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Nest Construction Costs Bald Eagles Time but not Breeding Success or Productivity

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ABSTRACT.—Constructing nests costs birds time and energy and may influence breeding success and productivity. The precise nature and extent of these costs is understudied, particularly among raptor species. We used linear and generalized linear mixed models to examine the time and reproductive costs of nest construction to Bald Eagles (*Haliaeetus leucocephalus*) in New Jersey, USA, from 2009 to 2021. To differentiate nest construction costs from the influence of experience, we separately analyzed the breeding performance and phenology of new pairs constructing nests, established pairs constructing nests, and established pairs reusing nests. We also considered the influence of weather, year, and ecoregion. New territorial pairs building nests were generally less successful and productive than established pairs building or reusing nests. However, these trends were largely attributable to a greater egg-laying rate among established pairs. Nest building pairs, new and established, were generally delayed in egg laying, hatching, and nestling fledging compared to established pairs reusing nests; new pairs were notably more delayed than established pairs building nests. Territorial pairs in the Atlantic Coastal Pine Barrens were less successful and productive than pairs in other ecoregions. Higher precipitation around the egg laying period was predictive of lower nest success and productivity rates but did not appear to affect phenology. Higher temperatures around this period also lowered these rates, with the further effect of advancing phenology. In New Jersey, climate change appears to be advancing breeding phenology and could constrain productivity by century's end, though we anticipate that density dependence will regulate and lower Bald Eagle breeding performance prior to this period. Breeding success and productivity rates, as well as the effects of year in our models, indicate that New Jersey's breeding Bald Eagle population is still healthy and growing. Overall, our results indicate that nest construction imposes minor temporal costs on Bald Eagles but does not meaningfully affect their breeding success or productivity, which may help inform management of Bald Eagle nests and populations.

KEY WORDS: *breeding*; *nest construction*; *nest management*; *productivity*; *raptor*; *reproductive rate.*

LA CONSTRUCCIÓN DEL NIDO LE CUESTA TIEMPO PERO NO ÉXITO REPRODUCTIVO O PRODUCTIVIDAD A *HALIAEETUS LEUCOCEPHALUS*

RESUMEN.—La construcción de nidos tiene un costo de tiempo y energía para las aves, y puede influir en el éxito reproductivo y la productividad. La naturaleza precisa y el alcance de estos costos están insuficientemente estudiados, especialmente entre las especies de aves rapaces. Utilizamos modelos lineales y modelos lineales mixtos generalizados para examinar los costos temporales y reproductivos de la construcción de nidos para *Haliaeetus leucocephalus* en Nueva Jersey, EEUU, desde 2009 hasta 2021. Para diferenciar los costos de construcción de nidos de la influencia de la experiencia en su construcción, analizamos por separado el resultado de la reproducción y la fenología en parejas nuevas que construían nidos, en parejas establecidas que construían nidos y en parejas establecidas que reutilizaban nidos. También consideramos la influencia

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del clima, el año y la ecorregión. Las parejas reproductoras nuevas que construían nidos fueron generalmente menos exitosas y productivas que las parejas establecidas que construían o reutilizaban nidos. Sin embargo, estas tendencias se debieron en gran medida a una mayor tasa de puesta de huevos entre las parejas establecidas. Las parejas nuevas y establecidas que construían nidos generalmente se retrasaron en la puesta de huevos, la eclosión y el emplumamiento de los volantones en comparación con las parejas establecidas que reutilizaban nidos; las parejas nuevas tuvieron un retraso notablemente mayor que las parejas establecidas que construían nidos. Las parejas reproductoras en los Bosques Costeros de Pino del Atlántico fueron menos exitosas y productivas que las parejas en otras ecorregiones. Una mayor precipitación alrededor del período de puesta de huevos predijo tasas de éxito y de productividad de los nidos más bajas, pero no pareció afectar la fenología. Temperaturas más altas alrededor de este período también redujeron estas tasas, con el efecto adicional de adelantar la fenología. En Nueva Jersey, el cambio climático parece estar adelantando la fenología de reproducción y podría limitar la productividad para finales del siglo, aunque anticipamos que la denso-dependencia regulará y disminuirá el resultado de la reproducción de *H. leucocephalus* antes de este período. En nuestros modelos, las tasas de éxito reproductivo y de productividad, así como los efectos del año, indican que la población reproductora de *H. leucocephalus* de Nueva Jersey sigue siendo saludable y está creciendo. En general, nuestros resultados indican que la construcción de nidos impone costos temporales menores a *H. leucocephalus*, pero no afecta significativamente su éxito reproductivo o productividad, lo que podría ayudar a la gestión de los nidos y de las poblaciones de esta especie.

[Traducción del equipo editorial]

INTRODUCTION

Nests are a nearly universal feature of avian reproduction. Although bird nests vary dramatically in form, they are generally consistent in basic function: they provide an environment for the safety and development of offspring. Nests protect against predation and weather (Hansell 2000, Mainwaring et al. 2014) and create a microclimate of temperature and humidity conducive to offspring development (Deeming 2011, Botero-Delgadillo et al. 2017). The act of constructing nests can also hold behavioral significance for adults. In certain species, nest construction plays an important role in sexual selection (Hansell 2000, Mainwaring et al. 2014). Nest building can also be integral to pair bonding and courtship (Hansell 2000, Newton 2010). For large, territorial species, conspicuous nests may serve as valuable warning signs to competitors (Newton 2010, Sergio et al. 2011, Canal et al. 2016).

However, for most avian species to achieve these benefits, one or both members of the breeding pair must build and maintain the nest. Breeding birds may commit significant time to constructing and improving nests (Conrad and Robertson 1993, Lens et al. 1994, Hansell 2000, Mainwaring and Hartley 2013) and may expend significant energy in the process of collecting and arranging nesting materials (Hansell 2000, Mainwaring and Hartley 2013). These costs can delay egg laying (Lens et al. 1994, Cavitt et al. 1999) and depress nestling fitness (Lens et al. 1994, Moreno et al. 2010). The tendencies of certain species to reuse nests in spite of increased risks of parasitism and predation, or to steal nests or nesting materials provide further indirect evidence of the costs of building nests (Hansell 2000, Jones et al. 2007).

