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LOCAL WEATHER EXPLAINS ANNUAL VARIATION IN NORTHERN GOSHAWK REPRODUCTION IN THE NORTHERN GREAT BASIN, USA

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ABSTRACT.—Weather is thought to influence raptor reproduction through effects on prey availability, condition of adults, and survival of nests and young; however, there are few long-term studies of the effects of weather on raptor reproduction. We investigated the effects of weather on Northern Goshawk (*Accipiter gentilis*; henceforth goshawk) breeding rate, productivity, and fledging date in south-central Idaho and northern Utah, USA. Using data from 42 territories where we found evidence of breeding attempts in ≥1 yr from 2011–2019, we analyzed breeding rates using 315 territory–season combinations, analyzed productivity for 134 breeding attempts, and analyzed fledging date for 118 breeding attempts. We examined 35 predictor variables from four categories: precipitation, temperature, wind, and snowpack. Of the variables we evaluated, April precipitation, previous year's April–July precipitation, April–May mean temperature, and March–May mean temperature were related to measures of goshawk reproduction. Greater April–July precipitation in the previous year and lower April precipitation in the current year were associated with higher breeding rates. Years with warmer average April–May temperatures were associated with increased goshawk productivity. Years with greater April–July precipitation during the previous year and lower mean March–May temperatures were associated with later fledging dates. Based on these relationships, we considered projected changes in weather in the northern Great Basin over the next 50 yr as a result of climate change (without directly accounting for habitat changes caused by climate change), and predicted that climate change will: (a) have no significant effect on goshawk breeding rate, (b) have a positive effect on goshawk productivity, and (c) cause a shift toward earlier goshawk breeding. Our results indicate that weather is significantly related to goshawk reproduction in the northern Great Basin, and we suggest that the relationship between raptor breeding and weather be further investigated to enable higher resolution predictions of how changes in the climate may influence their populations, particularly changes that may not have been captured by our study.

KEY WORDS: *Northern Goshawk*; Accipiter gentilis; *climate change*; *Idaho*; *nesting success*; *phenology*; *Utah*.

EL CLIMA LOCAL EXPLICA LA VARIACIÓN ANUAL EN LA REPRODUCCIÓN DE *ACCIPITER GENTILIS* EN EL NORTE DE LA GRAN CUENCA, EEUU

RESUMEN.—Se considera que el clima influye en la reproducción de las rapaces a través de su efecto sobre la disponibilidad de presas, la condición de los adultos y la supervivencia de los nidos y los polluelos; sin embargo, hay pocos estudios a largo plazo de los efectos del clima sobre la reproducción de las rapaces. Investigamos los efectos del clima sobre la tasa reproductiva, la productividad y la fecha de emplumamiento de *Accipiter gentilis* en el sur-centro de Idaho y norte de Utah, EEUU. Usando datos procedentes de 42 territorios donde encontramos evidencia de intentos reproductivos en ≥1 año desde 2011–2019, analizamos

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las tasas reproductivas usando 315 combinaciones de territorio y estación, analizamos la productividad para 134 intentos reproductivos y analizamos la fecha de emplumamiento para 118 intentos reproductivos. Examinamos 35 variables predictivas de cuatro categorías: precipitación, temperatura, viento y manto de nieve. De las variables que evaluamos, la precipitación de abril, la precipitación de abril-julio del año previo, la temperatura media de abril-mayo y la temperatura media de marzo-mayo estuvieron relacionadas con las medidas de la reproducción de *A. gentilis*. Una mayor precipitación en abril-julio del año previo y una menor precipitación del corriente año estuvieron asociadas con tasas reproductivas más altas. Los años con temperaturas promedio más elevadas en abril-mayo estuvieron asociados con un aumento de la productividad de *A. gentilis*. Los años con mayor precipitación en abril-julio del año previo y con menores temperaturas medias en marzo-mayo estuvieron asociados con fechas de emplumamiento más tardías. Tomando como base estas relaciones, consideramos a los cambios proyectados en el clima en el norte de la Gran Cuenca para los próximos 50 años como el resultado del cambio climático (sin considerar directamente los cambios de hábitat causados por el cambio climático), y predijimos que el cambio climático: (a) no tendrá un efecto significativo en la tasa reproductiva de *A. gentilis*, (b) tendrá un efecto positivo en la productividad de *A. gentilis*, y (c) causará un cambio hacia una reproducción más temprana de *A. gentilis*. Nuestros resultados indican que el clima está significativamente relacionado con la reproducción de *A. gentilis* en el norte de la Gran Cuenca, y sugerimos que la relación entre su reproducción y el clima sea investigada con más profundidad para permitir predicciones más precisas de cómo los cambios en el clima pueden influir en sus poblaciones, particularmente aquellos cambios que pueden no haber sido considerados en nuestro estudio.

[Traducción del equipo editorial]

Introduction

Weather can affect raptor fecundity by influencing individual condition, the availability of food and water, and habitat quality (e.g., Krüger 2002, McDonald et al. 2004, White 2008). Weather can influence raptor prey abundance and alter prey behavior, which is particularly important during the breeding season because the abundance and availability of prey directly influence raptors' ability to reproduce (e.g., Steenhof et al. 1997, Krüger 2002, McDonald et al. 2004). Weather-induced effects on prey can have long-term effects on the demographics of raptor populations, as low prey availability during the breeding season can cause decreased raptor brood sizes and increased mortality rates in raptor nestlings and fledglings (Olsen and Marples 1992, Salafsky et al. 2007).

