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DIFFERENTIAL MIGRATION IN FIVE SPECIES OF RAPTORS IN CENTRAL COASTAL CALIFORNIA

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ABSTRACT.—Using data from 17 144 hawks trapped during migration through the Marin Headlands in central coastal California, we evaluated the extent of differential migration within five species of raptors and compared our findings to those obtained at other raptor-migration sites in North America. This is the first description of patterns of differential migration for raptors migrating along the Pacific corridor, and the first investigation of differential migration in Red-shouldered Hawks (*Buteo lineatus*). We found that females migrated significantly earlier than males in Cooper's Hawks (*Accipiter cooperii*), Sharp-shinned Hawks (*Accipiter striatus*), hatch-year (HY) American Kestrels (*Falco sparverius*), HY Merlins (*Falco columbarius*), and HY Red-shouldered Hawks. In American Kestrels we found no difference in migration timing between AHY females and males or between adults and juveniles overall. Juveniles preceded adults in Sharp-shinned Hawks and Cooper's Hawks. We did not have sufficient samples of adult Red-shouldered Hawks, or Merlins, to compare migration timing among age classes. For Cooper's Hawks, Sharp-shinned Hawks, American Kestrels, Merlins, and Red-shouldered Hawks, our data agreed with the patterns of migration seen elsewhere in North America. Our description of the migration patterns in Red-shouldered Hawks provides a baseline for future comparisons with data from other migration sites.

KEY WORDS: age; differential migration; falcon; hawk; raptor; sex; timing.

MIGRACIÓN DIFERENCIAL EN CINCO ESPECIES DE RAPACES EN LA COSTA CENTRAL DE CALIFORNIA

RESUMEN.—Empleando datos de 17 144 halcones capturados durante la migración a lo largo de Marin Headlands en la costa central de California, evaluamos el alcance de la migración diferencial en cinco especies de rapaces y comparamos nuestros resultados con aquellos obtenidos en otros sitios migratorios de América del Norte. Esta es la primera descripción de patrones de migración diferencial para rapaces que migran a lo largo del corredor Pacífico y la primera investigación de migración diferencial en *Buteo lineatus*. Encontramos que las hembras migraron significativamente más temprano que los machos en *Accipiter cooperii*, y en *A. striatus*, y que los individuos del primer año de eclosión (PAE) de *Falco sparverius*, individuos del PAE de *Falco columbarius* e individuos del PAE de *B. lineatus*. En *F. sparverius* no encontramos diferencias en el momento de migración entre hembras y machos del PAE o entre adultos y juveniles. Los juveniles precedieron a los adultos en *A. striatus* y en *A. cooperii*. No tuvimos suficientes muestras de adultos de *B. lineatus* o de *F. columbarius* para comparar el momento de migración entre las clases de edad. Para *A. cooperii*, *A. striatus*, *F. sparverius*, *F. columbarius* y *B. lineatus*, nuestros datos concuerdan con los patrones de migración vistos en otros sitios en América del Norte. Nuestra descripción de los patrones de migración en *B. lineatus* brindan información de base para futuras comparaciones con datos de otros sitios migratorios.
[Traducción del equipo editorial]

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Among North American raptors differential migration, the differences in migration timing between age or sex classes (Ketterson and Nolan 1983, Berthold 2001), has been investigated mainly in species at eastern and midwestern migration watchsites (e.g., Duncan 1981, Duncan 1982, Bildstein et al. 1984, Mueller et al. 2000), with the few studies describing differential migration patterns in western North America limited in number of species examined (e.g., DeLong and Hoffman 1999, Worcester and Ydenberg 2008). The evolutionary and ecological factors responsible for differential migration have been examined, and a number of studies have provided alternative hypothetical explanations for the emergence of differential migration within species (see Kerlinger 1989). In a comprehensive examination of differential autumn migration among North American raptors east of the Rocky Mountains, adults generally migrated later than juveniles, and males migrated later than females (Mueller et al. 2000). These patterns were attributed to adults remaining on breeding grounds longer than juveniles, presumably to gain an advantage in either survival or subsequent breeding opportunities, and to males remaining on breeding grounds longer than females, presumably to defend feeding areas (Mueller et al. 2000), as males are primarily responsible for territory defense.

