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Juvenile and Adult Survival Estimates of American Kestrels Throughout the Full Annual Cycle in Eastern North America

Mercy Melo,[1,2] Joseph M. Kolowski,[3*†] Rebecca A. McCabe,[1] John A. Smallwood,[4]
Allison Cornell,[5] David King,[6] and Jean-François Therrien[1]

[1] *Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, Orwigsburg, PA 17961 USA*
[2] *University of Massachusetts-Amherst, Amherst, MA 01003 USA*
[3] *Smithsonian-Mason School of Conservation, Smithsonian's National Zoo and Conservation Biology Institute, Front Royal, VA 22630 USA*
[4] *Department of Biology, Montclair State University, Montclair, NJ 07043 USA*
[5] *Department of Biology, Pennsylvania State University-Altoona, Altoona, PA 16601 USA*
[6] *USDA Forest Service Northern Research Station, Amherst, MA 01003 USA*

ABSTRACT.—Measuring survival in a declining species provides the foundation for continued research, demographic modeling, and informed conservation strategies. Although American Kestrel (*Falco sparverius*) populations have continued to decline since the 1970s, little is known about their survival throughout the full annual cycle, making it difficult to identify factors responsible for these declines. We used radio telemetry to provide the first known-fate estimates of adult kestrel survival, and we present data across breeding stages, and between resident and migratory wintering individuals, in addition to separately modeling fledgling survival. Temporal and spatial stratification of study sites allowed for the investigation of different pressures and risks that may lead to variation in survival. We generated weekly survival estimates for 56 adult kestrels in Pennsylvania and Florida, and for 146 recently fledged kestrels at five study sites throughout northeastern North America from 2021 to 2023. Adult weekly survival varied by sex and season, with males in the nonbreeding season exhibiting the lowest values (0.9074). Overwinter survival at our Pennsylvania study site (0.9316) was lower than in Florida (0.9881), indicating potential survival costs to overwintering at these locations. Post-fledging juvenile weekly survival estimates varied among five study sites (0.9429 to 1.000) and were much higher than expected based on previous work and the presumed difficulty of surviving this vulnerable early life stage. This insight into where and when mortality occurs in this declining species provides key parameters for demographic modeling and refines potential targeted conservation planning.

KEY WORDS: *cause-specific mortality*; *falcon*; *known fate*; *seasonal survival*; *telemetry*.

ESTIMACIONES DE SUPERVIVENCIA DE JUVENILES Y ADULTOS DE *FALCO SPARVERIUS* A LO LARGO DEL CICLO ANUAL COMPLETO EN EL ESTE DE AMÉRICA DEL NORTE

RESUMEN.—Medir la supervivencia en una especie en declive sienta las bases para investigaciones continuadas, modelización demográfica y estrategias de conservación informadas. Aunque las poblaciones de *Falco sparverius* han seguido disminuyendo desde la década de 1970, se sabe poco sobre su supervivencia a lo largo del ciclo anual completo, lo que dificulta identificar los factores responsables de estos declives poblacionales. Utilizamos radio-telemetría para proporcionar las primeras estimaciones conocidas de la supervivencia de individuos adultos de *F. sparverius* y presentamos datos a lo largo de las etapas

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* Corresponding author: kolowskij@si.edu
[†] Present address: Pennsylvania Game Commission- Northcentral Region, 1566 PA 44, Jersey Shore, PA 17740 USA.

de cría, y entre individuos residentes e invernantes migratorios, además de modelar por separado la supervivencia de los volantones. La estratificación temporal y espacial de los lugares de estudio permitió investigar diferentes presiones y riesgos que podrían llevar a variaciones en la supervivencia. Generamos estimaciones semanales de supervivencia para 56 individuos adultos en Pensilvania y Florida, y para 146 individuos recientemente emplumados en cinco áreas de estudio en el noreste de América del Norte entre 2021 y 2023. La supervivencia semanal de los adultos varió según el sexo y la estación, siendo los machos en la temporada no reproductiva los que mostraron los valores más bajos (0.9074). La supervivencia invernal en nuestra área de estudio en Pensilvania (0.9316) fue más baja que en Florida (0.9881), lo que indica posibles costos de supervivencia asociados con invernar en estos sitios. Las estimaciones de supervivencia semanal de los juveniles después del emplumamiento variaron entre los cinco lugares de estudio (0.9429 a 1.000) y fueron mucho más altas de lo esperado según estudios previos y la supuesta dificultad de sobrevivir a esta etapa inicial vulnerable de la vida. Este análisis sobre dónde y cuándo ocurre la mortalidad en esta especie en declive proporciona parámetros clave para el modelado demográfico y mejora la planificación potencial para su conservación.

