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Author: Tomalty, Katharine M.

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DIFFERENTIAL MIGRATION AND PHENOLOGY OF ADULT RED-TAILED HAWKS IN CALIFORNIA

KATHARINE M. TOMALTY
Genomic Variation Laboratory, Department of Animal Science, Meyer Hall, University of California Davis, One Shields Avenue, Davis, CA 95616 U.S.A.

ANGUS C. HULL, ALLEN M. FISH, AND CHRISTOPHER W. BRIGGS
Golden Gate Raptor Observatory, Building 1064, Fort Cronkhite, Sausalito, CA 94965 U.S.A.

JOSHUA M. HULL[1]
Golden Gate Raptor Observatory, Building 1064, Fort Cronkhite, Sausalito, CA 94965 U.S.A.
and
Department of Animal Science, Meyer Hall, University of California Davis, One Shields Avenue, Davis, CA 95616 U.S.A.

ABSTRACT.—Differential migration by age and sex has been observed within several raptor species. Here, we report differential autumn migration timing between adult and juvenile Red-tailed Hawks (*Buteo jamaicensis*), and between adult males and females at the Golden Gate Raptor Observatory in the Marin Headlands of northern California. Because Red-tailed Hawks cannot be easily sexed in hand, we used discriminant function analysis (DFA) to identify morphometric measures useful for sexing adult Red-tailed Hawks captured during migration in the Marin Headlands and created a flowchart for in-hand field sexing of adult Red-tailed Hawks. The DFA correctly assigned sex 95% of the time, and provides an improved method for sexing adult Red-tailed Hawks in the Marin Headlands when compared to existing DFAs developed for other populations of this species in the western United States. Our ability to sex adult Red-tailed Hawks permitted examination of fall migration phenology, which differed markedly for adult and juvenile Red-tailed Hawks in the Marin Headlands. Juveniles displayed two distinct peaks of migration, one in mid-September and a second in mid-November. In contrast, the number of migrating adults increased steadily through mid-November, and declined thereafter, with adult females migrating earlier than adult males and the mean passage date for both sexes much later than documented at other North American hawk watch sites.

KEY WORDS: *Red-tailed Hawk*; Buteo jamaicensis; *count*; *migration*; *morphometric*; *sexing*; *timing*.

MIGRACIÓN DIFERENCIAL Y FENOLOGÍA DE INDIVIDUOS ADULTOS DE *BUTEO JAMAICENSIS* EN CALIFORNIA

RESUMEN.—La migración diferencial por edad y por sexo ha sido observada en numerosas especies de rapaces. Reportamos los tiempos de la migración diferencial de otoño entre individuos adultos y juveniles de *Buteo jamaicensis* y entre machos adultos y hembras en el Observatorio de Rapaces Golden Gate en Marin Headlands en el norte de California. Debido a que el sexo de los individuos de *B. jamaicensis* no puede ser determinado fácilmente cuando son capturados, utilizamos un análisis de función discriminante (AFD) para identificar las medidas morfométricas útiles para la determinación del sexo de los individuos adultos de *B. jamaicensis* capturados durando la migración en Marin Headlands y creamos un diagrama de flujo para la determinación del sexo en el campo de los individuos capturados de esta especie. El AFD asignó correctamente el sexo el 95% de las veces y representa un método mejorado para la determinación del sexo de los individuos adultos de *B. jamaicensis* en Marin Headlands en comparación con los AFD existentes desarrollados para otras poblaciones de esta especie en el oeste de los Estados Unidos. Nuestra capacidad para determinar el sexo de los individuos adultos de *B. jamaicensis* permitió estudiar la fenología de migración de otoño, la cual difirió marcadamente para los individuos adultos y juveniles de *B. jamaicensis* en Marin Headlands. Los individuos juveniles exhibieron dos picos de migración distintivos,

[1] Email address: jmhull@ucdavis.edu

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uno a mediados de septiembre y otro a mediados de noviembre. En contraste, el número de adultos migrantes aumentó continuamente hasta mediados de noviembre y a partir de este momento disminuyó, con las hembras adultas migrando con anterioridad a los machos adultos y con la fecha media de paso migratorio para ambos sexos mucho más tardía que la documentada en otros sitios de observación de *B. jamaicensis* en América del Norte.