Despite these significant implications, the costs of nest construction remain relatively understudied, particularly compared to the costs of incubation and nestling rearing (Hansell 2000, Mainwaring and Hartley 2013). The studies that are available on this topic tend to focus on passerines, particularly cavity nesters (e.g., Moreno 2010, Mainwaring and Hartley 2013, Tobolka et al. 2013). Raptors are notably neglected in this research area given that this taxon constructs some of the largest nests in the world (Newton 2010) and is of general conservation concern (McClure et al. 2018). The common practices of nest reuse and usurpation among raptors (Newton 2010) indicate that nest construction may be costly to these species (Hansell 2000).

Nonetheless, the limited research that is available suggests nest construction has negligible impact on phenology and performance of breeding raptors. For two raptor species in Spain, nest reuse did not increase the probability of breeding success or average productivity (Jiménez-Franco et al. 2014). Similarly, Rough-legged Hawks (*Buteo lagopus*) in the Canadian High Arctic showed no difference in clutch size or hatch date when using new versus old nests, suggesting negligible cost to nest construction for this species (Beardsell et al. 2016). Furthering this trend, Golden Eagles (*Aquila chrysaetos*) in southwestern Idaho constructing new nests were no less successful in breeding than those reusing nests (Kochert and Steenhof 2012). Among Eurasian Sparrowhawks (*Accipiter nisus*), nest reuse appeared to delay rather than advance laying date and to increase predation (Otterbeck et al. 2019).

However, Otterbeck et al. (2019) found nest reuse was more common among first-time breeders and speculated that these young breeders reused other pairs' old nests to compensate for their later start to breeding. Across these raptor species and populations, nest construction did not appear to reduce same-season breeding performance or delay subsequent phases of breeding.

As a member of this understudied taxon and builder of the largest nests in the world, the Bald Eagle (*Haliaeetus leucocephalus*) is an ideal subject for understanding the costs of nest construction. Bald Eagles commonly reuse nests across breeding seasons, occasionally for decades (Stalmaster 1987). This regular reuse comes despite possible increased risk of ectoparasites (Wimberger 1984, Grubb et al. 1986, Rendell and Verbeek 1996, Tomás et al. 2007). The species is also intensely monitored and managed over much of its North American range. In the USA, the Bald and Golden Eagle Protection Act (16 USC §§668-668d) prohibits the destruction of Bald Eagle nests without a permit from the US Fish and Wildlife Service (USFWS). The USFWS only authorizes take of Bald Eagles and their nests if it is consistent with stable or increasing populations (50 CFR §22). It uses a potential biological removal model and prescribed take level framework to implement sustainable thresholds for permitted take (USFWS 2016, Zimmerman et al. 2022). When authorizing disruption of normal breeding activity at a Bald Eagle nest, the USFWS debits the relevant management unit threshold by the assumed productivity loss (1.33 Bald Eagles per nest in the coterminous USA, excluding the Southwest).

Whether removing a Bald Eagle nest may disrupt subsequent breeding activity likely depends in part on how costly it is to Bald Eagles to build these structures. The massive size of Bald Eagle nests suggests a significant energetic cost to construction; Bald Eagles may place over a metric ton of material in their nests (Buehler 2022). Bald Eagles also typically require at least four days to build a nest and continue to maintain their nests throughout the breeding season (Stalmaster 1987), indicating significant time investment as well. Theoretically, if nest construction costs are sufficiently high, then breeding pairs forced to rebuild nests by natural or human circumstances may not have adequate time or energy to lay eggs and raise young. Examining these costs may help wildlife managers make more accurate assumptions about the potential productivity loss associated with removing Bald Eagle nests.

For this study, we used a dataset on Bald Eagle breeding performance and phenology in New Jersey, USA, from 2009 to 2021 to examine costs of nest construction to this iconic and intensively managed raptor (Smith and Clark 2021). Specifically, we tested whether territorial pairs reusing nests were more successful and productive than those constructing new nests. We differentiated nest construction in new territories from nest construction in established territories to help distinguish nest construction costs from experience-related effects. According to Hansell (2000), nest building costs can be inferred from observational study of the amount of time birds devote to this activity and relationships between construction effort and reproductive rate. Our hypotheses were that territorial pairs that built new nests (1) were less successful at fledging young, (2) fledged fewer young, and (3) laid, hatched eggs, and fledged young later in the year.

As a secondary objective, we attempted to determine whether factors recognized to influence the performance and phenology of other breeding raptors and Bald Eagle populations were also relevant to New Jersey's Bald Eagles. In particular, we examined the influence of weather, ecoregion, and year on Bald Eagle breeding productivity and phenology. We hypothesized (1) that colder, wetter winters would suppress breeding performance and warmer temperatures would advance phenology; (2) that ecoregion would affect phenology; (3) that breeding performance would decline with time because of intensifying density dependence; (4) that nest phenology would advance with time, either in response to increased competition or climate change.

METHODS

Data Sources. *Breeding data.* Our data were based on published reports of Bald Eagle breeding activity in New Jersey from 2009 to 2021 (Smith and Clark 2021). Each year, staff from New Jersey Fish and Wildlife and the Conserve Wildlife Foundation of New Jersey and their trained volunteers monitored Bald Eagle territories throughout the state and recorded occupancy status, success, and productivity, as well as incubation, hatching, and fledging dates (see Smith and Clark 2021 for full methodology). We considered a territory to be occupied if a pair of eagles were present at the nest and the nest appeared to be recently maintained. Observers also noted when territorial pairs (i.e., pairs of breeding-aged Bald Eagles occupying territories [Steenhof et al. 2017]) used newly constructed nests, both for new and established territories. Although consistent coordinates were not available for individual nests for the full study period, we were able to assign a county to each territory.

Covariates. Our main covariate of interest was the nest construction effort and pair experience associated with each breeding attempt—whether new pairs constructed nests, established pairs constructed nests, or established pairs reoccupied old nests. Conceivably, our dataset also included new pairs that used old nests (i.e., usurpers) and mixed pairs of established and new breeders. However, because Bald Eagles are challenging to identify individually without markings (e.g., patagial tags), we assumed all eagles on established territories were returning birds. Past research suggests such mate replacements are relatively infrequent (Jenkins and Jackman 1993).

