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Robert A. Miller
Boise State University

Jay D. Carlisle
Boise State University

Gregory S. Kaltenecker
Boise State University

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EFFECTS OF REGIONAL COLD FRONTS AND LOCALIZED WEATHER PHENOMENA ON AUTUMN MIGRATION OF RAPTORS AND LANDBIRDS IN SOUTHWEST IDAHO

Robert A. Miller[1], Jay D. Carlisle, and Gregory S. Kaltenecker

Idaho Bird Observatory, Department of Biological Sciences, Boise State University, 1910 University Dr., Boise, ID 83725

Abstract. Weather has a significant effect on avian migration, but whether the influence is similar across diverse geographic regions and across all species remains to be determined. We evaluated the effect of regional cold fronts and localized weather phenomena on the timing of autumn migration of multiple species of landbirds and raptors in southwest Idaho. The focus of the analysis was on total landbirds and the ten most common landbird species, along with total raptors and the eight most common raptor species. Using 13 years of data from the Idaho Bird Observatory in southwest Idaho (1997–2009), including standardized mist-net captures of landbirds and counts of raptors during autumn migration, we determined significant patterns that advance our understanding of the variables influencing avian migration in the West. Our data show a depression of numbers of most migratory species on the days immediately before, during, and after the passage of a cold front, with peak flights of most species occurring several days prior to or after cold fronts. This pattern was further substantiated by a detailed analysis of many weather variables illustrating that the majority of species choose to migrate during calmer winds, high pressure, and between cold fronts when the opportunity presents itself. In the Intermountain West, cold fronts are fewer in fall than in much of the rest of North America, so migrants may have greater choice of conditions under which to migrate and this behavior may be more common.

Key words: *autumn migration, cold front, landbirds, raptors, weather.*

Efectos de Frentes Fríos Regionales y de Fenómenos Climáticos Localizados sobre la Migración Otoñal de Rapaces y de Aves Terrestres en el Sudoeste de Idaho

Resumen. El clima tiene un efecto significativo sobre la migración de las aves, pero aún no se ha determinado si la influencia es similar entre diversas regiones geográficas y entre todas las especies. Evaluamos el efecto de los frentes fríos regionales y de fenómenos climáticos localizados sobre la fecha de la migración de otoño de múltiples especies de aves terrestres y de rapaces en el sudoeste de Idaho. El foco del análisis estuvo sobre el total de las aves terrestres y las diez especies de aves terrestres más comunes, junto con el total de las rapaces y las ocho especies de rapaces más comunes. Usando 13 años de datos provenientes del Observatorio de Aves de Idaho en el sudoeste de Idaho (1997–2009), incluyendo capturas estandarizadas de redes de niebla de aves terrestres y conteos de rapaces durante la migración otoñal, determinamos los patrones significativos que mejoran nuestro entendimiento sobre las variables que influencian la migración de las aves en el oeste. Nuestros datos muestran una disminución de los números de la mayoría de las especies migratorias en los días inmediatamente antes, durante y luego del pasaje de un frente frío, con un pico de vuelos de la mayoría de las especies ocurriendo varios días antes y después de los frentes fríos. Este patrón fue posteriormente confirmado por un análisis detallado utilizando muchas variables climáticas que muestran que la mayoría de las especies eligen migrar durante la presencia de vientos más calmos, alta presión y entre frentes fríos cuando se presenta la oportunidad. En el oeste inter-montano, los frentes fríos son más escasos en el otoño que en la mayoría del resto de América del Norte, por lo que las aves migratorias tienen mayor posibilidad de elección de las condiciones bajo las cuales migrar y este comportamiento puede ser más común.

INTRODUCTION

Migration is a very significant event in the annual cycle of many birds. Some of the challenges faced by migrants include gathering food to support a 10–25× increase in the basal metabolic rate (Gill 2007) and a significant increase in the risk of predation. Migrating birds are also important ecological indicators, and Bildstein and Klem (2001) argued that migrating raptors fulfill 13 of 14 properties desirable for an indicator species. According to the Breeding Bird Survey, 29% of neotropical migrant species have declined in the western United States since 1980 (Sauer et al. 2008), and conservation of these species requires a complete understanding of their life history and ecology, including migration and the effects

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[1]E-mail: RobertMiller7@u.boisestate.edu

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of weather. To this point, Sillett and Holmes (2002) showed that for some landbirds 85% of apparent annual mortality can occur during migration. The causes of this migration-related mortality are difficult to pinpoint, but weather is likely to play a significant role.

Indeed, weather has a large effect on the life of a migrating bird. It likely plays a role in initiating migration (Gill 2007), directly or indirectly influences the course and pace of migration (Gauthreaux 1971), and can affect survival during migration directly (Newton 2007). However, is the effect of weather on migration similar across diverse geographic regions and across all species? Many site-specific studies (Titus and Mosher 1982, Millsap and Zook 1983, Hall et al. 1992, Allen et al. 1996, Woltmann and Cimprich 2003) and syntheses (Richardson 1978, 1990) document our current understanding with regard to weather and avian migration. With respect to cold fronts, some studies have shown peak migration of raptors on the day a front passes (Millsap and Zook 1983), on the day after it passes (Richardson 1978, Allen et al. 1996), or no significant relationship at all (Hall et al. 1992). Among local weather variables, some studies have shown only wind direction and visibility factors as significant predictors for some species (Titus and Mosher 1982), while others have found a much more diverse set of significant predictors such as wind direction and speed, temperature, pressure, cloud cover, and lunar phase (Pyle et al. 1993). Despite the variation in details of results, the pattern that biologists and birdwatchers alike have observed in the eastern United States is that large waves of migrants generally pass by monitoring sites within a day after the passage of a cold front (Richardson 1978, 1990).

