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THE INFLUENCE OF WEATHER ON GOLDEN EAGLE MIGRATION IN NORTHWESTERN MONTANA

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ABSTRACT.—We analyzed the influence of 17 weather factors on migrating Golden Eagles (*Aquila chrysaetos*) near the Continental Divide in Glacier National Park, Montana, U.S.A. Local weather measurements were recorded at automated stations on the flanks of two peaks within the migration path. During a total of 506 hr of observation, the yearly number of Golden Eagles in autumn counts (1994–96) averaged 1973; spring counts (1995 and 1996) averaged 605 eagles. Mean passage rates (eagles/hr) were 16.5 in autumn and 8.2 in spring. Maximum rates were 137 in autumn and 67 in spring. Using generalized linear modeling, we tested for the effects of weather factors on the number of eagles counted. In the autumn model, the number of eagles increased with increasing air temperature, rising barometric pressure, decreasing relative humidity, and interactions among those factors. In the spring model, the number of eagles increased with increasing wind speed, barometric pressure, and the interaction between these factors. Our data suggest that a complex interaction among weather factors influenced the number of eagles passing on a given day. We hypothesize that in complex landscapes with high topographic relief, such as Glacier National Park, numerous weather factors produce different daily combinations to which migrating eagles respond opportunistically.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *migration*; *weather*; *Montana*; *Glacier National Park*; *modeling*.

La influencia del tiempo en la migracion del noroeste de Montana

RESUMEN.—Analizamos la influencia de 17 factores del tiempo en la migración de *Aquila chrysaetos* cerca de la división continental en el Parque Nacional de Glacier, Montana U.S.A. Las mediciones locales fueron registradas en las estaciones automáticas de los flancos de dos picos dentro de la ruta migratoria. Durante un total de 506 horas de observación, el número de águilas doradas en conteos de otoño (1994–96) promedio 1973; los conteos de primavera (1995–96) promediaron 605 águilas. La tasa promedio de migración (águilas/hora) fué de 16.5 en otoño y 8.2 en primavera. las tasas máximas fueron de 137 en otoño y 67 en primavera. Mediante la utilización de un modelo linear generalizado, probamos los efectos del tiempo en el número de águilas contadas. En el modelo de otoño, el número de águilas aumentó con el incremento de la temperatura del aire, el aumento de la presión barométrica y la disminución de la humedad relativa y las interacciones entre estos factores. En el modelo de primavera, el número de águilas incrementó con el aumento de velocidad del viento, la presión barométrica y la interacción entre estos dos factores. Nuestros datos sugieren que la compleja interacción entre los factores del tiempo influenciaron el número de águilas pasando en un día dado. Formulamos una hipótesis la cual se basa en que en paisajes complejos con topografía marcada, como en el Parque Nacional de Glacier, numerosos factores climáticos pueden producir diferentes combinaciones a los cuales las águilas responden en forma oportunista.

[Traducción de César Márquez]

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The influence of weather on bird migration has been reviewed by Alerstam (1978), Richardson (1978, 1990), and others. During migration, the number of raptors moving on a given day may be influenced by barometric pressure (Kerlinger 1989), thermal updrafts (Gerrard and Gerrard 1982), wind speed and direction (Mueller and Berger 1967a, Titus and Mosher 1982, Kerlinger 1989, Liechti and Bruderer 1998), and frontal passage (Millsap and Zook 1983, Allen et al. 1996). Heintzelman (1975), Kerlinger (1989) and Spaar (1997) discussed weather variables related to migrating hawks, but in western North America few studies have provided empirical support for hypotheses concerning the influence of weather on raptor migration.

Although other studies have described raptor migration and weather influences, weather observations generally have not been made within the actual migration corridor. Additionally, few studies have examined weather and migration within complex mountainous terrain. In the Rocky Mountains north of Glacier National Park (GNP), in Alberta, Canada, Sherrington (1992) reported several thousand migrating eagles in autumn and spring. Large numbers of migrating eagles also have been reported by Omland and Hoffman (1996) in southwestern Montana. Although Golden Eagles (*Aquila chrysaetos*) were recorded in the GNP area in autumn as early as the mid-1880s (Grinnell 1888), their major migration route in GNP was not detected until 1987.

