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# Phenology effects on productivity and hatching-asynchrony of American kestrels (*Falco sparverius*) across a continent

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ABSTRACT

Optimal reproductive performance occurs when birds time reproduction to coincide with peak food availability. Deviation from optimal timing, or mismatch, can affect productivity, though birds may mediate some mismatch effects by altering their incubation behavior. We studied the consequences of nesting timing (i.e., clutch initiation relative to an index of spring start) on productivity across the breeding range of American kestrels (*Falco sparverius*) in the United States and southern Canada, and associations between nesting timing, incubation behavior, and hatching asynchrony. We used observations from long-term nest box monitoring, remote trail cameras, and community-scientist-based programs to obtain data on clutch initiation, productivity, incubation, and hatching synchrony. Kestrels that initiated clutches after the extended spring index (SI-x, start of spring estimate) had higher rates of nest failure and fewer nestlings than earlier nesters, and effects of nesting timing on productivity were strongest in the Northeast. In contrast, kestrels in the Southwest experienced a more gradual decline in productivity across the season. Spatial effects may be the result of regional differences in growing seasons and temporal nesting windows (duration of nesting season). Specifically, resource availability in the Northeast was highly peaked during the breeding season, potentially resulting in shorter nesting windows. Conversely, resource curves were more prolonged in the Southwest, and growing seasons are becoming longer with climate change, potentially resulting in longer nesting windows. We found an inverse relationship between nesting timing and the onset of male incubation. Males from breeding pairs that initiated clutches after SI-x began incubation sooner than males from breeding pairs that initiated clutches before SI-x. Early-onset of male incubation was positively associated with hatching asynchrony, creating increased age variation in developing young. In sum, nesting phenology relative to the SI-x has consequences for American kestrels'

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productivity, and these consequences vary across space. The early onset of incubation may act as a potential adaptive behavior to advance the average hatch date and spread out energetic demands. Given the effects of nesting timing on productivity, kestrels are likely to be sensitive to climate-driven advances in growing seasons and vulnerable to phenological mismatch, particularly in the Northeast.

## 1. Introduction

Optimal reproductive performance occurs when birds time reproduction to coincide with peak food availability (Lack, 1968). Within a population, variation in nesting phenology (i.e., the timing of clutch initiation) relative to prey phenology may result in variation in individual fitness (Visser and Gienapp, 2019). Specifically, deviations from optimal timing, or mismatch, can affect productivity (Both and Visser, 2005; Visser and Gienapp, 2019). In birds, mismatches between nesting phenology and peak food availability may result in lower food provisioning, slower growth, poor body condition, and high nestling mortality (Buse et al., 1999; Sanz et al., 2003; Visser et al., 2006). Hence, individuals that nest in synchrony with resource phenology tend to have higher nest success and productivity than individuals that are mismatched (Both et al., 2004; Visser et al., 2006). Given that climate change is impacting the onset of spring and the duration of the growing season across temperate regions (Schwartz et al., 2006; Christiansen et al., 2011) and phenology has shifted unequally among different taxa and trophic levels, it is important to understand population characteristics associated with vulnerability to phenological mismatch.

Although the evidence for consequences of phenological mismatch on productivity is widespread in birds, the effects are not homogenous across regions, even within a species (Visser et al., 2003; Both et al., 2004). Growing seasons and climatic conditions vary widely across North America, with some regions experiencing narrow, peaked resource availability during the breeding season, and others experiencing a prolonged, dampened resource curve (Eastman et al., 2013). The former (i.e., a short nesting window) may result in very high productivity for individuals that optimally time breeding, but may have extreme consequences for individuals that mistime breeding. Conversely, the latter (i.e., long nesting window) may result in lower productivity peaks, but mistiming effects may be less severe (Garcia-Heras et al., 2016). Indeed, seasonal declines in productivity (Garcia-Heras et al., 2016) and population declines (Both et al., 2010) are both more pronounced for species nesting in regions with strong seasonality and shorter nesting windows than those nesting in regions with weaker seasonality and longer nesting windows. Climate change effects also vary regionally, with the steepest spring warming and increases in frost-free days occurring in northern and western regions (Easterling, 2002; Peterson et al., 2013), extreme temperatures and drought occurring in southern and western regions (Peterson et al., 2013), and increasing extreme precipitation events occurring in eastern regions (Kunkel et al., 2013; Huang et al., 2017). This regional variation in climate change impacts will likely cause variation in the width and flexibility of nesting windows and potentially change the fitness consequences associated with nesting phenology.