We also created covariates based on weather, ecoregion, and year (Table 1). Precipitation and temperature can influence the timing, success, and productivity of breeding attempts for raptors generally (Newton 2010, Tapia and Zuberogoitia 2018) and Bald Eagles specifically (Gende et al. 1997, Mougeot et al. 2013, Wilson et al. 2018). In New Jersey, Bald Eagles typically lay eggs in February. Incubation is among the most sensitive phases of the breeding season for Bald Eagles; eggs may be killed by even brief (e.g., 15 min) exposure to precipitation or extreme temperature (USFWS 2007). We therefore used data from the National Oceanic and Atmospheric Agency (Vose et al. 2014) to determine county-level average temperature and total precipitation for February of each observation year. Although the brooding period following incubation is also a vulnerable time for young, we chose to focus solely on weather during incubation to limit our number of covariates, simplify model structure, and improve interpretability. Bald Eagle breeding phenology and productivity can also vary within states based on elevation (Isaacs et al 1983, Swenson et al. 1986), latitude (Buehler 2022), and general environment (Elliot et al. 1998). To capture this potential variation, we assigned territories to Environmental Protection Agency Level III Ecoregions based on the predominant ecoregion in each territory's county (Woods et al. 2007). During our study period, New Jersey's Bald Eagle breeding population was recovering from near extirpation and historic contaminant exposure (Clark et al. 1998). Additionally, beginning around 2010, recruitment of fourth-year Bald Eagles into the breeding population began to decrease nationally, suggesting an approach toward density dependence (Zimmerman et al. 2022). Climate change has also shifted the phenology of many breeding birds (Bates et al. 2022). To detect temporal trends in our dataset, we recorded the year of each observed breeding

Table 1. Model covariates with definitions, mean and standard deviation (continuous variables), frequency (categorical variables), range (continuous variables), and data source. The five ecoregions are Atlantic Coastal Pine Barrens (ACPB), Middle Atlantic Coastal Plain (MACP), Northeastern Highlands (NH), Northern Piedmont (NP), and Ridge and Valley (RV).

Covariate	Definition	Mean (SD) or Frequency	Range	Source
Year	Nesting season year	2016 (3.55)	2009–2021	Smith and Clark 2021
Status	Pair experience and nest age: new pairs building new nests (new pair), established pairs building new nests (new nest), or established pairs reusing nests (established)	New pair = 265, New nest = 130, Established = 1803		Smith and Clark 2021
Average February Temperature	Average temperature (°C) for February in a county in a particular year	1.89 (3.06)	−9.22–6.22	Vose et al. 2014
Total February Precipitation	Total precipitation (mm) for February in a county in a particular year	8.67 (3.88)	1.30–18.54	Vose et al. 2014
Ecoregion	US Environmental Protection Agency ecoregion, Level III	ACPB = 729, MACP = 982, NH = 101, NP = 228, RV = 158		Woods et al. 2007
Territory ID	Unique identifier for a geographic area that contains one or more nests associated with a particular territorial pair	386 unique territories (frequency range = 1–13)		Smith and Clark 2021

attempt. We centered and scaled all continuous covariates to facilitate computation.

Study Area. Our study area included the entire state of New Jersey, which spans five ecoregions from north to south. Eagle nests are found in all 21 counties, but about 50% of nests are located within 20 km of Delaware Bay in the Middle Atlantic Coastal Plain counties of Salem, Cumberland, and Cape May. These Delaware Bay counties are roughly 100 km from the center of Chesapeake Bay and farther from the central and northern portions of New Jersey. As a result, the USFWS Bald Eagle recovery plans split the state between the Northern States and Chesapeake Bay recovery regions (USFWS 1990). The New Jersey population declined during the DDT era of the mid-20th century with just one active nest remaining by the late 1970s. Biologists managed that single nest in the 1980s with artificial incubation of the thin-shelled eggs and fostering of 2-wk-old nestlings that enabled nest success; that management was suspended once the adult female was succeeded by a new (presumably less-contaminated) female. Hotspots of organochlorine contamination remained in the state (Clark et al. 1998) but the population grew well enough to recover nesting statewide, numbering 247 pairs in 2021 (Smith and Clark 2021).

Statistical Models. Using the *lme4* package (Bates et al. 2015) in R (R Core Team 2021), we constructed generalized linear mixed-effects models (GLMM) to examine the relationship between our covariates (Table 1) and breeding outcome; we constructed linear mixed-effects models (LMM) to examine the relationship between our covariates and phenology. For each model, we specified Territory ID as a random effect. We started model construction by creating full models containing all relevant covariates and tested for multicollinearity (variance inflation factor > 3; Zuur et al. 2010), overdispersion ($\hat{c} > 1$), and singularity using the *performance* package (Lüdecke et al. 2021). Next, we inspected model residuals for indication of outliers or exceptional violation of assumptions with assistance from the *DHARMa* package (Hartig 2022). As a measure of model performance, we calculated conditional and marginal R^2 based on the *performance* package's implementation of the Nakagawa calculation method (Nakagawa et al. 2017).

We fit models according to an information theoretic approach, using a corrected Akaike Information Criterion (AIC_c) threshold of $\Delta 2$ (Burnham and Anderson 2002; Arnold 2010) to select a set of best approximating models. To make models comparable during selection, we limited our data to complete cases (i.e., records without NAs). If we found evidence for overdispersion ($\hat{c} > 1$) with Poisson or binomial models, we used corrected Quasi AIC ($Q\ AIC_c$) for model fitting. When model selection identified more than one competitive model, we averaged predictions, weighting by relative AIC_c weights (MuMIn; Banner and Higgs 2016, Barton 2022). For prediction, we did not include any models that were simply embellishments of higher ranked models (i.e., differed only by inclusion of additional terms). We calculated 85% confidence intervals (CI) around covariates while holding other model covariates at their means (e.g., Arnold 2010). We considered covariates to be meaningful predictors if they were present in the competitive model set and, in the case of status and ecoregion, if the estimated 85% CIs of two or more categories did not overlap.

Breeding success. We considered a territorial pair successful if observers noted nestlings 9 wk or older (i.e., 80% of average fledging age; Bortolotti 1986, Steenhof et al. 2017). We constructed two GLMMs, one examining breeding success among territorial pairs and one examining breeding success among the subset of egg-laying pairs. For both models, we specified a binomial link function.

