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FACULTATIVE MIGRATION: NEW INSIGHT FROM A RAPTOR

MICHAEL D. MCCRARY¹ AND PETER H. BLOOM

Bloom Research, Inc., 1358 1/2 Cloverdale Avenue, Los Angeles, CA 90019 USA

SPENCER PORTER

Communications Specialists Inc., 426 West Taft Avenue, Orange, CA 92865 USA

KARYN J. SERNKA

Bloom Research, Inc., 1358 1/2 Cloverdale Avenue, Los Angeles, CA 90019 USA

ABSTRACT.—We studied migration of a female and male Red-tailed Hawk (*Buteo jamaicensis*) from southern California with satellite telemetry over 9.3 and 6.7 yr, respectively. Previous research suggested the migratory fraction of southern California's Red-tailed Hawk population was limited to juveniles and young adults, and that these hawks ceased migrating once they acquired a territory and mate, usually at 3 yr of age. Both hawks in this study ceased migrating at 3 yr of age, the year they both first nested, and did not migrate for the next 4 and 3 yr, respectively. However, both hawks resumed migrating in 2014, the year with the lowest recorded precipitation in California history. The male did not migrate in 2015, the last year we were able to track his movements, while the female switched between migrating (2015 and 2017) and residency (2016) over the next 3 yr. To our knowledge, our study is the first to document individual raptors displaying such switching behavior.

KEY WORDS: *Red-tailed Hawk*; *Buteo jamaicensis*; *California*; *facultative migration*; *satellite tracking*; *summering area*.

MIGRACIÓN FACULTATIVA: NUEVAS PERSPECTIVAS DESDE UNA RAPAZ

RESUMEN.—Estudiamos la migración de una hembra y de un macho de *Buteo jamaicensis* desde el sur de California a lo largo de 9.3 y 6.7 años, respectivamente, usando telemetría satelital. Investigaciones previas sugirieron que la fracción migratoria de la población de *B. jamaicensis* del sur de California se limitaba a juveniles y adultos jóvenes, y que estos individuos dejaban de migrar cuando adquirían un territorio y una pareja, usualmente a la edad de 3 años. Ambos individuos de este estudio dejaron de migrar a los 3 años de edad, siendo el año en que ambos anidaron por primera vez, y no migraron en los próximos 4 y 3 años, respectivamente. Sin embargo, ambos individuos volvieron a migrar en el año 2014, cuando se registraron las precipitaciones más bajas en la historia de California. El macho no migró en 2015, el último año en que pudimos seguir sus movimientos, mientras que la hembra alternó entre migrar (2015 y 2017) y residir (2016) en esos años. Hasta donde sabemos, nuestro estudio es el primero en documentar este comportamiento de alternancia migratoria en rapaces a nivel individual.

[Traducción del equipo editorial]

Migratory birds can be divided into two broad categories based on the causal mechanisms for migration: obligate migrants and facultative migrants (Berthold 2001). Obligate migrants tend to migrate at the same time, in the same

direction, and to the same wintering areas each year (Berthold 1996). Such genetically “hardwired” migration has obvious benefits, especially for young, inexperienced birds migrating for the first time across vast, unknown regions. Conversely, migration of facultative migrants tends to be more flexible (Newton 2012) and may be particularly

¹ Email address: mikedmccrary@gmail.com

sensitive to environmental factors that fluctuate widely between years, such as weather and food availability (Berthold 1996). Thus, facultative migrants may be more resilient to environmental change than obligate migrants (Gilroy et al. 2016).