[Traducción del equipo editorial]

INTRODUCTION

Measuring survival in a declining species provides the foundation for continued research and can orient conservation efforts. Survival estimation throughout the full annual cycle allows researchers to pinpoint when mortality occurs and, therefore, where resources should be allocated for potential mitigation and conservation action (Rushing et al. 2017). For migratory individuals, full-annual survival studies provide both spatial and temporal context that can be integrated with data on habitat quality, environmental conditions, and anthropogenic factors to inform population trends and identify areas of future conservation priority (Grande et al. 2009, Duriez et al. 2012).

Raptors face many threats throughout the full annual cycle. During the breeding season, adult raptors have greater energy expenditure due to increased foraging required to produce eggs and care for nestlings (Ydenberg and Forbes 1991, Daan et al. 1996). Further, incubation leaves breeding individuals at increased risk for predation (Low et al. 2010). Migration is known to be especially challenging due to increased metabolic requirements, human-induced mortality, and unfamiliar landscapes and routes (Newton 2008, Oppel et al. 2015, De Pascalis et al. 2020). Indeed, daily mortality rates in raptors are reported to be greater during migratory periods than during stationary periods (Klaassen et al. 2014, Sergio et al. 2019). After completion of autumn migration, survival rates of migratory raptors are typically greater for the duration of the overwintering period relative to the migratory period (Klaassen et al. 2014, Sergio et al. 2019); however, not all raptors migrate. For nonmigratory birds, the overwintering period may impose its own challenges such as unfavorable climatic conditions, decreased prey abundance, and increases in competition with species occupying similar niches (Lack 1968, Kostrzewa and Kostrzewa 1991, Robinson et al. 2007, Duriez et al. 2012). For partial migrants (i.e., some individuals in a region migrate while others remain resident year-round), ecological tradeoffs exist between (1) risky migration followed by potentially less demanding overwintering conditions or (2) foregoing migration to attempt persisting in suboptimal overwintering conditions (Duriez et al. 2012). Understanding survival consequences of these life history decisions is crucial to pinpointing when and where raptors are most vulnerable during the full annual cycle.

Challenges throughout the full annual cycle may vary based on intrinsic factors such as age and sex. Survival studies in raptors indicate that juveniles experience higher mortality than adults, with fatality events occurring in different stages throughout the annual cycle (Newton et al. 2016, Sergio et al. 2019). Most juvenile raptors do not survive their first year of life, with many dying in the first few weeks after fledging (Stupik et al. 2015, Newton et al. 2016). For juvenile raptors, autumn migration (Oppel et al. 2015) and the first overwintering period (McCabe et al. 2022) are especially challenging likely due to their lack of experience (Sergio et al. 2019). Survival may also differ based on sex in sexually dimorphic raptors: larger females are thought to have greater annual survival than their smaller male counterparts, as the sexes display different foraging strategies, migration habits, and breeding behaviors (Ydenberg and Forbes 1991, Newton et al. 2016).

The American Kestrel (*Falco sparverius*, hereafter kestrel) is a small falcon species native to the western hemisphere, ranging from southeast Alaska, USA, through Argentina. Since the 1970s, in North America and especially across the Atlantic Flyway, kestrel populations have declined across their annual cycle, triggering a wave of focused research into potential causes (e.g., Farmer et al. 2008, Farmer and Smith 2009, Smallwood et al. 2009, Oleyar et al. 2023). However, the driver behind the continental decline in kestrel populations remains unknown (Farmer et al. 2008, McClure et al. 2017, Bednarz and Therrien 2023, Bird and Smallwood 2023). Investigations of breeding season demography revealed generally high survival and reproductive success, suggesting that mortality may be elevated during other stages of the full annual cycle (Smallwood et al. 2009, McClure et al. 2017). Estimating survival for both migratory and resident populations may elucidate regional population trends as each strategy exposes kestrels to different sources of mortality.

Individual tracking via radiotelemetry enhances our understanding of raptor survival and reduces some of the challenges associated with band recoveries by increasing detection rate, distinguishing between death and emigration, and allowing for determination of the cause of death (Newton et al. 2016). Currently, many demographic models utilize mark-recapture or band recovery data but could be improved through the implementation of radiotelemetry data (McClure et al. 2017). Although telemetry-based studies of kestrel survival exist, none to our knowledge have tracked individuals throughout multiple seasons in both migratory and residential populations (Varland et al. 1993, Farmer et al. 2006, Stupik et al. 2015). Using radio telemetry, we aimed to document adult and fledgling survival during various stages of the annual cycle and test the following hypotheses: (1) adult kestrel survival varies between the breeding and nonbreeding season, (2) migratory adult kestrels overwintering in Florida have greater survival rates than adults overwintering in Pennsylvania, and (3) kestrel fledgling survival will vary geographically and will be lower than for adults.

