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High-resolution GPS Tracking of American Kestrels Reveals Breeding and Post-breeding Ranging Behavior in Northern Virginia, USA

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ABSTRACT.—Long-term monitoring data indicate a persistent decline in American Kestrel populations across North America. Loss or alteration of habitat have been listed as potential causal factors, but basic information on kestrel space use, including breeding home range size, is lacking. No study has provided robust estimates of the ranging behavior of breeding kestrels based on tracking data of any resolution. We fitted 19 adult female kestrels with solar-powered GPS transmitters during the incubation period in northern Virginia. High-resolution tracking began during the early nestling stage for 17 birds. We collected an average of 1710 locations per bird through the end of the breeding season (31 August), with 13 birds tracked through the fledging of their young. Autocorrelated kernel density home range estimation showed that female kestrels used breeding home ranges that were smaller (average: 0.32 km²) than most previously published range sizes. Home ranges did not vary significantly in size across breeding stages and demonstrated little overlap with the ranges of neighboring kestrels. Five females shifted their territories in the post-breeding stage (i.e., after disappearance or dispersal of fledglings) between 1.5 and 12.3 km from their nest box; they maintained these new ranges at least to the migration period. We also documented home range excursion forays ($n=128$) by all 12 consistently tracked females. Mean (4.0 km) and maximum (127.7 km) foray distances were some of the largest reported among birds and mammals relative to home range size. Weekly foray rates were highest during the nestling stage, and for birds that ultimately shifted from their breeding home range. The existence of long-distance foray behavior and the use of multiple summer home ranges, both shown here for the first time for this species, has a direct impact on interpretation of kestrel nest-site and habitat selection data, and on the assessment of potential threats to this species in the breeding season.

KEY WORDS: *Foray; home range; post-breeding; prospecting; space use; territory.*

EL SEGUIMIENTO CON GPS DE ALTA RESOLUCIÓN DE *FALCO SPARVERIUS* REVELA SU COMPORTAMIENTO EN EL RANGO REPRODUCTIVO Y POSTREPRODUCTIVO EN EL NORTE DE VIRGINIA, EEUU

RESUMEN.—Los datos de monitoreo a largo plazo indican una disminución persistente en las poblaciones de *Falco sparverius* en toda América del Norte. La pérdida o alteración del hábitat se han señalado como posibles factores causales, pero falta información básica sobre el uso del espacio por parte de *F. sparverius*,

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incluyendo el tamaño del área de campeo de la estación reproductiva. Ningún estudio ha proporcionado estimaciones sólidas del comportamiento en las áreas de cría de *F. sparverius* basadas en datos de seguimiento de cualquier resolución. Equipamos 19 hembras adultas de *F. sparverius* con transmisores GPS alimentados por energía solar durante el período de incubación en el norte de Virginia. El seguimiento de alta resolución comenzó para 17 aves durante la etapa temprana de polluelos. Recopilamos un promedio de 1710 localizaciones por ave hasta el final de la temporada reproductiva (31 de agosto), con 13 aves rastreadas hasta el emplumamiento de sus crías. La estimación del área de campeo mediante kernels de densidad que tienen en cuenta la autocorrelación espacial mostró que las hembras de *F. sparverius* tuvieron áreas de campeo durante la estimación de cría más pequeñas (promedio: 0.32 km^2) que la mayoría de los tamaños de las áreas de campeo previamente publicados. Las áreas de campeo no variaron significativamente en tamaño a lo largo de las etapas reproductivas y mostraron poco solapamiento con los áreas de campeo de los individuos de *F. sparverius* vecinos. Cinco hembras desplazaron sus territorios en la etapa postreproductiva (i.e., después de la desaparición o dispersión de los polluelos) entre 1.5 y 12.3 km desde sus cajas nido; ellas mantuvieron estas nuevas áreas de campeo al menos hasta el período de migración. También documentamos excursiones exploratorias fuera del área de campeo ($n = 128$) en las 12 hembras seguidas de manera consistente. La distancia media (4.0 km) y máxima (127.7 km) de las exploraciones fueron algunas de las más grandes reportadas entre las aves y los mamíferos en relación con el tamaño del área de campeo. Las tasas de exploración semanal fueron más altas durante la etapa de cría y para las aves que finalmente cambiaron su área de campeo. La existencia de comportamientos de exploración de larga distancia y el uso de múltiples áreas de campeo en verano, ambos demostrados aquí por primera vez para esta especie, tienen un impacto directo en la interpretación de los datos de selección de hábitat y de lugares de cría de *F. sparverius*, y en la evaluación de las posibles amenazas para esta especie en la temporada reproductiva.

[Traducción del equipo editorial]

INTRODUCTION

The American Kestrel (*Falco sparverius*; hereafter, “kestrel”) is a widespread, cavity-nesting falcon found throughout most of the western hemisphere that inhabits open to semi-open habitats, including grasslands, agricultural fields, shrublands, and urban and suburban areas (Smallwood and Bird 2020). The species has experienced a marked decline in recent decades according to a variety of data sources (US Geological Survey Breeding Bird Survey routes: Sauer et al. 2017; migration counts: Farmer and Smith 2009; nest box occupancy rates: Smallwood et al. 2009a), with some of the most persistent declines in the northeastern USA (Oleyar et al. 2023). Suggested potential causes of the declines have included climate change (Steenhof and Peterson 2009), pesticide exposure (Smallwood et al. 2009, Rattner et al. 2020), and habitat degradation and loss (Bolgiano et al. 2015, Wommack et al. 2015), but the observed steady rate of decline may be due to a combination of factors varying over time and space (McClure et al. 2017).

Improved understanding of kestrel movement ecology has significant potential to inform assessments of regional threats and evaluate potential management solutions (Fraser et al. 2018, Katzner and Arlettaz 2020). The home range of a species, originally framed by Burt (1943:352) as the “area traversed by an individual in its normal activities of

food gathering, mating, and caring for young,” is the most basic and common descriptor of a species’ movement ecology. It describes the space requirements of individuals of the species, and when combined with knowledge of home range overlap, informs key population parameters including density, carrying capacity, and number of potential breeders (Morales et al. 2010). Placement and size of raptor home ranges has been used to assess the utilization and effectiveness of protected areas (Margalida et al. 2016, Blakey et al. 2020), whereas seasonal variation in range size has clarified the potential threat of wind energy development (Braham et al. 2015). Home range size may also serve as a useful metric of habitat quality (e.g., Forsman et al. 2005, Kouba et al. 2017).

Description of the home range concept by Burt (1943) goes on to state that “Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.” As a central-place forager where both sexes share parenting duties, breeding kestrels are closely tied to their nest site (natural cavities or nest boxes) for at least part of the breeding season, and their movements reflect that important association; yet the extent and duration of this connection has not been evaluated. The “occasional sallies,” also called forays, are challenging to document, yet advances in tracking technology have improved our understand-

ing of this behavior in birds. Recent studies have documented previously unknown long-distance forays in both raptors and songbirds during the breeding (Blakey et al. 2019, 2020, Cooper and Marra 2020) and post-breeding (Heggøy et al. 2021, Curk et al. 2022) periods. The existence, timing, and potential drivers of these movements have important conservation relevance. For example, the spatial extent of these movements can inform risk of exposure to agricultural chemicals (e.g., Santolo and Yamamoto 2009) and the extent to which protected areas include regions utilized by focal species (Blakey et al. 2020). In addition, timing and extent of movements directly impact knowledge of habitat available on the larger landscape for foraging and breeding dispersal decisions (Reed et al. 1999, Ponchon et al. 2013).

