

6-2023

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AMERICAN KESTREL MIGRATION: INSIGHTS AND CHALLENGES FROM TRACKING INDIVIDUALS ACROSS THE ANNUAL CYCLE

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ABSTRACT.—Natural variation in migratory strategies across the range of the American Kestrel (*Falco sparverius*) creates a unique opportunity for comparative research of annual cycles. However, it can be logistically and technically challenging to track such a small but highly mobile species. We tagged American Kestrels with light-level geolocators or satellite transmitters with the aim of estimating migration timing and connectivity, and we monitored a subset of satellite-tagged individuals during the breeding season to assess transmitter function and wear. We recovered geolocators from six of 49 (12%) tagged individuals. One geocator-tagged individual migrated approximately 1235 km from its Idaho breeding grounds to New Mexico near the Arizona border for the winter and returned to Idaho the following spring. The other five recaptured individuals remained near (<200 km) the breeding grounds year-round. The low reliability of recovery and low precision of locations suggested major limitations of using geolocators to track this species. Most satellite transmitters (18 of 22, 82%) failed prior to migration, but one satellite-tagged individual migrated approximately 5945 km from Canada to Nicaragua, and three others transmitted ≥ 1 location during migration. Transmitters stopped functioning while on live individuals despite showing no visible damage and maintaining adequate battery levels. These results suggest further testing and development are needed before these recently developed tags are deployed again on American Kestrels. Both individuals with complete migration tracks showed evidence of short distance (250–350 km) post-breeding movements to southern stopover sites where they stayed 1–3 mo before migrating onward. Although sample sizes were small, migration patterns were consistent with latitudinal leap-frog patterns described in previous studies and revealed an interesting pattern of a prolonged post-breeding stopover before longer migration. Further, the migration track from Canada to Nicaragua represents the longest recorded migration path for this species.

KEY WORDS: *American Kestrel*; *Falco sparverius*; *full annual cycle*; *geocator*; *satellite transmitter*; *stopover*.

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MIGRACIÓN DE *FALCO SPARVERIUS*: INFORMACIÓN Y DESAFÍOS DEL SEGUIMIENTO DE INDIVIDUOS A LO LARGO DEL CICLO ANUAL

RESUMEN.—La variación natural en las estrategias migratorias de *Falco sparverius* a través de su área de distribución proporciona una oportunidad única para la investigación comparativa de los ciclos anuales. Sin embargo, puede ser un desafío logístico y técnico rastrear una especie tan pequeña pero altamente móvil. Marcamos individuos de *F. sparverius* con geolocalizadores de nivel de luz o transmisores satelitales con el objetivo de estimar el tiempo de migración y la conectividad. Igualmente, un subconjunto de individuos fue seguido con emisores satelitales durante la temporada reproductiva para evaluar la función y el desgaste del transmisor. Recuperamos geolocalizadores de seis de los 49 (12%) individuos marcados. Un individuo marcado con un geolocalizador migró aproximadamente 1235 km desde su área de reproducción en Idaho hasta la frontera de Nuevo México y Arizona durante el invierno y regresó a Idaho la primavera siguiente. Los otros cinco individuos recapturados permanecieron durante todo el año cerca (<200 km) de sus lugares de cría. La baja fiabilidad de la recuperación y la baja precisión de las ubicaciones sugirieron importantes limitaciones en el uso de geolocalizadores para rastrear esta especie. La mayoría de los transmisores satelitales (18 de 22, 82%) fallaron antes de la migración, pero un individuo seguido con satélite migró aproximadamente 5945 km desde Canadá a Nicaragua, y otros tres transmitieron ≥ 1 ubicación durante la migración. Los transmisores dejaron de funcionar mientras estaban en individuos vivos a pesar de no mostrar daños visibles y de mantener niveles de batería adecuados. Estos resultados sugieren que se necesitan más pruebas y desarrollo antes de que estos emisores desarrollados recientemente sean colocados nuevamente en *F. sparverius*. Ambos individuos con rutas migratorias completas mostraron evidencia de movimientos post-reproductivos de corta distancia (250–350 km) hacia sitios de parada en el sur donde permanecieron de uno a tres meses antes de seguir migrando. Aunque los tamaños de muestra fueron pequeños, los patrones migratorios fueron consistentes con los patrones de “salto de rana” latitudinales descritos en estudios previos y mostraron un patrón interesante de una escala post-reproductiva prolongada antes de una migración más larga. Además, la ruta de migración de Canadá a Nicaragua representa la ruta de migración más larga registrada para esta especie.

