Seasonal Trends in Adult Apparent Survival and Reproductive Trade-Offs Reveal Potential Constraints to Earlier Nesting in a Migratory Bird

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Abstract

Birds aim to optimize resources for feeding young and self-maintenance by timing reproduction to coincide with peak food availability. When reproduction is mistimed, birds could incur costs that affect their survival. We studied whether nesting phenology correlated with the apparent survival of American kestrels (*Falco sparverius*) from two distinct populations and examined trends in clutch initiation dates. We estimated apparent survival using multistate mark-recapture models with nesting timing, nesting success, sex, age, and weather covariates. Nesting timing predicted the apparent survival of successful adults; however, the effect differed between populations. Early nesting kestrels had higher apparent survival than later nesters in the western population, where kestrels have a relatively long nesting season. At the eastern site, where kestrels have a relatively short nesting season, the pattern was reversed — later nesters had higher apparent survival than earlier nesters. Nesting timing did not affect the apparent survival of adults with failed nests suggesting that the energetic cost of producing fledglings contributed to the timing effect. Finally, clutch initiation dates advanced in the western population and remained static in the eastern population. Given that both populations have seasonal declines in

productivity, population-specific survival patterns provide insight into seasonal trade-offs. Specifically, nesting timing effects on survival paralleled productivity declines in the western population and inverse patterns of survival and reproduction in the eastern population suggest a condition-dependent trade-off. Concomitant seasonal declines in reproduction and survival may facilitate population-level responses to earlier springs, whereas seasonal trade-offs may constrain phenology shifts and increase vulnerability to mismatch.

Keywords: American kestrel, climate change, mismatch, winter, phenology

Introduction

Optimal timing of avian reproduction coincides with peak food availability to exploit resources not only for feeding young but for self-maintenance (Lack 1968). Relationships between nesting phenology and productivity are well-researched. Earlier nesting birds typically have higher productivity than later nesting birds (Reed et al. 2013; Saino et al. 2017). However, the consequences of nesting phenology on other fitness components, such as survival, and potential trade-offs between adult survival and productivity, are less-studied (Reed et al. 2013; Bastianelli et al. 2021). Understanding relationships between nesting phenology and fitness is increasingly important as climate change drives advances in spring green-up, and prey availability, in many regions (Dunn 2004). If birds do not advance nesting timing accordingly, phenological mismatch (i.e., when reproduction is out of synchrony with prey resources) could lead to fitness costs that culminate in population declines (Møller et al. 2008). Indeed, species that have shifted their timing of reproduction least in response to climate change have experienced more severe population declines than species that have shifted more (Møller et al. 2008). Therefore, it is important to understand the associations between nesting phenology and survival.

Breeding at suboptimal times (i.e., lower food availability compared to the peak of the season) can lead to decreased survival (Golet et al. 1998; Lof et al. 2012). Earlier nesting adults may increase survival by obtaining high-quality nesting sites with abundant resources by synchronizing their reproduction with regional resource peaks, or both (Møller 1994). This may result in better physical condition at fledging for both early-breeding adults and their young, increasing their likelihood of survival. Adults who fledge young early in the breeding season have more time to complete molt and improve their physiological condition prior to migration, which may allow them to depart earlier for overwintering areas. This may ultimately result in early breeders obtaining higher quality winter territories than later breeding adults (Smallwood 1988). Additionally, earlier nesting adults may be more competitive, higher quality individuals than later nesting adults, with inherent traits that result in higher survival and productivity (Verhulst and Nilsson 2008). Earlier hatched young have more time before autumn migration to gain foraging experience, establish breeding territories for subsequent years, and gain mass before migration, which could result in increased survival compared to later hatched young (Smallwood and Smallwood 1998; Catry et al. 2016). Because raising young is the most energetically expensive time of the nesting season for species with altricial young (Hillström and Moreno 1992), there may be trade-offs between adult survival and productivity if resources are limited. For example, adults raising young at suboptimal times (i.e., mismatched with peak food availability) may have to reallocate resources spent on self-maintenance to provisioning their young, which could result in poor body condition, increased metabolic stress, and decreased adult survival (Nilsson and Svensson 1996; Reed et al. 2013). Offspring reared at suboptimal times may be provisioned with less food, which can result in slow growth, poor body condition, high nestling mortality, and lower probabilities of fledging and recruitment (Visser et al. 2006).

The strength of timing effects on survival, and the capacity of individuals to shift their timing of reproduction, may depend on regional patterns of climate and resource availability, species life history traits, or variability in adaptive capability among individuals within a population. For example, thermoregulation costs, lasting snow cover, low food availability, and inclement spring weather may inhibit early nesting (Stevenson and Bryant 2000; Irons et al. 2017). Steeper seasonal declines in productivity (Garcia-Heras et al. 2016) and population declines (Both et al. 2010) are more pronounced for species that nest in regions with strong seasonality and shorter nesting windows than those nesting in regions with weaker seasonality and longer nesting windows. Migrant birds, particularly long-distance migrants that often nest in highly seasonal environments, have incomplete knowledge of breeding ground conditions, which may impede their ability to adjust the timing of migration departure, duration, and arrival to match resource peaks (Rubolini et al. 2010). Conversely, resident birds have real-time information about breeding area resources and do not need to time their migration to match resource peaks, which may facilitate a shift to earlier nesting in response

to changing local conditions, like advancing green-up dates (Samplonius et al. 2018). Long-distance migrants show fewer and weaker phenological responses (Rubolini et al. 2010; Samplonius et al. 2018), and stronger negative population effects of climate change than residents (Møller et al. 2008; Both et al. 2010).

American kestrels (*Falco sparverius*) are a widespread, generalist predator, breeding across much of North America (Smallwood and Bird 2020). Kestrel migration tendency and distance covaries with latitude. At northern latitudes, kestrels are complete, long-distance migrants. Whereas at southern latitudes kestrels migrate shorter distances, and populations are partial migrants or complete residents (Smallwood and Bird 2020). There is extensive evidence of kestrel declines in eastern populations (Smallwood et al. 2009), but population trends in other regions are less clear and, in some cases, stable or increasing (McClure et al. 2017). The causes of declines and the reason for geographic differences in trends are still unclear, but regional differences in patterns of seasonality and climate change, and differing adaptive capacity of distinct genetic groups and migratory phenotypes (Smallwood et al. 2009; Ruegg and Brinkmeyer et al. 2021) may contribute to these discrepancies. Western populations are advancing their nesting phenology in response to climate change (Heath et al. 2012; Smith et al. 2017), whereas this phenomenon has not been observed in eastern populations, creating a unique opportunity for comparative studies of the impacts of nesting phenology on survival. Nesting phenology of kestrels is positively correlated with the start of spring (estimated from the extended spring index, see supplement) and increasing Normalized Difference Vegetation Index (NDVI) values, which are a good proxy for small mammal and insect abundance (Lafage et al. 2014; Smith et al. 2017). Further, kestrels that nest before the start of spring (measured by extended spring index) have higher nesting success (i.e., ≥ 1 young fledged) and productivity (i.e., number of young fledged) than later nesters across their breeding range (Callery et al. 2022). However, the relationship between nesting phenology and survival is not as well understood, even though the population dynamics of kestrels are particularly sensitive to changes in adult survival (McClure et al. 2021). Here we examined how nesting phenology relates to the apparent survival of adult and juvenile birds so that we can better understand how climate-driven changes in spring might impact populations.

We used long-term mark-and-recapture data from sites in western (Idaho) and eastern (New Jersey) North America (Figure 1a) to investigate how the timing of nesting relative to the start of spring affected the apparent survival of adult American kestrels and their offspring. We hypothesized that variation in nesting phenology and parental investment in raising young within sites, and regional differences in nesting windows between sites (~4 months in the West, ~2 months in the East) would explain the apparent survival of adults and that nesting phenology and regional differences would explain apparent survival of juveniles. We predicted that later-nesting adults and hatch-year (HY) birds from later nests would have lower apparent survival rates than early-nesting adults and hatch-year birds from earlier nests, respectively, and we expected this effect to be stronger at the eastern site, where the nesting window is shorter. We also expected a stronger negative effect of late nesting on the apparent survival of adults raising young, compared to adults with failed nests, because of higher energy demands. Finally, we included sex and winter temperatures in apparent survival analyses because of their effects on juvenile recruitment rates of kestrels (Steenhof and Heath 2013) and we examined temporal trends in clutch initiation dates for both populations.

Methods

We collected mark and recapture data from nest box networks in Idaho and New Jersey (Figure 1a) with long-term monitoring programs. The study site in southwestern Idaho (43°N, 116°W) encompasses approximately 1000 km^2 within a mixture of sagebrush steppe, agriculture, and rangelands, alongside exurban and suburban areas in the municipalities of Kuna, Meridian, and Boise. Wooden nest boxes were erected on roadside utility poles or trees and spaced 1 km apart on average. The number of nest boxes at this study site ranged from 98 – 113, depending on the year. Occupancy averaged 42% (± 14.4 SD) and, on average, occupied boxes (i.e., American kestrels with ≥ 1 egg) were 1.5 km apart. The magnitude of seasonal changes in primary productivity is relatively low and variable across landscapes and years (Figure 1b, see supplement for NDVI methods). The study site in northwestern New Jersey (41°N, 74°W) encompasses approximately 200 km^2 and is comprised of agricultural lands with open fields embedded within forested areas in Sussex and Warren counties (Smallwood et al. 2009). Wooden nest boxes were erected on roadside utility poles, trees, and barns or other buildings, and spaced 1 km apart. The number of nest boxes at this study site ranged from 96 – 127, depending on the year. Occupancy averaged 28% (± 9.5 SD) and, on average, occupied boxes were 1.5 km apart. Seasonal changes in primary productivity at the New Jersey site are relatively higher in magnitude and consistent from year to year (Figure 1c).

We captured and marked adult American kestrels nesting in nest boxes in Idaho from 2008 – 2017, and in New Jersey from 1997 – 2017. We monitored nest boxes from March – July and systematically checked for occupancy (every 1 – 3 weeks in Idaho; every 3 – 4 weeks in New Jersey). We hand-captured adults in nest boxes during the incubation stage. We then banded birds with US Geological Survey aluminum bands, measured and sexed (by plumage) adults, and returned them to the nest box. Recaptured adults, or birds that had been banded previously elsewhere, were recorded as already banded. On average we trapped 80% ($\pm$ 7.4 SD) and 39% ($\pm$ 16.6 SD) of nesting adults in Idaho and New Jersey, respectively. Unless kestrels were first captured and marked as nestlings, we were unable to age after-hatch year (adult, AHY) birds to more specific age categories. We returned to the nest box to band, measure, and sex nestlings when they were between 18 – 25 days old. We considered a nesting attempt to be successful if it produced at least one young that reached 25 days old (Anderson et al. 2016; Smallwood 2016).

We recorded the clutch initiation date for each nesting attempt by different methods, depending on the status of the nest when it was discovered. When we discovered an incomplete clutch of eggs in a nest box, we back-calculated clutch initiation dates assuming kestrels laid one egg every other day (Bird and Palmer 1988). For clutches that were discovered complete and the eggs hatched, we back-calculated 30 days from the hatching date and twice the clutch size to estimate clutch initiation. If complete clutches never hatched, we used the midpoint between the earliest and latest possible date of clutch initiation. The earliest possible date of clutch initiation was the date we last found the box empty or, if we removed another species nest (i.e., a European starling, *Sturnus vulgaris,* made the box unavailable to kestrels), the date we removed the nest material plus one. We estimated the latest possible date through back-dating, as described above. If the range of possible dates was >15, we considered the clutch initiation date as unknown. For clutches that were discovered complete and hatched, we used the ages of the nestlings, determined by plumage characteristics (Griggs and Steenhof 1993), to back-calculate the clutch initiation date by subtracting the plumage age of the most mature nestling, 30 days for incubation, and twice the clutch size.