Although obligate migrants have been studied in both the laboratory and the field, facultative migrants have received far less attention (Newton 2012). Because many decisions regarding migration in facultative migrants are made by individuals, in the past research was limited by the difficulty in tracking individual migrants (Robinson et al. 2010). With the advent of radio and satellite transmitters and geolocators, recent studies have documented a previously unknown range of migratory flexibility of individuals. Individuals may vary the timing of migration (Kjellén et al. 2001), route taken (Bobek et al. 2008), and wintering area (Dias et al. 2011) between years. However, migration comes with certain inherent risks (Klaassen et al. 2014), and the ultimate degree of flexibility would be for an individual to choose between migration and residency each year. Although there is indirect evidence that facultative migrants regularly make this decision (e.g., irruptive species, Newton 2012), switching back and forth between migration and residency by known individuals has been documented for only a few species (Great Bustards [*Otis tarda*], Palacín et al. 2011; Eurasian Skylarks [*Alauda arvensis*], Hegemann et al. 2015; and American Dippers [*Cinclus mexicanus*], Gillis et al. 2008). Accordingly, the circumstances that drive individuals to migrate in some years and not others remain largely unknown.

We tracked the daily movements of a female and a male Red-tailed Hawk from southern California via satellite telemetry from fledging until their transmissions ceased after 9.3 and 6.7 yr, respectively. Here, we describe the migrations of the two hawks, their incidence of switching between migration and residency, and the apparent influence of severe drought on their behavior.

METHODS

In 2008, we tagged a female nestling with a GPS satellite transmitter (Transmitter ID 65994-3) and in 2009, a male fledgling with a Doppler satellite transmitter (65999-2; see Bloom et al. 2015 for details on study area, transmitter weight, attachment method, and duty cycles). The female's GPS transmitter consistently provided more accurate locations, which allowed us to track her movements from one night to the next. Fewer accurate locations were available with the Doppler transmitter, and in some cases, the male's daily movements were determined from a few hours after sunrise or a few hours before sunset.

We considered northward migrations of the two hawks to begin at either their natal territory or home range, and end at a summering area. We define a summering area as an area of concentrated use (>15 d) and localized, randomly oriented daily movements (mean ≤ 5 km/d) as

compared to the longer (mean >100 km/d) north- or south-oriented daily movements characteristic of migration. We considered the hawks to have completed a migration when they returned south to a previously occupied or newly established home range.

We used NCSS statistical software (Hintze 2007) for statistical analyses. Means are reported \pm SD unless otherwise specified, and we used $\alpha = 0.05$ as the level of significance for statistical tests. Daily precipitation data were compiled from three weather stations near (<25 km) each hawk's southern California home range. Precipitation data were from the Global Historical Climatology Network-Daily Database (Menne et al. 2012) and were obtained from the National Centers for Environmental Information website (<https://www.ncdc.noaa.gov>).

RESULTS

Female (65994-3). We tracked the female's movements from when we tagged her with a satellite transmitter as a nestling in June 2008 until her satellite transmissions ceased in September 2017, a period of 9.3 yr. During this time she migrated six times (Fig. 1A and 1B); all six were in a northward direction, which is the typical direction of summer migration of Red-tailed Hawks from southern California (Bloom et al. 2015). During her northward migrations and southward returns, she remained within an approximately 200-km-wide corridor east of the Sierra Nevada Mountains (Fig. 1A and 1B). Her movement rates during migration were similar to those of other large raptors (see Kjellén et al. 2001). Daily rates of northward (mean = 181 ± 94 km/d, $n = 33$, range = 52–428) and southward (203 ± 110 km/d, $n = 23$, range = 19–433) migrations were not significantly different (t -test = 0.4, $P = 0.42$), and her overall mean rate was 190 ± 101 km/d ($n = 56$).

The female's migrations in her first year (Fig. 1A) were more complex and varied than her subsequent migrations. She first migrated north from the vicinity of her natal nest in August 2008 when approximately 13 wk of age. She traveled 1059 km to the Great Basin Desert of southeastern Oregon (Fig. 1A), where her daily movements decreased sharply (mean = 4 ± 3 km/d, $n = 17$) compared with her daily movements during migration (see above). After remaining in Oregon for 17 d, she began traveling south on 27 August, reaching a point 38 km from her natal nest 4 d later (Fig. 1A). She remained in southern California for only 2 d, and then returned north to a new summering area (mean = 2.5 ± 1.9 km/d, $n = 36$) in the Sonoma Range of northern Nevada, 140 km south of her previous summering area (Fig. 1A). This was the only year she made such a brief back-and-forth trip. After 41 d in the Sonoma Range, she returned south in October 2008 and settled just east of San Diego, California (Fig. 1A). In all subsequent migrations, she traveled directly to the Sonoma Range and remained there until returning south to her home range near San