METHODS

Study Areas. We tracked adult kestrels in Pennsylvania (PA, Hawk Mountain Sanctuary: $n = 18$ males, 14 females) and Florida (FL, Cape Coral: $n = 12$ males, 12 females). In addition, we tracked fledgling kestrels at three study sites in Pennsylvania (Hawk Mountain Sanctuary: $n = 22$ males, 31 females; Pennsylvania State University-University Park [PSU]: $n = 9$ males, 7 females; and Lancaster County: $n = 5$ males, 7 females), one study site in New Jersey (NJ, Montclair State University: $n = 17$ males, 22 females), and one study site in Virginia (VA, Virginia Piedmont: $n = 12$ males, 8 females; Fig. 1). As part of a multi-scale research project examining kestrel declines in eastern North America, our six study sites were selected based on collaborative nestbox programs and do not necessarily represent ecologically independent populations. Populations are known to be partially migratory at our Pennsylvania, New Jersey, and Virginia sites, with a portion of the population being year-round residents and others migrating south during the nonbreeding period. Kestrels overwintering at the Cape Coral, Florida site are fully migratory and are present only as winter residents.

Transmitter Deployment and Tracking. We captured adult kestrels using baited bal-chatri traps deployed from a vehicle along public roadsides at the beginning of each season (i.e., breeding, overwintering; see dates below) between December 2020 and December 2022. We captured nestlings at the nestbox about 5 d before fledging and returned them to the nestbox after handling. We banded both adults and nestlings with an aluminum US Geological Survey band and either a plastic wrap-around alpha-numeric color band (Pro-Touch Engraving Ltd., Saskatoon, Saskatchewan, Canada) or a vinyl-coated nylon patagial tag (only at New Jersey site based on bander's preference; Varland et al. 2007, Smallwood 2016).

We deployed both Holohil BD-2 radio VHF tags ($n = 180$) and Lotek NTQB2-6-1 NanoTags ($n = 22$) using backpack-style harnesses built from Teflon ribbon (Bally Ribbons Mills, Bally, PA, USA) that crossed the breast of the bird and were held in place with a 1-cm^2 leather patch (Steenhof et al. 2006). Both transmitter types were equivalent in weight, shape, and size, ultimately being indiscernible once affixed to the bird. Transmitter deployment and bird handling concluded within 20 min of capture, whereafter the bird was immediately released at the capture site or nestbox. All auxiliary markers, including bands/tags, transmitter, and attachment materials, did not exceed 3% body mass (total weight 3.2–3.6 g). Both transmitter types were battery operated, lasting approximately 6 mo once activated.

When tracking individuals, we followed a standardized protocol to eliminate site-based heterogeneity of effort. We located adult kestrels weekly by scanning for the radio frequency at the last known location. If a signal was not detected at the last known location, we scanned for the signal at four different locations approximately 1.5 km away (our limit of detection under typical habitat characteristics) from the last known location. We attempted to maximize separation

