

## NATAL DISPERSAL DISTANCE AND POPULATION ORIGINS OF MIGRANT RED-TAILED HAWKS AND COOPER'S HAWKS

CHRISTOPHER W. BRIGGS<sup>1</sup> AND ANGUS C. HULL  
*Golden Gate Raptor Observatory, Sausalito, CA 94965 USA*

JOSHUA M. HULL  
*Department of Animal Science, University of California, Davis, CA 95616 USA*

JILL A. HARLEY  
*Golden Gate Raptor Observatory, Sausalito, CA 94965 USA*

PETER H. BLOOM  
*Bloom Research Inc., Los Angeles, CA 92705 USA*

ROBERT N. ROSENFELD  
*Department of Biology, University of Wisconsin, Stevens Point, Stevens Point, WI 54481 USA*

ALLEN M. FISH  
*Golden Gate Raptor Observatory, Sausalito, CA 94965 USA*

ABSTRACT.—We used a two-step process to determine region of geographic origin for migratory Red-tailed Hawks (*Buteo jamaicensis*) and Cooper's Hawks (*Accipiter cooperii*). First, we used encounter data from the USGS Bird Banding Laboratory to estimate natal dispersal distances of Red-tailed Hawks and Cooper's Hawks. Then we used this information to assess whether hawks banded at migration stations and later encountered as breeding birds could be assigned to an approximate region of origin. Across the USA, the average apparent natal dispersal distance of Red-tailed Hawks was  $137 \pm 287$  km ( $n = 127$ , median = 23 km) and of Cooper's Hawks was  $40 \pm 90$  km ( $n = 70$ , median = 13.5 km). There were no differences in apparent natal dispersal as a function of latitude or longitude across the continent. From data on birds banded at migration stations and then encountered later as likely breeders, we inferred that these encounter locations will, on average, reflect these birds' region of origin. Because individuals of these two species tend to have short natal dispersal distances, we can infer regions of origin from breeding-season encounters of banded individuals originally trapped at migration sites across North America. As an example, we used data from migrating Red-tailed and Cooper's Hawks trapped in the Marin Headlands, California, that were later encountered as likely breeders to assign the region of origin of these individuals. Using this information, we inferred that early-migration-season Red-tailed Hawks originated in central California and that later-migration-season Red-tailed Hawks were a mix of individuals originating from central California and eastern Oregon. Cooper's Hawks captured during migration at Marin originated west of the Cascade and Sierra Nevada Mountains, including areas in northern California, Oregon, and British Columbia. Encounter data for hawks banded during migration then captured later during the breeding season may help migration researchers better understand origins of birds captured at migration sites and better link population trends at migration stations with population trends of breeding birds.

KEY WORDS: *Red-tailed Hawk*; *Buteo jamaicensis*; *Cooper's Hawk*; *Accipiter cooperii*; *banding*; *breeding*; *migration*; *natal dispersal*.

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<sup>1</sup> Present address: Department of Biology, Hamilton College, Clinton, NY 13323; email address: cwbriggs@hamilton.edu

DISTANCIA DE DISPERSIÓN NATAL Y ORÍGENES DE LAS POBLACIONALES DE INDIVIDUOS MIGRATORIOS DE *BUTEO JAMAICENSIS* Y *ACCIPITER COOPERII*