When mismatch does occur, the behavioral plasticity of individuals offers one potential mechanism for species to respond and adapt to resource-limited conditions. For example, initiating continuous incubation before clutch completion results in an earlier average hatch date (i.e., less mismatched, Both and Visser, 2005), and staggers egg hatching dates and nestling development in a phenomenon called "hatching asynchrony" (Clark and Wilson, 1981). Producing offspring that reach their peak growth rate at different times lessens the *per diem* energy burden on parents during brood-rearing (Wiebe and Bortolotti, 1994; Mainwaring et al., 2014), which could be adaptive if brood-rearing is occurring under mismatched, resource-limited conditions. Costs of hatching asynchrony to parents are not well-studied, but Slagsvold et al. (1995) found that post-breeding survival of parents was affected by brood synchrony, with females having lower survival after raising asynchronous broods, while males had lower survival after raising synchronous broods. Further, although asynchronous broods have similar, or in some cases higher, fledging success than synchronous broods during periods of food scarcity, asynchrony appears to be costly in food-rich periods (Magrath, 1989; Parejo et al., 2015) because of the higher frequency of brood reduction (death of the smallest nestling) in asynchronous nests compared to synchronous broods (Wiebe and Bortolotti, 1995; Viñuela, 2000).

American kestrels (*Falco sparverius*) are small falcons with a widespread breeding distribution across much of North America. Kestrels are leap-frog migrants with northern populations being more migratory and migrating farther distances than southern populations (Heath et al., 2012). Kestrels are dietary generalists and prey on insects, small mammals, birds, and lizards (Smallwood and Bird, 2020). Clutch initiation of kestrels is positively correlated with the start of spring (estimated from the extended spring index, SI-x, Callery et al., 2022) and Normalized Difference Vegetation Index (NDVI) values, which are a good proxy for small mammals (Smith et al., 2017) and insect (Lafage et al., 2014) abundance. Specifically, the timing of NDVI peaks is positively correlated with the timing of peaks in small mammals, regardless of land cover type (Smith et al., 2017). Furthermore, the median timing of kestrel clutch initiation is 12 days before the SI-x (Fig. S1B), suggesting that incubation and brood-rearing would coincide with increasing and relatively high NDVI values (Fig. 2S) and prey abundance based on known durations of egg-laying (8 – 12 days) and incubation (26 – 32 days) for the species (Smallwood and Bird, 2020). Kestrel clutch initiation dates are advancing with earlier springs in western populations (Smith et al., 2017), but remain unchanged in eastern populations, despite advancing springs (Callery et al., 2022). The causes of geographic variation in phenological shifts, and potential fitness consequences are unknown. Further, geographic variation in population trends, specifically steeper declines in eastern populations (Smallwood et al., 2009; McClure et al., 2017), emphasizes the importance of understanding population characteristics associated with vulnerability to mismatch consequences.

Our objectives were to study the consequences of American kestrel nesting phenology on productivity across a large spatial scale, and determine whether kestrels alter incubation behavior to mitigate mismatch effects. Specifically, we quantified mismatch of clutch initiation relative to SI-x, and kestrel productivity (i.e., number of fledglings produced per nesting attempt) using data from long-term monitoring projects and community science programs across North America spanning nearly 25 years. We quantified the onset of incubation and degree of hatching asynchrony using images from remote trail cameras in nest boxes located on study sites across the United States in 2018 – 2019. We predicted that productivity would decline as phenological mismatch increased, but that this pattern would vary spatially because of regional differences in seasonality. Finally, we predicted that clutch initiation dates after the SI-x would result in earlier onset of incubation behavior and lead to hatching asynchrony.

## 2. Methods

### 2.1. Clutch initiation date, nest outcome, and productivity

We obtained nest records from the Cornell Lab of Ornithology's NestWatch program (1997 – 2018; https://nestwatch.org/) and The Peregrine Fund's American Kestrel Partnership (AKP, 2007 – 2019; https://kestrel.peregrinefund.org/). Additionally, we collected data as part of our long-term Southwestern Idaho Kestrel Study (2008 – 2018), and the Full Cycle Phenology Project (2018 – 2019) where we monitored nest boxes on Department of Defense (DoD) installations in Washington, New Mexico, California, New York, North Carolina, and Kansas (Fig. 1).