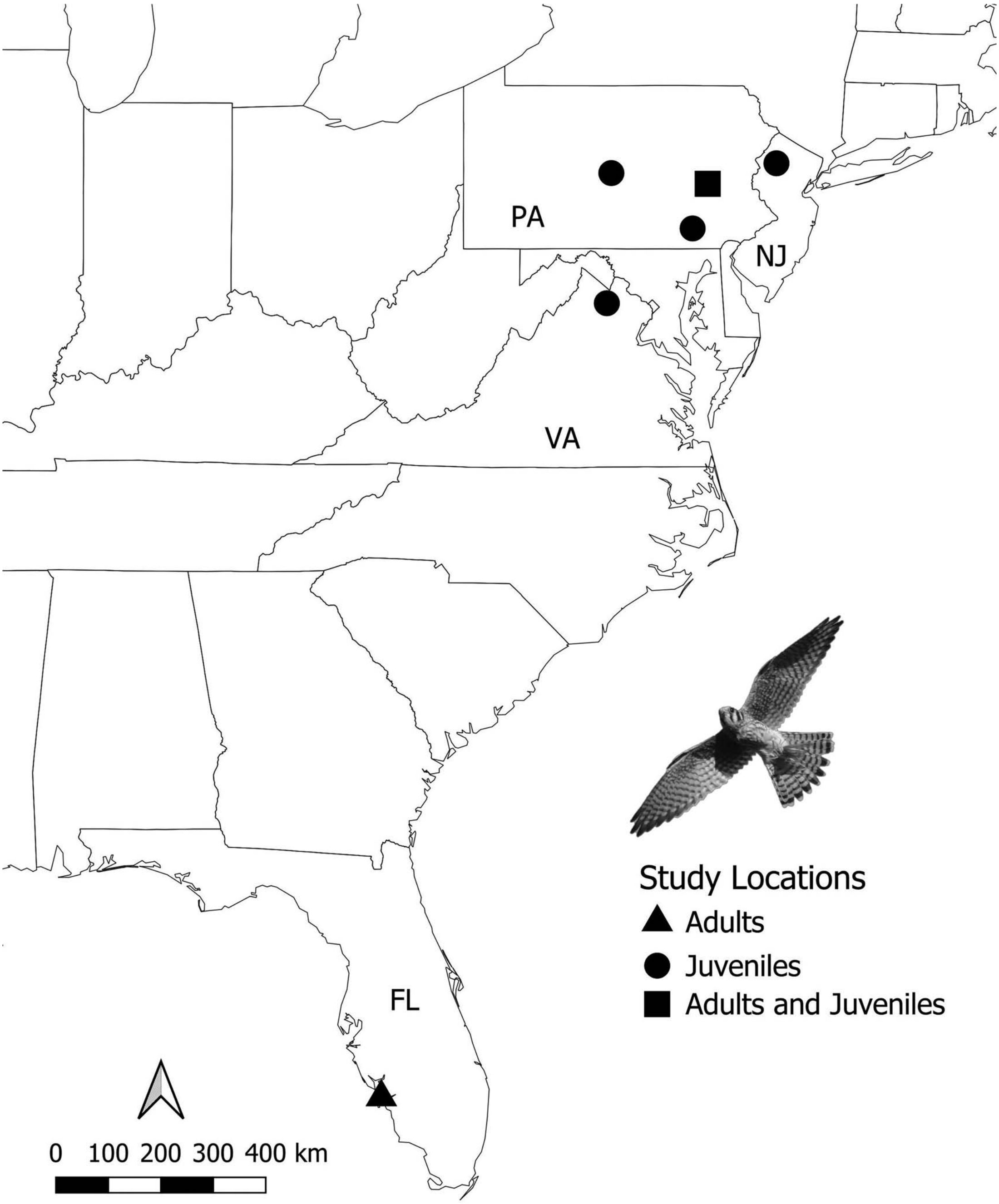

Figure 1. Study locations of American Kestrels ($n = 202$) tracked with VHF transmitters between December 2020 and December 2022 in Pennsylvania (PA), New Jersey (NJ), Virginia (VA), and Florida (FL), USA.

and elevation of each of the four locations while accounting for variable property access. A confirmed live encounter required both visual (using color bands, patagial tags, or presence of transmitter antenna wire) and audible detection using transmitter signal. If we heard a transmitter signal but were unable to visually confirm a re-sighting, we triangulated the location and ensured the individual was re-sighted on the following attempt or that the location of the signal origin moved between re-sight attempts to confirm the bird was alive during the previous attempt. If an individual's signal did not move between re-sighting attempts, we searched the area for any signs of a fatality. We confirmed deaths by locating the carcass and determining cause of death in the field following methods of Stupik et al. (2015). We conducted necropsies of recovered carcasses to confirm suspected causes of death and elucidate unknown causes. All fatality events were designated to have occurred the week after the last live sighting (Stupik et al. 2015). If we did not detect a signal for an individual and the bird was not re-sighted for 4 consecutive weeks, we discontinued search efforts with the assumption that the individual dispersed from the study area.

We began tracking fledglings approximately 28 d old (mean age of fledging) and located fledglings in the field three times per wk. Triweekly tracking continued for the first 2 wk post-fledging and subsequently reduced to twice per wk tracking until individuals remained undetected for 4 consecutive wk. Heightened tracking effort early in the tracking period assisted in recovering carcasses promptly after fatalities to allow for proper necropsy and determination of cause of death.

Statistical Analysis. Although individual adult birds were not tracked for a full year period due to battery limitations (approximately 6 mo), we were able to collect survival data for adults in all ecological life history periods of the year except migration at our Hawk Mountain Sanctuary site. These periods (i.e., seasons) were defined as breeding: 1 May (PA mean lay date)–14 July (PA mean fledge date); summer-dispersal: 15 July–31 August (PA onset of fall migration); and nonbreeding: 1 September–31 March. We first constructed known-fate survival models to compare adult survival among seasons, including terms for sex, year, and linear time. For this and all subsequent analyses, we aggregated our tracking data into encounter histories (LDLD format; Cooch and White 2012) with 1-wk occasions. For individuals re-sighted multiple times per wk (i.e., fledglings) we included only the first re-sighting attempt per wk in the encounter history to maintain consistent effort.

