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Research Paper

Weather and climate change drive annual variation of reproduction by an aerial insectivore

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ABSTRACT. For many bird species, but especially aerial insectivores, reproduction depends on weather. Climate change is likely to intensify effects, but with uncertain consequences. We report 22 years of data on Eastern Kingbird (*Tyrannus tyrannus*) reproduction for two populations located in different hygric environments undergoing climate change; mesic central New York, USA, (NY; 12 years) and xeric southeastern Oregon, USA, (OR; 10 years). Laying date became earlier with increasing temperature in the 30-day period preceding laying in identical fashion at both sites, and in years of early laying, clutch size was larger, length of laying season increased, and failed initial nesting attempts were more often replaced. High temperature in the 10-days preceding mean laying date was associated with shorter laying seasons, while a site by 10-day temperature interaction reflected an increase and decrease of clutch size with increasing 10-day temperature in NY and OR, respectively. Seasonal rate of clutch size decline was higher when the laying season was short but also slowed in xeric OR when rain was abundant in the 10-days prior to mean laying date. Nest predation drove annual variation in young fledged/nest, but the latter also increased and decreased with increasing maximum temperature during the nestling phase in mesic NY and xeric OR, respectively. Potential effects of climate change on kingbird populations are thus high given the dependence of reproduction on weather, and climate change likely contributed to declines of kingbirds in OR. Declines of kingbirds in NY appear unrelated to warming climates because higher temperatures advanced laying dates and yielded greater nest productivity. However, length of laying season declined across years at both sites, and thus early season gains may be negated by poor conditions late in the season that may be causing shorter laying seasons. Further work is needed to identify causes for the latter changes.

Les conditions météorologiques et les changements climatiques entraînent la variation annuelle de la reproduction d'un insectivore aérien

RÉSUMÉ. Pour de nombreuses espèces d'oiseaux, mais surtout les insectivores aériens, la reproduction dépend des conditions météorologiques. Les changements climatiques sont susceptibles d'intensifier les effets, mais les conséquences sont incertaines. Nous avons analysé 22 ans de données sur la reproduction du Tyran tritri (*Tyrannus tyrannus*) pour deux populations situées dans des environnements hygriques différents qui subissent les effets des changements climatiques : le centre mésique de l'État de New York, É.-U. (NY : 12 ans) et le sud-est xérique de l'Oregon, É.-U. (OR : 10 ans). La date de ponte a été plus hâtive avec l'augmentation de la température dans la période de 30 jours précédant la ponte de manière identique sur les deux sites, et dans les années de ponte hâtive, la taille de la ponte était plus grande, la durée de la saison de ponte augmentait, et les tentatives de nidification ratées étaient plus souvent remplacées. Une température élevée dans les 10 jours précédant la date de ponte moyenne a été associée à des saisons de ponte plus courtes, tandis que l'interaction entre le site et la température sur 10 jours s'est traduite par une augmentation et une diminution de la taille de la ponte avec l'augmentation de la température sur 10 jours dans NY et l'OR, respectivement. Le taux saisonnier de diminution de la taille de la ponte était plus élevé lorsque la saison de ponte était courte, mais il a également ralenti dans l'OR lorsque la pluie était abondante dans les 10 jours précédant la date de ponte moyenne. La prédation au nid était responsable de la variation annuelle du nombre de jeunes envolés par nid, mais ce nombre a également augmenté et diminué avec l'augmentation de la température maximale pendant l'élevage des oisillons dans NY et l'OR, respectivement. Les effets potentiels des changements climatiques sur les populations de tyrans sont donc élevés étant donné que la nidification dépend des conditions météorologiques, et les changements climatiques ont probablement contribué à la baisse des tyrans en OR. La baisse des tyrans dans NY ne semble pas liée au réchauffement climatique, car les températures élevées se sont soldées par le devancement des dates de ponte et ont permis une plus grande productivité des nids. Toutefois, la durée de la saison de ponte a diminué au fil des ans aux deux sites; les gains réalisés en début de saison ont donc peut-être été annulés par de mauvaises conditions en fin de saison, et ces dernières pourraient être responsables des saisons de ponte plus courtes. Des travaux supplémentaires sont nécessaires à ce sujet pour qu'on puisse identifier les causes.

Key Words: *climate change; clutch size; laying date; length of laying season; nest predation; rate of seasonal decline of clutch size; weather*

“And I feel, so much depends on the weather”
Plush, Scott Weiland of Stone Temple Pilots

INTRODUCTION

Many North American birds, including aerial insectivores (tyrannid flycatchers, nightjars, swallows, and swifts), are experiencing population declines (Rosenberg et al. 2019). Aerial insectivores are ecologically diverse, however, and the timing and geographic extent of declines of flycatchers often differ from other aerial insectivores (Smith et al. 2015). Among tyrannids, downward population trends are also not uniform (Spiller and Dettmers 2019) and when they occurred they began earlier in mesic central and eastern North America than in the xeric west (Smith et al. 2015). Spiller and Dettmers (2019) suggested that declines of aerial insectivores were possibly linked to habitat loss, climate change, or nonbreeding season events, but proposed declining food quantity or quality as the main driver. However, given that the mid-1980s was a period of accelerated climate change (Arias et al. 2021) and also the beginning of the decline of aerial insectivores (Nebel et al. 2010, Smith et al. 2015), climate change may be a more important contributor than recognized (e.g., Berzins et al. 2020, Cox et al. 2020).

Reproductive responses to climate change are potentially numerous but the most immediate is an earlier start to laying (Dunn and Winkler 2010, Kluehn et al. 2017) arising from an acceleration of spring phenology (Cayan et al. 2001, Slayback et al. 2003, Arias et al. 2021). Timing of laying is important for birds because not only does clutch size often decline with laying date (e.g., Murphy 1986, Dhondt et al. 2002, Winkler et al. 2002), but delayed laying can reduce chances of raising replacement or second broods (Cooper et al. 2011, Townsend et al. 2013, Berzins et al. 2020), reduce the probability of offspring recruitment (Saino et al. 2012, Öberg et al. 2014), and, delay molt (Dhondt and Smith 1980), departure of fall migrants (Mitchell et al. 2012), and reproduction in the following year (Low et al. 2015).

However, understanding the full effect of climate change for birds is complicated because responses vary with ecology and/or behavior. For example, phenotypic plasticity of resident and short-distance migrants appears sufficient to enable timing of laying to track phenology (Phillimore et al. 2016), but long-distance migrants (which include nearly all aerial insectivores) may be less capable of timing reproduction to track early season changes in food abundance caused by warming climates (Källander et al. 2017, Kluehn et al. 2017, Samplonius et al. 2018). An earlier start to laying also has the potential to increase the length of laying seasons, and length of the laying season has increased in many multi-brooded species. But, for reasons not yet clear, laying season length has either not changed or even shortened in single-brooded species (Dunn and Møller 2014, Halupka and Halupka 2017). A possible explanation for unchanging laying season lengths is that timing of laying has not advanced, but this fails to account for the shortening seen in others (Halupka and Halupka 2017).

How climate change will affect clutch size is also uncertain. Clutch size generally declines seasonally in single-brooded species and has increased over time in some species as laying dates advanced (e.g., Schaefer et al. 2006, Nilsson et al. 2020). However, it is not clear that an acceleration of spring phenology will lead to greater population productivity because advancement of laying date may

be constrained by inflexible migration schedules (Lany et al. 2016), antagonistic selection on other traits (Winkler et al. 2002, Sheldon et al. 2003), or increased likelihood of failure of early nests because of extreme weather that occurs most often in the early laying season (Shipley et al. 2020). Although evidence exists to tie annual variation in timing of laying by birds to ambient temperature, including effects of climate change, the extent to which changing laying date affects other life history traits is poorly explored.