RESUMEN.—Usamos un proceso de dos pasos para determinar el origen geográfico de los individuos migratorios de *Buteo jamaicensis* y *Accipiter cooperii*. Primero, usamos datos de recapturas del Laboratorio de Anillado de Aves del Servicio Geológico de Estados Unidos para estimar las distancias de dispersión natal de *Buteo jamaicensis* y *Accipiter cooperii*. Luego, usamos esta información para evaluar si los halcones anillados en las estaciones de migración y posteriormente encontrados como aves reproductivas podrían ser asignados a una región aproximada de origen. A lo largo de Estados Unidos, la distancia de dispersión natal aparente promedio de *B. jamaicensis* fue de  $137 \pm 287$  km ( $n=127$ , mediana=23 km) y la de *A. cooperii* fue de  $40 \pm 90$  km ( $n=70$ , mediana=13.5 km). No hubo diferencias en la dispersión natal aparente en función de la latitud o longitud a través del continente. A partir de datos de aves anilladas en las estaciones de migración y posteriormente encontradas como aves reproductivas probables, inferimos que estas ubicaciones de encuentro reflejarán, en promedio, el lugar de origen de estas aves. Debido a que los individuos de estas dos especies tienden a tener distancias de dispersión natal cortas, podemos inferir las regiones de origen a partir de los encuentros en la estación reproductiva de individuos originalmente atrapados en los sitios de migración a través de América del Norte. Como ejemplo, usamos datos de individuos migratorios de *B. jamaicensis* y *A. cooperii* atrapados en el Promontorio Marin, California, que luego fueron encontrados como reproductores probables, para asignar la región de origen de estos individuos. Usando esta información, inferimos que los individuos de *B. jamaicensis* de principios de la estación migratoria se originaron en el centro de California, y que los individuos de *B. jamaicensis* de fines de la estación migratoria fueron una mezcla de individuos que se originaron en el centro de California y el este de Oregón. Los individuos de *A. cooperii* capturados durante la migración en Marin se originaron al oeste de las Montañas de las Cascadas y de Sierra Nevada, incluyendo áreas en el norte de California, Oregón y Columbia Británica. Los datos de encuentros de halcones anillados durante la migración y luego capturados durante la estación reproductiva pueden ayudar a los investigadores a entender mejor los orígenes de las aves capturadas en los sitios de migración y a vincular mejor las tendencias poblacionales en las estaciones de migración con las tendencias poblacionales de las aves reproductivas.

[Traducción del equipo editorial]

Datasets from raptor migration sites have become important conservation tools in the last century because they can be used to estimate changes in raptor population sizes and even to help identify underlying causes of those changes (Farmer et al. 2007). For example, understanding the Bald Eagle (*Haliaeetus leucocephalus*) and Peregrine Falcon (*Falco peregrinus*) population declines that resulted from DDT use was facilitated by examining raptor migration data in the 1960s (Carson 1962; Hickey and Anderson 1968). More recently, migration count data have been useful for detecting American Kestrel (*F. sparverius*) population declines across much of the species' range (Smallwood et al. 2009; Farmer and Smith 2009), and for investigating possible causes of these declines (Ely et al. 2018). Since the 1950s, over 300 raptor migration sites have been monitored within North America, making their data a potentially valuable resource for understanding migrating raptor populations (Dunn and Hussell 1995, Farmer et al. 2007, Martín et al. 2016). However, the geographic region of origin of raptors documented at migration sites is often unknown. Uncertainty of region of origin of raptors captured

at any given migration site limits our ability to understand the implications of apparent population trends because we cannot determine which breeding population(s) may be influencing the migratory population (Farmer et al. 2007). Without knowledge of "catchments" of a migration site (i.e., geographic areas from which a migration site draws birds), we cannot understand which populations are actually being monitored at the migration station, limiting our ability to look for causes of any observed changes in the migrant population(s). Developing an understanding of migration catchments of each raptor migration site may allow data collected at multiple, isolated migration sites to be synthesized to better explain local and regional trends in breeding populations (Bildstein et al. 2008).

Although a number of methods to aid in determining the region of origin of individuals have become available to researchers in recent years, none have proved to be a panacea for assigning regions of origin. For example, stable isotopes (Hobson et al. 2004) may not be reliable for determining origins of at least some raptors due to a lack of reproducibility within a population or

individual (Briggs et al. 2017, Smith et al. 2008, 2009; but see Meehan et al. 2003). Because many methodologies often lack fine-scale spatial resolution, we examined the utility of band encounters as a method of determining geographic region of origin of migrant raptors (i.e., region where an individual fledged). Following the United States Geological Survey Bird Banding Lab (BBL) protocol, we consider a band encounter as any report of a banded hawk, dead or alive. If natal dispersal distances (distance from the natal site to the first nesting territory; Greenwood and Harvey 1982) is short (e.g., <100 km) across a species' range, then the future encounter location of a breeding individual originally banded at a migration site could be used as a proxy for assigning region of origin of that individual (Hoffman et al. 2002). Based on this, migration researchers could use encounter locations of banded birds during the breeding season to assess each migration station's catchment. Additionally, we could potentially assess any intra-seasonal or long-term changes in region of origin of individuals captured at a migration banding site and look for migration patterns.