Farmer and Wiens (1998:405) recently suggested: "The landscape and the physical environment shape migration schedules and influence one's ability to interpret patterns . . . Modeling these factors may lead to new insights about migration adaptations in heterogeneous environments." The installation of high elevation weather stations for climate change studies in GNP afforded the opportunity to examine relationships between weather variables and eagle migration counts over a 3-yr period. In this paper, we report numbers of migrating Golden Eagles within a narrow corridor in northwestern Montana and describe patterns of migration. We evaluated the influence of 17 weather variables on numbers of eagles counted in autumn and spring, seeking the simplest model that would provide the greatest interpretive value.

STUDY AREA

We conducted our study in GNP, northwestern Montana (approximately 48°30′N, 114°00′W). The northern boundary of GNP is coincident with the southern boundaries of Alberta and British Columbia, Canada. GNP is bisected from north to south by the Continental Divide, from which major spur ridges extend east and west to or beyond the GNP border (Fig. 1). Elevations range from 948–3190 m. The climate is transitional between northern Pacific coastal and continental regimes. The Pacific influence is characterized by maximum cloudiness and precipitation in late autumn through winter (Finklin 1986). Annual precipitation averages 76 cm at West Glacier and more than 250 cm along the Continental Divide. Prevailing wind generally is from the west or southwest throughout the year. Cold fronts approach predominantly from the Pacific Northwest, but occasional Arctic cold fronts influence GNP during autumn and spring migration. Mean daily minimum and maximum temperatures at West Glacier during October (peak autumn migration) are −0.3°C and 11.8°C; during March (peak spring migration), they are −4.4°C and 6.2°C (Western Regional Climate Center, Reno, Nevada, TD-3200 Data Base).

METHODS

Field Procedures. During autumn, migrating eagles traveling south along the Livingston Range cross the McDonald Valley from Stanton Mountain to Mount Brown (Fig. 1) (first reported by E. Caton, October 1987, pers. comm.). Some eagles that follow the Continental Divide south also converge at Mount Brown. The same routes are used in reverse by eagles migrating northward in the spring. We counted migrating eagles within this path of convergence and passage during autumns 1994–96 and springs 1995 and 1996. Our observation site (976 m) was near the base of Mount Brown (peak height 2610 m) and near the head of Lake McDonald, about 9 km west of the Continental Divide (Fig. 1). All counts were made from this location because it was easily accessible and it provided an unobstructed view of the migration corridor. Observation locations nearer to the eagles, on the slopes of Mount Brown, required a day-long hike and reduced the field of view, leaving many eagles undetected. Such observations were made occasionally to check observer reliability, but they were not included in our analyses. Observers used 10× binoculars and 15–60× spotting scopes to identify eagles passing Mount Brown. Most observations (>90%) were made by the same seven individuals, each of whom had more than five years experience in GNP eagle research.

Incidental to our focus on Golden Eagles, we tallied all other raptors observed. Most Golden Eagles were easily distinguished from less frequent Bald Eagles (*Haliaeetus leucocephalus*) (5.6%) by plumage and morphology (Wheeler and Clark 1995). However, if specific identification between Bald and Golden Eagles was problematic, we tallied eagles without assigning species. These unidentified eagles (12%) were not included in our analyses; thus, our counts probably are underestimates of the actual number of Golden Eagles. We also could not always be confident of accurately separating subadult and adult Golden Eagles under some lighting conditions. The variable amount of white plumage that characterizes Golden Eagle age classes through 4 yr (Wheeler and Clark 1995) could result in some misidentifications at our observation distance. Therefore, our analyses involving age classes in-

