PHENOLOGICAL MISMATCH IS CORRELATED WITH FITNESS OUTCOMES

AND ADAPTIVE BEHAVIOR IN A GENERALIST AVIAN PREDATOR

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by

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DEDICATION

To my family.

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ABSTRACT

Climate-driven advances in the start of spring may result in a phenological mismatch between peak-prey abundance and the breeding season of secondary consumers. Phenological mismatch has been well-studied in insectivorous birds for which reproductive productivity is strongly linked to caterpillar abundance. The effects of mismatch on the productivity of dietary generalists, that forage on several types of prey, are less well-understood. Further, few studies have addressed questions about the effects of mismatch on survival, an important component of fitness that can be affected by breeding in sub-optimal conditions. We examined the relationship between phenological mismatch and fitness for a widespread generalist raptor, the American kestrel (Falco sparverius). In the first chapter, we collected productivity data from nest observations across the contiguous US and southern Canada and quantified phenological mismatch on each nest as the difference in days between the start of spring and clutch initiation. Then, we examined the relationship between mismatch, location, and productivity. Also, we investigated whether incubation behavior leading to hatching-asynchrony was related to phenological mismatch. Kestrels that laid eggs after the start of spring had fewer nestlings and higher rates of nest failure compared to kestrels that laid eggs before the start of spring. The strength of the mismatch effect depended on location. In the northeast, the number of fledglings per brood and rates of nest success were high for pairs nesting before the start of spring, but the effect of phenological mismatch was strongest here, with rapid declines in nest success associated with mismatch. Whereas, in the

southwest, early-laying pairs had lower productivity and success relative to the northeast, but the effects of phenological mismatch were not as strong as the northeast. The effect of location is likely related to climatic constraints on the growing season and the time window for kestrel breeding that are becoming stronger in the northeast and weaker in the southwest. The timing of male incubation behavior was associated with hatching asynchrony, and males breeding after the start of spring were more likely to initiate incubation early as opposed to males breeding before the spring index date, suggesting that hatching asynchrony is a possible mechanism to cope with phenological mismatch.

In the second chapter, we investigated the relationships between phenological mismatch and survival using mark-and-recapture data from two distinct, long-term study sites in Idaho and New Jersey where kestrel exhibit difference migration strategies. We created a multistate mark-recapture models to estimate the annual survival of adult (after-hatch-year) and juvenile (hatch-year or yearling) kestrels. For the multistate framework, we categorized the phenological mismatch of nests at each site "earlier" or "later" relative to the yearly median difference in days between clutch initiation date and the start-of-spring date, which was estimated at each nest box location. In addition, we included covariates for nesting success, sex, and minimum winter temperature anomaly in our survival models. Mismatch was associated with the survival of kestrels that produced young; however, the direction of this effect differed between populations. In Idaho, successful kestrels had higher survival when they bred "earlier" rather than "later." In New Jersey, successful kestrels had higher survival when they bred "later" rather than "earlier." Differences in survival between sites may reflect differences in seasonality, climate change patterns, or consequences of migration strategies. For partially migrant

populations (i.e, Idaho kestrels), mismatch may rapidly drive directional selection for birds to breed earlier by favoring survival and productivity, but for fully migrant populations (i.e., New Jersey) that have a limited window of time to reproduce, mismatch may create trade-offs between reproduction and survival. Mismatch did not affect the survival of adult birds with failed nests, and there was no difference in survival between hatch-year birds produced from "earlier" or "later" nests. In Idaho, males had higher survival rates than females and warmer winter temperatures positively correlated with survival in all age and sex classes. In New Jersey, sex and winter temperature did not explain survival. In sum, we found negative consequences of phenological mismatch on the fitness of American kestrels, generalist predator. For both productivity and survival, the effect of mismatch was more severe for kestrels in the northeast, where the breeding season is shorter and kestrels more migratory when compared to the west. These results demonstrate that duration of breeding season is an important factor to consider when assessing vulnerability to climate change, and that a generalist diet does not ensure resilience to phenological mismatch.

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LIST OF ABBREVIATIONS AND TERMS

AHY   After hatch-year

AKP   American Kestrel Partnership

CI   Confidence Interval

CI-date   Clutch-initiation date

DoD   United States Department of Defense

FCP   Full Cycle Phenology (Project)

HY   Hatch-year

SERDP   Strategic Environmental Research and Development Program

SI-x   Extended spring-index date

US / USA   United States / United States of America

INTRODUCTION

Phenological mismatches have been increasing in frequency and magnitude over the past half-century with the progression of climate change (Parmesan, 2007; Thackeray et al., 2016); and can decrease species fitness by facilitating mistimed breeding relative to seasonal food abundance (Visser & Gienapp, 2019). Most studies concerning the effects of phenological mismatch and mistimed breeding on fitness are conducted on regional spatial scales, on dietary specialist species, and solely focus on the productivity component of fitness. Few studies are conducted that compare effects of mistimed breeding for a species on a continental scale, that consider the effects of mistimed breeding on survival (Thomas et al., 2001), or that focus on dietary generalists (Tucker et al., 2019). The impacts of mistimed breeding on fitness for widespread dietary generalists may not be as severe or striking as they are for narrowly-distributed specialist species, but these impacts are important to consider given that generalists are linked to many other species in their ecosystems, and given the increasing prevalence of climate-driven phenological mismatches in recent years (Hegland et al., 2009).

My research attempts to address the gap in knowledge of how phenological mismatch and mistimed breeding can affect both the productivity and survival of a widespread generalist, and how these effects may vary across a species's range. American kestrels (*Falco sparverius*) consume taxonomically diverse prey (e.g. invertebrates, reptiles, small mammals, songbirds), and exists in variety of habitat types across a large geographic range. In Chapter 1, I present research concerning effects of

phenological mismatch and mistimed breeding on American kestrel productivity in terms of probability of nest failure and the number of young produced from successful nests; and considered how these effects varied across our study area of the contiguous US and southern Canada. We also examined the mechanisms behind and environmental drivers of hatch asynchrony in American kestrels at specific breeding sites across their range, where detailed incubation behavior and within-brood nestling ages were recorded, because hatch asynchrony is a hypothesized adaptation to increase fitness when breeding is mistimed (Clark & Wilson, 1981; Wiebe & Bortolotti, 1994a). In Chapter 2, I present research concerning how the survival of American kestrel adults and their offspring is affected by phenological mismatch and mistimed breeding in two distinct breeding populations. These populations exist in climate types, occupy different migratory flyways, and exhibit different propensities for migration; the differences between our study populations allowed us to consider the effects of weather and migration behavior on annual survival.

My thesis chapters are prepared as manuscripts that will ultimately be submitted to peer-reviewed scientific journals. The co-authors of these manuscripts are identified in the individual 'Acknowledgements' section for each chapter.

PHENOLOGICAL MISMATCH PREDICTS LOWER PRODUCTIVITY AND
INCREASED HATCH-ASYNCHRONY IN AMERICAN KESTRELS (FALCO
SPARVERIUS)

Abstract

Climate-driven advances in spring phenology can result in mismatched timing
between peak-prey abundance and the breeding season for insectivorous birds, resulting
in decreased productivity. The fitness consequences of phenological mismatch for dietary
generalists are unclear. We examined the relationship between phenological mismatch
and productivity of American kestrels (Falco sparverius), a predatory generalist with an
extensive breeding range across North America where there is evidence of population
declines in some parts of their range. In addition, we investigated incubation behavior
leading to hatching-asynchrony as a possible facultative adaptation to suboptimal
breeding conditions associated with phenological mismatch. We used nest observations
collected across the contiguous US and southern Canada, and quantified phenological
mismatch as the difference in days between the start of spring and clutch initiation date.
We used zero-inflated generalized linear mixed-effect models with Generalized Poisson
distributions to examine the effect of phenological mismatch and location on
productivity. Also, we examined how the onset of incubation behavior by each parent
contributes to variance in nestling age, and then modeled the association between
mismatch and location on incubation behavior. We found that pairs who laid eggs after
the start of spring had fewer nestlings and higher rates of nest failure, and that the

strength of this effect depended on location. In the northeast, the number of fledglings per brood and rates of nest success were high for pairs nesting before the start of spring, but the effect of phenological mismatch was strongest here, with rapid declines in nest success associated with mismatch. In contrast, early laying pairs in the southwest had lower productivity and success than similarly early pairs in the northeast, and experienced a more gradual decline in productivity with seasonal mismatch than northeastern birds. We attribute the effect of location to the growing season and time window for breeding being shorter in the northeast than in the southwest, where climate change is lengthening the growing season, and the kestrel breeding season can span several months. These seasonal differences have been further exacerbated by climate change leading to milder winters and advancing springs in the west, along with wetter winters and static last frost dates in the east. The timing of male incubation behavior was associated with hatching asynchrony, and males breeding after the start of spring were more likely to initiate incubation early as opposed to males breeding before the spring index date, suggesting that hatching asynchrony is a possible mechanism to cope with phenological mismatch. In sum, we demonstrate that dietary generalists are vulnerable to phenological mismatch and that seasonality may be a more informative predictor of risk than diet. Vulnerability to mismatch may be one factor contributing to declines in kestrels in the northeast.

Introduction

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). Phenology has shifted unequally among different taxa and trophic levels, even between

species that are ecologically linked (Walther et al., 2002). Consequently, changes in

spring season plant phenology have led to timing mismatches between animal breeding

seasons and food availability (Visser et al., 1998; Buse et al., 1999). Long-term studies of

phenological mismatch and productivity have been conducted on regional populations of

avian insectivores in Europe, which specialize on caterpillar prey during their breeding

season (Cresswell & McCleery, 2003; Visser et al., 2006). Productivity and recruitment

were strongly affected by breeding time relative to the emergence of caterpillars in these

study systems (Visser et al., 2006; Reed et al., 2013). Generalist predators may be less

vulnerable than specialists are to shifts in prey phenology for one (or a few) species

because generalists can switch between various prey as they peak in abundance at

different times or in different habitat types, lessening the severity of any one phenological

mismatch and broadening the overall peak in prey availability (Both et al., 2010; Mallord

et al., 2017). However, the productivity of generalists may decline if phenology mismatch

is severe, which has been found for some long distance migrants that breed at northern

latitudes (Both & Visser, 2001; Clausen & Clausen, 2013), where spring phenology is

advancing more rapidly than at lower latitude migration staging areas (Ahola et al., 2004;

Høye et al., 2007). Here, we investigate the effects of phenological mismatch on a

widespread avian generalist, American kestrels (*Falco sparverius*), across a large spatial

scale. Kestrels are experiencing disparate regional population trends in North America,

with marked population declines in the northeastern United States, and the reasons

behind these different population trends remain largely unknown. Studying which factors

influence regional and temporal kestrel productivity is important to further understanding

their different regional population trends, and would be timely and critical for informing conservation efforts.

Since the mid-20th century, hypotheses about phenological mismatch have been tested on insectivorous, cavity-nesting passerine systems in Europe, producing an incredible wealth of knowledge about the consequences of phenological mismatch on productivity. These studies mainly focus on regional populations of Great tits (*Parus major*) and Blue tits (*Cyanistes caeruleus*), which provision their young with caterpillars during the breeding season (Royama, 1970; Perrins, 1991). In studies of these birds, productivity and recruitment were strongly affected by breeding time relative to caterpillar emergence (Thomas et al., 2001; Visser et al., 2006). It is hypothesized that generalists fare better than specialists when faced with phenological mismatch (Miller-Rushing et al., 2010) and environmental change (Devictor et al., 2008). For example, tree swallows (*Tachycineta bicolor*; Dunn et al., 2011), wood warblers (*Phylloscopus sibilatrix*; Mallord et al., 2016), and ruddy turnstones (*Arenaria interpres*; Tucker et al., 2019), did not show negative fitness effects of phenological mismatch because these species were able to switch between different type of arthropod prey. Presumably, this pattern would hold true for predatory generalists that can switch between many groups, such as insects, reptiles, mammals, and birds; however, this has not been studied. Further, studies of phenological mismatch are often done at the local scale where all individuals may experience similar climate or phenological constraints. Increasing the spatial scale allows for investigation of factors such as environmental seasonality, or local adaptation or behavior that may ameliorate or exacerbate the consequences of mismatch.