We used banding and encounter data from the BBL to estimate the apparent natal dispersal distance of Red-tailed Hawks (*Buteo jamaicensis*) and Cooper's Hawks (*Accipiter cooperii*) across North America. Here we define apparent natal dispersal distance as the distance between the natal site and the assumed first nesting territory. Because we did not have accurate data on breeding status of birds banded as nestlings, we created simple rules to indicate when we assumed an encountered individual should have been on a breeding territory based on date, latitude, and age of the individual (i.e., excluding pre-breeding individuals). That is, any individual encountered within the defined breeding season and older than a specific age was defined as a likely breeder (e.g., Amar et al., 2019).

To demonstrate the utility of data for birds banded at migration sites then encountered later during the breeding season, we used these criteria (i.e., encounters during the breeding season of individuals old enough to be breeding) to infer regions of origin for birds migrating through the Marin Headlands, California (37.83° N, 122.50° W; Hull et al. 2009). The Marin Headlands lie just north of the city of San Francisco, California, along the Marin peninsula, which funnels raptors between the Pacific Ocean to the west and San Francisco Bay to the east. Genetic research indicates that migrating Red-tailed

Hawks that arrive earlier in the fall migration season at the Marin Headlands generally originate from central California, and individuals that arrive after 1 October (late season) generally originate from both central California and the Intermountain West (Hull et al. 2009, Jasper et al. 2014). In addition, the majority of the migrants observed or captured are juveniles (Hull et al. 2009). We predict that our encounter data will generally reflect the genetic work of Hull et al. (2009). To further demonstrate the potential of utilizing encounter data, we examine whether later migrants originate farther from the Marin Headlands than early arrivals, and whether encounter data suggest shifts in the regions of origin of birds captured at Marin over the course of the 30 yr of data collected, e.g., as a result of climate change (Jenni and Kéry 2003).

#### METHODS

**Natal Dispersal Distance.** We obtained data for Red-tailed Hawks and Cooper's Hawks banded as nestlings then encountered across the US from 1940 through 2014, from the BBL. Because we wanted to include only apparently breeding birds, we first eliminated any individual whose encounter code indicated timing of encounter was unknown (i.e., codes 50 [Found dead: band with skeleton or bone only], 56 [Obtained: letter simply states in effect "I obtained this bird"], and 98 [Band or band number only obtained. No further information available]).

We split the breeding range for both Red-tailed Hawks (Table 1) and Cooper's Hawks (Table 2) into three regions (north, central, and south) based on latitude, to account for differences in nest-initiation date across latitudes. We defined the south region from 26<sup>th</sup> to 37<sup>th</sup> parallel, the central region from the 37<sup>th</sup> to 46<sup>th</sup> parallel, and the north region as everywhere north of the 46<sup>th</sup> parallel. We defined the breeding period, the portion of the breeding season during which individuals were likely breeding and on territory, according to published average dates of incubation within each region (i.e., north, central, and south), which generally corresponded to the start of incubation, and average dates of fledging (Tables 1 and 2). We shifted the date of the beginning of the breeding period for the southern region to approximately the middle of the incubation period to avoid including northern migrants that had not yet started their northward migration.

To determine a cut-off for identification of breeders vs. nonbreeders during the described

Table 1. Dates used to define the breeding period for each region of North America for Red-tailed Hawks.

REGION	BREEDING START DATE	BREEDING END DATE	SOURCE
North	April 20	July 30	Craighead and Mindell 1981; Luttich et al. 1971; Johnson 1975
Central	April 10	July 20	Minor et al. 1993; Orians and Kuhlman 1956; Smith and Murphy 1973
South	April 1	July 1	Mader 1978

periods above, we examined movement distance by age for both species. We used an ANOVA to examine differences among age classes with distance from natal site to encounter site as the response variable and each age class as a predictor, with the oldest birds pooled together due to sparse data. Based on these dispersal distances (Fig. 1A) and other sources, we believe that Red-tailed Hawks 33 mo or older were likely breeding, so we then removed from the dataset all Red-tailed Hawks encountered within 33 mo of hatching. Similarly, based on qualitative differences between age groups (Fig. 1B) and other sources (Rosenfield et al. 2019), we removed Cooper's Hawks < 21 mo old from the dataset, as they were likely to be nonbreeders.

