# Earlier nesting by generalist predatory bird is associated with human responses to climate change

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### Summary

**1.** Warming temperatures cause temporal changes in growing seasons and prey abundance that drive earlier breeding by birds, especially dietary specialists within homogeneous habitat. Less is known about how generalists respond to climate-associated shifts in growing seasons or prey phenology, which may occur at different rates across land cover types.

**2.** We studied whether breeding phenology of a generalist predator, the American kestrel (*Falco sparverius*), was associated with shifts in growing seasons and, presumably, prey abundance, in a mosaic of non-irrigated shrub/grasslands and irrigated crops/pastures. We examined the relationship between remotely-sensed normalized difference vegetation index (NDVI) and abundance of small mammals that, with insects, constitute approximately 93% of kestrel diet biomass. We used NDVI to estimate the start of the growing season (SoGS) in irrigated and non-irrigated lands from 1992 to 2015 and tested whether either estimate of annual SoGS predicted the timing of kestrel nesting. Finally, we examined relationships among irrigated SoGS, weather and crop planting.

**3.** NDVI was a useful proxy for kestrel prey because it predicted small mammal abundance and past studies showed that NDVI predicts insect abundance. NDVI-estimated SoGS advanced significantly in irrigated lands ($\beta = -1.09 \pm 0.30$ SE) but not in non-irrigated lands ($\beta = -0.57 \pm 0.53$). Average date of kestrel nesting advanced 15 days in the past 24 years and was positively associated with the SoGS in irrigated lands, but not the SoGS in non-irrigated lands. Advanced SoGS in irrigated lands was related to earlier planting of crops after relatively warm winters, which were more common in recent years.

**4.** Despite different patterns of SoGS change between land cover types, kestrel nesting phenology shifted with earlier prey availability in irrigated lands. Kestrels may preferentially track prey in irrigated lands over non-irrigated lands because of higher quality prey on irrigated lands, or earlier prey abundance may release former constraints on other selective pressures to breed early, such as seasonal declines in fecundity or competition for high-quality mates.

**5.** This is one of the first examples of an association between human adaptation to climate change and shifts in breeding phenology of wildlife.

**Key-words:** adaptation, agriculture, *Falco sparverius*, growing season, minimum temperature, NDVI, phenology, prey, spring, winter

## Introduction

Shifts in breeding phenology are a common biological response to climate change. There is evidence of earlier breeding in amphibians (Beebee 1995; Gibbs & Breisch 2001), reptiles (Telemeco, Elphick & Shine 2009), birds (Brown, Li & Bhagabati 1999; Dunn & Winkler 1999; Hussell 2003; Torti & Dunn 2005) and mammals (Reale *et al.* 2003; Millar & Herdman 2004). Earlier breeding is a common pattern affecting diverse taxa, but most hypotheses regarding climate change and breeding phenology have been generated from studies of passerine birds that specialize on insects (Crick *et al.* 1997; Forchhammer, Harris

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& Stenseth 1998; Both *et al.* 2004; and others). In these systems, warming spring temperatures have affected plant phenology and insect emergence. Early peaks in prey abundance increase the selective pressure to nest earlier because birds benefit by timing their reproduction to coincide with periods of high food abundance (Lack 1954) and, for some species, breeding phenology has advanced (Crick *et al.* 1997; Dunn & Winkler 1999; Both & Visser 2005; Pearce-Higgins, Yalden & Whittingham 2005; Bauer *et al.* 2010).

The ability of primary productivity and prey phenology to drive change in avian breeding phenology is most likely to occur when birds specialize on relatively few prey species that exhibit synchronous, highly peaked abundance (van Noordwijk, McCleery & Perrins 1995), or when most of a bird's different prey species experience common phenology shifts (Dunn & Winkler 1999). The extent to which generalists or species that forage in mixed land cover types are affected by changes in primary productivity and prey abundance is unclear. Generalists may be less likely to advance their breeding phenology in response to one (or a few) prey species because they often forage on a variety of prey items with asynchronous abundance patterns (Both *et al.* 2010) or heterogeneous distributions. These species may have the potential to switch among possible prey items or change their distribution, whereas specialist species may be forced to adjust their breeding phenology to match the timing of their prey. Further, rates of change in primary productivity and prey abundance will vary with different plant species that require different numbers of growing degree days to germinate or flower. Species that live in a mosaic of vegetation types may experience different rates of phenological changes in prey abundance.

Phenology shifts may be further confounded by changes in human activities for species that nest in human-dominated landscapes (Plummer *et al.* 2015). In the Northern Hemisphere, growing seasons are lengthening and late frosts are occurring significantly earlier (Schwartz, Ahas & Aasa 2006). Farmers are adapting to these changes by planting crops earlier each year and introducing new cultivars, which has resulted in plants with higher biomass and increased yield (Kucharik 2006). Without these adaptations to climate change, crops such as maize may have experienced substantial losses in yield, but they have instead increased their overall yield (Liu *et al.* 2013). Changes in planting and growing degree days could result in accelerated changes in breeding phenology in human systems when compared to natural systems.