We used extended spring-index (SI-x) models to estimate the start of spring. SI-x provides a fine-scale (1 km), validated model of the start of spring across North America (Izquierdo-Verdiguier et al. 2018). These models were developed using daily maximum and minimum surface temperatures to predict the first-bloom dates of lilac (*Syringa chinensis* and *S. vulgaris*), and honeysuckle cultivars (*Lonicera tatarica* and *L. korolkowii*, Schwartz et al., 2006; Rosemartin et al., 2015). SI-x measures are highly correlated with land surface metrics (e.g. NDVI; Zurita-Milla et al. 2017), but in North America SI-x values have proven more predictive of bird phenology than NDVI (Kelly et al. 2016) and are positively associated with American kestrel nest initiation (supplemental information). We extracted SI-x dates derived from Daymet climate datasets (Thornton et al., 2018) at the latitude and longitude of each occupied nest box per year using Google Earth Engine code modified from Izquierdo-Verdiguier et al. (2018). We used NDVI to represent seasonal patterns in primary productivity because NDVI captures year-round green-up and senescence (methods in supplement information).

Ideally, nesting timing would be best represented as a continuous representation of the degree of overlap between seasonal resources and resource requirements of nesting birds (Miller-Rushing et al. 2010). However, multi-state survival models require individual time-varying covariates to be categorical. We calculated the difference (in days) between the clutch initiation date and the year-specific SI-x date for each nest attempt and compared the difference to the median difference for each study site. Then, we categorized nesting attempts as "early" or "late" depending on whether the individual nesting attempt was before (early) or after (late) the median. If a bird attempted to nest more than once in a season (n = 16), the latest successful nesting attempt was considered when assigning the bird to a timing group for that year (n = 8), or if both nesting attempts were unsuccessful (n = 8), the latest nesting attempt was considered.

We calculated winter minimum temperature anomalies for each study site to determine winter severity. We used minimum temperatures because, especially in winter months, minimum temperatures limit species distributions (Root 1988; Zuckerberg et al. 2011) and lower minimum temperatures affect energetic requirements associated with thermoregulation (Meijer et al. 1999). The use of anomaly values allowed for standardized representation of climate change across locations with different minimum temperatures. We used Google Earth Engine (Gorelick et al. 2017) to extract minimum temperatures from the Daymet dataset, which provides daily gridded climate data at 1-km resolution (Thornton et al. 2018). For each year we averaged daily minimum temperature values within a minimum bounding box of all nest box locations for each study area. For each study site we calculated winter minimum temperature anomalies for each year as the difference between the mean winter minimum temperature and the mean winter minimum temperature from a 30-year (1981 – 2010) baseline period.

Statistical Analysis

For the survival analysis, we created mark-recapture models using the multistate model framework in Program MARK (White and Burnham 1999), using the RMark package and interface (Laake 2008). Multistate mark-recapture models estimate apparent survival (S), and capture probability (p) similar to Cormack-Jolly-Seber mark-recapture survival models (Lebreton and Pradel 2002); additionally, these models estimate transition probability (Ψ) between categorical states (Schwarz et al. 1993). We created six states, hereafter referred to as strata, to represent nesting timing, age, and nesting success of adults:

(1.) HY from a brood initiated "early"
(2.) HY from a brood initiated "late"
(3.) a successful AHY that initiated egg-laying "early"
(4.) a successful AHY that initiated egg-laying "late"
(5.) an unsuccessful AHY that initiated egg-laying "early"
(6.) an unsuccessful AHY that initiated egg-laying "late"

In addition to individual strata, we included sex as an individual-level, static covariate and winter minimum temperature anomaly as a population-level, time-varying covariate to explain apparent survival.

We created capture histories for each bird by coding their presence or absence in each year of the study and assigning the appropriate stratum according to their age, timing category, and nesting-success, for each year they were present. Most (> 85%) American kestrels breed in their second year, and there was no difference between clutch initiation dates between second year and older kestrels (Steenhof and Heath 2009). We had few known-age birds, so we did not consider age effects other than categorical hatch-year and after-hatch-year designations. We designed a model set for apparent survival that included all additive and interactive models of the multistate variable stratum, sex, and annual minimum winter temperature anomaly ("winter temperature"). We examined models for p that included the covariates of winter temperature and sex because we typically capture a higher proportion of females compared to males (Steenhof and Heath 2013), and we created a candidate model set for Ψ that included an intercept-only model and an effect of current stratum membership. We did not have the sample size to build more complex models for Ψ. We fixed the Ψ estimates of transition from AHY to HY and between HY strata to 0 (Figure S5). We used an iterative process to find the best model by selecting the top model for p, then the best model for Ψ, and used the top models for p and Ψ to build models for S. We ran separate mark-recapture analyses for western and eastern sites, using the same model set for each analysis. We ran goodness of fit tests on survival models with the variable 'strata' using functions from the package R2UCare (Gimenez et al. 2018). Specifically, we used the functions *overall_JWV* to test the fit of the model, *test3Gsr* to test for the presence of transients, and *test3Gwbwa* to test for the presence of memory. For all tests we failed to reject the null hypotheses (p > 0.05) indicating model fit, and lack of issues with transients and memory.

We examined temporal trends in clutch initiation dates for each study site using generalized linear models with Gamma distributions and log link functions in the R package glmmTMB (Brooks et al. 2017). We used a Gamma distribution because clutch initiation dates are positive data. We plotted residual dispersion to check model assumptions.

We compared models using Akaike's information criterion corrected for small sample size (AICc) and considered the models with the lowest AICc to be most informative (Anderson and Burnham 2004). We estimated 85% confidence intervals for model parameters to be compatible with model selection criteria (Arnold 2010), and we considered effects statistically unclear if 85% confidence intervals overlapped zero (Dushoff et al. 2019). We report parameters as estimate ± standard error and with their 85% confidence intervals. We conducted all analyses in R (R Core Team 2021, version 4.0.5).

Results

We captured and marked 1430 (first marked as AHY = 507, HY = 923) individual kestrels at the western site in Idaho and 1405 (first marked as AHY = 284, HY = 1121) individual kestrels at the eastern site in New Jersey. These individuals were associated with 369 nest attempts from 2008 – 2017, and 301 nest attempts from 1997 – 2017, at western and eastern sites, respectively. At the western site, clutch initiation ranged from early March through late June (Figure 2a), and the median difference between clutch initiation and the start of spring was -17 days (std. deviation = 21 days, Figure 2b). At the eastern site, clutch initiation ranged from late March through early June (Figure 2a), and the median difference between clutch initiation and the start of spring was -8 days (std. deviation = 12 days, Figure 2b).

The best-supported model for recapture probability contained a covariate for sex. Western males were more likely to be recaptured than females (β = 0.44; 85% CI: 0.06 – 0.81, Table S2) and eastern males were less likely to be recaptured than females (β = -1.21; 85% CI: -1.7 – 0.71, Table S3). The best-supported model for the transition probability was the intercept-only model (Table S4, Table S5). Previous strata state did not explain the transition probability to alternate states.

The best-supported model for apparent survival at the western site included additive effects for the multistate variable stratum (includes nesting timing, age, and nesting success), sex, and winter temperature (Table 1). The best-supported model for apparent survival at the eastern site contained the stratum and sex covariates (Table 2). Successful "early" nesting birds had higher apparent survival rates compared to successful "late" nesters in the West (Figure 3, Table 3). Successful "late" nesting birds had higher apparent survival rates compared to successful "early" nesters in the East (Figure 3, Table 3). At both sites, successful adults had higher apparent survival rates than unsuccessful adults, and there was no difference in apparent survival of unsuccessful "early" and "late" adults. Also, there was no difference in apparent survival of "early" versus "late" hatch-year birds. Overall, hatch-year birds had lower apparent survival estimates than after-hatch-year birds.

Winter minimum temperature anomalies were positively associated with higher apparent survival estimates (β = 0.43; 85% CI: 0.21 – 0.64, Figure 3) in the West, and males tended to have higher survival estimates than females, but the 85% confidence interval for sex crossed zero so we considered this effect statistically unclear (β = 0.11; 85% CI: -0.23 – 0.45). The top model did not include winter temperature in the East. It did include sex, but the confidence interval for sex crossed zero (β = -1.04; 85% CI: -1.30 – 0.01); therefore, we considered this effect statistically unclear.

Clutch initiation date advanced (β = -0.009; 85% CI: -0.014 – -0.003) over the nine-year study period in the West (Figure 4), whereas clutch initiation dates did not change over the 20-year study period in the East (β = 0.003; 85% CI: -0.002 – 0.004, Figure 4).

Discussion

Our comparative study on the effects of nesting phenology on the apparent survival of American kestrels showed differing trends at two distinct long-term monitoring sites in western and eastern North America. At both sites, nesting phenology affected the apparent survival of adult kestrels that raised young, but the direction of the effect differed between populations, with earlier nesters having higher apparent survival than later nesters in the West, and later nesters having higher apparent survival than earlier nesters in the East. Given that both populations have seasonal declines in productivity (Callery et al. 2022), these results suggest that condition-dependent trade-offs between reproduction and survival exist for eastern kestrels, whereas this trade-off is not apparent for western kestrels. Furthermore, despite advancing springs across North America, clutch initiation dates tended not to change at the eastern site, but they are advancing at the western site. Seasonal trade-offs may constrain shifts in nesting phenology in response to earlier springs in the eastern population, whereas the high apparent survival and productivity of early nesters in the West may make that population well-suited to respond to directional pressure to breed earlier (Figure 5).

Results from the western site were consistent with our predictions that earlier nesting adults raising young during peak availability of resources would have higher apparent survival than later nesting adults. Further, because early nesting American kestrels also have high productivity (Callery et al. 2022), results suggest that, in the West, resources do not create a trade-off between survival and reproduction, that early nesters are higher quality individuals, or both. Without experimental manipulation, the effects of nesting timing and individual quality are difficult to tease apart, and most likely a combination of nesting timing and individual effects contribute to the success of early nesters (Verhulst and Nilsson 2008). Winter temperatures have warmed over the past two decades at the western site (Heath et al. 2012, unpub data) and spring is advancing, especially on irrigated croplands within the study area (Smith et al. 2017). Warming winters and earlier springs may have removed previous constraints to early nesting, such as early-season cold temperatures that increase thermoregulation costs of survival and delay egg production, or low food availability that affects incubation and raising young (Stevenson and Bryant 2000; Woodworth et al. 2017). Indeed, our results show that western kestrels had higher apparent survival with increasing winter temperature anomalies, and Heath et al. (2012) showed earlier nesting after warmer winters. Late summer at the western site is subject to extreme heat and drought conditions, increasingly so with climate change (Sohrabi et al. 2013), which may have negative effects on

both the survival and productivity of later breeders (Albright et al. 2010). Together, the removal of early constraints, additional costs of late nesting, and seasonal declines in survival and productivity may explain the advancement of nesting phenology in response to climate change in the West.