Once the data had been narrowed to individuals encountered while likely breeding (hereafter likely breeders), we used ArcGIS 10.2 to determine distances between natal site and assumed nesting territory. As most BBL data were reported only to the nearest 10-minute block, we used the center of the block as the natal or encounter location. We assumed a natal dispersal distance of 9.7 km when both natal banding and subsequent encounter (breeding) locations were reported within the same 10-minute block, because 9.7 km is the approximate distance between the center and edge of a 10-minute block (Gustafson et al. 1997).

We used a general linear model (glm) to examine associations between year, latitude of encounter, longitude of encounter, and age class at encounter and apparent natal dispersal distance of the likely breeders, for each species. Age was treated as a continuous variable in our glm analyses.

**Regions of Origin for Hawks Banded in Marin Headlands.** We used data from migrants trapped in the Marin Headlands of California to assess the utility of these types of data for estimating regions of origin and migration patterns. We trapped migrant raptors from mid-August through early January from 1983 through 2014. We used *staffelmauser*, or wave molt, of Red-tailed Hawks (Clark 2004, Pyle 2006) and retained back or breast coverts of Cooper's Hawks (Boal 2001) to identify second-year (SY) and after-second-year (ASY) individuals. If an individual's age could not be determined more precisely than after-hatch-year (AHY) by its plumage, then we conservatively treated it as an SY bird in this analysis. For example, a Red-tailed Hawk banded during fall migration and classified then only as AHY would be excluded from our analysis if it was encountered during the next breeding period following capture. We tried to verify the timing and coordinates of each encounter, and confirm the encounter code provided by the BBL by contacting the person who reported the band. We applied the same rules described above to the individuals originally banded at the Marin Headlands and later encountered to define likely breeders. We mapped the locations of encounters that met all criteria to examine regions of origin relative to migration patterns.

*Red-tailed Hawks.* For simplicity, we defined encounter areas similar to those outlined by Hull et al. (2009): central California and the Intermountain West. For migration patterns, we differentiated between two distinct peaks of juvenile (HY) Red-tailed Hawk migration, where the first peak of Red-tailed Hawk migration lasted from mid-August

Table 2. Dates used to define the breeding period for each region of North America for Cooper's Hawks.

REGION	BREEDING START DATE	BREEDING END DATE	SOURCE
North	May 15	July 30	Craighead and Mindell 1981; Campbell et al. 1990; Nennenman et al. 2002
Central	May 5	July 20	Henny et al. 1985; Meng and Rosenfield 1988; Reynolds and Wight 1978
South	May 1	July 15	Asay 1987; Layne 1986; Millsap 1981

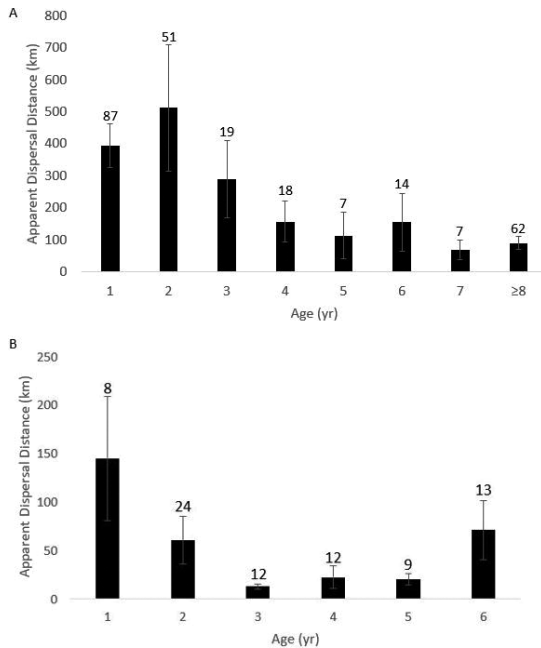


Figure 1. Mean apparent dispersal distances and SE by age (in yr) of (A) Red-tailed Hawks and (B) Cooper's Hawks banded as nestlings and later encountered during the breeding period from across the United States. Age is rounded; therefore, a bird labeled as 1-yr-old is actually a second-year bird (i.e., age approximately 10–14 mo). For Red-tailed Hawks age  $\geq 3$  yr, and Cooper's Hawks  $\geq 2$  yr, apparent dispersal distance is considered to be apparent natal dispersal distance. Sample size is shown above bars.

through 30 September (early), and the second peak from 1 October through 31 December (late) each year. We used linear models to evaluate the variation in distance between encounter location (i.e., region of origin) and Marin as a function of migration pattern (early vs. late) and year of capture. We used a backward stepwise method to distinguish significant variables.