[Traducción del equipo editorial]

INTRODUCTION

Tracking birds throughout the full annual cycle can help identify distinct populations, determine unique spatio-temporal challenges, unravel carry-over effects, and ultimately inform population-specific management and conservation efforts (Marrá et al. 2015). Migratory phases in particular may have large effects on population trends because of high mortality during migration (Klaassen et al. 2014) and carry-over effects of migration phenology and arrival condition on fitness in subsequent seasons (Robinson et al. 2020). Migration distance and phenology can impact birds' ability to synchronize with seasonally available resources across geographically dispersed habitats (Rubolini et al. 2010), which has implications for individual fitness outcomes and population trends (Both et al. 2006, Møller et al. 2008), particularly in light of climate-driven changes in phenology of seasonally available resources (Schwartz et al. 2006, Christiansen et al. 2011). Migration distances, routes, and stopover sites determine the conditions and threats that individuals face and can impact survival and physical condition upon arrival to the breeding and winter-

ing grounds (Newton 2010). Hence, understanding migration ecology is an important first step to elucidating drivers of individual fitness outcomes, population trends, and vulnerability to threats like climate change.

The American Kestrel (*Falco sparverius*) is a small-bodied, cavity-nesting raptor species that breeds and winters over a large and diverse geographic area across North and South America (Smallwood and Bird 2020). Natural variation in migratory strategies across their North American range (Smallwood and Bird 2020) creates a unique opportunity for comparative research of annual cycles, and regional variation in population trends (Smallwood et al. 2009) underscores the importance of understanding population-specific annual cycles. Banding mark-recapture studies and migration counts have provided some insights into kestrel migration ecology, namely the tendency for leap-frog migration, increasing propensity to migrate with increasing breeding latitude (Goodrich et al. 2012, Heath et al. 2012), and average timing of migrant kestrel passage (Smallwood and Bird 2020), but higher spatial and temporal resolution data are needed to identify migration stopover behavior, routes, timing,

and connectivity. Finally, American Kestrel population growth is sensitive to adult survival and highly correlated with immigration (McClure et al. 2021), so obtaining higher-resolution data on migratory ecology and seasonal survival rates could help explain regional variability in population trends.

For highly mobile species with widespread geographic ranges and migratory life histories, like American Kestrels, it can be logistically and technically challenging to track individuals. External tracking devices (e.g., geolocators, archival transmitters, satellite transmitters) have become increasingly popular to study bird movements and ecology, and provide valuable information about migratory behavior, connectivity, phenology, and even vital rates of birds (Robinson et al. 2010, Bridge et al. 2011). However, devices have only recently become miniaturized enough to use on American Kestrels, and loss, damage, or technical failure of tracking devices can impact the amount and reliability of data and cost-effectiveness (Scarpignato et al. 2016).

We aimed to learn more about migratory phenology and routes of American Kestrels using light-level geolocators and satellite transmitters. Here, we describe the outcomes and challenges of these tracking efforts. Specifically, we (1) used location data from both types of devices to estimate migration initiation and end dates, distance, routes, and stopover sites of a small sample of individuals; (2) reported on the reliability of recovering data from geolocators and receiving locations from transmitters; and (3) monitored a subset of individuals with transmitters during the breeding season to determine whether individuals were removing or damaging transmitters.

METHODS

Capture and Tagging. From April through May (2013 and 2014), we deployed geolocators (battery-powered Intigeo, model W-65, Migrate Technology Ltd, Coton, Cambridge, UK, approximately 2.8 g) on adult female and adult male American Kestrels in Ada County, Idaho, USA. We captured incubating individuals by hand in nest boxes, banded individuals using US Geological Survey (USGS) aluminum leg bands, collected morphometric measurements, and used a leg loop harness (Rappole and Tipton 1991, 3.2-mm Teflon ribbon, Bally Ribbon Mills, PA, USA) to attach geolocators (<2.5% of body weight including attachment materials). Once fit, we fixed the harness size by closing a small silver crimp around the ribbon passing through each side of the

tracking unit. We released individuals back into the nest box. If an individual flushed from the nest box immediately after being returned, we visually observed them for as long as possible or up to 30 min to ensure the harness did not impede routine flight and behavior. We attempted to resight and recapture individuals by hand in nest boxes in subsequent breeding seasons to recover the geocator and download the data.