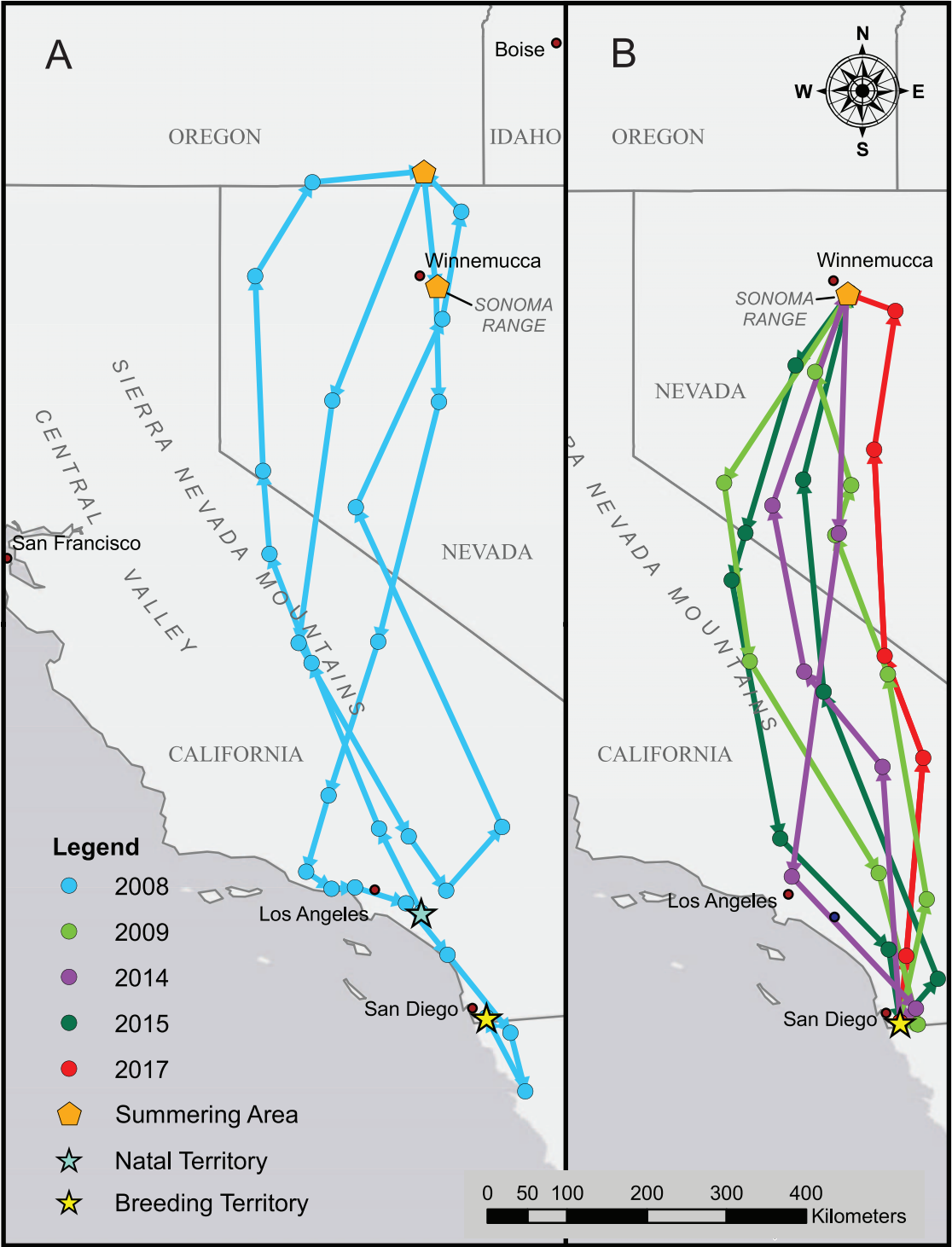


Figure 1. Migrations of Red-tailed Hawk female 65994-3 as determined by satellite telemetry in (A) 2008, and (B) 2009, 2014, 2015, 2017.