**Cooper's Hawks.** We used linear models to evaluate the variation in distance between encounter location (i.e., region of origin) and Marin as a function of day of year (i.e., standardized dates across all years) and year of capture to examine migration timing and changes in migration catchment over time. Because Cooper's Hawks did not display multiple peaks of migration, we used day of year captured rather than a dichotomous variable as in the Red-tailed Hawks.

For both species we tested residual normality with a Shapiro-Wilk test and tested model residual

homoscedasticity using a Breusch-Pagan test. For all tests we assumed  $\alpha = 0.05$ .

## RESULTS

**Natal Dispersal Distance. Red-tailed Hawks.** A total of 12,364 encounters of Red-tailed Hawks were reported to the BBL between 1940 and 2014. After reducing the data to include only encounters that occurred during the defined breeding periods, we found no differences in dispersal distance among age classes ( $F_{7, 257} = 1.81$ ,  $P = 0.08$ ,  $n = 265$ ; Fig. 1A). ANOVA results met assumptions of both residual normality and homoscedasticity ( $P > 0.05$ ). Then, as described in Methods, we removed hawks  $< 33$  mo old at the time of encounter from the dataset.

After removal of younger hawks, only 127 of the encountered Red-tailed Hawks met our criteria as likely breeders. Of those, 35 were banded as nestlings in the southern region, 78 in the central region, and 14 in the northern region. Of these 127 birds, 21 (16.5%) were encountered within the same 10-min block in which they were banded as nestlings. Average apparent natal dispersal distance was  $137 \pm 287$  km (median = 23 km) and range was 9.7–2071.8 km. There was no association between apparent natal dispersal distance and year of capture ( $t = -0.62$ ,  $P = 0.55$ ,  $n = 127$ ,  $\beta = -1.08 \pm 1.79$ ), age at encounter ( $t = -1.29$ ,  $P = 0.20$ ,  $n = 127$ ,  $\beta = -7.20 \pm 5.58$ ), latitude ( $t = 0.09$ ,  $P = 0.93$ ,  $n = 127$ ,  $\beta = 0.48 \pm 5.04$ ), or longitude ( $t = -0.29$ ,  $P = 0.77$ ,  $n = 127$ ,  $\beta = -0.54 \pm 1.86$ ).

**Cooper's Hawks.** A total of 4743 encounters of Cooper's Hawks were reported to the BBL. After reducing the data to include only encounters that occurred during the defined breeding periods, we found no differences in dispersal distance among age groups ( $F_{5, 103} = 0.95$ ,  $P = 0.45$ ,  $n = 109$ ; Fig. 1B). ANOVA results met assumptions of both residual normality and homoscedasticity ( $P > 0.05$ ). Then, as described in Methods, we removed hawks  $< 21$  mo old at the time of encounter from the dataset.

After removal of younger hawks, only 70 of the encountered Cooper's Hawks met our criteria as likely breeders. Of those, 9 were banded as nestlings in the southern region, 46 in the central region, and 15 in the northern region. Of these 70 birds, 20 (29%) were encountered within the same 10-min block in which they were banded as nestlings. Average apparent natal dispersal distance was  $43 \pm 88$  km (median = 13.5 km) and range was 9.7–350 km. There was no relationship between apparent natal dispersal distance and age at encounter ( $t =$

0.93,  $P = 0.36$ ,  $n = 70$ ,  $\beta = 5.61 \pm 6.05$ ), latitude ( $t = 0.98$ ,  $P = 0.33$ ,  $n = 70$ ,  $\beta = 2.26 \pm 2.31$ ), or longitude ( $t = -1.53$ ,  $P = 0.13$ ,  $n = 70$ ,  $\beta = -1.31 \pm 0.86$ ). The average natal dispersal distance of likely breeding Cooper's Hawks trended down by 3.3 km each year between 1974 and 2014 ( $t = -3.08$ ,  $P = 0.003$ ,  $n = 70$ ,  $\beta = -3.27 \pm 1.06$ ); however, when an outlier banded on 7 August 1974 was removed, the relationship was no longer significant ( $t = -1.546$ ,  $P = 0.13$ ,  $n = 69$ ,  $\beta = -1.27 \pm 0.82$ ). Residuals were normally distributed (Shapiro-Wilk test  $P > 0.05$ ) and homoscedastic (Breusch-Pagan test  $P > 0.05$ ).