The data set from the Idaho Bird Observatory's Lucky Peak site, consisting of 13 years of captures of migratory landbirds and counts of raptors, enables a robust analysis of the influences of weather on avian migration. Initial qualitative evaluations of weather and bird movements suggested that in Idaho birds were not moving immediately after cold fronts as found elsewhere. Therefore, we hypothesized that other weather variables play more important roles in the West or that western birds respond to cold fronts differently from their eastern counterparts.

METHODS

STUDY SITE

The study was conducted at Lucky Peak (1845 m), the southernmost peak of the Boise Foothills, located 12 km east of Boise, Ada County, Idaho (43° 36' N, 116° 05' W). The Boise Foothills, consisting of north–south trending peaks and hills in the Boise Mountains, form the northern boundary of the Snake River Plain and the southernmost extension of the central Idaho mountains. The study site lies along the migratory flyway of the Intermountain corridor (Goodrich and Smith 2008) and is located at the boundary between the mostly forested mountains to the north and the shrub steppe to the south (Carlisle et al. 2004).

MIST-NET CAPTURES OF LANDBIRDS

We captured landbirds with standard 12 m × 2.5 m × 36-mm mesh mist nets in mountain shrubland (Carlisle et al. 2004). The standard operation consisted of ten nets operated daily for 5 hr beginning at sunrise from mid-July to mid-October, except in the case of high winds or continuous precipitation. Birds were captured, identified to species, age, and sex (Pyle 1997), and fitted with individually numbered aluminum leg bands issued by the U.S. Geological Survey Bird Banding Laboratory. Hummingbirds were not banded but individually marked on their tail feathers to prevent double counting of individuals. Date, time, and certain morphological characteristics of each bird were also recorded. For the purpose of this analysis, birds were not counted on their second and subsequent captures.

We summed the total numbers of captured landbirds of all species (all migrant passerines plus hummingbirds and migratory woodpeckers) to provide a daily total, then divided this number by effort to provide an index per net hour for each day. We also analyzed the ten most common landbird species individually. To determine if age was a factor, we analyzed each species and all birds pooled by age (hatch year vs. after hatch year); however, there were no significant differences by age in migration relative to weather. Furthermore, to account for the separation of the nocturnal flight patterns of most migrant passerines and their subsequent capture during the morning, we shifted capture rates plus or minus one day relative to weather patterns, with little effect on results.

RAPTOR MIGRATION COUNTS

Following standardized methods recommended by Hoffman and Smith (2003), a minimum of two trained observers counted migrating raptors daily from 25 August through 31 October. Counts were curtailed only during periods of prolonged precipitation. Counts began at 12:00 MST during August and at 10:00 MST for the remainder of the season and continued throughout the day until raptor flights ceased, usually between 17:00 and 19:00 MST. For each passing raptor we recorded hour of observation, species, and—when possible—age, sex, and color morph . Best efforts were made to ensure that only migrating raptors were counted (Kaltenecker et al. 2010). We totaled all raptors counted for a given day and divided the total by the number of watch hours for that day to provide a rate for each day per watch hour. These data were not adjusted for the number of observers, and as with the landbird data, we analyzed the age classes separately but do not include the results as there were no significant age-related patterns.

COLD FRONTS

Following Millsap and Zook (1983), Hall et al. (1992), and Allen et al. (1996), we determined passages of cold fronts by analyzing synoptic weather maps obtained from the National Oceanic and Atmospheric Administration's (NOAA) *Daily*

Weather Map series (U.S. Department of Commerce 2010a). We interpolated the timing of each front through examination of subsequent daily maps. Fronts had to pass the study site directly to be included in analyses. Fronts that appeared or disappeared on subsequent maps, with no evidence that they had passed the study site, were not included in analyses. We counted stationary fronts on the last day they remained over the study site (Hall et al. 1992, Allen et al. 1996). For the purposes of modeling, we classified days as "under the influence of a cold front" if they fell the day before, the day of, or the day after passage of a cold front. All other days were classified as "not under the influence of a cold front."

LOCAL WEATHER PHENOMENA

We obtained historical weather data, including daily average temperatures, average wind speed, wind direction, and average pressure, from the National Climatic Data Center (U.S. Department of Commerce 2010b). These data were recorded at the Boise Air Terminal weather station, the weather station closest to Lucky Peak (approximately 12 km away, and 983 m lower in elevation). We obtained the change in each weather variable (daily average temperature, daily average pressure, daily average wind speed) by subtracting the previous day's value from the following day's value. Wind direction was recorded at midnight Mountain Standard Time each day, and we use it in our analysis as a value for the new day (00:00 hr), expressing it as a Boolean value representing a tailwind (1) or headwind (0). We defined a tailwind as a wind blowing from a compass direction <35° or >225°. We evaluated a cosine function of the wind direction, but it provided little incremental resolution, so we retained the simpler Boolean measure. These values not only align with the general flight direction of our migrating birds but also represent the two primary directions of wind in the area, northwest and southeast. We obtained lunar data from the U. S. Naval Meteorology and Oceanography Command portal (U. S. Naval Meteorology and Oceanography Command 2010).