Northern Goshawk (*Accipiter gentilis*; henceforth goshawk) reproductive success is affected by weather (e.g., Fairhurst and Bechard 2005, Herfindal et al. 2015, Reynolds et al. 2019) and weather is also related to goshawk prey availability, which influences goshawk productivity (Rutz and Bijlsma 2006, Wiens et al. 2006, Herfindal et al. 2015). Furthermore, long-term changes to weather patterns are a driving factor of ongoing precipitous declines in the extent, abundance, and distribution of quaking aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*), which compose many of the forest stands that goshawks use for nesting in western North America (Rehfeldt et al. 2009, Perovich and Sibold 2016).

We studied goshawks in the northern Great Basin of southern Idaho and northern Utah, USA, where goshawks are currently designated as an indicator species of forest health by the US Forest Service (US Forest Service 2011). In the northern Great Basin, goshawk occupancy and productivity are more variable than in most other locations where they have been studied (Bechard et al. 2006, Jiménez-Franco et al. 2011, Reynolds et al. 2017), which may be the result of the available suite of prey (Miller et al. 2014, Miller 2017), individual and territory quality (Reynolds et al. 2019), weather conditions (Fairhurst and Bechard 2005, Reynolds et al. 2019), or a combination of these factors. Based on 9 yr of research in the fragmented forests of the northern Great Basin, we hypothesized that weather had a significant influence on goshawk breeding rate, productivity, and fledging date. We investigated the association of weather and goshawk reproduction by assessing the relationships of precipitation, temperature, wind, and snowpack with breeding rate, productivity, and fledging date. In addition to analyzing direct weather factors similar to those evaluated by Fairhurst and Bechard (2005), we investigated factors that may act indirectly through their influence on prey abundance and availability. Lastly, we explored how these factors may influence future goshawk population ecology using a model of future climate conditions.
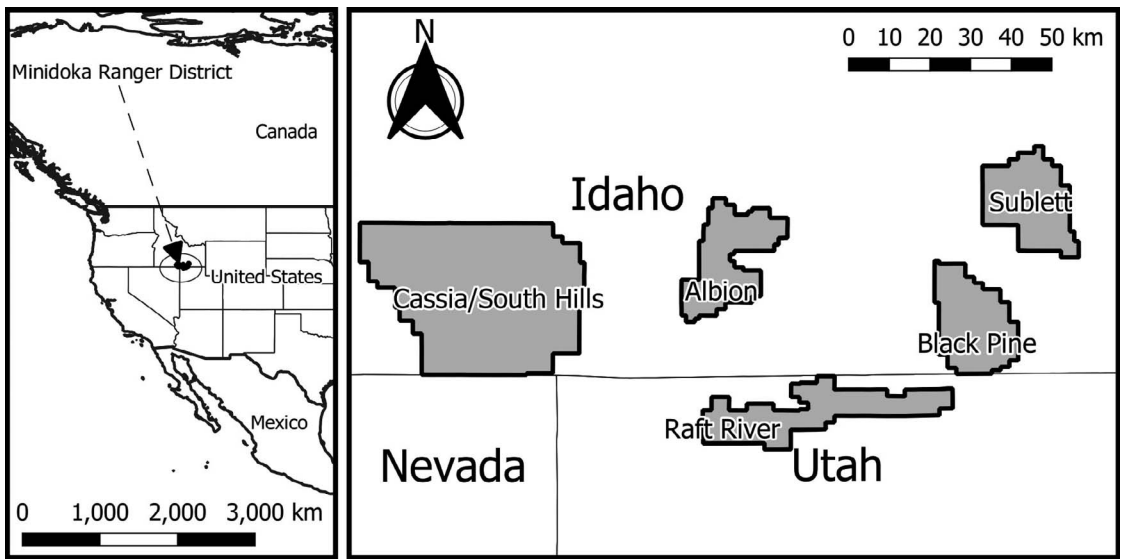
Figure 1.　Northern Goshawk study areas in Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in south-central Idaho and northern Utah, USA (left); with five isolated divisions highlighted (right).

Methods

Study Area. Our study area encompassed all five divisions of the Minidoka Ranger District, Sawtooth National Forest in south-central Idaho and northern Utah, USA (41.98–42.50°N, 112.89–114.48°W; Fig. 1). All divisions were bordered primarily by land administered by the Bureau of Land Management (US Forest Service 2003).

Landscapes within our study area consisted of isolated patches of forested land cover surrounded by shrublands, agriculture, and developed areas (US Forest Service 2003). The forested portions were naturally fragmented and adjacent areas were dominated (approximately 80%) by grasslands and mountain big sagebrush (*Artemisia tridentata vaseyana*; US Forest Service 2003). Forest stands in the western portion of our study area consisted predominantly of quaking aspen, lodgepole pine, and subalpine fir (*Abies lasiocarpa*; US Forest Service 2003). Douglas fir (*Pseudotsuga menziesii*) was the predominant tree species in the eastern portions of our study area, interspersed with quaking aspen throughout and mixed with piñon pine (*Pinus edulis*) and juniper (*Juniperus* spp.) in northern Utah (US Forest Service 2003).

In 2011 and 2012, we monitored goshawks only in the Cassia Division on the western edge of our study area (Fig. 1). In 2013, we collected data in the Cassia, Black Pine, and Sublett Divisions. In 2014–2019, we collected data in all five divisions. Within each division, we surveyed areas with historical observations of goshawk breeding attempts (i.e., nest where eggs were laid) and prospective new areas prioritized by predictive Geographic Information System (GIS) habitat suitability models (Miller et al. 2013). Based on a prior radiotelemetry investigation of male home range in the same study area (Hasselblad and Bechard 2007), we delineated "territories" as circular areas extending 1370 m (588 ha) from the last occupied nest structure or, if no known nest structure existed in the area, from the core of the area with the highest suitability as established by our predictive model (Miller et al. 2013). We restricted our analyses to territories where we observed a breeding attempt at least once during the 9-yr study period and included data in our analyses only from years in which territories were surveyed.

