

# Migration and seasonal ranges of the Eastern Tehama deer herd in northern California

SCOTT C. HILL<sup>1\*</sup> AND PETER J. FIGURA<sup>2</sup>

<sup>1</sup>*California Department of Fish and Wildlife, Northern Region, 1530 Schwab St., Red Bluff, CA 96080, USA*

<sup>2</sup>*California Department of Fish and Wildlife, Northern Region, 601 Locust St., Redding, CA 96001, USA*

\*Corresponding Author: [scott.hill@wildlife.ca.gov](mailto:scott.hill@wildlife.ca.gov)

We investigated the movements and seasonal ranges of deer from the Eastern Tehama deer herd in northern California, USA. Twenty-eight adult female black-tailed deer (*Odocoileus hemionus columbianus*) were captured and fitted with GPS collars during 2013–2015. Average annual migration distances between summer and winter ranges was approximately 69 km. Deer used a variety of seasonal ranges including fall and spring stopovers during migration. Summer ranges averaged 3.3 km<sup>2</sup>, winter ranges averaged 2.7 km<sup>2</sup>, and fall and spring stopovers averaged 1.6 km<sup>2</sup> and 1.1 km<sup>2</sup>, respectively. Fall migration (duration) averaged 30 days and spring migration averaged 21 days. The deer spent approximately 87% and 67% of the migration period at fall and spring stopovers, respectively. This study reinforces the importance stopover site use during migration. Conservation actions to benefit this herd should not only be focused on summer and winter ranges but also stopovers and migratory corridors which will require landscape-scale collaborations.

Key words: black-tailed deer, California, Eastern Tehama deer herd, migration, *Odocoileus hemionus columbianus*, seasonal ranges, stopovers

---

Migration is an important part of the life history of many ungulate species (Mysterud et al. 2001; Bolger et al. 2008; Bischof et al. 2012; Fryxell and Holt 2013). In many areas, long-distance migrations of ungulates are being altered by human population growth, barriers to movement, habitat loss and modification, and climate change. These alterations are likely to result in population declines and a functional loss of migration (Berger 2004; Bolger et al. 2008; Sawyer et al. 2009; Lendrum et al. 2013; Sawyer et al. 2013; Monteith et al. 2018; Wyckoff et al. 2018). In 2018, the U.S. Secretary of the Interior signed Secretarial Order

3362, which directed the U.S. Department of the Interior to collaborate with state fish and wildlife management agencies to improve habitat quality on winter ranges and migration corridors used by big game species, including antelope (*Antilocapra americana*), elk (*Cervus canadensis*), and mule deer (*Odocoileus hemionus*) in the western U.S.

An integral part of migration behavior is use of seasonal ranges for rest, nutritional replenishment, reproduction, and predator avoidance (Monteith et al. 2011; Sawyer and Kauffman 2011; Middleton et al. 2013; Sawyer et al. 2013; Monteith et al. 2018; Wyckoff et al. 2018). The identification and characterization of seasonal ranges (including fall and spring stopover sites) is of great importance as these sites are vital to migratory ungulates (Sawyer et al. 2005; Monteith et al. 2011; Sawyer and Kauffman 2011; Bischof et al. 2012; Sawyer et al. 2013; Wyckoff et al. 2018). Mule deer migration in California has been well documented in the southern Sierra Nevada Mountains (Loft et al. 1989; Kucera 1992; Nicholson et al. 1997; Monteith et al. 2011) and to a lesser extent black-tailed deer in the Klamath-Trinity Mountains in northwestern California (Loft et al. 1984; Bowyer et al. 1998; Wittmer et al. 2014). However, relatively little is known about the migratory behaviors and seasonal ranges of California's largest migratory population of deer, the Eastern Tehama deer herd (ETDH) in northern California, USA (CDFG et al. 1981).

The ETDH is highly valued by the public for recreational uses and has declined in number over the past several decades (CDFW, unpublished data), which has resulted in a loss of recreational opportunities (26% reduction of hunting tags over the last 20 years; CDFW unpublished data), wildlife viewing opportunities, reduced contributions to local economies, and increased public concern regarding the status of the ETDH. The ETDH decline is thought have resulted from anthropogenic factors (e.g., land management activities and fire suppression) which have decreased habitat quality (CDFG 1998). Although several telemetry studies have been conducted on the ETDH (CDFW unpublished data), migration stopover sites had not previously been investigated. CDFW has long recognized the importance of stopover sites as key foraging sources for the ETDH, as stated in the Eastern Tehama deer herd management plan (CDFG 1981):

“Holding areas [i.e., stopovers] on intermediate range are of extreme importance to deer since it's there deer delay on their migrations between seasonal ranges. Deer heavily utilize these areas during the spring while awaiting forage development on the summer range. Deer also feed heavily on acorns within these types during the fall migration. Holding sites must be more accurately delineated for management purposes.”

As stated above, several previous studies using telemetry collars were conducted on the ETDH and provided information that allowed for coarse-resolution identification of summer and winter ranges and some migration routes, but those collars did not include GPS technology, and the resulting data lacked the accuracy, resolution, and sample sizes to accurately delimit migration routes and important seasonal habitats used by the ETDH.

We initiated this project to identify areas of seasonal importance to deer in the ETDH. Our objectives were to: (1) document and characterize seasonal ranges and spring and fall stopover sites of the ETDH, and (2) quantify timing and duration of migration, including use of stopover sites. Project results will provide CDFW with information needed to prioritize areas for habitat conservation (e.g., conservation easements, fee title purchase, and management recommendations for both public and private lands) and enhancement, and will be used to update management planning for the ETDH.