Various factors influence the movement behavior of individual raptors including sex (Pfeiffer and Meyburg 2015, Blakey et al. 2020), and breeding status (e.g., juvenile, nonbreeder, breeding adult; van Eeden et al. 2017, Wheat et al. 2017). Range sizes and travel distances may expand with the transition from incubation to nestling stages as energetic demands on adults rise (Hernández-Pliego et al. 2017, Blakey et al. 2020, López-López et al. 2022). Improved tracking tools have allowed increased investigation of breeding bird movements in the less-studied fledgling and post-breeding stages, when adult movements are likely to be less predictable and wider ranging. For example, parents with dependent fledglings may expand their home range (Blakey et al. 2020), alter habitat selection (Vitz and Rodewald 2006, Wohner et al. 2020), or abandon their breeding territories (van Overveld et al. 2017). Adults in the post-breeding period, when fledglings are no longer dependent, may show large-scale regional transition movements prior to actual migration (Brown and Taylor 2015, Bégin-Marchand et al. 2022), make temporary long-distance excursions (Heggøy et al. 2021, Curk et al. 2022), and shift their home ranges to entirely new locations (Arlt and Pärt 2008, Cooper and Marra 2020).

Although the American Kestrel is a well-studied species, current knowledge of its movement ecology is surprisingly limited. Home range size information comes primarily from early studies relying on visual observations. Average estimates of home range size range in area from 0.18 to 1.94 km² and in diameter from 0.66 to 2.36 km (Craighead and Craighead 1956, Cruz 1976, Gard and Bird 1990), but very little tracking information has been collected to confirm

these estimates. A single study used very high frequency (VHF) radio telemetry to track seven adult males during the breeding season (Santolo and Yamamoto 2009), but the location data were lost and only maximum foraging distances are presented. Various authors have used radii to represent circular kestrel home ranges as a key parameter for habitat investigations (e.g., 900 m: Strasser and Heath 2013; 500 m: Brown et al. 2014, Miller et al. 2019; 2.4 km: Buers et al. 2019), but these estimates have been based on early observational studies, or on unpublished personal observations. Until recently, high-resolution tracking of kestrels has been impossible due to the weight of GPS transmitters and no study has provided robust estimates of the ranging behavior of breeding kestrels based on tracking data of any resolution.

Our objective was to document home range size and overlap in the American Kestrel using high-resolution tracking data. We also aimed to investigate ranging behavior more broadly by describing the frequency and distance of movements outside of established home ranges (i.e., forays). We focused on females during the breeding and post-breeding seasons and investigated how ranging behavior varied across all breeding stages, including after fledglings have dispersed or disappeared. We hypothesized that foraging demands on adults would be highest at the fledgling stage and predicted that the largest home ranges and movements would be during this period.

METHODS

Study Area. Our study area was located in Fauquier and Rappahannock Counties in Virginia, USA, approximately 80 km west of Washington, DC, USA, and was bordered to the west by the forested Shenandoah National Park. In this two-county region we regularly monitored a network of 163 kestrel boxes. Monitored boxes stretched in a roughly NE-SW orientation from just north of the city of Warrenton (pop: 10,057 in 2020; US Census Bureau) to just south of the town Sperryville (pop: 302 in 2020; US Census Bureau; <https://www.census.gov/quickfacts/fact/table/warrentontownvirginia/HSD310219>). The area defined by a 500-m buffered 100% minimum convex polygon around monitored boxes covers 1326 km² and includes a diverse mosaic of land uses that are typical of the Mid-Atlantic Piedmont: livestock pastures (primarily for beef cattle), hay fields, and grasslands (37.3%); scattered fragments of deciduous forest (51.1%); row crops

which are primarily livestock feed corn (2.6%); and human development in various forms and intensities (7.2%; National Land Cover Database, <https://www.mrlc.gov/>). The majority of nest boxes were located in cattle pasture, hay fields, or meadows. Elevation ranges from approximately 100 to 480 masl. Temperature ranges from an average high of 5.6°C in January to a high of 29.0°C in July, with an average annual precipitation of 1100 mm (Warrenton, VA; <http://www.usclimatedata.com/>).

Nest Monitoring. Beginning in mid-March 2021, we checked nest boxes (with a camera mounted on a pole to minimize disturbance) approximately once a week, in an attempt to observe a clutch in the process of completion. We estimated clutch initiation date in two ways. If a nest was found containing <5 eggs (i.e., less than a typical full clutch), we assumed one egg would be laid every other day (Smallwood and Bird 2020). If the first check with eggs revealed a full clutch of five or more eggs, we estimated clutch initiation date by backdating from nestling ages, determined during a single check during the nestling stage and using a photographic key (Klucsarits and Rusbuldt 2007). Here we assumed an incubation period of 30 d plus 5–9 d for clutch completion based on egg laying rate (Bird and Palmer 1988). We estimated the hatch initiation date as 30 d from clutch initiation date, but this date was refined based on observation of nestlings when available. We estimated fledging date as 30 d from hatching (Bird and Palmer 1988). Once nestlings fledged, we visited their natal ranges at least once a week and used visual/auditory detections to estimate when fledglings dispersed or disappeared.

Capture and Tracking. We captured adult female kestrels and fitted them with miniature solar-powered GPS data loggers from April to May 2021. Because we were interested in investigating kestrel habitat selection, we prioritized tagging females in boxes surrounded by a diversity of field cover types. Once a subset of birds was tagged, we also targeted nearby boxes to maximize collection of home range overlap data. We captured kestrels by hand from nest boxes at least 7 d after the last egg of the clutch had been laid. We attached loggers (Remote Gypsy XS; TechnoSmart, Rome, Italy, 3.3–3.9 g) using a backpack harness (Chan et al. 2016) created from two sections of 3.75 mm diameter Spectra tubing (Bally Ribbon Mills, Pennsylvania, USA) with shrink tubing at the breast knot connection. No height adjustment or additional modification was made to prevent feather coverage of the solar panel, aside

from feather trimming near the panel. We only attached loggers when the combined weight of the harness and logger (range: 3.8–4.6 g) did not exceed 3% of the kestrel's body weight.

We initially set the location collection schedule to low resolution (<4 locations per day) due to the lack of solar charging while females were incubating. We switched loggers to a high-resolution schedule (typically 10-, 15-, or 20-min intervals from 0800 H to 1600 H or 1800 H EDT) when batteries sufficiently charged, which was typically about 1 wk after estimated hatch date. Therefore, we recorded few locations during incubation and only at low temporal resolution.

We manually downloaded data from the loggers at least one time per week using a remote base station. We adjusted the collection schedule if battery charge was insufficient to maintain continuous collection. Downloads and adjustments could be made from up to approximately 400 m away, allowing for minimal disturbance to the birds after initial capture and logger fitting.

We defined the different periods of the breeding season (hereafter “stage”) for each tracked female as: (1) incubation: before and including the estimated hatch initiation date; (2) nestling: between the estimated hatch initiation date and either the last date nestling heads were seen poking out of the nest box, or the estimated fledge date if frequent nest checks were not possible; (3) fledgling: between the confirmed fledge date, when it was certain the box was empty and the last observation of a fledgling in the home range, or 3 wk after the confirmed fledge date when fledglings are independent (Varland et al. 1993), whichever was earlier; and (4) post-breeding: after the fledgling stage and through 31 August, or until a home range “shift” was observed (see Forays and Home Range Shifts below). In these cases, an additional shifted post-breeding stage was assigned, beginning at the date of the range shift (when the bird no longer returned to its breeding home range) and ending on 31 August.

