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DIFFERENTIAL MIGRATION BETWEEN DISCRETE POPULATIONS OF JUVENILE RED-TAILED HAWKS (*BUTEO JAMAICENSIS*)

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Abstract.—Migratory species are of increased conservation concern because of their reliance on multiple, geographically disjunct habitats. An understanding of how long-term ecological processes and contemporary population genetic patterns are related is critical for effective management and conservation of such species. Combining traditional long-term census and mark–recapture data with temporally focused molecular genetic data can help inform these efforts. We used 24 years of banding data, 15 years of migration counts, and molecular genetic data from 17 microsatellite loci to describe the migration phenology, direction, and population connectivity of Red-tailed Hawks (*Buteo jamaicensis*) migrating through the Marin Peninsula, California. Count data indicated two distinct peak periods of movement across years: 15 August–30 September and 1 October–30 November. Band-encounter data from these two periods revealed a significant difference in movement: individuals in the early period of migration (15 August–30 September) displayed little net movement, whereas individuals from the second period (1 October–30 November) showed directional, southward movement. Finally, molecular genetic data suggest that the early-season period primarily involves a population from central California, whereas the second period includes both individuals from central California and individuals from desert regions of the Intermountain West. These analyses provide important information for interpreting long-term Red-tailed Hawk count and banding data and offer an example of how traditional population-monitoring methods can be combined with molecular genetic markers. *Received 2 July 2008, accepted 23 December 2008.*

Key words: banding, *Buteo jamaicensis*, hawk-watch counts, microsatellite, migration, Red-tailed Hawk.

Migración Diferenciada entre Poblaciones Discretas de Juveniles de *Buteo jamaicensis*

Resumen.—Las especies migratorias tienen una prioridad de conservación creciente debido a su dependencia de múltiples hábitats que se encuentran geográficamente disyuntos. El entendimiento de cómo se relacionan los procesos ecológicos de largo plazo con los patrones contemporáneos de estructura genética es de gran importancia para la conservación y el manejo efectivo de estas especies. La combinación de datos provenientes de censos de largo plazo tradicionales y de marcado y recaptura con datos moleculares genéticos enfocados en un tiempo determinado, puede ayudar a informar estos esfuerzos. Usamos datos de 24 años de anillamiento, de 15 años de conteos migratorios y datos genéticos de 17 loci microsatelitales para describir la fenología y dirección migratoria, así como la conectividad de individuos migratorios de *Buteo jamaicensis* en la península Marin, California. A través de los años, los datos de conteo indicaron dos periodos diferentes de pico de movimiento: 15 de agosto a 1 de septiembre y 1 octubre a 30 de noviembre. Los datos de recaptura de individuos marcados en estos dos periodos revelaron una diferencia significativa en movimiento: los individuos del periodo temprano de movimiento (15 de agosto–30 de septiembre) presentaron poco movimiento neto, mientras que los individuos del segundo periodo (1 de octubre – 30 de noviembre) presentaron un movimiento direccional hacia el sur. Finalmente, los datos genéticos sugieren que el periodo inicial de la temporada involucra principalmente una población de California central, mientras que el segundo periodo incluye individuos de California central y de regiones desérticas del oeste intermontano. Estos análisis proveen información importante para interpretar los conteos de largo plazo y de anillamiento de *B. jamaicensis*, y ofrecen un ejemplo de cómo los métodos tradicionales de monitoreo pueden ser combinados con marcadores genéticos moleculares.

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Human alteration of landscapes and global climate change are two of the greatest threats to species persistence (Sala et al. 2000, Thomas et al. 2004, Jetz et al. 2007). Migrants are at particular risk, because they rely on specific breeding, migration, and non-breeding habitats; consequently, conservation efforts aimed at single habitats may not be sufficient to maintain viable populations (Huntley et al. 2006, Amano and Yamaura 2007). Avian migrants are of particular conservation concern, because their ranges may span thousands of kilometers and cross multiple political boundaries, resulting in logistical challenges in identifying where specific populations are distributed and limited throughout the annual cycle of breeding, migration, and wintering (Lemoine and Böhning-Gaese 2003, Holmes 2007).