[Traducción del equipo editorial]

Studies of migration phenology can provide insights into broad-scale environmental changes, and have recently provided evidence of the effects of climatic change on populations of migratory birds (Parmesan and Yohe 2003, Parmesan 2006). Among raptors, long-term studies at northern migration concentration points have documented a shift toward later migration for a variety of North American raptor species (Rosenfield et al. 2011, Van Buskirk 2012). The ability of studies such as these to successfully detect phonological changes among species depends upon an accurate preexisting description of the underlying migration patterns for each species being monitored. Additionally, detection of intraspecies changes in migration phenology depends on understanding the differences in migration phenology between adults and juveniles, males and females, and differences among populations. Describing baseline migration phenology can be a challenging task particularly for broadly distributed species with both resident and migratory populations and at migration sites where both resident and migrant populations comingle during migration and winter.

Previous studies of the phenology of raptor migration have demonstrated age and sex differences for several species (Rosenfield and Evans 1980, Bildstein et al. 1984, Smallwood 1988, DeLong and Hoffman 1999). Several studies of sex-specific autumn migration timing of raptors have demonstrated that female raptors migrate earlier than males (Rosenfield and Evans 1980, Mueller et al. 2000, Hull et al. 2012), perhaps so males can maintain control of territories longer (Mueller et al. 2000). Similarly, age is known to affect migration timing in some species, with juveniles often migrating earlier than adults (Rosenfield and Evans 1980, Hull et al. 2012).

Red-tailed Hawks (*Buteo jamaicensis*) are one of the most widely distributed North American raptors, with complex migratory patterns that vary among populations (Preston and Beane 1993, Hull et al. 2009). Because of year-round availability of prey, breeding and wintering Red-tailed Hawks achieve high densities in central California (Fitch et al. 1946, Preston and Beane 1993, Pandolfino et al. 2011). Similarly, the greatest number of migrating Red-tailed Hawks in North America are observed and banded in the Marin Headlands along the central California coast where annual totals average 9409 Red-tailed Hawks observed and 317 banded (Golden Gate Raptor Observatory 2012). Based on genetic analysis, the Red-tailed Hawks captured in the Marin Headlands represent both a resident central California population and a migratory Intermountain West population (Hull et al. 2008, 2009).

The distribution of juvenile Red-tailed Hawk migration in the Marin Headlands is bimodal, with the first peak in numbers representing dispersal by the local California population and the second peak representing migration of the Intermountain West population (Hull et al. 2009). Examination of adult Red-tailed Hawk migration timing is important in order to provide a more complete understanding of the species migration ecology and provide a context for future phenological studies. However, because of the lower total number of sightings per year and additional time required to obtain sufficient sample size, the migration phenology of adult Red-tailed Hawks through the Marin Headlands has not yet been described.

To better describe the migratory behavior of Red-tailed Hawks observed in the Marin Headlands we addressed three objectives. First, we provided a description of the timing of migration for adult Red-tailed Hawks. Second, we developed a site-specific discriminant function for sexing adult Red-tailed Hawks captured in the Marin Headlands. Though previous work has developed tools for sexing migrant and wintering Red-tailed Hawks in the Intermountain West (Donohue and Dufty 2006) and the Central Valley of California (Pitzer et al. 2008), the origins of the Marin Headlands migrants are unclear and may include California breeding birds. Therefore, we developed a separate function to accurately assign sex to migrating adult Red-tailed Hawks. Our third objective was to then use the tailored discriminant function to describe sex-specific differences in the migration phenology of adult Red-tailed Hawks. This information will provide a baseline for future analyses of trends in migration phenology, including

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examinations of potential responses to environmental changes.

METHODS

The Golden Gate Raptor Observatory is located along the central coast of California in the coastal scrub headlands at the southern terminus of the Marin peninsula, between San Francisco Bay to the east and the Pacific Ocean to the west (37°49.82′N, 122°29.98′W). The north–south orientation of the Marin peninsula and bordering shorelines funnel migrating raptors southward toward the narrowest bay crossing, which creates an opportunity to study a large concentration of migrating raptors at the southern point of the peninsula. Annual raptor migration counts are conducted from Hawk Hill at a high point on the southern peninsula (Binford 1979), and raptor banding occurs at four nearby sites.