STATISTICAL ANALYSIS

The Box–Cox method revealed that natural log was a suitable transformation for the number of landbirds captured per net-hour (Faraway 2005), so we transformed the data by ln $(n + 1)$. To remove the influence of individuals not actively migrating early in the season, we restricted the dates for total landbirds to 15 August through 15 October. Also, to eliminate potential nonmigrants, we restricted the analysis of each species of landbird to the central 75% of its numbers between 16 July and 15 October. Specific dates for each species are represented in Table 1.

For raptors as for landbirds, we used a Box–Cox procedure to determine an appropriate transformation for the counts, again leading us to use $\ln(n + 1)$ (Faraway 2005). Total raptor counts used the full monitoring window of 25 August through 31 October. Because of more precise counting of migrating raptors than of landbirds, for analysis of individual species we used a broader date range encompassing the central 90% of a season's numbers of migrants. Specific dates for each species are represented in Table 1.

TABLE 1. Intervals of migration defined for statistical analysis of species and groups of species. Intervals for species represent the central 75% of migrating landbirds counted and the central 90% of migrating raptors counted at Lucky Peak, Idaho, during autumn migration (1997–2009).

Species	Beginning day	Ending day
Overall landbirds	Jul 20	Oct 14
Ruby-crowned Kinglet	Sep 15	Oct 5
Oregon Junco	Sep 18	Oct 11
Gambel's White-crowned Sparrow	Sep 9	Sep 27
Dusky Flycatcher	Jul 24	Aug 26
Audubon's Warbler	Aug 22	Oct 1
MacGillivray's Warbler	Jul 24	Sep 11
Western Tanager	Aug 8	Sep 4
Spotted Towhee	Aug 22	Oct 1
Chipping Sparrow	Jul 31	Oct 7
Orange-crowned Warbler	Aug 13	Sep 19
Overall raptors	Aug 25	Oct 31
Sharp-shinned Hawk	Sep 3	Oct 16
American Kestrel	Aug 29	Oct 4
Turkey Vulture	Sep 9	Sep 28
Red-tailed Hawk	Aug 29	Oct 22
Cooper's Hawk	Sep 3	Oct 6
Northern Harrier	Aug 30	Oct 19
Swainson's Hawk	Aug 25	Sep 25
Osprey	Aug 30	Oct 3

For multivariate analysis we used linear regression and an information-theoretic approach with Akaike's information criterion (AIC; Burnham and Anderson 2002). We created independent models for total landbirds, total raptors, and each species of landbird and raptor. Predictor variables included daily average temperature, change in daily average temperature, daily average atmospheric pressure, change in daily average atmospheric pressure, daily average wind speed, change in daily average wind speed, wind direction at 00:00 MST, moon illumination (percent), moon phase (waxing/waning), cold-front influence, day of year, day of year^2, and lag of the response variable (previous day's count value). We calculated Pearson correlations between each pair of variables to rule out over correlated variables (Faraway 2005). For interpreting directional relationships between weather variables and migrating birds, we used coefficient signs from models including day of year, day of year^2, and lag to mitigate any autocorrelation.

Each weather variable was included in a separate "univariate" model including the variable, day of year, day of year^2, and lag. We retained the latter three values in all models as these variables are important to mitigate the autocorrelation of the response variable. We removed from further consideration for that species or group of species any weather variable for which the value of *P* in the univariate model was greater than 0.25 (Hosmer and Lemeshow 2000). We combined the variables passing this threshold to form a set of regression models including all possible combinations of the remaining variables, including the null model which included only day of year, day of year^2, and lag. For each model in the set, we calculated a value of AIC along with an Akaike weight (Burnham and Anderson 2002, Lavoue and Droz 2009). For all models in a set including a given variable, we summed the weights to produce a weight of relative importance of that variable for that set (Lavoue and Droz 2009).

All statistical analyses were run with software from the R Development Core Team (2009).

RESULTS

The Pearson correlations (Table 2) between the ten weather variables ranged from –0.52 to 0.45, well below the threshold of 0.70 established for this study. However, evaluating the multiple correlation of the weather variables to predict cold fronts produced a model in which a decrease in the daily average temperature ($P < 0.001$), a decrease in the change in daily average temperature ($P < 0.001$), a decrease in daily average atmospheric pressure ($P < 0.001$), and an increase in daily average wind speed ($P < 0.001$) were all significant predictors for cold-front influence ($F_{4,\,1040} = 28.78$, $P < 0.001$, $R^2 = 0.14$). This indicates a multiple correlation between these variables that does not invalidate the analysis but helps in the interpretation (Buckland et al. 1997).

In no model set did the null model (no weather variables, only day of year, day of year^2, and lag) rank in the top half of weights for the model set. No two species of landbirds or of raptors resulted in the same set of variables included in the final set of models (Table 3), although the American Kestrel did have the same model set as the Oregon Junco. No individual model produced convincing evidence of being superior (Akaike weight > 0.90) for the total or any single species of landbird or raptor, so we used multi-model averaging for all analyses (Burnham and Anderson 2002).

LANDBIRDS

We included a total of 65 253 landbirds in analyses, encompassing 100 species captured over 13 years. The ten most common species included the Ruby-crowned Kinglet (*Regulus calendula*, n = 14 136), Oregon Junco (*Junco hyemalis*, *oreganus* group, n = 7717), Gambel's White-Crowned Sparrow (*Zonotrichia leucophrys gambelii*, n = 5422), Dusky Flycatcher (*Empidonax oberholseri*, n = 3578), MacGillivray's Warbler (*Oporornis tolmiei*, n = 3270), Audubon's Warbler (*Dendroica coronata, auduboni* group, n = 3193), Western Tanager (*Piranga ludoviciana*, n = 3143), Spotted Towhee (*Pipilo maculatus*, n = 2677), Chipping Sparrow (*Spizella passerina*, n = 2138), and Orange-crowned Warbler (*Oreothlypis celata*, n = 2066).