## METHODS

### Study area

We conducted this study in northern California, in portions of Tehama, Plumas, Lassen, Shasta, and Butte counties (40.169 N, -121.560 W), occupied by migratory individuals in the ETDH. The study area encompassed 6,580 km<sup>2</sup> (Figure 1). Deer in the ETDH generally use low-elevation winter range, high-elevation summer range, and stopovers at intermediate elevations.

*Winter range.*—The winter range of the ETDH is in eastern Tehama and north-central Butte counties, in the western foothills of the southern Cascade and northern Sierra Nevada Mountains. The habitat types are primarily blue oak (*Quercus douglasii*) woodlands, annual grasslands, blue oak-foothill pine (*Pinus sabinina*) woodlands, and montane hardwoods (in the creek canyons) (Mayer and Laudenslayer 1988). Common woody plant species include blue oak, foothill pine, interior live oak (*Quercus wislizeni*), and numerous shrubs including wedgeleaf ceanothus (*Ceanothus cuneatus*), birch-leaf mountain mahogany (*Cercocarpus betuloides*), and manzanita (*Arctostaphylos* spp.). Annual grassland habitats are primarily composed of introduced annual grasses and forbs including wild oats (*Avena* spp.), brome grasses (*Bromus* spp.), and redstem filaree (*Erodium cicutarium*). Common terrestrial wildlife species in the area include wild pig (*Sus scrofa*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and mountain lion (*Puma concolor*). Elevations range from 107 m near the valley floor to 820 m in the upper elevations of the winter range. Temperatures range from an average low of 3.7° C to an average high of 15.6° C from October–April (when deer are present). Most of the 85.5 cm of precipitation per year, falls from October–April (mean accumulation from 1995–2016, weatherbase.com, Manton, CA).

*Summer range.*—The summer range is located in the southern Cascades and northern Sierra Nevada Mountains in eastern Tehama, western Plumas, northeastern Butte, northwestern Lassen, and southeastern Shasta counties. Important habitat types include Sierran mixed-conifer forest, wet meadow, white fir (*Abies concolor*) forest, and montane chaparral (Mayer and Laudenslayer 1988). Primary tree species are white fir, ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Common shrub species include mountain whitethorn (*Ceanothus cordulatus*), snowbrush ceanothus (*Ceanothus velutinus*), bush chinquapin (*Castanopsis sempervirens*), and willow (*Salix* spp.). Common wildlife species in the area include black bear (*Ursus americanus*), coyote, mountain lion, and bobcat. Gray wolf (*Canis lupus*) may also be present at very low densities. Elevations range from 1300 m near the transitional point between conifer and hardwood-dominated habitats to 3100 m near Lassen Peak. We did not conduct captures in Lassen Volcanic National Park (due to permitting issues), which contains most of the highest elevation summer range. Temperatures range from an average low of 4.6° C to an average high of 25.8° C from May–September (when deer are present). The area receives approximately 81 cm of precipitation per year, with most falling as snow from December–March (mean accumulation from 1995–2016, Western Regional Climate Center, Chester, CA).

*Stopover sites.*—Typical habitat types of stopovers include ponderosa pine, Sierran mixed-conifer forest, and montane hardwood-conifer. Although both ponderosa pine and Sierran mixed-conifer forests are conifer-dominated, several oak species including California black oak, Oregon white oak (*Quercus garryana*), and canyon live oak (*Quercus chrysolepis*)



also occur in those forests and are important forage species during fall migration (mast and foliage) (CDFG 1981).

## Captures

We conducted two capture efforts each year from 2013–2015. We captured deer during migration in April and May and on summer range in late July and August. We did not capture in June and early July to avoid the parturition period and any potential complications to does or fawns resulting from handling does during late stages of pregnancy or early lactation (Casady and Allen 2013).

All deer were chemically immobilized via free-range darting using a combination of Telazol® (tiletamine HCl and zolazepam HCl, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine HCl (Anased, LLOYD Laboratories, Shenandoah, Iowa, USA) at maximum dosages of 4.4 mg/kg (2.0 mg/lb) and 2.2 mg/kg (1.0 mg/lb), respectively. Tolazoline (LLOYD Laboratories, Shenandoah, Iowa, USA) was used as the antagonist for xylazine and was administered at a dosage of approximately 6.6 mg/kg (3.0 mg/lb) at least 80 minutes post immobilization (CDFW Wildlife Restraint Handbook 2012). Immobilization drugs were administered by CDFW staff with advanced training in chemical immobilization and in consultation with a wildlife veterinarian from the CDFW Wildlife Investigations Laboratory (WIL). The use of immobilization drugs was consistent with the CDFW Policy on the Use of Pharmaceuticals in Wildlife.

During captures, each deer was fitted with a store-onboard GPS collar (G2110B, Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) equipped with VHF and mortality sensors. Collars also included a drop-off mechanism.

## Monitoring

GPS collars were programmed to collect a location every four hours (six locations per day) and automatically release one year after deployment. We attempted to locate all collared deer for survival monitoring and to assess collar function using VHF telemetry, from the ground or fixed-wing aircraft, at least once a month while collars were active. After release, collars were recovered, and location data was downloaded.