Populations of raptors in California and the Pacific coast may display different patterns of differential migration than observed in eastern and midwestern North America. Many North American raptor species have genetically discrete eastern and western populations or subspecies, including Red-tailed (*Buteo jamaicensis*), Red-shouldered (*B. lineatus*), and Sharp-shinned hawks (*Accipiter striatus*; Pearlstine 2004, Hull and Girman 2005, Hull et al. 2008a, Hull et al. 2008b), and in some cases clear differences in morphology are apparent, including size (see Smith 1988, Pearlstine and Thompson 2004, Dykstra et al. 2008, Hull et al. 2008) and plumage (Clark and Wheeler 2001, Wheeler 2003) polymorphism.

The geography and climate of California also may influence patterns of migration timing. The mild winter climate in coastal and central California may cause changes in the behaviors and timing of migrant raptors. In addition to having mild winters, the Marin Headlands study site is at a lower latitude than many of the study sites in midwestern and eastern North America where differential migration among raptors has previously been examined (e.g., Rosenfield and Evans 1980, Duncan 1981, Duncan 1982, Mueller 2000) and consequently, the timing of autumn migration may differ in California. For example, if differences in migration speed among groups are partially responsible for differential migration (see Mueller et al. 2000), then the degree of differential migration may become more pronounced at southern sites. These considerations, combined with observed genetic and anatomical geographical differences, suggest that comparison of differential migration of populations of western raptors with midwestern and eastern raptors is warranted.

Rather than relying on hawk-count data, where identification errors in sex identification may confound data interpretation (Hull et al. 2010), we used data gathered during raptor capture and banding operations at the Golden Gate Raptor Observatory to determine the patterns of differential migration at a coastal California migration bottleneck. These data provide a good opportunity for examination of differential migration, because after raptors have been captured and are in hand, their ages and sexes can be easily determined (see Mueller et al. 2000). A thorough analysis of band encounters has yet to be completed for the raptor species banded at the Golden Gate Raptor Observatory; however, some general patterns are apparent from the band encounters reported to date. Encounters extended from southern Baja California to northern British Columbia and from the Farallon Islands, 43 km west of the California coastline, east to Jerome, Idaho. Encounters were frequent in the hills and valleys of the Coast Range with smaller numbers in California's Sacramento Valley and few encounters within the Sierra Nevada (Weeks 2001, 2009; Harn 2010). In total, these band encounters suggested that the raptors banded at the Golden Gate Raptor Observatory migrated primarily within the Pacific migration corridor; however, these preliminary data cannot be used to infer breeding origins of the various species. In this report, we identify patterns of differential migration among five species of hawks and falcons at a Pacific coast site and compare these findings with those described at other North American raptor migration stations.

METHODS

We trapped, and analyzed data from, 17 144 raptors of six species during the autumn migrations (mid-August through mid-December, corresponding with the timing of the migration season) of

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1983–2010 at the Golden Gate Raptor Observatory (37°49′49″N, 122°29′59″W) in the Marin Headlands north of San Francisco, California. A total of 10 906 Cooper's Hawks (*A. cooperii*; 1983–2005), 4700 Sharp-shinned Hawks (1986–2008), 861 American Kestrels (*Falco sparverius*; 1984–2008), 395 Merlins (*F. columbarius*; 1988–2008), and 282 Red-shouldered Hawks (1986–2010) were trapped. The Golden Gate Raptor Observatory captured a large number of Red-tailed Hawks each year; however, differential migration timing of genetically distinct populations through the Marin Headlands (Hull et al. 2009) confounded our ability to determine whether the sexes of these distinct populations differ in their migration timing.

We determined sex for all species using morphology and plumage (American Kestrel) keys developed in the Golden Gate Raptor Observatory Manual for coastal California migrant raptors (Golden Gate Raptor Observatory 2010). The key for Red-shouldered Hawks was previously validated using molecular sexing techniques (Pitzer et al. 2008); age was determined using plumage characteristics (see Clark and Wheeler 2001), and raptors were classified as hatch-year (HY) or after-hatch-year (AHY). Raptor trapping was authorized through U.S. Geological Survey (Federal Bird Banding Permit # 21827), State of California (Department of Fish and Game Scientific Collecting Permit # SC-001259, and U.S. National Park Service (GOGA-2001-SCI-0009) permits. Each hawk was captured using standard techniques in a mist-net, dho gaza, or bow net (Bloom 1987), and banded with a federal aluminum leg band. Due to potential sex-based trapping bias, the trapping data presented here should not be used to infer natural sex ratios. The capture dates for each species across seasons were compiled and converted to Julian dates in order to produce continuous distributions. The Julian date distributions for males and females of each species and age class were compared using Mann-Whitney *U*-tests in SYSTAT 11.0 (SYSTAT Software, Inc. 2004).