Field Methods. In our study area, April is the nest-building and egg-laying period, and the majority of incubation occurs in May. Eggs hatch during late May and early June. We established call-broadcast points every 300 m in all areas with forest cover within delineated territories. Due to the highly fragmented nature of forest cover in our study area, we manually positioned call-broadcast points on a map using satellite imagery to minimize the number of points while ensuring all forest areas fell within 180 m of a point (a point offset technique suggested

by Joy et al. [1994]). The resulting number of call-broadcast points ranged from four to 24 per territory and varied with the amount of forest cover across territories.

In territories with previously identified nests, we first checked all known intact nest structures for evidence of occupation by goshawks each year starting in late May or early June and before beginning a call-broadcast survey. A nest was considered occupied if signs of reproduction were observed. If we found no occupied nest, we began a survey at call-broadcast points located closest to the last known occupied nest.

At each call-broadcast point, we broadcasted three calls separated by silent listening periods, following Kennedy and Stahlecker (1993) and Joy et al. (1994). During June and early July (local nestling-rearing period), we broadcasted three adult goshawk alarm calls. During mid-to-late July (local fledgling period), we switched to two alarm calls followed by one begging call at each point (Joy et al. 1994). For each broadcast (alarm and begging), we broadcasted the call for 10 sec at approximately 100 dB with a game caller (FoxPro Inc., Lewistown, PA, USA, models FX3, NX3, or NX4) followed by a silent listening and searching period of 50 sec. We then rotated the game caller 120° on the horizontal plane and repeated the procedure (rotating in the same direction) until we completed three full broadcasting and listening intervals (Kennedy and Stahlecker 1993).

When we detected a goshawk, we ceased broadcasts and began searching for an occupied nest. If we discovered an occupied nest, we ceased all broadcasts within 2 km to minimize potential disturbance until returning to assess productivity. If we failed to detect evidence of a breeding attempt while surveying a territory, we classified that territory as having no evidence of a breeding attempt for that year, acknowledging that measurement error may have occurred as a result of early nest failure or inconspicuous behavior of breeding goshawks (Woodbridge and Hargis 2006). We quantified breeding rate as the proportion of territories surveyed with evidence of breeding attempts each year. Our survey protocol did not always include repeat visits to individual territories within years, so we were unable to account for imperfect detection in our assessment of territory status and therefore report unadjusted estimates of breeding rate.

Nest success and productivity. Using a photographic key (Boal 1994) to estimate nestling age, we classified a breeding attempt as successful if at least one nestling reached 34 d of age, which is the minimum acceptable age for assessing goshawk nesting success (80% of average fledging age; Steenhof et al. 2017). We define productivity as the number of fledglings per breeding attempt.

During the late nesting period and early fledging period, we visited all territories where we previously observed breeding to count fledglings and used these observations to quantify nesting success, quantify productivity, and estimate fledging date (assuming a fledging age of 42 d for the oldest fledgling; Boal 1994, Franke et al. 2017). If nestlings had fledged, we attempted to locate all fledglings, alive or dead, by searching within 150 m of the nest structure. If we failed to locate all fledglings previously known to be present, we broadcasted begging calls in an attempt to elicit a response. Because the likelihood of detecting fledglings decreased as the period between fledging and our visit increased, we used these visits only to confirm nesting success, whereas we quantified productivity based on the greatest number of nestlings we observed in nests. In two cases, while searching for fledged young, we discovered nestlings older than 34 d that had died prior to fledging. In these two cases, we considered the nesting attempt as successful, but we subtracted the dead nestlings from estimates of productivity.

Statistical Analyses. For each year during our study period, we classified territories based on whether we observed a goshawk breeding attempt, quantified productivity, and estimated fledging date (Franke et al. 2017, Steenhof et al. 2017). We examined 35 predictor variables from five categories (precipitation, large storm precipitation, temperature, snowpack, and wind; Appendix 1) and developed models of goshawk breeding rate, productivity, and fledging date. We selected variables that we hypothesized could affect goshawk reproduction through specific mechanisms. Precipitation may affect goshawk hunting success, particularly if precipitation influences prey availability by causing prey to become more difficult to capture (Dawson and Bortolotti 2000, Sergio 2003). Precipitation may also affect thermoregulation of young and cause hypothermia (Anctil et al. 2014). We evaluated the previous year's April–July precipitation because it may affect ground squirrel abundance through its effects on foraging conditions before squirrels move underground to breed (Yensen et al. 1992) and goshawks in our study area depend heavily on Belding's, golden-mantled,

and Uinta ground squirrels (*Urocitellus beldingi, Callospermophilus lateralis, U. armatus*; approximately 75% of biomass consumed in some areas; Miller et al. 2014). Temperature could affect survival rates of eggs and young nestlings, especially if the female goshawk leaves the nest to forage in times of prey scarcity or poor hunting success. We examined snowpack because ground squirrels do not emerge from hibernation until snow melts sufficiently to expose greenery (Morton and Sherman 1978, Sheriff et al. 2011). We also considered wind in our analysis because it occasionally destroys goshawk nests and causes nest trees to fall (R. Miller unpubl. data).