Home Range Analysis. We created 95% home ranges for each female and each breeding stage in 2021 (excluding incubation) using autocorrelated kernel density estimation (AKDE: Fleming et al. 2015, Fleming and Calabrese 2017) in the R package *ctmm* (Calabrese et al. 2016). This technique improves upon classic kernel density estimation by explicitly modeling the degree of autocorrelation of locations and identifying an optimal smoothing bandwidth that incorporates a more appropriate

continuous-time movement process (Fleming and Calabrese 2017). Home range estimation is only appropriate when animals exhibit range residency (Fleming and Calabrese 2017), also referred to as site fidelity (i.e., repeated, consistent use of the same area). We therefore excluded breeding stages where inspection of the variogram (Fleming et al. 2014) or plotting of tracking locations did not indicate range-resident behavior. We also screened location data for inaccurate or implausible locations based on estimated travel speed (function *outlie*). We then fit location data for the remaining samples to a suite of possible movement models ($n = 9$), which varied primarily in how position and velocity autocorrelation were represented (Calabrese et al. 2016). The full model set included a null model that assumed complete independence among locations as in a standard kernel density approach. Using the most appropriate model for each individual data set (i.e., lowest corrected Akaike's information criterion [AIC_c]), we generated a 95% home range kernel density estimate (Calabrese et al. 2016) and employed optimized weighting of location data to account for irregularity in sampling intervals. The amount of independent information included in a potentially autocorrelated movement data set is best represented by the effective sample size. This adjusted sample size is proportional to the observed home range crossing events, and almost certainly lower than the recorded number of locations (Fleming et al. 2019). Although current methods in *ctmm* effectively account for potential area estimation bias, even at low effective sample sizes (Fleming and Calabrese 2017, Fleming et al. 2019), we conservatively included only those home ranges based on effective sample sizes of greater than 15 locations. To compare home range size estimates across breeding stages, we calculated an average home range size for each stage across sampled individuals, and compared these averages based on overlap of confidence intervals calculated with the function *meta*. This method ensures that uncertainty in each range size estimate, as well as variability across individuals is accounted for in confidence intervals.

The loggers used do not record horizontal accuracy, so we incorporated GPS device error into each movement model and subsequent home range estimation based on calibration data collected with stationary loggers (Fleming et al. 2020). Calibration tests included a range of sampling intervals (1–15 min) and included 17 of the 19 loggers that were

ultimately affixed to kestrels. A total of 16,210 calibration locations was recorded, with between 95 and 2258 points recorded for each of the 17 loggers. The average straight-line distance between each location and the known location of the loggers was 21.8 m. A single error model (function *uere*) was generated for the pooled calibration data and applied to each movement model (Fleming et al. 2020) for each individual and breeding stage.

We created a single full-season home range for each bird to describe overall breeding home range sizes and to assess the degree of overlap between adjacent ranges. For these calculations we used the entire period of the bird's summer resident behavior including only birds that were tracked from incubation to the time their young fledged. Home range overlap was quantified using the Bhattacharyya coefficient (BC; Winner et al. 2018), which ranges from 0 to 1, for all pairs that shared a home range boundary. Overlap was assessed using the nestling stage home range, as well as the pooled full-season range; the nestling stage home range represented less behavioral variation than the fledgling stage across individuals, due to the variable survival and dispersal times of fledglings.

Forays and Home Range Shifts. We described foray flights for birds for which we could construct full-season home ranges. The average distance from the nest to the nearest home range boundary for these birds was 162.7 m, so we defined a foray as any location or series of locations that was more than twice this distance (325.4 m) outside each bird's home range boundary. In this way, forays were meant to represent movements not only outside an established home range, but also substantially farther than a typical movement distance within the home range. Intervening points within our cutoff distance signaled the end of a foray, which could continue for more than one day. To account for uncertainty in boundary estimation, we defined the boundary here as the line representing the outer 95% confidence interval for the 95% autocorrelated kernel density estimator home range.

To investigate variation in foray frequency and length across breeding stages, we calculated weekly foray counts, as well as total duration and maximum distance of forays. Only forays observed during high-resolution tracking were considered, and only weeks in which the bird was tracked in high resolution each day of that week were included. Here we defined high-resolution tracking as a maximum daytime sampling interval of 30 min and a total daily

collection of at least 16 locations. The restriction to high-resolution samples was designed to minimize severe underestimation of foray distance or the missing of an entire daytime foray event. To place foray distances in broader context, we divided average and maximum foray distances by home range radius (assuming a circular shape for our full-season home range average; Cooper and Marra 2020).

We defined a home range shift as occurring when a kestrel's daily movements were consistently and predictably located within an area that was distinct and non-adjacent to the nestling stage home range and where no future movements were detected to this original range within that season. All documented range shifts occurred after the dispersal or disappearance of fledglings (i.e., post-breeding). We investigated whether this range shift behavior was related to earlier foray behavior during the breeding season. We considered long distance movements to be forays for these range-shifted birds through their period of transition to new ranges, but not after these shifted ranges were permanently established (i.e., no return to nestling home range). Using a regression framework, we investigated the influence of breeding stage and range consistency (whether a bird maintained its breeding home range or shifted to a new one) on weekly foray frequency and foray distances. In the case of weekly foray counts we used a generalized linear mixed model with individual bird as a random effect (intercept term) and a negative binomial error distribution. For foray distance, we used a linear mixed model framework (Gaussian error distribution) again with individual as a random intercept. We used AIC_c to compare null models to models including stage, range consistency, as well as the addition and interaction of the two. We report the pseudo- R^2 values (tri-gamma in the case of the negative binomial model; Nakagawa et al. 2017) as assessments of model predictive power, and we assessed model fit through inspection of scaled simulated residuals in the *DHARMA* package (Hartig 2021) and its associated tests for uniformity.

We performed all modeling in the R environment (R Core Team 2020). We used package *lme4* (Bates et al. 2015) to run regression models, *AICcmodavg* (Mazerolle 2020) for model comparisons, *MuMIn* (Barton 2020) for marginal r^2 and *DHARMA* (Hartig 2021) for calculation and plotting of scaled residuals. Plotting was performed with *ggplot2* (Wickham

2016) and maps prepared with *tmap* (Tennekes 2018).

RESULTS

We tagged 19 adult female kestrels with GPS transmitters from 12 April to 21 May 2021. We successfully tracked 18 birds between 13 and 140 d (mean = 100 d) through 31 August 2021 (considered end of breeding season; Table 1), with a range of 0 to 91 d tracked at high resolution (mean = 44.8 d). One female disappeared before any locations were recorded. We recorded between 139 and 3369 locations per bird (mean = 1710). No recorded locations were implausible based on estimated travel speed. Twelve study nests were confirmed to have fledged young. We suspected that two others had young that fledged because the nests were empty after observations of large nestlings.

Home Range Size and Seasonal Stability. Twelve kestrels displayed resident behavior and provided tracking data at least through fledging of young. We pooled locations from these birds to estimate a full breeding season range even though these birds were tracked for varying periods of time before 31 August. Average full season home range size for these resident female kestrels was 0.315 km^2 (CI: 0.193–0.488); sizes varied from 0.056 to 0.905 km^2 (Fig. 1, Supplemental Material Table S1). Average home range size tended to be smallest in the nestling stage (mean = 0.219 km^2 ; CI = 0.124–0.359) compared to the fledgling (mean = 0.400 km^2 ; CI = 0.170–0.811), and post-breeding (mean = 0.391 km^2 ; CI = 0.279–0.533) stages (Fig. 1, Table S1). High individual variation, however, resulted in at least some overlap in 95% confidence intervals, with variation across individuals highest in the fledgling stage (Fig. 1), where sample size was limited by the apparent loss of fledglings in some cases, and nonresident behavior of adults in others.