## Data analysis

GPS location data were analyzed using ArcGIS software (ArcMap 10.6.1, Environmental Systems Research Institute, Redlands, California, USA). Home ranges were estimated for individual deer using Brownian bridge movement models (BBMM: Horne et al. 2007; Nielson et al. 2013; Nicholson et al. 2016) in R (R Development Core Team 2019). Before determining utilization distributions (UDs), we separated locations by seasonal range based on a visual inspection that approximated the date when a deer left its summer or winter range to begin migration (Bunnefeld et al. 2011). Stopovers were also delineated by visually separating clusters of GPS locations within the migration and running BBMM analysis for each cluster. Summer home range, winter home range, and stopover sites were then delineated by generating the 95% isopleth upon the individual UD.

## RESULTS

### Capture

Thirty female deer were captured from May 2013–August 2015 (Table 1). We affixed GPS collars to 28 of the captured deer (one doe died during capture processing and one yearling doe was too small to collar). Captures during spring migration were not as successful as post-parturition summer captures, as below normal precipitation during the study influenced the timing and predictability of spring migration.

**Table 1.** Dates and number of does captured from the ETDH 2013–2015.

Date	Number of Deer Captured
May 2013	2
July 2013	8
May 2014	3
July 2014	7
April 2015	5
August 2015	5

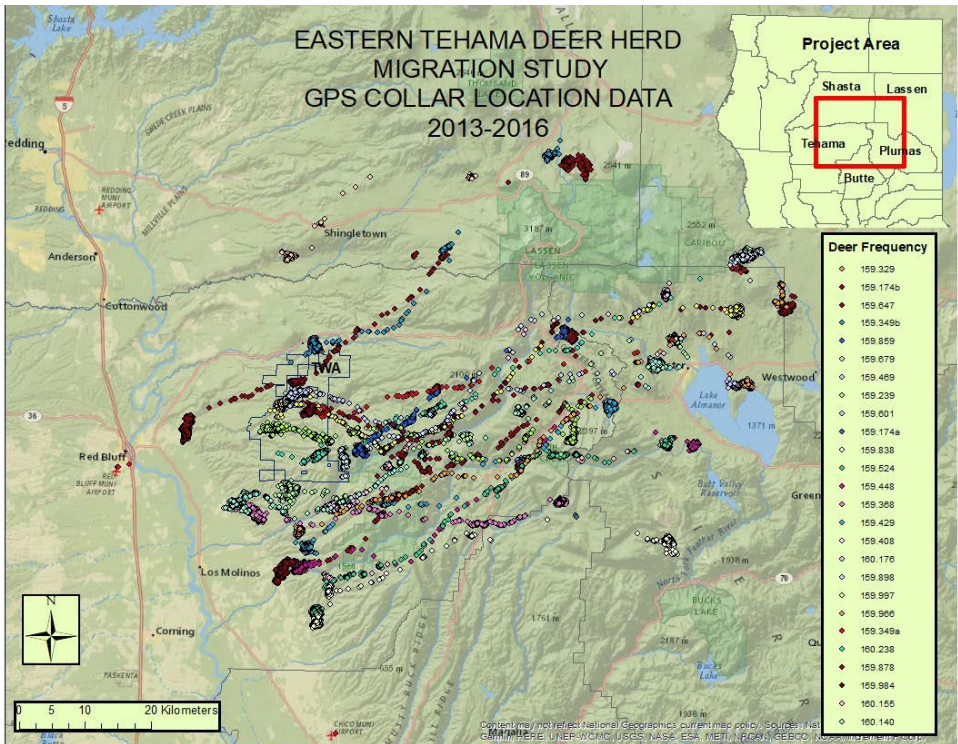
### Telemetry

Between May 2013–June 2016, we collected 39,203 locations from GPS-collared deer ( $n = 26$ ; two collars were not recovered) (Figure 2). Fix rate success by collar (i.e., proportion of collar fix attempts that successfully resulted in obtaining a GPS location) ranged from 53–94% ( $\bar{X} = 83\%$ ,  $SE = 1.78$ ). The proportion of fixes by collar that were 3-dimensional (i.e.,  $\geq 4$  satellites used to determine location) ranged from 38–85% ( $\bar{X} = 74\%$ ,  $SE = 2.01$ ). Three-dimensional fixes are assumed to be more accurate than 2-dimensional fixes (Di Orio et al. 2003). GPS collars generally collected locations as scheduled on summer and winter ranges and stopovers; however, during migration the frequency of locations was reduced on some animals due to long distance movements through closed canopy areas (Rempel et al. 1995; Di Orio et al. 2003). The mean number of GPS locations collected for individual deer that completed both fall and spring migrations was 1,841 (range 1,363–2,057,  $SE = 31.73$ ). The GPS collar collection interval (four hours) was too long to conduct BBMM analysis on an entire migration sequence because it over-approximated the width of the migration route. Therefore, migration routes were delineated by connecting successive GPS fixes from beginning to end of the migration sequence.

### Sizes of home ranges and stopover sites

Seasonal home ranges were broken down into four classifications: summer, fall stopover, spring stopover, and winter (Figure 3). Only deer that had  $\geq 2$  months of location data for summer or winter range were included in the analysis. Summer range areas for collared does ranged from 0.85–9.93 km<sup>2</sup> ( $\bar{X} = 3.29$ ,  $SD = 2.52$ ,  $n = 19$ ). Winter range areas ranged



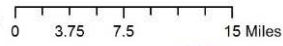


**Figure 2.** GPS location data for 26 female deer in Tehama, Plumas, Butte, Lassen, and Shasta counties, CA, USA, 2013–2016.