Egg laying. We categorized pairs as egg-laying using the definition of Steenhof et al. (2017): "territorial pairs that lay at least one egg in a given year, as evidenced by eggs, young, or a bird in incubation posture." For coding, we assigned egg-laying $= 1$ and non-laying $= 0$. In constructing our GLMM, we specified a binomial link function.

Productivity. We constructed GLMMs to examine three measures of productivity: number of young per territorial pair, number of young per egg-laying pair, and number of young per successful pair. We specified a Poisson distribution for each based on the count nature of our data. Our productivity values represented either number of nestlings observed fledged or, if an observer missed fledging, number of nestlings >9 wk old.

Phenology. We constructed LMMs for Julian date of incubation, hatching, and fledging, which corresponded to three subpopulations: egg-laying pairs, egg-hatching pairs (i.e., pairs that successfully hatched eggs, as inferred by brooding posture, feeding of chicks, or chick presence), and successful pairs. Observers assigned incubation and hatching dates according to when they first witnessed or were able to infer these milestones and reported fledging date as the date on which they witnessed the first nestling fly in a sustained and controlled manner. We checked for date outliers using the *performance* package (Lüdecke et al. 2021).

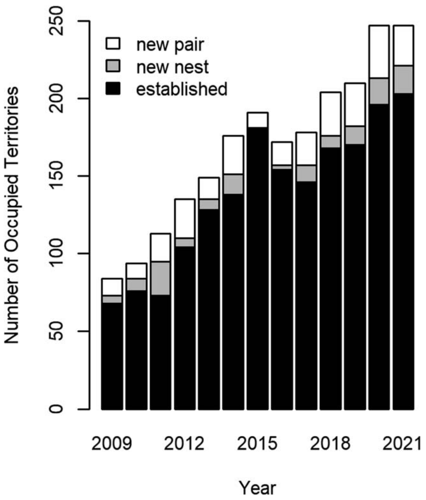

Figure 1. Annual total number of occupied territories used by established pairs reusing nests (established), established pairs constructing new nests (new nest), and new pairs constructing new nests (new pair) across study period (2009–2021).

RESULTS

Between 2009 and 2021, observers monitored 386 occupied Bald Eagle breeding territories in New Jersey, many for multiple years, representing a total of 2200 territory-year records (Fig. 1). Counting within our study timeframe, the average nest age was 4.11 (SD = 3.03) yr and average territory age was 4.97 (SD = 3.41) yr. Most territorial pairs laid eggs (mean = 0.91, SD = 0.29). Breeding success was 0.72 (SD = 0.45) for territorial pairs and 0.80 (SD = 0.40) for egg-laying pairs. Productivity averaged 1.2 ± 0.9 young per territorial pair and 1.3 ± 0.9 young per egg-laying pair. Presumed first-time breeders and established breeders using new nests constituted an average of 0.12 (SD = 0.33) and 0.06 (SD = 0.23) of breeding attempts, respectively, with the remaining 0.82 (SD = 0.38) of attempts attributed to established pairs reusing existing nests.

Nest phenology was typical for Bald Eagles in the Mid-Atlantic USA. The average laying date was 19 February (SD = 17.5 d), followed by average hatching on 26 March (SD = 16.3 d), and average fledging on 17 June (SD = 16.2 d). Averaging hatching date followed 35 d after average laying, and average fledging followed approximately 12 wk after average hatching. These timeframes match the typical incubation and rearing durations for individuals of this species (Buehler 2022). The earliest recorded laying date was 31 December. For summary statistic and modeling purposes, we assigned this record a Julian laying date value of –1 to define the value according to the relevant breeding season year and to avoid unnecessarily removing the record as an outlier.

Breeding Success. Our full model explained a limited amount of the variation in breeding success among territorial pairs (marginal pseudo-R^2 = 0.032; conditional pseudo-R^2 = 0.106), and the variation for which it accounted was mainly attributable to our random effect for Territory ID. The full model was also our best approximating model ($\omega_i = 0.298$). Averaged predictions from our competitive models indicated that new territorial pairs constructing nests were less successful (69.0%; 85% CI = 63.8–73.8) than established pairs reusing (76.2%, 85% CI = 73.5–78.7) or constructing nests (82.2%; 85% CI = 76.5–86.7; Fig. 2). Established pairs constructing nests were more successful than those reusing nests, but not meaningfully. The only significant difference among these groups was between new pairs and pairs rebuilding nests. Year positively influenced breeding success, indicating improved breeding success in the study population between 2009 and 2021 (Table 2). Increased average temperature and total precipitation in February were associated with decreased breeding success. Territorial pairs in the Atlantic Coastal Pine Barrens were significantly less successful than pairs in the Middle Atlantic Coastal Plain and Northern Piedmont.

As with the full model for breeding success among territorial pairs, the full model for breeding success among the narrower segment of egg-laying pairs offered limited explanation for variation in this reproductive metric (marginal pseudo-R^2 = 0.048; conditional pseudo-R^2 = 0.101). The most competitive subset model included terms for precipitation, ecoregion, and year. Three models fell within 2 AIC$_c$ of the top model, though we eliminated these models as more complex versions of the top model. In our top model, year remained a positive influence on breeding success and February precipitation was still highly predictive of nest failure among the smaller dataset of egg-laying pairs (Table 2). Breeding success also remained lower in the Atlantic Coastal Pine Barrens than in the Middle Atlantic Coastal Plain and Northern Piedmont. Examined within the full model, there were no differences in breeding success between new pairs constructing nests (85.1%, 85% CI = 80.9–88.5), established pairs constructing nests (88.2%, 85% CI = 83.3–91.8), or established pairs reusing nests (83.3%, 85% CI = 80.9–85.4).