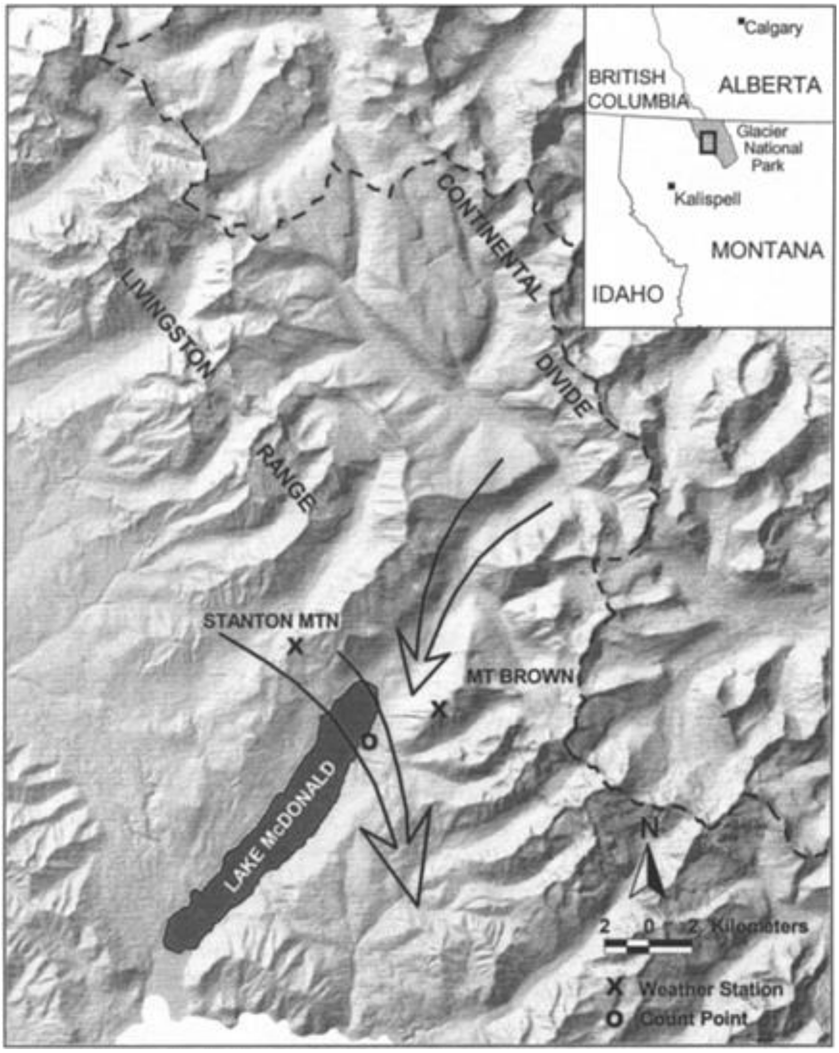

Figure 1. Study area within Glacier National Park, Montana U.S.A., showing Golden Eagle migration routes (arrows), observer counting point, and weather station locations.

cluded only those eagles that were reliably identified as adults or immatures.

To minimize variation of temporal patterns, observations were restricted to 1000–1700 H (Mountain Standard Time). Counts were made during days and hours when precipitation and clouds did not completely obscure visibility. As a result, some days were not represented by count data, and the number of observation hours per day varied.

Weather Data. During 1994–96, weather data were continuously recorded at two automated Omnidata® meteorological stations within the eagle migration corridor (Fig. 1). These stations had been established and maintained by the GNP Global Change Research Program since 1993 (White et al. 1998) and measured variables were applicable to modeling eagle migration. Both weather stations were equipped with EasyLogger® 900 series data recording systems powered by solar-charged, 12-volt batteries. At both stations, meteorological variables (Table 1) were measured at approximately 3 m above the ground. Data loggers operated on a 1-min sampling interval, with maxima and means recorded for each hour. The Mount Brown weather station was 2276 m, 334 m below the mountain's summit and relatively unobstructed by topography or trees. Weather data from this station were used in our analyses of autumn periods only. No spring data were available from Mount Brown because snow accumulations exceeding 3 m inactivated the solar panel. We used spring weather data from the other station (1735 m), on a west-facing ridge 627 m below the

Table 1. Source of weather variables included in analyses of influences on eagle migration in Glacier National Park, Montana.