We acquired daily precipitation and temperature data from Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group (2019) and procured wind data from the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Laboratory (2019). We derived mean and maximum wind speed using National Center for Environmental Prediction/National Center for Atmospheric Research Reanalysis 1 near-surface projections, interpolating these datasets up to the resolution of our precipitation and temperature data (Kalnay et al. 1996). We obtained average snowpack data (snow water equivalent; SWE) from the National Weather Service (2019). We restructured the precipitation, temperature, and wind data into monthly and multiple-month time scales based on our hypothesized effects for each variable. We calculated the previous year's April–July precipitation as a possible predictor of ground squirrel abundance (Yensen et al. 1992). We defined heavy precipitation days as all days within the upper 5% of daily precipitation readings in our study area (the equivalent of exceeding two standard deviations above the mean), which consisted of days with precipitation exceeding 10.39 mm. We derived predictor variables related to precipitation using the total heavy precipitation days between March and May and the maximum number of consecutive days of heavy precipitation during the same period. We calculated the SWE for early April, mid-April, and late April, as we hypothesized that these times would be the most ecologically relevant for analysis given how snowpack might affect incubating female goshawks. We applied our analyses to the incubation and nesting periods because they coincided with the timing of our observations, thereby providing an opportunity for more direct inference.

We used generalized linear mixed models in all analyses (Zuur et al. 2009, 2010). We performed three analyses, each with a separate response variable of breeding rate (binomial distribution), productivity (Poisson distribution), or fledging date (Gaussian distribution). For all models, we included division (within the Sawtooth National Forest), territory, and year as random effects to account for pseudo-replication and spatial autocorrelation (Zuur et al. 2009, 2010).

In each analysis, we ranked competing models with Akaike Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002). To address the issue of correlated variables, we used a two-tier approach to model selection (Lebreton et al. 1992, Doherty et al. 2012). In the first tier, we placed variables within each category (e.g., precipitation or temperature), many of which were correlated, into univariate models and ranked them against the other univariate models in their category, using AIC_c to choose the best-supported univariate model for each category if that univariate model ranked above the null model. We chose the best-supported univariate model including precipitation, previous year's April–July precipitation, temperature, wind, snow, and severe storms, propagating the variables from those models into the second tier of model selection. In evaluating models considering all combinations of these six variables, we ensured that no two highly correlated variables appeared within the same model (Pearson's $|r| < 0.6$; Zuur et al. 2010). We identified the best-supported model in each analysis by removing models that were >2 ΔAIC_c from the best-supported model, models that ranked below the null model, and models including variables that were uninformative (Burnham and Anderson 2002, Arnold 2010).

Future Climate Projections. For climate projections, we used the Hadley Centre Global Environment Earth System Model version 2 and Representative Conservation Pathway (RCP) 8.5 *a priori* (Collins et al. 2011). This model is based on the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 5 (CMIP5) multi-model dataset (Taylor et al. 2009). We used the Bias Corrected and Downscaled WCRP CMIP5 Climate Projections (Bureau of Reclamation 2013). This model assumes a radiative forcing value of +8.5 watts/m^2 in the year 2100 relative to pre-industrial values, which is the climate scenario that most closely aligns with the current greenhouse gas emission trend (Moss et al. 2008, US Global Change

Table 1. Best-supported models and null models of breeding rate, productivity, and fledging date of Northern Goshawks within the Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in Idaho and Utah, USA, 2011–2019. We present only models where $\Delta AIC_c \leq 2.00$ and the null model for comparison.

RESPONSE VARIABLE (ANALYSIS)	MODEL[a]	K^b	AIC_c^c	ΔAIC_c^d	DEVIANCE	df
Breeding rate (binomial)	PrecipApril + PrecipLagAprJul	6	385.7	0.00	373.4	309
	Null	4	399.8	14.09	391.7	311
Productivity (Poisson)	TempMeanAprMay	6	399.9	0.00	387.2	128
	Null	5	402.5	2.64	392.1	129
Fledging date (Gaussian)	PrecipLagAprJul + TempMeanMarMay	7	808.2	0.00	793.2	111
	Null	5	827.0	18.84	816.5	113

[a] All models include division and territory as random effects. Model variables defined in Appendix 1.
[b] K = number of parameters in the model.
[c] AIC_c = Akaike's Information Criterion adjusted for sample size.
[d] ΔAIC_c = difference in AIC_c values between individual model and model with lowest AIC_c.

Research Program 2017). We chose an arbitrary period of 50 yr for projections.

We integrated RCP climate projections of the relevant weather variables into our models of goshawk reproduction to create predictions for breeding rate, productivity, and fledging date over the next 50 yr. For each of our projections (breeding rate, productivity, and fledging date), we evaluated significant trends using linear models of the projection and reported them if the 95% confidence intervals of the coefficients did not overlap zero. The confidence interval represents the uncertainty of the predicted trend rather than the uncertainty of the models themselves.

Statistical Reporting. We report coefficient estimates for all models with standard errors and 95% confidence intervals (hereafter CIs). We report relationships from the best-supported model(s) of projected goshawk reproduction with 95% CIs determined by altering the variable of interest across its measured range while holding all other variables at their mean values. We conducted all statistical analyses in R (R Core Team 2019) and fit all models using R package glmmTMB (Magnusson et al. 2019). We ranked models using R package MuMIn (Bartoń 2019).

RESULTS

We found evidence of breeding attempts in 42 territories over our 9-yr study period (2011–2019). We quantified breeding rate using 315 territory–season combinations, quantified productivity based on 134 breeding attempts, and estimated fledging date for 118 successful breeding attempts.