Data collection protocols varied depending on the monitoring program, but nest records were typically collected through repeat monitoring by community science volunteers, professional biologists, time-lapse camera imagery, or a combination of these approaches. We restricted our analysis to nests in which (1) eggs or nestlings were observed and clutch initiation date was directly observed or could be reliably back-calculated from the information provided, (2) nest outcome could be assigned from nestling age or participant comments, and (3) the number of young fledged was provided. Additional details on data collection for each of these nest monitoring programs, data processing steps, and determination of breeding parameters are provided in Supplementary Material.

### 2.2. Incubation onset and hatch asynchrony

We quantified incubation onset and hatch asynchrony at a subset of DoD nest boxes equipped with cellular or non-cellular trail cameras (Spypoint, see Supplement Material) that captured complete time-lapse imagery from clutch initiation date through the end of the incubation period. Cameras were initially programmed to capture three images per day, but cellular cameras were switched remotely via the Spypoint website to take hourly images once the clutch was initiated. We defined the relative onset of incubation behavior as the difference in days between clutch initiation and the first day in which each parent began incubation (i.e., laying prone over the eggs and the majority of the eggs are covered). For hatch asynchrony, we calculated the variation in plumage-determined ages (Griggs and Steenhof, 1993) among nestlings approximately 23 – 25 days after the first egg hatched.

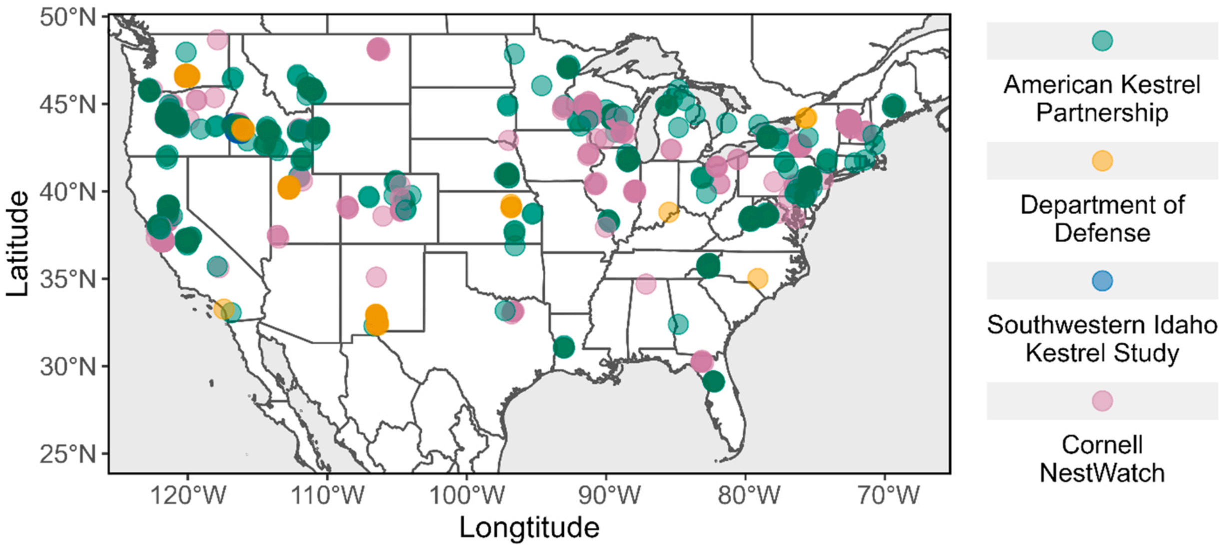


**Fig. 1.** Map of American kestrel nests included in the productivity analysis (n = 2144). Each point represents one nest, darker points represent multiple nests, and the color of the point indicates the source of data: the American Kestrel Partnership (2007 – 2019, n = 758), the Full Cycle Phenology Project on Department of Defense land (2018 – 2019, n = 67), the Southwestern Idaho Kestrel Study (2008 – 2018, n = 416), or Cornell NestWatch (1997 – 2018, n = 903).