To further investigate sources of seasonal variation in survival, we pooled the breeding and summer-dispersal seasons for a combined breeding/summer dispersal (1 May–31 August) vs. nonbreeding (1 September–31 March) comparison. We included additive models containing all combinations of covariates with the following exceptions: (1) we avoided the combination of the season covariate with the simplified breeding/summer dispersal vs. nonbreeding covariate as they both described temporal patterns and (2) neither the season covariate nor the breeding/summer dispersal vs. nonbreeding covariate were modeled with linear time for the same reason. We included interaction terms to allow seasonal effects to vary by sex. In total, we tested 20 models including the null model.

To compare overwintering survival of adult kestrels, we conducted a second analysis using data from tracking individuals concurrently during the overwintering period (1 December–31 March) at our Hawk Mountain Sanctuary (PA) and Cape Coral (FL) sites, and compared survival using models including terms for sex, year, time, and site with all combinations tested as additive models (total of 16 models).

Finally, we conducted a third analysis to investigate sources of variation in survival of fledgling kestrels using tracking data from the post-fledging season, which was truncated on 31 August. We first investigated potential patterns associated with sex, site, and region. Because sites in PA and NJ are ecologically similar and geographically contiguous, we also combined them and compared them to our VA site as different "regions." We compared single variable and additive models of each combination of these covariates, resulting in a total of six models including the null model (i.e., all combinations of covariates except for "site" with "region"). To identify potential patterns associated with linear time and year, we compared a separate set of models using data from only those sites that recorded at least one fatality. Here we compared all additive model combinations of sex, year, and linear time for a total of eight models.

Known-fate models were run using the R package *RMark* (Laake 2013). We used corrected Akaike's Information Criterion (AIC_c) values to rank models and identify the top model in each analysis. Survival estimates are reported for the top model in each analysis and are presented strictly as weekly values.

RESULTS

Of the 202 individuals we tracked ($n = 146$ fledglings, 56 adults; Supplemental Material Table S1), we had 19 confirmed deaths (8 fledglings, 11 adults).

Table 1. Known-fate model comparison results for full-annual adult kestrel survival analysis conducted using tracking data from December 2020 through December 2022 at Hawk Mountain Sanctuary, Pennsylvania. Included models have $\Delta AIC_c < 2$.

Model	n	AIC_c	ΔAIC_c	Weight
(Breeding/Dispersal vs. Nonbreeding) + Sex	3	84.088	0	0.136
Breeding/Dispersal vs. Nonbreeding	2	84.115	0.027	0.134
Season (Breeding vs. Dispersal vs. Nonbreeding)	3	85.112	1.025	0.082
Season (Breeding vs. Dispersal vs. Nonbreeding) + Sex	4	85.192	1.104	0.078
Breeding/Dispersal vs. Nonbreeding * Sex	4	85.574	1.487	0.065
Breeding/Dispersal vs. Nonbreeding + Year	3	85.713	1.625	0.060
Sex + Year + Breeding/Dispersal vs. Nonbreeding	4	85.899	1.811	0.055
Intercept only (Null)	1	85.988	1.901	0.053

Known causes of death included automobile collisions ($n = 2$ fledglings, 4 adults), predation by other raptor species ($n = 3$ adults), and entrapment in buildings ($n = 1$ fledgling, 2 adults), where structures (e.g., closed garage door) prevented or complicated the departure of birds. One adult kestrel was killed by a domestic cat (*Felis catus*). The causes of the remaining fatalities ($n = 5$ fledglings, 1 adult) were undetermined. For adults, all deaths due to entrapment occurred during the breeding season, and all other causes of death occurred during the nonbreeding season. As juveniles were only tracked during the breeding season, all deaths (two automobile collisions, one entrapment in building, and five undetermined causes) occurred during the breeding season.

For adult kestrels in PA, model comparisons indicated weekly survival was higher across seasons for females than males, and survival was higher during the breeding/summer dispersal season (females = 0.9911, SE = 0.0078; males = 0.9767, SE = 0.0169) compared to the nonbreeding season (females = 0.9629, SE = 0.0216, males = 0.9074, SE = 0.0362; Table 1). However confidence intervals for both the sex and season model coefficients overlapped zero (Table 2).

For the overwintering period, model comparisons showed strong support for the influence of site (occurred in all models with $\Delta AIC_c < 2$), suggesting that survival was lower for adults wintering in PA (0.9316, SE = 0.0233) than in FL (0.9881, SE = 0.0068; Tables 2 and 3). There was no evidence that overwintering survival varied by sex, linear time, or year (Table 3).