Mismatched breeding pairs may adopt different strategies for coping with relative late nesting and reduced prey availability. For example, birds can shift the dates their eggs hatch by altering their incubation behavior. Great tits responded to cold spells by delaying their incubation behavior (Naef-Danzer et al., 2005). Although delayed hatching was correlated with egg failure, delayed fledglings had higher survival compared to those from broods that were not delayed, likely because delayed broods were reared at a time of greater food abundance than those that hatched during the cold spell. Average egg hatching date can be facultatively advanced if continuous incubation starts before the clutch is complete (Clark & Wilson, 1981). Both and Visser (2005) found that great tits advanced the average egg hatching dates of their broods more frequently in years with early caterpillar emergence and this behavior has been hypothesized to be an adaptation for suboptimal breeding time (van Balen, 1973). In addition to advancing the average egg hatching date, incubation prior to clutch completion staggers egg hatching dates and nestling development in a phenomenon called "hatch asynchrony." Having offspring that reach their peak growth rate at different times lessens the per diem energy burden on parents during brood-rearing (Wiebe & Bortolotti, 1994a), which would be adaptive if brood-rearing is occurring under mismatched, resource-limited conditions. Both and Visser (2005) found that a great tit population had broods with more hatch asynchrony in years with earlier caterpillar emergence times where breeding time was relatively later. Amundsen and Slagsvold (1998) found that asynchronous great tit broods had less variable recruitment rates than synchronous broods when environmental conditions were poor or unpredictable, and cited that asynchronous broods tend to have fewer and higher quality offspring, than synchronous broods, which have more and lower quality offspring

(Amundsen, 1991). While the effects of incubation timing and hatch asynchrony have been widely documented in many bird species, there have been few studies of facultative hatch asynchrony in response to phenological mismatch, aside from studies of great tits. American kestrels (*Falco sparverius*) are widespread, small falcons that have broad dietary niches and can prey on insects, small mammals, birds, and lizards (Smallwood & Bird, 2002). In this species, egg-laying is positively correlated with the start of spring, which predicts the availability of prey resources (Smith et al., 2017). Climate-driven shifts in prey phenology could cause phenological mismatch between kestrel brood-rearing and peak prey abundance; however, given their wide range and diverse diets, the consequences of mismatch may vary and depend on location. For example, kestrels breeding in the northeast tend to be migratory and have short breeding seasons compared to kestrels in the intermountain west that are partial migrants and have longer breeding seasons. The regionally different lengths of the breeding seasons could reflect differences in the abundance trends of prey based on biome, differences in the severity of environmental constraints on the optimal time window for breeding, or behavioral constraints like migratory strategy exhibited by a particular population. Hatch asynchrony may be a possible adaptation for kestrels that are mismatched with prey availability. Previous studies have shown that hatch asynchrony is more likely in kestrel broods during years when food is scarce (Wiebe & Bortolotti, 1994b), but no studies have quantified variation in hatch asynchrony for kestrels across their North American range.

Here, we investigate how breeding time relative to the start of spring relates to kestrel productivity and the prevalence of hatch asynchrony in American kestrel broods, and how these relationships may vary across the contiguous United States. To compare

phenological mismatch across years and locations, we defined relative breeding time as the difference in days between clutch-initiation date and the start of spring (Schwartz et al., 2006). We used data from four monitoring programs from across the country spanning nearly 30 years. We predicted that productivity would decline as phenological mismatch increased and that the rate of productivity decline would vary spatially, because breeding season lengths and seasonal resource abundance differ regionally. Also, we hypothesized that if variation in nestling age may be a way to offset the energetic costs of mismatched breeding time, then there would be an association between phenological mismatch and onset of incubation behavior that leads to hatch asynchrony.

Methods

We obtained American kestrel egg-laying dates, productivity (number of young produced per pair), and nest location data from two community-based science projects, the Peregrine Fund's American Kestrel Partnership (AKP) and Cornell NestWatch. Data from the AKP were collected from 2007-2019. AKP volunteers checked nest boxes for eggs every two weeks starting in early March. Upon finding eggs in a box, volunteers revisited the box again 30 days later to check for hatch and nestling age. For each observation, volunteers were asked to record the date, time, number of kestrel adults, number of kestrel eggs, number of kestrel nestlings, age of kestrel nestlings, and report their results online. Cornell NestWatch data were contributed for nests between 1997-2018. NestWatch volunteers observed nests from a distance once every 3-7 days; recorded the presence of adults, eggs, and nestlings for each observation; and reported nest contents after it was certain that birds had vacated the nest (e.g. unhatched eggs, dead offspring, etc.) (https://nestwatch.org).

In addition to the community science data, we monitored American kestrel nest boxes in Ada County, Idaho from 2008-2018 and nest boxes installed on Department of Defense (DoD) installations in Washington, New Mexico, California, New York, North Carolina, and Kansas from 2017-2019 (Figure 1.1 and 1.2). We monitored nest boxes with in-person visits or via trail cameras installed in the lid of the nest box. Nest box visits occurred between March-July every 1-3 weeks. We defined occupancy by the presence of one or more kestrel eggs (Smallwood & Collopy, 2009; Heath et al., 2012). We trapped adult kestrels in the nest box while they were incubating a complete clutch of eggs, and then banded and measured the adults. A nesting attempt was considered successful if the pair raised at least one offspring to 25 days old (80% of fledging age). We recorded the clutch initiation date for each nesting attempt by different methods, depending on the state of the nest when it was discovered. When we discovered an incomplete clutch of eggs in a nest box, the clutch initiation date (lay-date of the first egg in the clutch) was calculated by subtracting the number of eggs in the clutch multiplied by two from the date that the clutch was discovered (Anderson et al., 2017), because kestrels tend to lay 1 egg every other day (Bird & Palmer, 1988). For clutches that were discovered complete and hatched, we used the ages of the chicks, determined by plumage characteristics (Griggs & 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 from the hatching date. If complete clutches never hatched, we estimated the clutch initiation date by backdating from the date of clutch discovery times the number of eggs. At nests monitored by cameras, we installed SPYPOINT trail cameras that were programmed to take 3 pictures per day. prior to nest box occupancy. In

areas with adequate cell service, we installed SPYPOINT cellular trail cameras and these cameras transmitted images to the SPYPOINT website once a day, which allowed us to monitor boxes remotely. Once these nest boxes were occupied, trail cameras were programmed to take one picture per hour to capture fine-scale data about the egg-laying period and sex-specific incubation behavior. Nest box photos taken around the clutch initiation date (CI-date), with an unobstructed view of nest box floor, were used to estimate CI-date. For successful nests with incomplete photo records, CI-date estimates were improved by subtracting the plumage age in days of the most mature nestling (using the aging guide by Griggs & Steenhof, 1993), 30 incubation days, and twice the clutch size in days from the banding date. For nesting attempts with complete photo records of the early incubation period, we defined the relative onset of incubation behavior for each bird in the breeding pair as the difference in days between the lay-date of the first egg in the clutch and the date of the first day-time picture where that bird appears to be incubating the eggs (applying its brood patch to the eggs, and the majority of the eggs are covered). For successful nests with full photographic records of adult incubation behavior (n = 16), we calculated the variation in plumage ages among fledglings.

To estimate the start of spring, we used extended spring-index (SI-x) models 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). Lilac and honeysuckle first-bloom dates have been used to indicate the onset of spring, and the ubiquitous nature of these ornamental plants allows for the meaningful comparison of spring phenology across space, time, and different biomes (Schwartz & Hanes, 2010). We estimated these indicator dates at the latitude and longitude of each

occupied nest box per year with SI-x models using Daymet climate datasets (Izquierdo-Verdiguier et al., 2018; Thornton et al., 2018). We created an index of phenological mismatch by calculating the difference in days between the CI-date and the SI-x date (Figure 1.3).

Statistical analysis

We used a zero-inflated generalized linear mixed-effect models 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). Each model in this candidate set included the random effect of the categorical year. Covariates included in the conditional and zero-inflation model candidate sets for productivity were phenological mismatch, latitude, and longitude. All covariates were scaled and centered. We evaluated candidate models for the zero-inflation model with an intercept-only conditional model. Then, we used the best supported zero-inflated model to evaluate candidate models for the conditional model.

We created gamma-distributed generalized linear models with log links to examine the relationship within-brood variation   in nestling age and the timing of the onset of incubation behavior for each sex parent. Then, we used generalized linear models with negative binomial distributions and a log link to if see if parental incubation behavior was predicted by phenological mismatch or location. For these models we used data from both successful and unsuccessful nest attempts with complete photographic records of incubation behavior (n = 27).

We compared candidate models using Akaike's information criterion corrected for small sample size (AICc), and considered the models within 2ΔAICc to be

informative (Burnham & Anderson, 2002). We estimated 85% confidence intervals for parameters in the top model to be compatible with model selection criteria (Arnold, 2010). We did all analyses in R (R Core Team, 2020).

Results

Our data set for productivity consisted of 2144 American kestrel nest attempts that occurred between 1997-2019 in the contiguous US and southern Canada (Figure 1.2). Clutch initiation dates ranged from March 1st - June 14th. Most kestrel nests were successful (n = 1642) and raised 1 - 7 young. Some kestrel nests failed (n = 502). Kestrels tended to nest before the start of the growing season (-8 ± 0.5 days).

The best zero-inflation model included an interaction between phenological mismatch, latitude, and longitude (Table 1.1.A). Kestrels were more likely to fail if they nested after the start of spring and this effect was strongest in the northeast. The best conditional model for American kestrel productivity was the additive effect of phenological mismatch with an interaction between latitude and longitude (Table 1.1.B). These results suggest that productivity was lower for successful pairs that nested after the start of spring, regardless of location. When kestrel nested earlier relative to the SI-x date, kestrels in the northeast had more young per brood and less brood failure than kestrels in the west and southwest (Figure 1.4). However, northeastern kestrels experienced a sharper decline in productivity than kestrels from other regions included in our study. The effects of phenology mismatch in the southwest were more gradual (Figure 1.4).

Male kestrels initiated incubation 1 - 20 days after clutch initiation and females initiated incubation 0 - 8 days after clutch initiation. Within-brood nestling ages ranged from 0 – 3 days old. Within-brood nestling age variance (a probable consequence of

hatch-asynchrony), was best explained by the onset of male incubation behavior, (β = -0.33 $\pm$ 0.01) (Table 1.2). If the male kestrels started to incubate shortly after clutch initiation, then eggs hatch asynchronously, which produced greater variance in nestling ages (Figure 1.5)

The onset of male incubation behavior was best predicted by the additive effects of phenological mismatch and latitude (Table 1.3). At nests where clutch initiation was before the start of spring, males tended to delay incubation, likely producing similarly aged nestlings (Figure 1.6). As clutch initiation dates became relatively later, males tended to incubate shortly after clutch initiation, likely creating hatch asynchrony and variation in nestling ages. Southern kestrels were the most likely to delay start of incubation and northern kestrels were most likely to initiate incubation after the first egg was laid (Figure 1.6).