In 2018 and 2019 we deployed satellite transmitters manufactured by Lotek (battery-powered Lotek PinPoint GPS-Argos-75, Newmarket, Ontario, Canada, approximately 4 g) or Microwave Telemetry Inc. (solar-powered Microwave Platform Transmitter Terminal, Columbia, MD, USA, approximately 2 g) on adult female American Kestrels across their North American breeding and wintering range. We captured incubating adult females by hand in nest boxes (May–June) and captured wintering adult females using a bal-chatri trap with a live lure mouse (December–January; Berger and Mueller 1959). We collected morphometric measurements, and used a pre-constructed backpack-style harness with shrink wrap tubing over the chest knot (Steenhof et al. 2006, Chan et al. 2016, 2.5-mm Spectra ribbon, Bally Ribbon Mills, PA, USA) to attach transmitters, which we secured with superglued knots once fit on the individual. We focused our efforts on adult females that met the minimum weight requirement (males were not large enough to carry the 4-g transmitters) and we did not band individuals with USGS leg bands to keep the weight of the transmitter and attachment materials <3% body weight (MacDonald and Amlaner 1980). We released individuals at the capture location and monitored behavior for a minimum of 30 min post-release. We did not attempt to recapture or resight individuals at capture sites in the subsequent year because of the large geographic scale across which we deployed transmitters, and the expectation that transmitted data would preclude the need to recover transmitters.

Tag Programming and Data Collection. Geolocators use recorded light intensities and an accurate internal clock to estimate sun elevation, and geographical position (Hill 1994). Latitude is determined using day or night length, while longitude is determined using the time of local noon or midnight (Porter and Smith 2013); geolocators provide two fixes per day with an average accuracy of 186 ± 114 km (Phillips et al. 2004) and have a maximum lifespan of 23 mo. We programmed geolocators to

Mode 1 (i.e., recording full range light, maximum and minimum temperatures, and wet/dry data; Porter and Smith 2013). We focused our analysis on the light data for location information and did not assess the temperature or wet/dry information. Because data is stored on the unit, geolocator-tagged individuals require recapture to retrieve the data. After recovery, we analyzed data using BASTRAK software written by the British Antarctic Survey, using techniques described by Porter and Smith (2013). We used light-level data recorded by units on the individuals during the period between hatching and fledging to calibrate subsequent positional information. During this period, adults remain relatively close to the nest box to brood and feed nestlings, but generally stop entering the box overnight, providing a known location with an unobscured view of the sky. Because day and night length are approximately the same at all latitudes during an equinox, it is impossible to calculate latitude during this period, so we determined the migration period by longitude changes alone (Hill 1994, Porter and Smith 2013). We calculated average longitudes (to compensate for cloud-shaded dusks and dawns) for all stationary periods and trial periods investigating possible movements. If we visually detected significant stationary periods on either side of equinoxes, we calculated the latitude between the clusters mirrored on either side of the equinox (Porter and Smith 2013). We visually identified the beginning of the migration period by the clear shift in longitude values, followed by a directional and sharp variation in longitude (of approximately two degrees of longitude per day). Similarly, arrival dates were considered as the day at which longitude values stabilized (Catry et al. 2011). We plotted and examined fixes sequentially, visually scanning for clusters that would indicate stopovers and wintering regions. We assumed that an individual did not migrate if there was only one cluster of fixes. Because the estimated error in locations is so large, only movements of >200 km could reliably be distinguished from locational error.

Satellite transmitters acquire locations and send signals to satellites, and data from satellites are relayed to processing centers via ground antennas across the globe and then processed and distributed to users (Meyburg and Fuller 2007). Prior to deployment on American Kestrels, we tested both Lotek and Microwave transmitters by placing them in a location with an unobstructed view of the sky and antennae pointing upward, and confirming that