In an effort to identify population connectivity between habitats, stable-isotope and molecular genetic analyses have been used to study a variety of organisms (Kelly et al. 2005, Gómez-Díaz and González-Solís 2007, Hobson et al. 2007). These intrinsic markers provide information about each individual, which allows data to be accumulated rapidly. Although capable of describing long-term patterns, traditional methods such as banding often have recovery rates of <1% and require many decades to develop information about population movements (e.g., Newton and Rothery 2000, Bakken and Mehlum 2005, Piersma et al. 2005).

Long-term field research combined with molecular genetic or stable-isotope analyses provides an opportunity for gaining powerful insights about migratory movements and population connectivity. This approach has been used in several studies that have described connectivity between breeding sites and migration routes (Lopes et al. 2006, Literák et al. 2007), identified source populations associated with migration monitoring stations (Mazerolle et al. 2005), and described a pattern of chain migration (R. B. Smith et al. 2003). Because molecular genetic methods can identify discrete breeding populations, combining genetic data with long-term banding and count data may provide insights into migration and habitat use.

Diurnal raptors, in particular, provide a useful system for investigating how band-encounter and count data can be combined with genetic data to yield new ecological information. During migration, raptors rely on thermal and wind-driven updrafts to conserve energy and provide lift; consequently, most raptor migration occurs during the day, and concentrated migrants can be easily observed and counted (Bildstein 2006). Further, a network of raptor banding stations throughout northern temperate latitudes and extending into the tropics presents ample opportunity to develop long-term mark–recapture data. The Red-tailed Hawk (*Buteo jamaicensis*) can be used as a model raptor system for a combined approach to investigating migration and habitat connectivity.

Red-tailed Hawks are among the most abundant North American raptors, breeding throughout grasslands and open areas of North America and Central America (Preston and Beane 1993). Population genetic analyses of microsatellite and mitochondrial data indicate an east–west population distinction coinciding with the range of the subspecies *B. j. calurus* (western) and *B. j. borealis* (eastern) (Pearlstine 2004, Hull et al. 2008). Further population structure is evident within western North America, corresponding to the arid Intermountain West and central California (Hull et al. 2008).

Within western populations, discerning population-specific regions of conservation importance is difficult. The migratory behavior of these populations is complex; most of the northern populations are complete migrants, whereas populations of middle and lower latitudes display a mixture of partial migration and year-round residency (Lowe 1978, Preston and Beane 1993). Migratory populations of Red-tailed Hawks are studied at several raptor migration stations throughout North America, where between 1,000 and 3,000 Red-tailed Hawks are banded, and ~40,000 counted, annually (Hawk Migration Association of North America 2007, Bildstein et al. 2008, Goodrich and Smith 2008, A. Hull unpubl. data). Both mark–recapture and daily counts are conducted during autumn migration at some of these stations, and they provide settings for additional investigations of migration patterns of genetically distinct populations. One such station, the Golden Gate Raptor Observatory, is in central California at the southern end of the Marin Peninsula (37°50′N, 122°30′W), along the Pacific migration corridor (Binford 1979). Here, a migration bottleneck provides an opportunity to study large numbers of raptors; >25,000 sightings of 19 species are counted annually.

We used long-term count and band-encounter data from the Marin site, in concert with molecular genetic data, to investigate population connectivity, direction of migration, and migration phenology of Red-tailed Hawks. This investigation provides an example of how long-term data sets from birds and other organisms can be combined with data from intrinsic markers to increase the detection of biologically relevant patterns.

Methods

Migration counts.—The Golden Gate Raptor Observatory in the Marin Headlands conducts standardized daily raptor counts between mid-August and mid-December each year, using a site-specific quadrant system (McDermott and Fish 1991, Fish 2001). The counts yield an annual average of >9,000 sightings of Red-tailed Hawks, of which ~65% are juveniles. We summed and plotted total daily counts of sightings of juvenile Red-tailed Hawks for each date of the migration season across 15 years (1992–2006). Modes of movement by Red-tailed Hawks were identified by eye, and the season was subsequently divided into distinct periods of movement. We used the bimodality coefficient, b (SAS Institute 1989, based on Darlington 1970), as an index of bimodality, where $b > 0.55$ indicates bimodality.