For all species except the Audubon's Warbler, Spotted Towhee, and Orange-crowned Warbler, the model sets, utilizing weather variables as predictors for total number of captured landbirds, included at least one weather variable with a relative importance weight >0.90, (Table 3). The Audubon's Warbler and Spotted Towhee did have values above 0.85, indicating reasonably strong influence. Daily average wind speed and change in daily average wind speed were included in 10 of 11 model sets, with wind speed having a very strong relative importance weight for overall landbirds and the Ruby-crowned Kinglet and change in daily average wind speed being most influential for overall landbirds, MacGillivray's Warbler, and Chipping Sparrow. Daily average temperature

TABLE 2. Values of Pearson correlation between 10 weather variables used in analyses of bird migration at Lucky Peak, Idaho, during autumn migration (1997–2009): daily average temperature (Temp), change in daily average temperature (chTemp), daily average atmospheric pressure (Press), change in daily average atmospheric pressure (chPress), daily average Wind speed (Wind), change in daily average wind speed (chWind), wind direction (Tail), cold-front influence (Cfront), lunar illumination (MoonIll), and moon phase (waxing/waning; Wax).

	Temp	chTemp	Press	chPress	Wind	chWind	Tail	Cfront	MoonIll	Wax
Temp	1									
chTemp	0.22	1								
Press	–0.52	0.07	1							
chPress	–0.06	–0.48	0.45	1						
Wind	0.12	–0.19	–0.15	0.07	1					
chWind	–0.06	0.14	–0.25	–0.23	0.62	1				
Tail	0.00	–0.35	–0.2	0.10	0.13	0.02	1			
Cfront	–0.06	0.14	–0.21	0.00	0.25	0.13	0.14	1		
MoonIll	0.00	–0.01	0.001	0.01	0.01	0.01	0.04	–0.01	1	
Wax	0.02	0.00	–0.06	0.00	–0.06	0.01	–0.02	–0.08	0.06	1

TABLE 3. Relative importance weights and direction associations (signs) for each weather variable for landbirds and raptors counted at Lucky Peak, Idaho, during autumn migration (1997–2009). Blank cells indicate variables that were dropped from consideration. Bold type highlights the most influential variables (>0.90) in each model set.

	Temp	ΔTemp	Press	ΔPress	Wind speed	ΔWind speed	Wind dir.	Cold-front influence	Moon illum.	Moon phase
Total landbirds	−0.81		+0.58	+0.29	**−0.99**	**−0.91**		−0.46		
Ruby-crowned Kinglet				−0.46	**−0.97**	−0.53	−0.31	−0.31		
Oregon Junco	**−0.99**	−0.36	+0.35	+0.28	−0.90	−0.49	**+0.96**	−0.65		
Gambel's White-crowned Sparrow			**+0.92**		−0.31	−0.68				
Dusky Flycatcher	**+0.91**	+0.67		−0.31	−0.40	−0.88	−0.35	**−0.99**	−0.73	
Audubon's Warbler		+0.34	+0.38		−0.88	−0.31				
MacGillivray's Warbler		+0.34	**+0.98**	**−0.99**	−0.30	**−0.94**		−0.62	−0.36	
Western Tanager	**+0.96**	−0.42		−0.29	−0.47		−0.28	+0.84		
Spotted Towhee			+0.43	+0.57	−0.42	−0.89			+0.78	
Chipping Sparrow		+0.54	+0.49		−0.36	**−0.93**		−0.28		
Orange-crowned Warbler	−0.42	−0.21		+0.56		−0.57	+0.40			
Total raptors			+0.89	+0.85	**−0.99**	−0.28		−0.68		
Sharp-shinned Hawk		**+0.99**	+0.36	**+0.96**	**−0.99**	−0.38	−0.31	−0.80		
American Kestrel	**+0.99**	+0.40	**+0.99**	−0.48	**−0.99**	−0.28	**+0.99**	**−0.94**		
Turkey Vulture		+0.38	**+0.99**	+0.33	**−0.93**	−0.52	−0.30	−0.28		+0.53
Red-tailed Hawk		−0.52	**+0.99**	+0.81	**−0.99**	−0.33		−0.39		
Cooper's Hawk	+0.29	+0.57	+0.82	+0.75	**−0.99**	−0.28		−0.55		
Northern Harrier			**+0.96**		**−0.99**	−0.55		−0.29	−0.58	
Swainson's Hawk	+0.58				−0.79	−0.38	−0.33	−0.42		
Osprey				+0.44	−0.77	−0.46				

was the next most influential variable with high relative importance weights for three species, the Oregon Junco, Dusky Flycatcher, and Western Tanager. Daily average atmospheric pressure was well represented for many species, and its relative importance for the Gambel's White-crowned Sparrow and MacGillivray's Warbler was high. Directional relationships (Table 3) were consistent for the most important values such as daily average wind speed (negative association), change in daily average wind speed (negative association), and daily average atmospheric pressure (positive association) but varied for values such as daily average temperature, change in daily average temperature, change in daily average atmospheric pressure, wind direction, cold-front influence, and moon illumination.