At the eastern site, results did not fit our predictions — later nesting adults that raised young had higher apparent survival than earlier nesters. This survival pattern contrasts with the observed seasonal decline in productivity (Callery et al. 2022). The narrow distribution of clutch initiation dates and seasonal changes in primary productivity suggest that there is a very narrow window of high resources for raising young at the eastern site. Seasonally limited resources may cause condition-dependent trade-offs between survival and reproduction (Stearns 1989). Early in the season adults may allocate resources to raising young at a cost to survival, whereas later in the season this pattern is reversed. Alternatively, winter and early spring weather events such as increased severity and frequency of blizzards (Cohen et al. 2018) and extreme precipitation events in spring (Huang et al. 2017) may decrease survival through delay in arrival time, and a decrease in prey activity, hunting efficiency, and provisioning rates (Olsen and Olsen 1992). Unpredictable early season conditions suggest that the potential survival costs of arriving at the breeding grounds and nesting early are high and nesting later may be a safer strategy (Stevenson and Bryant 2000). Inverse seasonal patterns in survival and reproduction may represent different investments by individuals of different ages or experiences. Though we did not find evidence of associations between age and timing. Hatch-year birds transitioned to both early or late states, and previous research at the western site found no difference in clutch initiation dates between second-year birds and older birds (Steenhof and Heath 2009). Narrow resource windows and inverse seasonal patterns of survival and reproduction may constrain eastern American kestrels from nesting earlier in response to climate change.

Migratory phenotype is another individual-level trait that can affect nesting phenology, with long-distance migrants generally nesting later than residents and short-distance migrants because of arrival time constraints and incomplete knowledge of breeding ground conditions (Rubolini 2010). In American kestrels, the arrival time of short-distance migrants is earlier in years with warmer spring temperatures, whereas the arrival time of long-distance migrants remains unchanged (Powers et al. 2021). The kestrel population at the western site is partially migratory (i.e., some individuals migrate, while others are year-round residents; Anderson et al. 2016), and migration distances are becoming shorter with warming winters (Heath et al. 2012). Hence, flexible migratory strategies may work in concert with reduced environmental constraints to allow for earlier nesting in Idaho. Less is known about migratory phenotypes and distances of kestrels from the eastern site, although Smallwood and Bird (2020) suggest that at these mid-latitudes, juveniles tend to be fully migratory, whereas adult migratory strategy may be dependent on weather patterns. Results showed that the apparent survival of eastern kestrels was not affected by winter temperatures, which could suggest that a large proportion of the population are migratory, so do not experience local winter weather conditions. Furthermore, because migration is the life history stage with the highest mortality risks (Klaassen et al. 2014; reviewed in Robinson et al. 2020), it is difficult to tease apart whether migratory strategy is directly affecting apparent survival or indirectly affecting apparent survival through nesting phenology. Finally, genetic differences between earlier and later breeding birds (Saino et al. 2017) and between migrants and residents (Ruegg and Brinkmeyer et al. 2021) suggest that underlying genetic composition may be affecting nesting phenology directly or indirectly through migratory phenotype. American kestrels in western North America are genetically distinct from those in eastern North America and may have differing levels of adaptive capacity to shift phenology (Ruegg and Brinkmeyer et al. 2021).

Overall, adults with failed nests had lower apparent survival rates than adults that raised young, which could reflect lower inherent individual fitness (Blums et al. 2005), or higher dispersal and permanent emigration rates of unsuccessful adults compared to successful adults (Steenhof and Heath 2009). We did not detect effects of nesting phenology in adults with failed nests, but only in those that raised young. The brood-rearing stage is when concurrent parental and offspring energy demand is at its highest (Hillström and Moreno 1992), so limited resources are most impactful during this stage. The majority of unsuccessful nests at both sites failed at the egg stage (Idaho: 87%, New Jersey: 78%), suggesting these individuals did not invest as much energy and resources as those raising young, so were unaffected by nesting timing. Additionally, nesting adults may mitigate their own mortality risk by abandoning nests when survival costs are too high compared to potential productivity benefits (Clutton-Brock 2019).

Consistent with previous studies (reviewed by Martin 1995), the apparent survival of hatch-year birds was lower than that of adults. However, contrary to previous studies of kestrels and other birds (Verhulst and Tinbergen 1991; Catry et al. 2016; Robinson et al. 2020), the apparent survival of hatch-year birds was not affected by the timing of nests they were hatched from. Nestlings hatched later in the season may have fewer siblings than those hatched earlier in

the season because of reduced clutch size, hatching success, or nestling survival (Callery et al. 2022). This could potentially mitigate the costs of later hatching on size, condition (Shutler et al. 2006), and subsequent survival of the remaining nestlings. Alternatively, the low overall apparent survival of hatch-year birds in our study may have limited our ability to detect a significant effect of nesting timing on apparent survival of this age class.

It is important to note that our model, like most survival models, estimates apparent survival as opposed to true survival (Lebreton and Pradel 2002; Schaub and Royle, 2014) and hence cannot distinguish between death and permanent emigration (Schaub and Royle, 2014). American kestrels with higher dispersal rates (e.g. unsuccessful breeders, Steenhof and Heath 2009) or longer dispersal distances (e.g. later hatched young, Miller and Smallwood 1997; migrants, McCaslin et al. 2020) have lower recapture likelihood and hence lower apparent survival estimates, so we cannot disentangle whether nesting phenology or dispersal patterns decreased apparent survival estimates.

In summary, although spring is advancing at both the western and eastern sites, American kestrel populations are responding differently. Western kestrels are nesting earlier, whereas nesting phenology did not change for eastern kestrels. In the West, flexible migratory strategies and warmer winters may reduce early nesting constraints and allow kestrels to maximize fitness by nesting earlier when both productivity and survival rates are highest. Hence, this population may be well-suited to respond to directional pressure to breed earlier with a warming climate. Conversely, at the eastern site, potential constraints from early inclement weather and narrow seasonal availability of resources may result in trade-offs between seasonal declines in productivity and seasonal increases in survival. These trade-offs may constrain nesting phenology in eastern populations in response to climate-driven advances in spring, which is particularly concerning in light of steep declines in eastern populations.

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Conflict of Interest

The authors have no conflicts of interest to declare.

Ethics Approval

American kestrels were handled and marked under the authority of federal bird banding permits (JAH: 23307, JAS: 21378), New Jersey scientific collecting permit SC 2017023, and its predecessors, Idaho scientific collecting permits, and institutional IACUCs.

Data Availability Statement

Data are available at an institutional DOI (TBD).

References

Albright TP, Pidgeon AM, Rittenhouse CD, Clayton MK, Wardlow BD, Flather CH, Culbert PD, Radeloff VC (2010) Combined effects of heat waves and droughts on avian communities across the conterminous United States. Ecosphere 1:1-22

Anderson AM, Novak SJ, Smith JF, Steenhof, K, Heath JA (2016) Nesting phenology, mate choice, and genetic divergence within a partially migratory population of American kestrels. The Auk: Ornithological Advances 133:99-109

Anderson D, Burnham K (2004) Model selection and multi-model inference Second NY: Springer-Verlag 63:1007

Arnold, TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175-1178

Bastianelli O, Charmantier A, Biard C, Bonamour S, Teplitsky C, Robert A (2021) Is earlier reproduction associated with higher or lower survival? Antagonistic results between individual and population scales in the blue tit. bioRxiv

Bird DM, Palmer RS (1988) American kestrel. In: Palmer RS (ed) Handbook of North American birds, vol 5: diurnal raptors, part 2. Yale University Press, New Haven, pp 253-290

Blums P, Nichols JD, Hines JE, Lindberg MS, Mednis A (2005) Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia 143:365-76

Both C, van Turnhout CA, Bijlsma RG, Siepel H, van Strien AJ, Foppen RP (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B: Biological Sciences 277:1259-1266

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal 9:378-400

Callery KR, Schulwitz SE, Hunt AR, Winiarski JM, McClure CJ, Fischer RA, Heath JA (2022) Phenology effects on productivity and hatching-asynchrony of American kestrels (*Falco sparverius*) across a continent. bioRxiv

Catry T, Moreira F, Alcazar R, Rocha PA, Catry I (2016) Mechanisms and fitness consequences of laying decisions in a migratory raptor. Behavioral Ecology 28:222-232

Clutton-Brock TH (2019) The evolution of parental care. Princeton University Press

Cohen J, Pfeiffer K, Francis JA (2018) Warm Arctic episodes linked with increased frequency of extreme winter weather in the United States. Nature Communications 9:1-12

Dunn P (2004) Breeding dates and reproductive performance. Advances in Ecological Research 35:69-87

Dushoff J, Kain MP, Bolker BM (2019) I can see clearly now: reinterpreting statistical significance. Methods in Ecology and Evolution 10:756-759

Garcia-Heras MS, Arroyo B, Mougeot F, Amar A, Simmons RE (2016) Does timing of breeding matter less where the grass is greener? Seasonal declines in breeding performance differ between regions in an endangered endemic raptor. Nature Conservation 15:23-45

Gimenez O, Lebreton J-D, Choquet R, Pradel R (2018) R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. Methods in Ecology and Evolution 9: 1749 – 1754.

Golet GH, Irons DB, Estes JA (1998) Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67:827-841

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18-27

Griggs GR, Steenhof K (1993) Photographic guide for aging nestling American kestrels. USDI Bureau of Land Management Raptor Research Technical Assistance Center, Boise, Idaho, USA

Heath JA, Steenhof K, Foster MA (2012) Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. Journal of Avian Biology 43:376-384

Hillström L, Moreno J (1992) Variation in time and energy budgets of breeding wheatears. Behaviour 120:11-39

Huang H, Winter JM, Osterberg EC, Horton RM, Beckage B (2017) Total and extreme precipitation changes over the northeastern United States. Journal of Hydrometeorology 18:1783-1798

Irons RD, Harding Scurr A, Rose AP, Hagelin JC, Blake T, Doak DF (2017) Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. Proceedings of the Royal Society B: Biological Sciences 284:20170412

Izquierdo-Verdiguier E, Zurita-Milla R, Ault TR, Schwartz MD (2018) Development and analysis of spring plant phenology products: 36 years of 1-km grids over the conterminous US. Agricultural and Forest Meteorology 262:34-41

Lack DL (1968) Ecological adaptations for breeding in birds. London, Methuen & Co

Kelly JF, Horton KG, Stepanian PM, de Beurs KM, Fagin T, Bridge ES, Chilson PB (2016) Novel measures of continental-scale avian migration phenology related to proximate environmental cues. Ecosphere 7:e01434

Klaassen RH, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo KM, Bairlein F, Alerstam T (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176-184

Laake J, Rexstad E (2008) RMark–an alternative approach to building linear models in MARK. In Cooch E and White GC (eds) Program MARK: a gentle introduction.