RESULTS

American Kestrel. HY females migrated before HY males ($U = 51\,689$; $P = 0.002$; Fig. 1; Tables 1, 2). No difference in migration timing was detected between AHY females and males ($U = 2910$; $P = 0.123$), or between either HY males or females and AHY males or females ($U = 12\,392$; $P = 0.274$ and $U = 18\,828$; $P = 0.348$).

Merlin. HY females migrated before HY males ($U = 15\,741$; $P = 0.002$; Fig. 1; Tables 1, 2). We lacked a sufficient sample size to examine the relationships between AHY females and males or between HY and AHY individuals.

Cooper's Hawk. HY females migrated before HY males and AHY females before AHY males ($U = 9\,708\,752$; $P < 0.001$ and $U = 12\,791$; $P < 0.001$; Fig. 2; Tables 1, 2). HY females migrated before AHY females ($U = 1\,749\,490$; $P < 0.001$), and HY males before AHY males ($U = 318\,475$; $P < 0.001$).

Sharp-shinned Hawk. HY females migrated before HY males and AHY females before AHY males ($U = 1\,536\,007$; $P < 0.001$ and $U = 7403$; $P < 0.001$; Fig. 2; Tables 1, 2). HY females migrated before AHY females ($U = 93\,945$; $P < 0.001$), and HY males before AHY males ($U = 144\,866$; $P < 0.001$).

Red-shouldered Hawk. HY females migrated before HY males ($U = 8208$; $P = 0.025$; Fig. 3; Tables 1, 2). We lacked a sufficient sample size to examine the relationships between AHY females and males or between HY and AHY individuals.

DISCUSSION

We found that HY females migrated significantly earlier than HY males in American Kestrels, Merlins, Cooper's Hawks, Sharp-shinned Hawks, and Red-shouldered Hawks. We also found that AHY females migrated significantly earlier than AHY males in Cooper's Hawks and Sharp-shinned Hawks; no difference was detected among AHY American Kestrels, and we lacked sufficient samples to test for a difference in AHY Merlins and Red-shouldered Hawks. In both Cooper's and Sharp-shinned Hawks, HY males and females migrated before their AHY counterparts. No difference in timing was found between HY and AHY American Kestrels.

Our results indicating that HY female American Kestrels migrated before HY males were consistent with those of Mueller et al. (2000) from Cedar Grove, Wisconsin, and Stotz and Goodrich (1989) from Kittatinny Ridge, Pennsylvania. However, although we found no difference in timing between AHY males and females, and no difference between HY and AHY, Mueller et al. (2000) found AHY females migrated before AHY males, and HY individuals migrated before AHY. The discrepancy may be explained by lack of sufficient statistical power due to few samples of AHY American Kestrels (94 AHY females and 72 AHY males) at our site. That said, Mueller et al. (2000) had a smaller sample and detected a significant difference in migration timing. Another possible explanation for the differing pattern between regions is the difference in winter

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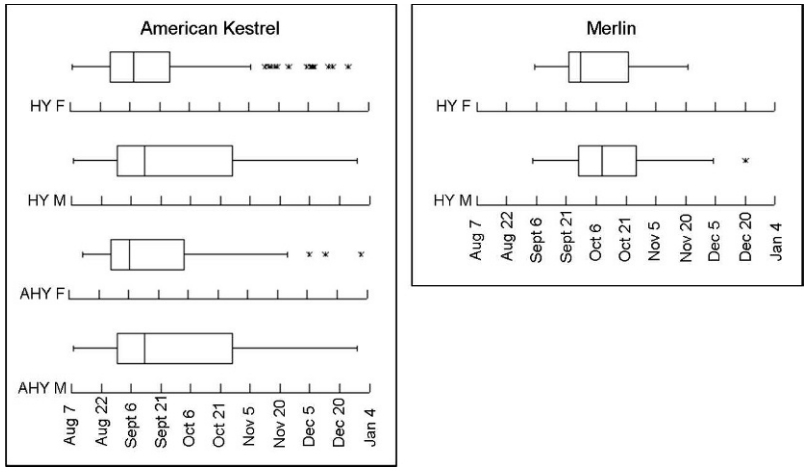


Figure 1. Temporal distribution of American Kestrels and Merlins trapped during autumn migration through the Marin Headlands, California. The vertical line indicates the median migration date. The box encompasses 50% of observations from the first to third quartiles; whiskers extend to include minimum and maximum values while asterisks indicate statistical outliers.

climate at the two sites. American Kestrels in midwestern North America experience a much harsher continental winter climate there and are generally not able to overwinter there, in contrast to populations in central California, which are able to remain on territories throughout the winter. The abundant resident population of American Kestrels in central California (e.g., Shuford 1993) may dilute the migrant pool to such an extent as to obfuscate patterns of differential migration between ages.