Unfortunately, it can be difficult to establish coupled phenology change without long-term studies on both predators and prey. In lieu of prey data, many studies have used remote sensing data to measure land cover characteristics that may act as a proxy for prey abundance (Pettorelli *et al.* 2005; Balbontín *et al.* 2009; Trierweiler *et al.* 2013; Cole *et al.* 2015; McKinnon, Stanley

& Stutchbury 2015). Specifically, the amount of infrared and visible red light absorbed or reflected back into space can be indexed by normalized difference vegetation index (NDVI) (Reed *et al.* 1994; Pettorelli *et al.* 2011). Growing, green vegetation has higher NDVI values than sparse, less photosynthetically active plants (Pettorelli *et al.* 2011). Seasonal changes in NDVI can be used to estimate the start of growing season (SoGS) and track the increase in vegetation greenness that may elicit a response from primary consumers like insects and small mammals (Reed *et al.* 1994). For example, Trierweiler *et al.* (2013) used NDVI as a proxy for grasshoppers and found that wintering Montagu's harriers (*Circus pygargus*) tracked grasshoppers across west Africa spatially and temporally. Cole *et al.* (2015) showed that NDVI predicted prey abundance for great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) and that reproductive phenology for both species could be predicted using NDVI.

American kestrels (*Falco sparverius*) are small falcons that feed primarily on small mammals, and insects, and occasionally on birds and reptiles (Smallwood & Bird 2002). Kestrels are secondary cavity nesters and use a variety of land cover types that include shrub and grasslands and agricultural and suburban areas (Bird & Palmer 1988). In south-western Idaho, for instance, American kestrel nesting territories often contain both sagebrush steppe and invasive grass lands and irrigated lands (e.g. crops, pastures, and lawns). For American kestrels in this region, the start of nesting (nest initiation) has advanced approximately 15 days between 1992 and 2015. Earlier nesting by American kestrels has been associated with warmer winter minimum temperatures, but not concomitant changes in spring temperatures (Heath, Steenhof & Foster 2012).

Here, we used prey surveys, remote sensing and data from 24 years of nest monitoring to evaluate whether advancing nest phenology of American kestrels living in heterogeneous landscapes is associated with changes in the timing of prey abundance and the onset of the growing season, and assess the potential influence of weather and human activities on changes in the start of the growing season. Several previous studies have shown that NDVI is a useful proxy for insect abundance (Lassau & Hochuli 2008; Jepsen *et al.* 2009; Deveson 2013; Lafage *et al.* 2014), but less is known about the relationship between NDVI and small mammals (Pettorelli *et al.* 2011). Therefore, we first verified that NDVI reliably predicted seasonal changes in small mammal abundance. Next, we used NDVI to estimate changes in the SoGS and, thus, seasonal changes in kestrel prey abundance from 1992 to 2015. Then, we evaluated the relationship between the changes in NDVI-based estimates of SoGS and nest initiation dates of American kestrels. Finally, we assessed the relationship between the SoGS in irrigated land cover with winter temperatures and the timing of crop planting by local farmers.

## Materials and methods

### STUDY AREA AND SPECIES

The south-western Idaho study area (43°N 116°W) included between 90 and 126 nest boxes available to kestrels depending on the year (Steenhof & Heath 2009). The nest boxes were placed on highway signs along Interstate 84, on trees in rural residential areas near Kuna, Idaho and on wooden poles throughout agricultural and exurban areas south of Boise and Meridian, Idaho. Kestrels also had the opportunity within our study area to nest in old trees and buildings as well as boxes erected by others. A 900 m radius around each nest box was considered a 'nesting territory' because it represented a confined location where kestrels nested and no more than one pair bred there at a time (Newton & Marquiss 1982; Steenhof & Heath 2013).

The study area was 65 × 22 km and encompassed approximately 1000 km$^2$ of open agricultural and sagebrush steppe land cover. The agricultural areas (referred to as irrigated land cover) primarily consisted of irrigated cropland where potatoes, barley, spring wheat, winter wheat, alfalfa and sugar beets were often planted. The sagebrush steppe (referred to as non-irrigated land cover) was primarily a mixture of sagebrush and invasive grasses. Most kestrel territories in our study area contained both irrigated and non-irrigated land covers. For example, 53 kestrel territories sampled within our study area contained an average of 59·4 ± 32·4% irrigated and 39·8 ± 32·4% non-irrigated land cover ($\bar{x} \pm$ SD, Strasser & Heath 2013).

American kestrels in south-western Idaho have a relatively broad food-niche breadth, similar to other generalist predators (Marti *et al.* 1993). In the early 1990s, Marti *et al.* (1993) used prey remains and pellet analysis to study American kestrel diets and found that the majority of prey items were insects (68%) and mammals (27%). From 2012 to 2014, we used images from motion-activated cameras and observations to identify prey items American kestrels brought to their nestlings. Results from recent years were strikingly similar to Marti *et al.* (1993) with 64% of 488 prey items consisting of insects (Orthoptera and Coleoptera) and 29% small mammals (*Microtus* and *Peromyscus*). Approximately 80% of the diet biomass comes from mammals and approximately 13% comes from insects. The remaining 7% consists of birds, lizards and worms.