### 2.3. Start of spring estimates

We estimated the start of spring using extended spring-index (SI-x) models. These models predict the first-bloom dates of lilac (*Syringa chinensis* and *S. vulgaris*), and honeysuckle cultivars (*Lonicera tatarica* and *L. korolkowii*) using daily maximum and minimum surface temperatures (Schwartz et al., 2006; Rosemartin et al., 2015). Lilac and honeysuckle first-bloom dates have been used to indicate the onset of spring, and the ubiquitous distribution of these ornamental plants allows for the meaningful comparison of spring phenology across space, time, and different biomes (Schwartz and Hanes, 2010). SI-x models have been validated across North America and provide fine-scale (1 km) estimates of the start of spring (Izquierdo-Verdiguier et al., 2018). SI-x measures are highly correlated with land surface metrics (e.g., NDVI; Zurita-Milla et al., 2017, Fig. S2), and in North America SI-x has proven more predictive of bird phenology than NDVI (Kelly et al., 2016). Further, Callery et al. (2022) found that the timing of American kestrel clutch initiation was positively associated with SI-x. 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 created an index of phenology mismatch by calculating the difference in days between the clutch initiation date and the SI-x date.

### 2.4. Statistical analysis

We used a zero-inflated generalized linear mixed-effect model with a Generalized Poisson distribution and log-link to evaluate candidate model sets for predicting productivity in the “glmmTMB” package (Brooks et al., 2017) for R (R Core Team, 2020). This model included two sub-models: (1) a zero-inflation to model the probability of nest failure, and (2) a conditional generalized Poisson to model count data (i.e., number of young fledged from successful nests). Each sub-model included a random effect of categorical year. Covariates included in the conditional and zero-inflation model candidate sets for productivity were phenological mismatch, latitude (lat), and longitude (long). All covariates were scaled and centered. We assessed correlations among covariates and all were $|r| < 0.5$. Candidate models included all possible combinations of the three covariates. We evaluated candidate models for the zero-inflation model with an intercept-only conditional model first. Then, we used the best supported zero-inflated model to evaluate candidate models for the conditional model. We examined dispersion and residuals of the top model using the DHARMa package (Hartig, 2020) to check model assumptions.

We created gamma-distributed generalized linear models with log links to examine the relationship between within-brood variation in nestling age and the onset of incubation behavior for each parent. One male did not incubate until 20 days after clutch initiation, much later than the other males. We ran models with and without this observation to ensure the value did not have an undue influence on results. We used generalized linear models with negative binomial distributions and a log link to determine if male incubation behavior (number of days between clutch initiation date and the first day of incubation) was predicted by phenological mismatch or location (lat and long). For these models, we used data from both successful and unsuccessful nesting attempts with complete photographic records of incubation behavior.

We compared candidate models using Akaike’s information criterion corrected for small sample size (AICc) and considered the models within the lowest AICc to be the most informative (Burnham and Anderson, 2002). We estimated 85% confidence intervals for parameters in the top model to be compatible with model selection criteria (Arnold, 2010). We conducted all analyses in R (R Core Team, 2020).

**Table 1**
Candidate models for predicting the number of American kestrel young fledged per nesting attempt. The zero-inflation models represent the probability of nest failure, whereas the conditional models predict the number of young that fledge from successful nests. Zero-inflated generalized Poisson mixed-effect linear models included the covariates of phenological mismatch (the difference between the clutch initiation date and the SI-x), longitude in °W, and latitude in °N. During the evaluation of zero-inflated models (A) the conditional model was an intercept-only model. All conditional models (B) included the top model for zero-inflation (all two-way interactions among mismatch, latitude, and longitude). Each conditional and zero-inflation model included a random effect of year. Tables show models with weights > 0.01 and an intercept-only model, the number of parameters estimated (K), ΔAICc, and model weights ($w_i$). We evaluated 15 candidate models for each sub-model.