Discussion

We show negative consequences of phenological mismatch exists for American kestrels, a dietary generalist species; but the severity of these consequences depended on location. The negative effects of phenological mismatch were strongest in the northeast, where kestrels have shorter breeding seasons compared to kestrels in the west, where clutch initiation can span months. Results show support for the hypothesis that kestrels mediated the effects of phenological mismatch by altering incubation behavior, which results in hatch asynchrony and variation in nestling ages. We also found that males at higher latitudes started incubation earlier than males at lower latitudes throughout the season, suggesting that hatch asynchrony may be more prevalent in northern nests. Collectively, this study provides evidence that kestrels experience productivity declines

from phenological mismatch differentially across their range, and that the ability for kestrels to adapt to phenological mismatch may vary regionally as well.

To our knowledge, this is the first paper to demonstrate negative effects of phenological mismatch on a predatory generalist. The effect of mismatch depended on location. Specifically, effects were strongest in the northeast. These results suggest that kestrels may have been unable to compensate for advancing resources by switching prey, altering incubation behavior, or breeding earlier. The breeding season for American kestrels in the northeast is constrained by the increasing incidence of winter and early spring extreme precipitation events (Overland et al., 2011; Huang et al., 2017). These weather events can delay arrival time on their breeding grounds (Powers et al., in prep). Northeastern kestrels arriving to their breeding grounds too early may experience severe precipitation, which has been linked to decreased foraging ability, prey availability, and lower productivity in raptor species (Olsen & Olsen, 1992; Dawson et al., 2000; McDonald et al., 2004). Severe precipitation events can actually delay the growing season for farmers in the east by water-logging the soil, causing a mismatch between the correct temperature conditions for plant growth with the soil conditions (Wolfe et al., 2018), and potentially impacting the prey peak for eastern kestrels. The growing season in the northeast and midwest is also constrained by the lack of advance in the last-frost date (Easterling, 2002; Kunkel et al., 2004), and the increased probability of "false springs," where early warm temperatures followed by frost cause the growth and destruction of primary productivity (Marino et al., 2011; Allstadt et al., 2015). These climatic conditions are creating an increasingly inflexible and narrow time window within which northeastern kestrels can breed without experiencing a decrease in

productivity. On the other hand, western kestrels may be better adapted to breeding at different times throughout the season, ultimately increasing their fitness. Winters are becoming milder in the west, which has been associated with shorter migration, and could be facilitating the overwintering observed in mountain west kestrels (Cohen et al. 2018). The onset of spring is advancing more rapidly in the mountain west than anywhere else in our study region (Schwartz et al., 2006; Allstadt et al., 2015). Farmers in the west are advancing the start of their planting season earlier in the year to coincide with the warm temperatures, consistent advancing in the last frost date, and mild precipitation of late winter and early spring (Christiansen et al., 2011; Smith et al., 2017). Deciduous forest habitats - like those that dominate the northeast - may have higher but narrower food peaks in the spring than in other habitats – like the coniferous forests or dry shrub-lands of the west (van Balen et al., 1973; Both et al., 2010). This may explain why on-time nesters in the northeast have higher productivity than western kestrels; however, the long spring growing season and mild weather conditions for breeding may allow for western breeders to have more flexibility in their breeding time. Longer breeding seasons and wider prey peaks in the west may contribute to their resistance to phenological mismatch.

Hatch asynchrony could confer some resistance to phenological mismatch for birds in the northeast by advancing the average hatch date to lessen the mismatch, and by increasing the age spread of nestlings in the brood, which is a hypothesized adaptation to suboptimal brood-rearing conditions (Wiebe, 1995). We found evidence that the mechanism for age spread in kestrel broods is incubation behavior, which is similar to other species (Clark & Wilson, 1981), and that the timing of male incubation behavior

may be the factor controlling when incubation becomes continuous in this species. Species where both parents incubate tend to start incubating earlier in the laying sequence than species where only one parent incubates (Nilsson, 1993), so the presence of early-onset incubation was expected for this species, as well as the variation in incubation behavior observed (Bortolotti & Wiebe, 1993; Wiebe, 1995). Onset of female incubation did not explain the variance in nestling ages. Our methods may have more accurately measured male incubation behavior because it was unlikely he would lay on the eggs for any other purpose but incubation. However, females laying eggs could have been confused for a female in incubation posture. The timing of male incubation behavior may be related to the onset of continuous incubation behavior, but we may have needed a data set with time intervals smaller than an hour between pictures to study this. Unfortunately, we were unable to measure the hatching span or, in some cases, exact hatch date from the hourly pictures so we derived it from age spans of nestlings. The onset of sex-specific incubation behavior, as well as direct estimation of the hatching span and the average hatch date of the brood, would be better estimated with continuous video camera footage in future research. Nevertheless, even with a small sample size, we found an association between male incubation behavior and age variance.

Onset of male incubation was associated with the additive effects of phenological mismatch of clutch initiation date with the start of spring, latitude, and migratory flyway, though the estimate of this last effect was statistically unclear. There was a negative association between phenological mismatch and male onset. Specifically, males from breeding pairs that laid eggs late, relative to the SI-x date, started incubating shortly after the first eggs were laid, which is consistent with the "hurry-up" hypothesis (Clark &

Wilson, 1981), in advancing the average hatch date of later broods, and increasing the developmental range of nestlings through hatch asynchrony. Males breeding at higher latitudes were more likely to initiate incubation earlier; the strong negative effects of phenological mismatch at higher latitudes may increase the adaptive potential of this behavior and advancing average hatch date. Asynchronous hatching has also been seen more frequently in American kestrel breeding populations in years of food scarcity, and less so in birds that were provided supplemental food (Wiebe & Bortolotti, 1994b). It has been experimentally demonstrated that asynchronous broods need less provisioning per day than synchronous broods for this species (Wiebe & Bortolotti, 1994a). Hatch asynchrony in American kestrels has been hypothesized as an adaptation to unpredictable or low food resources (Wiebe, 1995); these results provide evidence that hatch asynchrony may be adaptive during times of phenological mismatch, which is associated with environmental unpredictability and declining resources.

For western kestrels, breeding at a particular time in the spring season is not as limiting of a factor for productivity as it is for northeastern kestrels, where the probability of nest failure increases rapidly if clutches are initiated after the start of spring. This result is striking, and it is especially interesting that kestrels in the northeast have a limited window for maximizing productivity, because kestrel populations are declining in the northeast. Future work should investigate the proximate, causal mechanisms driving the sharp decrease in kestrel productivity as the season progresses in the northeast.

Acknowledgements

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Tables and Figures

Table 1.1. **Top models for the number of young fledged per brood ("young_fledged"). Models in the candidate set were zero-inflated generalized Poisson mixed-effect linear regressions, and included combinations of the covariates of phenological mismatch (the timing of clutch-initiation relative to the spring index date; "mismatch"), longitude in °W ("long"), and latitude in °N ("lat"). Models in (A) used the null conditional model in order to compare and find the best for zero-inflation. Each model in (B) included the best model for zero-inflation. Each conditional and zero-inflation model also included the random effect of year.**

A.

Zero-Inflation Model Formulas (young_fledged ~ 1)	df	AICc	ΔAICc
zero-inflation ~ mismatch * lat * long	12	7042.7	0.0
zero-inflation ~ mismatch + lat * long	9	7056.6	13.8
zero-inflation ~ mismatch * lat	9	7072.8	30.0
zero-inflation ~ mismatch + lat	8	7073.2	30.4

B.

Conditional Model Formulas (zero-inflation ~ async * lat * long)	df	AICc	ΔAICc
young_fledged ~ mismatch + lat * long	16	6538.6	0.0
young_fledged ~ mismatch * lat * long	19	6540.5	3.4
young_fledged ~ mismatch * lat	15	6540.6	14.5
young_fledged ~ mismatch	13	6542.6	15.2

Table 1.2.   Parameter estimates, intercepts, standard error, and 85% confidence intervals (LCI = lower confidence interval; UCI = upper confidence interval) from the best zero-inflation model (A), and the best conditional model (B) of kestrel productivity. The zero-inflation models represent the probability of total nest failure, whereas the conditional models predict the number of young that fledge from successful nests.

A. Top zero inflation model formula: zero-inflation ~ async * lat * long

Parameters	Estimate	85% LCI	85% UCI	Std. Error
(Intercept)	-1.32	-1.58	-1.07	0.18
async	0.97	0.83	1.12	0.10
lat	-0.01	-0.12	0.09	0.07
long	-0.29	-0.40	-0.19	0.07
async * lat	0.18	0.09	0.27	0.07
async * long	0.38	0.22	0.53	0.11
lat * long	-0.32	-0.45	-0.19	0.09
async * lat * long	-0.03	-0.13	0.08	0.07

B. Top conditional model formula: young_fledged ~ async + lat * long

Parameters	Estimate	85% LCI	85% UCI	Std. Error
(Intercept)	1.36	1.35	1.39	0.01
async	-0.07	-0.08	-0.05	0.01
lat	0.00	-0.01	0.01	0.01
long	0.00	-0.01	0.01	0.01
lat * long	0.03	0.02	0.04	0.01

Table 1.3. **Candidate set of gamma linear regression models for fledgling age variance per brood ("age_var"). The covariates included are the standardized difference in days between the first observation of male incubation and the clutch-initiation date ("male_incub"), and the standardized difference in days between the first observation of female incubation and the clutch-initiation date ("female_incub").**

Model Formulas	df	AICc	ΔAICc
age_var ~ male_incub	3	40.3	0.0
age_var ~ male_incub + female_incub	4	43.5	3.2
age_var ~ 1	2	46.5	6.2
age_var ~ female_incub	3	48.9	8.6

Table 1.4. **Candidate set of gamma linear regression models for difference in days between the first observation of male incubation and the clutch-initiation date ("male_incub"). The covariates included are phenological mismatch ("mismatch") defined as the standardized difference in days between the clutch-initiation date (CI-date) and extended spring index date (SI-x date); standardized latitude ("latitude"); and longitude ("longitude").**