Autumn raptor migration counts, including Red-tailed Hawks, were conducted each year from 1992 to 2006. Weather permitting, counts occurred daily from 0930–1530 H from mid-August through mid-December. A standardized count methodology using a site-specific quadrant system (McDermott and Fish 1991) has been used since 1986. Rotating teams of 7 to 17 volunteers conducted the counts; each team was led by an experienced hawk counter with ≥5 yr of experience counting hawks in the Marin Headlands. Unlike many raptor migration sites where the statistical properties of observer identification rates have not been examined, previous studies examining the utility and accuracy of raptor counts at the Golden Gate Raptor Observatory have found that this method results in consistent identification rates across years, allowing for detection of population trends (Lewis and Gould 2000, Hull et al. 2010).

Banders captured adult Red-tailed Hawks during autumn migration each year from 1984 to 2012 using bow nets, mist nets, and dho-gazas, (Clark 1970, Bloom 1987, Bub 1991). Banders collected seven morphometric measurements from each captured hawk: unflattened and flattened wing-chord (from tip of longest primary to wrist), tail length (from feather insertion to tip of longest tail feather), tarsus depth (greatest anterior–posterior width at the narrowest point of tarsus), hallux length (from tip of hallux to flesh), exposed culmen length (from cere to tip of culmen), and mass (Golden Gate Raptor Observatory 2010). From 2002 to present, banders collected two contour feathers from the breast of each individual for subsequent genetic analysis. Prior to release all hawks were banded with a U.S. Geological Survey leg band.

Using genomic DNA obtained from contour feathers, we determined the sex of 93 randomly selected adult Red-tailed Hawks trapped between 2002 and 2012 through molecular analysis of the Z and W chromosomes. To obtain the DNA samples, we cut the proximal 3–4 mm of each feather shaft into several small pieces, and digested for 48 hr at 56°C in a reaction of 180 ml tissue lysis buffer (Qiagen ATL buffer) and 20 µl proteinase K. We added an additional 20 µl proteinase K at hour 24 of the digestion. We isolated DNA using the Qiagen DNeasy®Blood and Tissue Kit, and the associated animal-tissue extraction protocol. We performed polymerase chain reactions (PCR) in a 10 µl volume mixture containing 50 mM KCl, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.6 µM of primers AWS03 (5'-ACAGTTTGT CTGTCTCCGGGGAA-3') and USP3 (5'-AGCTGGAY TTCAGWSCATCTTCT-3'), 0.4 µM of primers CPE 15F (5'-AAGCATAGAA-ACAATGTGGGAC-3') and CPE15R (5'-AACTCTGTCTGGAAGGACTT-3'; Itoh et al. 2001), and 0.75 units Taq polymerase. We used the following thermal profile: 94°C for 5 min, 15 cycles of 94°C for 30 sec, 65°C for 90 sec, 72°C for 45 sec, 15 cycles of 94°C for 30 sec, 53°C for 90 sec, 72°C for 45 sec, and a final extension cycle of 72°C for 10 min. Primers were previously validated using samples from 36 Red-tailed Hawks of known sex (Pitzer et al. 2008). We fluorescently labeled forward primers with FAM and VIC, respectively, and analyzed the PCR product on an ABI 3730 DNA Analyzer (Applied Biosystems, Carlsbad, CA, U.S.A.) in a 10-µl reaction volume containing 1 µl of PCR product (diluted 1:5 with ddH_2O), 0.2 µl LIZ500 size standard, and 8.8 µl HiDi formamide (Applied Biosystems, Carlsbad, CA, U.S.A.). We analyzed electropherograms using GENEMAPPER 4.0 software (Applied Biosystems, Carlsbad, CA, U.S.A.) and confirmed them by visual inspection.