RAPTORS

In our analyses we included 91 850 raptors representing 18 species counted over 13 years. The eight most common species were the Sharp-shinned Hawk (*Accipiter striatus*, n = 18 060), American Kestrel (*Falco sparverius*, n = 17 035), Turkey Vulture (*Cathartes aura*, n = 17 011), Red-tailed Hawk (*Buteo jamaicensis*, n = 15 251), Cooper's Hawk (*Accipiter cooperii*, n = 11 735), Northern Harrier (*Circus cyaneus*, n = 3500), Swainson's Hawk (*Buteo swainsoni*, n = 1143), and Osprey (*Pandion haliaetus*, n = 975).

For most raptors, with the exception of the Swainson's Hawk and Osprey, the model sets included at least one weather variable with a relative importance weight >0.90, (Table 3). Daily average wind speed and change in daily average wind speed were included in all model sets, with daily average wind speed having a very strong relative importance weight for overall raptors and many of the individual species. Cold-front influence was the next most widely used variable, appearing with overall raptors and seven individual species. Directional relationships (Table 3) were consistent for the most important values such as daily average wind speed (negative association), change in daily average wind speed (negative association), daily average atmospheric pressure (positive association), cold-front influence (negative association), and daily average temperature (positive association) but varied for values such as change in daily average atmospheric pressure, daily average temperature, and wind direction.

COLD FRONTS

For the length of the study season, 16 July through 31 October of each year, Lucky Peak averaged 12.5 cold fronts passing per season. The median value was 12, the range 5 (1998) to 17 (2005 and 2007). The average number of days between cold fronts was 8.8 with a median of 7. The first quartile was 5 days, and the third quartile was 11 days. The number of days between cold fronts ranged from 1 to 49.

The passage of cold fronts was correlated with the number of landbirds caught and the number of raptors counted

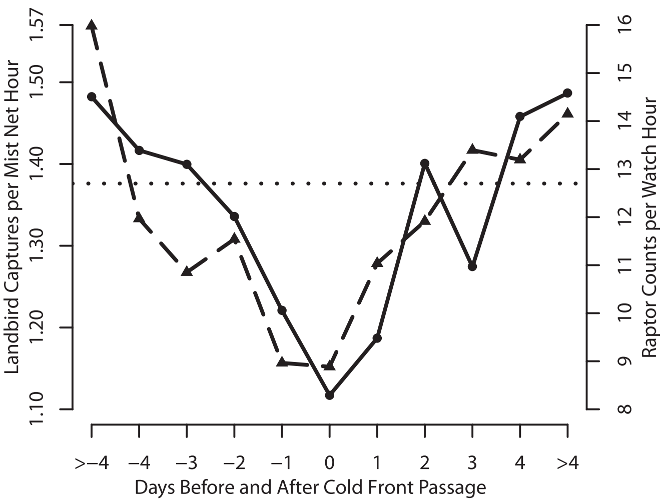

FIGURE 1. Average daily numbers of landbirds captured (solid line) and raptors counted (dashed line) relative to passage of cold fronts over Lucky Peak, Idaho, during autumn migration (1997–2009). Grand mean values (dotted line) for each group are aligned.

daily (Fig. 1). Numbers of both landbirds and raptors started declining a few days prior to a cold front and did not fully rebound until a few days after the front's passage. All of the raptors and most of the landbirds evaluated followed this general pattern, but there were a few exceptions. Figure 2 highlights the most significant exception, the Western Tanager, the only

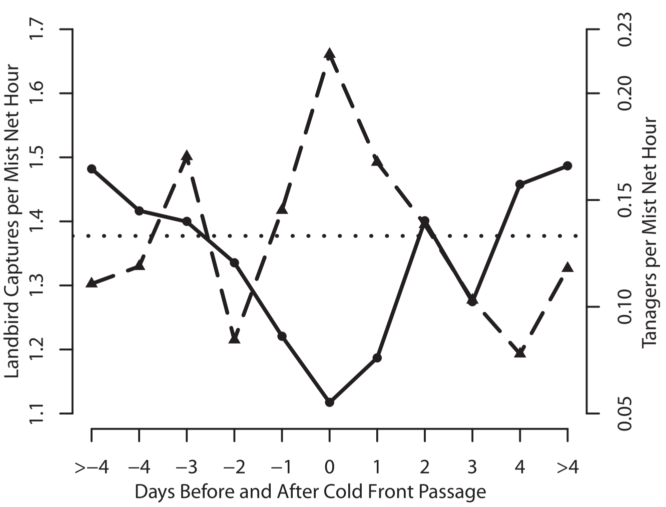

FIGURE 2. Average daily numbers of total landbirds captured (solid line) and Western Tanagers captured (dashed line) relative to passage of cold fronts over Lucky Peak, Idaho, during autumn migration (1997–2009). Grand mean values (dotted line) for each group are aligned.

species evaluated with a maximum average capture rate on the day of a cold front's passage.

Cold-front influence appeared in the model sets for overall landbirds, six landbird species, overall raptors, and seven raptor species, but its relative importance weight was very high (>0.90) only for the Dusky Flycatcher and American Kestrel and fairly high for the Western Tanager (0.84) and Sharp-shinned Hawk (0.80; Table 3). Cold-front influence had a negative association with all species except the Western Tanager (Table 3).