### NDVI

NDVI values were estimated using Landsat 5 and 8 images (U.S. Geological Survey, http://earthexplorer.usgs.gov) of the study area (path 42, row 30) taken every 16 days from 1992 to 2015 (except for January 2012–mid-April 2013 when the Landsat 5 satellite was down until Landsat 8 satellite started). All image files were calibrated in ENVI version 5.2 (Exelis Visual Information Solutions, Boulder, CO, USA) by calculating the radiance values and then calculating the top of atmospheric (TOA) reflectance values. Landsat 5 images were calibrated and TOA reflectance was determined using calculations described by Chander & Markham (2003) and Chander, Markham & Helder (2009). Landsat 8 images were calibrated and TOA reflectance was determined using the calculations described in the Landsat 8 (L8) Data Users Handbook (U.S. Geological Survey 2015). NDVI was calculated using the calibrated images and eqn 1 for Landsat 5 and eqn 2 for Landsat 8.

$$\text{Landsat 5 NDVI: (Band 4 − Band 3)/(Band 4 + Band 3)} \quad \text{eqn 1}$$

$$\text{Landsat 8 NDVI: (Band 5 − Band 4)/(Band 5 + Band 4)} \quad \text{eqn 2}$$

We selected 34 non-irrigated and 37 irrigated, 80 × 70 m sites within our study area using ArcGIS 10.1 (Esri 2012, Redlands, CA, USA) for NDVI analysis. Small mammal surveys were conducted at 28 of these 71 sites. All sites were selected in a stratified random fashion from kestrel territories where no land-use change had occurred between 1992 and 2015 and were in close proximity to a kestrel nest box. The NDVI layers created in ENVI were loaded into ArcGIS 10.1 and maximum NDVI values were extracted for each site (Pettorelli *et al.* 2005; Bradley *et al.* 2007). All images were visually inspected for cloud cover and any images with greater than 25% cloud cover across the entire study area were excluded from analysis. Additionally, any individual 80 × 70 m sites that were obscured by clouds were excluded from the analysis. Once maximum NDVI values for each site were extracted, all values were sorted and combined into two groups based on land cover type (irrigated or non-irrigated) within the 80 × 70 m site. We created separate estimates for small mammal abundance and NDVI in irrigated and non-irrigated land covers because of differences in vegetation (Bradley *et al.* 2007). Seasonal trends in NDVI for the same 80 × 70 m grid where small mammal surveys were conducted were compared for the seasonal trends in small mammal abundance for each of the 28 sites.

We used a combination of approaches to account for any missing NDVI values from cloud contamination or unavailable data. When missing two data points or less, linear interpolation was used to fill the missing data. When three or more consecutive data points were missing, the values from a third-order harmonic regression analysis that was trained by the year before and the year after were used (Brooks *et al.* 2012). At times the third-order harmonic regression was influenced by large data gaps and would estimate erroneously high NDVI values. Annual curve values were not used if they were greater than adjacent known NDVI values because erroneous maximums could influence the estimated start of the growing season. In these cases, remaining data gaps were replaced by average date-specific values of NDVI from other years. Annual NDVI curves and three-day moving averages were plotted and the date at which the moving average intercepted the annual NDVI curve was considered the SoGS because this point signifies the date NDVI makes a sudden increase and because of photosynthetic activity (Reed *et al.* 1994).

### PREY SURVEYS

Seasonal abundance of small mammals was assessed using presence/absence data collected from track plates enclosed in tubes modified from the design of Drennan, Beir & Dodd (1998), Glennon, Porter & Demers (2002) and Wiewel, Clark & Sovada (2007). The tubes were 30 cm long on top and 20 cm long on the bottom and were constructed of two halves of plastic rain gutter taped together on one side and held shut by one rubber band. This design allowed the track plates to be rainproof, light weight and easy to deploy (Drennan, Beir & Dodd 1998; Glennon, Porter & Demers 2002; Wiewel, Clark & Sovada 2007). The track plates were 18 cm long aluminium flashing placed on the bottom of the tube and held in place by Velcro. Each end of the track plate was covered by a felt pad that was coated in ink, a 1 : 1

mixture of lamp black (Daniel Smith, Inc., Seattle, WA, USA) and paraffin oil (STE Oil Company, Inc., San Marcos, TX, USA). A piece of white paper between each felt pad recorded footprints. Traps were baited with a small amount of peanut butter along the top half of the track plate tube. Traps were secured in place by two tent stakes.

Small mammals were sampled near 28 kestrel nest boxes in 2014. At each nest box, 20 track plates were placed in a 5 × 4 rectangular trapping grid with 20 m between each track plate and all within 100 m of the nest box. Cover types were classified based on the vegetation present where small mammals were sampled regardless of cover type in the territory surrounding the nest box. Ten track plate plots were in irrigated land cover and 18 were in non-irrigated land cover. Track plates were deployed at each nest box site for three consecutive days each month from March through July. Trapping order was selected in a stratified random fashion so that the sites sampled last during a previous month were not the first sampled the next month, and sites were not trapped in the same order each month. Track plates were checked once per day during which time tracks were recorded as present or absent. If tracks were present the paper was replaced, the location of trap was recorded, and bait was reapplied.

Animal tracks were identified using Murie & Elbroch (2005) and, at some trap sites, motion-activated trail cameras (Bushnell® HD Trophy Cameras, Overland Park, KS, USA). We used trail cameras placed near several track plates within different kestrel territories to obtain visual confirmation of the identity of small mammals visiting traps. Ultimately tracks were classified as being from mountain cottontail (*Sylvilagus nuttallii*), ground squirrel (*Urocitellus* sp.) or small mammal, which typically were either deer mice (*Peromyscus maniculatus*) or voles (*Microtis* sp.). Voles and deer mice were grouped together because their footprints were of similar size and both were important kestrel prey.