locations were recorded on the device and transmitted. Microwave transmitters are solar-powered and are preprogrammed by the manufacturer to transmit data continuously when battery voltage is deemed sufficient by internal sensors (i.e., voltage/transmission rates depend on how the computer on the tag assesses and responds to the amount of voltage coming in). Hence, the user does not specify the fix rate, but the suggested operating life is 2 yr, and we received 10 usable locations per d during the tag testing phase. Lotek transmitters have a fixed battery life, so to ensure that batteries would last through migration we programmed them at a low fix rate (i.e., one location every 2 d), which the Lotek software predicted would allow the tags to function for 101–157 d. We ensured Lotek transmitter batteries were fully charged prior to deployment (i.e., green rather than red indicator light and no error message upon activation) using the Lotek software and a DLC-1 Interface reader. After deployment, we processed received GPS-Argos transmissions using the manufacturer's data processor software ("PinPoint Host"), discarded GPS locations that did not meet the criteria for accurate data transmission (i.e., we retained 2D and 3D GPS points that passed the parsing software and removed "fail" points and erroneous dates), and retained high-quality Argos locations (i.e., Argos classes 3 [<250 m], 2 [250 – 500 m], and 1 [500 – 1500 m], Douglas et al. 2012). We considered migration as the period between when directional movement >100 km from the capture site began and when individuals reached the wintering grounds (for fall migrants) or breeding grounds (for spring migrants) and directional movement ceased (Airoola et al. 2019). We defined stopover sites as areas where individuals remained and did not proceed along the main travel route for at least 4 d (Airoola et al. 2019).

We used different approaches for calculating migration distance depending on type of tracking device and apparent track completeness. We used ArcGIS 10.8.2 (Redlands, CA, USA) to calculate either: (1) total migration distance (TMD; i.e., cumulative distance between all high-quality locations from the last location preceding the migration period and the first location after the end of the migration period, excluding movements within stopover areas) for satellite-tagged individuals with complete tracks; (2) straight-line minimum migration distance (SLMMD; i.e., distance between capture location and last migration period location) for satellite-tagged individuals with incomplete

tracks (i.e., at least one location transmitted that met the migration period criteria, but locations stopped transmitting prior to end of migration period); or (3) straight-line migration distance (SLMD; i.e., distance between breeding capture location and average wintering location) for geolocator-tagged individuals. For both geolocator-tagged and satellite-tagged individuals we defined seasonal movement rate (km/d) as the migration distance divided by the number of days in the migration period (i.e., including stopover days), and migration speed (km/d) as the distance traveled on days when migration movements occurred (i.e., excluding stopover days) following Airola et al. (2019).

Testing Transmitter Wear and Status. After experiencing extensive transmitter failure, we deployed Lotek transmitters on adult females nesting at our local study sites in Salt Lake County, Utah and Ada County, Idaho, to monitor and assess potential causes of failures. We used a combination of in-person visits and still images from trail cameras installed on the ceiling of nest boxes facing downward to the nest box floor (Spypoint LINK-EVO) to assess whether individuals were removing or damaging transmitters. We programmed cameras to take images in motion-detection mode and transmit images via cellular data to our laboratory computers. We randomly selected 10 images per day for each camera-monitored individual and annotated whether the bird was biting the transmitter or harness. In addition, to confirm points were recording and transmitting despite the tagged individual being inside of the nest box, we noted whether the individual was inside the nest box (i.e., detected in images) at the time that GPS points were recorded. We attempted to recapture individuals in the nest boxes 1–2 wk after tagging to check wear patterns on the transmitters and harnesses, download stored data to compare with remotely transmitted data, and test battery levels. Once we confirmed the nestlings had hatched, we returned a third time to recapture individuals to remove transmitters and check wear patterns, download data, and test battery levels a final time. We attempted to resight individuals that did not return to the nest box or that did not have a trail camera installed in the nest box to confirm whether individuals were alive and still carrying transmitters.

RESULTS

Migration Ecology. We deployed 49 geolocators on incubating adult female ($n=28$) and adult male ($n=21$) American Kestrels. We recaptured six individuals

(four females and two males) with intact geolocators and recovered one detached geolocator inside a nest box. We did not recapture or resight the remaining individuals after deployment, and they did not nest within the local nest box project in subsequent years. We identified one recaptured male as a migrant (D993), whereas the other five individuals had locations within a single cluster <200 km from the breeding area (i.e., within the margin of location error) and were considered nonmigrants.

We deployed 22 satellite transmitters on adult female American Kestrels during incubation (Canada: Alberta, $n=1$, Lotek; Saskatchewan, $n=8$, Lotek) and wintering periods (United States: California, $n=2$, Microwave; Texas, $n=10$, Lotek; Florida, $n=1$, Lotek). One individual provided a complete migration track, while three others provided incomplete migration tracks (Fig. 1).