LOCAL WEATHER PHENOMENA

Daily average temperature appeared in models for total landbirds, five landbird species, and three raptor species, whereas change in daily average temperature appeared in 11 model sets (Table 3). The direction of the association for both variables differed by species (Table 3). Daily average atmospheric pressure appeared in model sets for overall landbirds, six landbird species, overall raptors, and six raptor species (Table 3). Pressure was positively associated with numbers of migrants in all model sets in which it appeared (Table 3). Change in daily average atmospheric pressure appeared in model sets for overall landbirds, seven landbird species, overall raptors, and six raptor species (Table 3). The direction of the association varied by species: for all but one raptor species the interaction with higher pressure was positive, yet landbirds were nearly evenly split with three positive and four negative (Table 3). Daily average wind speed appeared in all model sets except that for the Orange-crowned Warbler and was negatively associated in all model sets (Table 3). Overall numbers of migratory landbirds captured and overall numbers of raptors counted were negatively associated with wind speed for both favorable and unfavorable wind directions (Figs. 3, 4). Change in daily average wind speed was represented in all but one model set (the Western Tanager), and the direction of the association is negative for all species. Wind direction appeared in the model set for five landbirds and four raptors but had a very high relative importance weight only for the Oregon Junco and American Kestrel (Table 3). Moon illumination and moon phase (waxing/waning) appeared in fewer model sets than did the variables mentioned above, and the direction of the association varied by species (Table 3).

Taken together, these results indicate that multiple weather variables have important influence on daily numbers of both landbirds and raptors in autumn migration. Each species responds differently to the various aspects of weather systems, but all species are affected with a reasonably high degree of consistency. Wind and atmospheric pressure had the broadest and most consistent effects with more birds migrating during periods of higher pressure and reduced winds. The effects of cold fronts were fairly consistently negative except on the Western Tanager.

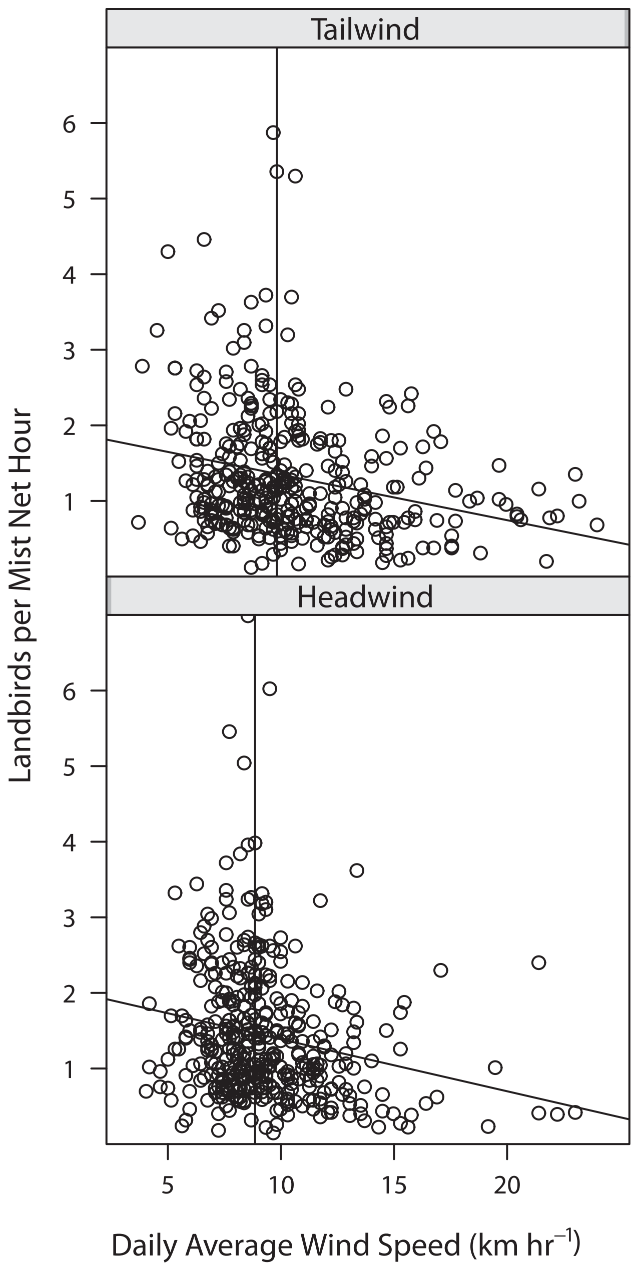

FIGURE 3. Overall rates of capture of landbirds (per net-hour) as compared to daily average wind speed (km hr^{-1}) for favorable tailwinds (upper) and unfavorable headwinds (lower). Vertical line, median; diagonal line, trend.