Of 13 birds tracked into the post-breeding stage, seven remained in their original nesting territories at least through 31 August. One logger failed early in the post-breeding stage, and five birds gradually shifted to unique territories either during or at the end of the fledgling stage. These shifted post-breeding territories were 1.5, 3.2, 3.5, 4.8, and 12.3 km from the female's nest box (e.g., Fig. 2) and were established permanently (i.e., female ceased to return to nesting range) by 4 to 31 July, 19 to 57 d after the estimated fledge dates of their young. Average size of these five shifted ranges was most similar to fledgling and post-breeding stage ranges,

Table 1. Tracking data and nest fates for 18 American Kestrel females in Fauquier and Rappahannock Counties of Virginia, USA, tagged with solar-powered GPS backpack loggers. The start and end dates of each bird's tracking period in 2021, along with the total duration of tracking (days tracked), the total number of locations, and the total days the bird was tracked at a high-resolution sampling interval (Days at HRes; see Methods). This summary includes all tracking locations, regardless of whether they could be assigned to a breeding stage. An end date of 31 August indicates the bird was tracked through the entire breeding season. ID values in bold indicate birds for which a home range could be estimated in at least one breeding stage.

Bird ID	Start Date	End Date	Days Tracked	Days at HRes	Total Number of Locations	End of Nest Attempt	Nest Fate
1007	30 Apr	30 Aug	122	91	3369	10 Jun	fledged
1011	30 Apr	30 Aug	122	90	3180	04 Jun	fledged
1013	14 May	31 Aug	109	86	3146	18 Jun	fledged or depredated very late
1019	30 Apr	31 Aug	123	75	3027	10 Jun	fledged
1010	13 Apr	31 Aug	140	78	2800	01 Jun	fledged
1017	21 May	31 Aug	102	67	2506	25 Jun	fledged
1004	25 May	31 Aug	98	76	2379	28 Jun	fledged
1005	09 May	27 Aug	110	63	2294	21 Jun	fledged
1002	12 Apr	30 Aug	140	47	2065	28 May	fledged
1008	07 May	31 Aug	116	56	2014	18 Jun	fledged or depredated very late
1009	14 Apr	25 Aug	133	20	1170	04 Jun	fledged
1006	30 Apr	05 Jul	66	29	870	18 Jun	fledged
1015	12 Apr	21 May	39	14	548	02 Jun	female disappeared; nest fledged with only male attending
1001	01 May	27 Aug	118	4	521	10 Jun	fledged
1012	15 May	28 May	13	5	286	07 Jun	abandoned due to depredation attempt
1016	09 May	01 Jun	23	4	282	07 Jun	depredated
1003	13 Apr	31 Aug	140	0	182	13 Apr	abandoned after capture
1014	07 May	05 Aug	90	1	139	17 Jun	depredated

with relatively low variation among individuals (mean = 0.428 km²; CI = 0.302–0.588; Fig. 1; Table S1). Once established, these shifted post-breeding ranges were maintained at least through 31 August.

A single female (Bird ID no. 1009), not included in the full season range analysis, displayed a different movement pattern. In mid-June, after a few apparently exploratory flights in late May, this female began regularly using a new pasture 2.5 km from the nest box, which required travel across an adjacent occupied kestrel home range. The female never completed a permanent shift to this new area but continued to use both areas through the rest of the breeding season, rarely using the intervening area occupied by the neighboring pair (Fig. S1).

Home Range Overlap. Bhattacharyya coefficient overlap values for six female kestrels (i.e., five sets of two neighboring birds with adjacent home ranges) ranged from 0 to 0.267 in the nestling stage, and 0 to 0.421 for full season ranges (Table 2). However, even for the neighbors with the highest overlap (Bird ID no. 1001 and no. 1011), few actual tracking locations

were found in the same areas (Fig. 3). To put this level of overlap in spatial context, the average distance between adjacent nest boxes within this group, including two occupied nest boxes without tracked females (Fig. 3) was 573 m (range: 405–956 m).

Foray Behavior. We documented 128 foray flights by the 12 females for which we could create full-season home ranges. The maximum distance from the home range boundary was 127.7 km (second longest = 32.9 km), with 11 forays exceeding 10 km from the home range boundary. The mean distance of all 128 forays was 4.00 km (SE = 0.35 km; median = 1.65 km). The average home range radius was 0.319 km, assuming a circular home range. Maximum and average observed foray distances were therefore 400.3 and 12.5 times larger than the average home range radius, respectively. The total number of detected forays for individual females during our 4-mo study period ranged from 2 to 26, with a mean of 10.7 (SE = 3.1), but birds were tracked for varying lengths of time and at varying temporal resolutions