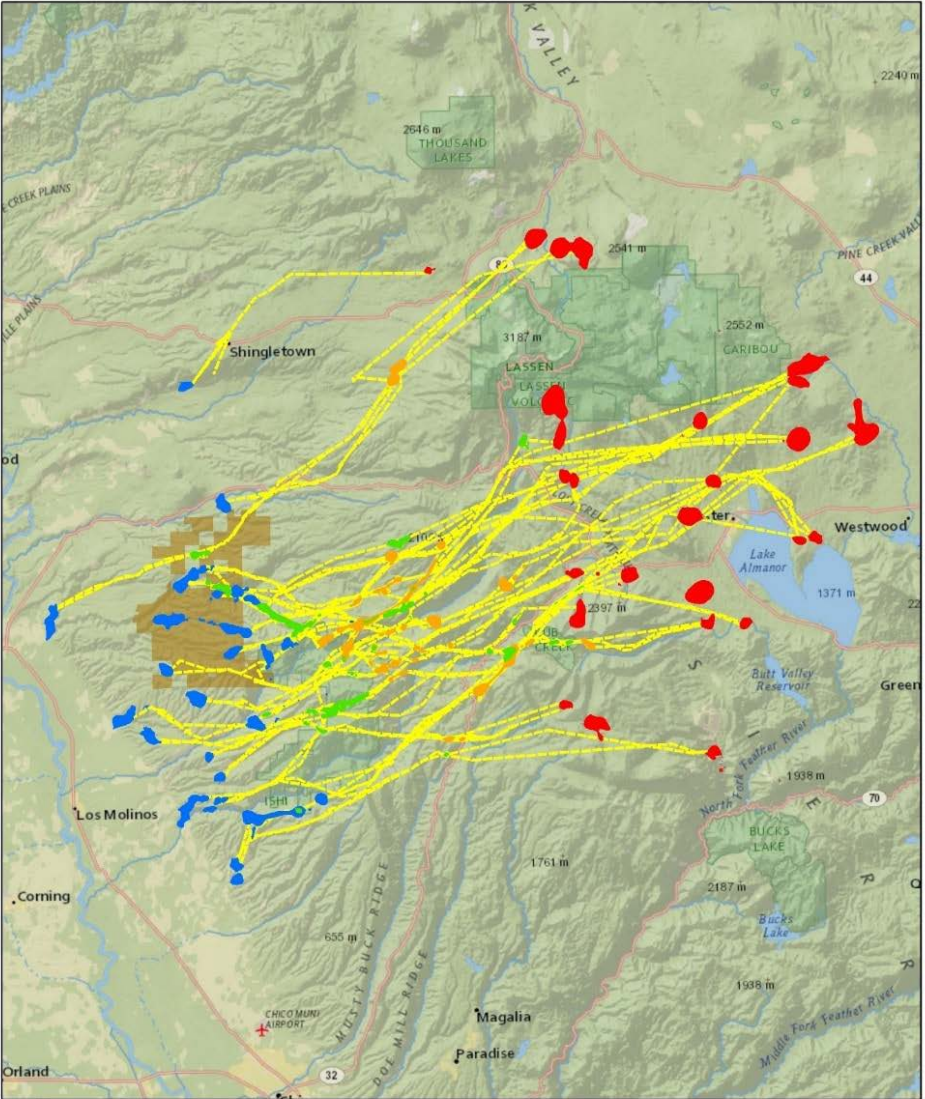
from 0.89–8.42 km<sup>2</sup> ( $\bar{X}$  = 2.67,  $SD$  = 1.67,  $n$  = 21). Fall stopovers ranged from 0.18–4.65 km<sup>2</sup> ( $\bar{X}$  = 1.64,  $SD$  = 1.43,  $n$  = 23) and spring stopovers ranged from 0.10–4.67 km<sup>2</sup> ( $\bar{X}$  = 1.06,  $SD$  = 0.99,  $n$  = 36). In some instances, does used more than one fall and spring stopovers during one migration which we analyzed independently. The mean number of fall and spring stopovers for individual does was 0.95 ( $SD$  = 0.50, range 0–2) and 1.28 ( $SD$  = 0.57, range 0–2), respectively (Table 2).

*Seasonal range elevation, habitat types, and land ownership.*—Mean elevation of summer ranges was 1650 m ( $n$  = 28, range 1300–1900 m). Typical habitat types within summer ranges were Sierran-mixed conifer forest, white fir forest, wet meadow, and montane chaparral. The majority of the of the collared does summer ranges were on USDA Forest Service (USFS) lands (54%) followed by private timberlands (31%) and other private lands (15%). Mean elevation of winter ranges was 460 m ( $n$  = 25, range 200–825 m), and typical habitat types were blue oak woodlands and blue oak-foothill pine woodlands. The majority of the winter ranges were on private ranches (58%), followed by CFDWs Tehama Wildlife Area (TWA) (21%), Gray Davis Dye Creek Preserve (13%), and USFS (8%). The mean elevation of spring and fall stopovers were 1073 m ( $n$  = 36, range 640–1675 m) and 1240 m ( $n$  = 23, range 775–1465 m), respectively. Typical habitat types were Ponderosa pine forest, Sierran-mixed conifer forest, and montane hardwood conifer forest. Land ownership of the

### East Tehama Deer Herd Seasonal Ranges



- ✚ Spring Holding Area
- ✚ Fall Holding Area
- ✚ Summer Range
- ✚ Winter Range
- Migration Paths
- Tehama Wildlife Area



**Figure 3.** Seasonal ranges and approximate migration routes of collared does from the ETDH 2013–2016.

fall stopovers was private timberlands (55%) and USFS (45%). Ownership of the spring stopovers was USFS (72%), private timberlands (22%), and TWA (6%).