**Regions of Origin for Hawks Banded in the Marin Headlands.** Fifty-seven Red-tailed Hawks banded as migrants in the Marin Headlands and encountered elsewhere met our criteria for likely breeder. These hawks had apparent regions of origin in central California and throughout California and the Intermountain West (Fig. 2). Red-tailed Hawks captured and banded during the first peak of migration (early period) at Marin apparently originated an average of  $163 \pm 250$  km ( $n = 34$ ) from the site, in areas clustered in central California. For individuals captured and banded during the second peak of migration (late period), the distance to the region of origin averaged  $339 \pm 342$  km from Marin ( $n = 23$ ) and regions of origin were more broadly distributed across the northern California coast and eastern Oregon (Fig. 2). The Intermountain West seemed to be the origin of birds from both the early ( $n = 3$ ) and late ( $n = 5$ ) migration periods. Migration period (early vs. late) was a significant predictor of distance of the region of origin from the Marin Headlands ( $t = -2.09$ ,  $P = 0.04$ ,  $\beta = -161.32 \pm 77.02$ ), but year of capture was not ( $t = -1.91$ ,  $P = 0.06$ ,  $\beta = -9.10 \pm 4.76$ ). Residuals were normally distributed (Shapiro-Wilk test  $P > 0.05$ ) and homoscedastic (Breusch-Pagan test  $P > 0.05$ ).

Thirty-four Cooper's Hawks banded as migrants in the Marin Headlands and encountered elsewhere met our criteria for likely breeders. These birds had apparent regions of origin west of the Sierra Nevada and Cascade Mountains, ranging from Oregon to Baja California (Fig. 3). There was no relationship between distance from presumed nesting area to the Marin Headlands and day of the year ( $t = 0.32$ ,  $P = 0.75$ ,  $\beta = 0.92 \pm 2.81$ ) or year captured ( $t = 0.14$ ,  $P = 0.89$ ,  $\beta = 1.29 \pm 9.15$ ).

#### DISCUSSION

Overall Cooper's Hawks and Red-tailed Hawks appeared to have relatively low apparent natal

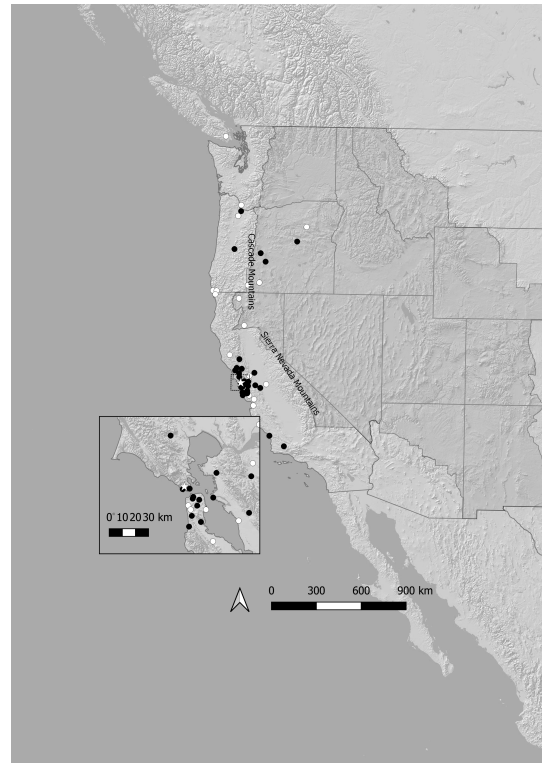


Figure 2. Locations of encounters of likely breeding Red-tailed Hawks originally banded as migrants between 1983 and 2014 in the Marin Headlands, California (white star). Likely breeders were encountered during the breeding period and were at least 33 mo old. Dark gray areas represent the Intermountain West, black circles indicate individuals trapped during the first migration peak (i.e., mid-August – 30 September), and white circles indicate individuals trapped during the second migration peak (i.e., 1 October – 31 December).

dispersal distances, and usually return to near their natal areas to breed (e.g., within 10 territory lengths; Shields 1982), though there were a few outliers, which indicates median may be a more appropriate metric of natal dispersal distance. Because apparent natal dispersal distance was low, we could investigate assumed regions of origin of migrants from each species. In addition, this noninvasive approach can utilize historical encounter data to better refine our understanding of migrant population(s) and address questions regarding migration in relation to climate change or migration strategy (e.g., differences in migration timing or location between age or sex classes).