## BREEDING PHENOLOGY

From 1992 to 2015, except for 2007, American kestrels nesting in boxes in south-western Idaho were monitored (Steenhof & Heath 2009; Steenhof & Peterson 2009). Prior to the nesting season each year, nest boxes were cleaned and lined with pine shavings. Beginning in early March, boxes were visited every 7–21 days to determine kestrel occupancy and clutch size. The mean nest discovery dates (average date when eggs were first discovered in a nest, regardless of number of eggs) each year were used as an index of annual timing of kestrel nesting. Nest discovery dates correlated well with hatching dates, as nests discovered early hatched early (Pearson correlations analysis: $r = 0.89$, $n = 577$, $P < 0.001$), so we considered them to be a reliable index of clutch initiation date (Steenhof & Heath 2009). Nest discovery dates for the years 1992 to 2015 ranged from 14 March to 12 July and averaged 26 April. All methods and protocols described above were approved by the Boise State University IACUC review board (IACUC Approval Numbers 006-AC14-005, 006-01-006, and 006-05-004) and conducted under scientific permits issued to K. Steenhof or J. Heath from state and federal authorities.

## CROP PLANTING AND WEATHER

We obtained Idaho Crop Progress and Condition reports for our study area from the USDA National Agricultural Statistics Service (https://www.nass.usda.gov) to evaluate whether the timing of crop planting has changed over the study period. These reports give the percentage of land that has been planted for each crop by the report date, but they do not contain the date of first planting. We assumed that an increase in the percentage of planted land by the first annual report represented earlier planting rather than a faster rate of planting (i.e. the start of planting remained constant). This assumption was verified by comparing the percentage of planted land with the SoGS estimated by NDVI for each year. Planting patterns for barley, potatoes, spring wheat and sugar beets were examined for years 1992 to 2013. The USDA did not report district-specific data and transitioned to statewide data in 2014 so years 2014 and 2015 were excluded from our analysis.

We used daily winter minimum temperature anomaly data from the Global Historical Climatology Network gridded data set (HadGHCND, www.ncdc.noaa.gov/oa/climate/ghcn-daily) station nearest the study area (station 1295) to examine the potential effect of winter temperature change on crop planting dates from 1992 to 2013 (see Heath, Steenhof & Foster 2012). Winter months were November through February (Heath, Steenhof & Foster 2012). Daily anomalies were the difference of each daily minimum temperature from a daily 'base value' (Caeser, Alexander & Vose 2006). Daily 'base' minimum temperatures were calculated from the climate station's minimum temperature records for 1961–1990 using a five-day window centred on each day (Caeser, Alexander & Vose 2006).

## STATISTICAL ANALYSES

The hypothesis that NDVI reliably predicted small mammal abundance was tested using generalized linear mixed-effects models with binomial distributions and logit links (i.e. mixed logistic regression, Zuur *et al.* 2009). We analysed data from irrigated and non-irrigated sites separately. The response variable was the presence (1) or absence (0) of small mammals (i.e. mice and voles) at each track plate during each trapping occasion. Our small mammal index was therefore the probability that a track plate had a positive detection of small mammals during a given trapping occasion. Each model included a fixed effect of NDVI and random effects that controlled for the repeated sampling of track plates and their nested nature within kestrel territories. Also, the seasonal peak in the small mammal index was estimated using mixed logistic regression models with a quadratic effect of ordinal date and the same random effects as the NDVI models. Seasonal changes in NDVI were examined at the territory scale using linear models with quadratic effects of ordinal date. Ordinal dates were z-transformed to aid in statistical convergence (Steen *et al.* 2012). We used the method described by Nakagawa & Schielzeth (2013) and the R (R Core Team 2015) package MuMIn (Barton 2016) to calculate $R^2$ values for mixed models. All mixed models were built using the package lme4 (Bates *et al.* 2014) in R (R Core Team 2015).

We examined the potential relationship between mean nest discovery date and SoGS for irrigated and non-irrigated land covers using a linear model. We did not separate nest discovery dates based on land cover type as with small mammal and NDVI analyses because kestrels had access to both land covers surrounding their nest box. We examined seasonal changes in maximum NDVI values for 2014 separately for irrigated and non-irrigated land covers using linear models with ordinal date and ordinal date-squared as predictors. We assessed potential trends in the annual SoGS for irrigated and non-irrigated land covers

separately using linear models. Annual trends in kestrel breeding phenology were examined using linear models with average nest discovery date as the dependent variable and year as the independent variable.

We used linear models to determine whether the percentage of land planted with each crop was higher earlier in the year from 1992 to 2013. All crop types were combined within a single linear model and we used crop type, initial reporting date and year to examine whether the proportion of land planted at initial reporting had changed over time. The predictor variable winter temperature anomaly, instead of year, was used to examine whether the proportion of land planted with a crop depended on the preceding winter weather. Finally, we examined whether the proportion of land planted predicted SoGS from 1992 to 2013. All analyses were performed in R v. 3.1.1. Results are presented as $\beta \pm$ SE throughout.