| **A.** Zero-Inflation Models | K | ΔAICc | $w_i$ |
|---|---|---|---|
| Mismatch*Latitude + Latitude*Longitude + Mismatch*Longitude | 11 | 0.0[a] | 0.70 |
| Mismatch*Latitude*Longitude | 12 | 1.9 | 0.27 |
| Mismatch*Longitude + Latitude*Longitude | 10 | 6.4 | 0.03 |
| Intercept-only | 5 | 159.1 | 0 |
| **B.** Conditional Models | K | ΔAICc | $w_i$ |
| Mismatch + Latitude*Longitude | 15 | 0.0[b] | 0.64 |
| Mismatch*Latitude + Latitude*Longitude + Mismatch*Longitude | 17 | 1.9 | 0.25 |
| Mismatch*Latitude*Longitude | 18 | 3.4 | 0.12 |
| Intercept-only | 11 | 64.0 | 0 |

[a] AICc = 7040.9
[b] AICc = 6976.9

## 3. Results

We collected data from 2144 American kestrel nesting attempts that occurred between 1997 and 2019 in the contiguous United States and southern Canada (Fig. 1). Most kestrel nests were successful (n = 1642, 77%) and raised 1 – 7 young (mean = 3.9, standard deviation = 1.1). Clutch initiation dates ranged from 1 March – 14 June (Fig. S1A). The median timing of clutch initiation was 12 days before SI-x (range −67 to 64, Fig. S1B).

The best zero-inflation model for predicting nest failure included all two-way interactions between phenological mismatch, latitude, and longitude (Table 1A). Kestrels were more likely to fail if they nested after the SI-x, and this effect was strongest in the northeast (Table 2A). The best conditional model for American kestrel productivity was the additive effect of phenological mismatch with an interaction between latitude and longitude (Table 1B, Table 2B). These results suggest that productivity was lower for successful pairs that nested after the SI-x, regardless of location. When nesting earlier relative to the SI-x, kestrels in the northeast had more young per brood than kestrels in the west and southwest (Fig. 2). However, northeastern kestrels experienced a sharper decline in productivity with increasing mismatch than kestrels from other regions included in our study (Fig. 2).

There were 27 nests with complete photographic records of incubation to use for our analysis of incubation behavior. The onset of male incubation was 1 – 20 days (mean = 8.0, standard deviation = 4.2) after clutch initiation and females started to incubate 0 – 8 days (mean = 2.0, standard deviation = 2.3) after clutch initiation. Of the 27 nests, we had 16 successful nests where we measured variance in nestling age within broods. Within-brood nestling age variance ranged from 1 to 4 days (mean = 2.1, standard deviation = 1.0) and was best explained by the onset of male incubation behavior ($\beta = -0.33$, 85% CI: −0.47 to −0.19, Table 3, Fig. 3). The early onset of male incubation resulted in more asynchronous hatching, producing a greater variance in nestling ages.

The onset of male incubation was best predicted by the additive effects of phenological mismatch ($\beta = -0.33$, 85% CI: −0.51 to −0.14) and latitude ($\beta = -0.34$, 85% CI: −0.52 to −0.16, Table 4, Fig. 4). Males from breeding pairs that initiated clutches after the SI-x began incubating sooner than males from breeding pairs that initiated clutches before the SI-x. Males breeding in northern regions were more likely to initiate incubation soon after clutch initiation, whereas males breeding in southern regions were more likely to delay the onset of incubation.

## 4. Discussion

We showed that mismatch, specifically clutch initiation after the SI-x, decreased both nest success and productivity of American kestrels across their range. The effect of mismatch was strongest in the Northeast, where kestrels experience highly peaked resource availability compared to other regions (Fig. S2). Geographic variation in the strength of mismatch effects (i.e., stronger effects in the Northeast) may be related to variation in growing seasons and climate change impacts (Both et al., 2010; Garcia-Heras et al., 2016; Taylor et al., 2021). Growing seasons in the Northeast have a higher peak in primary productivity in the spring than in other regions, where green-up is less peaked and more heterogeneous (Fig. S2). This may explain why "on-time" nesters in the Northeast have higher productivity peaks, but have steeper productivity declines because of mistimed breeding (i.e., shorter nesting window), compared to kestrels in regions where less-peaked, but prolonged growing seasons allow more flexibility in breeding time (i.e., longer nesting window). Similarly, black harriers (*Circus maurus*) in regions with short breeding seasons had more pronounced seasonal declines in productivity than those in regions with long breeding seasons (Garcia-Heras et al., 2016).