FACTOR DESCRIPTION	DATA SOURCE
Mean hourly maximum wind speed (m/s)[a]	RM-Young ES-050[b]
Vector mean wind speed (m/s)[a]	RM-Young ES-050[b]
Vector mean wind direction (cosine°)[a]	RM-Young ES-050[b]
Mean air temperature (°C)[a]	Viasala ES-120[b]
Maximum air temperature (°C)	Viasala ES-120[b]
Minimum air temperature (°C)	Viasala ES-120[b]
Relative humidity (%)	Viasala ES-120[b]
Soil temperature (°C)	Omnidata ES-060-SW[b]
Solar radiation (Langleys/min)	Li-Cor ES-230[b]
Barometric pressure at Kalispell, Montana (millibars, daily mean)	NCDC[c]
Barometric pressure at Calgary, Alberta, Canada (millibars, daily mean)	NCDC[c]
Change in barometric pressure from previous day at Kalispell, Montana	NCDC[c]
Barometric pressure from previous day at Kalispell, Montana	NCDC[c]
Barometric pressure from previous day at Calgary, Alberta, Canada	NCDC[c]
Barometric pressure from two days prior at Kalispell, Montana	NCDC[c]
Barometric pressure from two days prior at Calgary, Alberta, Canada	NCDC[c]
Frontal System (day of passage)[d]	Natl. Weather Serv.

[a] Averaged over each 7-hr period of eagle observation.

[b] Instrument located on site, at Mount Brown and Stanton Mountain.

[c] National Climate Data Center (http://www.ncdc.noaa.gov/onlineprod/tfsod/climvis/main.html).

[d] Each day was assigned to one of four classes: (1) day before frontal passage, (2) day of, (3) day after, or (4) not associated with a cold front passage.

summit of Stanton Mountain. This site had some obstruction of north and east winds, but it accumulated less snow and the station continued to operate through spring. Hours between 1000–1700 were aggregated to provide maximum and mean values per daily observation period.

On-site weather stations were not equipped with barometers; therefore, we obtained barometric pressure records from the nearest National Weather Service station at Kalispell, Montana (50 km SW of the study site), and the Environment Canada station at Calgary, Alberta, Canada (260 km to the north). In autumn models, we included Calgary's barometric pressure, recorded one and two days before count days at GNP, because weather conditions to the north along the migration route could influence the number of eagles migrating south through GNP. Eagles would have passed the Calgary vicinity one or two days before passing through GNP in the autumn (McClelland et al. 1994). We obtained the dates of cold front passage at GNP from maps in the National Weather Service archives.

Statistical Modeling. We tested for the effects of weather on the number of eagles counted within a generalized linear modeling framework. We initially considered counts of eagles as a Poisson random variable. However, preliminary results showed a moderate degree of overdispersion with respect to the Poisson assumption, a common outcome for biological count data. Therefore, we treated counts as an overdispersed Poisson variable, generally regarded as appropriate for analysis of such data in the presence of overdispersion (McCullagh and Nelder 1989, Diggle et al. 1994). We used the PSCALE option of PROC GENMOD (SAS Inst. 1997) to provide the appropriate variance inflation for overdispersion under a quasi-likelihood testing framework.

To account for observation effort, the log of the number of hours of observation was treated as an offset (McCullagh and Nelder 1989, Agresti 1990), such that the number of eagles counted on a given day was modeled per hour of effort (i.e., eagles/hr of observation).