The Eastern Kingbird (*Tyrannus tyrannus*; hereafter kingbird) is an aerial insectivorous New World Flycatcher (Tyrannidae) that annually migrates between North and South America (Murphy and Pyle 2018). Breeding Bird Survey data (Sauer et al. 2020) indicate a range-wide population decline of kingbirds since at least the mid-1980s (Nebel et al. 2010, Rosenberg et al. 2019, Spiller and Dettmers 2019), a finding corroborated by 10-plus year field studies from the 1990s in central New York (NY), USA, (Murphy 2001) and the 2000s in southeastern Oregon (OR), USA (Murphy et al. 2020). If climate change is responsible for diminished reproductive processes and contributed to the observed population declines, then weather should be an important determinant of annual variation in reproduction. To test this expectation, and to assess the potential contribution of climate change to kingbird population declines, we here report 22 years of reproductive data for the climatically distinct declining NY and OR kingbird populations.

Assuming initiation of laying is temperature-dependent, we (a) identified the prelaying period at both sites when annual variation in ambient temperature appeared to trigger the start of egg-laying. We then (b) evaluated the contributions of prelaying temperature, weather just prior to egg-laying, and resources (i.e., surrogates of food) to annual variation in the timing of laying, and (c) established the degree to which annual variation in clutch size, length of the laying season, the rate at which clutch size declined seasonally, and nest productivity were influenced by laying date, weather at the start of the laying season, and resources. By combining data from long-term studies at two very climatically different sites during which time climates were changing (see Methods), we, lastly, sought (d) to establish the extent to which climate change contributed to population declines of kingbirds in NY and OR.

METHODS

Species and study sites

Kingbirds are obligate tree/shrub nesting birds that are strongly associated with grasslands, savannah, riparian zones, and edges of ponds and lakes (Murphy and Pyle 2018). Socially monogamous pair bonds form on territories established by males. Females build open-cup nests in trees and incubate eggs without male assistance, but both sexes feed and defend young against predators (Murphy and Pyle 2018). One brood is raised annually, but replacement of failed first nesting attempts is common. Early laying increases the probability of recruiting young (Dolan et al. 2009).

Twelve years of research was conducted on private lands in central NY (1989 to 2000) primarily along the riparian zone of Charlotte Creek and surrounding fields in Delaware County (42.47 N, -74.84

W; 354 m above sea level [asl]). Research in southeastern OR (2002 to 2011) was conducted on the southern half of Malheur National Wildlife Refuge (MNWR) in Harney County (42.97 N, -118.87 W; 1279 m asl), located at the northern end of the Great Basin Desert. Kingbirds nested almost exclusively along the riparian zone of the Donner und Blitzen River that transects MNWR.

Climate is highly seasonal at both sites (National Oceanic and Atmospheric Administration; <http://www.noaa.gov/>). Annual monthly mean temperature (average of daily low and high temperatures) from Cooperstown, NY (42.702 N, -74.977 W) and Burns, OR (43.585 N, -119.061 W), the weather stations with long-term records nearest our sites (30 and 75 km distant, respectively), is highest in July at both sites (19.7 °C and 19.2 °C, in NY and OR, respectively), with annual mean monthly low being either December (OR: -4.4 °C) or January (NY: -10.0 °C). Monthly mean temperatures during the breeding season tend to be higher in NY in May (12.8 °C vs. 10.6 °C), June (17.5 °C vs. 14.7 °C), July (as noted), and August (18.9 °C vs. 18.3 °C). However, wide swings of daily temperature in the desert throughout the breeding season results in daily low and high temperatures that average 6.1 ± 0.38 °C SE lower and 3.1 ± 1.28 °C SE higher, respectively, in OR. Total annual precipitation is four times greater in NY (1,109.5 mm) than OR (277.4 mm), but just as importantly, precipitation is distributed equally among months in NY but falls mostly in the nonbreeding season (September through April) in southeastern OR (74.7% of annual total).

Field methods

The same methods were used in all years and are detailed elsewhere (Murphy 1986, Murphy et al. 2020 and Appendix 1). Field studies yielded data on (a) laying dates (= date of first egg of clutches), (b) clutch size, (c) mean egg mass per clutch, (d) whether failed (= 0 young fledged) initial nests were replaced, and (e) number of young fledged from successful nests. Analyses of laying date, clutch size, seasonal rate of clutch size decline, and proportion of initial nests that were replaced were limited to first nests of the year. However, because nest failure was common, the contribution of replacement nests to productivity (= number of young to fledge/nest) was potentially high and thus length of laying season and productivity included both first and replacement nests. Mean number of pairs per year for calculating annual laying date and clutch size was 50 (± 3.5 pairs) in NY and 40 (± 4.3 pairs) in OR. For calculation of proportion of failed first nests that were replaced, sample sizes were 66 (± 3.5 pairs) in NY and 58 (± 3.0 pairs) in OR. Annual sample sizes for calculation of productivity of successful nests and the combined sample of successful and failed nests were 38 (± 2.9 nests) and 87 (± 5.8 nests), respectively, in NY and 26 (± 1.3 nests) and 74 (± 5.0 nests), respectively, in OR.

Statistical analyses

Laying date was counted continuously from 1 May (i.e., 1 June = day 32). Length of the laying season was the difference between laying dates of the last replacement nest and first initial nest of the season. Fresh egg mass (M) was estimated from maximum length (L) and breadth (B) measurements of eggs using the formula $Mass = C \cdot (L \cdot B^2)$, where $C (= 0.545)$ was determined from measurements of eggs weighed on the day of laying (M. T. Murphy, unpublished data). Clutch mean egg mass was used instead of mass of individual eggs to calculate annual mean egg mass.

To determine whether annual variation in mean laying date was tied to ambient temperature during particular weeks prior to the initiation of laying, we used correlation analysis to compare mean annual laying date to mean daily ambient temperature averaged over a sliding 30-d window beginning with 1 April. Each subsequent time period shifted by 10 days so that the next period began on 11 April, then 21 April, and on to the last 30-d period beginning on 21 May. We refer to this as “prelaying temperature.” Response variables in our other analyses were annual variation in (a) laying date, (b) length of the laying season, (c) clutch size, (d) seasonal rate of clutch size decline, (e) the proportion of failed first nests that were replaced, (f) number of young fledged from successful nests, and (g) number of young fledged from the combined sample of successful and failed nests. The seasonal rate of clutch size decline was the slope of the regression of first clutch size against laying date. The predictor variables used to examine annual variation in response variable are given in Table 1.

Table 1. Model structure for the general linear model analyses of reproductive traits of Eastern Kingbirds (*Tyrannus tyrannus*) breeding in central New York (1989 to 2000) and southeastern Oregon (2002 to 2011). Ten-d temperature and 10-d rainfall describe average temperature and total precipitation, respectively, in the 10-day period preceding the mean laying date in each year. Mean nestling phase maximum temperature was averaged over the 20-day period over which most nestlings were being fed. Analyses of laying date, length of laying season, and clutch size and its seasonal rate of decline included interaction terms between year and site, site and 10-d temperature, and site and 10-d rainfall. Proportion of failed nests to be replaced also included a year by site interaction, while analyses of nest productivity included interactions between year and site and mean nestling phase maximum temperature and site.

Response variable	Predictors variables
Laying date	Site, prelaying temperature, 10-d temperature, 10-d rainfall, year
Length of laying season	Site, laying date, 10-d temperature, 10-d rainfall, success of first nests, year
Clutch size	Site, laying date, 10-d temperature, 10-d rainfall, egg mass, year
Rate of seasonal decline in clutch size	Site, laying date, length of laying season, 10-d temperature, 10-d rainfall, egg mass
% of failed first nesting attempts replaced	Site, laying date, length of laying season, success of first nests, egg mass, year
Young per successful nesting attempt (first & replacement)	Site, laying date, clutch size, success of first nests, length of laying season, rate of seasonal decline of clutch size, mean nestling phase maximum temperature, year
Young per nesting attempt (first & replacement)	Site, laying date, clutch size, success of first nests, length of laying season, rate of seasonal decline of clutch size, mean nestling phase maximum temperature, year