Egg Laying. After noting that the disparity in breeding success between first-time breeders and established pairs disappeared when we narrowed our focus from territorial pairs to egg-laying pairs

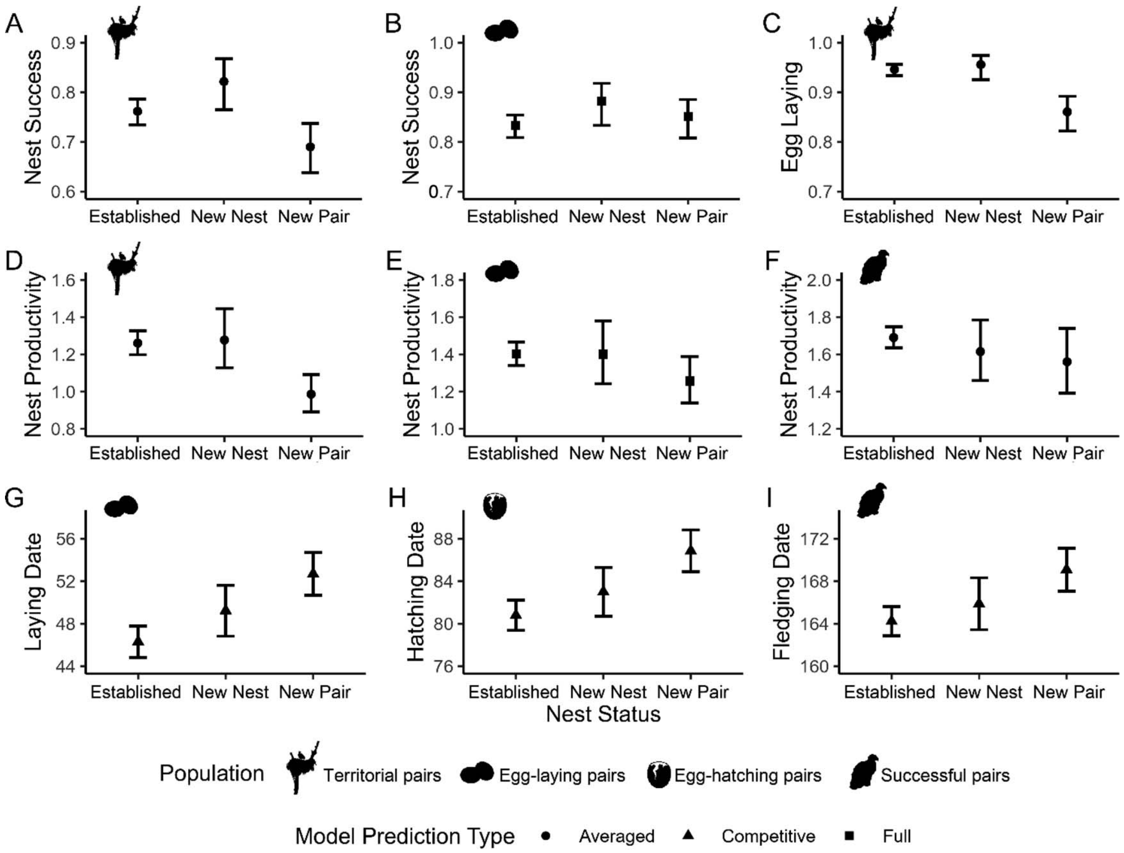

Figure 2. Modeled relationships between nest success (A–B), egg laying rate (C), nest productivity (D–F), and phenology (G–I) and nest construction status of breeding Bald Eagles in New Jersey from 2009 to 2021. Pairs are either established pairs reusing nests (established), established pairs building new nests (new nest), or new pairs building new nests (new pair). Relationships are modeled among territorial pairs, egg-laying pairs, egg-hatching pairs, and successful pairs. Model predictions are taken from either the averaged predictions of the competitive model set (Averaged), the sole competitive model (Competitive), or the full model if status was not a covariate in the competitive model set (Full).

(Fig. 2), we suspected that new pairs' lower breeding performance was due to a lower rate of egg laying. We therefore decided to model whether pair status was predictive of egg laying among territorial pairs. We also considered whether year, weather, and ecoregion were predictive of this behavior. Our full model accounted for a modest amount of the variation in egg laying rate, although, again, much of this explanation was due to the random effect for Territory ID (marginal pseudo-R^2 = 0.060; conditional pseudo-R^2 = 0.302). From the averaged predictions of our competitive model set, we found that new territorial pairs were notably (86.1%, 85% CI = 82.2–89.2) less likely to lay eggs than either type of established territorial pair (established-new nest, 95.6%, 85% CI = 92.6–97.4; established-old nest, 94.6%, 85% CI = 93.3–95.6; Fig. 2). Year was a parameter in our top ranked model and appeared to negatively influence the rate of egg laying (Table 2). Similarly, temperature, which was present in both competitive models, showed a negative association with egg-laying. Precipitation only appeared in the competitive model set as an extraneous parameter and did not seem to have a meaningful association with the territorial pairs' propensity to lay eggs. Ecoregion appeared to have no appreciable influence on egg-laying rate and was absent from the top ranked models.

Productivity. Our full model containing all covariates of interest addressed only a negligible amount of the variation in productivity (young per territorial pair; marginal pseudo-R^2 = 0.030; conditional

Table 2. Summary of modeled relationships between breeding success, egg laying, productivity, laying date, hatching date, and fledging date, and nest construction status (STATUS), February total precipitation (PCP2), February average temperature (TAVG2), breeding season (YEAR), and EPA Level III Ecoregion (ECO3: Middle Atlantic Coastal Plain [MACP], Northeastern Highlands [NH], Northern Piedmont [NP], and Ridge and Valley [RV]). Statistical relationships were either meaningfully positive (+) or negative (−), entirely unmeaningful (blank), or unmeaningful at a particular factor level (x). Relationships are considered within relevant breeding Bald Eagle populations: territorial pairs, egg-laying pairs, and successful pairs.

Response Variable	Eagles Included	STATUS[a]		PCP2	TAVG2	YEAR	ECO3[b]			
		New Nest	New Pair				MACP	NH	NP	RV
Success	Territorial pairs	x	−	−	−	+	+	x	+	x
	Egg-laying pairs			−		+	+	x	+	x
Egg laying	Territorial pairs	x	−		−	−				
Productivity	Territorial pairs	x	−	−	−		+	x	+	x
	Egg-laying pairs			−			+	x	+	x
	Successful pairs	x	x							
Laying date	Egg-Laying pairs	x	+		−	−	x	+	+	+
Hatching date	Egg-laying pairs	x	+		−	−	x	+	+	+
Fledging date	Successful pairs	x	+		−	−	x	+	+	+

[a] Reference category = established pairs.