The migrant geolocator-tagged individual (D993) nested in an agricultural and sagebrush steppe habitat near Kuna, Idaho, and departed for fall migration on approximately 13 July 2013. Following a 2-mo stopover approximately 230 km southeast of the capture location, it migrated southeast to New Mexico near the Arizona border (the exact location could not be determined because of spikes in the light curve at night), where it overwintered from October 2013 to March 2014. On 13 March 2014, it began its northward spring migration and returned to Idaho within 5 d of departure (Fig. 1). The SLMD was approximately 1235 km, with seasonal movement rates of 14.5 km/d (fall) and 247 km/d (spring), and a migration speed of 247 km/d in both fall and spring.

The satellite-tagged individual (#174019) with a complete migration track nested in an aspen parkland habitat near Manning, Alberta, and departed for fall migration between 28 July and 3 August 2018. Following a stopover from 5 August to 4 September 2018 near Athabasca, Alberta (approximately 345 km southeast of capture location), it migrated southeast through the Great Plains (stopping over for approximately 1 wk near Kearney, Nebraska), eastern Mexico, Guatemala, Honduras, and arrived in northwestern Nicaragua (near Hato Viejo) on 28 October 2018. It remained at this location through 11 November 2018 (when the battery likely failed), suggesting that this area was being used for the winter (Fig. 1). The TMD was 5945 km, with a seasonal movement rate of 66.8 km/d and a migration speed of 112.2 km/d.



Figure 1. Migration tracks for American Kestrels tagged with a geolocator ($n=1$, symbol with a dot) or transmitter ($n=4$, symbols without a dot) that collected data in multiple seasons. Locations for each tagged individual are represented by a unique shape. Locations and straight line distances between successive locations during fall migration are shown in orange (light grey in print), and those during spring migration are shown in blue (dark grey in print). Complete migration tracks are represented by solid lines and incomplete migration tracks (i.e., tags failed prior to migration completion) are represented by dotted lines. Deployment (D), stopover (S), and wintering sites (W), and departure and arrival dates for the two tagged individuals with complete migration tracks are shown in corresponding labels in orange (light grey in print) for fall and blue (dark grey in print) for spring.

Another satellite-tagged individual (#174025) with an incomplete migration track wintered in coastal grassland habitat on Mustang Island, Texas, departed its wintering grounds between 10 and 11 April, and was migrating northward on 12 April based on locations approximately 375 km north of Mustang Island near Huntsville, Texas. Subsequent locations transmitted on 6 May showed that this individual had migrated as far north as Cheboygan, Michigan (Fig. 1) after which no further points were transmitted. It is unclear whether this individual settled to breed in Michigan or was still migrating at this time, but the SLMMD was ≥ 2230 km.

Two more satellite-tagged individuals (#175486, #175487) with incomplete migration tracks nested

in agricultural habitat near Regina, and Moose Jaw, Saskatchewan, respectively, and migrated at least as far southeast as Wall, South Dakota (≥ 721 km SLMMD) and Wingate, Texas (≥ 2079 km SLMMD), respectively, but each only transmitted a single high-quality location along migration, after which both transmitters failed (Fig. 1). For both of these individuals, the long temporal gap (>1 mo) between the locations immediately preceding the migration period and migration locations themselves prevented us from determining fall migration departure dates. For all three individuals with incomplete tracks, we were unable to calculate seasonal movement rates or migration speeds because of long gaps between locations and lack of data on stopovers.

Reliability of Geolocators and Transmitters. We recovered 12% of deployed geolocators. For the five geocator-tagged individuals that were located <200 km from the breeding grounds, light signals during dusk and dawn indicated shading events that changed the recorded day length (characterized by a vertical drop and a step at dusk and the opposite shape at dawn) and were not consistent from day to day, resulting in the estimated locations being shifted dramatically and unpredictably. In addition, the midday light signal for these individuals appeared dimmed for days or weeks well below full sunlight level.