In addition to prelaying temperature, we also expected annual variation in mean laying date to result from variation in weather on shorter time scales. We thus calculated the mean daily temperature and total precipitation occurring in the 10 days prior to the mean laying date in each year (= 10-d temperature and 10-d rain). We chose 10 days because egg formation requires 4 to 5 days in passerines, and we felt that this and an additional period

of equal length would reflect conditions experienced by females as they produced eggs. Other predictor variables were population parameters. For instance, nest success (number of successful nests/total nests) of first nests of the season was included as a predictor of length of the laying season in the expectation that frequent nest failure would lead to longer laying seasons. Laying date was included in analyses of length of laying season and clutch size because early laying provides more time to produce replacement clutches and clutch size declines seasonally (Murphy 1986). For analyses of clutch size and its seasonal rate of decline we included egg mass as a surrogate of quality of conditions for laying in any given year. Our rationale was based on the fact that egg mass is the most repeatable of avian reproductive traits (Christians 2002), including kingbirds (Murphy 2004), and thus little annual variation is expected. However, kingbirds in Kansas produced larger eggs in years of high food abundance (Murphy 1986), and thus contrary to expectations of energetic trade-offs between number and size of eggs (Smith and Fretwell 1974), we expected large clutches and a slower rate of seasonal decline in years when large eggs were produced if egg production responded directly to energetic conditions at laying. Lastly, nestling kingbirds grow poorly when ambient temperatures are high (Murphy 1985), and thus to evaluate the role of weather on production of fledglings we computed average maximum temperature over the period when most young were being fed in the nest (“nestling phase”). To do so we obtained mean annual hatching date by adding days to lay a clutch (= clutch size - 1 to account for hatching asynchrony; Gillette et al. 2021) and mean incubation length (15 days; Gillette et al. 2021) to mean laying date. Most nests (75%) hatch eggs over a 3-week period that is skewed to the right of mean hatching date because of the influence of replacement nests. We thus calculated mean maximum temperature over the nestling phase beginning 5 days before the mean hatching date, the hatching date, and the 14 days after mean hatching date (= MaxTemp). Number of days of rain and total rainfall in the nestling phase were so low in OR that it was impossible to include precipitation variables in analyses of nest productivity.

We used all subsets analysis of the predictor variables listed in Table 1 to identify sources of variation in each response variables using generalized linear models (GLMs). Competitive models were identified using an information theoretic framework with Akaike’s Information Criterion (corrected for small sample size, AICc) as our measure of model fit; model weights (w_i) and log-likelihood values are reported for all competitive models (≤ 2.0 AICc units of the top model). We then modeled averaged parameter estimates from competitive models. In lieu of year, year of study (1 to 12 in NY and 1 to 10 in OR) was included in all analyses as there was no overlap in years between sites, and our goal was to determine if response variables changed over time. To account for possible different yearly trends across sites, we included a site by year interaction in all analyses. Moreover, because of the pronounced climatic differences between sites, we included a site by 10-d temperature and site by 10-d rain interaction term in analyses of laying date, length of laying season, clutch size, and rate of seasonal decline of clutch size, and a site by MaxTemp interaction term in analyses of productivity. GLMs were run with distribution set at normal and an identity link function. Ten-d rain exhibited right-skewed distributions and therefore they were \log_{10} transformed. All predictor and response

variables were standardized to a mean of zero and standard deviation of 1.0.

We used STATISTX (ver. 9.0) or JMP PRO (ver. 14) for analyses; statistics are reported as means \pm SE (n). Although we report P-values, evaluation of the statistical contribution of predictor variables were based upon whether 85% confidence intervals (Arnold 2010) of model averaged parameter estimates overlapped zero.

RESULTS

Temporal aspects of reproduction

Annual variation in mean laying date (Appendix 1, Table A1.1) was dependent on prelaying temperatures (Fig. 1A). The strongest association of temperature with the start of laying in NY was the 30-d period beginning on 1 May, but in OR it came three weeks later (Appendix 1, Table A1.2). Scaling calendar laying date to a mean of zero at both sites showed that laying became progressively earlier with increasing prelaying temperature in an identical manner in NY and OR (Fig. 1B; ANCOVA: slope, $F_{1,19} = 0.08$, $P = 0.774$; elevation: $F_{1,20} = 0.01$, $P = 0.90$; $r^2 = 78.1\%$, $P < 0.001$).

Fig. 1. Relationship between the (A) average date of clutch initiation (date of 1st egg) of initial clutches of Eastern Kingbirds (*Tyrannus tyrannus*) and average ambient temperature over a 30-day period preceding the start of the breeding season. The 30-day periods for central New York (open circles; $r^2 = 0.834$, $P < 0.001$) and southeastern Oregon (filled circles; $r^2 = 0.767$, $P = 0.001$) were 1 to 30 May and 21 May to 19 June, respectively. In (B), average breeding date in both New York and Oregon were rescaled by subtracting the grand mean from each year’s average value so that the grand mean equaled zero for both sites (r^2 for combined sample = 0.747, $P < 0.001$). Dashed lines around regression lines are 95% confidence intervals.

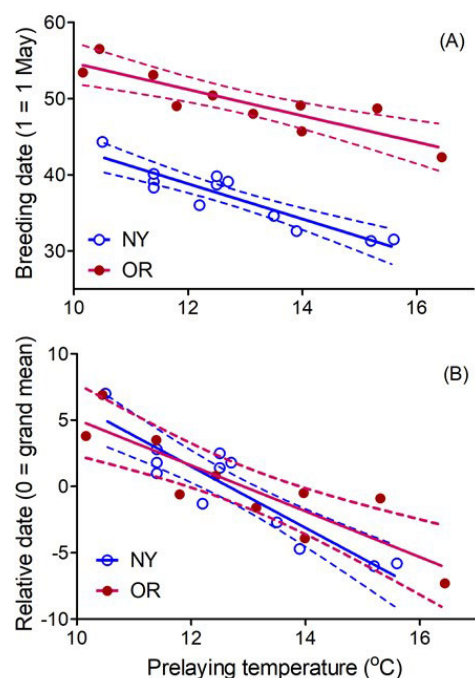


Table 2. Results of analyses of reproductive traits of Eastern Kingbirds (*Tyrannus tyrannus*) breeding in central New York (1989 to 2000) and eastern Oregon (2002 to 2011) using generalized linear models of all possible combinations of predictor variables. Output of all competitive models ($\Delta AICc \leq 2.0$) include number of parameters (k), AICc and $\Delta AICc$ scores, along with model weights and log likelihood of each model.

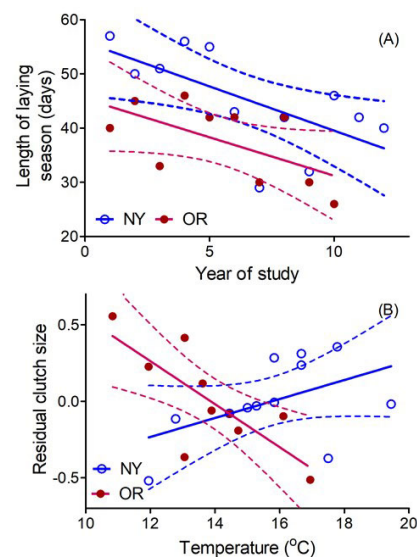
Response variable	Model	k	AICc	$\Delta AICc$	w_i	Log likelihood
Laying date (LayDate)	Site + Prelying temperature	4	9.251	0.000	0.320	-0.551
	Site + Prelying temperature + 10-d Rain	5	9.673	0.422	0.259	-2.039
	Site + Prelying temperature + Site*Year	5	9.760	0.509	0.248	-1.995
	Site + Prelying temperature + Site*10-d temp	5	10.479	1.228	0.173	-1.430
Length of laying season (LoLS)	LayDate + NestSucc + Year + 10-d temp + Year*Site	7	44.449	0.000	----	11.224
Clutch size (ClSize)	Site + Egg mass + LayDate + Site*Year + Site*10-d temp	7	12.023	0.000	----	-4.989
Rate of decline of clutch size	LoLS + Site*10-d rain	4	59.200	0.000	----	24.424
Prop. failed first attempts replaced	LayDate	3	63.050	0.000		27.858
	LayDate + NestSucc	4	64.309	1.259		26.978
Young per successful nest	MaxTemp x Site + ClSize + CSdecline + LoLS	6	50.675	0.000	0.385	16.538
	MaxTemp x Site + Site + NestSucc	5	51.485	0.810	0.253	18.867
	MaxTemp x Site + ClSize + LoLS	5	51.880	1.205	0.208	19.065
	MaxTemp x Site + LayDate + ClSize	5	52.423	1.748	0.159	19.337
Young per nesting attempt	NestSucc + MaxTemp x Site + LoLS + ClSize + CSdecline	7	3.887	0.000	0.434	-9.057
	NestSucc + MaxTemp x Site + Site	5	4.684	0.797	0.291	-4.534
	NestSucc + MaxTemp x Site + Site + MaxTemp	6	4.796	0.909	0.275	-6.402

10-d temp and 10-d rain = mean temperature and total rainfall in 10 days preceding mean laying date, respectively; NestSucc = proportion of first nestling attempts to fledge young; CSdecline = rate of seasonal decline of clutch size; MaxTemp = mean maximum temperature when young were in the nest being fed by parents.