Breeding Rate. Of the 315 territory–season combinations, we found evidence of breeding attempts on 146 occasions, resulting in an unadjusted estimate of breeding rate of 46%. The best-supported model of breeding rate incorporating precipitation variables from the same year that we assessed breeding rate included April precipitation (–0.02 ± 0.005; CI: –0.03, –0.01). The model of breeding rate that incorporated the previous year's April–July precipitation (0.01 ± 0.005; CI: –0.003, 0.02) ranked above the null model in our first tier of model selection. The best-supported model of breeding rate considering temperature variables included minimum May temperature (0.17 ± 0.05; CI: 0.07, 0.27) and the maximum number of consecutive days with heavy precipitation (–0.54 ± 0.26; CI: –1.05, –0.02). No models including wind speed or snowpack ranked above the null model. In our second tier of modeling breeding rate, we considered variables identified in each category in our first tier of model selection. The best-supported model of breeding rate in our second tier of model selection included April precipitation and previous year's April–July precipitation (Table 1). Goshawks were more likely to be present, detected, and breeding in areas and years with lower April precipitation (–0.02 ± 0.004; CI: –0.03, –0.01; Fig. 2a), and greater precipitation in April–July the previous year (0.009 ± 0.003; CI: 0.003, 0.01; Fig. 2b).

Productivity. Of the 134 breeding attempts for which we were able to assess productivity, average productivity was 2.12 (±1.06 SD) fledglings per breeding attempt. In our first tier of modeling productivity, no model including precipitation from the current year or previous year, no model
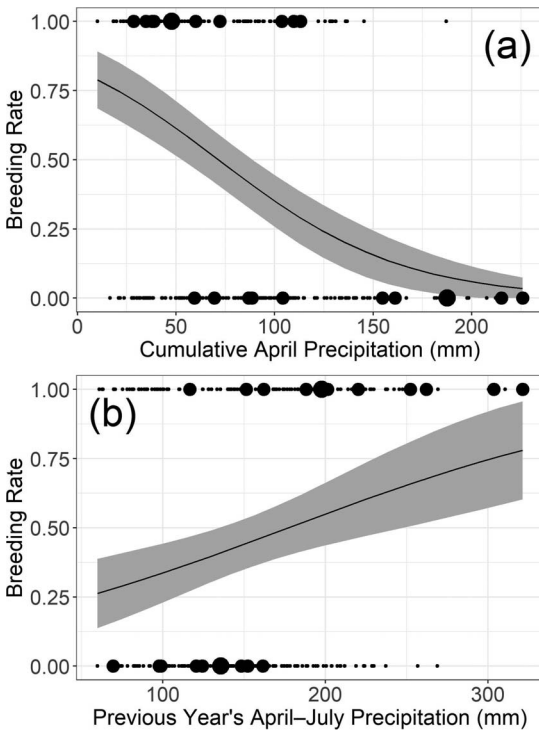
Figure 2. Predicted relationship between Northern Goshawk breeding rate and (a) cumulative April precipitation; and (b) previous year's April–July precipitation from the best-supported model of Northern Goshawk breeding rate within the Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in Idaho and Utah, USA, 2011–2019. Black line = model prediction; gray area = 95% confidence interval; and points = data used to build the model with point size relative to the number of similar values.

including snowpack, and no model including wind variables ranked above the null model. The best-supported model of productivity considering temperature variables was also our best supported overall model, including only mean April–May temperature (0.06 ± 0.03; CI: 0.007, 0.11; Table 1). Productivity was higher in years with warmer April–May temperatures (0.06 ± 0.03; CI: 0.007, 0.11; Fig. 3).

Fledging Date. For the 118 breeding attempts for which we were able to estimate fledging date, average fledging date was 10 July (±8.7 d SD). The best-supported model of fledging date incorporating precipitation variables from the same and previous year included previous year's April–July precipitation (0.08 ± 0.02; CI: 0.05, 0.11). The best-
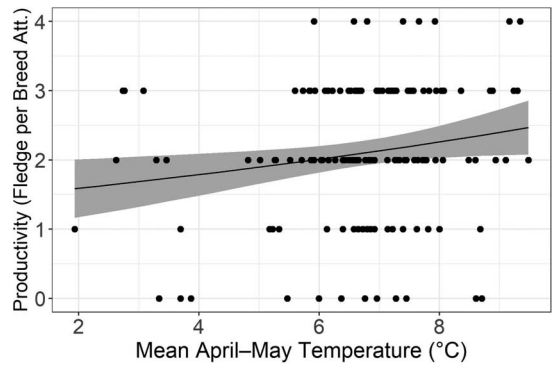

Figure 3. Predicted relationship between Northern Goshawk productivity (fledglings per breeding attempt) and mean April–May temperature from best-supported model of Northern Goshawk productivity within the Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in Idaho and Utah, USA, 2011–2019. Black line = model prediction; gray area = 95% confidence interval; and points = data used to build the model.

supported model of fledging date considering temperature variables included mean March–May temperature (−4.31 ± 0.90; CI: −6.07, −2.55). The best-supported model of fledging date considering snowpack variables included early April SWE (0.02 ± 0.006; CI: 0.01, 0.03). Considering variables identified within variable categories (i.e., precipitation, temperature, and snowpack) in our second tier of model assessment, previous year's April–July precipitation and mean March–May temperature were related to fledging date (Table 1). Goshawks bred later on average in years with more previous year's April–July precipitation (0.04 ± 0.02; CI: 0.004, 0.08; Fig. 4a) and lower mean March–May temperatures (−3.06 ± 0.97; CI: −4.97, −1.16; Fig. 4b).