Capture and banding.—Juvenile Red-tailed Hawks were captured during autumn migration using bow nets, mist nets, and dho-ghazzas during 24 years, 1984–2007, at the Golden Gate Raptor Observatory (Fig. 1; Berger and Mueller 1959, Clark 1970, Bloom 1987, Bub 1991). Analysis was focused on individuals trapped during the migration season; therefore, we constrained our sampling to the period 15 August–30 November to reduce the possibility of including late-breeding individuals or those that had settled onto wintering grounds (Goodrich and Smith 2008). Hawks were leg-banded with federal metal bands and released.

Analysis of banding data.—Of the 7,006 Red-tailed Hawks banded during the study period, 123 of 402 recoveries were suitable for inclusion in the present study. To allow the birds an opportunity to move away from Marin, we included only those recoveries that were reported at least one week after initial capture.

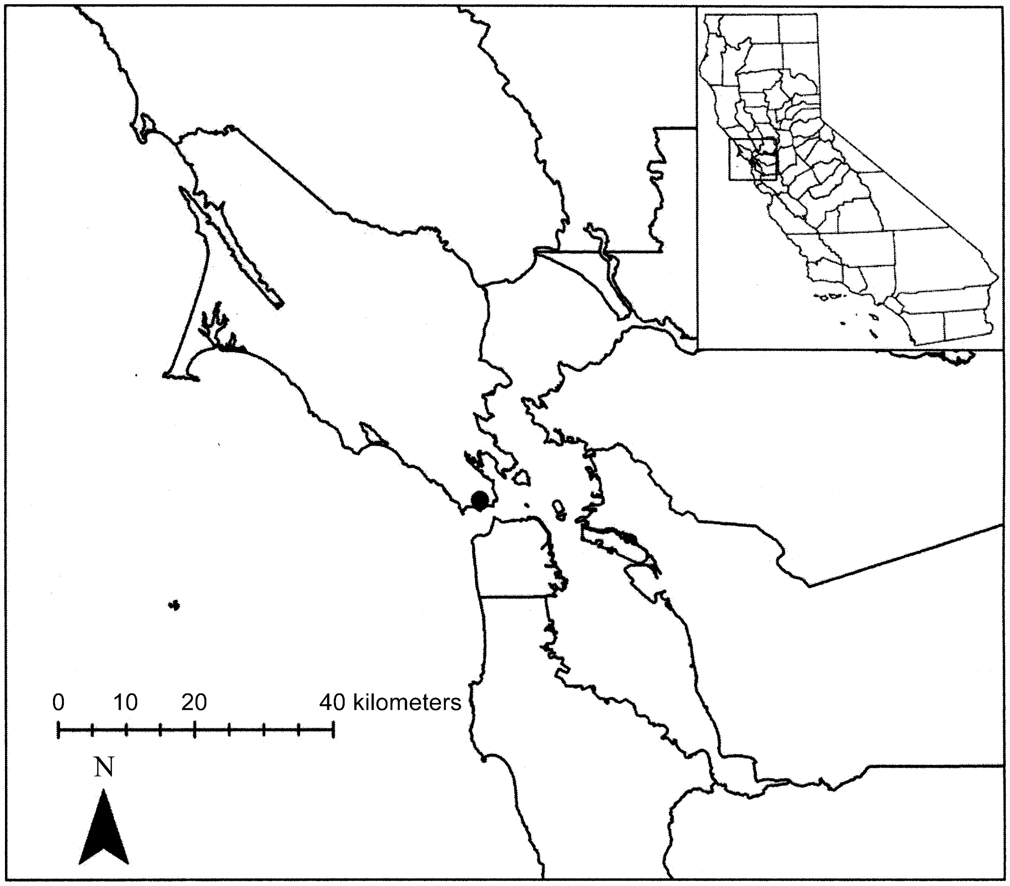

FIG. 1. Map of the San Francisco Bay region and the Marin Headlands, California, sampling station (black circle) positioned at the southern tip of the Marin peninsula.

Radio- and satellite-telemetry data (HawkWatch International; see Acknowledgments) indicated that a Red-tailed Hawk frequently moves hundreds of kilometers in one week (A. Hull unpubl. data). Adults generally migrate later (Gauthreaux 1985, Kerlinger 1989; but see Bildstein 2006) and overwinter farther north (Hoffman et al. 2002) than juveniles. Consequently, we included only data from juvenile Red-tailed Hawks recovered during the same migration and wintering season in which they were banded. Finally, to reduce the likelihood of including individuals that had initiated spring migratory movements, which would bias our estimation of the direction of autumn migration, we included only those recoveries reported as "fresh" before 1 March of the year after capture (Preston and Beane 1993).