Site and prelying temperature comprised the top model from the GLM analyses of laying date (Table 2), but three additional competitive models emerged (Table 2). At both sites laying was delayed by high 10-day rainfall (Table 3). A year by site interaction also existed as a result of the difference between sites in coefficients (β) describing the relationship between laying date and year (ANCOVA: $F_{1,18} = 5.90$, $P = 0.026$); laying date was increasingly delayed in the later years of our study in OR ($\beta = 0.417 \pm 0.149$, $F = 2.80$, $P = 0.023$), but was independent of year in NY ($\beta = -0.123 \pm 0.149$, $F = 0.82$, $P = 0.431$). Change of date with year in OR remained (GLM: $\beta = 0.212 \pm 0.080$, $X^2 = 5.29$, $P = 0.021$) after accounting for the relationship between laying date and prelying temperature ($\beta = -0.324 \pm 0.063$, $X^2 = 13.02$, $P < 0.001$). Date and year remained unrelated in NY ($\beta = -0.041 \pm 0.057$, $X^2 = 0.50$, $P = 0.480$) after accounting for the association of laying date and prelying temperature ($\beta = -0.535 \pm 0.070$, $X^2 = 21.28$, $P < 0.001$). Confidence intervals of parameter estimates for 10-d rain, the year by site interaction, and year by temperature interaction included zero.

Length of the laying season yielded a single competitive model (Table 2); longer laying seasons occurred in years with early onset of laying, when success of first nests of the season was low, in earlier years of study at both sites (Fig. 2A), and when 10-d temperature was low. A year by site interaction also existed because of the stronger relationship between length of the laying season and year of study in NY ($\beta = -0.598 \pm 0.163$, $t = 3.67$, $P = 0.004$) than OR ($\beta = -0.135 \pm 0.225$, $t = 0.60$, $P = 0.565$) after removing effects of other variables in the model.

Fig. 2. (A) Length of the laying season (clutch initiation date of last replacement nest of the year–clutch initiation date of first initial nest of the year) in relation to year of study for Eastern Kingbirds (*Tyrannus tyrannus*) breeding in central New York (open circle; $r^2 = 0.424$, $P = 0.022$) and southeastern Oregon (filled circle; $r^2 = 0.360$, $P = 0.066$). (B) Residual clutch size (effects of site, date, and egg mass removed by regression analysis) in relation to mean temperature in the 10-d period preceding the mean breeding date for Eastern Kingbirds breeding in central New York and southeastern Oregon. Dashed lines around regression lines are 95% confidence intervals.



Clutch size

Analysis of clutch size (Table 2) yielded one competitive model indicating that larger clutches were produced in OR, if it was a year in which laying was early (Table 3; Appendix 1, Fig. A1.1) and in years when large eggs were laid (Table 3; Appendix 1, Fig. A1.2). An interaction also existed between clutch size and temperature (Table 3) because smaller clutches were laid in years of high temperatures in OR but lower temperatures in NY (Fig. 2B). Clutch size also exhibited opposite tendencies with year in NY ($\beta = 0.206 \pm 0.137$, $t = 1.51$, $P = 0.163$) and OR ($\beta = -0.209 \pm 0.221$, $t = 0.94$, $P = 0.373$), leading to an interaction of site with year (Table 3).

The only competitive model (Table 2) for the rate at which clutch size declined seasonally indicated that the rate of decline was more rapid (i.e., more negative) when laying season was short (Table 3; Fig. 3A). An interaction also existed between site and 10-d rain. No relationship existed in NY, but rate of decline dropped sharply (i.e., slope approached zero) when 10-d rain was abundant in OR (Fig. 3B).

Fig. 3. Rate of seasonal decline of clutch size of initial nests of the season in relation to (A) length of the laying season, and (B) total rainfall in the 10-day period preceding each year's mean laying date for Eastern Kingbirds (*Tyrannus tyrannus*) breeding in central New York (open circles) and southeastern Oregon (filled circles). Dashed lines around regression lines are 95% confidence intervals.

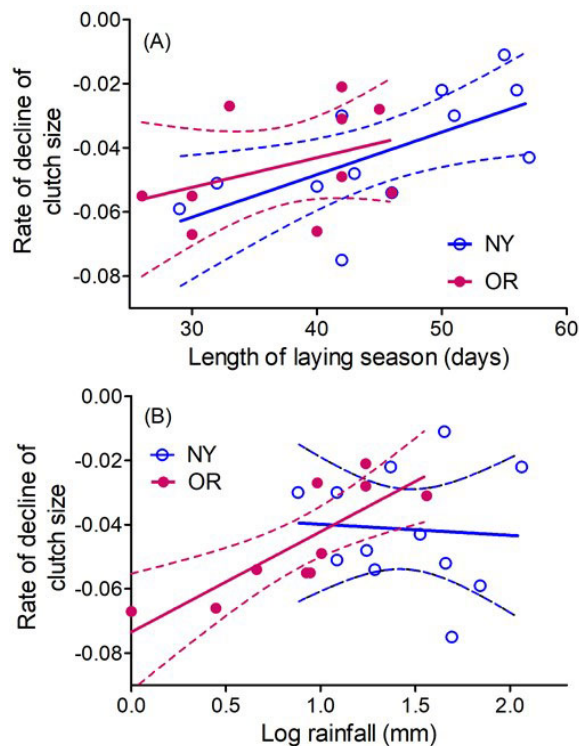


Table 3. Model averaged standardized coefficients (standard error in parentheses) and 85% confidence (i.e., compatibility; Wasserstein et al. 2019) intervals from analyses of reproductive traits of Eastern Kingbirds (*Tyrannus tyrannus*) in New York (1989 to 2000) and Oregon (2002 to 2011) in relation to a suite of environmental and population traits (Table 1). Predictor variables with 85% CI (Arnold 2010) that excluded zero are highlighted in bold font.