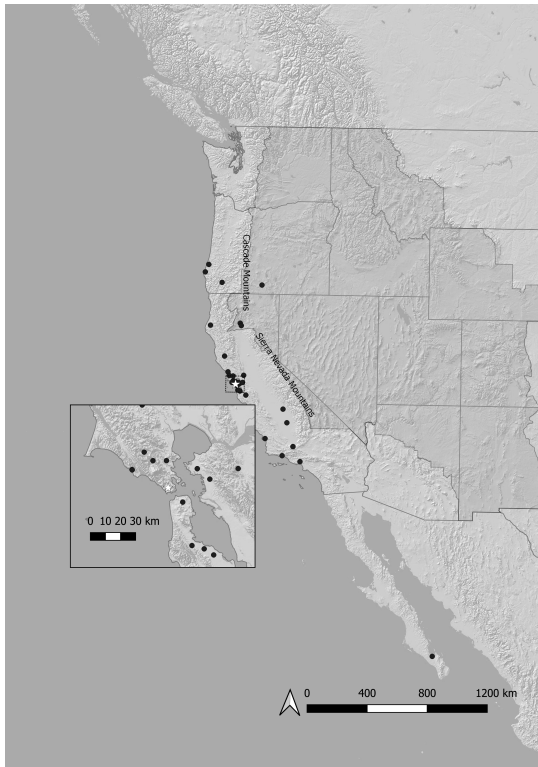


Figure 3. Locations of encounters of likely breeding Cooper's Hawks originally banded as migrants between 1983 and 2014 in the Marin Headlands, California (white star). Likely breeders were encountered during the breeding period and were at least 21 mo old.

Apparent natal dispersal distance of likely breeders for both species was greater than what has been reported previously. Our estimate of  $101 \pm 201$  km for apparent natal dispersal distance of Red-tailed Hawks was greater than that reported in southern California, using both recaptures and encounters (Bloom et al. 2011), or in the northeastern US (Morrison and Baird 2016). Both these studies also used encounter data from the BBL, allowing us to compare our estimates. Cooper's Hawks encountered in our study had an apparent natal dispersal distance of  $43 \pm 88$  km, which was greater than the 12.4 km reported for Wisconsin Cooper's Hawks, though this study relied only on local encounters (Rosenfield and Bielefeldt 1992). The differences between our results and previous research may be due to a combination of factors, e.g., previous studies missing individuals that dispersed outside

the study area or variations in sample size or population residency status.

Alternatively, our higher estimates of apparent natal dispersal distance relative to previous studies might be the result of inherent limitations in the methodology. We note that our estimates of apparent natal dispersal distance should not be taken as a precise estimate, because we could not verify breeding status of encountered birds during the breeding period, and due to the lack of precision when individuals were reported within a 10-minute block. Thus, our estimates may be biased high due to the accidental inclusion of individuals that were not actually breeding but were still on their wintering grounds or in migration, or were reported to the BBL with incorrect information. Another possible reason our estimates were higher than those of Morrison and Baird (2016) might be that those researchers excluded individuals that dispersed  $>250$  km from their analysis, assuming individuals that were  $>250$  km from their natal site were not breeding. However, from the viewpoint of a migration bander, we cannot know which individuals may be outliers and we must acknowledge that there will be uncertainty in our estimates of regions of origin (i.e., that some individuals that otherwise met the criteria established here either were not breeders or were long distance-dispersers). We found some evidence of possible error in using our criteria with BBL encounter data: of the six Red-tailed Hawks that dispersed  $>1000$  km, five were  $<6$  yr old and five were banded north of the 43<sup>rd</sup> parallel, suggesting they were still on their wintering grounds or migrating, or were not yet breeding adults (P. Bloom unpubl. data). Therefore, we might be able to improve the precision of our estimates at the cost of losing data by further restricting the timeframes associated with breeding in the northern region.