Among kestrel young that fledged in northeastern USA, model comparisons indicated survival varied by site and was generally higher for females. Weekly survival was lowest at two PA sites (Hawk Mountain Sanctuary: females = 0.9800, males = 0.9429; and Lancaster County: females = 0.9893, males = 0.9687), compared to NJ (females = 0.9966, males = 0.9899), VA (both sexes = 1.000), and the third PA site (PSU: both sexes = 1.000; Tables 2 and 4). However, the absence of any deaths at two sites and the recording of only single deaths at two others prevented estimates of standard error and suggests these sex- and site-specific estimates should be viewed with caution. The null model ignores potential site and sex-based variation but capitalizes on our large overall sample size to produce a global fledgling survival estimate of 0.9869 (SE = 0.0043). Our second analysis, which focused on sites that recorded mortalities, showed no evidence for an impact of year or linear time on fledgling survival, but continued to support a sex effect as above (Table 4), although the confidence interval for the sex coefficient here overlapped zero (Table 2).

DISCUSSION

Little is known about causes of mortality in either adult or juvenile kestrels. For adults, a single telemetry study reported avian predation as the top cause of death for kestrels wintering in PA (Farmer et al. 2006; $n = 5$ of 8 confirmed deaths). In contrast, most adult deaths in our study were related to anthropogenic causes (70%), with 30% categorized as natural (e.g., avian predation). Although based on a low sample of confirmed deaths, these results suggest that kestrel reliance on human landscapes for nesting and foraging comes with associated costs to survival in addition to previously documented costs to nest success (Strasser and Heath 2013). For most of our recovered fledglings we could not determine the cause of death (i.e., carcass found far from road with little to no body damage, or body damage that was so severe that a cause could not be identified), which likely represents a combination of natural sources of mortality such as exposure, starvation, and predation. Similarly, Stupik et al. (2015) and Varland et al. (1993) assigned 100% (6

Table 2. Known-fate beta estimates and confidence intervals (CI) for each covariate in best-ranked (lowest AIC_c) models across all four kestrel survival analyses. Intercept reference values are noted for each separate analysis. CI could not be calculated for column 3.

Parameter	Adult Full Annual (Intercept = Nonbreeding Season, Female) Beta (CI)	Adult Overwintering (Intercept = Florida Region) Beta (CI)	Fledgling (all five sites) (Intercept = Hawk Mountain Site, Female) Beta	Fledgling (three sites) (Intercept = Hawk Mountain Site, Female) Beta (CI)
Intercept	3.26 (2.07 to 4.46)	4.42 (3.28 to 5.56)	3.89	4.42 (3.29 to 5.57)
Sex M	−0.97 (−2.36 to 0.41)		−1.09	−1.14 (−2.54 to 0.26)
Breeding/Dispersal	1.45 (−0.12 to 3.02)			
Site PA		−1.81 (−3.16 to −0.47)		
Site Lancaster			0.629	
Site NJ			1.78	
Site PSU			20.72	
Site VA			20.03	
Year				
Time				

of 6) and 78.6% (11 of 14) respectively, of all categorized fledgling deaths to either predation or exposure based on similar telemetry-based methods. Some survival studies may underestimate nonhuman causes of death due to the lack of carcass recovery in remote locations, therefore we suggest future studies employ telemetry-based approaches and focus on cause-specific mortality.

Although an elevated mortality risk during migratory periods for raptors has been well documented (Klaassen et al. 2014, Sergio et al. 2019), less is known about seasonal variation in survival for resident birds, or for birds on breeding vs. nonbreeding grounds. This knowledge gap is likely due to reliance on band recoveries, and the resulting necessary focus on annual survival rates. Lower survival during the nonbreeding season for resident raptors, as found here, has been shown for the Eurasian Eagle-Owl (*Bubo bubo*; Leon-Ortega et al. 2016) and the Little Owl (*Athene noctua*; Thorup et al. 2013) but in both cases differences were either small or inconsistent. Although breeding birds experience increased energy demands associated with the entire reproductive effort, the nonbreeding season brings its own challenges for resident birds including prey abundance dynamics (Oro et al. 2021), reduction of foraging efficacy by snow cover (Sonerud 1986), and increased energy demands of thermoregulation (Alves et al. 2013). In addition, reduced body condition from breeding efforts could carry over to exacerbate challenges in the nonbreeding season (Robinson et al. 2020). Many of these challenges are likely intensified at higher latitudes, which may explain our lower survival rates for kestrels wintering in PA compared to FL. Indeed, PA winter survival rates were notably lower than those reported for kestrels wintering in Texas, with Crouch et al. (2019) reporting winter/nonbreeding weekly rates of 0.980–0.992, and Biles (2022) reporting an average 3-mo adult winter survival of 0.985–0.998 (converts to weekly rate of 0.9987–0.9998). Although these estimates compare well to our overwintering adults in FL, our lower winter survival rates in PA may result from the relatively harsh winters there and represent the first overwinter survival estimate of the species at northern latitudes. This pattern reflects a key element of the life history trade-off between taking on the risk of migration for potential increased winter survival (supported here) vs. remaining resident and facing potentially more challenging winter conditions.