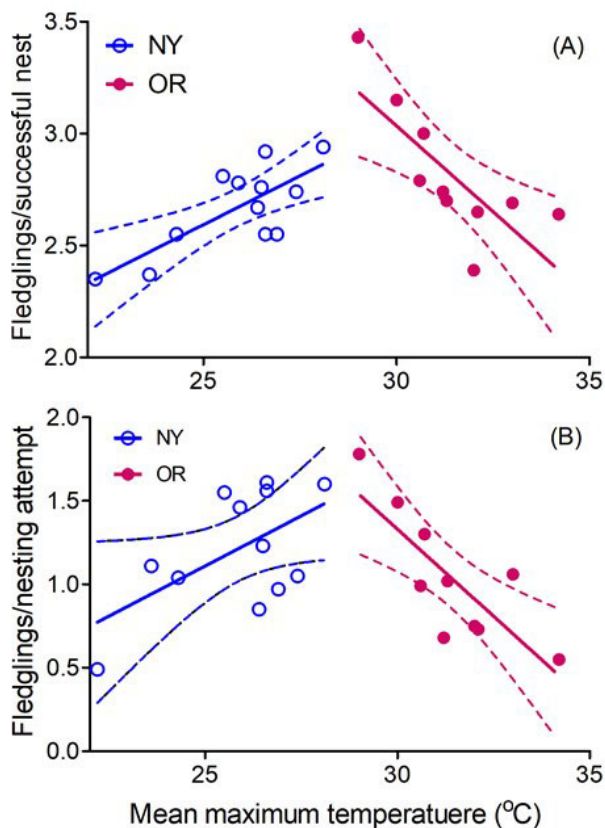
Response variable	Predictor variable	Estimate (SE)	85% CI
Laying date	Site	0.886 (0.063)	0.794 to 0.978
	Prelying temp	-0.465 (0.054)	-0.544 to -0.385
	10-d rain	0.028 (0.027)	-0.010 to 0.066
	Site*Year	0.024 (0.022)	-0.009 to 0.056
	Site*10-d temp	0.014 (0.015)	-0.008 to 0.036
Length of laying season	Laying date	-0.980 (0.121)	-1.157 to -0.803
	Nest success	-0.479 (0.102)	-0.628 to -0.330
	Site*Year	0.398 (0.103)	0.247 to 0.549
	Year	-0.356 (0.098)	-0.499 to -0.212
	10-d temp	-0.342 (0.114)	-0.509 to -0.175
Clutch size	Site	0.804 (0.132)	0.611 to 0.997
	Egg mass	0.517 (0.088)	0.388 to 0.646
	Laying date	-0.513 (0.094)	-0.651 to -0.375
	Site*10-d temp	-0.244 (0.050)	-0.317 to -0.171
	Site*Year	-0.137 (0.052)	-0.213 to -0.061
Rate of CS decline	LoL season	0.478 (0.162)	0.241 to 0.715
	Site*Rain	0.467 (0.200)	0.174 to 0.760
Failed first nests replaced	Laying date	-0.504 (0.192)	-0.785 to -0.223
	Nest success	-0.089 (0.088)	-0.218 to 0.039
Young/successful nest	Site x MaxTemp	-1.227 (0.295)	-1.660 to -0.795
	LoLS	-0.260 (0.139)	-0.464 to -0.056
	Clutch size	0.255 (0.119)	0.081 to 0.429
	Site	0.155 (0.121)	-0.022 to 0.332
	CSdecline	0.121 (0.090)	-0.011 to 0.253
	Laying date	0.055 (0.052)	-0.022 to 0.132
	Nest success	0.078 (0.077)	-0.034 to 0.190
	Year	0.078 (0.077)	-0.034 to 0.190
Young/nesting attempt	Nest success	0.908 (0.057)	0.825 to 0.991
	Site x MaxTemp	-0.307(0.112)	-0.472 to -0.143
	LoLS	-0.069 (0.044)	-0.134 to -0.005
	Rate of CS decline	0.054 (0.035)	0.002 to 0.106
	Clutch size	0.052 (0.035)	0.001 to 0.104
	Site	0.144 (0.074)	0.036 to 0.252
	MaxTemp	-0.046 (0.088)	-0.176 to 0.084
	Year	0.078 (0.077)	-0.034 to 0.190

Nest replacement and nesting productivity

On average, 50% or less of first nesting attempts in NY (0.46 ± 0.034 SE, range = 0.21-0.63) and OR (0.35 ± 0.038 , range = 0.19-0.56) produced fledglings ($t = 2.08$, $df = 20$, $P = 0.051$), and nest predation was the main cause of failure in both NY ($82.6 \pm 2.4\%$, range = 67.4% to 93.3%) and OR ($92.4\% \pm 2.2\%$, range = 79.0% to 97.4%). In only one year (in NY) did starvation of entire broods claim more than 3% of nests and in 18 of 22 years no nests failed because of nestling starvation. The proportion of failed first nests that was replaced was higher ($t = 1.93$, $P = 0.068$) in NY (0.59 ± 0.051 , range = 0.30-0.92) than OR (0.45 ± 0.050 , range = 0.24-0.80). However, laying date, not site, was retained in both competitive models from the GLM analysis of nest replacement (Table 2); nests were more likely to be replaced in years when laying was early (Table 3). Confidence limits for nest success, which was included in the second ranked model, included zero (Table 3).

All models of the production of young from first and replacement nests, whether restricted to successful nests (Fig. 4A) or both successful and failed nests (Fig. 4B), included a MaxTemp by site interaction (Table 2). The interaction arose from a pattern of increasing offspring production in warmer years in NY, but declining production of young in warmer years in OR (Fig. 4). For successful nests, the top model of the four competitive models indicated that more young were also produced in years when clutch size was large, the seasonal rate of clutch size decline was low, and laying season was short (Table 2). However, confidence intervals of model averaged parameter estimates for site, nest success, rate of clutch size decline, and laying date all included zero (Table 3). When the analysis was expanded to include failed nests, nest success, and the MaxTemp by site interaction appeared in all competitive models (Table 2; Fig. 4). Nest productivity was also highest in years when clutch size was large, seasonal rate of clutch size decline was low, and when laying season was short (Table 3).

Fig. 4. The relationship between mean number of Eastern Kingbirds (*Tyrannus tyrannus*) young fledged per successful nest (A) and mean number of young fledged from both successful and failed nests (B) from central New York (open circles) and Oregon (filled circles) in relation to mean maximum temperature during the nestling period. Both analyses included initial nests of the season and nests that replaced failed initial nesting attempts. Dashed lines around regression lines are 95% confidence intervals.



DISCUSSION

Kingbird reproduction and weather

Annual variation in weather must drive variation in reproduction or survival if climate change is to have consequences for populations, and previous work on kingbirds showed that foraging rate (Murphy 1987), nestling growth (Murphy 1985), nestling starvation (Murphy 1983, 2001), and incubation and hatching asynchrony (Gillette et al. 2021) depend on weather. Our current findings, from sites on opposite sides of North America where climates differ greatly, yielded additional evidence that kingbird reproduction depends on weather. First, the equally tight relationship between the start of laying and the absolute temperatures experienced early in the laying season (Fig. 1B), despite the nearly two-week difference in average laying date between sites, clearly shows the importance of early laying season weather for the timing of reproduction. Plant (Crimmins et al. 2010) and ectothermic invertebrate prey (Bale et al. 2002, Hassall et al. 2007, Roy et al. 2015) growth and development are tightly tied to temperature and the identical responses of kingbirds to temperature at the two sites, albeit at different dates (Fig. 1A), was likely a direct response to growth and abundance of invertebrate prey as ambient temperatures rose (Jamieson et al. 2012). Length of the laying season was also shorter in years when 10-d temperature was high. Although it is unclear why, high temperatures just prior to peak laying date may portend poorer conditions (i.e., hotter and drier) for breeding later in the season.

Clutch size and its seasonal rate of decline also responded to annual variation in 10-d temperature and rainfall, but oppositely in NY and OR. Higher temperatures in mesic NY possibly enhanced primary productivity and invertebrate prey abundance, enabling larger clutches to be laid, but without affecting its seasonal rate of decline. Smaller clutch size in drier years is common for passerines from xeric environments (Bolger et al. 2005, Illera and Diaz 2006), and in xeric OR, smaller clutches were laid when 10-day temperature was high, and clutch size declined more rapidly when 10-day rainfall was low. Summer primary productivity in OR is most dependent on winter precipitation (Rotenberry and Wiens 1989), and abundant rain just prior to the peak laying period in OR may have helped maintain primary productivity (Lauenroth and Sala 1992, Knapp et al. 2001) and invertebrate food supplies into summer.

The different MaxTemps experienced in NY and OR, and the responses of nest productivity to those temperatures was striking (Fig. 4). Nestling starvation can be eliminated as a cause for the opposite response to MaxTemp because nest predation caused nearly all nest failures. That productivity of successful nests also exhibited the same MaxTemp by site interaction suggests that predation during years of high nest failure also caused partial brood loss within successful nests. We speculate that both low and high temperatures caused parents to spend extra time away from nests, leaving them unattended and exposed to predators. Low attendance at low temperatures may have occurred because low temperatures limit insect flight activity (Järvinen and Väisänen 1984, Nooker et al. 2005) and reduce kingbird foraging rate (Murphy 1987), leading possibly to low parental foraging success. Cox et al. (2013) showed that nest predation rates by snakes and birds increased with temperature, and low attendance at high

MaxTemp may also have occurred if high temperatures caused parents to seek shelter away from nests because of heat stress, or because parents spent more time away from nests because high MaxTemp reduced parental foraging success. Further research is needed to identify the cause for the decline in productivity at high temperatures.