Future Climate Projections. We assessed the effects of climate change on breeding rate by integrating projections from climate models of April precipitation and previous year's April–July precipitation in our best-supported model of breeding rate. Predicted breeding rate exhibited no change over the next 50 yr (−0.0006 ± 0.002; CI: −0.004, 0.003; Fig. 5a). We projected a significant increase in productivity over the next 50 yr (0.01 ± 0.002; CI: 0.009, 0.02; Fig. 5b) based on predicted future April–May mean temperatures. Lastly, we projected a significant shift toward earlier breeding over the next 50 yr (−0.34 ± 0.04; CI: −0.43, −0.26; Fig. 5c)
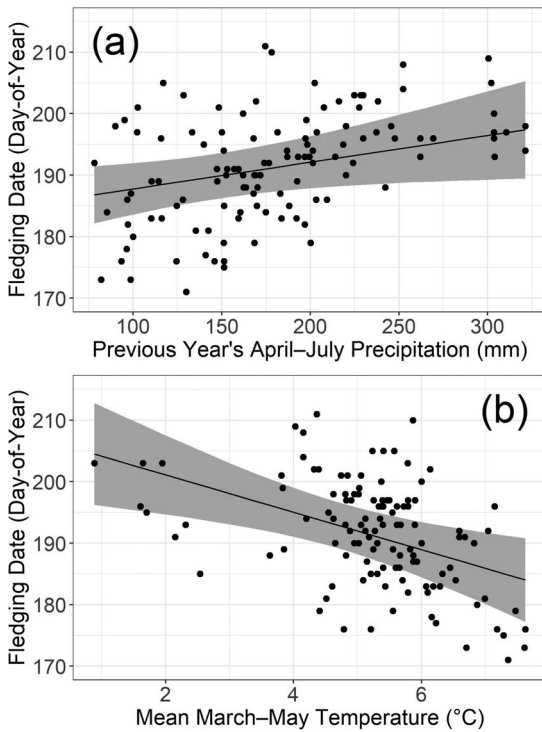
Figure 4. Predicted relationship between Northern Goshawk fledging date and (a) previous year's April–July precipitation; and (b) mean March–May temperature from best-supported model of Northern Goshawk fledging date within the Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in Idaho and Utah, USA, 2011–2019. Black line = model prediction; gray area = 95% confidence interval; and points = data used to build the model.

based on predicted March–May mean temperatures and previous year's April–July precipitation.

DISCUSSION

We evaluated weather factors related to goshawk breeding rate, productivity, and breeding phenology (i.e., fledging date) in the northern Great Basin region of western North America and demonstrated that spring precipitation and temperature were related to goshawk reproduction. We then used our best-supported models of goshawk breeding rate, productivity, and fledging date—combined with weather projections from climate models—to predict future goshawk reproduction. Our projections for goshawk reproduction suggest that changes to weather as a result of climate change over the next 50 yr will likely (1) have no effect on breeding rate,
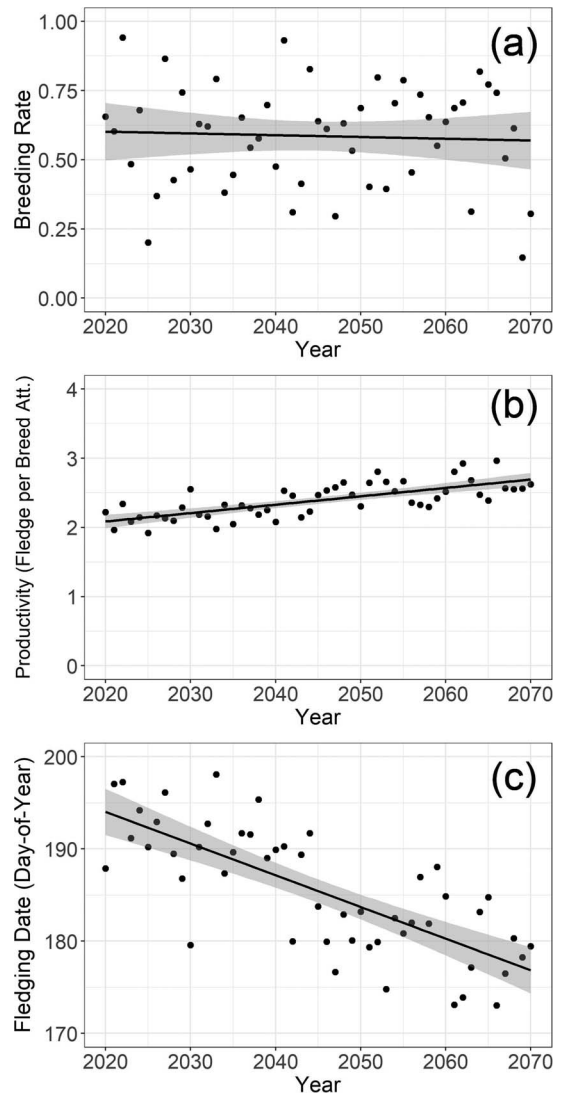

Figure 5. Predicted trends from best-supported models of Northern Goshawk (a) breeding rate; (b) productivity; and (c) fledging date using weather data from the Hadley Centre Global Environment Earth System Model version 2 and Representative Conservation Pathway (RCP) 8.5 climate model over the next 50 yr for the 42 Northern Goshawk territories within the Minidoka Ranger District, Sawtooth National Forest in the northern Great Basin in Idaho and Utah, USA. Black line = linear regression line of yearly predictions; gray area = 95% confidence interval for the regression line (Does not include climate model uncertainty). There was no trend for breeding rate, but a positive trend for productivity and a negative trend for fledging date.