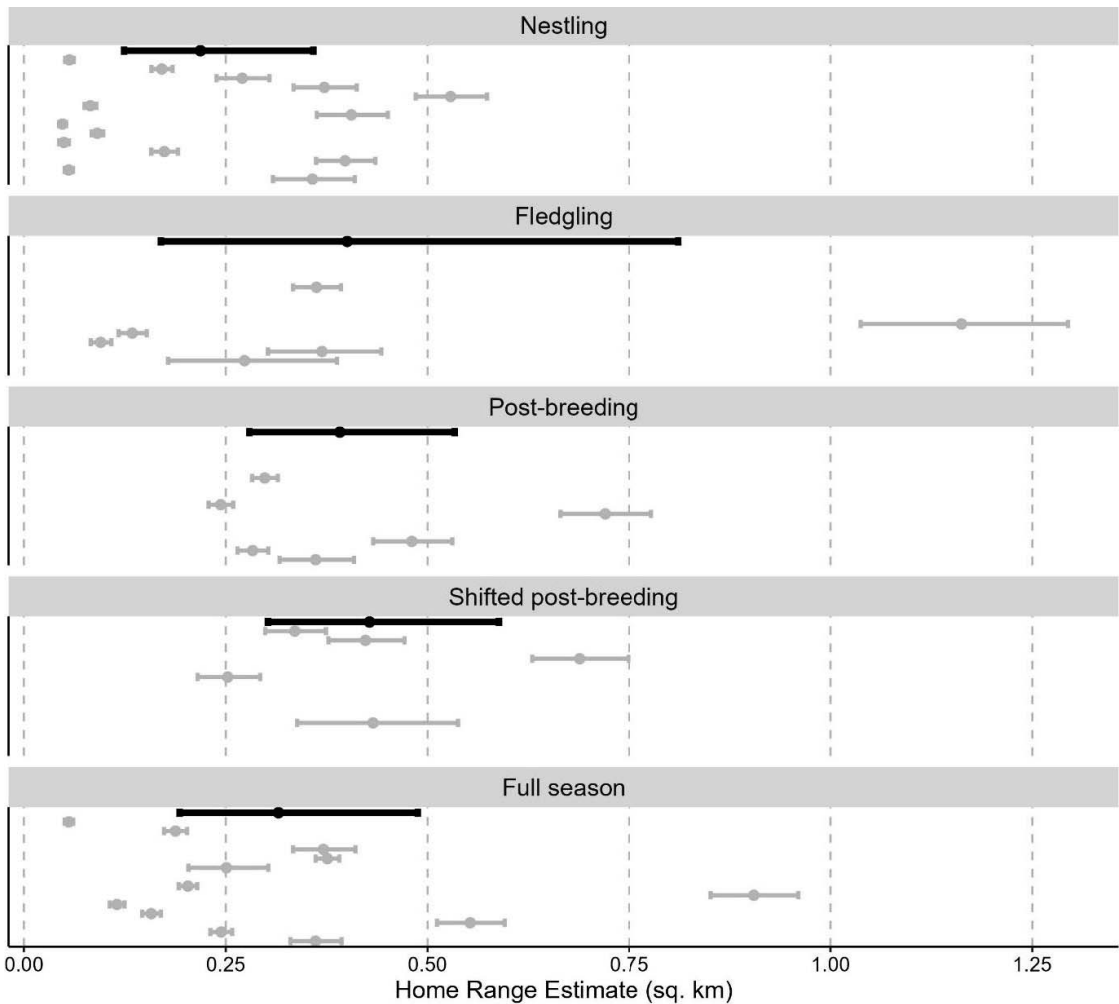


Figure 1. Autocorrelated kernel density home range sizes for adult female American Kestrels during four stages of the breeding season as well as across available stages. Colors (in digital version) indicate individual kestrels and thicker black point and error bars at the top of each section represent the overall mean and 95% confidence interval for each stage.

(Table S2). A subset of these forays ($n = 119$) occurred on high-resolution tracking days from 12 different females, five of which would ultimately shift their ranges, and it is these forays that we analyzed for foray rate and distance. It was difficult to estimate foray duration because many (45.3%) high-resolution forays recorded were based on a single location, and because lack of nighttime tracking prevented confirmation of whether birds temporarily returned to their home ranges during the night within multi-day forays. If we assume that birds did not return to their home ranges during the night, 11 (9.2%) forays extended beyond 24 hr in duration. All of

these multi-day forays were for birds that ultimately shifted their ranges, whereas the longest recorded foray for a resident bird was 2 hr. Of 46 forays lasting >1 hr, all but one was by eventual range-shifted birds, and all but one occurred in the fledgling or post-breeding stage.

Considering 65 weekly samples of foray rate across 12 females, the mean number of daily tracking locations ranged from 18.9 to 48.6 (mean = 34.3 ± 4.3 [SE]), with average daytime location intervals ranging from 10 to 25.6 min (mean = 16 min). Model comparisons indicated that both breeding stage and range consistency (shifted or not) were

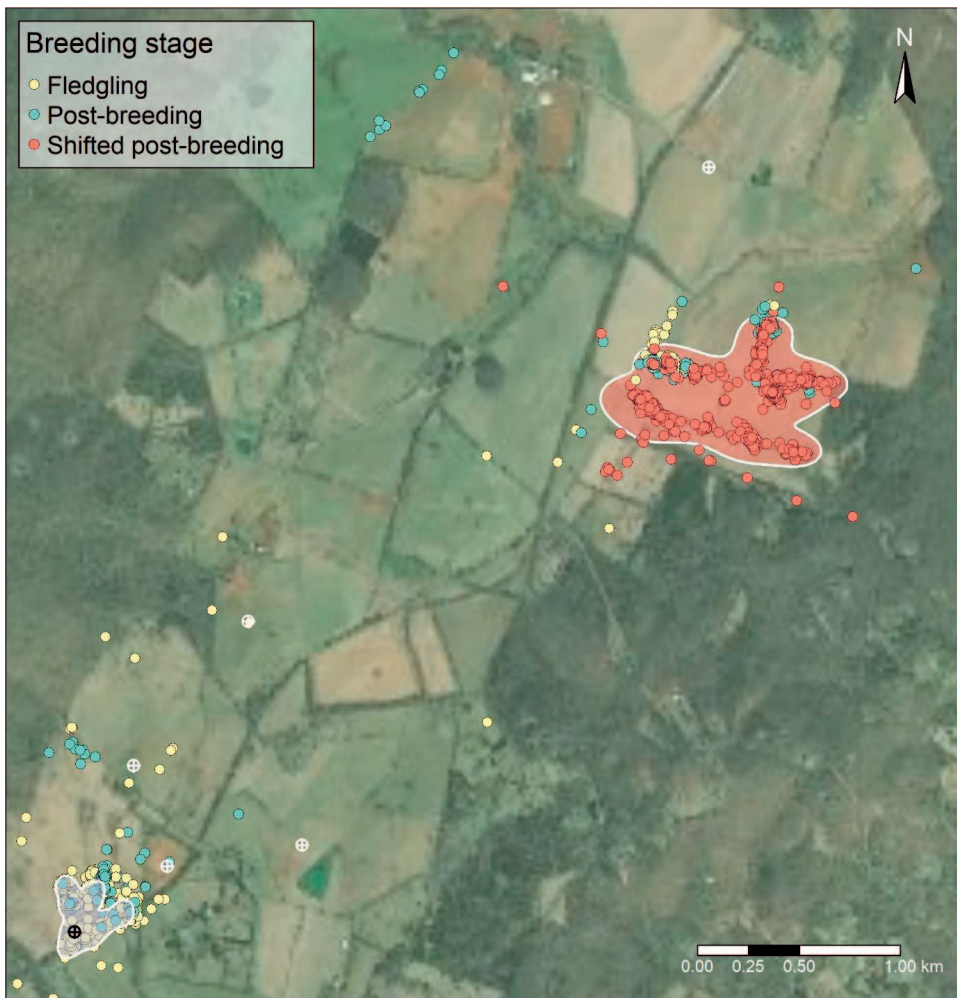


Figure 2. Estimated nesting stage (light purple) and shifted post-breeding stage (orange) home range boundaries (95% AKDE) for female 1019. Tracking locations during the fledgling (yellow) and post-breeding (blue) stages are included, but no ranges were estimated for these stages because of nonresident behavior. Nestling stage locations were excluded to allow visualization of locations from other stages. This bird's nest box is shown as a black target, all other confirmed active nest boxes are shown as white targets. Not all tracking locations are shown in this map extent.

Table 2. Extent of overlap and inter-box distances for adjacent American Kestrel female home ranges in the nesting stage and across the breeding season. Overlap is represented by the Bhattacharyya coefficient (BC), which ranges from 0 to 1, with a 95% upper and lower confidence limit.

