The Condor 98:633–636

SEASONAL, DIEL, AND SPATIAL DISPERSION PATTERNS OF GOLDEN EAGLE AUTUMN MIGRATION IN SOUTHWESTERN MONTANA[1]

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Key words: Golden Eagle; Aquila chrysaetos; *differential migration; dispersion.*

In this report we describe three behavioral phenomena of Golden Eagle (*Aquila chrysaetos*) fall migration: age-specific seasonal differential migration, age-specific diel patterns of migration, and the spatial dispersion pattern of migrating Golden Eagles. Immature individuals of many North American raptor species migrate earlier in the season than adults (see Appendix 2 in Kerlinger 1989). As resource levels decline in the fall, less efficient foragers (Hoffman 1985) or subordinate birds (Gauthreaux 1978) are likely to be the first to seek resources elsewhere. Hoffman and Potts (1985) reported that immature Golden Eagles migrate earlier in the season than adults although Kerlinger (1989) reported the reverse. We examined our data to address whether there was seasonal differential migration between age classes of Golden Eagles migrating along the Bridger Range. Because different travel requirements or behavioral differences between age classes may result in age-specific migration patterns within periods of the day, we also investigated whether immature and adult eagles had different diel patterns of migration.

A migrating raptor searching for lift may locate an updraft by flying towards other soaring birds. Such visual interaction among migrants would result in aggregation. This is similar to Kerlinger's (1985) aggregation model for flock formation. While his model applies to species that typically migrate in flocks, other species that do not form discrete flocks may still exhibit nonrandom dispersion due to visual interaction. Alternatively, Golden Eagles may avoid other eagles during migration. Pairs of Golden Eagles space out the nests that they use in a given year more regularly than random (Watson and Rothery 1986) and their territorial behavior may carry over to the migration season. In that case we would observe even dispersion. For aggregation or repulsion due to visual interaction to occur, concentrations of migrants would have to be sufficiently dense that individuals could see each other. Furthermore, aggregations of aerodynamically dissimilar birds would be ephemeral because of different climb and glide characteristics so it is appropriate to focus on concentrations of aerodynamically similar birds, e.g., birds of the same species, when testing for nonrandom dispersion. Golden Eagles passed our lookouts in sufficient densities that if they respond to the presence of other soaring Golden Eagles we should have observed nonrandom dispersion.

METHODS

We observed the fall hawk migration from ridgetop lookouts along the Bridger Range near Bozeman, Montana (110°55′ W, 45°48′ N). Observers (generally single, occasionally in pairs or threes) identified migrating raptors using binoculars and recorded their time of passage (MST). We assumed that an eagle was migrating unless it flew in a direction inappropriate for migration, perched for a prolonged period, or displayed sustained foraging behavior. Birds exhibiting such behaviors were excluded from our analyses; out of 1,305 sightings we excluded only 35. We distinguished two age classes of Golden Eagles based on plumage characteristics. Birds with white at the base of their primaries were classified as immatures and birds without white at the base of their wings were classified as adults or older subadults. Data for the dispersion analysis were times (recorded to the nearest 5 sec) that eagles crossed an imaginary east-west line. Birds flying more than approximately 200m on either side of the lookout were excluded from the dispersion analysis. We conducted observations between 09:00 hr and 17:00 hr (earlier or later on exceptional days) from 15 September to 3 November 1991 whenever weather was suitable for ridgetop flight. Observations included in the dispersion analysis were made on the five days (8, 9, 10, 16, and 21 October) in the later part of the season when large numbers of Golden Eagles were passing.

For our dispersion analysis we used time of passage as a proxy variable for position along the linear path of migration. We analyzed the dispersion pattern by comparing the range standardized variance of the intervals between passing eagles to critical values of that statistic tabulated by Williams (1995). For each period the times of passage were normalized so that the first eagle passed at $t = 0$ and the last at $t = 1$. The variance of the intervals between those normalized times is the range standardized variance. Because we wished to test both alternative hypotheses, that visual interaction among migrating eagles results in aggregated or repulsed dispersion, we used the critical values for α of 0.975 (aggregated dispersion) and 0.025 (repulsed dispersion). Nonrandom dispersion due to visual interactions among migrating eagles would be revealed on a scale over which eagles can see each other. We were

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[1] Received 14 December 1995. Accepted 22 March 1996.