Data Analysis. We used the genetically assigned sex of the 93 adult Red-tailed Hawks to develop a discriminant function that would allow for sex identification from morphometric data. We excluded individuals with missing data from the analysis. We tested each of the seven morphological measurements for normality using a one-sample Kolmogorov-Smirnov test. We used a backwards step-wise discriminant function analysis (DFA) to identify the most parsimonious model. We also conducted a classification-tree analysis and developed a flowchart for

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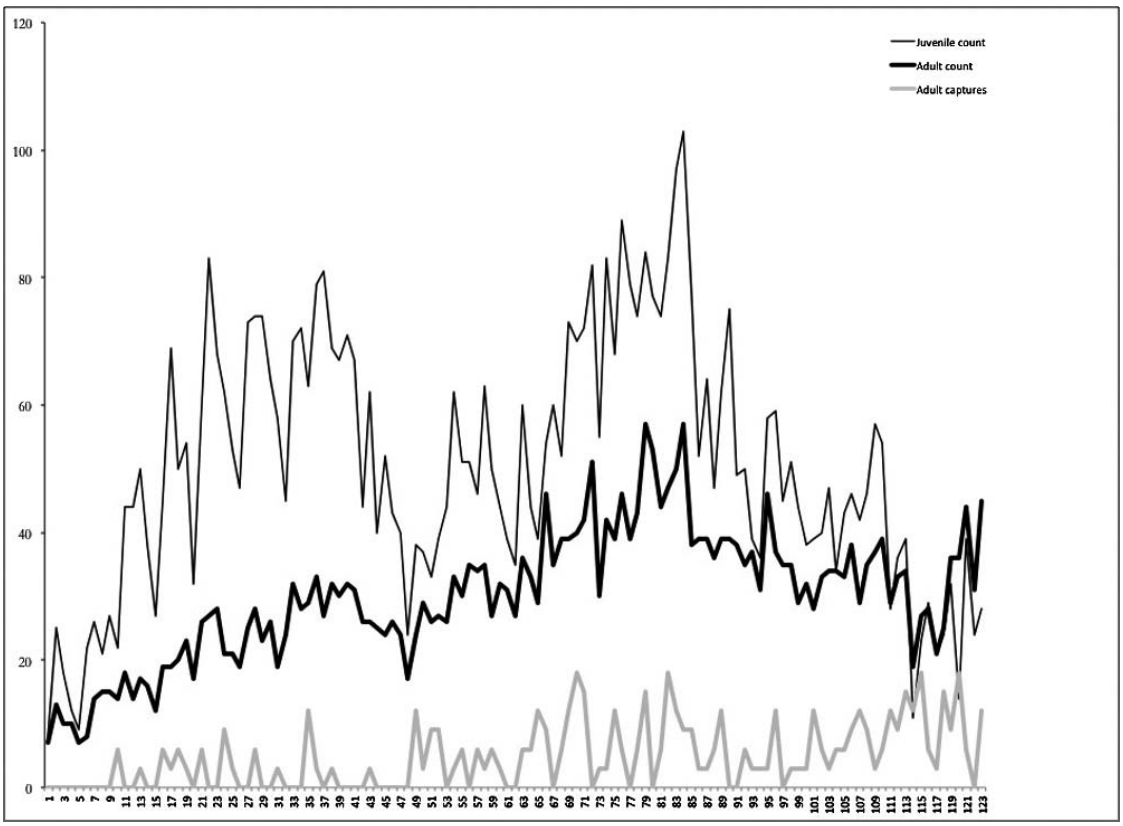


Figure 1. Averaged daily counts between 15 August and 15 December, 1992–2006 for juvenile (light black line) and adult (bold black line) Red-tailed Hawks. For comparison, the temporal distribution of adult Red-tailed Hawk captures (1984–2012) is also included (gray line; this value has been increased by a factor of three in order for the pattern of captures to be discernable on the same scale as the count data).

determining sex from the resulting tree. All statistical tests were performed using SYSTAT 11.0.

We used the discriminant function derived from the 93 known-sex adult Red-tailed Hawks to assign sex to 460 additional, adult Red-tailed Hawks captured since 1984. We used the data from these 460 individuals to investigate differences in the migration timing of males and females. We compiled the capture dates from banding operations across seasons and converted to Julian dates in order to produce continuous distributions for males and females. Similar to the pattern seen in the count data, the majority of adult Red-tailed Hawk captures occurred during the second half of the migration season (1 October through mid-December); however, a small proportion of hawks were captured in August and September (25 of 217 females and 16 of 243 males; Fig. 1). Because the early migration period in the Marin Headlands (mid-August through September) has been associated with a genetically distinct population of juvenile Red-tailed Hawks (Hull et al. 2009), we examined differential migration timing across both the entire season and constrained to the second half of the season. We compared the Julian date distributions for males and females using Mann-Whitney *U*-tests in SYSTAT 11.0.