Model Formulas	df	AICc	ΔAICc
male_incub ~ mismatch + latitude	4	150.5	0.0
male_incub ~ mismatch + latitude + longitude	5	151.3	0.7
male_incub ~ 1	2	153.7	3.2
male_incub ~ latitude	3	154.2	3.7
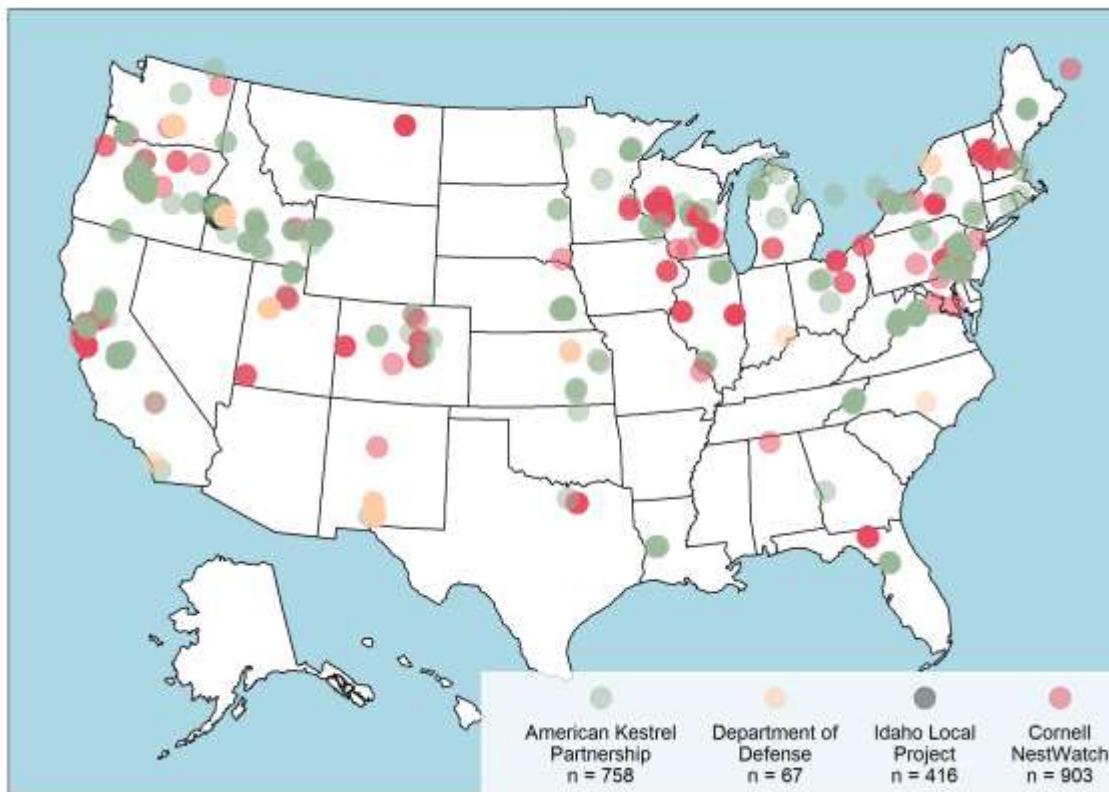
Figure 1.1.   Map of American kestrel nests included in the productivity analysis (n=2179). Each point represents one nest, and the color of the point indicates the group by which the nest was monitored: the American Kestrel Partnership (2007-2019), the SERDP Full Cycle Phenology (FCP) Project on Department of Defense land (2018-2019), the Heath Lab field crew at the long-term monitoring site in southwestern Idaho (2008-2018), or Cornell NestWatch (1997-2018).
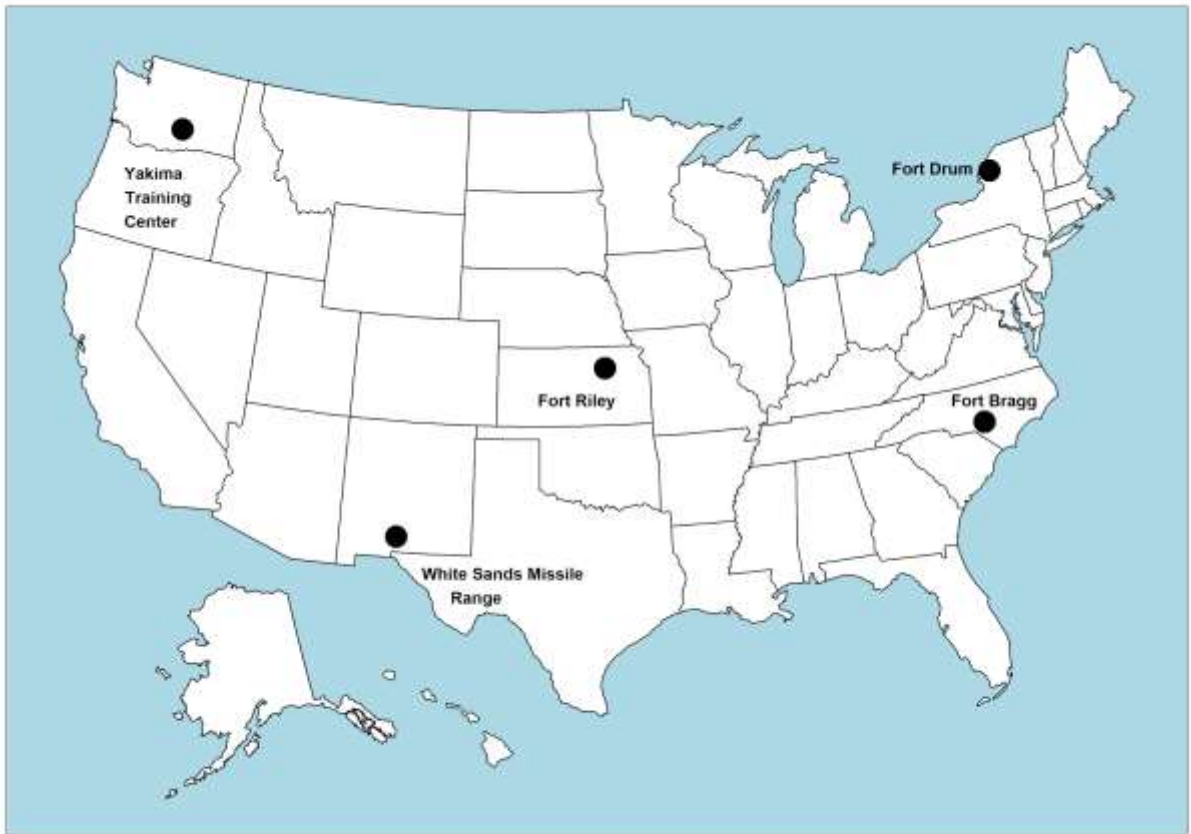
Figure 1.2.   The Department of Defense sites with American kestrel nests during the 2018-2019 breeding seasons. The SERDP FCP Project monitored the incubation behavior of these nests through the use of trail cameras installed inside the nest boxes, which would take pictures at regular intervals. Out of the nests with complete incubation data (n=27), around half were successful with more than one fledgling banded (n=16); plumage age variance on banding day was calculated for these nests.
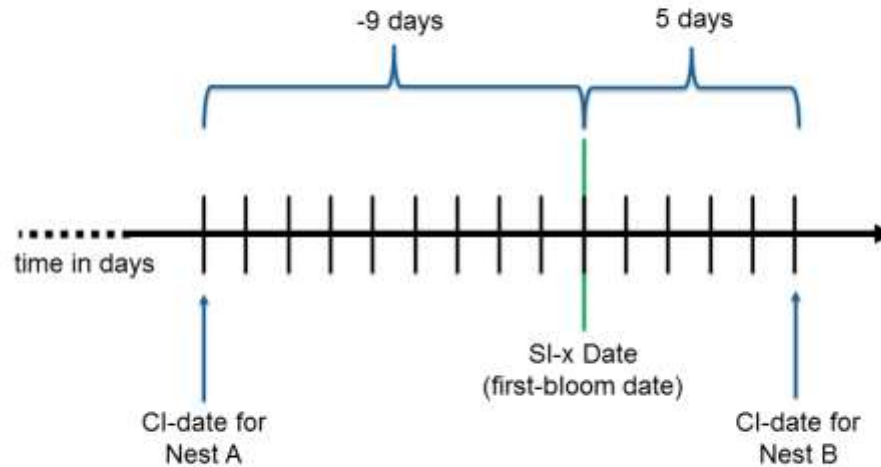
Figure 1.3.   A conceptual diagram of our index for phenological mismatch. We quantified phenological mismatch as the difference in days between clutch-initiation date (CI-date) and the extended spring index date (SI-x date) at each nest-box. A negative number indicates that a CI-date occurred before the SI-x, and a positive number indicates that CI-date occurred after the SI-x. It is important to note that the SI-x date was based on the environmental conditions around each nest box , so it varied within and among study sites, and in different years of the study. Nest A and Nest B happen to have the same SI-x date for ease of visualization.
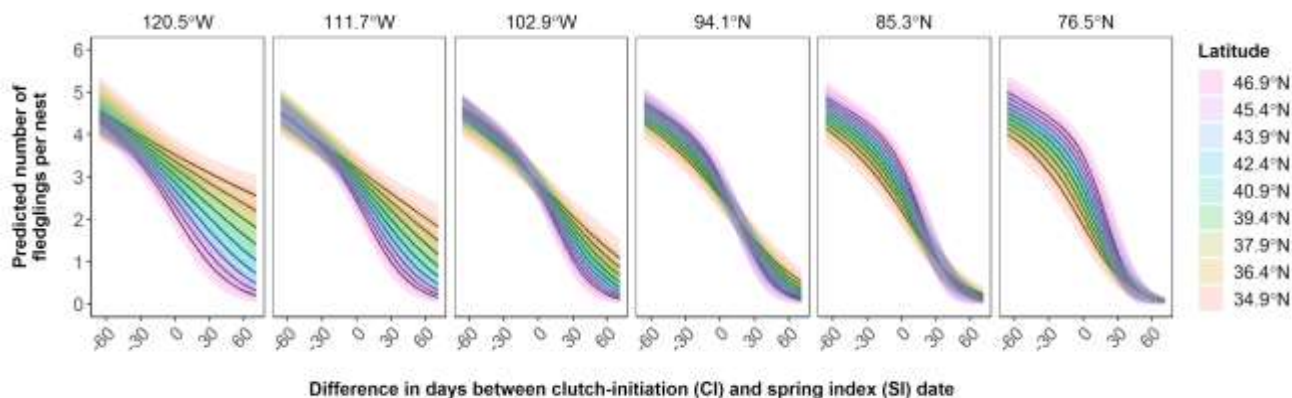
Figure 1.4. The trend in the number of fledglings produced per nest attempt (n = 2136) was best predicted by the additive effect of phenological mismatch (the difference in days between the clutch initiation date (CI-date) and the extended spring index date (SI-x) for that nest attempt, and the interactive effect of latitude and longitude. This model has a zero-inflation parameter that was best predicted by the interactive effect of phenological mismatch, latitude, and longitude; however, the estimation of this effect was statistically unclear as the 85% confidence intervals for the beta crossed zero. We instead plotted the predictions based on the estimates of the two-way interactive effects of phenological mismatch, latitude, and longitude from this model, for which the beta estimates were reliable. The lines represent the model prediction, the shaded regions are the 85% confidence intervals of the prediction, the facets display predictions at different longitudes, and the colors indicate predictions at different latitudes.
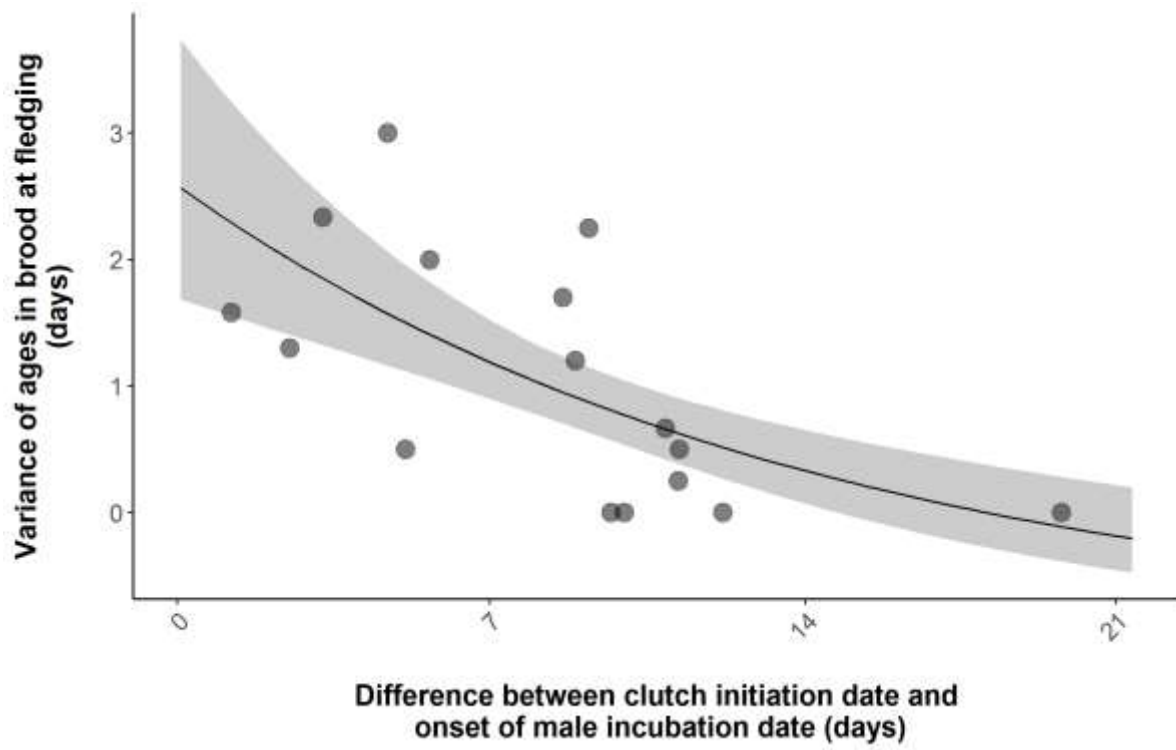
Figure 1.5. **Age variance of brood at fledging was best predicted by the difference in days between the onset of male incubation and the clutch initiation date (CI-date). Each point is a nest monitored by FCP on DoD land with complete incubation data that had at least two fledglings during the breeding seasons of 2018 (n=8) and 2019 (n=8). The line represents the model prediction, and the shaded region is the 85% confidence interval for that prediction.**
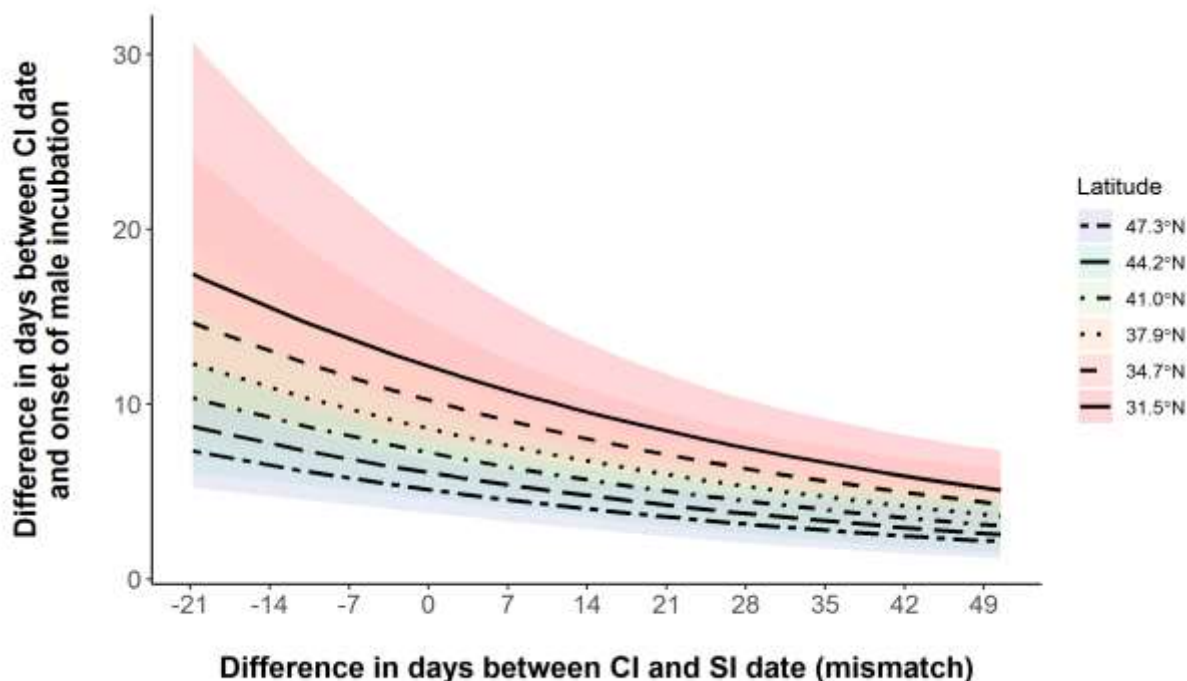
Figure 1.6. **Difference between the clutch-initiation date (CI-date) and the onset of male incubation is predicted by the additive effects of phenological mismatch and latitude. As mismatch and latitude increase, the difference in days between CI-date and the onset of male incubation behavior decreases. The earlier onset of male incubation behavior is a predictor for increased age variance of the nestlings, and an indicator of hatch asynchrony. This analysis included nests with complete incubation data with nestlings that were aged and banded (n=16), nestlings that were neither aged nor banded (n=2), and unsuccessful nests (n=9), from the 2018-2019 breeding seasons at the DoD site nest box installations. 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.**