Our model selection was a combination of the approach suggested by Hosmer and Lemeshow (1989) and interactive approaches suggested by Henderson and Velleman (1981) and Aitkin and Francis (1982). We began by exploring individual main effects of each explanatory variable. We tested main effects using a likelihood-ratio test. At this preliminary stage of the analysis, we used a liberal rejection criteria ($\alpha = 0.30$) because some effects that are important as interactions can be obscured as main effects (Hosmer and Lemeshow 1989). Where terms were different measures of the same effect, and/or highly correlated (e.g., average and maximum temperature), we retained the more significant term in further models. However, we periodically substituted the alternative form to verify that we had chosen the best representation of the effect. We then used a combination of AIC and likelihood-ratio tests to determine the most parsimonious model based on combinations of effects, including interactions among variables, as indicated from preliminary univariate analyses. The general form of the final model was:

$$\log(E/hr) = \beta_0 + \beta_1 X_1 \ldots + \beta_k X_k$$

where, E/hr is the number of eagles per hour of observation, β_0 is the intercept, and $\beta_1 X_1 \ldots + \beta_k X_k$ are the main effects plus any interaction effects.

RESULTS

We counted 7131 migrating Golden Eagles in 506 hr of observation during three autumns and two springs (Table 2). The seasonal distribution of our sampling effort varied (Table 3). We also recorded 427 Bald Eagles, 1065 eagles unidentified

Table 2. Golden Eagle migration counts for the Mount Brown corridor in Glacier National Park, Montana, 1994–96.

YEAR	SEASON	TOTAL NO. EAGLES	TOTAL hr OBSERVATION	OVERALL EAGLES/hr
1994	Autumn	1941	81.1	23.9
1995	Autumn	1730	117.9	14.7
1996	Autumn	2249	158.9	14.2
1995	Spring	507	66.4	7.6
1996	Spring	704	81.9	8.6

to species, 422 accipiters, 201 buteos, and 23 falcons. Compared with spring, Golden Eagle migrations in autumn had higher numbers, longer durations, and more pronounced seasonal distributions (Fig. 2). The number of eagles in autumn counts averaged about three times more than in spring counts (1973 and 605 eagles, respectively). Average passage rates (eagles/hr) were 16.5 in autumn and 8.2 in spring. Maximum passage rates occurred in early October (high of 137 eagles/hr on 6 October 1994) and the second to third weeks of March (high of 67 eagles/hr on 17 March 1995). The proportion of immature eagles illustrated no apparent trend during autumn, but increased as migration progressed in the spring (Fig. 3).

Our models for both spring and autumn suggested seasonal variation in the number of eagles counted, but neither model supported the inclusion of a year effect. The most parsimonious model for autumn indicated eagle numbers were influenced (increased) most by rising barometric pressure (at Kalispell, Montana), rising air temperature, decreasing relative humidity, and several interactions among these variables (Table 4). The final spring model (Table 5) supported inclusion of wind speed (increasing), barometric pressure (rising), and interaction between these two factors.

DISCUSSION

Migration Patterns. Although we recorded 12 species of raptors, the GNP migration corridor was primarily a Golden Eagle route. Eagles constituted 92% of all raptors counted and 76% were confirmed as Golden Eagles. Other raptor species may use this general route in greater numbers earlier or later during the season, and over a wider passageway. For example, peak autumn migrations of Bald Eagles through GNP usually occur in November (McClelland et al. 1982, 1994). Compared to Golden Eagles, Bald Eagles are more apt to follow water courses such as the North Fork of the Flathead River, about 20 km west of the route we describe in this paper (pers. observ.). However, a full evaluation of other species was beyond the scope of our study.