Migration corridors primarily followed the major east-west creek canyons, as indicated by previous telemetry studies (CDFG, unpublished data). Mill, Deer, and Antelope Creeks were most frequently used by collared does (33%, 25% and 13%, respectively). Typical habitat types include montane riparian and valley foothill riparian.



**Table 2:** Seasonal home ranges (km<sup>2</sup>) of 21 does from the ETDH 2013–2016.

Deer #	Summer range	Winter range	Fall stopover	Spring stopover
3	0.9	2.1	4.2	2.1,0.4
4	2.5	2.9	2.4	0.5,0.7
5	4.8	2.9	0.6	0.6
6	5.7	3.4	*	2.2,4.7
7	4.6	5.2	3.1	3.4
9	2.2	3.2	4.7	0.2
10	2.4	2.0	1.3	1.7
11	8.2	1.8	1.7	0.3
12	1.4	0.9	0.8	1.7
13	2.4	1.2	1.2	1.8,1.6
14	1.4	1.5	0.3	1.2
15	0.8	1.6	0.4	0.9,0.4
16	1.9	1.9	*	0.2
19	1.2	2.5	1.0	*
20	1.8	1.4	0.7,0.2	*
21	1.2	1.9	0.4	*
22	1.5	1.6	*	0.1
23	4.5	3.8	0.3,2.3	0.3,0.4
24	4.3	8.4	0.7	0.4
27	*	2.5	1.9	*
28	9.9	3.7	1.6	1.4

\*did not use a fall or spring stopover area or collar dropped prior to arrival on seasonal range

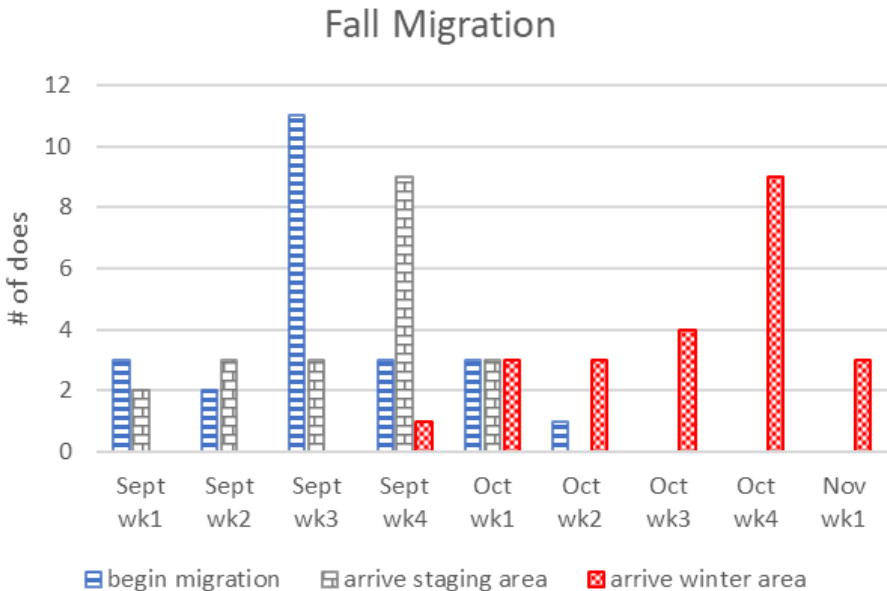
### Migration distances

Twenty-three collared does made at least one migration from summer range to winter range and 21 migrated from winter range to summer range. Migration distance ranged from 38–101 km ( $\bar{X}$  = 68.5,  $SD$  = 14.4). Most deer used both fall ( $n$  = 20) and spring ( $n$  = 19) stopovers during migration. Spring stopover sites tended to be more westerly ( $P$  < 0.001) and at lower elevations ( $P$  = 0.049) than fall stopover sites. Mean distance from the summer range to fall stopovers was 35 km (range 11–60 km). Mean distance from fall stopover sites to winter ranges was 28 km (range 11–57 km). Mean distance from winter range to spring stopover area was 23 km (range 9–44 km). The mean distance from the spring stopover area to summer range was 40 km (range 7–65 km).