The 123 recoveries that met our criteria were subsequently divided into groups (period 1, $n = 52$; period 2, $n = 71$) based on the date on which an individual was captured and banded. Because differential migration between males and females has been observed in many raptor species (Bildstein 2006), we identified the sex of the birds we caught using the genetically validated anatomical methods of Pitzer et al. (2008) and, subsequently, determined whether there were qualitative differences in the proportions of males and females between periods of migration activity. The distance each recovered individual moved north or south from Marin was subsequently calculated in decimal degrees of latitude. A two-sample t-test was used to detect any difference in mean movement between periods.

Analysis of microsatellite data.—Using genetic data from 17 microsatellite loci (BswA110w, BswD122w, BswA204w, BswA317w, BswD210w, BswD220w, BswA303w, BswB111aw, BswD234w, BswD310w, BswD313w, BswB220w, BswB221w, BswD327w, BswA302w, BswA312w, and BswD127w; Hull et al. 2007), Hull et al. (2008) found that the breeding subspecies of Red-tailed Hawks in western North America (*B. j. calurus*) can be divided into two regional populations: an Intermountain West population found throughout the Great Basin and western deserts of North America, and a central California population. This pattern was supported by Bayesian cluster analysis without prior information about geography, Monmonier's algorithm (designed to identify genetic barriers), unweighted pair-group method with arithmetic mean and neighbor-joining trees, and pairwise F_{ST} comparisons. Further, a sample of 265 juvenile Red-tailed Hawks collected in the Marin Headlands during autumn migration indicated the presence of both populations (Intermountain West, $n = 91$; central California, $n = 174$). We constrained our sample set to include only individuals that had been trapped between 15 August and 30 November during 2003, 2004, and 2005 (corresponding to the dates of the count and banding efforts). Consequently, we included 233 of the 265 juvenile Red-tailed Hawks genotyped by Hull et al. (2008).

We compared the relative genetic diversity between periods of migration. Heterozygosity and number of alleles per regional population were determined using MICROSATELLITE TOOLKIT (Park 2001); the number of private alleles (alleles occurring in only a single migration period) was calculated in CONVERT (Glaubitz 2004); and allelic richness, which accounts for variation in sample sizes, was calculated in FSTAT (Goudet 1995). Using the Bayesian clustering results from Hull et al. (2008), we employed a Yates corrected chi-square test (correction for noncontinuity) to determine whether the different periods of Red-tailed Hawk movement observed in Marin involved significantly different proportions of the Intermountain West and central California populations. We tested for differences in the total sample, among years, and within each year (2003–2005). Because of the smaller within-year sample size, we used Fisher exact tests. Significance was assessed following a sequential Bonferroni correction for multiple tests (Rice 1989).

RESULTS

Analysis of count data.—The combined-count data set for 1,454 count-days from 1992 through 2006 included 134,060 sightings of juvenile Red-tailed Hawks and showed a bimodal distribution of autumn movement of Red-tailed Hawks through the Marin Headlands ($b = 0.61$; Fig. 2). The first mode occurred at ~15 September. Numbers of juvenile Red-tailed Hawks began increasing to this mode in mid-August and declined to a trough at 30 September. After 30 September, Red-tailed Hawk sightings began to increase, and a second mode occurred in the second week of November. Bimodal distributions corresponding with these dates were observed separately within the yearly data for each year, 1992–2006 (b ranged from 0.56 to 0.73). On the basis of these observations, we divided the Red-tailed Hawk movements through Marin into two discrete phases (period 1: 15 August–30 September; period 2: 1 October–30 November).

Analysis of band-encounter data.—We found a significant difference in the average movement away from the Marin Headlands of juvenile Red-tailed Hawks trapped in period 1 and those trapped in period 2 ($t = 3.04$, df = 121, $P = 0.003$; Fig. 3). The mean movement for juvenile Red-tailed Hawks trapped during period 1 was 0.28° (31 km) south of Marin ($n = 52$), whereas the mean movement for period 2 was 1.16° (129 km) south of Marin ($n = 71$). Comparison of the proportion of males and females suggested a strong similarity between periods of migration. Period 1 included 46% females, whereas period 2 included 41% females (Yates corrected chi-square test, $\chi^2 = 0.06$, $P = 0.80$). As noted by Pitzer et al. (2008), the sexing methodology is more accurate during August and September and is more likely to misidentify females as males in October and November. Therefore, the estimation of 41% females in the period 2 is likely an underestimation.