Lower survival estimates for adult males across seasons in PA suggest that the breeding season workload for males may reduce their survival compared to their female counterparts. Female kestrels spend more time incubating while males spend more time foraging (Liébana et al. 2009), making them vulnerable to predation or anthropogenic-related deaths, and there is evidence this parental role is more costly than incubation across taxa (Owens and Bennett 1994). In addition, during the nonbreeding period males may be forced into suboptimal habitats with a lower quality food source or to occupy risky human-dominated habitats (Smallwood 1988, Ardia and Bildstein 1997). The smaller size of male kestrels

Table 3. Known-fate model comparison results for overwintering adult kestrel survival analysis conducted using tracking data from December 2020 through December 2022 at two sites (Hawk Mountain Sanctuary, Pennsylvania and Cape Coral, Florida). Included models have $\Delta AIC_c < 2$.

Model	n	AIC_c	ΔAIC_c	Weight
Site	2	94.969	0	0.254
Site + Sex	3	95.503	0.533	0.195
Site + Time	3	96.559	1.589	0.115
Site + Sex + Time	4	96.670	1.701	0.109
Site + Year	3	96.842	1.873	0.100

may also make them more susceptible to starvation during low resource periods, particularly when temperatures are low (see Lundberg 1986, Kenward et al. 1999). The only previous study comparing kestrel survival between sexes also found evidence for lower male annual survival (New Jersey, USA; Callery et al. 2022). Patterns outside this region are less clear. Some evidence for higher male annual survival was found for kestrels in Idaho (Callery et al. 2022), and although Biles (2022) found evidence for lower annual survival of males compared to females, the pattern was not consistent within years. Little evidence of sex-biased adult annual survival for kestrels was found at wintering grounds in FL (Hinnebusch et al. 2010). Indeed, across owls and raptors, the direction and magnitude of survival differences based on sex appear highly variable (Newton et al. 2016).

Our estimates of weekly fledgling survival are high considering the typically low reported survival rates of other juvenile raptors (7–41% lower than adult survival [Newton et al. 2016]). The only other known-fate analysis of fledgling kestrel survival estimated daily survival at 0.270 ($n = 11$), which converts to a weekly survival rate of 0.0001 (Stupik et al. 2015). Although the source of such a large difference with the results of Stupik et al. (2015) is unclear, it could be due in part to their attachment of transmitters to the fledglings' legs, which may potentially hinder foraging ability (Biles et al. 2023). If reduced foraging ability occurred, it may have led to the natural deaths observed (primarily predation and exposure). Other than transmitter attachment methods, our study utilized the same transmitters, tracking equipment, and tracking methods, pointing to possible differences at the site level including prey resources, predator abundance, and climatic conditions. Varland et al. (1993) reported 26% mortality of VHF-tracked fledglings, with all but one dying in the first week, which also contrasts broadly with our confirming only 6% dead across a similar period. Yet their results suggest potentially high annual variation in fledgling survival, with two of three years resulting in just 8% of birds found dead.

Regardless of the reason for these differences, our study shows that fledgling kestrels, across multiple geographic locations, can have high survival during a risky period in their development. Like Stupik et al. (2015), we observed that most fledgling individuals made substantial movements out of our tracking area by 4 wk post-fledging. As a result, tracking fledglings with VHF telemetry proved to be difficult beyond this period, and our data therefore best reflect survival of juvenile individuals between fledging and post-natal movements. If juvenile survival is equivalent to adult survival once individuals

Table 4. Known-fate model comparison results for juvenile kestrel survival analyses conducted using tracking data from December 2020 through December 2022 at five sites (two regions) throughout eastern North America. All models are shown.

Sites Included	Model	n	AIC_c	ΔAIC_c	Weight
All five sites	Sex + Site	6	92.307	0	0.338
	Site	5	92.752	0.446	0.270
	Sex + Region	3	93.349	1.043	0.200
	Region	2	93.838	1.531	0.157
	Intercept only (Null)	1	97.893	5.586	0.021
	Sex	2	98.628	6.322	0.014
Sites with mortality ($n = 3$)	Sex	2	88.249	0	0.210
	Sex + Time	3	88.517	0.268	0.183
	Time	2	88.947	0.698	0.148
	Intercept only (Null)	1	88.990	0.741	0.145
	Sex + Year	3	89.473	1.224	0.114
	Sex + Year + Time	4	90.240	1.991	0.077
	Year	2	90.531	2.282	0.067
	Year + Time	3	90.859	2.611	0.057

arrive at their overwintering areas (Biles 2022), juvenile mortality may be greater between late summer and prior to arrival in overwintering areas. Additional research comparing juvenile and adult survival in other overwintering areas is critical to assessing the consistency of this finding and identifying the riskiest periods for kestrel juveniles.