## Migration timing

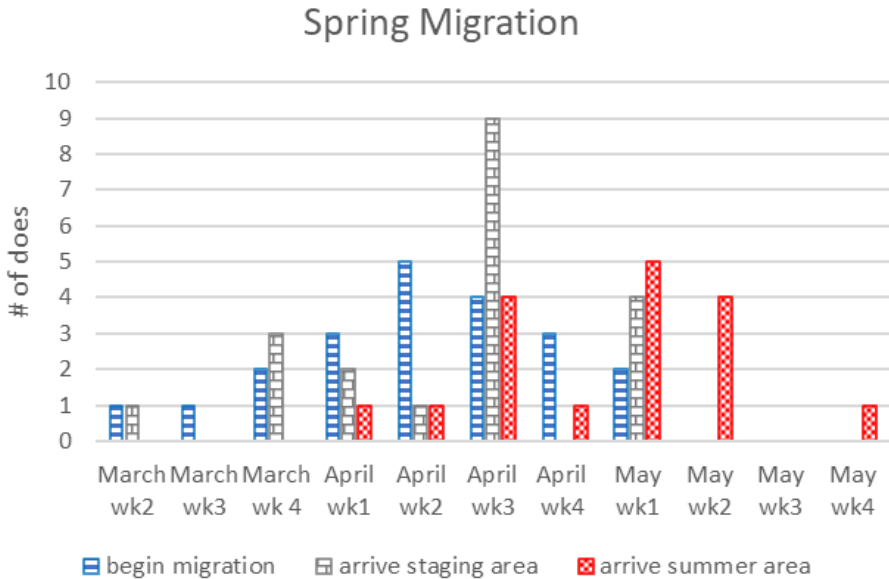
*Fall migration.*—The largest number of collared does left the summer range during the third week of September ( $n = 11$ ) and the median date of departure was 19 September ( $SD = 10$  days). The earliest a doe began fall migration was 30 August and the latest was 12 October. Collared deer arrived at fall stopovers between 5 September and 7 October, with the most common arrival time being the fourth week of September ( $n = 9$ ). The median fall stopover arrival date was 23 September ( $SD = 9.9$  days). Deer spent an average of 26 days (range 5–50 days) at fall stopovers before moving to winter ranges. Two does did not use a fall stopover site, including a doe that began its migration on 12 October and arrived on the winter range on 20 October after travelling almost 60 km. Most collared deer arrived on winter ranges around the fourth week of October ( $n = 9$ ) and the median date of arrival was 22 October ( $SD = 11.2$  days). The earliest arrival on winter range was 25 September and the latest was 3 November (Figure 4). The average number of days moving (i.e., not at a stopover) during migration was 5.1 (range 2–8 days). Total migration time from when a deer left summer range to arrival on winter range (including use of the fall stopovers) averaged 30 days ( $n = 23$ , range 7–51 days).

*Spring migration.*—The largest number of collared does left the winter range during the second or third week of April ( $n = 9$ ) and the median departure date was 13 April ( $SD = 12.9$  days). The earliest a doe began spring migration was 14 March and the latest was 30 April. Collared deer arrived at spring stopovers between 15 March and 2 May, with the most common arrival time being the third week of April ( $n = 9$ ). The median arrival date was 18 April ( $SD = 14.6$  days). Only one doe did not use a spring stopover. Does spent an



**Figure 4.** Fall migration timing, by week, of 23 collared does from the ETDH 2013–2015.

average of 14 days (range 3–37 days) at stopovers and most arrived on the summer range during the first or second week of May ( $n = 8$ ) and the median date of arrival was 2 May ( $SD = 13.1$  days). The earliest summer range arrival was 5 April (during 2015, an extremely low snow year) and the latest was 25 May (Figure 5). The average number of days moving during migration was 5 (range 3–8 days). Total migration time averaged 21 days ( $n = 16$ , range 3–53 days).



**Figure 5.** Spring migration timing, by week, of 21 collared does from the ETDH 2014–2016.

## Discussion

Deer in the ETDH migrate long distances from summer to winter ranges compared to many deer herds throughout California (Longhurst et al. 1952; CDFG 1981). Migration distance for ETDH collared does in the study averaged 69 km and the longest distance a collared doe migrated was 101 km. Additionally, a doe marked in a CDFW study in central Plumas County (outside the typical ETDH summer range), migrated approximately 125 km to ETDH winter range (CDFW unpublished data). In contrast, Loft et al. (1984) recorded an average migration distance of 21 km ( $n = 16$ , range 11–35) for black-tailed does in Trinity County. Wittmer et al. (2014) found even shorter migration distance of 5–10 km for black-tailed does in the Mendocino National Forest. Although ETDH migration distances are shorter than migrations of deer in other western states (Sawyer and Kauffman 2011; Sawyer et al. 2016), ETDH deer encounter similar challenges to migration from various anthropogenic factors (Berger 2004; Bolger et al. 2008). Sawyer et al. (2016) found longer distance migrants had a higher exposure to anthropogenic mortality factors (i.e., highways and fences), however, reduced time on winter range by long-distance migrators may alleviate

competition for limited forage. This suggests that there may be fitness trade-offs between migration strategies (long vs. short distance). We surmise that the longer distances between summer and winter ranges for the ETDH relative to those for herds in northwestern California are likely a function of differing elevation gradients and relief in each area.

Summer range areas for ETDH collared does averaged 3.29 km<sup>2</sup> and were slightly larger than winter ranges which average 2.67 km<sup>2</sup> and were larger than two other studies of black-tailed deer in northern California. Using local convex hull (95% isopleth), Wittmer et al. (2014) found average seasonal home range size for deer during summer were 0.61 km<sup>2</sup> and winter were 0.86 km<sup>2</sup> in Mendocino National Forest. In northwestern California, Loft et al. (1984) estimated 1.55 km<sup>2</sup> for summer ranges in Trinity County using the minimum convex polygon (MCP) method. However, in southern California, Nicholson et al. (1997) used both adaptive kernel (AK: 95%) and MCP methods to estimate average summer and winter range size of mule deer. Both methods showed larger average summer (AK = 5.54 km<sup>2</sup>, MCP = 3.15 km<sup>2</sup>) and winter range sizes (AK = 13.57 km<sup>2</sup>, MCP = 7.67 km<sup>2</sup>) than ETDH animals. The relative habitat quality and productivity of each study area (e.g., northwestern California conifer forest vs. arid southern California mountain ranges) may largely explain differences in home range sizes (Relyea et al. 2000).