Kestrel Neighbors	Nesting Stage Overlap	Full-season Overlap	Inter-box Distance (m)
1001 - 1011	0.267 (0.231–0.306)	0.421 (0.403–0.440)	704
1001 - 1017	0.154 (0.130–0.180)	0.153 (0.138–0.169)	405
1004 - 1006	0.040 (0.023–0.068)	0.024 (0.019–0.029)	956
1006 - 1019	0.000	0.000	525
1017 - 1019	0.058 (0.046–0.072)	0.058 (0.046–0.072)	434

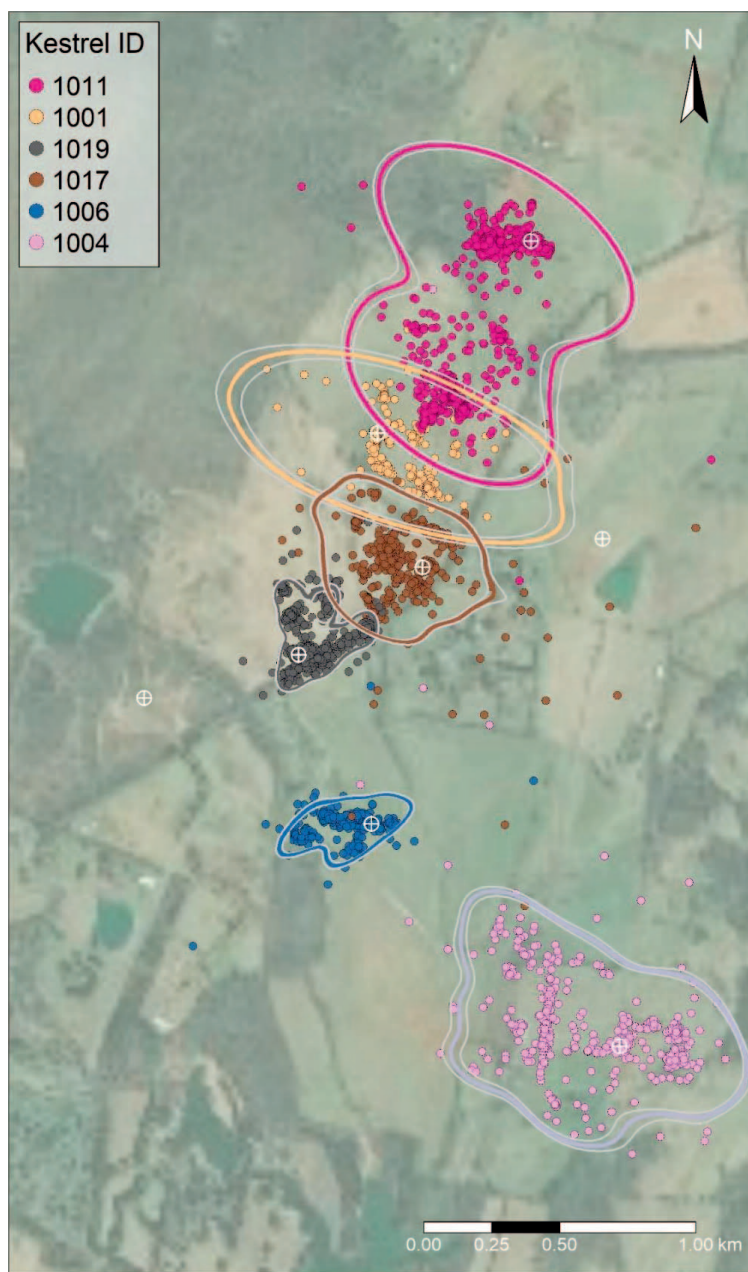


Figure 3. Nestling stage home range boundaries (95% AKDE with 95% CI) and nesting stage tracking locations of all tracked kestrels with adjacent territories. All active nest boxes (white targets) are depicted. Some tracking locations occur outside of the map extent.

associated with weekly foray rate (Table 3, S3). Birds that eventually shifted their ranges demonstrated higher rates of weekly forays across all three breeding stages, and both resident and range-shifted

birds displayed their lowest foray rates in the post-breeding stage (Fig. 4A). This model explained 38.0% of the variation in weekly foray rate. Average foray distance for high-resolution data was 4.17 km

Table 3. Final model summaries for analysis of weekly foray rate (generalized linear mixed model with negative binomial error distribution and log link) and foray distance (linear mixed model) in American Kestrels including model coefficients (Beta), and their standard errors, and associated test statistics. The nestling stage was coded as the baseline category.

Predictors	Weekly Foray Rate				Foray Distance			
	Beta	SE	Statistic	<i>P</i>	Beta	SE	Statistic	<i>P</i>
Intercept	0.13	0.29	0.43	0.665	5511.11	2764.63	1.99	0.049
Stage (Fledgling)	-0.45	0.35	-1.27	0.203				
Stage (Post-breeding)	-0.96	0.33	-2.90	0.004				
Consistency (shifted)	1.38	0.29	4.79	<0.001				

(median = 1.70 km). Modeling indicated that neither breeding stage nor range consistency were associated with foray distance (Table 3, S4, Fig. 4B). However, the nine longest-distance forays all occurred during the post-breeding stage and all nine were conducted by range-shifted birds ($n = 3$).

DISCUSSION

Home Range Size. We documented the first robust estimates of home range size for the American Kestrel and the first home range estimates of any kind for this species in the eastern USA. Breeding females' home range size (full breeding season average = 0.32 km^2) was smaller than averages

previously reported in the literature across the central and western USA ($0.74\text{--}1.94 \text{ km}^2$; Table 4), with similar values reported only for a study area in southeastern Quebec (average of 0.22 km^2 across three groups). Other studies ($n = 3$) reported only home range diameter, resulting in average home range sizes from 0.34 to 3.97 km^2 assuming a circular home range (Table 4). Assuming a circular home range, the average home range size of kestrels in our study would have a diameter of 0.64 km .

Our study's small home range sizes relative to previous findings were somewhat surprising, given that GPS-based tracking is much more likely to

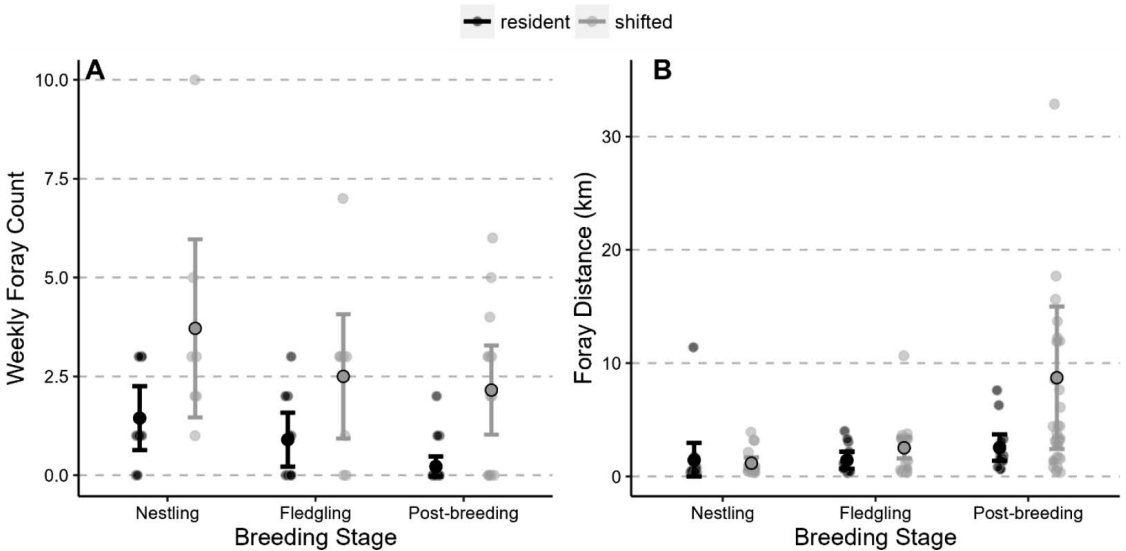


Figure 4. Mean weekly count (A) and mean distance from the home range boundary (B) for forays (with 95% confidence intervals) for 12 breeding female American Kestrels during high-resolution tracking periods. Raw data values are shown as points. Each week or foray was associated with a specific breeding stage based on nest monitoring observations. Shifted birds are those that permanently left their breeding home range and established a new post-breeding range. Presented data do not include forays once these new ranges were established. For visual purposes, Figure B excludes the longest foray of 127.7 km for a shifted bird in the post-breeding period.