Although Golden Eagles may use the same general path for spring and autumn migration (Brodeur et al. 1996), habitat selection for foraging can influence routes and rates of raptor migration (Niles et al. 1996). The strong disparity between our peak eagle counts in spring and autumn may result in part from different route selections. In northwestern Montana, many eagles use a spring route along the East Front of the Rocky Mountains rather than the heavily used autumn route at Mount Brown. Along the East Front, ground squirrels (*Spermophilus richardsonii*) provide an abundant food source (McClelland et al. 1994) during March and April. In autumn, however, the squirrels are hibernating and advantages of the eastern route diminish. The increasing proportion of immature eagles we recorded as spring migration progressed was consistent with the pattern reported for migrating Bald Eagles in the GNP area by McClelland et al. (1994). Adult raptors are under pressure to establish a nesting territory early, whereas immatures may benefit from a later arrival on the summering grounds (Newton 1979:191).

Influences of Weather on Migration. Among migrating bird species, there are substantial differences in response to weather (Richardson 1990). Titus and Mosher (1982), in the central Appalachians of Maryland, and Hall et al. (1992), in coastal northern California, found that different raptor species were influenced by different weather factors. The factors involved depend on which of the two main flight styles are used in migration: soaring/gliding and flapping/gliding (Spaar 1997). Ea-

Table 3. Observation time (days and hours) from which eagle count data were used, autumns 1994–96 and springs 1995 and 1996 in Glacier National Park, Montana.

OBSERVATIONS	AUTUMN				SPRING		
	1994	1995	1996	TOTALS	1995	1996	TOTALS
Count period[a]	28 Sep–3 Nov	22 Sep–4 Nov	24 Sep–9 Nov		28 Feb–5 Apr	8 Mar–10 Apr	
No. of d[b]	22	39	37	98	20	22	42
Total hr	59	92	125	276	45	61	106
Daily range (hr)	1–6	1–6	1–7	1–7	1–5	1–5	1–5
Mean hr/d (±SD)	2.7 (1.70)	2.4 (1.98)	3.4 (1.71)	2.8 (1.80)	2.2 (1.37)	2.8 (1.48)	2.5 (1.44)

[a] First and last day of count data.

[b] Numbers of days of count data within count periods are lower than totals within the count periods because of days on which view of the migration path was completely obscured or there were no eagles flying.

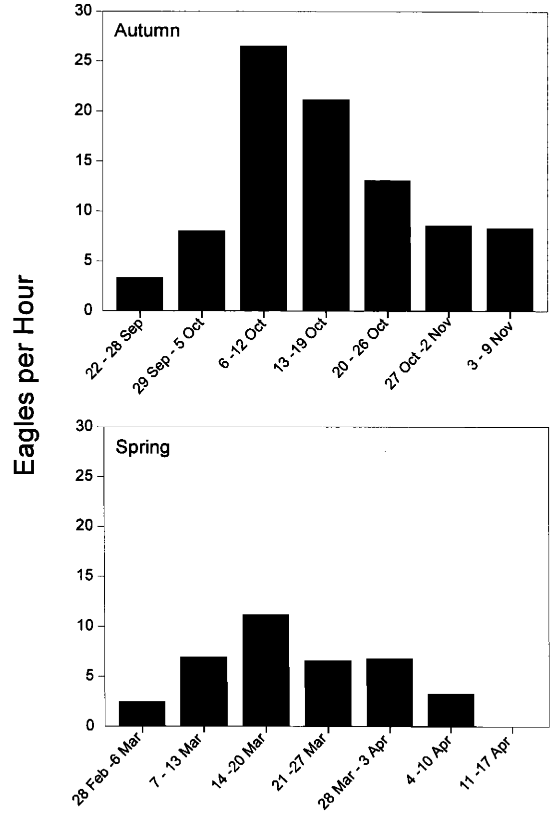

Figure 2. Average passage rates (Golden Eagles/hr), by date, in autumn (1994–96) and spring (1995 and 1996) migrations at Glacier National Park, Montana U.S.A.

gles primarily depend on the former style, which is facilitated by lifting winds. During the day, air near south- or west-facing mountain slopes warms more rapidly than air away from the slopes, producing a "mountain wind" [sometimes used interchangeably with "thermal"] that streams toward and up the mountain slopes (Petterssen 1958:165). Such winds are strongest when the air is clear, hot, and dry, and where exposed slopes are inclined toward the sun (Smith et al. 1990). Mountain winds produce the lift needed by eagles to gain sufficient altitude to glide between peaks. In autumn, we often saw eagles soar on mountain winds over Stanton Mountain, then glide to join eagles kettling above Mount Brown's slopes.