Lafage D, Secondi J, Georges A, Bouzillé JB, Pétillon J (2014) Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. Insect Conservation and Diversity 7:327-33

Lebreton JD, Pradel R (2002) Multistate recapture models: modelling incomplete individual histories. Journal of Applied Statistics 29:353-369

Lof ME, Reed TE, McNamara JM, Visser ME (2012) Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. Proceedings of the Royal Society B: Biological Sciences 279:3161-3169

Martin K (1995) Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35:340-8

McClure CJ, Schulwitz SE, van Buskirk R, Pauli BP, Heath JA (2017) Commentary: Research recommendations for understanding the decline of American kestrels (*Falco sparverius*) across much of North America. Journal of Raptor Research 51:455-464

McClure CJ, Brown JL, Schulwitz SE, Smallwood J, Farley KE, Therrien JF Heath JA (2021) Demography of a widespread raptor across disparate regions. Ibis 163:658-670

Meijer T, Nienaber U, Langer U, Trillmich R (1999) Temperature and timing of egg-laying of European Starlings. Condor 101: 124-132

Miller KE, Smallwood JA (1997) Natal dispersal and philopatry of southeastern American Kestrels in Florida. The Wilson Bulletin 1:226-32

Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3177-3186

Møller AP (1994) Phenotype-dependent arrival time and its consequences in a migratory bird. Behavioral Ecology and Sociobiology 35:115-122

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200

Nilsson JÅ, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London Series B: Biological Sciences 263:711-714

Olsen P, Olsen J (1992) Does rain hamper hunting by breeding raptors? Emu-Austral Ornithology 92:184-187

Powers BF, Winiarski JM, Requena-Mullor JM, Heath JA (2021) Intra-specific variation in migration phenology of American kestrels (*Falco sparverius*) in response to spring temperatures. Ibis 163: 1448-1456

R Core Team (2021) R: A language and environment for statistical computing R Foundation for Statistical Computing. Vienna, Austria URL https://wwwR-projectorg/

Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. Journal of Animal Ecology 82:131-144

Robinson RA, Meier CM, Witvliet W, Kéry M Schaub M (2020) Survival varies seasonally in a migratory bird: Linkages between breeding and non-breeding periods. Journal of Animal Ecology 89:2111-2121

Root T (1988) Energy constraints on avian distributions and abundances. Ecology 69: 330–339

Rosemartin AH, Denny EG, Weltzin JF, Lee Marsh R, Wilson BE, Mehdipoor H, Zurita-Milla R, Schwartz MD (2015) Lilac and honeysuckle phenology data 1956–2014. Scientific data 2:1-8

Rubolini D, Saino N, Møller AP (2010) Migratory behaviour constrains the phenological response of birds to climate change. Climate Research 42:45-55

Ruegg KC, Brinkmeyer M, Bossu CM, Bay RA, Anderson EC, Boal CW, Dawson RD, Eschenbauch A, McClure CJ, Miller KE, Morrow L, Morrow J, Oleyar MD, Ralph B, Schulwitz S, Swem T, Therrien J, van Buskirk RW, Smith TB, Heath JA (2021) The American kestrel (*Falco sparverius*) genoscape: Implications for monitoring, management, and subspecies boundaries. Ornithology 138:ukaa051

Saino N, Ambrosini R, Albetti B, Caprioli M, De Giorgio B, Gatti E, Leichti F, Parolini M, Romano A, Romano M, Scandolara C, Gianfranceschi L, Bollati V, Rubolini D (2017) Migration phenology and breeding success are predicted by methylation of a photoperiodic gene in the barn swallow. Scientific Reports 7:1-10

Samplonius JM, Bartošová L, Burgess MD, Bushuev AV, Eeva T, Ivankina EV, Kerimov AB, Krams I, Laaksonen T, Magi M, Mand R, Potti J, Torok J, Trnka M, Visser ME, Zang H, Both C (2018) Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. Global Change Biology 24:3780-3790

Schaub M, Royle JA (2014) Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods in Ecology and Evolution 5: 1316-1326.

Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. Global change biology 12:343-351.

Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag-recovery data. Biometrics 49:177-193

Shutler D, Clark RG, Fehr C, Diamond AW (2006) Time and recruitment costs as currencies in manipulation studies on the costs of reproduction. Ecology 87:2938-2946

Smallwood JA (1988) A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in southcentral Florida. Auk 105:36-46

Smallwood JA, Causey MF, Mossop DH, Klucsarits JR, Robertson B, Robertson S, Mason J, Maurer MJ, Melvin RJ, Dawson RD, Bortolotti G, Parrish JW, Breen TF, Boyd K (2009) Why are American kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest-box programs. Journal of Raptor Research 43:274-282

Smallwood JA (2016) Effects of researcher-induced disturbance on American Kestrels breeding in nest boxes in northwestern New Jersey. Journal of Raptor Research 50:54-59

Smallwood JA, Bird DM (2020) American Kestrel (Falco sparverius), version 10 In Birds of the World (A F Poole and F B Gill, Editors) Cornell Lab of Ornithology, Ithaca, NY, USA https://doiorg/102173/bowamekes01

Smallwood PD, Smallwood JA (1998) Seasonal shifts in sex ratios of fledgling American kestrels (*Falco sparverius paulus*): the early bird hypothesis. Evolutionary Ecology 12:839-853

Smith SH, Steenhof K, McClure CJ, Heath JA (2017) Earlier nesting by generalist predatory bird is associated with human responses to climate change. Journal of Animal Ecology 86:98-107

Sohrabi MM, Ryu JH, Abatzoglou J, Tracy J (2013) Climate extreme and its linkage to regional drought over Idaho, USA. Natural Hazards 65:653-681

Stearns, SC (1989) Trade-offs in life-history evolution. Functional Ecology 3:259-268.

Steenhof K, Heath JA (2009) American Kestrel reproduction: evidence for the selection hypothesis and the role of dispersal. Ibis 151:493-501

Steenhof K, Heath JA (2013) Local recruitment and natal dispersal distances of American kestrels. The Condor 115:584-592

Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. Nature 406:366-367

Thornton PE, Thornton M, Mayer BW, Wei Y, Devarakonda R, Vose RS, Cook RB (2018) Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 3. ORNL DAAC, Oak Ridge, Tennessee, USA

Verhulst S, Nilsson JA (2008) The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society of London, Series B 363:399-410

Verhulst S, Tinbergen JM (1991) Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus major*. Journal of Animal Ecology 60:269-282

Visser ME, Holleman LJ, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164-172

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120-S139

Woodworth BK, Wheelwright NT, Newman AE, Schaub M, Norris DR (2017) Winter temperatures limit population growth rate of a migratory songbird Nature Communications 8:1-9

Zuckerberg B, Bonter DN, Hochachka WM, Koenig WD, DeGaetano AT, Dickinson JL (2011) Climatic constraints on wintering bird distributions are modified by urbanization and weather. Journal of Animal Ecology 80:403-413

Zurita-Milla R, Goncalves R, Izquierdo-Verdiguier E, Ostermann FO (2017) Exploring vegetation phenology at continental scales: linking temperature-based indices and land surface phenological metrics. In Proceedings of the 2017 Conference on Big Data from Space, Toulouse, France pp. 28-30

Tables

Table 1. Candidate model set to estimate apparent survival (S) of western American kestrels in Idaho captured between 2008 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The recapture probability submodel contained a covariate for sex and the transition probability submodel included an intercept-only term for all apparent survival models. See methods for levels of the stratum variable.

Apparent survival (S)	K	ΔAICc	AICcWt
Stratum + Sex + Winter temperature	30	0	0.57
Stratum + Sex * Winter temperature	31	1.4	0.28
Stratum	28	3.7	0.09
Stratum + Sex	29	5.6	0.03
Stratum * Winter temperature	34	6.3	0.02
Stratum * Sex + Winter temperature	35	8.8	0.01
Stratum * Sex	34	14.4	0
Stratum * Sex * Winter temperature	46	17.3	0
Stratum + Winter temperature	29	51.7	0
Sex + Winter temperature	25	123.4	0
Sex * Winter temperature	26	125.1	0
Intercept only	23	126.4	0
Sex	24	128.3	0
Winter temperature	23	157.4	0

Table 2. Candidate model set to estimate apparent survival (S) of eastern American kestrels in New Jersey captured between 1997 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The recapture probability submodel contained a covariate for sex and transition probability submodel included an intercept-only term for all apparent survival models. See methods for levels of the stratum variable.

Apparent survival (S)	K	ΔAICc	AICcWt
Stratum + Sex	30	0.0	0.55
Stratum + Sex + Winter temperature	31	1.0	0.33
Stratum + Sex * Winter temperature	32	3.0	0.12
Stratum	29	25.1	0
Stratum + Winter temperature	30	26.5	0
Stratum * Winter temperature	35	31.8	0
Stratum * Sex	35	44.0	0
Stratum * Sex + Winter temperature	36	45.1	0
Stratum * Sex * Winter temperature	47	58.9	0
Sex	25	129.3	0
Intercept only	24	130.2	0
Sex + Winter temperature	26	130.4	0
Sex * Winter temperature	27	132.5	0
Winter temperature	24	141.2	0

Table 3. Effect size (β) for each covariate in the top apparent survival model for American kestrels captured at the western (Idaho) and eastern (New Jersey) site. Hatch-year birds had lower apparent survival rates than adult birds. Among successful adults, nesting timing had different effects between sites. Winter temperatures had a positive effect on apparent survival rates of western kestrels but that variable was not in the top model for eastern kestrels.

Covariate	Western (Idaho) Site			Eastern (New Jersey) Site		
	Effect size (β)	Lower CI (85%)	Upper CI (85%)	Effect size (β)	Lower CI (85%)	Upper CI (85%)
Stratum						
Earlier hatch-year	-3.52	-4.05	-2.99	-3.95	-4.66	-3.23
Later hatch-year	-3.76	-4.48	-3.05	-5.32	-6.80	-3.85
Earlier adult, nest-success	-0.44	-0.81	-0.07	-0.80	-1.19	-0.41
Later adult, nest-success	-1.18	-1.56	-0.80	-0.10	-0.53	0.34
Earlier adult, nest-failure	-1.74	-2.40	-1.08	-1.06	-1.94	-0.18
Later adult, nest failure	-1.91	-2.45	-1.37	-2.31	-3.86	-0.76
Sex (male)	0.11	-0.23	0.45	-1.04	-1.30	0.01
Winter Temperature (min anomaly °C)	0.43	0.21	0.64	-	-	-

Figure Legends

Fig. 1 Locations (a) of the long-term mark and recapture studies used to estimate apparent survival of American kestrels with insets of annual normalized difference vegetation index (NDVI) from Jan 1 – Dec 31 (2001 – 2020) from five locations within 1 km of nest boxes within the western site (Idaho, b) and eastern site (New Jersey, c). The blue lines represent a smoothed average. Though the study sites are at a similar latitude, growing seasons are more pronounced at the eastern site compared to the western site where vegetation green-up is more heterogeneous and less peaked.

Fig. 2 Density distributions of the clutch initiation (CI) dates (a), and the difference between clutch-initiation date and extended spring index date (SI-x, b) for nests at western (Idaho, shaded orange, n = 369, 2008 – 2017) and eastern (New Jersey, shaded blue, n = 301, 1997 – 2017) sites. The orange dashed line represents the median overall CI date for western nests in "a" (April 12th) and the overall median difference between CI and SI-x in "b" (-17 days). The blue dashed line represents the overall median CI date for eastern nesting attempts in A (April 27th) and the overall median difference between CI and SI-x in B (-8 days).

Fig. 3 Apparent survival estimates for female western (Idaho) American kestrels from 2008 –2017 (top) and eastern (New Jersey) American kestrels from 1997 – 2017 (bottom) categorized by age, whether or not an adult successfully raised young, and nesting timing category across winter minimum temperature anomalies. Circles and triangles are mean estimates and bars represent 85% confidence intervals. Apparent survival of successful adults depended on whether they were in the early (green) or late (coral) nesting timing category. Nesting timing did not affect apparent survival rates of hatch-year birds or adults that did not successfully rear offspring. Apparent survival rates of western kestrels increased as winter minimum temperature anomaly increased, but this result was statistically unclear for eastern kestrels.

Fig. 4 Trends in clutch initiation dates of American kestrel nests at the western (Idaho) site from 2008 – 2017 (blue) and eastern (New Jersey) site from 1997 – 2017 (orange). The shaded areas represent the 85% confidence interval around the predicted line, and each point represents the clutch initiation date at an occupied nest box. American kestrels are nesting earlier at the western site, but there is no change in nesting phenology at the eastern site.