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able to detect an oncoming eagle without the aid of binoculars on average 88 sec (SD = 17 sec, n = 26) before it passed our lookout. Assuming that an eagle's vision is 2.5 to 3 times more acute than ours (Gill 1990), we calculated that eagles separated by as much as 260 sec may be visible to each other. Therefore we analyzed the dispersion pattern for each period when three or more Golden Eagles passed with no interval greater than 260 sec between them. Nonrandom dispersion due to visual interaction would certainly be apparent among individuals migrating at that density; nonrandom dispersion among birds migrating at lower density might be due to factors other than visual interaction (e.g., weather changes).

RESULTS

Sightings of migrating immature Golden Eagles reached a peak earlier in the season than sightings of adults. The modal date of sightings of immatures was 2 October whereas that of adults was 7 October (Fig. 1; distributions significantly different, $\chi^2 = 137.4$, df = 6, $P < 0.001$). Early in the season most Golden Eagles sighted were immatures but the proportion of immatures decreased steadily over the course of the season ($r^2 = 0.59$, df = 29, $P < 0.001$). For example, 22 of 24 (92%) Golden Eagles counted on 25 September were immatures, on 5 October 22 of 42 (52%) were immatures, and on 19 October 3 of 28 (11%) were immatures. Conversely, the proportion of eagles that were adults increased over the course of the season. On 6 October and all subsequent days of observation the majority of Golden Eagles sighted were adults.

Immature Golden Eagles were more frequently sighted than adults between 08:00 hr and 12:00 hr and after 17:00 hr while adults were more abundant than immatures during the afternoon. Thus the diel distribution of immatures was more even than that of adults (Fig. 2; $\chi^2 = 22.9$, df = 7, $P < 0.01$). Between 11:00 hr and 17:00 hr the frequency of sightings of immature Golden Eagles remained within the range 2.5 to 3.5 eagles/hr whereas the frequency for adults ranged from fewer than 2.5 to more than 4.5 eagles/hr. Twenty-five percent of all immatures counted passed our lookout before noon while only 17% of the adults were seen before noon. In contrast, 72% of the adults passed our lookout between 12:00 hr and 16:00 hr while only 61% of the immatures passed during that period.

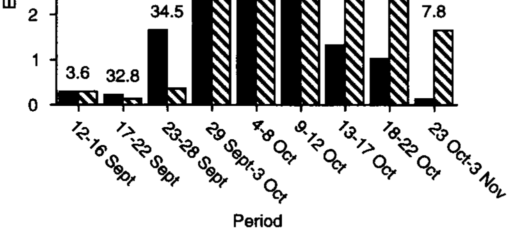

FIGURE 1. Seasonal distribution of sightings of immature and adult Golden Eagles migrating along the Bridger Range, fall 1991. Periods were delineated by peaks on a trace of barometric pressure (recorded at Montana State University, Bozeman) which accurately represented periods of eagle migratory activity. Numbers over bars represent the number of observer hours during each period.

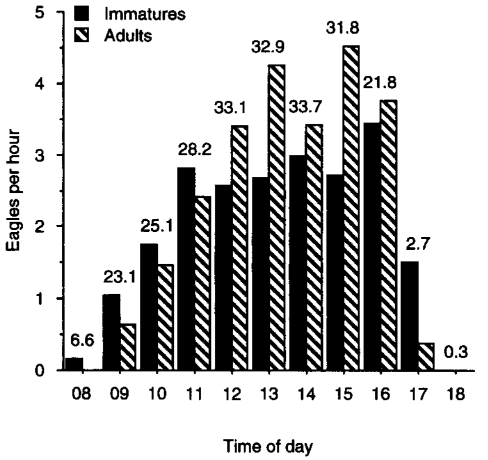

FIGURE 2. Diel distribution of sightings of immature and adult Golden Eagles migrating along the Bridger Range, fall 1991. Numbers over bars represent the number of observer hours at each time of day across the season.