Stopover sites have been extensively studied due to their importance in migratory ecology of mule deer (Kucera 1992; Sawyer et al. 2009; Monteith et al. 2011; Sawyer and Kaufman 2011). Most research into stopover ecology suggests that stopovers play a key role in the migration strategy by allowing individuals to migrate in concert with plant phenology and maximize energy intake rather than speed (Monteith et al. 2011; Sawyer and Kauffman, 2011; Bischof et al. 2012; Lendrum et al. 2014; Aikens et al. 2017). Sawyer and Kaufman (2011) found that mule deer in central Wyoming spent approximately 95% of the migration period at stopovers. Stopovers also appear important to the ecology of the ETDH, as collared does averaged approximately 87% (26 days) and 67% (14 days) of the migration period at fall and spring stopovers respectively. Loft et al. (1984) found similar periods of delay at spring stopovers in black-tailed deer in Trinity County (16 days). Sawyer and Kaufman (2011) also found high fidelity to stopover sites across season and years and concluded that the protection of stopover sites may provide an effective conservation strategy for migratory mule deer. In the ETDH, stopovers were often located on USFS lands and private timberlands. Management strategies for migratory sites should differentiate between stopover sites and movement corridors to be most effective (Sawyer et al. 2009).

Due to variability in weather patterns during the study period (2013–2016), including drought conditions during most of the study, our migration timing results may not be representative of a “normal” precipitation year. These conditions may have also affected our ability to capture deer during spring migration (migration timing predictability). Snowfall averages from Chester, CA in the heart of the summer range were 96%, 92%, and 50% below average during our study period (2013–2014, 2014–2015, 2015–2016; Western Regional Climate Center, Chester, CA).

Although the majority of collared does wintered on private ranches, our results emphasize the value of CDFW’s 190 km<sup>2</sup> Tehama Wildlife Area to the ETDH. The property has long been considered an important wintering area for the herd (Longhurst et al. 1952) and was specifically acquired in 1942 to protect deer winter range from being overgrazed by livestock. While TWA represents only about 9% of the total winter range for the ETDH, 46% ( $n = 11$ ) of the collared does either wintered on or moved through TWA. Addition-

ally, two does from a CDFW study in Plumas County wintered on or moved through TWA.

Anthropogenic factors can have a detrimental effect on mule deer migration and habitats (Monteith et al. 2018; Wyckoff et al. 2018). Stopovers for the ETDH are often located in areas of private timberlands managed primarily to maximize marketable lumber. Silvicultural systems used on private timberlands in California are diverse, and the effects of different systems on deer habitat quality and behavior are not well known. However, some silviculture practices (post-harvest herbicide use to control shrubs) can be detrimental to black-tailed deer forage quality (CDFG 1998; ODFW 2008; Ulappa 2015). Other types of human disturbance on stopovers (energy and residential development) have been shown to diminish use of stopovers thus increasing speed of migration (Wyckoff et al. 2018). Currently, the USFS administers a large portion of the ETDH summer range, fall and spring stopover sites, and to a lesser extent, winter range. Additional wildlife habitat restoration and improvement projects and forest management projects could be implemented on USFS and other lands to increase the quality and quantity of stands supporting valuable browse and forb species. While much of the herd's winter range is privately owned ranchlands, public lands such as TWA and the adjacent Gray Davis Dye Creek Preserve should be considered for additional deer habitat improvements. Although the TWA Vegetation and Fuels Management Plan (CDFW 2013) recommends prescribed burning to improve wildlife habitat, a lack of resources has limited the implementation of wildlife habitat improvement projects on TWA. Kie and Boroski (1995) recommended altered livestock grazing periods and stocking levels on TWA to benefit deer. Those recommendations are currently being implemented and continue to be assessed for effectiveness.

In conclusion, the ETDH is unique with respect to its migration and seasonal range use compared to other deer herds in California. The ETDH long-distance migrations may only be eclipsed by a few herds in the southern Sierra Nevada Mountains in California (CDFW unpublished data). Continued research into ungulate migration in California is crucial to conserving the migratory function of many herds. Seasonal ranges important to the ETDH and other herds, including stopover sites, need to be further studied and assessed to determine potential actions to improve habitats (Sutherland 1998; Sawyer and Kauffman 2011). The conservation of migratory ungulates is particularly challenging because entire regional landscapes must be managed in order to conserve migrations (Bolger et al. 2008). Effective conservation of the ETDH and other herds will require landscape-scale collaborations involving multiple parties and interests and the effective application of science, policy, and planning.

### ACKNOWLEDGMENTS

The project was funded and supported by the CDFW Northern Region, CDFW Wildlife Programs Branch (Deer Program), the Large Mammal Advisory Committee, and CDFW Wildlife Investigations Laboratory. We would like to thank Drs. P. Swift, B. Gonzales, and L. Woods for providing expertise and guidance in immobilization and safely handling of all deer. L. Konde provided equipment for capturing and handling. Warden Pilots J. Veal and G. Woelfel provided aerial telemetry surveillance. K. Morefield provided GIS analysis and map production. R. Schaefer, R. Shinn, B. Ehler, J. Carlson, P. Sater, T. Welch, and P. Raquel all assisted in darting, handling, collaring, and taking physical measurements. A special thanks to E. Smith, the Collins Pine Company, and Lassen National Forest who



granted access to their property to conduct the captures and telemetry work. And finally, R. Callas and R. Schaefer provided support, encouragement, and the knowledge from years of experience working with deer in northern California. And, we would also like to thank two anonymous reviewers who provided critical comments and suggestions to improve the previous version of this manuscript.