Of 22 satellite transmitters deployed, some did not transmit any locations after deployment ($n = 6$; 27%), whereas others transmitted locations but failed prior to ($n = 12$; 55%) or during ($n = 3$; 14%) migration. Of those that transmitted ≥ 1 location, the number of high-quality locations ranged from 3–74 ($\bar{x} = 21 \pm 18$ [SE]). Locations were often distributed unevenly across days and were inconsistent with the programmed schedule, and because of the uncertainty of the timing and locations of failure, we could not retrieve transmitters after they went offline.

In addition to the 22 transmitters we deployed to track migration, we also deployed four Lotek transmitters in Salt Lake County, Utah ($n = 1$) and Ada County, Idaho ($n = 3$) to investigate causes of transmitter failure using intensive in-person or trail-camera-assisted nest monitoring. All four transmitters failed within 2 wk of deployment while still intact on live individuals and transmitted from 7–15 locations. We resighted but were unable to recapture two individuals. We recaptured the remaining two individuals (and recovered their test transmitters) 20 d and 30 d after transmitter deployment. Motion-triggered nest box images were taken for 13 d (total of 8600 images) and 29 d (total of 7638 images) for these two individuals, after which the camera batteries failed and we did not replace them to avoid further disturbance of the nests. Although individuals extensively bit the transmitters and pulled on the harness material in 29% (38 out of 130) and 25% (74 out of 290) of the sampled motion-triggered images during incubation and brooding, the transmitters remained on the individuals and there was little visible evidence of external damage to the units or harnesses. Transmitters recorded points regardless of whether the individual was inside or outside the nest box (individuals were inside the nest box for 4 of 7 and 10 of 15 recorded

points), and all of the data stored on the units themselves had also been transmitted. Battery levels displayed as charged when transmitters were recovered. After removing transmitters, and without recharging the battery, we conducted further testing of the two recovered transmitters in an open, controlled yard setting. Both transmitters successfully recorded and transmitted 2–4 locations over a 24-hr period.

DISCUSSION

Migration Ecology. Although our sample size was small, our results were consistent with previously reported leap-frog migration patterns for American Kestrels, with northern breeders migrating farther than more southern breeders (Goodrich et al. 2012, Heath et al. 2012). Further, results suggested that external devices that do not require recovery might be particularly useful for uncovering long-distance migrations, as the Alberta individual represents the farthest recorded migration distance for the species. Previous band recovery studies have been limited in detecting long-distance and leap-frog migrations because of lower banding rates in northern breeding populations (B. Peterjohn and E. Nakash unpubl. data) and the low number of recoveries south of the United States (McClure et al. 2017). Despite known fall passage through southern migration sites (Ruelas et al. 2005, Lott et al. 2006), reviews of banding data show that only 3% of banded American Kestrel recoveries were reported south of the United States during winter, and over half of them were high latitude ($>45^\circ$) breeders (Goodrich et al. 2012). Furthermore, higher latitude breeders and more migratory populations tend to have longer dispersal distances (McCaslin et al. 2020) and lower breeding site fidelity (Miller et al. 2012), making them difficult to recapture from year to year, and suggesting limited utility of devices that require recovery.

Despite the Alberta individual traveling approximately five times the distance of the Idaho individual during fall migration, the duration of the migration period was surprisingly similar (89 d and 85 d, respectively), because of differing stopover durations. Both individuals made post-breeding movements to areas southeast of their breeding locations (approximately 345 km and approximately 230 km, respectively) prior to continuing southward migration, with the Alberta individual's (longer-distance migrant) stopover lasting only half the duration of the Idaho individual's (shorter-distance migrant; 30

d and 80 d, respectively). Because of the limited time to reach a far-away destination, long-distance migrants may prioritize optimizing migration speed, whereas shorter-distance migrants, who can afford to wait, may adjust migration speeds and take longer stopovers according to local weather conditions to reduce energy expenditure (Packmor et al. 2020). Dorian et al. (2020) found shorter post-breeding stopover duration for long-distance migrant passerines compared to shorter-distance migrants, but there can also be large intraspecific variation in stopover duration based on food availability (Steenhof et al. 2005). Prolonged stopovers that extend beyond the expected time needed for refueling are increasingly being documented with the use of tracking technology (McKinnon et al. 2013). Although causes vary, prolonged stopovers may allow the migrating bird to acquire necessary resources to cross large natural barriers (Delmore et al. 2012), to track seasonal resources using several consecutive nonbreeding areas (Stach et al. 2012), to molt during migration (Leu and Thompson 2002), or to congregate at hot-spots to forage on abundant prey (Newton 2010). American Kestrels complete molt during reproduction (Smallwood 1988), and congregations are not commonly observed as kestrels tend to migrate alone or in loose associations (Smallwood and Bird 2020). For our two tracked individuals, there were no obvious large natural barriers along their immediate post-stopover paths. However, American Kestrels could be tracking seasonal resources and moving to areas with higher prey abundance. Similarly, Steenhof et al. (2005) found that Prairie Falcons (*Falco mexicanus*) travel to postbreeding “summering areas” northeast of breeding sites, and remain there for several months prior to fall migration, likely following seasonal availability of ground squirrels. These results are the first reports of prolonged stopovers in American Kestrels. More work is needed to understand the frequency of these types of movements and to identify factors underlying this behavior.