[b] Reference category = Atlantic Coastal Pine Barrens.

pseudo-$R^2 = 0.066$). Averaged predictions of two competitive models indicated that precipitation and temperature were negatively associated with productivity and that territorial pairs in the Atlantic Coastal Pine Barrens were significantly less productive than pairs in two other ecoregions (Table 2). The averaged predictions also demonstrated that productivity did not differ meaningfully between established pairs reusing nests (1.26 young per territorial pair, 85% CI = 1.20–1.33) and building new nests (1.28, 85% CI = 1.13–1.45), but was lower for new pairs (0.99, 85% CI = 0.89–1.09; Fig. 2).

When we attempted to fit our full models for the two other measures of productivity (young per egg-laying pair and young per successful pair), the models achieved singular fit. We concluded that these singularities were not attributable to model complexity as the full models began with only five fixed effects and one random effect. Further, when we eliminated variables from the models, the singularity did not resolve. To help understand this issue, we ran simulations in which we randomly assigned each territory a status as a low (0–1 fledglings), medium (1–2 fledglings), or high (2–3 fledglings) productivity territory and then sampled their productivity each year from their assigned productivity range. When we fit models to these simulated productivity data, the singularities resolved, indicating that the issue was due to a lack of structure in productivity among territories. We then proceeded with fitting our full models for egg-laying and successful pairs as a generalized linear models (GLM), without the Territory ID random effect.

The full model for egg-laying pairs provided limited explanation for variation in productivity ($R^2 = 0.033$). Several redundant models fell within 2 AIC_c of the top model, which contained precipitation and ecoregion. Status only surfaced as a lower ranked, redundant model. Increased precipitation was predictive of lower productivity, as was location in the Atlantic Coastal Pine Barrens ecoregion (Table 2). The full model for successful pairs explained even less about variation in productivity ($R^2 = 0.026$) and there was little to differentiate competing subset models. Eight subset models fell within 2 AIC_c of the top ranked model, and we ultimately eliminated six of these as embellishments of higher ranked models, leaving only a model containing status and the intercept-only model. Ecoregion was absent from all models within 2 AIC_c of the top model. The averaged predictions of the status-only and intercept-only models indicated no meaningful difference in productivity among new breeders, established pairs building nests, and established pairs reusing nests (Fig. 2). Examining predictions from the top status-only model, the productivity of successful new territorial pairs that built nests (1.56 young per successful pair, 85% CI = 1.39–1.74) did not appear to differ from that of established pairs that reused nests (1.69, 85% CI = 1.63–1.75) or built new nests (1.62, 85% CI = 1.46–1.78).

Phenology. The full model for egg-laying date accounted for a sizeable proportion of the variation in date, though the random effect (Territory ID) was far more informative than the fixed effects (marginal pseudo-$R^2 = 0.093$; conditional pseudo-$R^2 = 0.450$). The most competitive subset model contained fixed effects for temperature, year, status, and ecoregion and was by far the most heavily weighted model (Table S13). The next most competitive model carried half the weight and differed only in the exclusion of temperature as a fixed effect. Averaged predictions from the competitive model set indicated that pairs laid eggs earlier with each year and with increasing average February temperature (Table 2). New pairs building nests (55.9 Julian days, 85% CI = 53.7–58.1) laid eggs later than established territorial pairs building nests (52.4 Julian days, 85% CI = 49.8–55.0) and established pairs reusing nests (49.5 Julian days, 85% CI = 47.7–51.2), though confidence intervals did not suggest a clear difference between new and established pairs building nests (Fig. 2). Pairs in three ecoregions (Northeastern Highlands, Northern Piedmont, and Ridge and Valley) laid eggs significantly later than pairs in the Middle Atlantic Coastal Plain and Atlantic Coastal Pine Barrens (Fig. S4).

These general patterns also emerged in our models of hatching date among egg-hatching pairs and fledging date among successful pairs. Both the full models for hatching date (marginal pseudo-$R^2 = 0.119$; conditional pseudo-$R^2 = 0.481$) and fledging date (marginal pseudo-$R^2 = 0.122$; conditional pseudo-$R^2 = 0.429$) explained moderate amounts of variation, though Territory ID continued to be the dominant explanatory factor. Subset models containing temperature, year, status, and ecoregion carried most of the model weight and were the sole competitive models for hatching date and fledging date (Table S13). Predictions from these top models showed a more pronounced negative effect of temperature. New pairs also continued to lag behind established pairs reusing nests, as did established pairs building nests, though not to the same degree as new pairs (Fig. 2). Similarly, pairs in the three northern ecoregions continued to lag significantly behind pairs in the two southern ecoregions (Fig. S4).

DISCUSSION

Nest Construction Costs. Our results refuted our hypotheses on the relationships between nest building and breeding outcome in Bald Eagles. Constructing nests costs Bald Eagles negligible time and has limited effect on their breeding success or productivity. Our dataset contained both new and established pairs building nests, but only the former registered lower rates of success or productivity when compared to established pairs reusing nests. As discussed below, we attribute these lower rates to inexperience, and not to energetic or time burdens imposed by nest construction. The lack of apparent nest building cost in breeding performance is consistent with observations for other raptor species (Kochert and Steenhof 2012, Jiménez-Franco et al. 2014, Beardsell et al. 2016).

The nest building status of territorial pairs was associated with dates of egg laying, hatching, and fledging. Established territorial pairs that built new nests achieved these milestones approximately 3 d after pairs that reused nests. We consider these delays meaningful even though CIs did not indicate significance because the pattern was consistent across all three phenological models. The difference in dates evident at egg laying persisted through hatching and fledging; established pairs building nests were lagging by 3 d by the time of egg laying and only made up approximately 0.75 d on their nest-reusing counterparts by the time of fledging. The lag of 3 d supports previously published estimates that Bald Eagles require 4 d to construct nests (Stalmaster 1987) and suggests marginal time costs placed on nest building Bald Eagles.

New territorial pairs constructing nests laid and hatched eggs and fledged young even later than established pairs building nests, which may be attributable to these birds' relative inexperience with nest construction or lower ability to successfully forage and achieve necessary body condition for egg laying. Although there were no clear links between these phenological delays and lower breeding performance, it is possible that later fledging may provide young a shorter post-fledging dependence period in which to receive parental support, leading to lower survival rates (López-Idiáquez et al. 2018). However, this effect may be less pronounced in nonmigratory populations such as New Jersey's.