Analysis of microsatellite data.—Of the 233 juvenile Red-tailed Hawks genotyped by Hull et al. (2008), 98 were sampled during period 1 and 135 during period 2. There was a significant difference in the proportions of Intermountain West and central California populations between the two periods of movement ($\chi^2 = 8.69$, df = 1, $P = 0.003$). Migrants in period 1 were primarily central California genotypes (80 vs. 18), whereas those in period 2 included large proportions of both populations (85 vs. 50). A similar between-period pattern in proportions of populations was observed in each year. However, analyzed by year, only 2003 and 2004 showed a significant difference ($P = 0.01$ and $P = 0.001$, respectively). In 2005, very few Red-tailed Hawks were observed or trapped, particularly during period 2 (only 12 individuals sampled), and no significant difference between migration periods was detected ($P = 0.29$). Period-specific heterozygosity, number of alleles, allelic richness, and private alleles are summarized in Table 1 and were generally similar between migration periods. However, twice as many private alleles were found in the second peak (32 vs. 16) and, of the private alleles found in the second peak, significantly more were found in individuals of the Intermountain West genetic group ($\chi^2 = 17.10$, df = 1, $P < 0.001$).

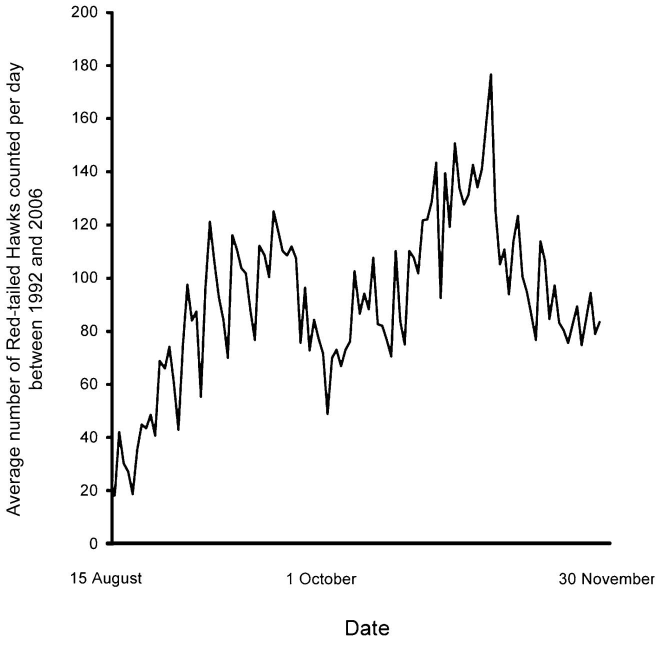

Fig. 2. Average numbers of daily Red-tailed Hawk sightings between 15 August and 30 November, 1992–2006. Two periods of migration activity occurred: the first from mid-August through the end of September and the second from the beginning of October through the end of November.

DISCUSSION

The combined analysis of count, band-encounter, and genetic data provides insight into the migration patterns of Red-tailed Hawk populations in western North America. We found that migration of juvenile Red-tailed Hawks through the Marin Headlands occurred in two distinct periods (Fig. 2). Red-tailed Hawks began to move through Marin in mid-August, and their activity reached a peak in mid-September, before declining to a low at ~1 October. Sightings increased again to a maximum in mid-November and then declined through the remainder of the autumn migration. Band encounters from these two periods of activity of juvenile Red-tailed Hawks revealed significantly different patterns of