RESULTS

The count dataset from 1992 through 2006, encompassing 1449 count-days, included 44,517 sightings of adult Red-tailed Hawks. Aggregated across all years, the numbers of adult Red-tailed Hawks observed in the Marin Headlands increased from mid-August through mid-December (Fig. 1). In contrast, the numbers of juvenile Red-tailed

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Table 1. Morphological measurements for 93 known-sex adult Red-tailed Hawks captured during autumn migration in the Marin Headlands, California between 2002 and 2012. Measurements are given as sample size (n), mean ± standard deviation, with range in parentheses. All measurements are in mm except mass, which is in g.

SEX	n	WING CHORD	FLAT WING	TAIL	MASS	CULMEN	TARSUS	HALLUX
Female	34	410 ± 12.5 (382–432)	417 ± 13.3 (389–437)	225 ± 9.7 (207–245)	1118 ± 100 (943–1406)	27.2 ± 1.2 (23.9–29.5)	12.1 ± 0.5 (11.0–13.3)	31.4 ± 1.5 (28.0–34.5)
Male	59	385 ± 9.9 (363–403)	392 ± 9.7 (370–407)	213 ± 8.7 (191–237)	889 ± 75 (691–1052)	25.3 ± 1.2 (21.8–28.1)	10.5 ± 0.6 (9.2–11.6)	28.0 ± 1.2 (25.1–31.5)

Hawks followed a bimodal distribution, with peaks of migration activity in mid-September and mid-November (Hull et al. 2009).

We successfully amplified DNA and scored PCR product from all 93 adult Red-tailed Hawks. PCR results indicated that the sample consisted of 34 females and 59 males. We detected no violations of normality or unequal variances in the morphometric data for the 93 known-sex individuals. The DFA indicated that mass, culmen length, tarsus depth, and hallux length were the most important factors for determining the sex of adult Red-tailed Hawks from the Marin Headlands (Table 1), and the resultant function correctly classified 95% of the individuals (33 of 34 females and 55 of 59 males; Table 2). We developed a flow chart for sexing adult Red-tailed Hawks from the classification tree analysis (Fig. 2) that correctly classified each of the 93 individuals to sex.

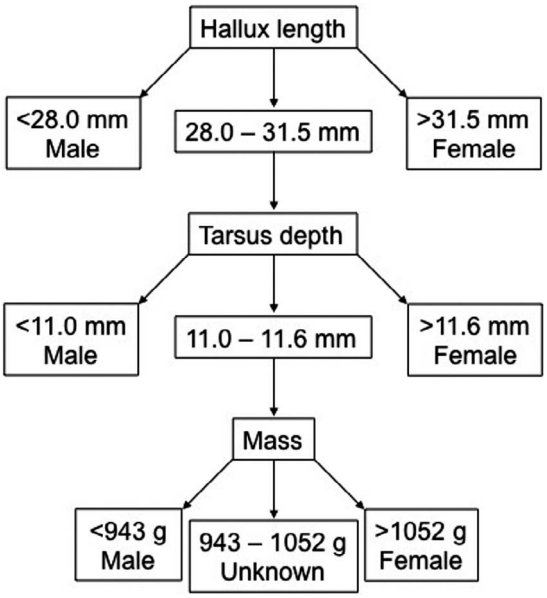


Figure 2. Flow chart for sexing adult Red-tailed Hawk captured in the Marin Headlands, California.

We subsequently used the results from the DFA to describe the differences in migration timing of adult male and female Red-tailed Hawks. Adult female Red-tailed Hawks migrated before adult males, whether analyzed for the entire migration season (8 November vs. 16 December, $n = 460$; $U = 16926.5$; $P < 0.001$) or only the late migration season (27 November vs. 2 December, $n = 419$; $U = 13698.5$; $P < 0.001$; Fig. 3; Table 3).