The seasonal movement rate was 17 times faster in spring than fall for the Idaho individual. The faster rate resulted from a lack of stopovers in spring, rather than an increase in migration speed. A review by Nilsson et al. (2013) reported higher speeds, shorter durations, and shorter stopover durations in spring compared to fall migration across a variety of species, which could be proximately due to seasonal differences in pre-migratory and migratory fueling conditions and behavior, and ultimately due to

higher selective pressure to arrive earlier on the breeding grounds vs. the wintering grounds (Nilsson et al. 2013).

Reliability of Geolocators and Transmitters. We recovered a small proportion of the total number of geolocators we deployed (12%), suggesting the other tagged individuals dispersed from the area or died. This return rate is comparable to that of banded American Kestrels in the same study area (17%; Steenhof and Heath 2009), so we do not suspect that low return rates of individuals with geolocators was an artifact of tagging (McKinnon et al. 2013), particularly because geolocators were lightweight (<2.5% body weight). The low precision of geolocators and inconsistent shading events masked movements of resident or short-distance migrants. In addition, the migrant individual’s wintering location was obscured by exposure to artificial light at night, and its flight path could not be determined because migration occurred during equinox periods. Low return rates and the variability in breeding site fidelity of American Kestrels (Steenhof and Peterson 2009) present major limitations for using geolocators, which require recovery. Further, although location precision of short-distance movements might be less of a limitation for tracking fully migratory and long-distance migrant populations (wherein movements would tend to be >200 km), American Kestrels with these population characteristics tend to have longer dispersal distances (McCaslin et al. 2020) and lower breeding site fidelity (Miller et al. 2012), making geolocator recovery difficult. Several aspects of American Kestrel ecology suggest that shading and light interference could impact the accuracy of geolocation in multiple seasons. American Kestrels use cavities not only during the breeding season, but also as roosts during migration (Bortolotti and Wiebe 1993) and winter periods (Davis et al. 2017) and inconsistent cavity entry and exit times can result in dramatic and unpredictable shifts in location estimates. Further, this species is often associated with urban and semi-urban areas (Smallwood and Bird 2020) increasing their exposure to artificial light at night.

Both transmitter models (Lotek and Microwave) experienced failures (82% of transmitters failed prior to migration), despite differing relative load and construction and despite the fact that all weighed <3% body weight (a generally accepted standard introduced by MacDonald and Amlaner 1980). Although causes of failure may be varied, we