Fig. 5 The density distributions of the difference between clutch-initiation (CI) dates and the start of spring (SI-x) in polygons, apparent survival estimates (mean and 85% confidence interval) of an early (green point and line) and late (coral triangle and line) successful, adult females, and seasonal trends in productivity (dark green line) based on Callery et al. (2022) for the western (Idaho) site (a) and eastern (New Jersey) site (b). At the western site, seasonal declines in both productivity and apparent survival may be allowing for earlier nesting in response to climate change via directional selection, whereas at the eastern site an inverse pattern between apparent survival and productivity may create a constraint for earlier nesting.
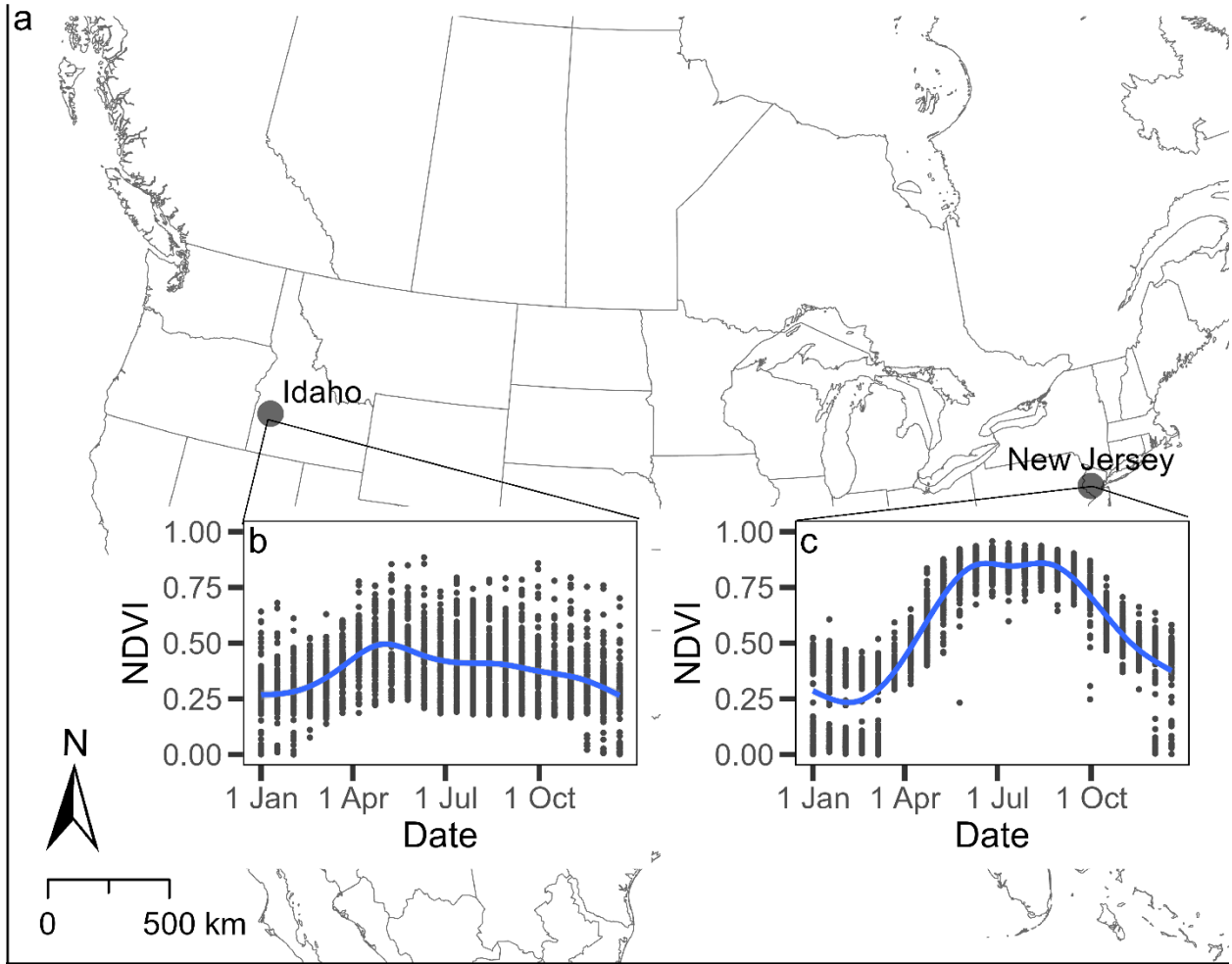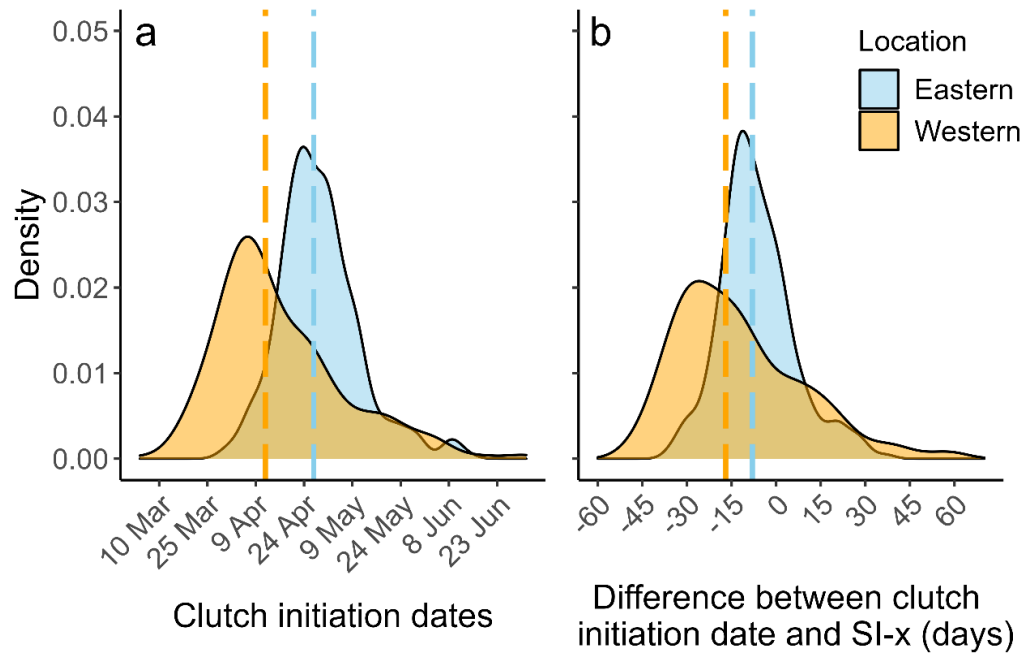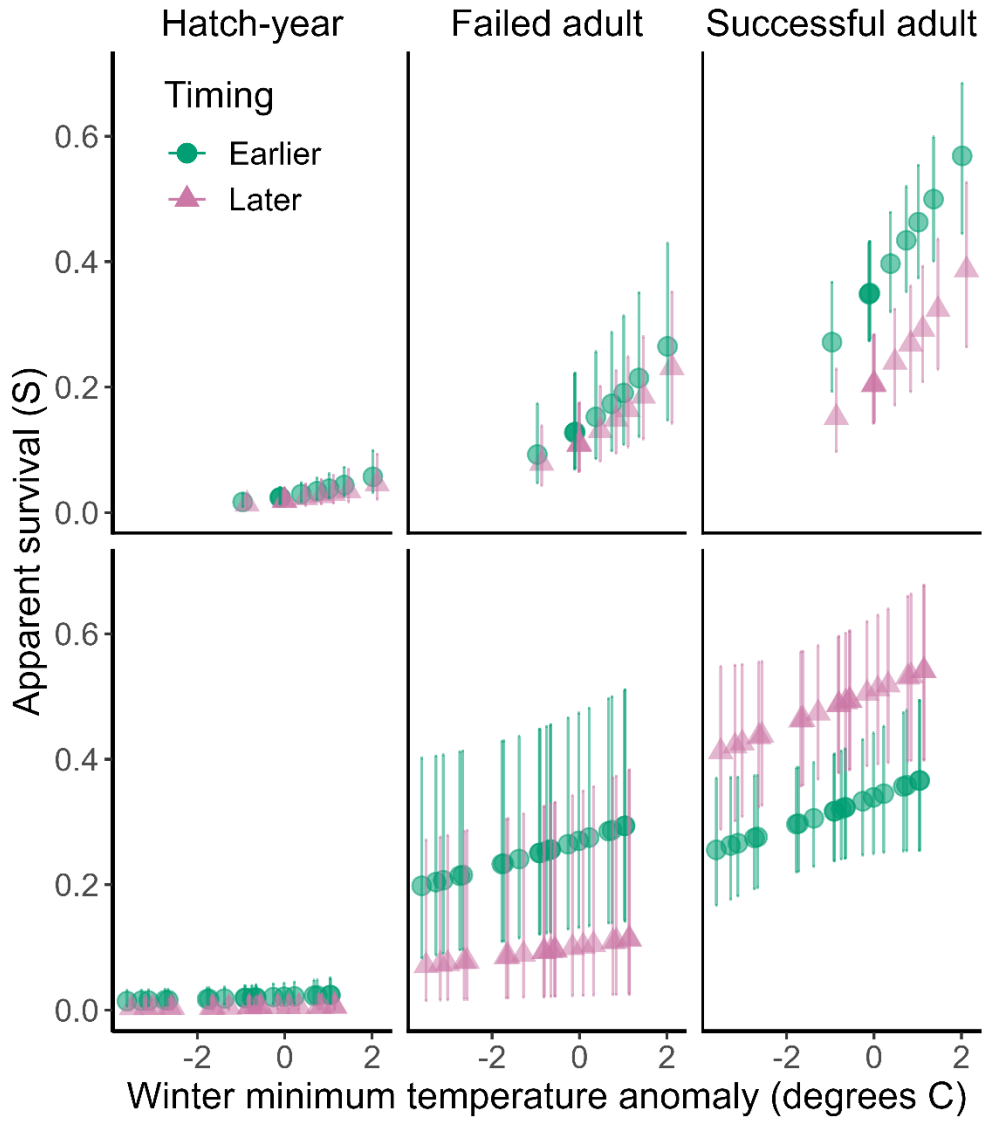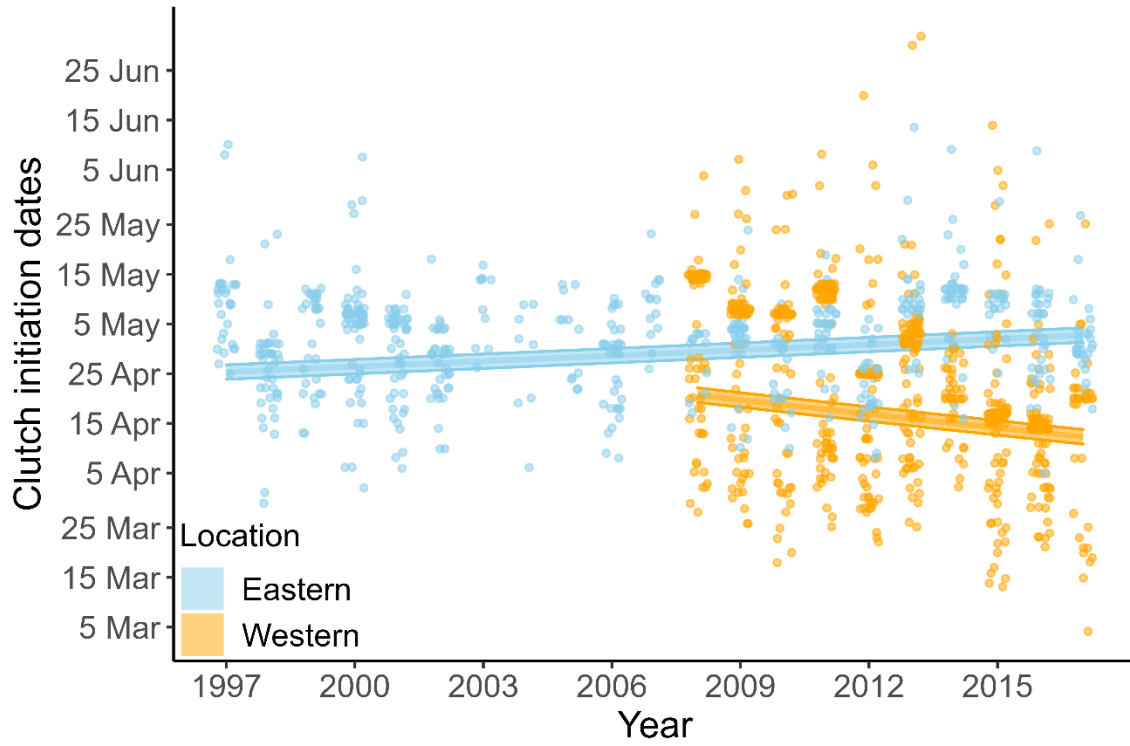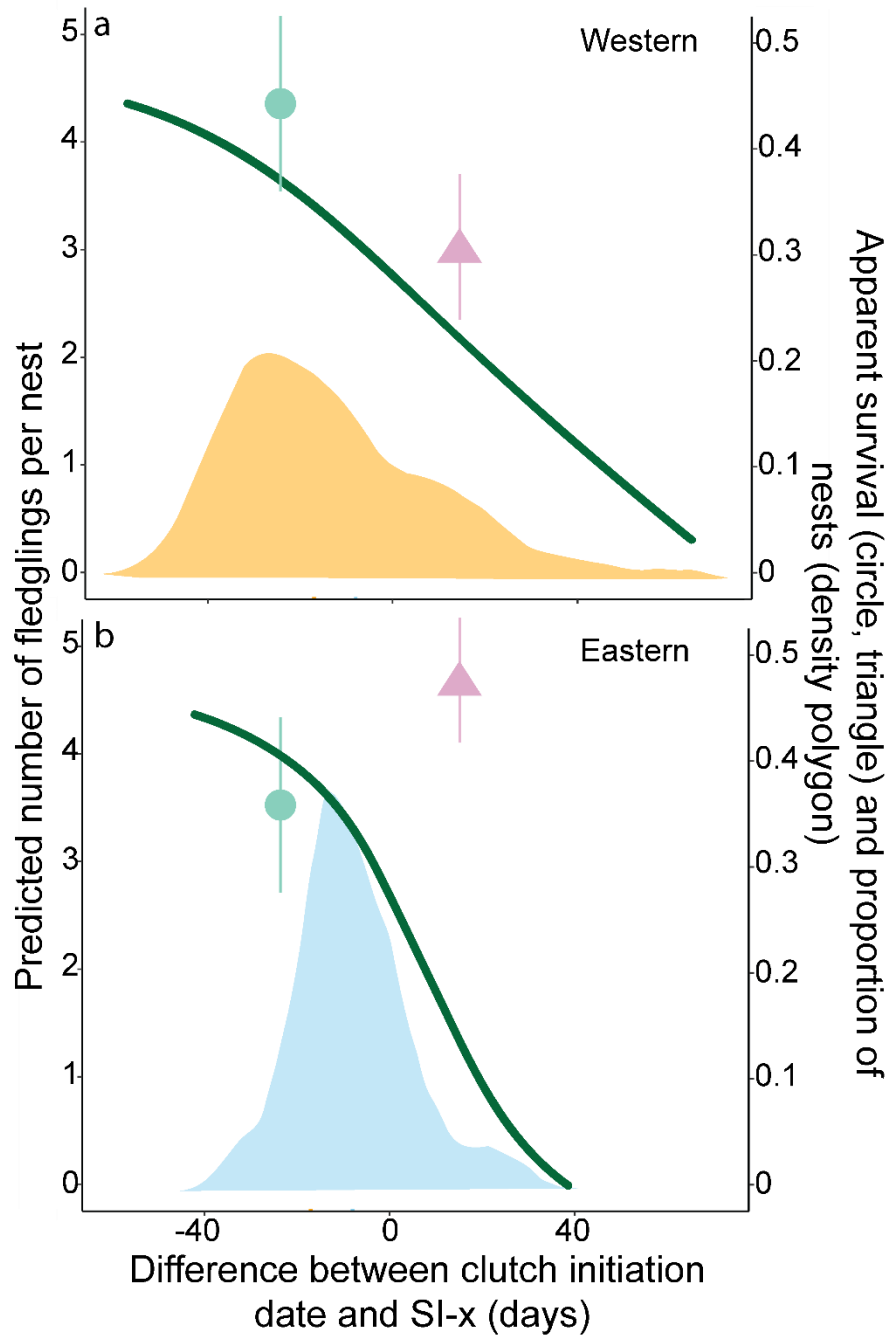
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5.