Table 4. Summary of published information on American Kestrel home ranges (HR) in the breeding season. Summary statistics include only breeding birds. Diameters are in km and areas are in km². All HR estimates, with the exception of this study, are based on a 100% minimum convex polygon estimation method, which includes all recorded locations.

Location	Min HR Diam.	Max HR Diam.	Avg HR Diam. (km)	Min HR Area (km ²)	Max HR Area (km ²)	Avg HR Area (km ²)	Samples	# Seasons	Reference
Michigan, USA	0.80	2.41	1.71	0.21	2.15	1.31	5 pairs	2	Craighead and Craighead 1956
Wyoming, USA	1.13	3.70	2.36	0.41	5.00	1.94	12 pairs	1	
Illinois, USA	1.93	2.57	2.25	-	-	-	4 birds	1	Enderson 1960 ¹
Illinois, USA	1.93	2.57	2.25	-	-	-	2 females	1	
Illinois, USA	2.09	2.41	2.25	-	-	-	2 males	1	
Utah, USA	0.89	3.70	0.82	-	-	-	12 pairs	2	Smith et al. 1972
Utah, USA	1.00	1.30	1.10	0.46	1.45	0.74	5 pairs	2	Smith and Murphy 1973
Jamaica	0.47	1.11	0.66	-	-	-	6 pairs	2	Cruz 1976
California, USA	-	-	-	-	-	1.09	32 pairs	2	Balgooyen 1976
Quebec, Canada ²	-	-	-	-	-	0.19	9 ranges	2	Bowman and Bird 1986
Quebec, Canada ³	-	-	-	-	-	0.28	11 ranges	2	
Quebec, Canada ⁴	-	-	-	0.08	0.36	0.18	31 pairs	2	Gard and Bird 1990
	1.04	2.47	1.48	0.29	2.24	0.82			Averages
Virginia, USA	-	-	-	0.06	0.91	0.32	12 females	1	This study 2023

¹ Area values estimated from figures in publication.

² Birds had replacement mate after one adult member of pair removed after 3 wk of incubation.

³ Birds had no replacement mate after one adult member of pair removed after 3 wk of incubation.

⁴ Brood sizes were manipulated.

detect long-distance movements than the observational methods used in all previous work. Our focus on females may explain in part the smaller home ranges documented here because most previous studies described home ranges of male-female pairs (Table 4). Little is currently known about variation in movement behavior between male and female kestrels. The single study comparing kestrel home ranges of two birds of each sex, based on observations only, found no differences (Enderson 1960). However, male kestrels may have larger space requirements for at least part of the breeding season because they are typically the sole food provider to nestlings for the first 7–10 d after hatching (Balgooyen 1976).

Two additional factors may explain the relatively small breeding ranges we documented. First, all previously published estimates have described home range size using a 100% minimum convex polygon (MCP), which would include all forays, regardless of distance, in the estimated home range boundary. The MCP approach, even when using the more conservative 95% threshold, is still likely to include areas rarely or never used (Harris et al. 1990, Barg et al. 2005), particularly if individuals show non-

uniform space use within the home range. When estimating 95% MCP home ranges with our data, the full breeding season home range average was not substantially larger than that of our AKDE estimate, changing from 0.32 km² to 0.36 km². However, full 100% MCP home ranges would be much larger, given the occurrence of foray behavior. Second, habitat quality may be high in our study area, resulting in relatively smaller foraging movements necessary to sustain adult birds and their young. At a nearby study area, box occupancy and nest success, potential indicators of habitat quality, were some of the highest reported throughout the kestrel's North American range (Kolowski et al. 2023). Home range size is smaller for many bird species, including small raptors, where resources are abundant and habitat is categorized as higher quality (Village 1982, Newton 1986, Marzluff et al. 1997, Santangeli et al. 2012). Additional studies documenting kestrel home range size using GPS loggers in other regions will help to confirm whether regional differences, habitat quality, or estimation method explain the variability documented to date in kestrel home range size.

We hypothesized that kestrels would maintain their largest home ranges during the fledgling stage,

when demands on parents were assumed to be highest, and there is evidence for this pattern in other raptors (e.g., Pfeiffer and Meyburg 2015, Blakey et al. 2020). The smallest female home ranges we documented were all within the nestling stage, but home range size did not change significantly across breeding stages. It may be that provisioning by male kestrels, who may be foraging over larger areas, allows the female to maintain consistently small home ranges even when feeding demands are highest. Importantly, three birds were nonresident during the fledgling stage, clearly exhibiting wider space use than those for which we could estimate home ranges, and thus home range size may not be the most appropriate metric of space use requirements during this period. Regardless, kestrel movements during the post-breeding stage, when females were unlikely to have been provisioned by males, demonstrate that independently foraging adult kestrels can be sustained on very small home ranges.

Home Range Overlap. We found little overlap in adjacent kestrel home ranges in our study area, where average nest box spacing was 573 m, which informs the potential utility of our home range estimates for broader estimates of density and numbers of potential breeders, at least in this region. Our high-resolution data demonstrated that movements rarely included the same areas, even when kestrels shared individual fields. However, it is unclear how these distinct boundaries are maintained and enforced as we observed very few intraspecific aggression events in kestrels. Other research suggests that active nests can be maintained at much closer spacing than was observed here, with high tolerance of neighbors (minimum spacing 12.2 m, Smith et al. 1972; 33.5 m, Nagy 1963). We found only one study documenting chasing and aggression between adult kestrels in the breeding season (Villarroel et al. 1998). However, these events were before or during egg-laying and occurred in the context of extra-pair copulation attempts as opposed to general territory incursions.

Post-Breeding Home Range Shifts. Our finding that some adult American Kestrels establish new disjunct home ranges in the post-breeding stage is novel information for the species. Intraspecific variation in movement strategies of raptors is often associated with age, sex, and breeding class (van Eeden et al. 2017, Wheat et al. 2017, Blakey et al. 2019). Much less is known about potential variation in movement strategies among breeding females,

particularly in the post-breeding stage. There are at least a few examples of breeding adult songbirds establishing new post-breeding territories, with evidence that these shifts are related to future breeding opportunities (Weggler 2000, Forstmeier 2002, Cooper and Marra 2020). In our study, these shifts are unlikely to be related to breeding opportunities within the same season. Shifts to new ranges occurred in July, a month in which no clutch initiations have been observed in our study area or another long-term kestrel monitoring project in Virginia (Kolowski et al. 2023). Home range shifts may have been related to selection of potential breeding territories for the following season, but we did not observe use of these shifted ranges the following year by any of these five females; two disappeared after apparent migration and did not return to the study area, one re-nested in her 2021 box, one nested in a box adjacent to her 2021 box. However, the fifth female did use a breeding range adjacent to her shifted post-breeding range.