Climate change

Although variability in temperature amongst years was high, and periods of stasis or reversals occurred (Appendix 2), breeding season temperature increased at both study sites between 1974 and 2013. Nevertheless, timing of egg-laying in NY was independent of year. By contrast, egg-laying was delayed over time in OR. Temperature in NY increased during June and July over our 12-year study, but this was not true of May (Appendix 2, Fig. A2.1), which likely explains the lack of a change in laying date with year in NY because May temperatures were the best predictor of annual laying date (Appendix 1, Table A1.2).

Mean maximum monthly temperature in southeastern OR over the 28 years preceding our study increased in May, did not change in June, but increased in July (Appendix 2, Fig. A2.2). That 28-year warming trend was followed by a 10-year decline in June and July temperature (but not May) as our study began (Appendix 2, Fig. A2.2). Pre-laying temperature did not decline between 2002 and 2011 ($r = -0.497$, $P = 0.144$). Hence, although temperature drove annual variation in laying date, the increasing delay with year in OR, after accounting for pre-laying temperature, indicates that other factors contributed to delayed laying. Southwestern North America, including our study site, has experienced an anthropogenically exacerbated megadrought over the years of our study (Williams et al. 2020). Hence, the increasing delay in annual laying date in OR, we suspect, was tied to increasingly dry weather driven by climate change.

Shortened laying seasons driven by climate change occur most often in single-brooded long-distance migrants such as kingbirds (Halupka and Halupka 2017), and indeed, we documented shortened laying seasons over time at both sites. Moreover, we showed that the seasonal decline of clutch size was more rapid in years of short laying seasons. The shorter laying season over time in NY was possibly caused by a decline in late season environmental conditions associated with rising June and July temperatures between 1989 and 2000 (Appendix 2, Fig. A2.1). In OR, despite the decline of daily maximum June and July temperatures between 2002 and 2011, temperatures remained higher during our study years than in the previous 28 (Appendix 2, Fig. A2.2). This, combined with severe regional drought (Williams et al. 2020), may have led to increasingly severe late season conditions that resulted in reduced laying season length.

Pinpointing a common cause for declines of aerial foragers is unlikely (Michel et al. 2016), but in kingbirds, we can narrow the possibilities. Quality or quantity of insect prey is an unlikely driver because nestling starvation was uncommon, nest predation was the cause of variation in nest productivity, and productivity was the driver of variation in kingbird population growth rate in both NY (Murphy 2001) and OR (Murphy et al. 2020). Events outside of the breeding season are also unlikely because neither adult nor first-year survival of kingbirds changed over the 10 years of study in OR (Murphy et al. 2020), and survival of adult kingbirds during

the periods of study in NY and OR were high and virtually identical (65%; Murphy 2001, Redmond and Murphy 2012). Murphy (2001) identified habitat loss caused by succession of the abandoned open habitats used by kingbirds as an important driver of population decline in NY. By contrast, declining nest productivity associated with high environmental temperature suggests climate change as a driver of population decline in OR with the underlying mechanism being elevated nest predation (a similar conclusion in shorebirds; Kubelka et al. 2018). Corvids, especially Black-billed Magpies (*Pica hudsonia*), are the primary nest predators of kingbirds in OR. Corvids are year-round residents at our OR study site, and increasingly warmer and/or shorter winters may result in greater overwinter survival and higher abundance of nest predators.

Assuming continuing climate change, kingbird populations in central NY may benefit because of the advancement of laying date, production of larger clutches, and greater nest productivity linked to increasing temperature, and greater likelihood of nest replacement with early laying. The same cannot be said for OR given falling nest productivity with rising ambient temperature. New York and OR likely represent climatic endpoints of what is a continuum of climate change across the kingbird's geographic range, and additional work is needed to ascertain likely trajectories for populations falling between these endpoints, and to understand the relationship between nest predator populations and weather, the influence of weather on kingbird parental behavior, and the link between nest predator and kingbird populations. Kingbirds, like most tyrannid flycatchers, are open-cup nesters that experience greater nest loss to predators than the primarily cavity/niche-nesting swifts and swallows (Martin and Li 1992), and additional work is needed to determine whether population declines of other tyrannids are linked to nest predation.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2203>

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Appendix 1

Michael T. Murphy, Lucas J. Redmond, Amy C. Dolan, Nathan W. Cooper, Karen Shepherdson, Christopher M. Chutter, and Sarah Cancellieri. Weather and climate change drive annual variation of reproduction by an aerial insectivore.

I. Field methods

Our field methods for documenting population size and reproductive statistics in New York (Murphy 1983, 2001) and Oregon (Redmond et al. 2009, Murphy et al. 2020) have remained unchanged over the period of study in New York. Briefly, daily surveys of the populations were conducted on foot, from vehicles along roads dissecting study sites, and from canoes on both Charlotte Creek and the Donner und Blitzen River beginning in mid to late May. Female kingbirds build conspicuous nests in trees (Murphy et al. 1997) and nests of most pairs were found prior to egg-laying (~80%). Nest checks occurred at 2 to 3 -d intervals, but more frequently as hatching and fledging neared, which allowed documentation of laying date, clutch size, egg size, and nesting success. When placed in trees over land, most nests could only be accessed by using either using ladders or climbing trees. Contents of the highest nests (>10 m) could generally only be viewed using a mirror attached to an extensible pole. Nest placed in trees over water were lower in the tree and were often accessible from a canoe, by wading in the water, or sometimes from ladders placed in the water.

Breeding date of each clutch, defined as the day the first egg was laid, was known for most nests by direct observation, and for others was backdated from hatching dates (assuming 1 egg laid/day and an incubation length of 15 days; Gillette et al. 2021) or by comparisons of young to nestling growth curves (Murphy 1981). Egg mass (nearest 0.1 g; Pesola scale) and maximum length and breadth (nearest 0.05 mm; dial calipers) were measured in all years except

2009. In some years eggs were weighed and measured on the day they were laid, but most were not measured until the full clutch was present. Fresh egg mass (i.e., mass recorded within a day of the egg's laying) was estimated for eggs weighed more than two days after laying by using maximum length (L) and breadth (B) measurements of eggs using the formula $\text{Mass} = C \cdot (L \cdot B^2)$, where $C (= 0.545)$ was determined from measurements of eggs weighed on the day of laying (Murphy 1983a). Identical data were collected from renesting attempts, but with only one exception (length of laying season), in this paper we limited all analyses to initial nests of the season. Observations of banded birds at both sites showed that pairs essentially never changed breeding locations after an initial nest failure. We thus assumed for all pairs that a nest appearing at a site after a failure was produced by the pair that nested there initially.

II. Geographic, annual and seasonal variation in reproduction

To test for intrasite annual variation in breeding date (i.e. date of the laying of the clutch's first egg) and clutch size we used analysis of variance (ANOVA) of individual clutches. Date was counted continuously from the start of May (May 1 = 1, June 1 = 32). For each year we then calculated annual means for breeding date and clutch size of initial clutches, length of the laying season (= breeding date of last replacement nest – breeding date of first initial clutch), breeding synchrony (number of days elapsed between the 10th and 90th percentile of breeding dates of initial clutches), and rate of the seasonal decline of clutch size (= slope of regression of size of initial clutch size against breeding date). Comparisons between sites were made using *t*-tests.

Both breeding date and clutch size differed among years at both sites (Table A1.1), while the only trait to not differ between sites was the rate at which clutch size declined seasonally (Table A1.1). EAKBs began to lay 12 days later, on average, in OR than NY, but at both, the

range of laying dates of individual clutches extended over a six-week period. In any given year, however, most initial clutches were laid within an approximate 2-week+ window (= breeding synchrony) that was nonetheless shorter in NY (Table A1.1). Length of laying season, which included replacement nests, was one week longer in NY (Table A1.1), while clutch size was larger in OR despite the later start to breeding (Table A1.1).

Despite site differences in clutch size (Table A1.1), annual variation in clutch size within sites was associated with mean annual breeding date in near identical fashion at both sites (Figure A1.1). Similarly, at both sites larger clutches were laid in years when mean egg mass was large (Figure A1.2). Egg size is highly repeatable within females in Eastern Kingbirds (Murphy 2004) and thus little annual variation is expected. However, Murphy (1986) showed that large eggs are laid in years of high food abundance and thus the positive association between mean annual clutch size and mean annual egg mass likely reflects a positive response for both variables to favorable breeding conditions, most likely high food availability.