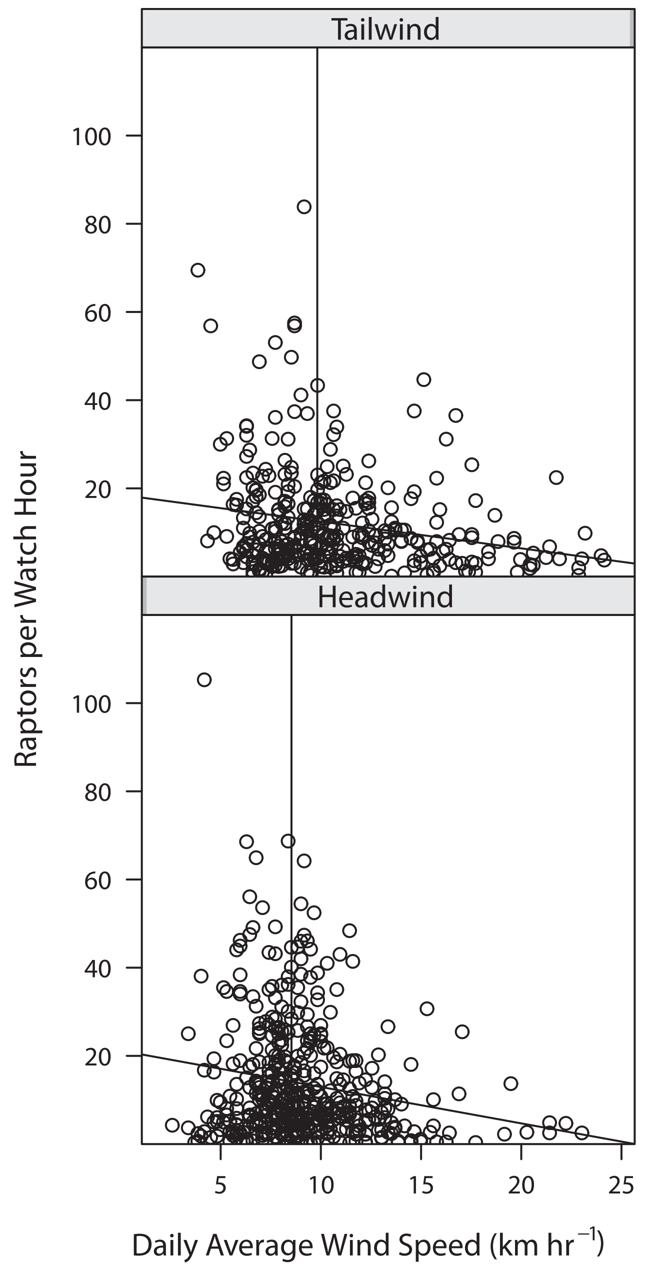

FIGURE 4. Overall counts of raptors (per watch hour) as compared to daily average wind speed (km hr^{-1}) for favorable tailwinds (upper) and unfavorable headwinds (lower). Vertical line, median; diagonal line, trend.

DISCUSSION

Weather systems vary by area in their effect on bird migration. Many locations have cold fronts, wind, and pressure changes, but the direction, intensity, and, importantly, their effect on avian migration can vary. Cyclone weather cells, of which the cold front is the leading edge, generally follow the flow of the jet stream (Lamb 1975). The jet stream, and so the cold fronts passing Lucky Peak, almost always approach from the northwest. The result is warmer southeast winds ahead of the front, which reverse to colder northwest winds just behind the front. The space between fronts is largely dominated by high pressure, warmer temperatures, and calmer winds. Local weather phenomenon such as wind and pressure are largely manifestations of synoptic patterns of cold fronts (Lamb 1975).

Although the results differed by species, the migration of most species we studied in southwestern Idaho was affected by a number of weather variables which were relatively influential and consistent in the model sets. The clearest pattern that emerged was that numbers of migrants were depressed immediately before, during, and after the passage of cold fronts. The response of migrating birds to other weather variables was consistent with the response to cold fronts in that numbers of migrants were depressed when wind speed was higher and atmospheric pressure was lower (local effects resulting from the passage of the fronts) than during periods separated from cold fronts by 2 or more days. The local weather variables most closely associated with cold fronts, wind and pressure, rated most influential in the analysis. We conclude that most individuals of most species choose to migrate past Lucky Peak during the periods of high pressure and calmer winds that occur between cold fronts.

Daily average wind speed was the most broadly important variable influencing migration, indicating a strong preference of calm winds for migration. Titus and Mosher (1982), Hall et al. (1992), and Pyle et al. (1993) also demonstrated this preference. The strong negative association with all species whose models included change in daily average wind speed indicates that the decrease in wind is not only a positive factor in migration, it might also be a strong influence in initiating migration. Interestingly, wind direction had a fairly weak effect on migration. The difference between a headwind and a tailwind shifted the median passage rate only mildly. This makes sense for larger raptors dependent upon thermal updrafts, which high winds, head or tail, eliminate. For smaller nocturnal migrants, strong winds create significant navigational challenges regardless of direction (Able 1974).

The next most influential variable was average daily atmospheric pressure, which was positively associated for all species whose model set included this variable. This supports the preference for days of high pressure between fronts. The relative importance weight of daily average temperature was high only for species that peaked either early or late in the count window, demonstrating that this weight was still suffering from autocorrelation. For example, the Dusky Flycatcher peaks early in the fall migration season and is positively associated with temperature whereas the Oregon Junco peaks late in the season and is negatively associated with temperature. Change in daily average temperature presents no such challenge but loses influence for most species. The Sharp-shinned Hawk was the only species to respond strongly to this variable, illustrated by its numbers rebounding sharply 2 days after the passage of a cold front when temperatures warm considerably. In contrast to Pyle et al. (1993), who studied over-water migration for which lunar illumination may be much more important, we found the importance of the moon to be relatively low for all species.

WHY MIGHT THE EFFECTS OF COLD FRONTS IN IDAHO CONTRAST WITH THOSE IN OTHER REGIONS?

From the perspective of a cold front, the general trend at Lucky Peak for nearly all species is the depression of numbers of migrants beginning a few days prior to a front's passage, hitting a low point near the passage, followed by a slow increase returning to average 2, 3, or even 4 days after passage. Richardson (1978) and Allen et al. (1996) found migration rates to peak the day after a cold front's passage. We believe differences in the frequency of cold fronts to be the primary factor behind this discrepancy.