## Results

### SMALL MAMMAL ABUNDANCE AND NDVI

We deployed a total of 8280 track plates from March to July and recorded 4949 (59·8%) track plates positive with small mammal foot prints, 3755 (75·9%) of which were deer mouse or vole. Both the NDVI and small mammal index showed similar patterns in seasonality with values peaking in May in non-irrigated areas and in July in irrigated areas (Fig. 1a and b). These seasonal patterns were statistically significant for the small mammal index on both irrigated ($\beta_{Date} = 0.90 \pm 0.07$, $P < 0.001$; $\beta_{Date}^2 = -0.28 \pm 0.07$, $P < 0.001$, $R^2 = 0.71$) and non-irrigated lands ($\beta_{Date} = 0.10 \pm 0.03$, $P = 0.003$; $\beta_{Date}^2 = -0.38 \pm 0.04$, $P < 0.001$, $R^2 = 0.33$) and for NDVI on irrigated ($\beta_{Date} = 0.05 \pm 0.01$, $P < 0.001$; $\beta_{Date}^2 = -0.02 \pm <0.001$, $P < 0.001$, $R^2 = 0.63$) and non-irrigated lands ($\beta_{Date} = 0.01 \pm <0.001$, $P < 0.001$; $\beta_{Date}^2 = -0.02 \pm <0.001$, $P < 0.001$, $R^2 = 0.54$). The small mammal index was therefore strongly correlated with NDVI in both irrigated ($\beta = 15.88 \pm 1.20$, $P < 0.001$, $R^2 = 0.76$) and non-irrigated areas ($\beta = 18.07 \pm 1.93$, $P < 0.001$, $R^2 = 0.40$, Fig. 1c). Therefore, we considered maximum NDVI values to be a predictor of seasonal small mammal abundance in both non-irrigated and irrigated land covers.

### YEARLY NDVI-ESTIMATED SOGS

Between 1992 and 2015, SoGS for irrigated and non-irrigated land covers ranged from 12 March to 29 April and from 4 February to 7 April, respectively (Fig. 2a). SoGS significantly advanced by $26 \pm 14$ days from 1992 to 2015 in irrigated land cover ($\beta = -1.09 \pm 0.30$, $P < 0.002$, $R^2 = 0.38$), but not for non-irrigated land cover ($\beta = -0.57 \pm 0.53$, $P = 0.30$, $R^2 = 0.05$, Fig. 2a).

### BREEDING PHENOLOGY

From 1992 to 2015, excluding 2007, there were 1069 kestrel nest discoveries ranging in date from 14 March to 9
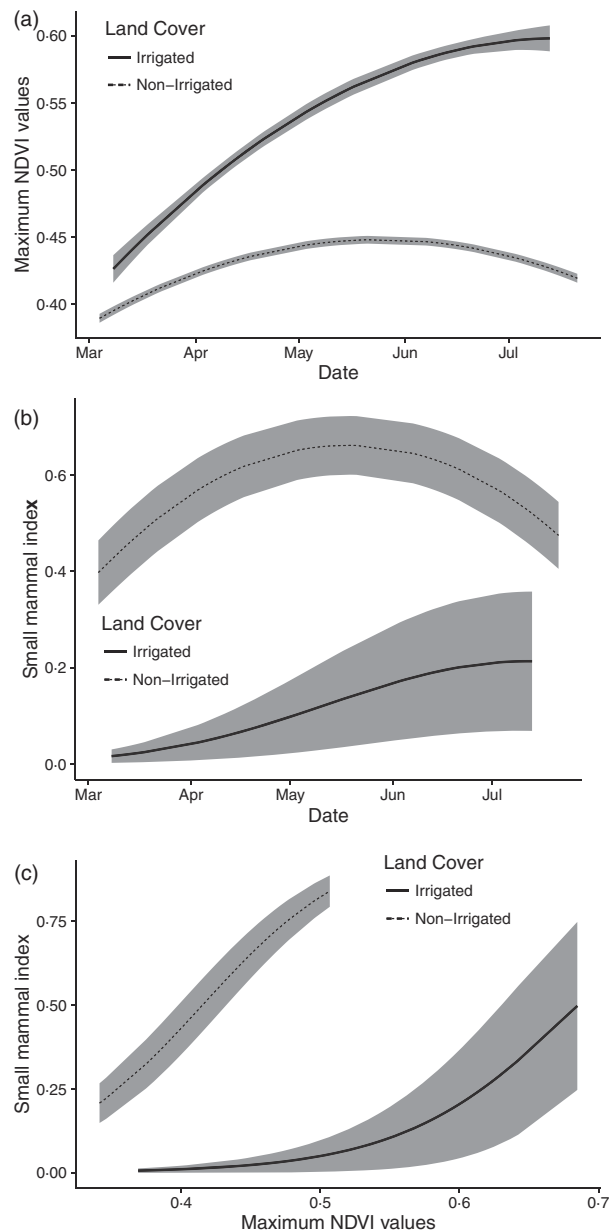


**Fig. 1.** Relationships between NDVI, date and small mammal index. (a) Changes in maximum NDVI values from March to late July 2014 in irrigated and non-irrigated land covers in south-western Idaho. (b) Changes in the probability that a small mammal (*Peromyscus* or *Microtus* sp.) will walk over a track plate (small mammal index) from March to late July 2014 in south-western Idaho. (c) Relationship between the small mammal index and maximum index values from March to late July 2014 in south-western Idaho. Shaded areas represent $\pm$ SE. NDVI, normalized difference vegetation index.