Weather and Implications of Climate Change. Our results demonstrated that factors commonly recognized to influence raptor breeding performance and phenology are relevant to Bald Eagles in New Jersey. Higher precipitation in February, which is the typical egg-laying month for our study population, was associated with reduced breeding success and lowered productivity, including among egg-laying pairs. Increased precipitation may affect breeding adults directly by forcing a reallocation of energy away from nest construction and egg development toward thermoregulation (Coe et al. 2015). Alternatively, precipitation may harm breeding performance by causing death of eggs and nestlings through exposure (Anctil et al. 2014) or impeding adults' ability to forage and feed young (Öberg et al. 2015). Although precipitation appeared influential over breeding success and productivity, it showed no association with phenology. However, average February temperature was associated with both breeding performance and phenology. Higher temperatures were related to lower success, egg-laying rates, and productivity. This outcome contradicted our hypothesis. Warmer temperatures conceivably create a more conducive environment for incubation and brooding, placing less temperature stress on both adults and offspring in the study area's temperate climate. Schmidt et al. (2020) observed a similar negative trend between spring warmth and nest success among breeding Bald Eagles in south-central Alaska and posited that warmer temperatures reduced access to salmon, an important food source for this population. Finding that higher air temperatures during incubation (April) were associated with reduced nesting success of Red-shouldered Hawks (*Buteo lineatus*) in Ohio, Dykstra et al. (2021) suggested that higher temperatures might lead to lower nest attendance by parents, thereby increasing the rate of nest predation. However, in that same study, higher temperatures during the nestling-rearing period (May) were associated with higher nest success as expected (Dykstra et al. 2021), suggesting potentially differing effects of higher temperatures depending on the timing. We also encourage research into the possibility that higher temperatures increase prevalence of ectoparasites and suppress nestling health (e.g., Martínez-de la Puente et al. 2010). We acknowledge that our analyses and results only reflect relationships between temperature and the incubation stage; temperature may have different relationships with nest success during brooding. Further, our results regarding the influence of temperature may be inconsistent with previous studies' findings simply because we limited our focus to the incubation phase, whereas other studies looked more broadly to the later brooding and rearing stages.

Results for phenology were more as anticipated, with warmer temperatures in February advancing the date of egg laying, with hatching date and fledging date then also appearing to advance. This pattern is consistent with general raptor ecology (Newton 2010). There are several potential mechanisms. Warmer temperatures may increase access to food resources by thawing lakes and rivers hosting fish or advancing the migration date of waterfowl. Alternatively, warmer temperature may require less energy for thermoregulation. In either situation, females may be able to achieve body condition necessary for egg development earlier in the season.

Our observed trends between weather and breeding performance and phenology hold potential implications under climate change scenarios. In the Northeastern USA, climate change is projected to increase temperature and precipitation (Wuebbles et al. 2017). Our models for territorial pairs predict that if greenhouse gas emissions continue unabated, by the final decade of the 21st century, increased average February temperatures and precipitation totals in New Jersey (Alder and Hostetler 2015) may cause established territorial pairs in New Jersey's Middle Atlantic Coastal Plain to fledge 3.7% fewer young. The reduced productivity would be equivalent to almost five fewer young fledging for every 100 breeding attempts. Increased competition among eagles will almost certainly intervene before century's end to lower and regulate Bald Eagle success and productivity, as observed in other populations (Elliott et al. 2011, Wilson et al. 2018). However, with all else equal, were future climate conditions to be imposed today, there would likely be fewer eagles on the landscape and a slower rate of population growth.

We also expect that based on the association we observed of laying date with average February temperature and year, phenology will continue to advance with climate change. Although Newton (2010) observed that earlier laying dates are associated with greater breeding success in raptors, he speculated that earlier laying and breeding success were both common products of greater experience and hunting ability among certain birds. Consequently, earlier laying dates caused by climate change will not necessarily benefit Bald Eagles. This phenological shift may even eventually harm Bald Eagles by desynchronizing their annual rhythms with those of their prey (Inouye 2022). Advancing laying dates may also challenge efforts to monitor Bald Eagle populations. Our model of egg laying phenology estimated that laying date advanced 3 d in the decade between 2010 and 2019. Managers conducting long-term studies of Bald Eagle populations with traditional aerial nest surveys may need to gradually adjust their survey timeframes to continue accurately tracking reproduction (Fraser et al. 1983).

Breeding Experience. Throughout our study period, Bald Eagle populations were continuing to recover (Fig. 1) and most individuals in the Lower 48 states were breeding as soon as sexually mature (Zimmerman et al. 2022). Therefore, we attribute the lower success and productivity rates among new pairs constructing new nests to inexperience. We also suspect that the positive association between breeding success and year was due to a general maturation of the breeding population and increase in individual breeding experience, as new territorial pairs remained a consistently small proportion (0.05–0.19) of the population each year and the total number of established territorial pairs typically increased each year. Although experience-related patterns of productivity in Bald Eagles have received limited attention, the recovering Scottish population of the congeneric White-tailed Sea-Eagle (*Haliaeetus albicilla*) shows similarly low success and productivity among young breeders (Murgatroyd et al. 2018). The unique distinction in our dataset between nest construction by new and established pairs allowed us to disentangle the effects of experience versus nest construction cost. Further, our results offer a caution that lower productivity due to high recruitment of young breeders in rapidly recovering raptor populations may easily be misinterpreted as the cost of building new nests, which may in turn lead to inflated valuation of nest structures in conservation management.

Post-recovery Population Trends. The Bald Eagle remains a state-listed threatened species in New Jersey. Nationally, USFWS delisted the species in 2007 (72 FR 37345). Federal post-delisting surveys found a four-fold increase in the number of breeding pairs in the Lower 48 states (excluding the Southwest) between 2009 and 2019 (USFWS 2020). Demographic modeling of populations in the Lower 48 states suggests that recruitment of fourth-year birds began steadily decreasing from the mid-2000s onward (Zimmerman et al. 2022), which potentially indicates population stabilization and increased competition for breeding territories, though the majority of after-third-year birds continued to breed. New Jersey's Bald Eagle productivity rate was comparable to previous national estimates for Bald Eagle productivity in the Lower 48 states (excluding the Southwest; USFWS 2016). In several of our models, year was a meaningful predictor, which indicates the breeding population has not yet stabilized. Breeding success appeared to increase with time, while the proportion of territorial birds that laid eggs decreased, though it remained generally high. The positive association of breeding success with year, coupled with the high mean productivity and breeding success (Sprunt et al. 1973), suggests that New Jersey's population is still growing and has not yet reached carrying capacity, contrary to our hypothesis. Although the population appears robust overall, the lower breeding success and productivity among Bald Eagles of the Atlantic Coastal Pine Barrens is not immediately explainable and warrants further investigation to determine whether it is due to natural factors, such as fewer large waterbodies and streams available for foraging, or anthropogenic issues, such as contaminant exposure.

