RELATIONSHIPS BETWEEN WINTER AND SPRING WEATHER AND NORTHERN GOSHAWK (ACCIPITER GENTILIS) REPRODUCTION IN NORTHERN NEVADA

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ABSTRACT.—Ecological factors, such as weather, play important roles in raptor population dynamics. We used logistic and Poisson regression analyses to investigate relationships between late winter, spring, and early summer temperatures and precipitation and Northern Goshawk (*Accipiter gentilis*) breeding, failure, and productivity in northern Nevada from 1992–2002. We also examined weather data for possible patterns that could explain reported trends in goshawk reproduction. Declines in occupancy of nesting territories by breeding goshawks were related to colder February and March temperatures and increased April precipitation. Warmer April temperatures and decreased precipitation in April–July favored reproductive success. Of all significant weather variables, only February and March temperatures had significant temporal trends. Although adverse weather is known to affect goshawk reproduction by decreasing nestling growth and survival, it is unlikely that direct weather effects were responsible for reported reproductive trends in our study area. Weather may have operated indirectly, influencing reproduction through changes in goshawk hunting behavior or food supply.

KEY WORDS: Northern Goshawk; Accipiter gentilis; weather, breeding, population trends; Nevada.

RELACIONES ENTRE EL CLIMA DE INVIERNO Y DE PRIMAVERA Y LA REPRODUCCIÓN DE *ACCIPITER GENTILIS* EN EL NORTE DE NEVADA

RESUMEN.—Factores ecológicos como el clima tienen un papel importante en la dinámica poblacional de las aves rapaces. Utilizamos análisis de regresión logística y de Poisson para investigar las relaciones entre las temperaturas y las precipitaciones de fines del invierno, de la primavera y del comienzo del verano, y los fracasos o éxitos reproductivos y la productividad de Accipiter gentilis en el norte de Nevada entre 1992 y 2002. También examinamos los datos de clima para encontrar posibles tendencias que puedan explicar las tendencias documentadas de la reproducción de estos halcones. La disminución en la ocupación de territorios de nidificación por halcones reproductivos se relacionó con las temperaturas más frías de febrero y marzo y el aumento de las precipitaciones en abril. Las temperaturas más cálidas de abril y la disminución de las precipitaciones en abril-julio favorecieron el éxito reproductivo. De todas las variables climáticas significativas, sólo las temperaturas de febrero y marzo presentaron tendencias temporales significativas. A pesar de que es sabido que las condiciones climáticas adversas afectan la reproducción de estos halcones al disminuir el crecimiento y la supervivencia de los polluelos, es poco probable que los efectos directos del clima fueran responsables de las tendencias reproductivas documentadas en nuestro sitio de estudio. Las condiciones climáticas pueden haber operado indirectamente, influenciando la reproducción a través de cambios en el comportamiento de caza de los halcones, o en la disponibilidad de alimento.

[Traducción del equipo editorial]

Weather can directly influence Northern Goshawk (*Accipiter gentilis*) population dynamics by affecting survival (Zachel 1985, Squires and Reynolds 1997, Bloxton 2002), movements (Marcström and Kenward 1981, Squires and Ruggiero 1995), and nestling development (Kostrzewa and Kostrze-

wa 1990). Temperature and precipitation may also indirectly affect prey populations (Van Horne et al. 1997, Bloxton 2002), foraging behavior (Zachel 1985), and other mortality factors (Newton 1979).

Studies addressing the relationships between weather and goshawk reproduction (Kostrzewa and Kostrzewa 1990, 1991, Patla 1997, Penteriani 1997, Ingraldi 1998, Bloxton 2002), generally agree that colder and wetter spring weather nega-

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tively affects goshawk reproduction; however, the association between winter weather and goshawk reproduction is not well studied. These studies have also only considered time periods <6 yr (Ingraldi 1998).

We previously reported declines in goshawk nesting territory occupancy and increases in breeding failure in northern Nevada from 1992-2002 (Bechard et al. in press). Determining the ecological factors responsible for these reproductive trends is difficult because any variable that showed a temporal trend from 1992-2002 will consequentially be correlated with reproduction. However, because of the known links between weather and goshawk reproduction and the abnormally low precipitation and drought conditions reported in the northern Great Basin from 1999-2002 (National Drought Mitigation Center 2003), we suspected that weather conditions affected goshawk reproduction in northern Nevada. Here, we address the associations between late winter, spring, and early summer temperature and precipitation and long-term trends in goshawk reproductive performance.

METHODS

Study Area. We conducted the study in the Independence and Bull Run Mountain ranges of Elko County, northern Nevada, during 1992–2002. The study area extended ca. 150 km north-to-south, 10–30 km east-to-west, and encompassed ca. 94 000 ha. The area is a mosaic of public lands administered by the United States Department of Agriculture Forest Service (Humboldt-Toiyabe National Forest) interspersed with private lands. Elevations range from ca. 1700–3000 m on the highest peaks. A mixture of land uses occurred in the study area, including cattle ranching, gold mining, and outdoor recreation (hunting, camping, and off-road vehicle use).

The sagebrush steppe was typified by big sagebrush (Artemisia tridentata), bitterbrush (Purshia tridentata), and rabbitbrush (Chrysothamnus spp.). Common native grasses included native bluebunch wheatgrass (Pseudoroegneria spicata) and Idaho fescue (Festuca idahoensis), and introduced cheatgrass (Bromus tectorum) and medusahead wildrye (Taeniatherum caput-medusae) also occur (Loope 1969; P. Jelinek, Humboldt-Toiyabe National Forest, pers. comm.). In the study area, goshawks nested exclusively in quaking aspen (Populus tremuloides), which occurred in naturally-fragmented stands where sufficient moisture was present. Subalpine fir (Abies lasiocarpa) replaces quaking aspen above elevations of 2500 m (Loope 1969).