(2) cause productivity to increase, and (3) cause fledging date to become earlier.

Breeding Rate. April precipitation and previous year's April–July precipitation were associated with goshawk breeding rate during our 9-yr study period. Greater April precipitation had a negative relation to breeding rate, similar to the relationship described by Kostrzewa and Kostrzewa (1990) and Fairhurst and Bechard (2005). There are several potential mechanisms for this relationship. Goshawk hunting success may be negatively affected by high precipitation, as it may cause prey to become less available (Dawson and Bortolotti 2000, Sergio 2003). If food resources are not sufficient for egg production, either because the male is unable to adequately provision the female or the female is unable to secure sufficient prey herself, a breeding attempt may fail (Newton 1986, Korpimäki 1990). Additionally, greater precipitation may result in higher energetic costs for an incubating female, and she may therefore be unable to successfully incubate eggs (Kostrzewa and Kostrzewa 1990).

Breeding rate was positively related to previous year's April–July precipitation. This association may have been related to increased prey availability, as most goshawks in our study are highly dependent upon ground squirrels during the nesting period and precipitation may be linked to ground squirrel abundance through its effects on vegetation (Younk and Bechard 1994, Van Horne et al. 1997, Miller et al. 2014).

In contrast to our results, Patla (2005) found no effect of weather on goshawk nest occupancy; her definition of nest occupancy rate was similar to what we termed breeding rate. However, her study used lower-resolution weather data from a single, central weather station, possibly contributing to the lack of an observed effect. Natsukawa et al. (2019) also found no effect of weather, but their study was limited to 3 yr of observations.

Productivity. Higher April–May mean temperatures were associated with increased goshawk productivity in the northern Great Basin, which was similar to the results of Kostrzewa and Kostrzewa (1990) and Fairhurst and Bechard (2005). In our study area, April is the nest-building and egg-laying period, the majority of incubation occurs in May, and eggs hatch during late May and early June. Temperatures during these periods could be related to productivity because colder temperatures increase the risk of hypothermia and subsequent death in nestlings, and temperature may affect goshawks indirectly by altering the behavior of prey species (e.g., the prolonged presence of snow is negatively correlated with the emergence of ground squirrels from their hibernation burrows; Morton and Sherman 1978). Although we did not observe a relationship between snowpack and goshawk productivity, we expect that the timing of the emergence of ground squirrels could impact goshawk productivity in our study area, with earlier emergence enabling goshawks to produce more young.

Fledging Date. Mean March–May temperature and previous year's April–July precipitation were related to goshawk fledging date, i.e., breeding date. Higher mean March–May temperatures were associated with earlier fledging dates, likely because warmer temperatures resulted in increased availability of ground squirrels earlier in the season and consequently enabled female goshawks to produce eggs earlier (Morton and Sherman 1978, Sheriff et al. 2011). Greater previous year's April–July precipitation could lead to improved ground squirrel condition when they estivate, leading to greater ground squirrel survival and productivity, thereby resulting in greater abundance the following year (Yensen et al. 1992). This increased prey abundance could enable female goshawks to attain higher body condition sooner, which may allow them to produce eggs earlier.

Years with greater previous year's April–July precipitation were also associated with later fledging dates, likely because greater previous year's April–July precipitation is associated with higher breeding rates. In years with higher breeding rates, the proportion of young, inexperienced breeding goshawks may also have been higher, as older, experienced breeders are more likely to breed consistently, even in poor years (R. Miller unpubl. data). Young goshawks lay eggs later than older goshawks, which could result in later average fledging dates (Kenward 2006).

Climate Change. Incorporating predicted weather conditions from the RCP8.5 climate model into our best-supported models of goshawk breeding rate, productivity, and fledging date over the next 50 yr indicated substantive potential effects on goshawk reproduction. Integrating April precipitation and previous year's April–July precipitation into our model of breeding rate resulted in no trend in breeding rate.

In contrast to our result for breeding rate, our model of goshawk productivity projects an increase in productivity based on predicted warmer April–

May mean temperatures derived from climate models. Furthermore, based on projected mean March–May temperatures and previous year's April–July precipitation, our model of fledging date predicts a trend toward earlier breeding, which we expect would have a neutral effect on goshawk reproduction. Overall, we expect that weather changes brought about by a climate scenario akin to RCP8.5 may have a slight positive effect on goshawk reproduction in the northern Great Basin by bolstering productivity.

However, our analysis does not fully account for all possible indirect effects that climate change may have on goshawk reproduction in our study area. Climate change is known to be a primary cause of continuing aspen declines in the western United States and is a factor that increases the vulnerability of lodgepole pine to mountain pine beetle (*Dendroctonus ponderosae*) infestation and subsequent death (Rehfeldt et al. 2009, Perovich and Sibold 2016). Furthermore, prey species and the vegetation on the open landscapes hunted by goshawks have experienced declines in the northern Great Basin linked to climate change (Keane et al. 2018, Reeves et al. 2018). These declines in tree, shrub, and prey species could result in a dramatic decrease in quantity and quality of breeding habitat available to goshawks in our study area, which would likely negatively influence their reproduction. We observed a decline in breeding rate that may be related to the indirect effects of climate change on forest structure (e.g., decreased canopy cover) during our 9-yr study period, but that trend is not apparent in the analysis of weather variables that we considered. We suggest that more long-term analyses investigating the relationship between weather, changes to forest structure, and annual variation in the reproduction of goshawks be conducted across their range; an understanding of these relationships is essential to inform predictions regarding the impact climate change may have on goshawk populations.