We find it more plausible that post-breeding home range shifts were driven by better late-season foraging opportunities. Shifting to new post-breeding ranges in better and unoccupied habitat eliminates the need to forage widely from the initial nesting home range at a time when birds are preparing for either migration or overwintering. These shifts also allow birds to breed in habitats that may otherwise not be favored for foraging in the post-breeding stage due to increased vegetation height and density (e.g., crops, native meadows). Broad shifts in preference for habitat type, structure, and location have been documented in forest-breeding birds during the post-breeding stage and are suggested to be driven at least in part by foraging resources (e.g., Vega Rivera et al. 1999, 2003, Vitz and Rodewald 2006, Chandler et al. 2012, Wohner et al. 2020). Complete post-breeding home range shifts in Northern Wheatears (*Oenanthe oenanthe*) provided higher proportions of shorter vegetation which were more conducive to foraging, compared to breeding territories (Arlt and Pärt 2008). This movement strategy has important implications for how breeding habitat quality and selection are assessed in kestrels. It is common to associate habitat surrounding nest boxes with metrics like box occupancy and nest success (e.g., Touihri et al. 2019, Kolowski et al. 2023), inferring that habitat surrounding occupied and successful boxes will be of higher quality. Yet our data suggest that kestrels may occupy and successfully raise young in habitat that may be suboptimal

after the breeding season. Studies of habitat selection of this species would therefore benefit from including the post-breeding stage, when foraging decisions are not influenced by nest site availability. Unfortunately, this is the hardest stage of the season to observe and monitor kestrels without GPS loggers. Studies of nesting home range habitat differences among resident and shifted females will elucidate whether shifts were ultimately driven by variation in habitat quality.

Foray Behavior. We documented foray flights, described for the first time in this species, for all 12 female kestrels for which we could estimate full-season ranges. Nonbreeding birds frequently exhibit foray behaviors and alternative space use strategies (e.g., Rohner 1997, Reed et al. 1999, Campioni et al. 2017, Wolfson et al. 2020), but relatively few studies have documented forays in breeding females. The ultimate driver of foray behavior can be challenging to identify, but breeding females may make forays to prospect for breeding locations in future seasons (Blakey et al. 2019, Cooper and Marra 2020) or in the event of nest failure (Ward 2005, Ponchon et al. 2015, Martinović et al. 2019). Prospecting flights by female songbirds and colonial seabirds peak in the nestling and fledgling periods, when information reflecting breeding success (e.g., adult or fledgling density) and therefore habitat quality, is most available (Boulinier et al. 1996, Doligez et al. 2004, Cooper and Marra 2020). This public information (i.e., collected from the behavior of others; Dall et al. 2005) would be most efficiently recorded when kestrel fledglings are present, as they can be vocal and visible in the weeks following fledging. Similarly, if forays were primarily motivated by immediate foraging needs, we would expect foray rate to peak during the fledgling stage, when energy demands on the female are highest. Instead, foray rates were highest during the nestling stage when females are often provisioned by males. These results suggest that prospecting was likely the primary motivation for forays, but that personal information (i.e., collected from direct interactions with one's environment; Dall et al. 2005) in the form of foraging habitat quality or nest site availability, was being collected. Our most convincing evidence that forays represented prospecting for near-future movement decisions was the consistently higher foray rate among females that ultimately shifted their home range in the post-breeding stage. That this pattern was detectable as early as the nestling stage implies that these females had already assessed the quality of

their nesting ranges and anticipated a need to locate an alternate post-breeding home range. The five females eventually shifting into new post-breeding home ranges made 4–18 foray flights into their eventual new home ranges, and these made up 14–59% of all their documented forays. We also show evidence that these five females, although not consistently taking longer forays than resident females, did gradually spend more and more time outside of their nesting range as the season progressed. Nearly all multi-hour forays (98%) were conducted by these five females, and nearly all of these (98%) were after the nestling stage.

Standardized maximum and average foray distances recorded here for kestrels are some of the largest recorded for any species, including mammals (review in Cooper and Marra 2020). Unlike the two leading species, Kirtland's Warbler (*Setophaga kirtlandii*) and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), kestrels are not habitat specialists with isolated remaining habitat patches scattered across large areas, and the drivers of these particularly long-distance movements in kestrels, which clearly traversed huge expanses of suitable habitat, are unclear. Tracking birds over multiple years may determine whether some long-distance forays are directed to locations of natal nests or previous breeding locations, as in Spotted Owl (*Strix occidentalis*; Blakey et al. 2019). The longest recorded foray in our study is particularly hard to explain without some influence of prior experience. In this case a female flew 127.7 km to southern Pennsylvania on 16 June (5 d after our last observation of fledglings) and remained there through 27 July, when she returned to our study area in Virginia for the fall and winter. This female nested in the same nest box the following year, and so this extended foray is difficult to explain from a foraging or prospecting perspective. As technological advances allow tracking of increasingly smaller species (Wikelski et al. 2007, Taylor et al. 2017), documentation of foray behavior is likely to increase, as will our ability to investigate the drivers of this behavior.

Although we are not aware of single objective method for defining movements as forays, definitions typically include a threshold distance from a nest location, time spent on these flights, or some combination of the two (e.g., Blakey et al. 2019, 2020, Cooper and Marra 2020). Whereas inter-nest distance has been used as a measure of typical movements (Blakey et al. 2019, 2020), we relied directly on our tracking data and home

range estimation to define average distance to the home range boundary. To be conservative, we then doubled this distance, and set the threshold from the home range boundary as opposed to the nest location itself. Forays presented here should then only consist of movements outside the boundary that are substantially farther than a typical movement for our study animals. Given that nearly half of forays were described by one location, there is a risk that some forays were simply high-error GPS locations. However, only 0.02% of straight-line error estimates from 16,210 calibration locations were greater than our foray definition of 325 m. We would also expect lower error for kestrel locations, given they would typically be recorded at much higher heights than the ground level calibration tests. Taken together this gives us confidence that GPS error could not play any marked role in our categorizations of kestrel forays. Regardless, foray definition distance should not impact our conclusions with respect to patterns in foray rate or distance across the breeding stages. Finally, weekly foray rates and total foray counts for kestrels in our study should be considered minimum estimates. Few birds were tracked at high resolution for every day of the breeding season (Table 1) and this likely resulted in at least some missed forays.

Conclusions. Our results indicate that American Kestrels are far more flexible and less predictable in their breeding season movements than previously documented, with a range of movement strategies used by breeding females, from full summer resident to post-breeding shifted, to a hybrid of the two. The small nesting home ranges of all monitored and successfully breeding females suggest that minimal space is required for successful reproduction in the mixed agricultural landscape in our study area. Nonetheless, late-season home range shifts in several tracked birds indicate that fields outside the breeding season home range serve as important foraging habitat. To fully understand the space requirements of a breeding kestrel pair, and the extent to which breeding season habitat management for this species can focus solely on nesting territories, space use of adult breeding males also must be studied. Recent work indicating that adult survival may be a key process in driving kestrel population dynamics (McClure et al. 2021) underscores the importance of describing the size and composition of areas used by adult kestrels, not only during nesting but during the post-breeding stage as

well. Our results also demonstrate that high-resolution tracking of this species, which has previously proven challenging (Hunt et al. 2023), is now feasible, opening the door to exciting new opportunities to study the ecology of the species and further investigate potential causes of its decline.

SUPPLEMENTAL MATERIAL (available online). Table S1: Summary information for all autocorrelated kernel density home ranges (AKDE HR) created for 14 adult breeding American Kestrels in northern Virginia, USA. Table S2: Summary of foray behavior across the twelve American Kestrels for which breeding season home ranges could be estimated. Table S3: Model comparisons for the set of generalized linear mixed models (negative binomial error distribution), predicting weekly foray count with individual bird as a random effect (intercept) and breeding stage and range consistency (resident vs. shifted) as fixed effects. Table S4: Model comparisons for the set of linear mixed models predicting foray maximum distance with the individual bird as a random effect (intercept) and breeding stage and range consistency (resident vs. shifted) as fixed effects. Figure S1: Estimated nestling stage (light purple) home range boundary (95% AKDE) for female 1009.

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