Among Merlins, our finding of HY females migrating before HY males was consistent with results from Cedar Grove (Mueller et al. 2000), as well as from Cape May, New Jersey (Clark 1985). Although the pattern of differential migration was similar among these locations, the magnitude of difference appeared to be greater in the Marin Headlands (females preceding males by 11 d) than at either Cedar Grove (2 d) or Cape May (4 d). The underlying reason for this difference was unclear. A potential cause for this pattern is that the Marin Headlands is farther from the core Merlin breeding range than either Cedar Grove or Cape May. If there is a significant difference in the flight speed of male and female Merlins during migration, a greater degree of differential migration would be expected at sites further removed from the origin of migration. Alternatively, the initiation of migration of males and females in populations of midwestern and eastern Merlins may be simultaneous, whereas males and females of western populations may initiate migration at different times. Currently, we lack information about both the flight speeds of migrating Merlins and the timing of departure from breeding grounds across North America; therefore, we cannot distinguish between these two alternatives.

Overall our migration-timing results for Cooper's Hawks and Sharp-shinned Hawks agreed with those

Table 1. Sample size (n) and median migration date through the Marin Headlands, California, for hawk and falcon age/sex categories.

SPECIES	AGE/SEX	n	MEDIAN DATE
American Kestrel	HY F	377	7 September
	HY M	318	13 September
	AHY F	94	6 September
	AHY M	72	12 September
Merlin	HY F	177	27 September
	HY M	218	8 October
Cooper's Hawk	HY F	6957	24 September
	HY M	3511	30 September
	AHY F	328	16 October
	AHY M	110	27 October
Sharp-shinned Hawk	HY F	2792	23 September
	HY M	1608	28 September
	AHY F	212	20 October
	AHY M	88	25 October
Red-shouldered Hawk	HY F	162	3 October
	HY M	120	8 October

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Table 2. Sample sizes and results of Mann-Whitney *U*-tests for differences in migration timing through the Marin Headlands, California, among hawk and falcon age/sex categories.

SPECIES	COMPARISON	*n*	*U*	*P*
American Kestrel	HY females vs. males	377; 318	51 689	0.002
	AHY females vs. males	94; 72	2910	0.123
	HY vs. AHY females	377; 94	18 828	0.348
	HY vs. AHY males	318; 72	12 392	0.274
Merlin	HY females vs. males	177; 218	15 741	0.002
Cooper's Hawk	HY females vs. males	6957; 3511	9 708 752	<0.001
	AHY females vs. males	328; 110	12 791	<0.001
	HY vs. AHY females	6957; 328	1 749 490	<0.001
	HY vs. AHY males	3511; 110	318 745	<0.001
Sharp-shinned Hawk	HY females vs. males	2792; 1608	1 563 007	<0.001
	AHY females vs. males	212; 88	7403	<0.001
	HY vs. AHY females	2792; 212	93 945	<0.001
	HY vs. AHY males	1608; 88	144 866	<0.001
Red-shouldered Hawk	HY females vs. males	162; 120	8208	0.025

from Cedar Grove (Mueller et al. 2000), Hawk Cliff, Ontario (Duncan 1981; Duncan 1982), Manzanos, New Mexico (DeLong and Hoffman 1999), and Goshutes, Nevada (DeLong and Hoffman 1999). The single point of disagreement among the results was that, unlike at the other four sites, at Cedar Grove the AHY male Cooper's Hawks precede AHY females. This discrepancy may be associated with the relatively low number of AHY Cooper's Hawks' samples at Cedar Grove (77 AHY females, 71 AHY males) or with the site's geographic location near the northern extent of the Cooper's Hawk's breeding range. Further investigation is needed to identify the cause of this pattern.