We also attempted to determine whether annual variation in mean breeding date was tied to ambient temperature during particular weeks prior to the initiation of breeding. We thus used correlation analysis to compare mean annual breeding date to mean daily ambient temperature averaged over a sliding 30-d window beginning with the 1st of April. Each subsequent time period shifted by 10 days so that the next period began on 11 April, then 21 April, and on to the last 30-d period beginning on 21 May. We refer to this as “prelaying temperature.” Results are given in Table A1.2. In New York, the strongest correlation existed between mean temperature averaged over the period 1 to 30 May, followed by the period between 11 May and 9 June (Table A1.2). Not surprisingly given the later breeding in Oregon than New York (Table A1.1), the strongest correlation between temperature and annual mean breeding date occurred roughly three

weeks later (Table A1.2), with the next strongest correlation being between breeding date and mean temperature over the 30-day period starting on 11 May (Table A1.2).

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TABLE A1.1. Summary of geographic and annual variation in breeding date, breeding synchrony, clutch size, length of the laying season, and seasonal rate of decline of clutch size of initial clutches for Eastern Kingbirds breeding in New York (1989-2000) and Oregon (2002-2011). Cell entries are mean \pm SE (N). Statistical comparison of geographic differences (Student's *t*-test) reported in far-right column. Annual comparisons (analysis of variance) within sites reported below mean values for breeding date and clutch size.

Trait	New York (12 years)	Oregon (10 years)	<i>t</i> (<i>P</i>)
Breeding date	6 June \pm 0.248 days (652) Range = 20 May to 30 June	18 June \pm 0.369 days (452) Range = 31 May to 10 July	26.59 (<0.001)
	<i>F</i> = 25.72, <i>P</i> < 0.001	<i>F</i> = 21.13, <i>P</i> < 0.001	
Breeding synchrony	13.4 \pm 0.81 days (12) Range = 10 to 20 days	17.2 \pm 1.51 days (10) Range = 10 to 29 days	2.31 (0.032)
Length of laying season	45.2 \pm 2.61 days Range = 29 to 57 days	37.6 \pm 7.15 days Range = 26 to 46 days	2.17 (0.042)
Clutch size	3.23 \pm 0.023 eggs (635) Range = 2 to 4 eggs	3.61 \pm 0.031 eggs (438) A Range = 2 to 5 eggs	9.48 (< 0.001)
	<i>F</i> = 2.03, <i>P</i> = 0.024	<i>F</i> = 3.16, <i>P</i> < 0.001	
Rate of seasonal decline of clutch size	-0.041 \pm 0.005 eggs/d (12) Range = -0.011 to -0.075	-0.045 \pm 0.005 eggs/d (10) Range = -0.021 to -0.067	0.51 (0.618)

TABLE A1.2. Correlation coefficients (r) describing the relationships between mean annual breeding date (i.e. laying date of 1st egg of a clutch) of Eastern Kingbirds and ambient temperature in 30-d periods beginning with the 1st of April. Time periods shift in successive 10-d intervals. The period in which temperature showed the strongest correlation with laying date is in bold.

Period	New York; r (P)	Oregon; r (P)
1 to 30 April	-0.431 (0.141)	-0.327 (0.357)
11 April to 10 May	-0.332 (0.268)	-0.164 (0.650)
21 April to 20 May	-0.551 (0.064)	-0.186 (0.608)
1 to 30 May	-0.913 (0.000)	-0.656 (0.040)
11 May to 9 June	-0.656 (0.021)	-0.757 (0.011)
21 May to 19 June	-0.462 (0.131)	-0.876 (0.001)

Figure legends

Figure A1.1. Relationship between mean annual clutch size of initial clutches for each year in relation to the average clutch initiation date (= Breeding date) of initial clutches for Eastern Kingbirds breeding in central NY (open circles; $r^2 = 0.637$, $P = 0.002$) and southeastern OR (filled circles; $r^2 = 0.377$, $P = 0.059$).

Figure A1.2. Mean annual clutch size in relation to mean annual egg mass for Eastern Kingbirds breeding in central NY (open circles; $r^2 = 0.300$, $P = 0.065$) and southeastern OR (filled circles; $r^2 = 0.467$, $P = 0.029$).

Figure A1.1

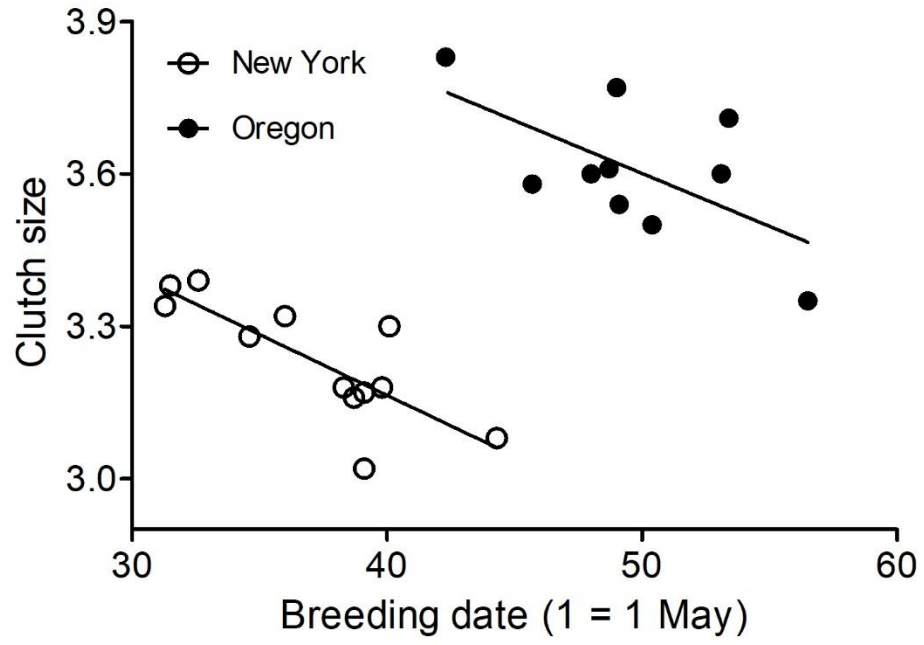
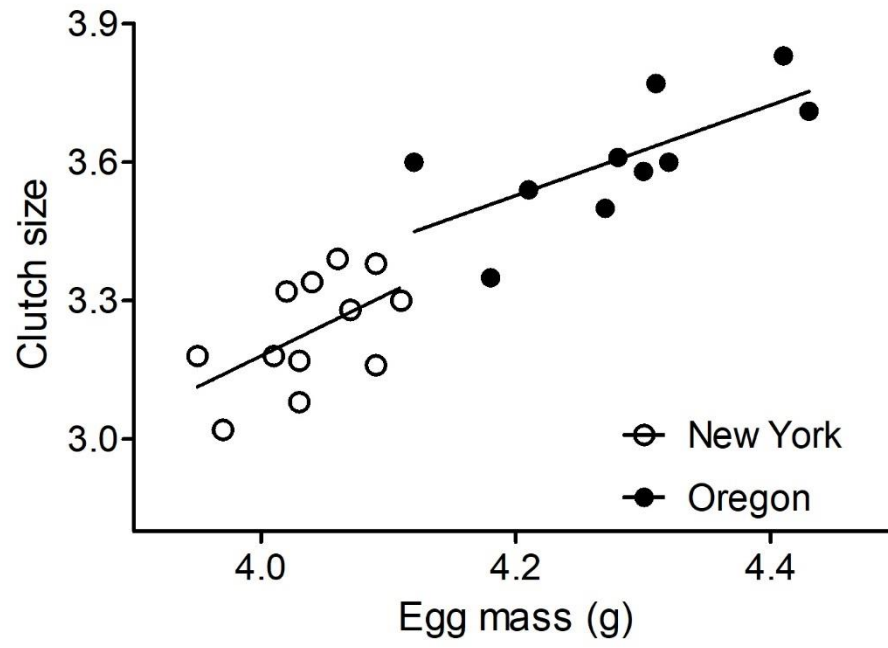


Figure A1.2



Appendix 2

Michael T. Murphy, Lucas J. Redmond, Amy C. Dolan, Nathan W. Cooper, Karen Shepherdson, Christopher M. Chutter, and Sarah Cancellieri. Weather and climate change drive annual variation of reproduction by an aerial insectivore.