PHENOLOGICAL MISMATCH CREATES FITNESS TRADE-OFFS THAT AFFECT

THE SURVIVAL OF BROOD-REARING AMERICAN KESTRELS (FALCO

SPARVERIUS)

Abstract

Climate-driven advances in spring phenology may lead to mismatch between the timing of peak prey abundance and bird reproduction. Mismatch can result in lower annual productivity, but the consequences of mismatch on survival of adults and hatch-year birds have received less attention. We investigated how breeding time relative to the start of spring was correlated with the survival of American kestrels (*Falco sparverius*) from two distinct breeding populations that exhibit different migration strategies. We used a multistate mark-recapture model to estimate the annual survival of adult and hatch-year kestrels. For each bird, in each year, we categorized its nesting attempt as "early" or "late" compared to the population's median number of days between clutch initiation and the start of spring to represent mismatch. In addition, we included covariates for nesting success, sex, and minimum winter temperature anomaly in survival models. Phenological mismatch predicted the survival of successful adults that produced young; however, the direction of the effect differed between populations. In Idaho, where kestrels are partial migrants, early- breeding kestrels had higher survival than later-breeding kestrels. In New Jersey, where kestrels tend to be fully migratory, later-breeding kestrels had higher survival compared to early breeding kestrels. Mismatch category did not affect the survival of adult birds with failed nests, suggesting that the energetic cost of producing fledglings contributed to the effect of mismatch on survival for successful

kestrels. There was no difference in survival between hatch-year birds produced from "early" or "late" nests. In Idaho, males had higher survival rates than females and winter temperatures positively correlated with survival in all age and sex classes. In New Jersey, sex and winter temperature did not explain survival. At both sites, there was a seasonal decline in productivity. Differences in survival between sites may reflect differences in seasonality, climate change patterns, or consequences of migration strategies. For partially migrant populations, mismatch may rapidly drive directional selection for birds to breed earlier by favoring survival and productivity, but for fully migrant populations that have a limited window of time to reproduce, mismatch may create trade-offs between reproduction and survival. Generalists are assumed to be less susceptible to negative fitness effects from phenological mismatch than specialists, so it is notable that we found negative effects on survival related to seasonal breeding time for our generalist study species. As climate change progresses, phenological mismatch may impact the survival of widespread generalist species more than was previously surmised.

Introduction

Many temperate bird species improve their productivity by synchronizing their breeding seasons with the timing of peak food abundance in the spring (Buse et al., 1999, Durant et al., 2005; Visser et al., 2006). Climate-driven advances in spring green-up may lead to an uncoupling between the timing of peak food availability and brood-rearing if species do not advance the timing of nesting attempts accordingly, as phenomenon called phenological mismatch (Cushing, 1990). There is ample evidence of the negative consequences of mismatch on reproductive success. Studies have shown that mismatched breeding time negatively affects productivity (Buse et al., 1999; Visser et al., 2006), nest

survival (Wann et al., 2019), and offspring recruitment (Reed et al., 2013). However, the consequences of mismatch on other fitness components, such as survival, are not well known. Raising offspring under mismatched conditions may create a trade-off for the parents between provisioning young and self-maintenance because of lower food availability when compared to the peak of the season, and this trade-off may lead to decreased adult survival. Offspring reared in mismatched conditions may be provisioned with less food, which can result in slow growth, poor body condition, high nestling mortality, and subsequently low probabilities of recruitment and hatch-year survival (Buse et al., 1999; Visser et al., 2006; Öberg et al., 2014). As climate-driven phenological mismatches become more common among species (Thackeray et al., 2010), more work is needed to understand the impacts of phenological mismatch on adult and juvenile survival.

Studies concerning the effects of mismatched breeding relative to environmental conditions and food availability during the breeding season may be confounded by seasonal patterns of individual quality and fecundity. Several studies have documented that later breeding birds are more likely to be of poorer body condition (Sassani et al., 2016), have lower productivity (Perrins, 1970; Sassani et al., 2016), and lower survival rates (Blums et al., 2005) than birds that breed earlier in the season. Offspring that fledged earlier in the season were are of higher quality in terms of body condition and weight (Perrins, 1970; Naef-Danzer & Keller, 1999; Öberg et al. 2014), and had have higher recruitment rates (Verhulst & Tinbergen, 1991; Catry et al., 2017), than young that fledged fledge later in the breeding season. Because both inherent parental quality and resource abundance vary seasonally, it is difficult to parse out the effects of these factors

on the fitness of breeding adults and their offspring (but see Koenig & Walters, 2018). Further, adult birds that failed fail to produce young in a season have lower breeding site fidelity than birds that were are successful (Harvey et al., 1979; Haas, 1998; Steenhof & Heath, 2009) - a tendency that could potentially bias apparent survival estimates (Schaub & Royle, 2014). Climate change may also affect environmental conditions in the non-breeding season that influence annual survival in the non-breeding season. Specifically, climate change has increased winter temperatures, especially in the western United States (Easterling, 2002), and this may improve the survival of bird species for which colder winters have been associated with lower survival (Peach et al., 1994; Leech & Crick, 2007; Woodworth et al., 2017). Changes in winter severity may also influence migration propensity and distance (Both et al., 2005). This may indirectly affect annual survival rates because migration is the part of the annual cycle when mortality is highest (Sillett & Holmes, 2002; Klaassen et al., 2014; Rushing et al., 2017). Decreased migration may also lead to decreased dispersal from the breeding grounds (Grinnell, 1922; Alonso et al., 2000), which could further influence apparent survival rate estimation (Schaub & Royle, 2014). For these reasons, studies of phenological mismatch should take the environmental conditions in different phases of the full annual life cycle into account.

American kestrels (*Falco sparverius*) are widespread, generalist, cavity-nesting falcons (Smallwood & Bird, 2002; Smith et al., 2017). In this species, egg-laying is positively correlated with the start of the growing season, which predicts the availability of important kestrel prey resources such as insects and small mammals (Smith et al. 2017). Hatch-year kestrels produced early in the season in years with warmer winters have higher recruitment rates than young birds produced later in the breeding season

(Steenhof & Heath, 2013). Adult kestrels that have a successful nesting attempt at a breeding site have higher return rates to that site than kestrels that failed there (Steenhof & Heath, 2009). Male and female kestrels exhibit different migratory behavior, with female kestrels tending to migrate farther than male kestrels (Heath et al., 2012). American kestrels also show different migration strategies along a latitudinal gradient across their range - with fully migrant populations in northern areas, to partial migrants, and fully resident populations in the south (Heath et al., 2012). A recent genetic study revealed distinct differences between kestrels in western and eastern North America (Ruegg et al., 2020) that are consistent with different responses to climate change. In the west, kestrels are migrating shorter distances in response to warmer winters (Heath et al., 2012), breeding distributions have shifted southward (McCaslin & Heath, 2020) and breeding phenology has advanced (Smith et al., 2017). In the eastern part of North America, kestrel migration remains unchanged (Heath unpublished data), breeding distributions have shifted northward (McCaslin & Heath, 2020), and breeding phenology has tended to not change (Smallwood, *unpublished data*). We considered the American kestrel to be an excellent species for studies of mismatch and survival because of their use in long term nest box programs, as well as the differences in migratory behavior and population trends of eastern and western kestrels.