Supplemental Material for Seasonal Trends in Adult Apparent Survival and Reproductive Trade-Offs Reveal Potential Constraints to Earlier Nesting in a Migratory Bird

American Kestrel Breeding Phenology and the Extended Spring Index

We used data from two community-science projects: the American Kestrel Partnership (https://kestrel.peregrinefund.org/; hereafter, 'AKP') and the Cornell Lab of Ornithology's NestWatch Program (https://www.nestwatch.org/) to examine environmental predictors of nest timing. For both of these data sets, volunteers throughout North America repeatedly monitor nests and collect information on nest contents for each nesting attempt. Nest data were also obtained from a long-term kestrel demographic study in southwestern Idaho (Heath et al., unpublished data) and the Full Cycle Phenology Project (FCPP; https://fullcyclephenology.com/), which monitored kestrel breeding at 13 Department of Defense (DoD) sites from 2017 – 2020. Nest monitoring approaches differed for each data source; clutch initiation dates were provided by NestWatch, but needed to be estimated for the AKP, Idaho, and DoD nest records. Briefly, clutch initiation dates for these sources were estimated by 1) counting backward from the number of eggs discovered in the box when an incomplete clutch was present [day of nest discovery - (number of eggs in box upon nest discovery × 2 days)] (Anderson et al. 2016), 2) by back-calculating if nests were first recorded with nestlings that were aged according to plumage characteristics, or 3) inferred directly using time-lapse imagery from camera-equipped nest boxes. Our final data set included nest records from 2012 – 2019 that spanned the contiguous US, Alaska, and southern Canada (Figure S1).

Breeding Phenology Covariates

We hypothesized that kestrels would time their breeding to coincide with vegetation green-up, which is an indicator of peak prey abundance (Smith et al. 2017). We used the extended spring index (SI-x; Schwartz et al. 2013, Ault et al. 2015) to determine spring green-up for each nest record. This data set provides the start-of-spring date (day-of-year), which is determined primarily by accumulated springtime warmth needed for leaf-out and bloom of lilac (*Syringa chinensis*) and honeysuckle species (*Lonicera tatarica* and *L. korolkowii*; Ault et al. 2015). Leaf-out dates are generally aligned with plant species that are active earliest in the spring, while bloom dates are associated with species that are active later in the spring. Extended spring indices have been shown to be strongly correlated with the timing of phenological events for native species and crops alike (Schwartz et al. 2013, Rosemartin et al. 2015, Gerst et al. 2020). Annual SI-x raster layers for leaf-out and first bloom dates were created using Google Earth Engine (Gorelick et al. 2017, Izquierdo-Verdiguier et al. 2018) and derived for each nest location using the raster package in R (Hijmans 2021).

We expected warmer spring temperatures to be associated with earlier clutch initiation dates, while colder winter temperatures and higher precipitation in spring could result in longer migration distances (Heath et al. 2012) or increase kestrel energetic demands, respectively, leading to later clutch initiation. Therefore, we included winter minimum temperature (November – February average), spring minimum temperature (March – May average), and spring precipitation (March – May total) in the analysis. Weather variables were obtained from the NASA Daymet daily surface weather and climatological summary dataset (Thornton et al. 1997). Daymet has a 1 km spatial resolution and provides daily modeled estimates of several weather variables. Data were extracted for each nest record using the daymetr package in R (Hufkens et al. 2018).

Statistical Analysis

Spatial Modeling

We tested for associations between environmental covariates and kestrel clutch initiation dates by fitting hierarchical generalized linear models in a Bayesian framework using integrated nested Laplace approximation (INLA; Rue et al. 2009). INLA is a fast and reliable alternative to Markov chain Monte Carlo, and allows for an efficient way of approximating Gaussian random fields (GRFs) to incorporate spatial effects in models (Simpson et al. 2016). We fit clutch initiation models using the R package inlabru (Bachl et al. 2019), which provides accessible and user-friendly functions for the widely-used RINLA package (Lindgren and Rue 2015).

In this framework, the spatial random effect represents processes that cannot be explained by covariates, including spatial dependence between observations. The spatial random effect was modeled as a continuous GRF using the stochastic partial differential equation (SPDE) approach (Lindgren et al. 2011). The INLA-SPDE approach overcomes

the computational challenges of modeling spatial data by approximating GRFs with sparser Gaussian Markov random fields (GMRF; Lindgren et al. 2011, Blangiardo and Cameletti 2015, Krainski et al. 2019). The GMRF was modeled across most of the United States and Canada using a spatial mesh created with constrained refined Delaunay triangulation (Figure S2). To build the mesh, a boundary layer of small triangles was created to cover the domain of kestrel nest records, and an outer layer of larger triangles was added to reduce boundary effects. We used the the inla.mesh.assessment function in the inlabru package to determine the appropriate triangle size for the inner portion of the mesh, which can affect the accuracy of model parameters. This tool visualizes the standard deviation, which should be uniform across the mesh (both at mesh nodes and inside triangles) when triangle edge lengths are properly chosen.

We analyzed kestrel breeding phenology using gamma-distributed models because clutch initiation dates (day-of-year) are always positive. We used default non-informative prior distributions from R-INLA for all regression coefficients and hyperparameters. Prior to analysis, we followed the data exploration and variable collinearity guidelines outlined by Zuur et al. (2017). As many of the covariates were highly correlated, we ran a null model (no spatial effect), and a null model and univariate models with a spatial random effect included. Models also contained a random effect for year to account for temporal variation in clutch initiation date. All covariates were centered and scaled by subtracting the mean value and dividing by the standard deviation prior to analysis.

Model Selection

Log pseudo-marginal likelihood (LPML) or the sum of the log conditional predictive ordinate values (CPO; Lindgren et al. 2011) was used to compare models. Calculation of CPO occurs as part of the model fitting process (Held et al. 2010) and is a leave-one-out cross-validation score (Hooten and Hobbs 2015). The top model was selected based on the lowest LPML value, and a covariate was considered significant if the 85% credible interval did not overlap zero. Finally, we used the mean absolute error (MAE) to evaluate the predictive ability of the top model.

Results

We analyzed predictors of breeding phenology from 3212 American kestrel nests (Figure S1). Comparing the spatial random effect models by LPML value, the best model included the effect of the extended spring index first bloom date (Table S1), which had a strong positive relationship with clutch initiation date ($\beta = 0.07$, 95% CI = 0.06 – 0.08; Figure S3). The second-highest-ranking model included the effect of the first leaf date but differed in LPML value by ~3 (Table S1).

The posterior mean of the range parameter, which is representative of the distance at which the spatial autocorrelation declines to a negligible level, was approximately 255 km (Figure S3). Predicted clutch initiation dates from the top model were heterogeneous across the study area (Figure S4). The model predicted the earliest clutch initiation dates in the Central Valley region of California, the interior Pacific Northwest, the Midwest, and mid-Atlantic states. Later clutch initiation dates were predicted for kestrels breeding in southern California, New Mexico, Florida, New England, and the Northern Great Plains. MAE for clutch initiation dates was ~11 days.