For the days that we recorded precise times of passage there were 17 periods during which three or more Golden Eagles passed with no interval greater than 260 sec between them. The duration of those periods ranged from 50 sec to 22 min 10 sec. During 15 of those periods the dispersion pattern was not different from random. One period had an aggregated pattern and one had a repulsed pattern (Table 1).

DISCUSSION

Our results show that immature Golden Eagles migrated somewhat earlier in the season than adults in southwestern Montana in the fall of 1991. Although both immatures and adults passed our lookouts throughout most of the season, the proportions shifted steadily from predominantly immatures in September to predominantly adults by mid-October. Advanced migration of immatures is consistent with Hoffman and Potts' (1985) representation of the fall Golden Eagle migration along the Wellsville Mountains in Utah and Hawk Mountain in Pennsylvania. Kerlinger (1989, Appendix 2) tentatively listed Golden Eagles among species in which adults migrate earlier than immatures in the fall. The results of this study as well as Hoffman and Potts' (1985) analysis provide grounds to change that listing. Advanced migration of immatures con-

TABLE 1. Dispersion of eagles migrating along the Bridger Range during 17 periods when at least three eagles passed without an interval greater than 260 sec between them. n = number of eagles that passed during that period; V = range-standardized variance of intervals between passing eagles (see text); the pattern of dispersion was evaluated according to Williams (1995).

Date	Time	n	V	Dispersion
8 October	9:20:40–9:36:45	10	0.0057	$0.10 > P > 0.90$ (random)
	9:43:50–9:49:50	4	0.1078	$0.10 > P > 0.90$ (random)
10 October	13:24:30–13:29:00	3	0.0830	$0.10 > P > 0.90$ (random)
	13:34:55–13:39:30	3	0.1205	$0.10 > P > 0.90$ (random)
	14:47:35–14:57:30	9	0.0185	$0.10 > P > 0.90$ (random)
	15:06:55–15:15:50	5	0.0175	$0.10 > P > 0.90$ (random)
	15:24:20–15:40:55	14	0.0048	$0.10 > P > 0.90$ (random)
	15:46:10–16:08:20	13	0.0038	$0.10 > P > 0.90$ (random)
	16:20:25–16:27:55	7	0.0182	$0.10 > P > 0.90$ (random)
	16:51:45–16:59:40	3	0.0001	$0.01 > P > 0.025$ (repulsed)
16 October	12:20:50–12:25:25	3	0.2025	$0.10 > P > 0.90$ (random)
	12:37:20–12:44:05	6	0.0580	$0.025 > P > 0.05$ (random)
21 October	12:30:40–12:40:05	11	0.0247	$P \approx 0.975$* (aggregated)
	13:10:35–13:16:35	3	0.1144	$0.10 > P > 0.90$ (random)
	13:27:20–13:29:45	3	0.0149	$0.10 > P > 0.90$ (random)
	15:08:50–15:10:30	3	0.3200	$0.10 > P > 0.90$ (random)
	15:17:35–15:18:25	3	0.3200	$0.10 > P > 0.90$ (random)

* Determined by extrapolation from Williams' (1995) table.

forms with Gauthreaux's (1978) prediction that during postbreeding movement subordinates will precede dominants since immature Golden Eagles are probably subordinate to adults. An alternative hypothesis is that a diminishing prey supply impinges on less-experienced foragers sooner, forcing them to abandon their summer range before more experienced foragers (Hoffman 1985).

Less-experienced foragers or subordinate birds generally migrate farther than more-experienced foragers or dominant birds (Gauthreaux 1985). To accomplish migration over greater distances these individuals must spend more time migrating. If they do that by migrating for a longer part of each day, sightings of immature migrants would be more evenly distributed throughout the day than sightings of adults. We observed that pattern among the Golden Eagles migrating along the Bridger Range in the fall of 1991. The observed pattern may also be accounted for in part by immature Golden Eagles being less selective about the time of day during which they migrate.