Here, we used long-term mark-and-recapture data from two research sites to investigate how the timing of breeding relative to the start of spring affected the apparent survival of adult American kestrels and their offspring. We used data from kestrels in southwestern Idaho, where kestrels are partial migrants and have shown advancing breeding phenology over the past 26 years (Smith et al., 2017) and from northwestern

New Jersey, where kestrels are fully migrant and breeding time has not advanced. We anticipated that different migratory strategies and changes in breeding phenology may reveal different consequences of mismatch. We categorized each bird's nesting attempt as "early" or "late" based on how it compared to the population's median number of days between clutch initiation and the spring index date. We predicted that later-breeding adults would have lower apparent survival rates than early-breeding adults, and that this may depend on their sex and whether or not they raised young that breeding season. We included hatch-year birds (HY) - birds that had fledged that year - in our analysis to see if their parent's clutch-initiation date was correlated with their survival. We anticipated that hatch-year birds (HY) would have lower apparent survival rates than the after-hatch-year breeding adults (AHY), because high juvenile mortality has been found in other species (Sullivan, 1990; Promislow & Harvey, 1989). Additionally, we expected to see higher survival rates associated with warmer winters, especially for birds breeding in Idaho, where part of the population overwinters on the breeding grounds.

Methods

We collected mark and- recapture data as part of long-term breeding season nest box monitoring programs at nest box networks in southwestern Idaho and in northwestern New Jersey. The study site in southwestern Idaho (43°N, 116°W) is within a mixture of sagebrush steppe, agricultural and rangelands, alongside exurban and suburban areas in the municipalities of Kuna, Meridian, and Boise (Steenhof & Petersen, 2009a). The number of nest boxes at this study site ranged from 98-113 during the study period. The study site in northwestern New Jersey (41°N, 74°W) is comprised of agricultural lands and, open fields embedded within, and some forested areas in Sussex and Warren

counties (Smallwood et al., 2009). The number of nest boxes at the New Jersey study site ranged from 96-127 during the years of our study period (Smallwood et al., 2009).

We captured and marked American kestrels for this study in Idaho from 2008-2017, and in New Jersey from 1997-2017. Nest boxes were monitored from March-July and were systematically checked for occupancy (every 1-3 weeks in Idaho; every 3-4 weeks in New Jersey), defined by the presence of one or more kestrel eggs (Smallwood et al., 2009; Heath et al., 2012). We trapped adult kestrels in the nest box during the incubation stage, recorded the sex of the adult as well as the number of eggs they were on. Upon finding a completed clutch of at least 5 eggs (or 4 eggs on consecutive visits), we then banded and measured the adults. Recaptured adults, or birds that had been banded previously elsewhere, were recorded as having already been banded. We banded, measured, and sexed nestlings by plumage when they were between 18-25 days of age; and we considered success as at least one nestling banded (Anderson et al., 2016; Smallwood, 2016).

We recorded the clutch initiation date for each nesting attempt by different methods, depending on the state of the nest when it was discovered. When we discovered an incomplete clutch of eggs in a nest box, we back-calculated lay-dates assuming kestrels laid 1 egg every other day (Bird & Palmer, 1988). For clutches that were discovered complete and hatched, we used the ages of the nestlings, determined by plumage characteristics (Steenhof & Griggs, 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 from the hatching date. If complete clutches never hatched, we

estimated the clutch initiation date by backdating from the date of clutch discovery times the number of eggs.

We used extended spring index (SI-x) models to estimate the start of spring by predicting the first-bloom dates of widespread, ornamental, early-spring plant species – specifically, lilac (*Syringa chinensis* and *S. vulgaris*), and honeysuckle cultivars (*Lonicera tatarica* and *L. korolkowii*) (Schwartz et al., 2006; Rosemartin et al., 2015). First-bloom dates for lilac and honeysuckle can be predicted by the accumulated spring temperatures required for leaf-out and bloom (Caprio, 1974). This method can more generally predict the onset of spring across different habitat types than remote sensing approaches, which often require adjustments across different biomes (Schwartz et al., 2002; Phillips et al., 2008; White et al., 2009). Early spring plant development has been found to predict the phenology and abundance of important kestrel prey items, such as insects and small mammals (Kemp et al., 1991; Reed et al., 1994; Smith et al., 2017), and SI-x first-bloom dates are positively correlated with the timing of egg-laying in American kestrels (Winiarski et al., in prep).   We extracted SI dates for each nest with an SI-x model parameterized with climate data from Daymet (Izquierdo-Verdiguier et al., 2018; Thornton et al., 2018).

We assessed the mismatch between breeding time and SI-x date for each nest-attempt by calculating difference in days between the clutch-initiation date and the SI-x date at the nest box where the clutch was initiated. We categorized the degree of mismatch as "early" or "late" depending on whether the individual nest event was before (early) or after (late) the median mismatch in days for each study site (See Figure 2.1B). If a bird attempted to breed 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.

To characterize winter severity, we calculated winter minimum temperature

anomalies for each study site to examine how winter temperatures changed over time

within our study period. 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., 1997; Thornton et al., 2018). First, for each year

we averaged daily minimum temperature values within a minimum bounding box of all

nest box locations for each study area. Study area-specific winter minimum temperature

anomalies were then calculated 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.

<u>Statistical analysis</u>

For each study site, we estimated whether SI-x dates and clutch-initiation dates

changed over the study period for each study site using generalized linear models with

Gamma distributions and log link functions with year as a covariate. For our survival

analysis, we created mark-recapture models using the multistate model framework in

Program MARK (White & Burnham, 1999; White et al., 2006), using the RMark package

and interface (Laake, 2013) Multistate mark-recapture models estimated survival (S), and

capture probability (p) similar to Cormack-Jolly-Seber mark-recapture survival models

(Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton et al., 1992); additionally, these

models estimate transition probability (Ψ) between categorical states (Arnason, 1973;

Brownie et al., 1993; Schwarz et al., 1993). In this model, birds transitioned from hatch-year (HY) to after-hatch-year (AHY) across a time-step in the analysis. We created six states, hereafter referred to as strata, to account for our hypotheses for age-structure, nesting success, and timing:

(1.)   HY from a brood initiated "early"

(2.)   HY from a brood initiated "late"

(3.)   AHY that was successful and initiated egg laying "early"

(4.)   AHY that was successful and initiated egg laying "late"

(5.)   AHY that was unsuccessful and initiated egg-laying "early"

(6.)   AHY that was unsuccessful and 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.

We created capture histories for each individual bird by coding their presence or absence in each year of the study, and further coding the present birds into the appropriate stratum according to their age, timing category, and breeding-success, for each year they were captured. Then, we designed models with all combinations of our multistate variable ("stratum"), sex, and annual minimum winter temperature anomaly ("winter"). We ran separate mark-recapture analyses for Idaho and New Jersey, using the same model set for each analysis. Then, we compared the models using Akaike's information criterion corrected for small sample size (AICc), and considered the top models within 2ΔAICc to be informative (Burnham & Anderson 1998, 2002). We estimated 85% confidence intervals for model parameters to be compatible with model selection criteria (Arnold, 2010); and we considered effects statistically unclear if

confidence intervals overlapped zero (Dushoff et al., 2019). We did all analyses in R (R

Core Team, 2020). We report parameters as estimate ± standard error and with their 85%

confidence intervals.

Results

We captured and marked 1430 individual birds in Idaho and 1405 individual birds

in New Jersey. These birds were associated with 369 nesting attempts from 2008-2017 in

Idaho, and 301 nest events from 1997-2017 in New Jersey. We found that birds in Idaho

laid eggs a median of 17 days before the start of spring (mean= -13 days; std. deviation =

21 days), and a median of 8 days before the start of spring in New Jersey (mean = -7

days; std. deviation = 12 days) (Figure 2.1). In Idaho, both clutch-initiation date (β = -

0.009 ± 0.004; 85% CI: -0.014, -0.003) and SI-x date (β = - 0.029 ± 0.001; 85% CI: -

0.030; -0.028) were advancing earlier in the year, but not at the same rate (Figure 2). In

New Jersey, the SI-x date did not significantly advance and was better predicted by the

null model than by year; however, clutch-initiation tended to shift later in the year over

the study period (β = 0.003 ± 0.001; 85% CI: -0.002, 0.004).   Given these trends, clutch-

initiation date is likely to surpass SI-x date in future years at both study sites.

The best model of survival was the same for both Idaho and New Jersey, and

included the additive effects of our multistate variable ("stratum"), minimum winter

temperature anomaly ("winter"), and sex (Tables 2.1 & 2.2), but the direction of the

effects differed between study sites. In Idaho, successful "early" breeding birds had

higher survival rates compared to successful "late" breeders (Figure 2.3). In New Jersey,

successful "late" breeding birds had higher survival rates compared to "early" successful

breeders (Figure 2.4). Successful adults had higher survival rates than unsuccessful adults

in both Idaho and New Jersey. Interestingly, mismatch category did not affect survival of unsuccessful birds at either study site. Also mismatch category did not have an effect on the survival of hatch-year birds. Hatch-year (HY) birds had lower survival estimates than after-hatch-year (AHY) birds.

In Idaho, increasing winter minimum temperature anomalies were positively associated with higher apparent survival estimates (Figure 2.3). Also, male birds had higher apparent survival rate estimates than female birds in Idaho (Figure 2.3). Though the model with winter temperature and sex was supported for the New Jersey site, the 85% confidence intervals for winter and sex covariates for the New Jersey study site crossed zero; therefore, we considered these effects statistically unclear. Recapture probability was not predicted by any of our covariates in Idaho. Model selection supported a model with sex predicting recapture probability (p) in New Jersey; however, this effect was statistically unclear. Current stratum membership, sex, and winter minimum temperature anomaly were not associated with the transition probabilities between stratum.

Discussion

We found that phenological mismatch affected the apparent survival of adult kestrels that successfully produced fledglings. The effect of mismatch and nest-success on survival was found for both Idaho and New Jersey kestrels, but the direction of the effect differed between study populations. When compared to earlier successful adults, later successful adults had lower survival rates in Idaho and higher survival rates in New Jersey. The window for breeding was narrower in New Jersey (April-June) than in Idaho (March-June), suggesting that seasonal constraints on nesting phenology may be stronger

in New Jersey than in Idaho. Migratory strategies may play a role in reinforcing or relieving these constraints. The New Jersey kestrel population is fully migratory, so breeding time may be constrained early in the season by arrival time at the breeding site, and constrained later in the season by the need to accrue fuel and complete molt before migration (Siikamaki 1998; Stutchbury et al., 2011). On the other hand, Idaho birds have the advantage of being able to overwinter on their breeding grounds, which relieves the constraints associated with migration for both earlier breeding and later breeding times. Also, female kestrels were estimated to have lower survival rates than male kestrels; this may be attributed to differences in migration behavior between the sexes. Winter weather conditions may also play a role in strengthening or weakening the constraints on breeding time, as well as having a direct impact on survival, with milder winters predicting higher survival in Idaho. These results reveal how breeding phenology mismatch affects the survival of American kestrels, how mismatch that is adaptive for productivity is not necessarily adaptive for survival outcomes (Lof et al., 2012), and why the effects of mismatch for productivity and survival may differ among regional populations of this widespread species.

In addition to influencing the extent of the breeding season, migratory strategy and regional climate may affect the magnitude of trade-offs between current reproductive success and adult survival. Adults that breed earlier relative to the spring index date are more productive in both Idaho and New Jersey (Callery et al., 2020; Smallwood & Luttmann, *unpublished data*). We found different trends for survival in Idaho and New Jersey, with earlier breeders having higher survival than later breeders in Idaho, and later breeders having higher survival than earlier breeders in New Jersey. Productivity and

survival both decline seasonally in Idaho, so there is no evidence of a trade-off between reproduction and survival for earlier birds – being early maximizes both components of fitness. Climate change is increasing minimum winter temperatures and decreasing the frequency of extreme winter precipitation in the western United States (Cohen et al., 2018), creating more suitable conditions for the Idaho population to overwinter and breed early. Productivity declines seasonally in New Jersey, but survival increases throughout the season, suggesting the existence of a trade-off between reproduction and survival, and that the direction of this trade-off depends on when the nesting attempt occurs. Climate change is increasing the severity and frequency of blizzards in the northeastern United States (Cohen et al., 2018); this could limit how early New Jersey breeders can migrate to their breeding grounds. Late winter storms could also impose harsh conditions on early arrivals. Earlier breeders in New Jersey may have the benefit of rearing their broods synchronously with peak-prey abundance, which will increase their productivity; however, they may have to divert energy from self-maintenance early in the season to keep warm and hunt in inclement winter weather – trading off their odds of future survival for reproductive success in the current breeding season. Later breeders in New Jersey have higher survival and lower productivity; they may be allocating more resources towards self-maintenance and investing less in their current nest attempt – trading off current reproductive success for survival.