DISCUSSION

The migration phenology of adult Red-tailed Hawks in the Marin Headlands differs from that of juveniles. In contrast to the pronounced bimodal pattern shown for juveniles (Hull et al. 2009), adult Red-tailed Hawk numbers generally increase through mid-November and then decline slowly through the end of the migration-monitoring season in mid-December (Fig. 1). Several underlying mechanisms may be responsible for the difference in migration phenology of adult and juvenile Red-tailed Hawks in the Marin Headlands. The first peak of juvenile activity is associated with a central California breeding population (Hull et al. 2009), likely reflecting primarily the multidirectional dispersal of fledglings from nests within central California. Because of the mild winter climate, adult Red-tailed Hawks that breed in central California are generally sedentary (Fitch et al. 1946, Preston and Beane 1993). Consequently, the number of adults of the central California population observed at the Golden Gate Raptor Observatory may be limited primarily to those with home ranges within or near to the Marin Headlands.

The peak of adult migration through the Marin Headlands in late November corresponds with the second peak of juvenile migration. These juveniles include some individuals from the central California population; however, a large proportion are juveniles from the Intermountain West that show directional southward migration (Hull et al. 2009). A similar phenomenon may be responsible for the peak in

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Table 2. Discriminant functions and classification error rates for using morphometrics to sex 93 known-sex adult Red-tailed Hawks captured during autumn migration in the Marin Headlands, California.

LOCATION	FUNCTION	PERCENT INCORRECT
Marin Headlands, California	D = –27.790 + 0.003 (mass) + 0.180 (culmen) + 0.911 (tarsus) + 0.342 (hallux)	5.4% (5/93)
Central Valley, California[a]	D = –41.505 + 0.844 (tarsus) = 0.385 (culmen) + 0.056 (wing)	9.7% (9/93)
Intermountain West[b]	D = –94.902 + 0.166 (wing) + 0.026 (mass)	9.7% (9/93)

[a] Based on data for hawks captured during winter (Pitzer et al. (2008).
[b] Based on data for hawks captured in Oregon, Washington, Nevada, and New Mexico (Donohue and Dufty 2006).

adult Red-tailed Hawks in late November, with a proportion of the birds associated with local breeding pairs and an additional input of adults migrating from the Intermountain West, although this hypothesis is supported only by limited telemetry data.

In spite of known regional differences in morphology of Red-tailed Hawks (Fitzpatrick and Dunk 1999, Pearlstine and Thompson 2004, Hull et al. 2008), the DFA specific to the Marin Headlands developed for sexing adult Red-tailed Hawks provided marginal improvement (5% versus 10% classification error rate) over functions developed for wintering Red-tailed Hawks in the Central Valley of California (Pitzer et al. 2008) and for migrant Red-tailed Hawks sampled at four migration sites in the Intermountain West (Donohue and Dufty 2006). Although the site-specific function was most accurate, all three functions achieved greater than 90% accuracy when applied to adult Red-tailed Hawks banded in the Marin Headlands, suggesting that useful sexing information can be obtained from any of these approaches when studying the western North American subspecies of Red-tailed Hawks, *B. j. calurus*. However, because the Bird Banding Laboratory requires a 95% accuracy of sexing protocols, local DFAs provide an important tool for field studies. Additionally, because of substantial size differences between *B. j. calurus* and other subspecies (Pearlstine and Thompson 2004, Hull et al. 2008), additional approaches should be developed when using morphology to sex other subspecies.

We found that the peak of adult female migration occurred prior to the peak of adult male migration in the Marin Headlands. This finding is consistent with the timing of male and female autumn migration of other raptor species observed in the Marin Headlands and at other banding stations across the United States (Rosenfield and Evans 1980, Bildstein et al. 1984, Smallwood 1988, DeLong and Hoffman 1999, Hull et al. 2012) and with findings from Cedar Grove, Wisconsin, where large adult Red-tailed Hawks (presumed to be mostly female) migrated before small adults (presumed to be mostly male; Mueller et al. 2000).

