


FIG. 4.—Average and standard error for (A) bird abundance and (B) species richness for short distance migrants and residents detected on four plot types during point counts on the Coconino National Forest, April 1997

migrants increasing was probably weather related. Numbers of individuals declined across all migratory guilds from 1996 to 1997 breeding seasons (Griffis, 1999), probably due to little rain in 1996 followed by several large snowstorms (January 12–14, 78.2 cm; January 25–27, 26.9 cm; February 25–28, 54.9 cm, NOAA, 2003) that did not occur in low elevation deserts where the short distance migrants were wintering. Such storms are expected to have the greatest impacts on residents with small body sizes (Graber and Graber, 1979) by altering winter resource availability (Kendeigh, 1934; Cody, 1985). This is demonstrated by dramatic declines between 1996 and 1997 breeding seasons in resident species with small body sizes such as pygmy nuthatches, white breasted nuthatches and brown creepers, and much smaller declines in Neotropical migrants (Griffis, 1999). This suggests that migratory strategy can have large impacts on population sizes in subsequent breeding seasons.

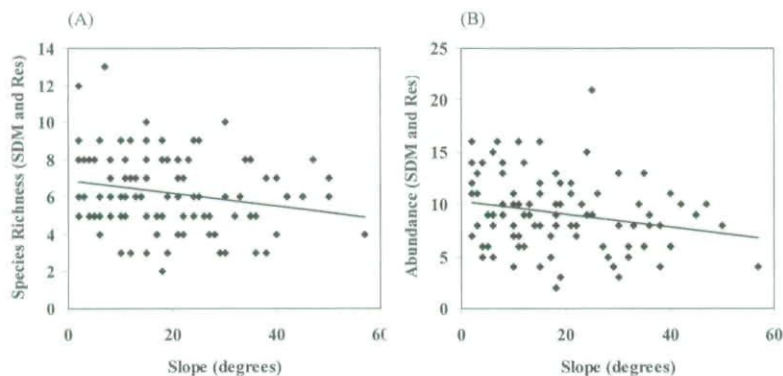


FIG. 5.—Scatter plot of detections of short distance migrant (SDM) and resident (Res) (A) abundance and (B) species richness in relation to degree of slope during point counts on the Coconino National Forest, summer 1996

Migratory guilds differed by numbers and by richness within season with all migrants most notably selecting aspen patches during the summer. This pattern continued through the breeding season of 1997. Aspen has been shown in numerous studies to be strongly associated with avian abundance and diversity both in the summer and winter (Winternitz, 1976; Yahner, 1986; Westworth and Telfer, 1993). We demonstrate that migratory birds, not residents, appear strongly attracted to aspen during the breeding season, but this association with aspen disappears as they are preparing to migrate and their habitat requirements are changing.

On our study area, migratory guilds are not associated with riparian corridors during the breeding season, a result consistent with results from overall bird abundance and richness (Griffis-Kyle and Beier, 2003). However, in the fall resident birds appeared to actively select these riparian areas. Residents may be using canyons and drainages as foraging areas or travel corridors protected from seasonally cold winds. Because no riparian sites in our study have perennial water flow, soil moisture probably differs little between upland and riparian sites; therefore, riparian areas may be more similar to upland areas (McGarigal and McComb, 1992) in these sites than in most other places. This lack of a relationship between bird diversity and riparian areas is unexpected given that most studies have demonstrated the importance of riparian areas to bird diversity and abundance in more xeric landscapes in the Southwest (Stevens *et al.*, 1977; Szaro, 1980; Knopf, 1985; Strong and Bock, 1990).

Both the presence of aspen and abundance of large aspen had a strong positive effect on patterns of total bird diversity during the breeding season, suggesting large trees are important to avian diversity. Because this pattern disappeared when Neotropical migrants were dropped from the analysis, large aspen apparently are important primarily to Neotropical migrants in northern Arizona, agreeing with other studies (Debyle, 1985; Rosenstock, 1998; Kirk and Hobson, 2001). In spring, long distance migrants are rapidly returning to their breeding areas. In this rush it may be easier for migrants to focus on these large deciduous trees as proximate cues for good resources, rather than search throughout the pine matrix for subtler cues of resource quality (Hilden, 1965).

Slope had a weak negative association with bird diversity probably because it is related to factors such as microclimate or vegetation that affect food supply, foraging substrates and nesting opportunities (Urban and Smith, 1989). This negative relationship with slope is consistent with results from habitat analyses of overall breeding bird species richness in aspen stands (Griffis-Kyle and Beier, 2003). Microclimate, influenced by slope, may be just as important as vegetation in determining bird communities because it has both direct effects (*e.g.*, nestling and adult survival, energetic needs) and indirect effects (*e.g.*, vegetation, insect abundance) on the avian community (Karr and Freemark, 1983). For a given aspect and orientation to prevailing winds, slope may increase wind velocity, water run off and evaporation of soil moisture, all of which lead to lower available moisture and decreased temperature. The mechanism between slope and bird diversity is as yet obscure, but is perhaps related to the effects of slope on floristics and food resources. We suggest that there should be further study into the interactions that slope has on factors that more directly affect bird fitness.

In summary, we have demonstrated seasonal differences in habitat selection for both migrants and residents as well as within season differences between birds of varying migratory strategy. Furthermore, we have highlighted the importance of old, large aspen as well as inclusions of aspen in general for Neotropical migrants in a coniferous forest matrix. Resources vary throughout the year in both timing and location; thus, birds should vary their selection of habitat to correlate with these changes (Alatalo, 1980; Morrison *et al.*, 1985; Strong and Bock, 1990). Furthermore, birds that use their environments in similar ways should be expected to select similar features of the environment.

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- KERRY L. GRIFFIS-KYLE<sup>1</sup> AND PAUL BEIER, Northern Arizona University, School of Forestry, P.O. Box 15018, Flagstaff 86011-5018. Submitted 9 January 2004; accepted 29 June 2004.

APPENDIX 1.—Potential habitat predictors measured on a 100-m<sup>2</sup> plot centered on the point count station, which we tested for relationships to resident and short distance migrant abundance and species richness using stepwise multiple regression. Starred variables (\*) were measured for aspen stands only

Variable	Measurement units; methods
Aspect	Degrees azimuth; hand-held compass
Slope	Degrees of slope; clinometer
Number of small aspen trees	Count of aspen less than 30.5 cm dbh
Number of large aspen trees	Count of aspen at least 30.5 cm dbh
Total number of aspen trees	Total count of aspen
Total numbers of coniferous trees	Count of coniferous trees
Total number of shrubs	Count of shrubs
Total number of small trees	Count of trees less than 30.5 cm dbh
Total number of trees	Total count of trees
Number of snags	Count of snags
Area*	Index calculated by multiplying perpendicular diameters
Isolation*	Nearest neighbor distance and mean nearest neighbor distance between stand centers

<sup>1</sup> Corresponding author: Present address: Department of Biology, 130 College Place, Syracuse University, Syracuse, New York 13244. Telephone (315) 443-1693; FAX (315) 443-2012; e-mail: klgriffi@syr.edu



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