There were no trends in latitude or longitude for either species in apparent natal dispersal distance. Because apparent natal dispersal distance was short across the US, migration banders could use encounters of breeding individuals to infer regions of origin of the migrants to determine the migration catchment for their site. Despite a few apparently relatively large errors in assigning regions of origin, the overall general short natal dispersal distance appears to lend credence to our ability to examine origins of migrants.

This approach provided insights on both species for individuals migrating through the Marin Headlands. Although our small sample sizes were small,

particularly in the Intermountain West, we found a similar pattern of Red-tailed Hawk region of origin as Hull et al. (2009). Specifically, early migrants were apparently from central California and later migrants more frequently originated from eastern Oregon (i.e., the Intermountain West). Individuals from all times in the migration season likely originated from west of the Cascade Mountains, suggesting that the Marin Headlands has migrants from coastal regions through southern British Columbia (e.g., Smith et al. 2003). Whereas the genetic information from Hull et al. (2009) was limited to describing birds from the large (over 500,000 km<sup>2</sup>) Intermountain West region, our analysis points to a more specific area within the Intermountain West. Specifically, our analysis points to areas east of the Cascade Mountains in Oregon and Washington as the likely origin of those individuals from the Intermountain West. These data suggest there could be differential migration and overwintering strategies of birds nesting in different parts of the Intermountain West (i.e., there could be high migratory connectivity within areas of the Intermountain West but not among areas). Thus, birds farther east or south within the Intermountain West may have different migration or overwintering strategies, though we will need larger sample sizes to assess specific hypotheses about movements among populations and trends over time.

Whereas most Cooper's Hawks we trapped apparently originated near (<100 km) the Marin Headlands or farther north, seven individuals apparently originated from south of the migration station. These data suggest that southern California Cooper's Hawks may undergo a northward summer migration, as already shown by Bloom et al. (2017) for birds banded in southern California. However, it is notable that this phenomenon may occur more broadly in the southern half of California, as the seven individuals were encountered in widely separated areas. These individuals may then follow the coastal route of other migrants moving south, or may still be heading north as indicated by some VHF telemetry data collected from the Marin Headlands (A. Hull unpubl. data). Interestingly, we found no temporal trend in region of origin for either Red-tailed Hawks or Cooper's Hawks, in contrast to Paprocki et al. (2014) who found that winter centers of migratory raptors may be moving north.

Although utilizing band encounters gives us a window into regions of origin for Red-tailed Hawks and Cooper's Hawks banded at Marin, we do not expect it to yield similarly rewarding results for all

populations of these species. For example, banded raptors breeding in and around the heavily populated Bay Area of California that surrounds the Marin Headlands (e.g., San Francisco, Oakland, San Jose) are more likely to be encountered than individuals in the less-populated Intermountain West or northern California coast. Without alternate methods that can eliminate reporting biases associated with human population density, such as satellite telemetry, banding cannot be used to determine the relative proportions of regions of origin for migratory birds, as band encounters will undoubtedly underrepresent birds coming from areas with low human population densities (Bildstein and Peterjohn 2012). In addition, some species have very low encounter rates as breeding adults. For example, Sharp-shinned Hawks (*A. striatus*) have low encounter rates (approximately 1%; Lutmerding et al. 2012). If encounter rates are low, few data will be available for analysis, particularly during the breeding season, when some species (e.g., Sharp-shinned Hawks and Broad-winged Hawks [*B. platypterus*]) may be difficult to find, thus limiting the utility of band encounters to determine regions of origin.

Though migrant encounter data during the breeding period may help provide information on regions of origin, there are limitations, such as inability to detect outliers or individuals who are not actually breeding. Therefore, we recommend that raptor migration sites employ multiple methodologies to determine regions of origin. This will have to be done separately for each species of interest, given different migration strategies and breeding distributions. However, for species that are caught in large numbers and have relatively high encounter rates, such as Golden Eagles (*Aquila chrysaetos*) and Peregrine Falcons (Lutmerding et al. 2012), this technique may begin to illuminate how birds migrate within the continental landscape and will allow analyses such as the Raptor Population Index (Farmer et al. 2007) to have a more nuanced description of trends occurring across a broad region.

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