July. The mean nest discovery dates ranged from 18 April to 11 May and showed a significant advancement of 15 days over 24 years ($\beta = -0.61 \pm 0.12$, $P < 0.001$, $R^2 = 0.55$, Fig. 2b). Kestrel nest discovery dates were related to SoGS in irrigated land cover ($\beta = 0.32 \pm 0.08$, $P < 0.001$, $R^2 = 0.43$, Fig. 3a), but not the SoGS in non-irrigated land cover ($\beta = 0.07 \pm 0.07$, $P < 0.32$, $R^2 = 0.05$, Fig. 3b).
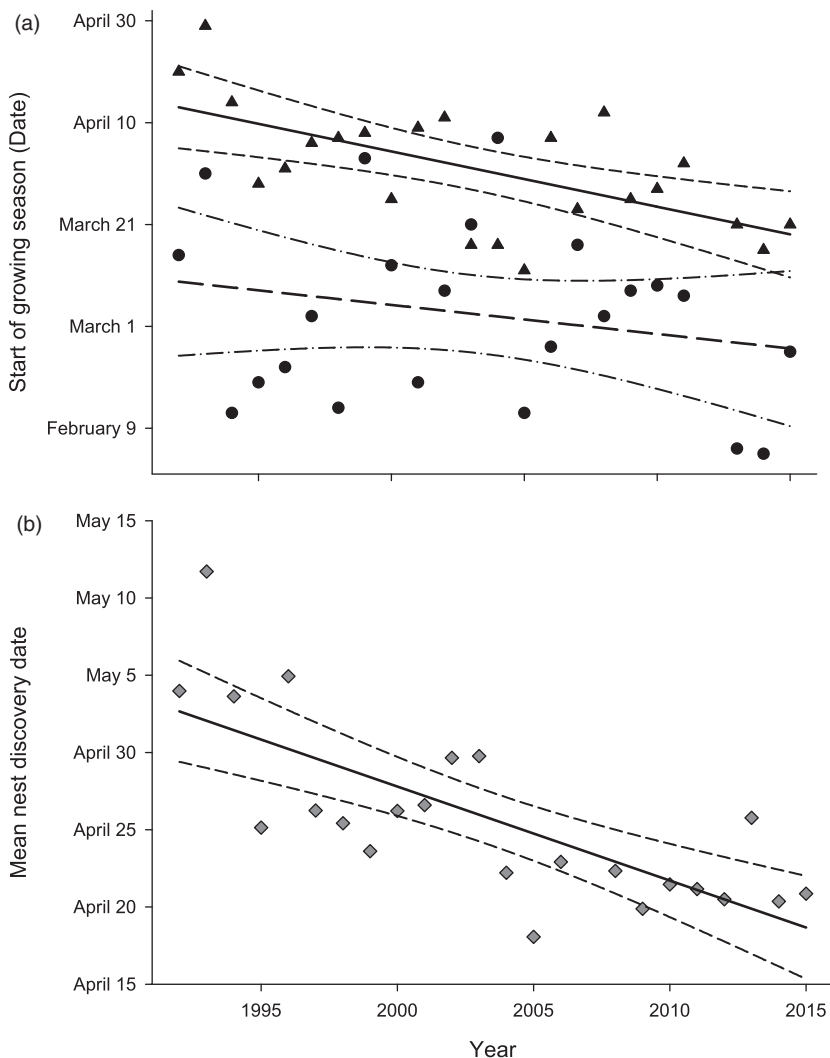
**Fig. 2.** Changes in growing seasons and American kestrel breeding phenology over time. (a) Relationship between start of growing season (SoGS) and year (excluding 2012) for irrigated (solid line) and non-irrigated (long dash line) land cover within the American kestrel study area, and (b) relationship between American kestrel mean nest discovery dates and year for 1992 to 2015 (excluding 2007) in south-western Idaho, USA. The SoGS has significantly advanced by 26 days in irrigated lands (triangles), but not non-irrigated lands (circles). American kestrel nest discovery dates have significantly advanced by 15 days. The solid and dotted lines represent the predicted relationship and the 95% confidence intervals, respectively.

CROP PLANTING AND WEATHER

From 1992 to 2013, the percentage of each crop planted was higher on the first day of reporting when controlling for crop type and day of report ($\beta = 0.87 \pm 0.39$, $P < 0.03$, $R^2 = 0.52$). Warmer winter temperature anomalies resulted in a higher percentage of crops being planted on the first day of reporting the following spring ($\beta = 6.59 \pm 2.41$, $P = 0.008$, $R^2 = 0.51$). As farmers planted their crops earlier in the year, the NDVI-estimated SoGS significantly advanced ($\beta = -0.75 \pm 0.21$, $P < 0.001$, $R^2 = 0.55$, Fig. 4). This suggests that farmers are having an impact on the SoGS in irrigated land cover by advancing the emergence of vegetation, and is consistent with NDVI-based SoGS for irrigated land cover.