The nesting window for American kestrels in the Northeast is also constrained by the increasing frequency of extreme precipitation events in winter and early spring (Huang et al., 2017) which can delay migrant arrival time (Powers et al., 2021), cause decreased foraging ability and prey availability, resulting in lower productivity in early-arriving kestrels (Olsen and Olsen, 1992; Dawson and Bortolotti, 2000; McDonald et al., 2004). These climatic conditions are creating an increasingly inflexible and narrow time window (e.g., ~2-month clutch initiation date range in New Jersey; Del Corso, 2016) within which northeastern kestrels can breed without

**Table 2**

Parameter estimates, standard errors, and 85% confidence intervals (LCI = lower confidence interval; UCI = upper confidence interval) from the top zero-inflation model (A), and the top conditional model (B) explain American kestrel productivity 1997 – 2019 across North America. The zero-inflation models represent the probability of nest failure, whereas the conditional models predict the number of young that fledge from successful nests.

| **A.** Parameters | Estimate | 85% LCI | 85% UCI | Std. Error |
|---|---|---|---|---|
| (Intercept) | -1.33 | -1.58 | -1.07 | 0.18 |
| Mismatch | 0.98 | 0.85 | 1.12 | 0.10 |
| Latitude | -0.01 | -0.11 | 0.09 | 0.07 |
| Longitude | -0.29 | -0.38 | -0.19 | 0.07 |
| Mismatch*Latitude | 0.18 | 0.09 | 0.27 | 0.07 |
| Mismatch*Longitude | 0.40 | 0.26 | 0.54 | 0.10 |
| Latitude*Longitude | -0.33 | -0.45 | -0.22 | 0.08 |
| **B.** Parameters | Estimate | 85% LCI | 85% UCI | Std. Error |
| (Intercept) | 1.365 | 1.35 | 1.38 | 0.01 |
| Mismatch | -0.067 | -0.08 | -0.05 | 0.01 |
| Latitude | 0.001 | -0.01 | 0.01 | 0.01 |
| Longitude | 0.004 | -0.01 | 0.01 | 0.01 |
| Latitude*Longitude | 0.034 | 0.02 | 0.04 | 0.01 |

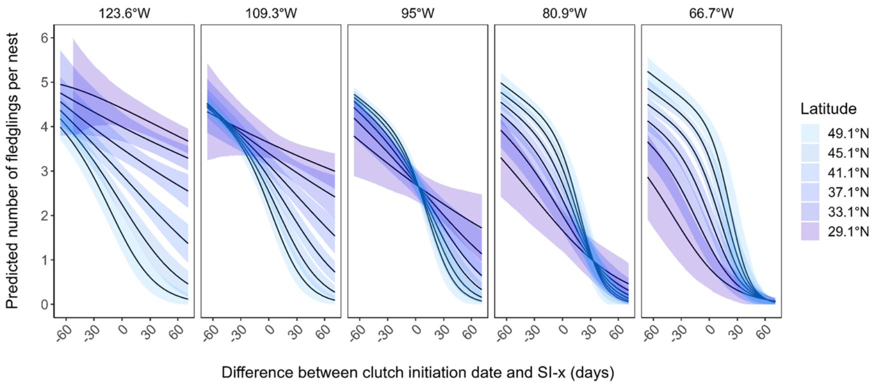


**Fig. 2.** The number of American kestrel fledglings per nesting attempt depended on phenological mismatch (the difference in days between the clutch initiation date and the extended spring index date, SI-x) latitude, and longitude. The lines represent the model predictions, the shaded regions are the 85% confidence intervals, the panels show predictions at different longitudes from west to east, and the colors indicate predictions at different latitudes. The number of young fledged per nesting attempt decreased as pairs laid eggs after the SI-x. The effect of late clutch initiation was strongest in the northeast, where productivity was high and then steeply declined.