As in an examination of Red-shouldered Hawk migration at Cedar Grove (Mueller et al. 2000), we found a significant difference in the timing of migration of this species, with HY females preceding HY males. The observation of differential timing of Red-shouldered Hawk movement through the

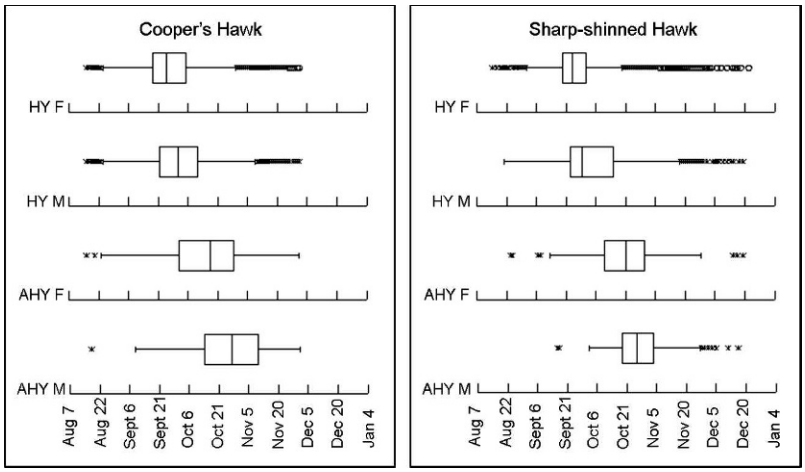


Figure 2. Temporal distribution of Cooper's and Sharp-shinned hawks trapped during autumn migration through the Marin Headlands, California. The vertical line indicates the median migration date. The box encompasses 50% of observations from the first to third quartiles; whiskers extend to include minimum and maximum values while asterisks indicate statistical outliers.

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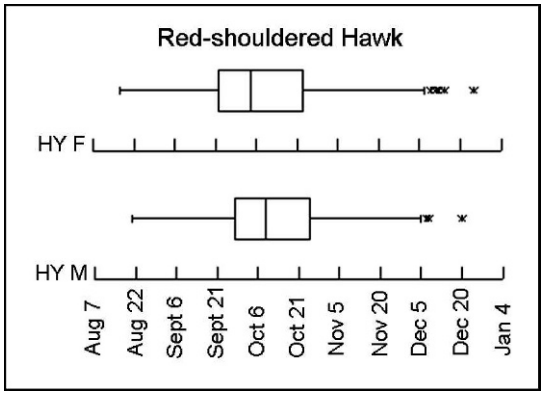


Figure 3. Temporal distribution of Red-shouldered Hawks and falcons trapped during autumn migration through the Marin Headlands, California. The vertical line indicates the median migration date. The box encompasses 50% of observations from the first to third quartiles; whiskers extend to include minimum and maximum values while asterisks indicate statistical outliers.

Marin Headlands was somewhat surprising. The subspecies of Red-shouldered Hawk in the upper Midwest, *B. lineatus lineatus*, is migratory and vacates northern latitudes during autumn and a difference in migration timing could be expected in this subspecies. In contrast, the California subspecies, *B. l. elegans*, is resident, and the movement of HY Red-shouldered Hawks through the Marin Headlands is more accurately described as dispersal from natal areas, rather than migration. Given the resident nature of the California subspecies, the finding of differential timing among males and females is unexpected. One explanation for this pattern would be differential timing in dispersal from natal areas between female and male Red-shouldered Hawks in California. However, the median passage dates of 3 October and 8 October were similar to those of northern migrants such as the Merlin, and were not consistent with resident juveniles that would have become independent of parental care in late summer. Alternatively, changes in weather and temperature in early autumn may cause a movement of juveniles away from habitats that are no longer suitable, resulting in an autumn flight through the Marin Headlands. How such a change in weather might result in differential timing between females and males is unclear. Additional data, including telemetry data that detail the movement patterns of individual HY Red-shouldered Hawks, are needed to address this question.

In general, the patterns of migration timing we observed in the Marin Headlands were similar to those observed in eastern, midwestern, and intermountain west, North America. The species examined here breed at temperate latitudes, and the pattern of HY individuals migrating ahead of AHY birds was consistent with the mechanism proposed by Mueller et al. (2000), that an advantage is conferred to adults that remain on breeding grounds as long as local weather and food resources permit. Similarly, males of the species examined here tend to be responsible for territory defense and consequently migrate later than females. Where our results depart from findings at other sites (American Kestrels and Red-shouldered Hawks), the difference may be attributed to the mild winter climate of central California and differences in migratory behaviors between regional populations and subspecies, although additional information is needed to determine the mechanism responsible for the differential timing of Red-shouldered Hawk movements in California. As additional data are gathered through ongoing banding and telemetry efforts, we may be able to better define the breeding origins of the raptor populations migrating through the Marin Headlands and understand the underlying causes for the patterns of differential migration observed at this site.

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