## Discussion

Previous studies have shown positive relationships between NDVI and insect abundance. Here, we showed that seasonal changes in NDVI predicted seasonal changes in small mammal abundance. Because insects and small mammals constituted 93% of the kestrel diet during our study, we considered NDVI-based estimates of growing season dates to be reliable indicators of the phenology of kestrel prey. NDVI patterns from 1992 to 2015 indicated that the SoGS has advanced in irrigated, but not non-irrigated, lands within our study area in south-western Idaho. American kestrel nest initiation was positively associated with the SoGS in irrigated lands, but not associated with the SoGS in non-irrigated lands. The SoGS in irrigated lands has advanced because farmers planted earlier after warmer winters, which have become more frequent on our study site (Heath, Steenhof & Foster 2012). To our knowledge, this is the first evidence of human adaptation to climate change affecting the breeding phenology of wildlife.

This study showed that generalist predators may advance nesting phenology in response to changes in prey, despite different rates of change within different types of land cover. Kestrels in our study area had access to both irrigated and non-irrigated land cover around their nest box, but shifts in kestrel phenology were only associated with SoGS in irrigated land cover. It is unclear why kestrels may track shifts in one land cover type and
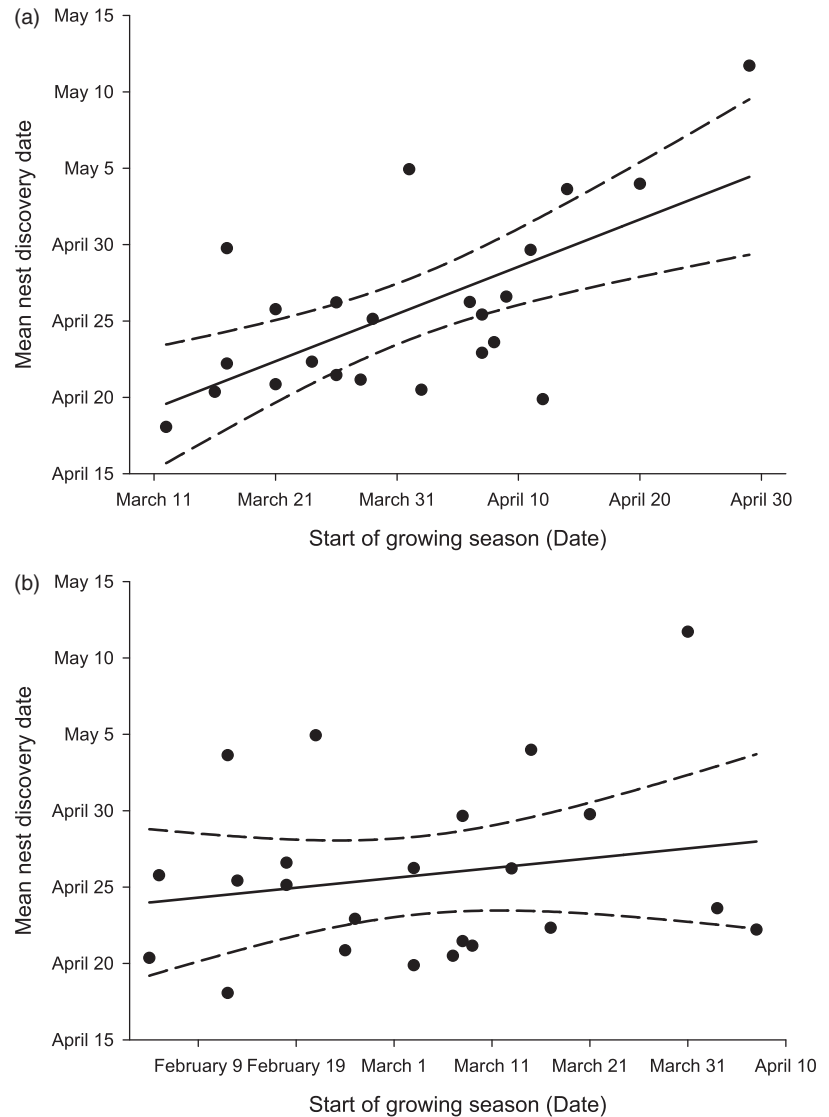
**Fig. 3.** Relationship (and 95% confidence intervals) between American kestrel mean nest discovery date and (a) the NDVI-estimated start of growing season (SoGS) in irrigated lands, and (b) NDVI-estimated SoGS in non-irrigated lands from 1992 to 2015 in south-western Idaho, USA. NDVI, normalized difference vegetation index.

not another. Animals may preferentially track shifts in prey if one class of prey is higher quality or quantity than another class of prey, but there is no evidence that kestrels choose to nest in one type of land cover preferentially over another (Strasser & Heath 2013) or that land cover determines diet quality (Sassani *et al.* 2016). Alternatively, shifts in prey may release former constraints on other selective pressures to breed early, such as seasonal declines in fecundity (Gienapp & Visser 2006) or competition for high-quality mates. Like many temperate birds species, American kestrels that breed earlier produce more recruits (Steenhof & Heath 2013) and have higher return rates (Steenhof & Heath 2009) than later breeding birds. Therefore, earlier SoGS in irrigated lands, and associated shifts in prey, may enable kestrels to nest earlier without consequences of nesting too early, before prey is abundant.

Although kestrel breeding phenology has advanced by 15 days since 1992, peaks in small mammal abundance in irrigated land cover have potentially advanced by 26 days

over the same time period. For most predators, there are fitness consequences associated with asynchrony between reproduction and peak food availability, creating a selective pressure to track shifts in prey (Reed, Jenouvrier & Visser 2013). However, access to prey in static non-irrigated systems may reduce the selective pressure to track changes on irrigated systems, resulting in differential rates of change between SoGS in irrigated lands and kestrels. For generalist species, or those feeding in heterogeneous habitats, mismatches between peaks of some prey in some areas are unlikely to have the same fitness consequences as mismatches for a specialist species (Visser & Both 2005) and so generalist consumers may not track shifts in primary productivity and prey as closely as specialists.