**Table 3**
Candidate models to explain age variation within broods of American kestrels. Covariates included the difference between the clutch initiation and incubation onset dates for male and female American kestrels. Models were generalized linear models with a Gamma distribution to represent age variance within broods. Tables show models, the number of parameters estimated (K), ΔAICc, and model weights ($w_i$).

| Candidate model | K | ΔAICc | $w_i$ |
|---|---|---|---|
| Male Incubation | 3 | 0.0[a] | 0.79 |
| Male Incubation + Female Incubation | 4 | 3.2 | 0.16 |
| Intercept-only | 2 | 6.2 | 0.04 |
| Female Incubation | 3 | 8.6 | 0.01 |

[a] AICc = 40.3

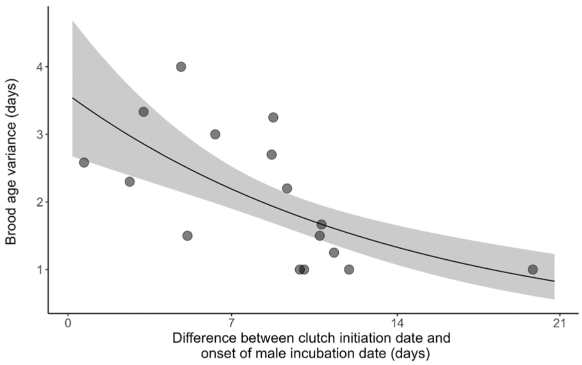


**Fig. 3.** Within brood age variance was best predicted by the difference in days between the clutch initiation date and the onset of male incubation. Each point represents a nest with complete incubation data that had at least two fledglings during the breeding seasons of 2018 (n = 8) and 2019 (n = 8). The line represents the model prediction, and the shaded region is the 85% confidence interval.

experiencing a decrease in productivity. Conversely, in western North America winters are becoming milder, which has been associated with shorter kestrel migration distances (Heath et al., 2012), northward shifts in wintering distributions (Paprocki et al., 2014), and earlier breeding (Heath et al., 2012). The onset of spring is also advancing more rapidly in the Mountain West than anywhere else in our study region (Schwartz et al., 2006; Allstadt et al., 2015), and farmers are advancing the start of their planting season (Christiansen et al., 2011; Smith et al., 2017), resulting in wider prey peaks and long nesting windows in the West (e.g., ~ 4-month clutch initiation date range in southwestern Idaho; Callery et al., 2022). Less is known about kestrel demographics in the Southwest, but southern populations are less migratory (Smallwood and Bird, 2020), and experience mild winters and long nesting windows (e.g., ~ 4-month clutch initiation date range in northwest Texas: Mullican, 2018), which may make them less vulnerable to mismatch.

Seasonal declines in productivity have been well-documented across several bird species (Perrins, 1970; Both et al., 2004;

**Table 4**
Candidate models to explain the difference between clutch initiation date and the onset of male incubation in American kestrels. The covariates included are phenological mismatch (the difference between the clutch initiation date and the SI-x), latitude, and longitude. Models were generalized linear models with a negative binomial distribution to represent the difference between clutch initiation date and the onset of male incubation. The table shows the model, number of parameters estimated (K), ΔAICc, and AICc weights ($w_i$).

| Candidate model | K | ΔAICc | $w_i$ |
|---|---|---|---|
| Mismatch + Latitude | 4 | 0.0[a] | 0.42 |
| Mismatch + Latitude + Longitude | 5 | 0.7 | 0.29 |
| Intercept-only | 2 | 3.2 | 0.09 |

[a] AICc = 150.5.

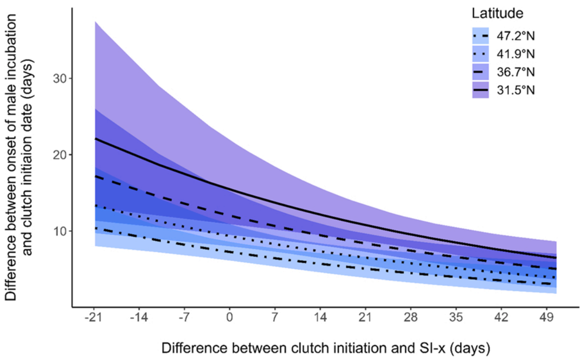


**Fig. 4.** The predicted relationships between phenological mismatch (the difference between clutch initiation date and SI-x) and the onset of male incubation relative to clutch initiation date (days) for different latitudes. As mismatch and latitude increase, the difference between clutch initiation date and the onset of male incubation behavior decreases. The earlier onset of male incubation behavior is a predictor for increased age variance of the nestlings and hatching asynchrony. The line represents the model predictions, the shaded regions are the 85% confidence interval for each prediction, and the line type of each prediction and the color surrounding it represent predictions at different latitudes.