Lucky Peak experiences fewer cold fronts during a migration season than do many other sites where migration has been monitored. For example, Allen et al. (1996) reported Hawk Mountain to range from 10 to 20 cold fronts per a restricted window of its migration season (restricted to maintain consistency from year to year). For a season of similar length, Lucky Peak ranges from 5 to 17 cold fronts. At Hawk Mountain, 50% of cold fronts passed within 3 days, 75% within 5 days, and 95% passed within 10 days of the previous cold front (Allen et al. 1996). At Lucky Peak, 50% of cold fronts passed within 7 days, 75% within 11 days, and 95% within 23 days of the previous cold front. At our study site, only 15–20% of cold fonts pass within 3 days, and 35–40% pass within 5 days of the previous front. Therefore, between cold fronts, many more calm days with high pressure are available for migration at our study site than at Hawk Mountain.

Migration rates for a given day can be influenced by a front that has already passed and the next front still approaching. At sites where cold fronts follow each other in close succession, the next approaching front acts to reduce numbers of migrants, causing the migration rate for a given day after a front to be lower than if the next front were still multiple days away. This process pulls down the average for days further from the previous front when there is a higher and higher likelihood of a new approaching front. Therefore it confounds the conclusions that can be drawn and likely explains the differing results in those regions. In southwestern Idaho, with many fewer cold fronts, approaching fronts play only a minor role, so the picture of birds' preferences for migration is clearer.

Days of high pressure between cold fronts provide calmer winds, which favor migration (Titus and Mosher 1982, Hall et al. 1992, Pyle et al. 1993). This conclusion is consistent with our detailed modeling, in which higher wind speed, independent of wind direction, was negatively associated with numbers of migrants of all species. It is also consistent with the cold-front analysis, in which numbers of migrants peaked on the calm days of high pressure between fronts.

During a cold front, migrating birds could be diverted toward or away from a site by wind drift (Mueller and Berger 1967). Millsap and Zook (1983) observed an increase in numbers of migrating *Accipiter* hawks that they believed to be the result of a shift in flight as a result of cold fronts. However, Allen et al. (1996) found that the number of cold fronts in a year did not affect the number of birds observed that year. A similar analysis at Lucky Peak produced similar results (R. A. Miller, unpubl. data). The degrees to which observations of flights are affected by cold fronts are likely site specific, but we feel confident that the differences in passage rates we have observed are caused by actual changes in the numbers of migrating birds, not by some migrants being steered away from our count site.

Many more calm days of high pressure favoring migration are available at Lucky Peak than at other sites of monitoring, the most logical explanation why at Lucky Peak peak numbers of migrants are delayed with respect to cold fronts.

ASSUMPTIONS AND POTENTIAL LIMITATIONS OF THE DATA

This study mixed two methods of data recording covering two different categories of birds into a single examination of the effects of weather on migration. We appreciate that this combination of datasets presents logistical challenges, including the question of whether or not counts of raptors passing by day and morning captures of landbirds migrating primarily at night are measuring the same movements and responses to weather. But we believe that this approach helps mitigate the potential for a procedural bias in either method and is strengthened by the two data sets leading to similar conclusions.

In our study, we did not mix the data from the two sources, only compared the interpretations of the independent analyses. Each method of counting, capture of landbirds in mist nets and counts of raptors, is widely recognized as valid for monitoring avian migration. Unlike raptor counts, however, landbird-capture data are not a measure of birds actually migrating at the time of observation, and Lucky Peak is a productive stopover point (Carlisle et al. 2005). Though our primary goal is to study birds during their migration, not all birds caught on a given day have necessarily been migrating that day or the night before, evidenced by the fact that up to 15% of individual birds are recaptured up to several days after initial capture (Carlisle et al. 2005). The quantitative use of mist-net data in this way has been criticized on the basis of the data being too variable for statistical conclusions to be drawn (Remsen and Good 1996), although later studies have shown mist-netting of landbirds to be effective in studies of their migration (Wang and Finch 2002). For example, Komenda-Zehnder et al. (2010) compared nocturnal measurements by radar with mist-net captures the next day and found a strong correlation in a similar mountainous environment. We feel confident that the overall number of new captures is a representative index of the total population on the move. This assertion is supported by several lines of evidence: capture rates agree with general observations of bird abundance in the area, stopovers are relatively short (Carlisle et al. 2005), large numbers of certain species are captured together (i.e., in migratory waves or pulses), most captured birds are carrying visible fat reserves for migration, captures and observations of birds decrease consistently starting multiple days ahead of the next cold front, and numbers captured are inconsistent with observations of grounded birds that might be predicted to be associated with cold fronts. Another possibility is that higher winds associated with a front's passage could act to reduce capture rates on those days by making nets more obvious or by reducing probability of capture when a bird hits the net. However, at our site fewer birds are observed *and* captured in inclement weather (when grounding might be expected), and this concordance of observations and captures suggests that there's a true reduction in landbird numbers. Furthermore, we shifted counts of landbirds captured by a day in either direction in order to determine if captures might by offset by a day from when the birds actually arrived, but this had minimal effect on the results, further supporting our conclusions about weather effects.

Since the breeding range of the migratory birds we are monitoring at Lucky Peak extends at least into central British Columbia, Canada (Kaltenecker et al. 2010), these birds could be affected by weather patterns not passing over Lucky Peak (i.e., cold fronts that stall far to the north of our site). Therefore, regionwide analysis could provide further resolution of the importance of weather patterns to the north of our site, especially in the initiation of migration.

CONCLUSIONS

The passage of cold fronts at Lucky Peak has the effect of depressing numbers of migrants of most landbirds and all raptors. These species' response to other weather variables such as wind speed, temperature, and pressure also support this conclusion. At our study site, this effect is most likely the result of birds choosing to migrate during periods of high pressure and calm winds. These results show avian migration in the Intermountain West to differ from that in areas where more frequent cold fronts diminish the availability of these conditions.

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