The long-term increase in global temperature since the beginning of the Industrial Revolution was interrupted mid-20th century, but began to increase again starting in the mid-1970s (Broecker 2017). We thus obtained temperature data (National Oceanic and Atmospheric Administration; <http://www.yourweatherservice.com/>) for the egg-laying months of the breeding season (May, June and July) for the 40-year period beginning in 1974 to evaluate whether climate change, as measured by temperature, was apparent at our central New York and southeastern Oregon study sites. Data came from weather stations in Cooperstown, New York (42.702 N, -74.977 W), and Burns, Oregon (43.585 N, -119.061 W), the weather stations with long-term records nearest our sites (30 and 75 km distant, respectively). We analyzed these data as a continuous 40-year record, but also separated into pre-study, study, and post-study periods to contextualize our field studies that occurred between 1989 and 2000 (New York) and 2002 to 2011 (Oregon). We examined mean month temperature (average of daily low and high temperatures) and average monthly daily high temperature

Mean monthly temperature in central New York increased from 1974 through 2013 in May ($r = 0.480$, $P = 0.002$), June ($r = 0.729$, $P < 0.001$), and July ($r = 0.589$, $P < 0.001$), but average maximum temperature did not (strongest relationship was May, $r = 0.192$, $P = 0.235$). We thus focused further analyses on mean temperature. Comparison of temperature records for the years preceding (1974 to 1988), during (1989 to 2000) and following (2001 to 2013) our research indicated that mean temperature trends in May trended upward after our study ($r =$

0.551, $P = 0.099$) but did not increase with time either before ($r = 0.136$, $P = 0.628$) or during ($r = 0.344$, $P = 0.274$; Figure A2.1A). On the other hand, June and July data indicated that our study took place during a period of rapidly climbing temperatures. Mean June temperature did not change with year during either the periods before ($r = -0.018$, $P = 0.948$) or after our study ($r = 0.246$, $P = 0.492$), but rose significantly between 1989 and 2000 ($r = 0.663$, $P = 0.019$; Figure A2.1B). Similarly, mean July temperature did not change with year in the years preceding our study ($r = -0.002$, $P = 0.993$), increased in July during our study ($r = 0.616$, $P = 0.033$) and tended to increase over the next 13 years as well ($r = 0.535$, $P = 0.060$; Figure A2.1C).

In Oregon, mean monthly temperature for May ($r = -0.056$, $P = 0.732$) and June ($r = -0.196$, $P = 0.227$) did not change over time, while the weak tendency for an increase in mean July temperature was not significant ($r = 0.243$, $P = 0.130$). Mean monthly maximum temperature showed a weak nonsignificant increase in May ($r = 0.254$, $P = 0.114$), no change in June ($r = 0.105$, $P = 0.518$), but a significant rise in July ($r = 0.604$, $P < 0.001$). Given the stronger signal produced by maximum temperature, we limited further analyses to this variable. Mean maximum temperature tended to increase in the years preceding our study (1974 to 2001) in May ($r = 0.333$, $P = 0.083$) and July ($r = 0.333$, $P = 0.083$), but not in June ($r = 0.093$, $P = 0.639$; Figure A2.2). Omitting one apparent outlier in July raised substantially the fit of maximum temperature to year ($r = 0.455$, $P = 0.017$). Although temperatures were high at the start of our study, 2002 marked the beginning of a 10-year downward trend in mean maximum temperature that was not significant in May ($r = -0.397$, $P = 0.256$), but was significant in June ($r = -0.706$, $P = 0.022$) and July ($r = -0.721$, $P = 0.019$; Figure A2.2). Despite the general cooling trend, mean maximum July temperature was higher between 2002 and 2011 than between 1974 and 2001 (Figure A2.2C; $t = 3.99$, $df = 38$, $P < 0.001$). The cooling trend in southeastern Oregon

appeared to be temporary as mean maximum temperatures in May, June, and especially July of 2012 and 2013 returned to high values consistent with long-term warming of climate (Figure A2.2).

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Figure legends

Figure A2.1. Mean monthly temperature for May (A), June (B), and July (C) from 1974 through 2013 in central New York. Data are presented and analyzed separately for the years before (open circles), during (filled circles), and after our study (half-filled circles).

Figure A2.2. Mean monthly temperature for May (A), June (B), and July (C) from 1974 through 2013 in southeastern Oregon. Data are presented and analyzed separately for the years before (open circles), during (filled circles), and after our study (half-filled circles).

Figure A2.1.

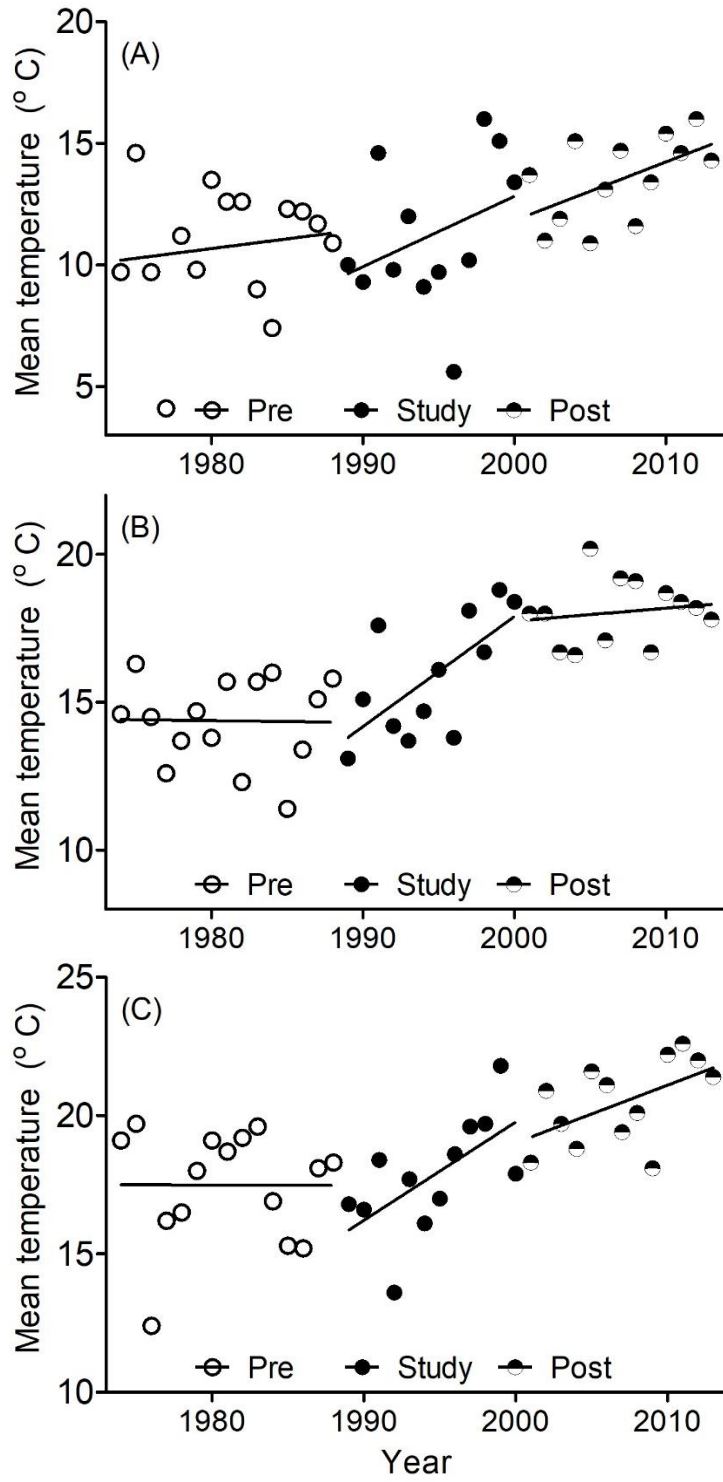


Figure A2.2.