The lower survival of adult males compared to adult females was also found in fledgling birds. To our knowledge, this is the first study comparing fledgling survival in the first weeks of development across sexes. Unlike for adults, where differing roles during breeding as well as potential timing of movements and migration help explain potential survival differences, reasons for fledgling sex differences are less clear. Body mass differences may be the primary explanation, as males are more susceptible to starvation/exposure, as noted above for adults. And although transmitter weights were well below 3% body weight threshold for all individuals in our study, it is possible even subtle transmitter impacts were more significant for these smaller males. We also observed site differences in fledgling survival, which were driven in part by a complete lack of fatalities in multiple sites. Site differences may also reinforce potentially large variation in fledgling survival both at the site and annual scale, which may be clarified only by additional study of fledgling survival across time and space.

Nearly all previous survival estimates for kestrels are based on band recovery or band-resighting data as opposed to tracking data used here (Table S2). Whereas traditional band recovery approaches may allow for relatively noninvasive estimation of survival across broad geographic areas, the method suffers from very low recapture rates (leading to high estimate uncertainty) and an inability to distinguish death from emigration (see Newton et al. 2016). Band-resight approaches, while often much narrower in geographic extent, can reach much higher detection rates and likely offer the best reference for comparison to our findings. Telemetry approaches used here have been suggested as a way of increasing the robustness of kestrel demographic modeling (McClure et al. 2017) and they offer much higher temporal resolution compared to band recoveries (weekly or seasonal survival vs. annual), and a much-improved ability to confirm death events and their cause, and to distinguish death from emigration. We have reason to believe that the units and attachment method used here had minimal impact on studied birds. First, although recently fledged birds would be the most likely to be impacted by the units as they are learning to fly and are dependent on their parents, we had two study sites with no mortality prior to dispersal. Second, these lightweight units made up <3% of body weight, well under recommended thresholds (US Geological Survey 2018). Third, our backpack harness attachment method has proven effective for this species, allowing adult birds to be tracked through successful breeding seasons (Kolowski et al. 2023) in some cases across multiple years (Biles et al. 2023, J. Kolowski unpub. data) as well as across migration flights (Biles et al. 2023, Hunt et al. 2023, J. Kolowski unpub. data) and there is evidence that negative impacts of device attachment are much reduced with backpack harnesses compared to leg loops (Constantini and Moller 2013).

Comparing our results with estimates from previous band recovery work offers additional challenges. Because of an inability to distinguish emigration from death, these methods report apparent, as opposed to true survival rates (Pollock et al. 1990), whereas the known-fate models used here calculate true survival for the focal region and time period. In addition, conversion of annual rates to the weekly rates presented here is mathematically possible but problematic, in that potentially large seasonal variation (including a demanding migration period) is ignored and spread evenly across the year, rendering converted weekly estimates less informative and potentially misleading. We therefore largely refrained from direct comparisons to previous work beyond broad reporting of value ranges, except for where weekly rates were directly estimated.

Our results suggest that fledgling survival while the young are on their natal territory is higher than previously thought, at least in our study areas, indicating that population declines may be influenced by survival patterns during other seasons and stages of the life cycle. One such stage could include adult survival during the nonbreeding season in northeastern North America, which our results suggest is lower than previously thought. Indeed, adult survival during the nonbreeding season and, more specifically, the overwintering period in PA appears to be lower than many of the previously published survival rates estimated using band recovery models. This discrepancy may stem from differences in methods as well as investigations at different study site latitudes, which we show can greatly impact overwintering survival. Our results ultimately direct conservation and research efforts toward adults during the nonbreeding season in northeastern North America, which may represent an exceptionally vulnerable stage marked with low survival rates. Our study also demonstrates the need for telemetry-based, multi-seasonal survival studies that are geographically broad to identify where and when conservation efforts and research investigations should be focused. Future studies utilizing emerging tracking technologies capable of assessing survival during the dispersal and migratory periods would fill a remaining knowledge gap in kestrel survival and elucidate the risks incurred by differing migratory strategies.

SUPPLEMENTAL MATERIAL (available online). Table S1: Duration of tracking efforts for each of the study sites and kestrel survival analyses conducted between December 2020 and December 2022. Table S2: Survival estimates of American Kestrels reported in previous studies.

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