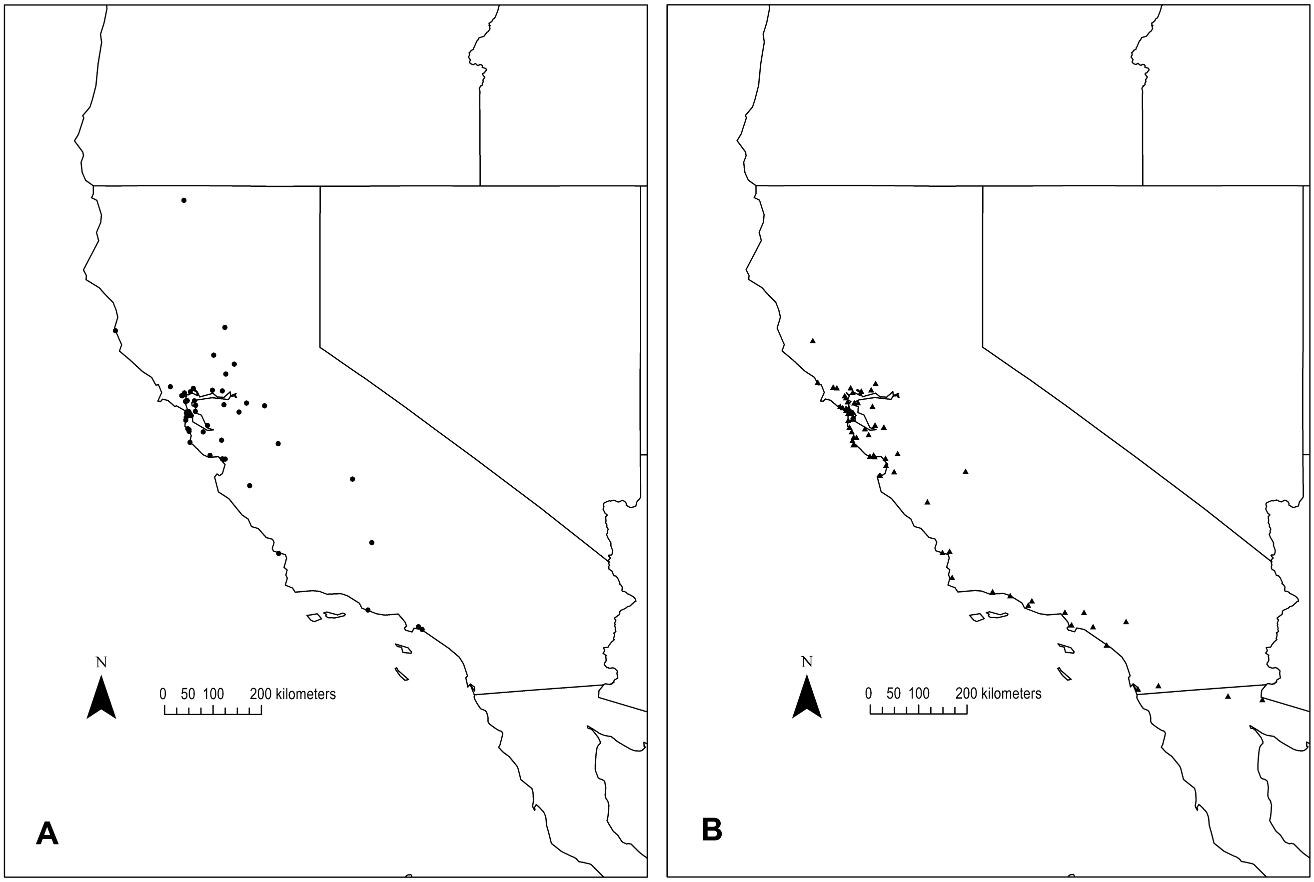

Fig. 3. Maps of 123 Red-tailed Hawk band recoveries (A) from the first period of migration ($n = 52$) and (B) from the second ($n = 71$). Net movement between groups was significantly different, with little net movement north or south during the first peak and more southward movement in the second peak. Each point represents a single band recovery.

movement (Fig. 3). During the early season (period 1), band encounters indicated little net movement north or south and were more suggestive of regional (central California) juvenile dispersal than of directed migration. By contrast, movements during period 2 included both regional movements and flights with a strong directional component to the south, which is more consistent with directed migration. This interpretation is supported by banding and radio- and satellite-telemetry results, which demonstrate that the Pacific Coast migration corridor is used by Red-tailed Hawks originating in both central California and the Intermountain West (Miller 2006, Goodrich and Smith 2008, Golden Gate Raptor Observatory unpubl. data).