Literature Cited

Anderson AM, Novak SJ, Smith JF, Steenhof K, Heath JA (2015) Nesting phenology, mate choice, and genetic divergence within a partially migratory population of American Kestrels. The Auk 133:99–109

Ault TR, Schwartz MD, Zurita-Milla R, Weltzin JF, Betancourt JL (2015) Trends and natural variability of spring onset in the coterminous United States as evaluated by a new gridded dataset of spring indices. Journal of Climate 28:8363–8378

Bachl FE, Lindgren F, Borchers DL, Simpson D, Scott-Hayward L (2019) Spatial inference using integrated nested Laplace Approximation. http://www.inlabru.org

Gerst KL, Crimmins TM, Posthumus EE, Rosemartin AH, Schwartz MD (2020) How well do the spring indices predict phenological activity across plant species? International Journal of Biometeorology 64:889–901

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27

Izquierdo-Verdiguier E, Zurita-Milla R, Ault TR, Schwartz MD (2018) Development and analysis of spring plant phenology products: 36 years of 1-km grids over the conterminous US. Agricultural and forest meteorology 262:34–41

Heath JA, Steenhof K, Foster MA (2012) Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. Journal of Avian Biology 43:376–384

Hijmans RJ (2021) raster: Geographic Data Analysis and Modeling. https://CRAN.R-project.org/package=raster

Hufkens K, Basler D, Milliman T, Melaas EK, Richardson AD (2018) An integrated phenology modelling framework in R. Methods in Ecology and Evolution 9:1276–1285

Krainski ET, Lindgren F, Simpson D, Rue H (2019) The R-INLA tutorial on SPDE models. https://www.math.ntnu.no/inla/r-inla.org/tutorials/spde/spde-tutorial.pdf

Lindgren F, Rue H, Lindstrom J (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society, Series B 73:23–498.

Lindgren F, Rue H (2015) Bayesian Spatial Modelling with R-INLA. Journal of Statistical Software. 63:1–25

Rosemartin AH, Denny EG, Weltzin JF, Marsh RL, Wilson BE, Mehdipoor H, Zurita-Milla R, Schwartz MD (2015) Lilac and honeysuckle phenology data 1956 – 2014. Scientific Data 2:150038

Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society, Series B 71:319–392.

Schwartz MD, Ault TR, Betancourt JL (2013) Spring onset variations and trends in the continental United States: past and regional assessment using temperature-based indices. International Journal of Climatology 33:2917–2922

Smith SH, Steenhof K, McClure CJW, Heath JA (2017) Earlier nesting by generalist predatory bird is associated with human responses to climate change. Journal of Animal Ecology 86:98–107.

Thornton P, Hasenauer H, White M (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. Journal of Hydrology 190:204–251.

Zuur AF, Ieno EN, Saveliev AA (2017) Beginner's guide to spatial, temporal and spatial-temporal ecological data analysis with R-INLA. Highland Statistics Ltd.

Table S1. Candidate models and model selection results using log pseudo-marginal likelihoods (LPMLs) for gamma regression of American kestrel nesting phenology in North America, 2012 – 2019. We used two versions of the extended spring index (SI-x) estimates of first bloom (SI-x-bloom) and leaf out (SI-x-leaf). SI-x-bloom best predicted nesting phenology and was used in analyses of survival.

Model	LPML
SI-x-bloom + site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13019
SI-x-leaf + site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13022
spring_tmin + site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13030
winter_tmin + site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13045
spring_prcp + site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13047
site(map = coordinates, model = spde1) + year(map = year_id, model = "iid", n = n_years)	13048
1 + year(map = year_id, model = "iid", n = n_years)	13880

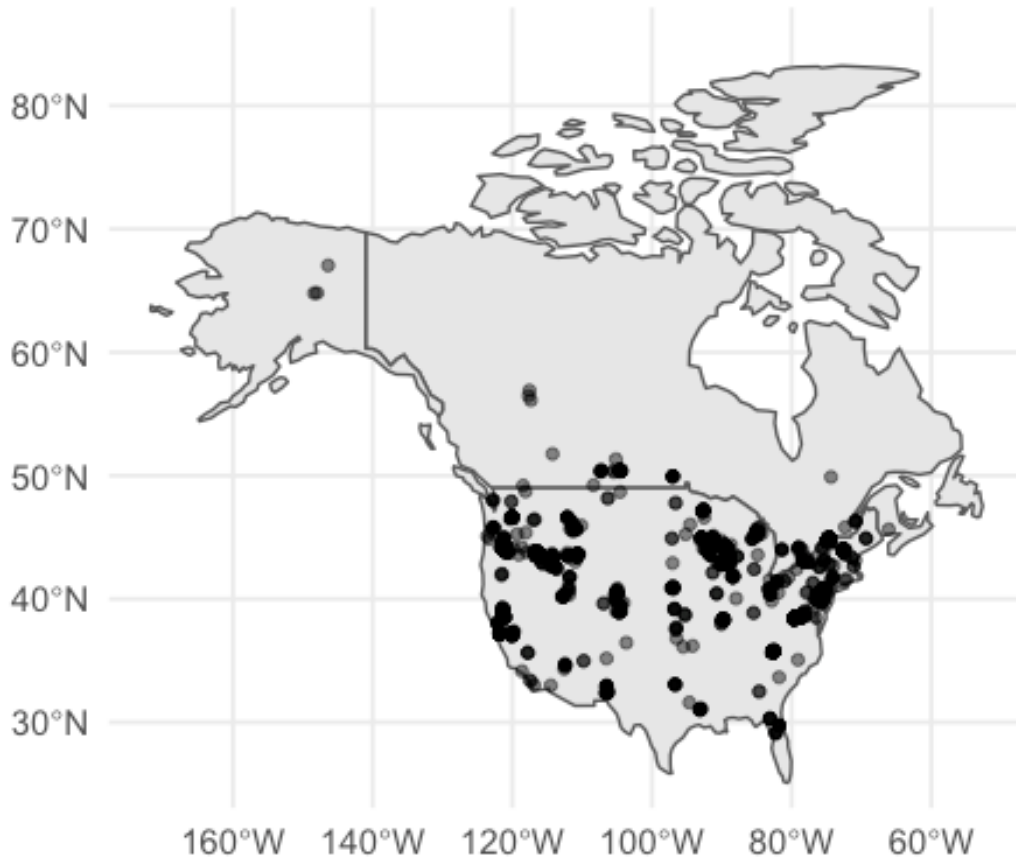Figure S1. Distribution of American kestrel nests (n = 3212) monitored in the continental US, 2012 – 2019 that were used to assess environmental predictors of clutch initiation dates.
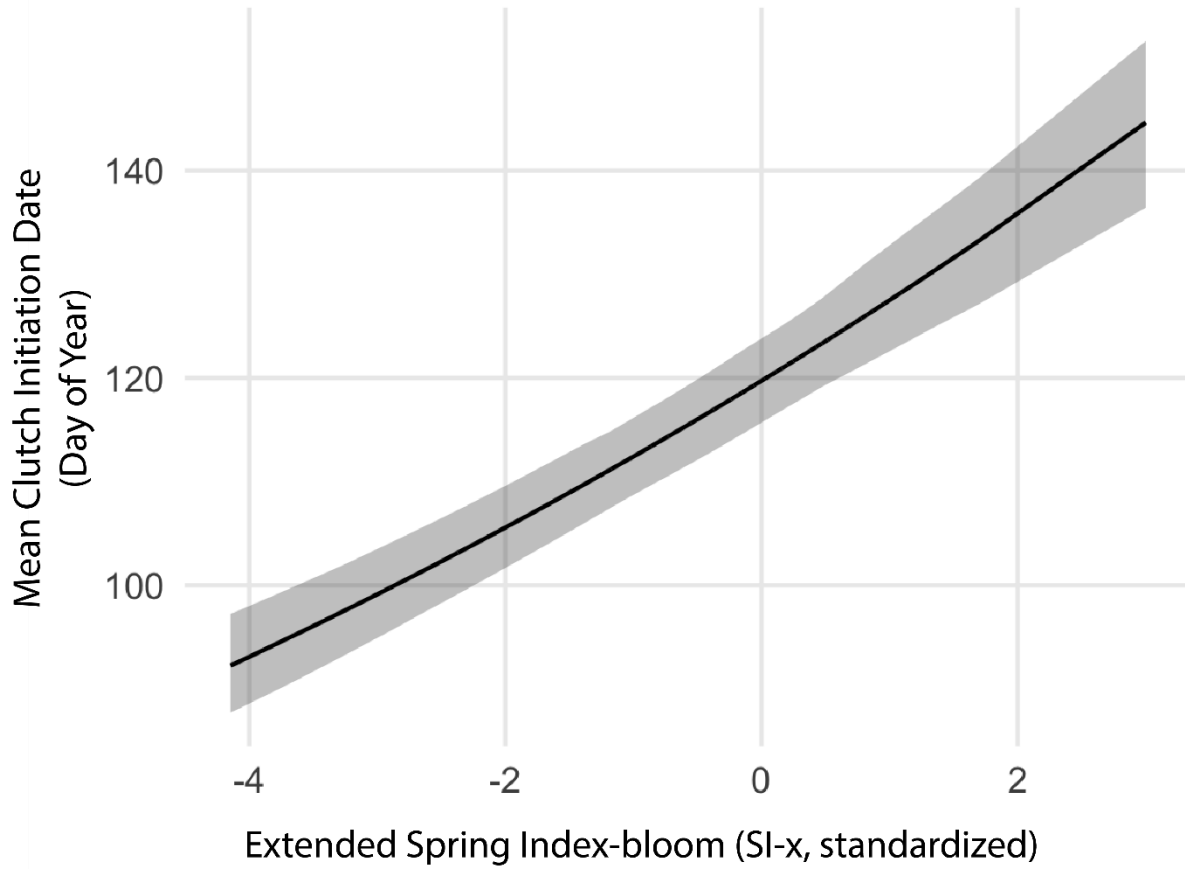
Figure S2. Relationship between clutch initiation date and the extended spring index estimating first bloom date (standardized). Black line and gray ribbon indicate mean predicted values and 95% credible intervals, respectively.
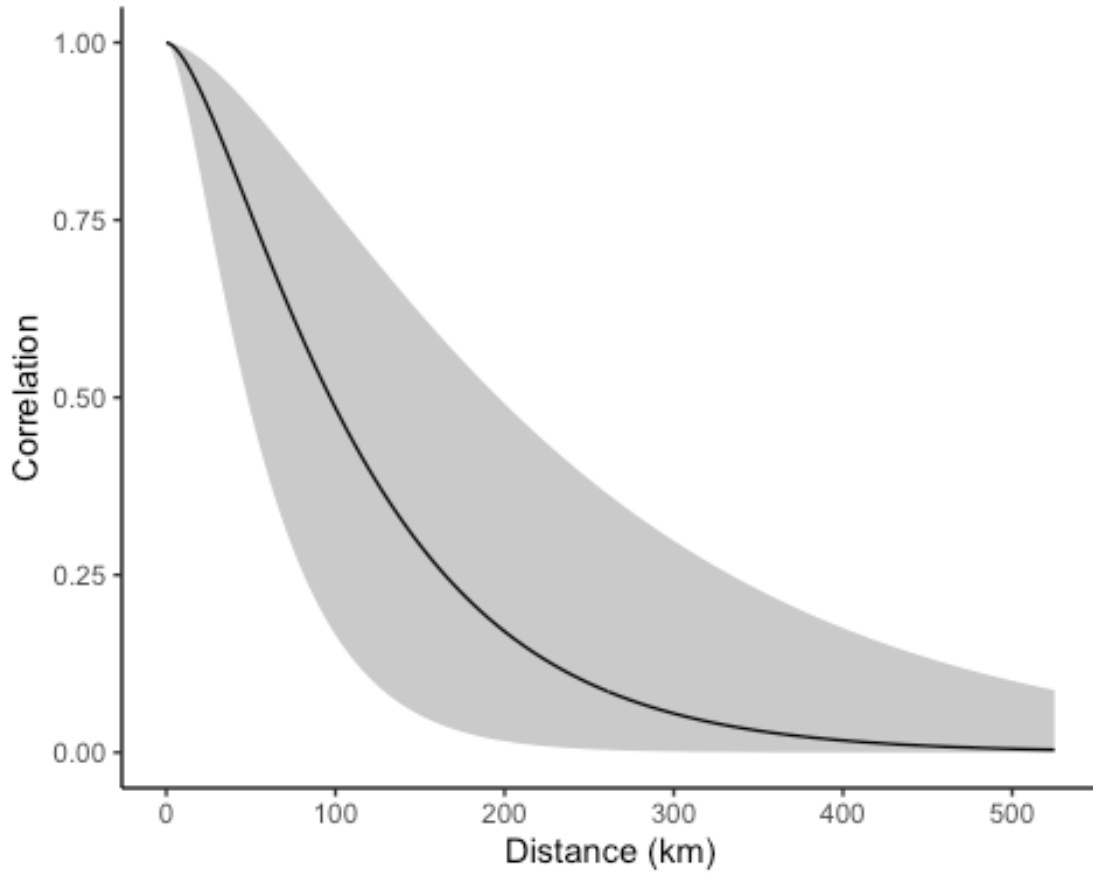
Figure S3. Matern correlation values showing spatial autocorrelation for American kestrel clutch initiation dates for nest records up to ~255 km apart from each other. Black line and gray ribbon indicate mean correlation values and 95% credible intervals, respectively.
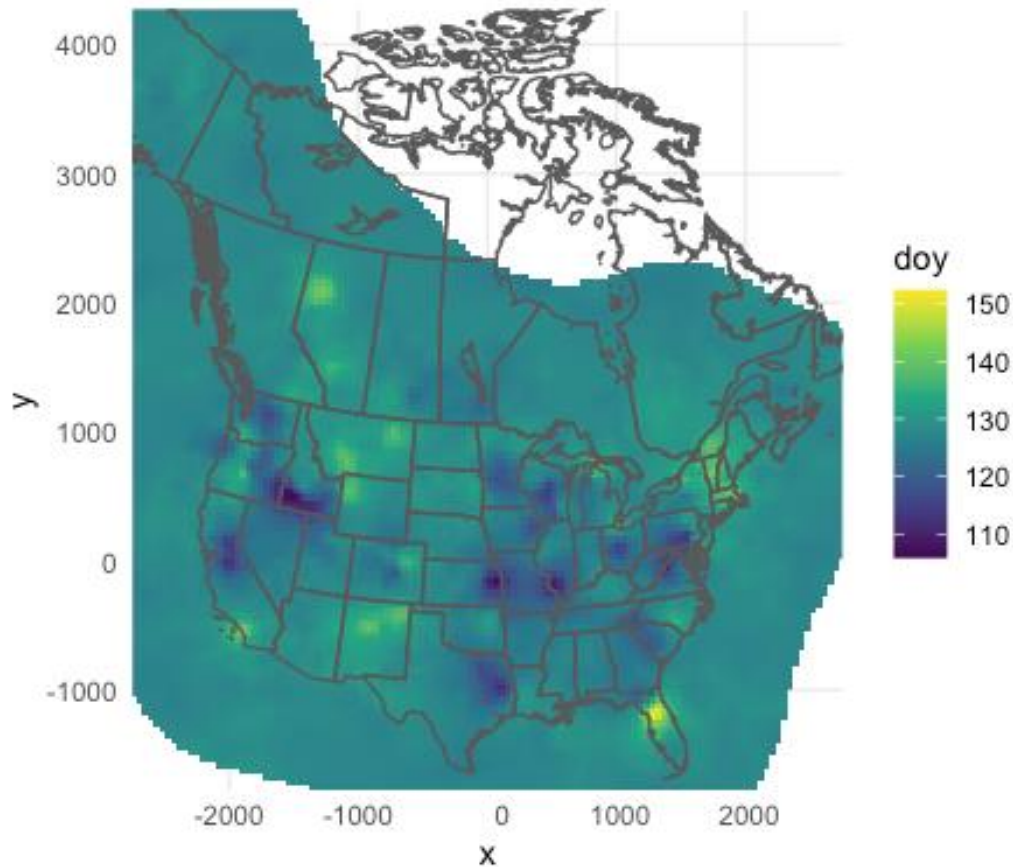
Figure S4. Posterior mean predicted clutch initiation dates shown as day-of-year (doy) from the inlabru model including SI-x as a fixed effect with a random spatial effect. Cooler colors represent earlier predicted clutch initiation dates, and warmer colors represent later predicted clutch initiation dates.