We also acknowledge that our inability to address imperfect detection could have influenced our results and their interpretation. If missed detections of goshawks in territories were random, any bias in our sample of goshawk territories may have been minimized. However, if missed detections were not random, estimates of breeding rate and productivity may have been biased. Our most likely source of imperfect detection was missing failed breeding attempts, especially those where failure occurred prior to our arrival in the study area. If missed failed breeding attempts correlated with any of our predictor variables, identification of the best-supported model and the nature of relationships we identified could have been compromised. Although we are unable to assess how imperfect detection may have influenced our results, we suggest that future studies account for imperfect detection.

Conclusions. Our results suggest that April precipitation, previous year's April–July precipitation, April–May mean temperature, and March–May mean temperature affect goshawk reproduction in the northern Great Basin, and we propose various explanations for these relationships. We found a neutral to positive influence of projected climate on goshawk breeding over the next 50 yr, primarily through an increase in productivity. Despite the trends indicated by our best-supported models, we suspect that climate change may have a long-term negative effect through its gradual influences on vegetation, but this will require additional time to validate. We suggest that future studies be conducted to determine what impact a changing climate will have on tree, shrub, and prey species relevant to breeding goshawks, which would improve future projections of how climate change may affect goshawk reproduction.

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Appendix 1. Category, variable name, mean, standard deviation (SD), range, and source of data used in models of Northern Goshawk breeding rate, productivity, and fledging date within the Minidoka Ranger District, Sawtooth National Forest, northern Great Basin in Idaho and Utah, USA, 2011–2019.

CATEGORY AND VARIABLE	MEAN $\pm$ SD	RANGE	DESCRIPTION
Precipitation (mm)[a]			
PrecipApril	80.2 $\pm$ 43.8	10.2–225.9	April precipitation
PrecipMarApr	151.6 $\pm$ 66.3	15.2–337.0	March–April precipitation
PrecipFebApr	212.4 $\pm$ 88.6	27.7–427.0	February–April precipitation
PrecipJanApr	296.8 $\pm$ 120.2	44.1–619.5	January–April precipitation
PrecipMay	62.3 $\pm$ 38.5	7.4–172.6	May precipitation
PrecipAprMay	142.6 $\pm$ 47.9	47.0–265.1	April–May precipitation
PrecipMarMay	214.0 $\pm$ 68.5	79.0–428.3	March–May precipitation
PrecipFebMay	274.7 $\pm$ 89.2	101.4–492.4	February–May precipitation
PrecipJanMay	359.1 $\pm$ 114.0	122.7–656.2	January–May precipitation
PrecipLagAprJul	157.7 $\pm$ 52.0	59.9–321.3	Previous year's April–July precipitation
Large storms precipitation (mm) or (d)[a]			
MaxDailyPrecip	24.7 $\pm$ 10.7	8.9–63.5	Maximum daily precipitation March–May
DaysHeavyPrecip	5.3 $\pm$ 2.9	0–14	Total number of days with heavy precipitation March–May
ConsDaysMaxPrecip	1.5 $\pm$ 0.6	0–3	Maximum consecutive days with heavy precipitation March–May
Temperature (°C)[a]			
TempMeanApril	5.3 $\pm$ 3.1	0.0–15.3	Mean April temperature
TempMeanMarApr	3.9 $\pm$ 2.5	−0.6–11.8	Mean March–April temperature
TempMeanFebApr	2.4 $\pm$ 2.6	−2.0–10.3	Mean February–April temperature
TempMeanMay	7.2 $\pm$ 3.9	−3.3–12.3	Mean May temperature
TempMeanAprMay	6.3 $\pm$ 1.5	1.9–9.5	Mean April–May temperature
TempMeanMarMay	5.0 $\pm$ 1.3	0.9–7.6	Mean March–May temperature
TempMeanFebMay	3.7 $\pm$ 1.5	−0.5–7.1	Mean February–May temperature
TempMinApr	−7.2 $\pm$ 2.9	−12.9–0.2	Minimum April temperature
TempMinMay	−5.2 $\pm$ 5.4	−22.9–2.4	Minimum May temperature
TempMinAprMay	−7.2 $\pm$ 4.0	−22.9–2.0	Minimum April–May temperature
TempMeanMinApr	−0.6 $\pm$ 2.8	−5.3–9.7	Mean minimum April temperature
TempMeanMinMay	1.5 $\pm$ 3.4	−9.8–6.6	Mean minimum May temperature
Snowpack (mm)[b]			
SnowDepth	375.9 $\pm$ 482.3	0.0–1669.7	Mid-April snow depth
EarlyAprSWE	133.0 $\pm$ 173.3	0.0–590.1	Early April snow water equivalent
MidAprSWE	108.0 $\pm$ 162.2	0.0–610.2	Mid-April snow water equivalent
LateAprSWE	76.2 $\pm$ 142.0	0.0–631.3	Late April snow water equivalent
Wind (m/sec)[c]			
MeanApr	4.6 $\pm$ 0.4	3.9–5.2	Mean April wind speed
MeanMay	4.1 $\pm$ 0.3	3.7–4.5	Mean May wind speed
MeanAprMay	4.3 $\pm$ 0.3	4.0–4.8	Mean April–May wind speed
MaxApr	6.8 $\pm$ 0.5	5.9–7.8	Maximum April wind speed
MaxMay	6.0 $\pm$ 0.4	5.5–6.7	Maximum May wind speed
MaxAprMay	6.4 $\pm$ 0.3	5.8–6.9	Maximum April–May wind speed

[a] PRISM Climate Group (2019).
[b] National Weather Service (2019).
[c] NOAA Physical Sciences Laboratory (2019).