Table 1. Genetic diversity data for 233 Red-tailed Hawks sampled during early-season (period 1) and late-season (period 2) migration in the Marin Headlands, California. Number of samples (n), heterozygosity corrected for sample size (H_C), average number of alleles per locus (A_N), allelic richness corrected for sample size (AR_C), and number of private alleles in each region (A_P).

Period	n	H_C	A_N	AR_C	A_P
1	98	0.66 ± 0.01	12.0 ± 8.9	12.0 ± 8.8	16
2	135	0.65 ± 0.01	13.2 ± 10.0	12.4 ± 9.3	32

To our knowledge, this description of migrations of juvenile Red-tailed Hawks through the Marin Headlands is the first statistically supported demonstration of a strongly bimodal avian migration associated with genetically discrete populations. Previous research has suggested bimodal migration among eastern North American Bald Eagle populations (*Haliaeetus leucocephalus*; Bildstein 2006), and bimodal migration has been correlated with sex, age, wintering latitude, and morphology (e.g., Francis and Cooke 1986, O'Hara et al. 2006, Tøttrup and Thorup 2008). The population-genetic migration pattern (central California birds preceding Intermountain West birds) that we observed in Red-tailed Hawks may be attributable, in part, to the Mediterranean climate of central California. The abundant prey base and mild winters in central California allow Red-tailed Hawks to breed at densities higher than those documented elsewhere (Fitch et al. 1946, Wiley 1975) and to remain near breeding territories throughout the year (Preston and Beane 1993). The rich winter prey base also attracts large numbers of wintering Red-tailed Hawks from other regions. As a result, the Marin site observes a combination of regional dispersal and directed migration, whereas stations in the Intermountain West observe individuals that are migrating directionally from more distant breeding populations (Hoffman et al. 2002).

Analysis of microsatellite data suggests that two genetically distinct populations of Red-tailed Hawks pass through the Marin Headlands during autumn migration. These populations are consistent with the central California and Intermountain West populations described in Hull et al. (2008). The first period of Red-tailed Hawk movement involves primarily the central California population, whereas the number of individuals from the Intermountain West population increases significantly in the second period. Band-recovery data suggest that the Intermountain West population originates in the arid regions of northeastern California and other regions within the northwestern Great Basin (Weeks 2006, A. Hull unpubl. data).

Genetic diversity was similar between both periods of migration activity and is consistent with genetic diversity observed among western North American breeding populations of Red-tailed Hawks (Hull et al. 2008). A notable exception was that we detected a much greater number of private alleles (alleles occurring in only a single migration period) in the second period of migration and, of these, significantly more were found in individuals of the Intermountain West population. This result is likely a consequence of the mixed central California–Intermountain West composition of period 2 and not a reflection of differing genetic diversity between peaks. Many unique central California alleles are present in both periods and are not identified as private alleles occurring in just one migration period.

Our data from banding, hawk counts, and molecular genetics provide guidance for interpreting annual Red-tailed Hawk counts and may assist in management decisions. Declines in early- or late-season migrants can be better interpreted as reflecting changes in specific populations of Red-tailed Hawks migrating through the Marin Headlands. The usefulness of these data is illustrated by the following examples taken from the migration count data. During the 2005 migration season, very few Red-tailed Hawks were observed during the time-frame normally associated with a late-season migration period, and this may suggest a phenomenon associated with the Intermountain West population. This is in contrast to the 1998 migration season, when few Red-tailed Hawks were observed throughout the autumn migration, and perhaps indicates a more widespread factor influencing both central California and Intermountain West populations.

Recently, Sergio et al. (2005) described a close relationship between the presence of top predators, particularly raptors, and high ecosystem biodiversity, and emphasized that understanding population connectivity and habitat use in raptors is broadly important for conserving biodiversity. In North America, 22 raptor-migration study sites each observe ≥12,000 Red-tailed Hawks each autumn (Zalles and Bildstein 2000). Many of these study sites have historically focused on either banding or counting but have not combined the two approaches into comprehensive studies. Where it is feasible, we encourage migration study stations to adopt both methodologies, as well as to collaborate with nearby sites where only one or the other approach is possible. We suggest that migration stations continue to share count and band-encounter data and to develop protocols to allow for the archiving of genetic material from raptors that are trapped for banding (e.g., T. B. Smith et al. 2003).

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