Garcia-Heras et al., 2016). In addition to being well-matched with prey resources, earlier nesting birds may be higher quality or obtain higher quality territories compared to later nesting birds (Møller, 1994; Verhulst and Nilsson, 2008). Our study was correlative and it is likely that additional factors, aside from clutch initiation relative to SI-x, contributed to the productivity patterns observed here. Unfortunately, it can be difficult to disentangle the confounding effects of seasonal declines in resources and individual quality without experimental manipulation of clutch initiation or resource availability. We used the timing of clutch initiation relative to SI-x, an environmental variable that is highly correlated with kestrel clutch initiation (Callery et al., 2022) and patterns of primary productivity and prey availability (Smith et al., 2017), rather than a relative index of timing-based off of the distribution of American kestrel clutch initiation dates alone (Fig. S1) to emphasize timing relative to resources rather than relative to other kestrels. Further, it is unlikely that age or experience contributed to seasonal effects because most kestrels breed in their first year and clutch initiation dates do not differ significantly between younger and older American kestrels (Steenhof and Heath, 2009).

We documented early-onset incubation, and resulting hatch asynchrony, as a potential adaptation to phenological mismatch in American kestrels. Similar to other species, we demonstrated the onset of continuous incubation as a mechanism for producing hatching asynchrony in American kestrels (Clark and Wilson, 1981). The onset of male incubation was associated with phenology mismatch and latitude. Males from breeding pairs that initiated clutches late relative to SI-x began incubating shortly after clutch initiation, which advanced the average hatch date and increased nestling age variance, consistent with the “hurry-up” hypothesis (Clark and Wilson, 1981). This relationship between mismatch and incubation onset suggests that hatching asynchrony may be an adaptation to low food resources resulting from sub-optimal breeding timing. Indeed, asynchronous hatching in American kestrels has been documented more frequently in years of food scarcity, and asynchronous kestrel broods need less provisioning per day than synchronous broods (Wiebe and Bortolotti, 1994).

Our results also showed that males breeding at higher latitudes were more likely to initiate incubation earlier after clutch initiation than those at lower latitudes. Hatching asynchrony at higher latitudes may ensure that some young have enough time to grow and develop hunting skills before departing for migration (Smallwood, 1998; Catry et al., 2016). Tendency to migrate decreases from north to south in American kestrels (Smallwood and Bird, 2020), and higher latitude breeders may be more constrained by migration timing. The fact that males from nests at high latitudes and nests where clutches were initiated after the SI-x were more likely to start incubating earlier suggest that this strategy is a response to lower food availability, a shorter duration of time before fall migration, or both. Unfortunately, we do not know whether early-onset incubation or hatching asynchrony has any effects on the annual survival of adults or fledglings because of challenges in tracking birds across the annual cycle. This would an important area of future research to determine whether this behavior is truly adaptive.

Interestingly, we found that male incubation, but not female incubation, predicted hatching asynchrony in American kestrels. Although females tended to start incubating early after clutch initiation, the contribution of the male may have provided the additional incubation necessary to stimulate embryo development (Nilsson, 1993). Alternatively, our methods may have more accurately measured male incubation behavior because it was unlikely males would lay on the eggs for any other purpose but incubation, whereas a female laying eggs could be confused for a female in incubation posture.

In summary, initiating clutches after the SI-x has negative consequences for the productivity of American kestrels across their range. With climate change causing earlier growing seasons and increasing the amount of mismatch between trophic levels, the demonstrated fitness consequences of mismatch could result in population-level effects for American kestrels. The steepest mismatch effects (i.e., declines in nest success and productivity) were seen in the Northeast, which is particularly concerning in light of declining trends in northeastern populations, and constraints on phenology shifts (i.e., short growing season and early inclement weather). Additionally, climate change is increasing the duration of growing seasons across North America (NOAA, 2021). Increased duration in growing seasons may decrease the negative consequences of later nesting if prey availability remains high. Further, kestrels may produce second broods in some areas as they nest earlier and the duration of the growing season increases (Smith et al., 2017). Early-onset of incubation may be an adaptive behavior to advance the average hatch date and spread out offspring demands when nesting is mismatched from prey resources or time to produce young before migration is brief. However, more work is needed to understand the effects of hatching asynchrony on the survival of adults and young to determine whether incubation flexibility might mitigate some of the fitness consequences of phenology mismatch.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02124.

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