Interestingly, the survival of birds that failed to rear fledglings was not impacted by breeding time mismatch. The vast majority of failed nests in our Idaho data failed at the egg stage (87%), and therefore, those adults never had to rear young. The result that phenological mismatch affected birds with nest success, but not birds with nest failure,

aligns with our prediction that the brood-rearing stage is the most important for determining the impacts of phenological mismatch on adult fitness, since this is when parental and offspring energy demand is at its highest. Overall, birds that failed to rear fledglings had lower apparent survival rates than birds that reared fledglings, which could reflect differences in inherent individual fitness, dispersal rates or permanent emigration rates between successful and unsuccessful birds. Like our model, most survival models survival estimate apparent survival as opposed to true survival (Lebreton & Pradel, 1992; Schaub & von Hirschheydt, 2009). Unless survival models are parameterized to be spatially-explicit or are telemetry-based, they cannot distinguish between death and permanent emigration (Ergon & Gardner, 2014; Schaub & Royle, 2014). Therefore, kestrels that failed may have died or dispersed.

We found that female kestrels have lower apparent survival rates than male kestrels in Idaho. A possible biological basis for this is unequal migration distances between the sexes. Migration is the life history stage with the highest mortality rate for other bird species – including raptor species (Sillett & Holmes, 2002; Klaasen et al., 2014). Female kestrels migrate farther than male kestrels (Steenhof & Heath, 2009b; Heath et al., 2012), and likely spend more time in this life history stage than males. If this species also has increased mortality during migration, female kestrels may have lower survival rates than males because females spend more time migrating than their male counterparts. It is also possible that the difference in estimated survival between the sexes could be an artifact of the apparent survival model. Because of their longer migrations, female kestrels are more likely to permanently emigrate from their breeding grounds than male kestrels. Migration length increases the chances of veering off course due to wind

drift or other stochastic environmental processes (Alerstam & Hedenstrom, 1998); incidentally, this could lead to more females permanently leaving the breeding grounds than males. Our survival model considers death and permanent emigration as the same, so if more females permanently emigrate than males, this effect would appear through lower apparent survival rate estimates (Ergon & Gardner, 2014; Schaub & Royle, 2014).

We also found that warmer winters predicted higher survival rates in Idaho, which was consistent with our hypothesis that birds overwintering in Idaho would benefit from more mild temperatures. Warmer, drier winter weather may improve survival of birds for which colder, wetter winters have been associated with lower survival rates (Peach et al., 1994; Leech & Crick, 2007; Woodworth et al., 2017). Winter temperature did not predict kestrel survival in New Jersey, perhaps because birds are seldom overwintering there. It is notable that winter warming due to climate change may be bolstering some regional populations of kestrels by increasing survival, while concurrently negatively impacting the numbers of kestrel prey species, like grasshoppers and small mammals, among others (Bierman et al., 2006; Ims et al., 2008; Jonas et al., 2015). It might be worth considering the population dynamics of regional kestrel prey-species when assessing the effects of warmer winters - and climate change in general - on a population of kestrels.

The timing of clutch-initiation is becoming uncoupled from the progression of spring phenology, with the clutch-initiation dates trending to become later in the season than the SI-x dates for both the Idaho and New Jersey study sites. Since breeding phenology affected the survival of productive and ostensibly high-quality adult kestrels, phenological mismatch could have serious consequences on kestrel population dynamics at these sites. We found that breeding phenology affected the survival of American

kestrels: a dietary generalist with a very diverse prey base. Most studies of phenological mismatch consider its effects on specialist species, because these effects are usually easier to connect to the dynamics of a specific prey species; however, as climate change impacts accumulate over time, affecting greater numbers of species, it makes sense that generalist species are starting to be at risk of suffering consequences from phenological mismatch. Studies should consider the consequences of life history phenology on survival, in addition to productivity, for a wider range of species if we aspire to further our understanding of how climate change will affect species and ecosystems.

Acknowledgments

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Tables and Figures

Table 2.1. AICc table comparing candidate models of survival for the Idaho
data, with all combinations of the covariates for the survival parameter (S), and the
best predictors for recapture (p) and transition between states or "strata" (Ψ) kept
constant. Previous model runs found the best predictor of p to be the intercept only,
and the best predictor for Ψ to be the intercept only, as well. Table includes the
number of model parameters (K), delta AICc (ΔAICc), and cumulative model
weights (AICcWt).

Survival (S)	Recapture (p)	Transition (Ψ)	K	ΔAICc	AICcWt
stratum + sex + winter	intercept only	intercept only	29	0.000	0.618
stratum + sex * winter	"	"	30	1.320	0.319
stratum + sex	"	"	28	5.621	0.037
stratum	"	"	27	7.167	0.017
stratum * sex + winter	"	"	34	8.734	0.007
stratum * sex	"	"	33	14.34	0.000
stratum * sex * winter	"	"	45	17.05	0.000
stratum + winter	"	"	28	55.72	0.000
stratum * winter	"	"	33	64.08	0.000
sex + winter	"	"	24	123.8	0.000
sex * winter	"	"	25	125.4	0.000
intercept only	"	"	22	127.7	0.000
sex	"	"	23	128.1	0.000
winter	"	"	22	158.6	0.000

Table 2.2.   **AICc table comparing candidate models of survival for the New Jersey data, with all combinations of the covariates for the survival parameter (S), and the best predictors for recapture (p) and transition between states or "strata" (Ψ) kept constant. Previous model runs found the best predictor of p to be sex, and the best predictor for Ψ to be the intercept only, as well. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).**

Survival (S)	Recapture (p)	Transition (Ψ)	K	ΔAICc	AICcWt
stratum + sex	sex	intercept only	29	0.000	0.394
stratum + winter	"	"	29	0.703	0.277
stratum + sex + winter	"	"	30	0.976	0.242
stratum + sex * winter	"	"	31	3.018	0.087
stratum	"	"	28	25.10	0.000
stratum * winter	"	"	34	31.81	0.000
stratum * sex	"	"	34	44.00	0.000
stratum * sex + winter	"	"	35	45.06	0.000
stratum * sex * winter	"	"	46	60.78	0.000
sex	"	"	24	129.4	0.000
sex + winter	"	"	25	130.4	0.000
intercept only	"	"	23	130.8	0.000
winter	"	"	24	131.8	0.000
sex * winter	"	"	26	132.5	0.000

Table 2.3.   **Effect size (β) for each covariate in the best model of the survival parameter (S) for Idaho (S ~ stratum + sex + winter). Hatch-year birds had significantly lower survival rates than adult birds. Among successful adults, earlier birds had significantly higher survival rates than later birds. Warmer winters and being male had a positive effect on survival rates.**

Covariate	Effect size (β)	Lower CI (85%)	Upper CI (85%)
Stratum			
Earlier hatch-year	-3.680	-4.204	-3.157
Later hatch-year	-3.923	-4.644	-3.203
Earlier adult, nest-success	-0.599	-0.945	-0.253
Later adult, nest-success	-1.335	-1.764	-0.906
Earlier adult, nest-failure	-1.896	-2.560	-1.232
Later adult, nest failure	-2.078	-2.622	-1.533
Sex (male)	0.394	0.103	0.684
Winter (min temp anomaly ℃)	0.424	0.201	0.646

Table 2.4. **Effect size (β) for each covariate in the top model of the survival parameter (S) for New Jersey (S ~ stratum + sex + winter). Hatch-year birds had significantly lower survival rates than adult birds. Among successful adults, later birds had significantly higher survival rates than earlier birds. Though winter temperature and sex were in the top model for survival, the estimates of the effect sizes for each of these covariates have confidence intervals that overlap zero, making the estimates statistically unclear.**

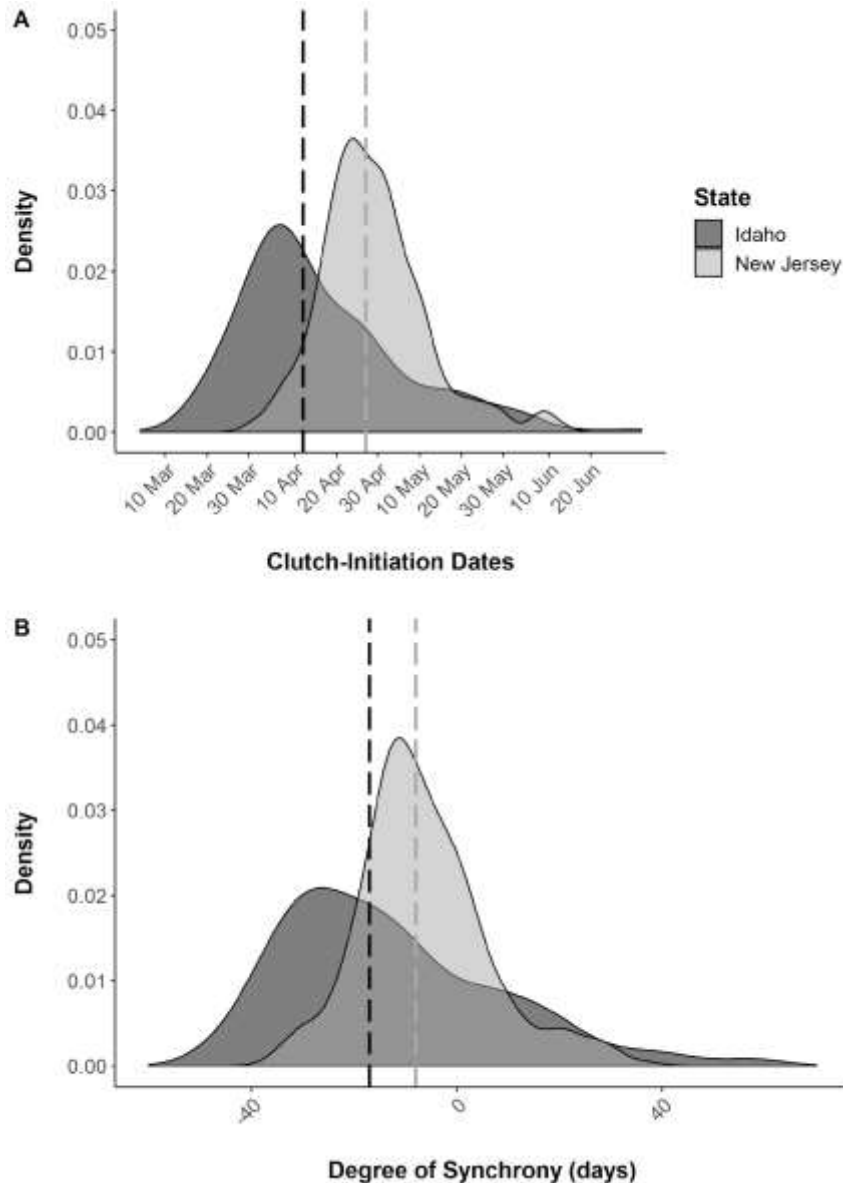| Covariate	Effect size (β)	Lower CI (85%)	Upper CI (85%)
Stratum			
Earlier hatch-year	-3.830	-4.562	-3.099
Later hatch-year	-5.206	-6.689	-3.724
Earlier adult, nest-success	-0.671	-1.104	-0.238
Later adult, nest-success	-0.043	-0.441	0.527
Earlier adult, nest-failure	-0.999	-1.891	-0.107
Later adult, nest failure	-2.180	-3.739	-0.621
Sex (male)	-0.655	-0.131	0.005
Winter (min temp anomaly °C)	0.112	-0.042	0.266