### **Author contributions**

Conceived and designed the study: SCH

Collected the data: SCH, PJF

Performed the analysis of the data: SCH

Authored the manuscript: SCH

Provided critical revision of the manuscript: PJF

### **LITERATURE CITED**

- Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters* 20:741–750.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. V. Moorter, and A. Myrsetrud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist* 180:407–424.
- Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.
- Bowyer R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Sexual segregation in black-tailed deer: effects of scale. *Journal of Wildlife Management* 60:10–17.
- Bunnfeld N., L. Borger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- California Department of Fish and Game (CDFG). 1981. Management plan for the Eastern Tehama Deer herd. California Department of Fish and Game, Sacramento, CA, USA.
- California Department of Fish and Game (CDFG). 1998. An assessment of mule and black-tailed deer habitats and populations in California. California Department of Fish and Game, Sacramento, CA, USA.
- California Department of Fish and Wildlife, Wildlife Investigations Lab (CDFW). 2012. Wildlife restraint handbook. Tenth edition. California Department of Fish and Wildlife, Rancho Cordova, CA, USA.
- California Department of Fish and Wildlife (CDFW). 2013. Tehama Wildlife Area vegetation and fuels management plan. California Department of Fish and Wildlife, Paynes Creek, CA, USA.
- Casady, D. S., and M. L. Allen. 2013. Handling adjustments to reduce chemical capture related mortality in black-tailed deer. *California Fish and Game* 99:104–109.

- Di Orio, A. P., R. Callas, and R. J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. *Wildlife Society Bulletin* 31:372–379.
- Fryxell, J. M., and R. D. Holt. 2013. Environmental change and the evolution of migration. *Ecology* 94:1274–1279.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian Bridges. *Ecology* 88:2354–2363.
- Kie, J. G., and B. B. Boroski. 1995. The effects of cattle grazing on black-tailed deer during winter on Tehama Wildlife Management Area. US Forest Service Report PSW-89-CL-030.
- Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. *Great Basin Naturalist* 52(2):122–130.
- Lendrum, P. E., C. R. Anderson, Jr., K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. *PLoS ONE* 8(5):e64548.
- Lendrum, P. E., C. R. Anderson, K. L. Monteith, J. A. Jenkins, and R. T. Bower. 2014. Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. *Mammalian Biology* 79:369–375.
- Loft, E. R., J. W. Menke, and T. S. Burton. 1984. Seasonal movements and summer habitats of female black-tailed deer. *Journal of Wildlife Management* 48:1317–1325.
- Loft, E. R., R. C. Bertram, and D. L. Brown. 1989. Migration patterns of mule deer in the central Sierra Nevada. *California Fish and Game* 75:11–19.
- Longhurst W. M., A. S. Leopold, and R. F. Dasman. 1952. A survey of California deer herds – their range management problems. *California Department of Fish and Game Bulletin #6*, Sacramento, CA, USA.
- Mayer, K. E., and W. F. Laudenslayer (editors). 1988. A guide to wildlife habitats of California. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station and California Department of Fish and Game. State of California, Resources Agency, Sacramento, CA, USA.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bower. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life history characteristics. *Ecosphere*, 2(4):art47.
- Monteith, K. L., M. M. Hayes, M. J. Kauffman, H. E. Copeland, and H. Sawyer. 2018. Functional attributes of ungulate migration: landscape features facilitate movement and access to forage. *Ecological Applications* 28:2153–2164.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70:915–923.
- Nicholson, K. L., S. M. Arthur, J. S. Horne, E. O. Garton, and P. A. Del Vecchio. 2016. Modeling caribou movements: seasonal ranges and migration routes of the central Arctic herd. *PLoS ONE*, 11(4):e0150333.
- Nicholson, M., C., R. T. Bowyer, and J., G. Kie. 1997. Habitat selection and survival tradeoffs associated with migration. *Journal of Mammalogy* 72:483–504.

- Nielson, R. M., H. Sawyer, and T. L. McDonald. 2013. BBMM: Brownian bridge movement model for estimating the movement path of an animal using discrete location data. R package, version 22. 2011. Available from: <http://CRAN.Rproject.org/package=BBMM>
- Oregon Department of Fish and Wildlife (ODFW). 2008. Oregon black-tailed deer management plan. Oregon Department of Fish and Wildlife, Salem, OR, USA.
- R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>
- Relyea, R. A., R. K. Lawrence, and S. Demarias. 2000. Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. *Journal of Wildlife Management* 64:146–153.
- Rempel, R. S., A. R. Rogers, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. *Journal of Wildlife Management* 59:543–551.
- Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, 19:2016–2025.
- Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. *Journal of Animal Ecology* 80:1078–1087.
- Sawyer, H., M. J. Kauffman, A. D. Middleton, T. A. Morrison, R. M. Nielson, and T. B. Wyckoff. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology* 50:68–78.
- Sutherland, W. J. 1998. The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology* 35:418–421.
- Ulappa, A. C. 2015. Using forage dynamics to answer landscape management questions: the nutritional ecology of black-tailed deer. Dissertation, Washington State University, Pullman, USA.
- Wittmer, H. U., T. D. Forrester, M. L. Allen, L. Marescot, and D. S. Casady. 2014. Black-tailed deer population assessment in the Mendocino National Forest, California. Report to the California Department of Fish and Wildlife, Sacramento, CA, USA.
- Wyckoff, T. B., H. Sawyer, S. E. Albeke, S. L. Garman, and M. J. Kauffman. 2018. Evaluating the influence of energy and residential development on migratory behavior of mule deer. *Ecosphere* 9(2):ecs2.2113.

*Submitted 4 November 2019*

*Accepted 6 December 2019*

*Associate Editor was K. Denryter*