NDVI Methods

We extracted NDVI values from points within 1 km of five nest boxes at each study site using Google Earth Engine. We used the satellite view to select likely foraging areas of kestrels (i.e., we attempt to select fields and avoid streets, water, or other non-habitat). We extracted NDVI estimates from 1 Jan 2021 through 31 Dec 2020 based on data collected from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Version 6 data generated every 16 days at 250 m spatial resolution (Didan 2015). We graphed annual patterns of NDVI over the calendar year and fit data with geom_smooth from the tidyverse package (Wickham et al. 2019) in R.

Didan K (2015) MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD13Q1.006

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. *Journal of Open Source Software* 4:1686
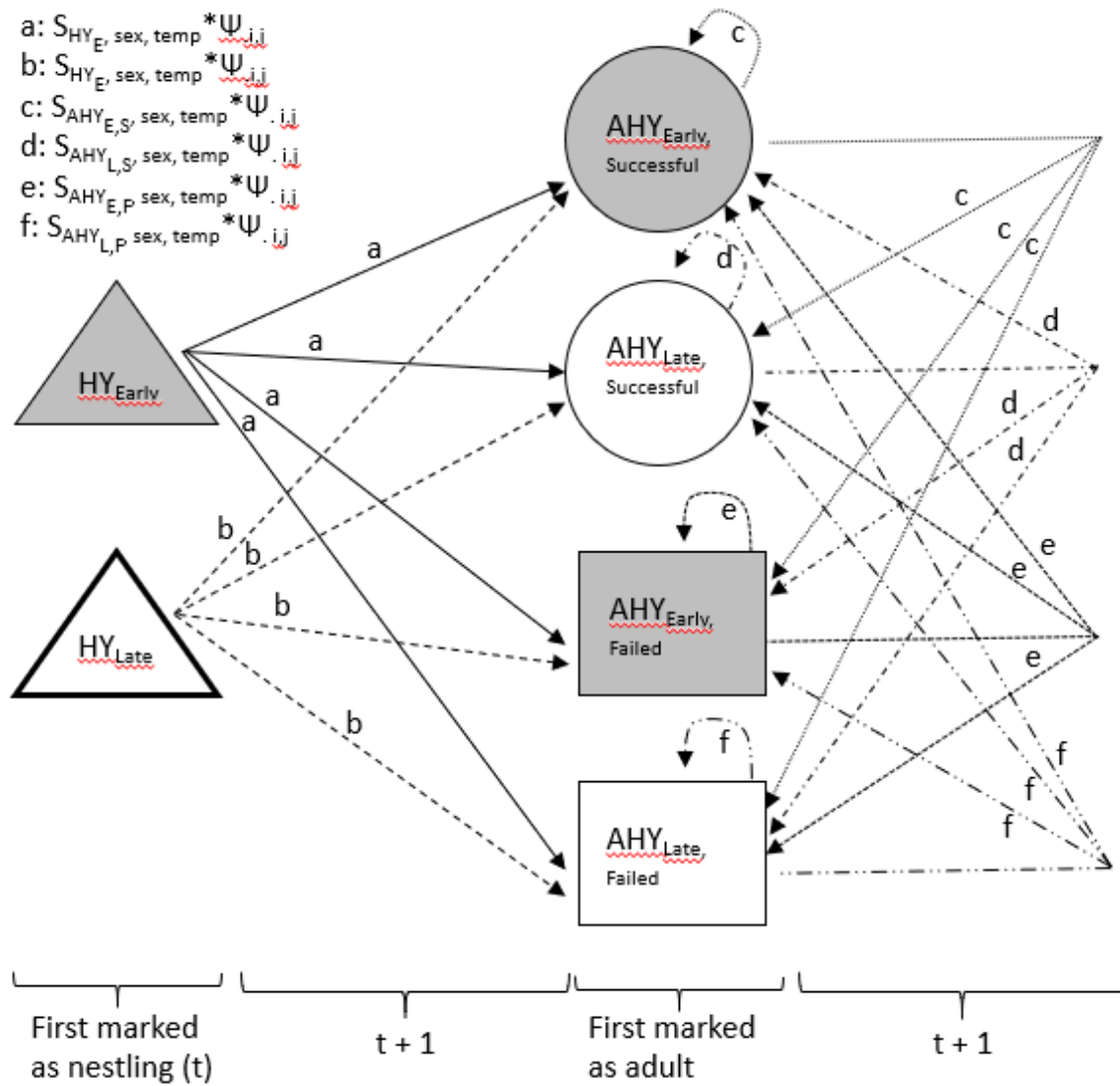
Survival Model Structure

Figure S5. Model structure for the top model of apparent survival of American kestrels at the western (Idaho) site showing the 6 levels of strata stratified by age (HY or AHY), nesting timing (Early or Late), and whether adults were successful (Successful, Failed). The probability of a kestrel surviving and transitioning between the first state (i) and next state (j) is shown in lettered paths. Transition probabilities between HY groups and from AHY groups to HY were fixed to zero and are not shown.

Supplemental Tables Showing Candidate Model Sets for Recapture Probability and Transition Probability

Table S2. Candidate model set to estimate recapture probability (p) of American kestrels in the western (Idaho) site captured between 2008 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The transition probability and apparent survival terms included an intercept-only term for these models.

Recapture (p)	K	ΔAICc	AICcWt
Sex	23	0	0.44
Winter temperature	23	0.8	0.29
Intercept-only	22	0.9	0.27

Table S3. Candidate model set to estimate recapture probability (p) of American kestrels in the eastern (New Jersey) site captured between 1997 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The transition probability and apparent survival terms included an intercept-only term for these models.

Recapture (p)	K	ΔAICc	AICcWt
Sex	23	0	0.99
Intercept-only	22	11.7	0.01
Winter temperature	23	12.9	0

Table S4. Candidate model set to estimate transition probability (Ψ) of American kestrels in the western (Idaho) site captured between 2008 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The recapture probability and apparent survival terms included an intercept-only term for these models.

Transition (Ψ)	K	ΔAICc	AICcWt
Intercept-only	23	0	0.74
Stratum	24	2.07	0.26

Table S5. Candidate model set to estimate transition probability (Ψ) of American kestrels in the eastern (New Jersey) site captured between 1997 – 2017. The table includes the model, number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt). The recapture probability and apparent survival terms included an intercept-only term for these models.

Transition (Ψ)	K	ΔAICc	AICcWt
Intercept-only	23	0	0.68
Stratum	24	1.5	0.32