Agostini's (1992:95) description of migrating Honey Buzzards' (*Pernis apivorus*) attraction to thermals at the Straits of Messina, Italy, aptly depicted the same pattern we observed for Golden

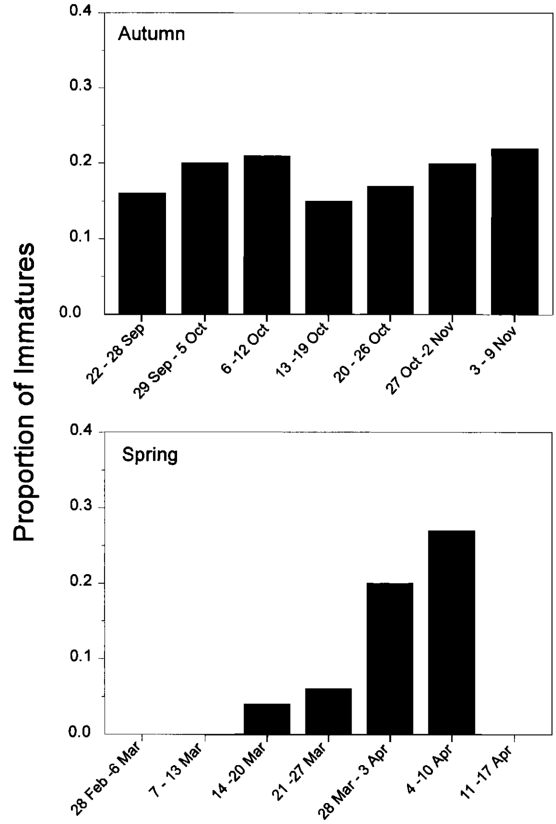

Figure 3. Average proportions of immature Golden Eagles by date, in autumn (1994–96) and spring (1995 and 1996) migrations at Glacier National Park, Montana U.S.A.

Eagles: "lone individuals and flocks were seen joining other birds of the same species in thermals. This was done from remarkable distances . . . [and] seems to confirm that flock location can provide a clue for the location of the thermal currents (Kerlinger 1989). On some occasions, groups split and used different thermals." In GNP, besides mountain winds and localized thermals, eagles used orographic deflection to achieve altitudes that allowed gliding with minimum flapping. When weather conditions required continuous flapping flight, eagles usually descended to cliff or tree perches.

In addition to daily and seasonal effects, our selected model for autumn included the main effects of average air temperature, barometric pressure, relative humidity, and interaction among these. Air temperature and barometric pressure were both positively associated with the number of eagles, whereas relative humidity was negatively associated. The interactions with relative humidity were likely influenced by several eagle responses. When the air is cool and moist (high relative humidity), thermals do not develop strongly and opportunities for eagle flight are more limited. On some occasions, high humidity was associated with precipitation. In cases when precipitation obscured our visibility, the effect was not simply a visibility bias. We observed birds taking shelter at the onset of heavy rain or snow, regardless of other favorable conditions (e.g., wind). Although the interactions with relative humidity were readily apparent, the nature of the interactions between air temperature and barometric pressure were less clear, even when explored using various multi-way graphical plots. This was probably because the effects of selected weather variables were confounded by other subtle variables and seasonal effects. In GNP, wind speed and

Table 4. Analysis of variance table of likelihood-ratio tests for weather factor and interaction effects on number of eagles counted during autumns 1994–96.