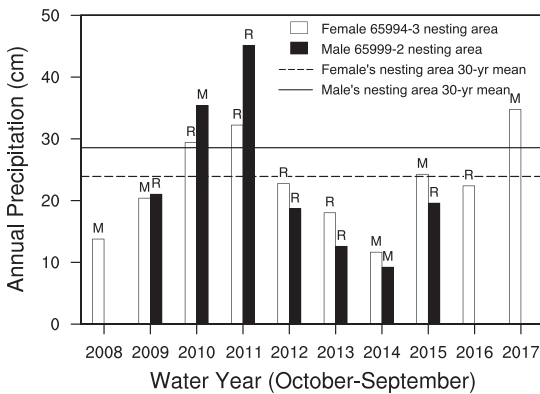


Figure 2. Trends in annual precipitation (October–September) from weather stations in the vicinity of summer home ranges of female 65994-3 and male 65999-2. M above a bar indicates the hawk migrated that year, while R indicates the hawk was resident.

Diego (Fig. 1B). She again migrated north in July 2009 and returned south in September 2009 (Fig. 1B). She did not migrate for the next 4 yr but remained in her home range for the entire period. We first observed her with two nestlings in 2011 when she was 3 yr old. In August 2014, she once again migrated north to her summering area (Fig. 1B). Her resumption of migration after 4 yr occurred during an extreme drought; precipitation in the vicinity of her home range in 2014 was $<50\%$ of the 30-yr average for the area and was the lowest during the period we tracked her movements (Fig. 2). She also migrated in July 2015 (Fig. 1B) but remained in her home range throughout 2016. She again migrated in July 2017 (Fig. 1B), but her satellite transmissions ceased in September while she was still in her summering area in the Sonoma Range.

Male (65999-2). We tracked the movements of the male from when we tagged him with a satellite transmitter in June 2009 shortly after he fledged until he either died or his transmitter detached in February 2016, a period of 6.7 yr. During this period he migrated north twice (Fig. 3). The two migrations covered a much broader area than those of the female and included both the eastern and western sides of the Sierra Nevada Mountains (Fig. 3). His daily rates of northward (mean = 109 ± 94 km/d, $n = 30$, range = 3–385) and southward (155 ± 103 km/d, $n = 17$, range = 18–378) migrations were not significantly different ($t = 0.1$, $P = 0.14$), and his overall mean rate was 126 ± 99 km/d ($n = 47$).

The male's two migrations were both different from each other and from those of the female. Unlike the female, he did not migrate during his first year but remained <30 km from his natal nest throughout 2009. He migrated north for the first time in August 2010, at approximately 16 mo of age. He traveled 800 km (Fig. 3) to an area in northern Nevada approximately 90 km east of

the Sonoma Range, where his daily movements decreased sharply (mean = 3.1 ± 2.9 km/d, $n = 22$). After remaining in his first summering area for 36 d, in September he traveled approximately 600 km southwest to an area in the Central Valley of California (Fig. 3), where his daily movements again decreased sharply (3.4 ± 3.6 km/d, $n = 21$). After occupying his Central Valley summering area for 27 d, in October 2010 he flew south to his home range near his natal nest in southern California (Fig. 3), where he remained for 15 d before returning north to his Central Valley summering area (Fig. 3). In December 2010 after 38 d, he returned to his home range in southern California (Fig. 3) and did not migrate for the next 3 yr. We first observed him at a nest with two nestlings in 2012 when he was 3 yr old. In July 2014, he once again migrated north. Precipitation in the vicinity of his home range in 2014 was $<30\%$ of the 30-yr average for the area and was the lowest during the period we tracked his movements (Fig. 2). While migrating north in 2014, he passed through his 2010 summering area in northern Nevada but continued on farther north into Idaho (Fig. 3). After occupying a summering area in southern Idaho for 70 d (mean = 3.4 ± 2.9 km/d, $n = 28$), in October 2014 he returned south to his home range in southern California (Fig. 3). He did not migrate in 2015 but remained in his home range for the entire year. In February 2016, he left his home range for the first time since October 2014 and traveled ≥ 150 km south (Fig. 3) where he either died or his transmitter detached.