The random dispersion pattern suggests that migrating Golden Eagles do not respond to each other visually. They do not aggregate as would be expected if they were using the presence of other soaring birds to indicate the locations of updrafts. The negative result may be peculiar to the observation site: Golden Eagles migrating along a ridge may find such a regular updraft that they do not need to search for lift and therefore ignore other migrants. Eagles migrating over nonmountainous terrain where physical cues to the presence of updrafts are obscure may be more dependent on using other migrants to find thermals. On the other hand, Golden Eagles migrating over open terrain are not concentrated in a narrow flyway. Therefore they probably cannot often see other migrants and do not have access to the information other migrants might provide. Golden Eagles may not use other soaring birds as cues to the presence of updrafts simply because they do not typically migrate in such density that they can see other migrants.

In summary, we conclude that immature Golden Eagles migrated earlier in the season than adults. Immatures also spent more time each day migrating and/or were less selective about the time of day during which they migrated than adult Golden Eagles. Finally, we found no evidence of visual interaction among migrating Golden Eagles.

This work was funded by a Challenge Cost-Share Agreement between HawkWatch International, Inc. and Gallatin National Forest, USDA Forest Service as part of a long-term effort by HawkWatch International to better understand raptor movements and population trends in the northern Rocky Mountain region. Other observers were Phil West, Lisa Daly, and Craig Limpach. Neil Buckley, Kevin Omland, Bernd Heinrich, Valerie Banschbach, Paul Kerlinger, and S. A. Gauthreaux, Jr. provided helpful comments on the manuscript. Nick Gotelli suggested the statistical test used in the dispersion analysis.

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The Condor 98:636–639
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STATUS SIGNALING IN DARK-EYED JUNCOS: PERCEIVED STATUS OF OTHER BIRDS AFFECTS DOMINANCE INTERACTIONS[1]

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Key words: Dark-eyed Junco; Junco hyemalis; *status signal; plumage variation; dominance; individual recognition.*

In a number of avian species, individual members of the species vary considerably in appearance. Differences in plumage coloration may be correlated with social status (Rohwer 1975, Whitfield 1987, Butcher and Rohwer 1989). The status-signaling hypothesis states that variation in plumage has evolved to signal differences in individuals' abilities to win agonistic contests (Rohwer 1975, 1977, Butcher and Rohwer 1989). The fundamental assumption is that coloration is a reliable predictor of rank, so that an individual's color at least partially determines its acquired rank during hierarchy establishment (Rohwer 1985). According to this hypothesis, superior fighters benefit from distinctive color markings ("badges of status") because they reduce either the number or intensity of contests in which they are involved in order to maintain dominant status or priority access to resources (Rohwer 1985).

In addition, plumage variability may facilitate individual recognition (Shields 1977, Whitfield 1986, 1987, Rohwer and Røskaft 1989). Individuals that are superior fighters may benefit from clearly signaling their identity since it will lead to a reduced number of contests repeated with the same individuals (Whitfield 1986, 1987, Rohwer and Røskaft 1989).

Potential badges have been identified in a wide variety of avian species (Rohwer 1975, Whitfield 1987). However, experiments involving the manipulation of plumage have sometimes had mixed results: in some cases the manipulations resulted in changes in rank and in others they did not. For example, in White-crowned Sparrows (*Zonotrichia leucophrys*), the contrast in the crown stripes has been shown experimentally to signal status between age and sex classes, but in the closely related White-throated Sparrow (*Z. albicollis*), there appears to be no relationship between crown pattern and status (Fugle et al. 1984, Watt 1986). Although plumage characteristics were correlated with dominance status in both Harris' Sparrows (*Z. querula*) and Dark-eyed Juncos (*Junco hyemalis),* when subordinates of these species were dyed to mimic dominants, many of these cheaters did not rise in social status because their badge was constantly being checked (detected and persecuted) by already established dominants (Rohwer 1977, Holberton et al. 1989).

Plumage alone may not be sufficient to determine dominance; appropriate behaviors may also be needed (Shields 1977, Rohwer and Rohwer 1978, Cristol 1995a). In most research to date, the plumage of focal birds was manipulated, but the bird being manipulated was still viewing its peers in the same manner, and thus might not be expected to alter its behavior. When subordinate Harris' Sparrows were both dyed and injected with testosterone, the birds became successful

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