confirmed that in at least four cases, Lotek transmitters did not fail as a result of individual mortality, transmitter or antennae removal, or visible transmitter damage. Although shading and cavity use were not likely causes of failure for Lotek transmitters (our test transmitters recorded points when individuals were confirmed to be inside nest boxes), these factors could present issues for solar-powered Microwave transmitters. Field tests of an earlier transmitter model (Lotek 3.5-g PinPoint GPS-Argos) on several shorebird species had a comparable failure rate to our study (89% of tags failed to transmit locations, Scarpignato et al. 2016). Some of these failures were attributed to observed antenna loss, and Lotek engineers also theorized that electrostatic discharge damage caused by the rubbing of the tag against the birds' feathers could have prevented transmission (Scarpignato et al. 2016). In our study, we used a newer model of Lotek transmitters that had a reinforced antennae base, and antenna removal was not the cause of failure in at least four cases, but this could present issues for Microwave transmitters which did not have a reinforced antenna base. Although we cannot rule out electrostatic discharge damage, this issue had apparently been corrected in subsequent models following the field tests by Scarpignato et al. (2016). Regardless, both transmitter models we tested have successfully tracked (i.e., provided migration tracks) small, non-raptor species comparable in mass to American Kestrels (Lotek, Common Nighthawk [*Chordeiles minor*], approximately 90 g, Ng et al. 2018; Microwave, Aleutian Tern [*Onychoprion aleuticus*], approximately 110 g, Tengeres and Corcoran 2020), so causes of failure may be species-specific rather than the result of transmitter to body weight ratios. Although a variety of external tracking devices including geolocators, archival GPS transmitters, satellite transmitters, and loggers that download to UHF base stations have been used successfully for larger falcon species (e.g., Lesser Kestrels [*Falco naumanni*], Rodríguez et al. 2009, Lopez-Ricaurte et al. 2021; Prairie Falcons, Steenhof et al. 2005; Eleonora's Falcon [*Falco eleonorae*], Vansteelant et al. 2021), the differing life histories, larger size of these species and the size of tracking devices they are able to carry, as well as differing tag and harness construction make it difficult to directly compare to our results. To our knowledge, only one other published study has used external devices (archival GPS) to track American Kestrels in multiple seasons (Crandall and Craighead 2019). The one recovered

device was used successfully to determine the wintering range of an individual of known origin, but because of limited battery life (18 stored locations), the transmitter did not provide any locations along the migration route (Crandall and Craighead 2019). The small sample size and difference in study goals limits direct comparison between the Crandall and Craighead (2019) paper and our results.

Overall, because of American Kestrels' small body size and the <3% body weight standard for tracking devices, there are limited options for tracking their migration, and our study showed low reliability of several tracking devices for this species (i.e., 88% of geolocators were never recovered, 82% of transmitters failed prior to migration). We do not have sufficient evidence regarding whether the <3% body weight standard is appropriate for this species because in most cases we were unable to directly observe the cause of satellite transmitter failure or the fate of unrecovered geolocators, and the many other factors that may affect device function and recovery. However, a meta-analysis by Barron et al. (2010) did not show negative impacts on aspects of behavior, body condition, or vital rates of birds when tracking device weight exceeded 3% or even 5% body weight, and Pennycuick et al. (2012) found that increased drag, rather than transmitter weight, adversely affected migration performance. As mentioned above, these models have been used successfully for other species, so transmitter failures in our study and others (e.g., Scarpignato et al. 2016) may be the result of some aspects of species life history or interactions between life history and these particular tag models.

Conclusions. In summary, this study represents a significant investment to track American Kestrel migration. Although our sample size was small, we have provided some of the first published data on individual migration phenology and routes, including a record migration distance for the species and evidence of prolonged post-breeding stopovers. However, the overall reliability of recovery and low precision of data of geolocators, and the high failure rate of transmitters prior to migration suggest that the tracking technology we used was not suitable to identify population-specific migration ecology for this small-bodied, cavity-nesting raptor species.

ACKNOWLEDGMENTS

Funding for this project was provided by a grant from the Strategic Environmental Research and Development

Program (SERDP) of the US Department of Defense (US DoD; Award Number: RC2702), Adopt-a-box donations, and gifts from Scott Radford. Kestrels were handled and marked under the authority of US federal bird banding permits (JAH: 23307; JLW: 21384), Canadian federal bird banding permits (ARH: 10277AC; JLW: 10277Z), Alberta wildlife research permit (ARH: 18-566), Saskatchewan research bird banding permit (JLW: 18FWBB009, 19FWBB009), Idaho scientific collecting permits (JAH: 071119), Utah certificate of registration scientific collecting permit (JLW: IBAND2199), Texas scientific permit (JAH: SPR-0917-187), Florida scientific collecting permit (JAH: LSSC-17-00081B), California scientific collecting permit (JAH: 13779) and institutional IACUCs. We thank Erin Bayne and Jeremiah Kennedy for permit facilitation. We thank our partners who assisted with trip logistics and fieldwork: Mitchell Warne, Janet Ng, Jared Clarke, Ryan Fisher, Mike Blom, Rich Fischer, Jake Jung, Kashmir Wolfe, Dayan Espinosa, Joel Pagel, Dane Ferrell, and Libby Even. We thank Wouter Vansteelant and two anonymous reviewers for comments that improved an earlier draft of this report.

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Received 10 January 2022; accepted 28 August 2022
Associate Editor: Jean-François Therrien