DISCUSSION

The two Red-tailed Hawks in this study displayed a high degree of migratory flexibility. Although both hawks first migrated as juveniles, the female migrated for the first time as a fledgling directly from her natal territory. In contrast, the male did not migrate during his first calendar year but remained near his natal nest until the following summer, when he migrated north. Although we are not sure how to categorize these movements, both hawks made brief visits to their natal region during their first migration but then returned north. These may have been exploratory movements (Baker 1980) to assess conditions in their natal regions such as prey availability or density of territorial individuals. Subsequent migrations differed substantially between the two hawks. Although both hawks used two different summering areas during their first migration, in all subsequent migrations the female traveled directly to her summering area in the Sonoma Range. However, the male did not reuse either his summering area in Nevada or California during his second migration, but instead occupied a new summering area in Idaho.

Bloom et al. (2015) suggested the migratory fraction of the Red-tailed Hawk population of southern California was limited to young individuals, as is typical of many bird species (Gauthreaux 1978), and that they ceased migrating after acquiring territories and mates usually at 3 yr of age.

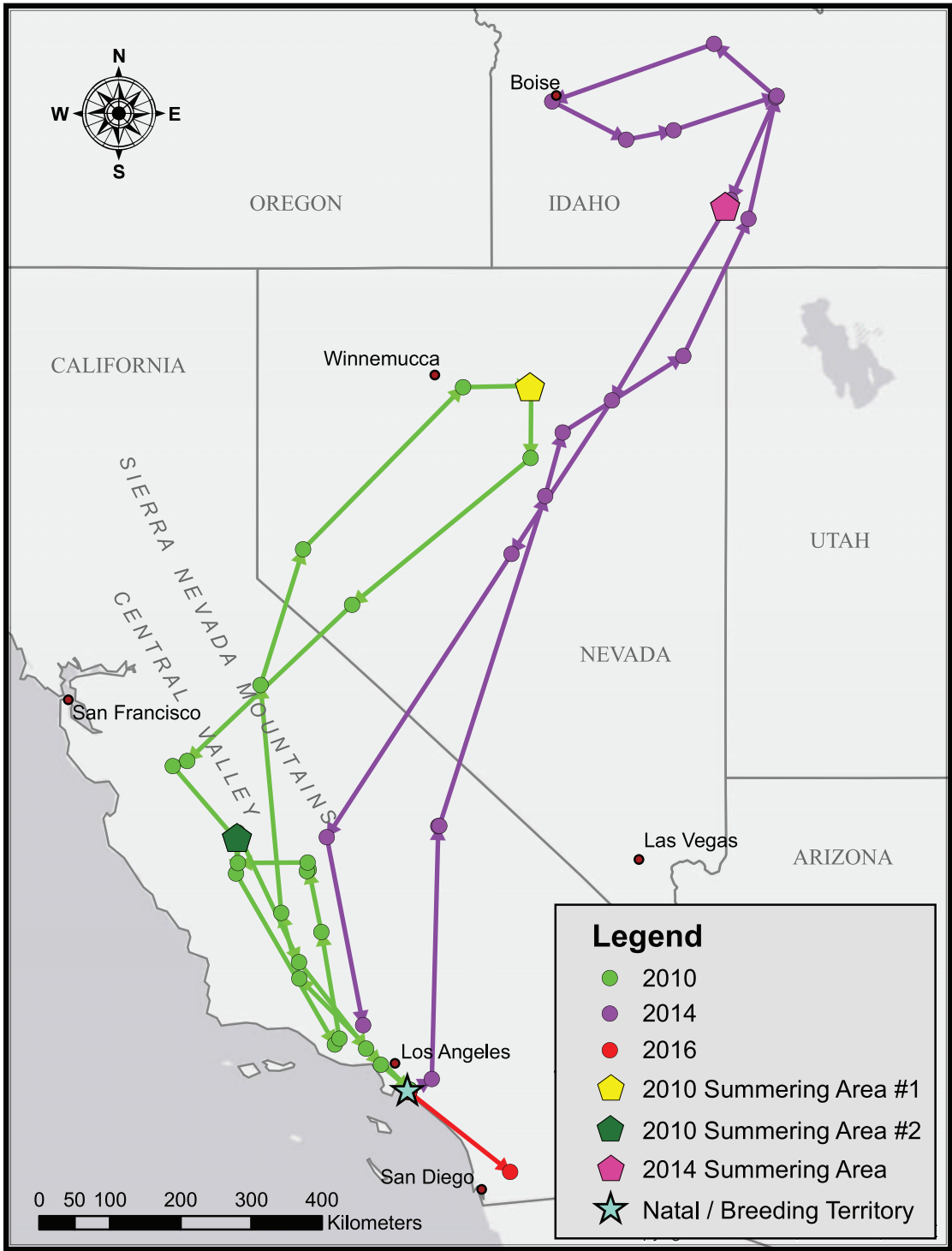


Figure 3. Migrations (2010 and 2014) of Red-tailed Hawk male 65999-2 as determined by satellite telemetry.

Although both hawks in this study ceased migrating at that age, the female and male both resumed migrating in 2014 at 7 and 6 yr of age, respectively. The male switched to residency the following year, while the female switched back and forth between migrating and residency over the next 3 yr. To our knowledge, our study is the first to document individual raptors displaying such switching behavior.

It seems likely that the resumption of migration of both hawks in 2014 was in response to severe drought. Water-years (WY, 1 October–30 September) 2012–2014 were the driest in California since record keeping began in 1885, and 2014 was the single driest WY on record (US Geological Survey 2017). Drought conditions improved in WY 2015 (Fig. 2), and the male switched back to residency. However, annual precipitation alone would not explain the female's