Because the SoGS in non-irrigated land cover starts earlier in the year than the SoGS in irrigated lands, the advancement of SoGS in irrigated lands increases the amount of overlap in growing seasons. The transition from a bimodal to unimodal growing seasons could result in a shorter period of relatively high prey availability.
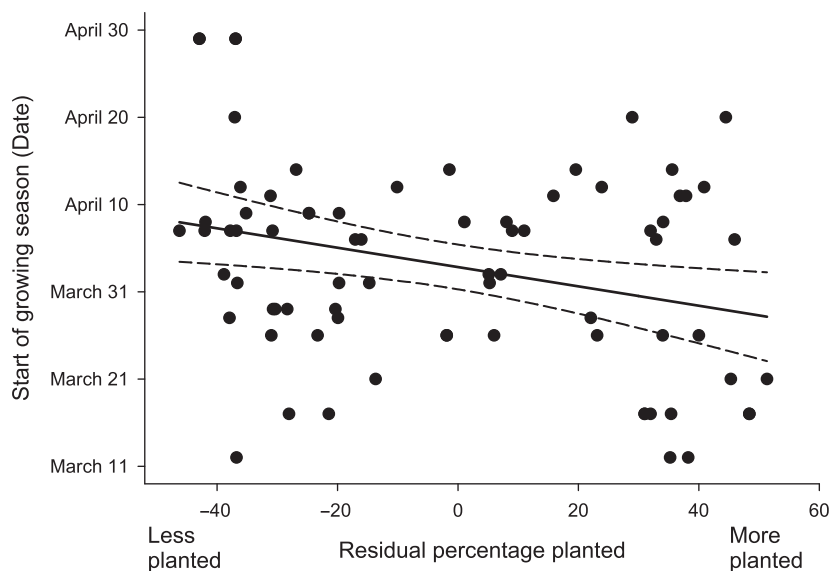
**Fig. 4.** Relationship (and 95% confidence intervals) between start of growing season (SoGS) and residual percentage of planted land, when accounting for crop type and date of reporting, for 1992 to 2013 in south-western Idaho, USA. As the proportion of planted lands increased, the NDVI-estimated SoGS significantly advanced. NDVI, normalized difference vegetation index.

This could have consequences for birds that tend to nest later in the season. For our partial migrant population, later breeders tend to be migrants (Anderson *et al.* 2016) that may be limited in their ability to arrive earlier to the breeding site. However, there is strong evidence that American kestrels in western North America have shorter migration distances following warmer winters (Heath, Steenhof & Foster 2012) and wintering distributions are shifting north (Paprocki, Heath & Novak 2014), which would imply that kestrels may be responding to changes in climate throughout their annual cycle. Further, in recent years when the nests were the earliest ever discovered, several pairs of early nesting kestrels successfully produced two clutches of offspring (J. Heath, unpublished data). Successful double clutching had been very uncommon through most of our long-term study (Steenhof & Peterson 1997). Whether these trends continue, and how higher rates of reproduction affect kestrel survival, is unclear.

Previously, kestrel breeding phenology was described as correlated with winter minimum temperature anomalies and not spring temperature anomalies (Heath, Steenhof & Foster 2012). Advancement in kestrel breeding phenology was hypothesized to be the result of reduced overwintering and pre-breeding constraints from warmer winters and seasonal declines in local fitness (Heath, Steenhof & Foster 2012). By using NDVI data and focusing on the vegetation across our study area, we found that, although spring temperatures have not increased, the SoGS has advanced, likely owing to human response to climate change. This result highlights the need for direct and reliable indicators of environmental change. Earlier planting after warmer winters is consistent with other studies that have found significantly earlier growing seasons in croplands after warm winters (Linderholm 2006). Further, other studies of common agricultural species, such as European starlings (*Sturnus vulgaris*), have found breeding phenology to be associated with winter temperatures rather than spring temperatures (Williams *et al.* 2015). Given the number of wildlife species that depend on agricultural systems for portions of their annual life cycle, agricultural climate adaptations are likely to be a significantly driver of biological change. Further, human activities such as land-use change, recreation and urbanization, which may not be climate adaptive, can act with climate change to affect species distributions, abundance and phenology (Pautasso 2012). Eurasian blackcaps (*Sylvia atricapilla*), for example, have altered wintering behaviour and migration strategies as a result of warmer winters and backyard bird feeding (Plummer *et al.* 2015).

This study demonstrates the multitude of factors that have potential to contribute to changes in reproductive phenology of individual species and in broader biological systems. As human systems begin to shift in response to climate change, understanding the relationships between alterations in either or both climate and human activity will become increasingly important. This study also demonstrates the importance of considering full annual cycles (Balbontín *et al.* 2009; Williams *et al.* 2015 & Sicurella *et al.* 2016) when discussing climate change, as winter, not spring, temperatures predict the timing of the SoGS, especially in agricultural systems (Smith 2016).

## Data accessibility

The data are available from http://doi.org/10.18122/B2PC78 (Smith *et al.* 2016).

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