Management Implications. Our results add to the growing body of evidence demonstrating breeding Bald Eagles' resilience to natural and anthropogenic challenges (Millsap et al. 2004, Goulet et al. 2021, Zimmerman et al. 2022). New pairs of nesting Bald Eagles in New Jersey were able to construct their massive nests while experiencing only minor delay to their subsequent breeding activities, compared to conspecifics using old nests. The results suggest that when nesting substrate and materials are readily available, as in the case of New Jersey's habitats, Bald Eagles may not be meaningfully affected by loss of alternate nests and the subsequent need to build new nests. If nests must be removed to protect public safety or other human interests, our results support removing them only when they are considered an alternate nest and risks to breeding productivity are negligible and indirect, versus while they are in use and impacts are more likely to be severe and direct (i.e., nest failure and death of offspring). Further, when Bald Eagle nests are removed outside breeding season and there is reasonable expectation that the resident pair will be able to construct a new nest within the territory, assuming lost productivity and debiting population management thresholds may be unwarranted. Alternatively, if there is evidence to suggest that alternate nesting substrate is significantly limited, it may be more accurate to assume the affected pairs may not be able to successfully breed for one or more seasons. For example, Watts and Byrd (2007) found that after Hurricane Isabel struck territories in the Lower Chesapeake Bay during the nonbreeding season, pairs that lost nests were less productive in following seasons, potentially due to the combined loss of nests and mature trees offering alternate nesting substrate.

To help determine whether removing an alternate nest may disturb Bald Eagle breeding activity, we recommend managers consider the following: (1) whether substrate for a new nest is readily and functionally available within the nesting territory, (2) whether sources for nesting material are present, and (3) whether the affected pair will have adequate time and physical space to build a new nest. If managers can confirm that all these requirements are met, we anticipate that Bald Eagle pairs will be able to build new nests and successfully breed. Revising expectations of productivity loss may help calibrate agencies' mitigation requirements and in turn alleviate social burden imposed on the regulated public (Watts and Byrd 2022).

SUPPLEMENTAL MATERIAL (available online). Table S1: Parameters, coefficients, standard errors, and *z*-values for full GLMM examining nest success among territorial Bald Eagle pairs in New Jersey, 2009–2021. Table S2: Parameters, coefficients, standard errors, and *z*-values for full GLMM examining nest success among egg-laying bald eagle pairs in New Jersey, 2009–2021. Table S3: Best approximating models (i.e., within 2 corrected Akaike Information Criterion [AIC$_c$] units of the top ranked model) in assessment of relationship between breeding success (SUC) and February total precipitation (PCP2), February average temperature (TAVG2), breeding season (YEAR), and nest construction status (STATUS) among occupied nesting territories in New Jersey, 2009–2021. Table S4: Parameters, coefficients, standard errors, and *z*-values for full GLMM examining egg laying among territorial Bald Eagle pairs in New Jersey, 2009–2021. Table S5: Best approximating models (i.e., within 2 corrected Akaike Information Criterion [AIC$_c$] units of the top ranked model) in assessment of relationship between egg laying (EGG) and February total precipitation (PCP2), February average temperature (TAVG2), breeding season (YEAR), and nest construction status (STATUS) among occupied nesting territories in New Jersey, 2009–2021. Table S6: Parameters, coefficients, standard errors, and *z*-values for full GLMM examining nest productivity among territorial Bald Eagle pairs in New Jersey, 2009–2021. Table S7: Parameters, coefficients, standard errors, and *z*-values for full GLM examining nest productivity among egg-laying Bald Eagle pairs in New Jersey, 2009–2021. Table S8: Parameters, coefficients, standard errors, and *z*-values for full GLM examining productivity among successful Bald Eagle pairs in New Jersey, 2009–2021. Table S9: Best approximating models (i.e., within 2 corrected Akaike Information Criterion [AIC$_c$] units of the top ranked model) in assessment of relationship between productivity (PRD) and February total precipitation (PCP2), February average temperature (TAVG2), breeding season (YEAR), and nest construction status (STATUS) among territorial, egg-laying, and successful territorial pairs in New Jersey, 2009–2021. Table S10: Parameters, coefficients, standard errors, and *t*-values for full GLMM examining Julian laying date among Bald Eagle pairs in New Jersey, 2009–2021. Table S11: Parameters, coefficients, standard errors, and *t*-values for full GLMM examining Julian hatching date among Bald Eagle pairs in New Jersey, 2009–2021. Table S12: Parameters, coefficients, standard errors, and *t*-values for full GLMM examining Julian fledging date among Bald Eagle pairs in New Jersey, 2009–2021. Table S13: Best approximating models (i.e., within 2 corrected Akaike Information Criterion [AIC$_c$] units of the top ranked model) in assessment of relationship between laying (LAY), hatching (HTC), and fledging (FLG) date and February total precipitation (PCP2), February average temperature (TAVG2), breeding season (YEAR), nest construction status (STATUS), and Level III Ecoregion (ECO3) among territorial territorial pairs in New Jersey, 2009–2021. Figure S1: Predicted nest success among territorial and egg-laying pairs according to (A) ecoregion, (B) year, (C) total February precipitation, and (D) February average temperature. Figure S2: Predicted rate of egg-laying among territorial pairs according to (A) ecoregion, (B) year, (C) total February precipitation, and (D) February average temperature. Figure S3: Predicted productivity rate among territorial, egg-laying, and successful pairs according to (A) ecoregion, (B) year, (C) total February precipitation, and (D) February average temperature. Figure S4: Predicted egg laying (A–E), hatching (F–J), and fledging (K–O) dates according to Level III ecoregion, year, total February precipitation, average February temperature. Supplemental Material 2. JRR-22-112 Wittig et al. 2023 Data.csv.

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