Although the demonstrated relationship between male and female adult Red-tailed Hawk migration timing is consistent with that of other raptors, the timing of the Red-tailed Hawk migration in the Marin Headlands is substantially later than that of any of the other species that migrates through the Marin Headlands, as well as any of the species that migrate through Cedar Grove, Wisconsin (Mueller et al. 2000, Hull et al. 2012). Additionally, the difference in passage date for peak migration of Red-tailed Hawks through northern sites and the Marin Headlands is much greater than for any of the other species observed at both sites (Mueller et al. 2000, Hull et al. 2012), although generally similar to some sites in eastern North America that also experience more mild winter weather (Goodrich and Smith 2008). The median passage date for adult female Red-tailed Hawks was 8 November (16 November if only late-season hawks are included) and the median passage date for adult males is 27 November (2 December if only late-season hawks are included). Because the Marin Headlands act as a concentration point for raptors during autumn migration and also provide suitable overwintering habitat, the late arrival of adult Red-tailed Hawks raises the question of whether the majority of these hawks are still in the process of migrating to wintering areas or if migration has already been completed and the adult Red-tailed Hawks observed in the Marin Headlands are in fact establishing winter ranges. If the adult Red-tailed Hawks are in fact using the Marin Headlands as wintering habitat, then the differential timing between adult males and females may indicate differential use of wintering habitat in combination

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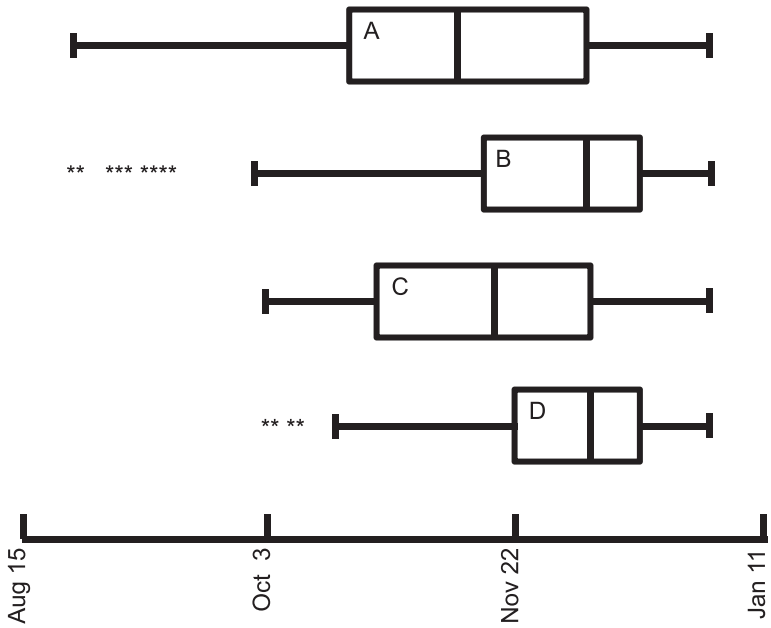


Figure 3. Temporal distribution of adult Red-tailed Hawks captured in the Marin Headlands, California, during (1) the entire autumn migration season, A = adult female, B = adult male, (n = 460, 217 female, 243 male; 15 August through 31 December) and (2) the late autumn migration season, C = adult female, D = adult male (n = 419, 192 female, 227 male; 1 October through 31 December). Vertical lines indicate the median passage date; the boxes encompass 50% of the observations, from the first to third quartiles; whiskers extend to include highest and lowest values with 1.5 times the interquartile range; and asterisks indicate statistical outliers.

with differential migration timing. In this case, the adult females may be arriving earlier on their way to wintering grounds, whereas males arrive later and preferentially use the Marin Headlands during winter. Sex-biased use of winter habitats has been previously suggested for several species (Newton 1979, Duncan 1982, Clark 1985, Hoffman et al. 2002); however, additional data are needed to confirm whether this is the case for adult Red-tailed Hawks wintering in central California.

The data described here provide a baseline for evaluating potential future changes in the migration phenology of adult Red-tailed Hawks observed in the Marin Headlands during autumn migration, which may be influenced by broad-scale environmental changes such as climate change. Because central California supports both a dense, resident breeding population and provides important winter habitat for other migratory Red-tailed Hawks from throughout western North America, continued monitoring of the trends in migration counts and migration phenology of Red-tailed Hawks in the Marin Headlands may provide valuable insights into the overall status of the species.

Table 3. Sample size (n) of Red-tailed Hawks captured from 1984 through 2012 during autumn migration in the Marin Headlands, California, for the entire migration season (15 August through 31 December) and the late migration season (1 October through 31 December).

Age / Sex	Median Date, Entire Season	n	Median Date, Late Season	n
Adult F	8 November	217	16 November	192
Adult M	27 November	243	2 December	227

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