Weather Factor or Interaction	χ^2	df	P
Julian day	25.34	1	<0.001
Julian day^{2}[a]	25.15	1	<0.001
Mean air temperature	9.97	1	0.002
Relative humidity	8.28	1	0.004
Barometric pressure (Kalispell, Montana)	7.02	1	0.008
Mean air temperature × Barometric pressure	9.72	1	0.002
Relative humidity × Barometric pressure	8.19	1	0.004
Mean air temperature × Relative humidity	7.66	1	0.006

[a] Julian day^{2} constitutes a quadratic seasonal effect.

Table 5. Analysis of variance table of likelihood-ratio tests for weather factor and interaction effects on number of eagles counted during springs 1995 and 1996.

WEATHER FACTOR OR INTERACTION	χ^2	df	P
Julian day	4.3	1	0.038
Vector mean wind speed	4.66	1	0.031
Barometric pressure (Kalispell, Montana)	6.47	1	0.011
Vector mean wind speed × Barometric pressure	4.71	1	0.03

direction may have been more important in spring migration than in autumn, as indicated by our models, due to generally greater atmospheric turbulence in spring (Gerrard and Bortolotti 1988). Additionally, mountain winds may be more important than indicated by our models; such winds have a strong vertical component that may not be suitably recorded by standard anemometers designed to measure horizontal winds.

Based on our data, we hypothesize that the more complex interactions among weather variables in GNP (compared with many other studies) derive from the relatively high topographic complexity in this area. Several variables may influence migration at any given time. Consistent with our hypothesis, Spaar and Bruderer (1996) found that Steppe Eagles (*Aquila nipalensis*) adjusted their flight tactics to existing wind and thermal conditions. Regions with less complex landscapes and fewer interactions between terrain and weather may provide fewer opportunities for favorable winds and lift to develop. In those areas, migrating eagles must rely on fewer atmospheric variables for favorable flight conditions.

In contrast to our results, some studies have associated high counts of migrating raptors with a single weather factor. In the Great Basin, Millsap and Zook (1983) found that high counts of migrating Sharp-shinned Hawks (*Accipiter striatus*) coincided with the passage of frontal systems. Mueller and Berger (1967a) found that numbers of migrating Sharp-shinned Hawks on the western shore of Lake Michigan were strongly influenced by westerly winds. In the Bridger Range of southwestern Montana, Omland and Hoffman (1996) suggested that peak numbers of migrating Golden Eagles were correlated with barometric pressure.

It is tempting to assume that further data exploration would yield insights into the complex interactions we found. However, we believe that the nature of this complexity represents a biological reality. At GNP, where the topography and weather are both complex and strongly interactive, eagles use the combination of factors which produce favorable conditions for migration at any given time. On days of high temperature they may use thermals. On windy days they may use orographic deflection, even if prevailing winds are not in a favorable direction. On days preceding autumn cold fronts, they make use of prevailing northerly winds. All of these effects are superimposed on a seasonal pattern that partially reflects conditions to the north (autumn) or south (spring) of GNP.

Analysis of weather influences on eagle passage rates at a specific location is complicated by the long distances and time periods involved in Golden Eagle migration (Britten et al. 1995). Nine juvenile Golden Eagles equipped with satellite transmitters in Denali National Park, Alaska (63°00'N, 152°00'W), since 1990, have passed through our study area during autumn migrations (C.L. McIntyre pers. comm.). It took these eagles 3–4 weeks to reach GNP (2700 km) before continuing to wintering areas as far south as New Mexico. During migration, eagles may be delayed by inclement weather far "upstream" from GNP. Consequently, on some days when weather conditions at GNP were otherwise conducive to high passage rates, there may have been few eagles in the vicinity due to unfavorable weather previously encountered. Thus, understanding geographically localized events in Golden Eagle migration requires a continental perspective.

In summary, the high western flanks along GNP's Livingston Range form an advantageous route for migrating eagles, a "leading line" (Mueller and Berger 1967b, Allen et al. 1996). In this complex topography, mountain winds, thermals, orographic deflection, prevailing winds, and resulting combinations and interactions create a variety of favorable conditions for eagle migration.

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