migratory behavior subsequent to 2014. Although precipitation in 2015 increased to approximately the 30-yr average for her home range (Fig. 2), the female migrated that year. With precipitation near average in 2016 and above average in 2017 (Fig. 2), the female switched to residency in 2016 and then back to migrating in 2017. Rather than annual precipitation, the hawks were most likely responding to changes in prey populations. Although we did not monitor rodents during our study, abundance of many rodents fluctuates with precipitation (Gillespie et al. 2008), and rodent abundance in southern California can decline sharply during drought (Spevak 1983). However, the relationship between rodent abundance and precipitation is complex (Brown and Ernest 2002) and varies among species and location. Some species can return to pre-drought numbers rapidly (Bradley et al. 2006), whereas others may not recover for a year or more (Dickman et al. 1999). Such variability in rodent abundance might explain the migratory behavior of the female once precipitation returned to average or above-average levels.

Berthold (2001) suggested that migrants may become increasingly resident if warmer conditions resulting from climate change permit overwintering on the breeding grounds. However, the opposite could occur with Red-tailed Hawks from southern California. One reason for summer migration of Red-tailed Hawks may be reduced aboveground activity of California ground squirrels (*Otospermophilus beecheyi*), an important prey species (Bloom et al. 2015). During the warmest, driest months, many adult ground squirrels estivate to avoid heat and water stress (Holekamp and Nunes 1989). Although literature is lacking on potential effects of climate change on California ground squirrels, one likely response to increasing temperatures would be a further reduction in their aboveground activity. Higher temperatures may also increase the frequency and severity of droughts for California (Diffenbaugh et al. 2015). Red-tailed Hawks might adapt to both reduced prey abundance due to drought and reduced ground squirrel activity by increasing the frequency of annual summer migrations. Further long-term studies of individual Red-tailed Hawks from southern California may

shed light on the role of other environmental cues in their decision to migrate and how they may respond to climate change.

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