Figure 2.1. Density distributions of the clutch initiation dates (A), and degree of synchrony between clutch-initiation date and SI-x date (B) for nest-attempts during the study periods in Idaho, shaded in black (n=369; 2008-2017) and in New Jersey, shaded in gray (n=301; 1997-2017). The black dashed line represents the median overall clutch initiation date for the Idaho nest-attempts in (A) (April 12th) and the overall median degree of synchrony for the Idaho nest-attempts (B) (-17 days). The gray dashed line represents overall median clutch initiation date for the New Jersey nest-attempts in (A) (April 27th), and the overall median degree of synchrony for the New Jersey nest-attempts in (B) (-8 days). Nest-attempts that occurred before the median degree of synchrony date for each state in (B) were classified as "earlier," and nests that occurred after that date were classified as later.
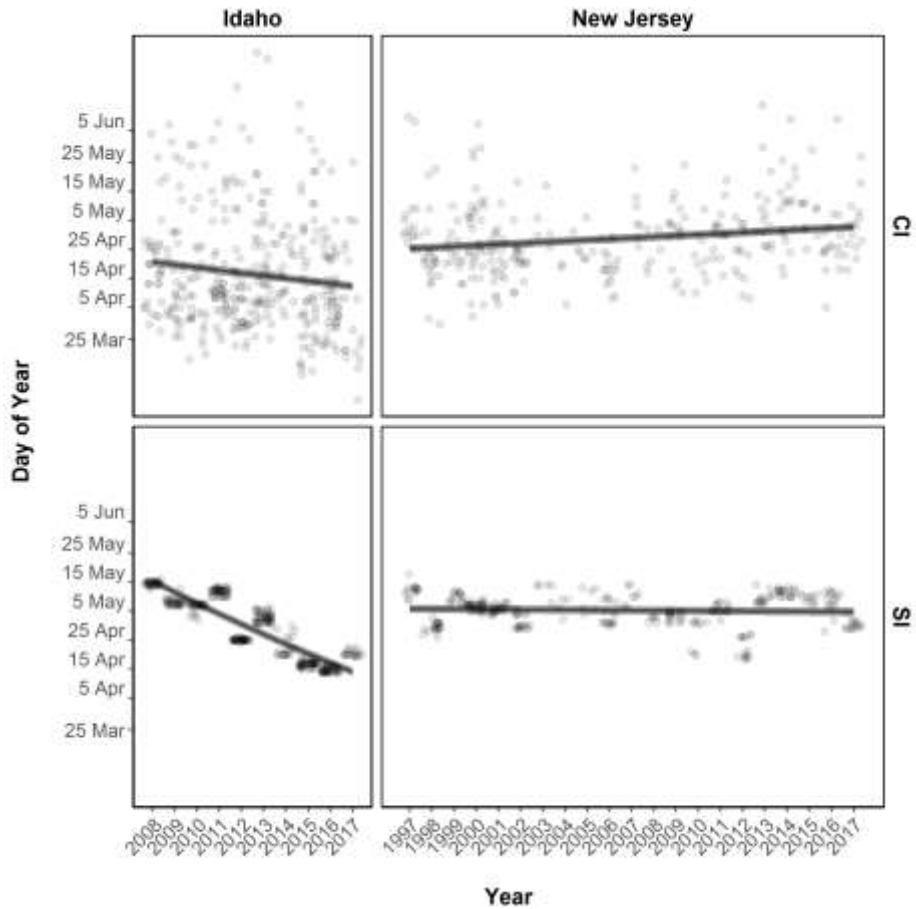
Figure 2.2. **Predictions of SI-x date and CI-date over time in Idaho (2008-2017) and in New Jersey (1997-2017). Predictions were made with generalized linear models with Poisson distributions. The gray shaded areas represent the 85% confidence interval around the model predictions, and each point represents the SI-x date at an occupied nest box. The degree of synchrony between SI-x date and clutch-initiation date is changing over time in both states.**
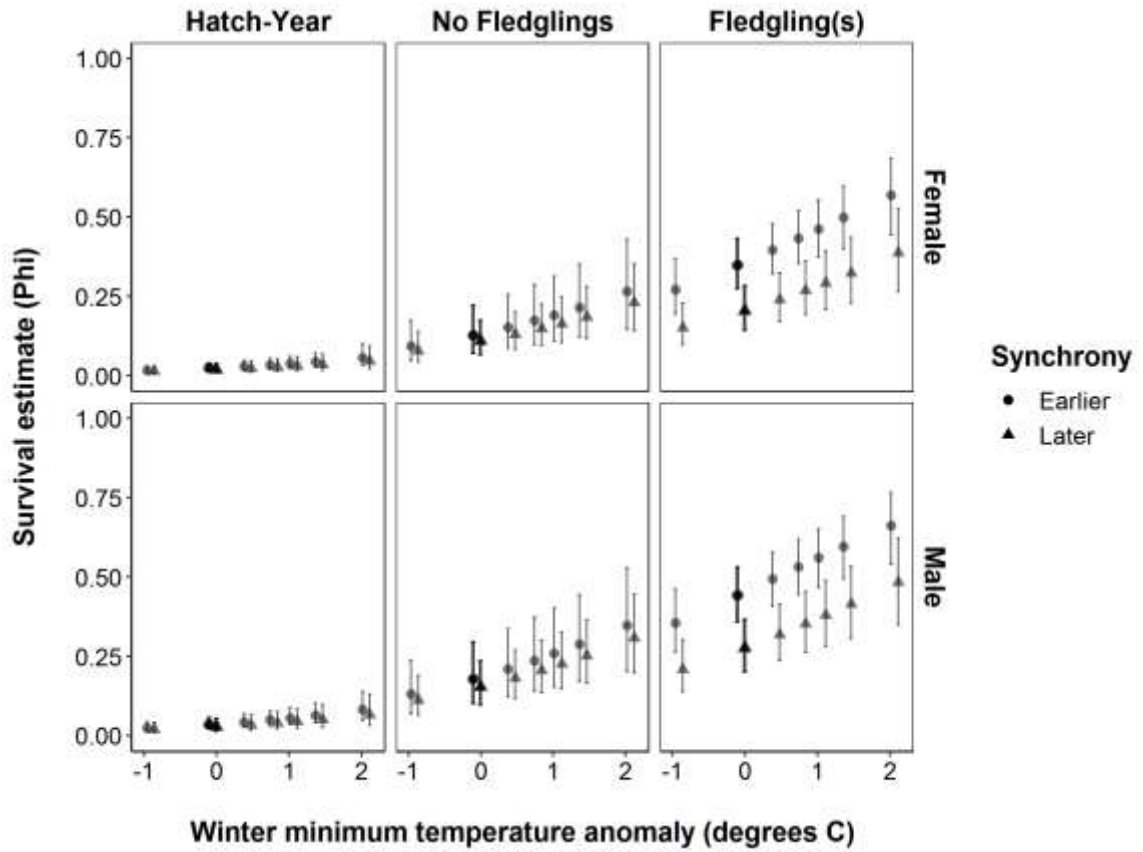
Figure 2.3. **Survival parameter estimates for American kestrels in Idaho categorized by age-structure, sex, and degree of synchrony of breeding time, related to winter minimum temperature anomaly. Error bars connote the 85% confidence intervals around the parameter estimate. Degree of synchrony of breeding time affected survival rates for breeding adults that reared fledglings, and did not affect survival rates of hatch-year birds or adults that did not rear offspring to fledge. Survival rates increased as winter minimum temperature anomaly increased.**
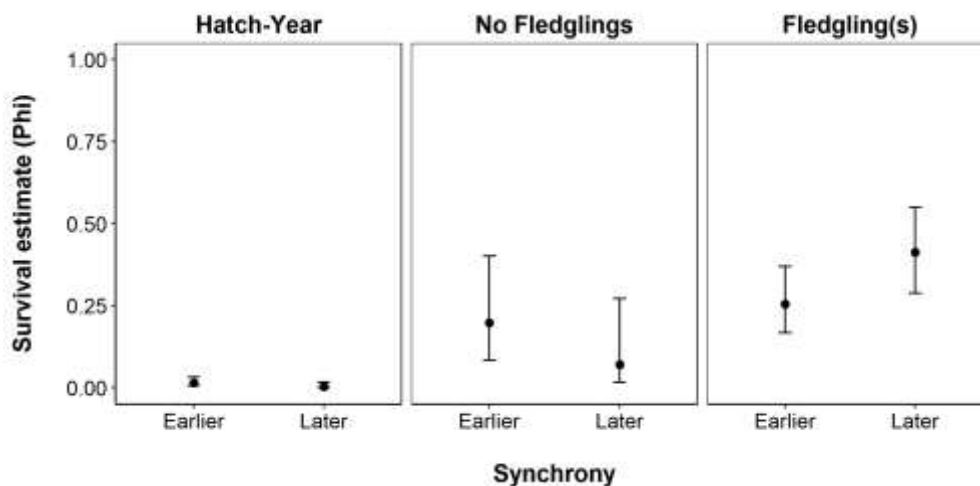
Figure 2.4. **Survival parameter estimates for American kestrels in New Jersey categorized by age-structure, and degree of synchrony of breeding time. Error bars connote the 85% confidence intervals around the parameter estimate. Degree of synchrony of breeding time affected survival rates for breeding adults that reared fledglings, and did not affect survival rates of hatch-year birds or adults that did not rear offspring to fledge. Winter minimum temperature anomaly and sex were in the top model for survival, but the estimates of their effect sizes were statistically unclear, as their 85% CI overlapped with zero.**

CONCLUSION

Overall, we found that western kestrels may have more flexibility in their breeding time than northeastern kestrels, which have a narrow window for optimal breeding time, outside of which they must make trade-offs between productivity and survival, according to the results of the New Jersey population's survival analysis. In the northeast, inclement winter weather mostly precludes the possibility of overwintering or arriving earlier due on the breeding grounds to decreased survival, and there is a large, rapid decrease in productivity later in the season. The challenge for northeastern kestrels to breed within this optimal time window, which will likely shift or shorten due to future climate change, is worth investigating in conjunction with the kestrel population declines documented in this region. In the west, where the breeding season is becoming earlier and longer, we may observe more kestrels overwintering than previously recorded, as well as a phenomenon known as double-brooding, which has been seen in other bird species when temporal constraints on breeding time are lifted (Dunn & Moller 2014), and for populations where overall productivity is less affected by optimal breeding time (Verboven et al. 2001). Overall, northern and eastern American kestrels experience more negative effects from phenological mismatch, whereas western American kestrels may be able to more easily adapt.

Through researching the fitness impacts of phenological mismatch on widespread generalists, we can begin to identify climatic and habitat-based drivers for mismatch by comparing the different effects of mismatch on distinct regional populations of

widespread species across broad spatial scales. We can also compare adaptations that regional populations of generalist species may be adopting to cope with phenological mismatch, such as the prevalence of hatch asynchrony, which may be based on the local breadth of their prey options or the length of the prey peak in their specific environment (Barrientos et al. 2016). Importantly, we can focus conservation efforts on parts of a generalist species' range where fitness is being negatively impacted the most by phenological mismatch. Hopefully, this research has illustrated the importance of studying the fitness effects of phenological mismatch on understudied species that do not fit the usual mold, and on different geographical scales.

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