Dense willow (*Salix* spp.), thickets, and cottonwoods (*Populus* spp.) occurred in riparian areas at all elevations.

Field Methods. In April of 1991, 1992, and 1994–96, we used helicopters to initially locate and subsequently survey all historical goshawk nesting territories in the study area. We defined a nesting territory as the area containing one or more nests occupied by a single pair of goshawks in any breeding season (Postupalsky 1974,

Woodbridge and Detrich 1994, Reynolds and Joy 1998). We discontinued helicopter surveys after 1996.

Beginning in mid-May of each year from 1992–2002, we conducted ground surveys of all historically-occupied nesting territories (i.e., previously located by helicopter and used by goshawks) to determine occupancy by goshawk breeding pairs. We conducted ground surveys on foot and with all-terrain vehicles by returning to nesting territories and thoroughly searching stands and adjacent stands for the presence of breeding goshawks. Because territories in our study area were relatively small and nest structures obvious, we were able to search each territory completely and, therefore, assume a uniform probability of detection. We were unable to reach all nesting territories each year because roads throughout the study area were periodically snow-covered or washed-out, and private land was not always accessible.

Beginning in mid-June of each year, we revisited occupied nesting territories to determine productivity (Bechard et al., in press). We climbed all occupied nest trees and counted and banded nestlings when they were approximately 21–31 d old (age based on nestling plumage; Boal 1994). We considered a pair failed if there was no sign of goshawks (adults or nestlings) at or near an occupied nest when it was revisited in June.

Data Analyses. We determined nesting territory occupancy, productivity per breeding pair, breeding failure, and productivity per successful pair. Because we visited most nests only twice during the breeding season, there was as much as a 30-d interval between our nest visits. Therefore, we could not always determine the cause of a nest failure. There were no instances that clearly indicated the nesting attempt had failed due to depredation or any other factor unrelated to weather; therefore, we included all failures in our analysis.

We downloaded weather data for the study area from the Natural Resources Conservation Service/SNOTEL website (Jack's Creek Upper weather station; Natural Resources Conservation Service 2003). Because SNOTEL considered temperature data for 2002 unreliable, we did not include those data.

To analyze 11-yr trends in reproduction, we used logistic regression for binary outcomes (i.e., nesting territory occupancy and nesting failures) and Poisson regression for counted outcomes (i.e., productivity). To account for the fact that repeated measurements on a nesting territory over time might not be statistically independent (Allison 1999), we used Generalized Estimating Equations ("GEE;" PROC GENMOD; SAS Institute, Inc., Cary, NC U.S.A.), which allowed us to cluster our data by nesting territory (Stokes et al. 2000).

We modeled mean daily temperature (°C), cumulative monthly precipitation (cm; Fig. 1, 2), and year as continuous explanatory variables. We used only weather data from January–July, as we felt that they were most biologically relevant. We considered individual months and groups of months (i.e., January and February, February and March) in analyses, resulting in 27 possible explanatory variables per reproductive outcome (13 for mean daily temperature, 13 for cumulative monthly precipitation, and 1 for year). Due to low sample sizes (N = 11 yr), we did not consider more than one explanatory variable per model. Therefore, to avoid over specifying our

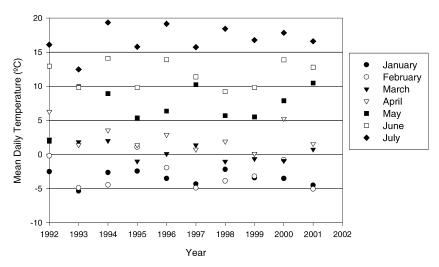


Figure 1. Mean daily temperature for January–July in the Independence and Bull Run mountains, Nevada for 1992–2002.

models, we ran separate univariate models for each explanatory weather variable and employed a pre-screening procedure to decide which models best explained the relationship between weather and goshawk reproduction.

During pre-screening, we only considered weather variables that appeared to be biologically relevant. For example, July weather would not be biologically related to occupancy in the same year because occupancy occurs before July. In addition, for each of the four reproductive outcomes, we ran several competing univariate models: each competing model used weather data from a single month or group of months as the explanatory variable. For example, 11 competing occupancy models used mean daily temperature as the explanatory variable, and an additional 11 occupancy models used cumulative monthly precipitation. For each reproductive outcome, we then selected the models with the single most statistically significant temperature and precipitation variables. Thus, for each reproductive outcome, we presented three separate univariate models: one for temperature, one for precipitation, and one for year. To avoid inflated Type I error rates, we assessed significance of all models using a step-down Bonferroni correction (Holm 1979). Although our statistical method has the potential to produce spurious results (Freedman 1983), the GEE has no other measure by which to assess multiple competing models.

We evaluated the results of logistic regression models by exponentiation of the model coefficient to obtain odds ratios, and we evaluated the results of Poisson regression by exponentiation of the model coefficient to obtain percent increase in the mean values of dependent variables. In the analyses, we only included nesting territories for which we knew the reproductive outcome.

To determine if any patterns existed in local weather variables, we used simple linear regression (JMP IN; SAS Institute, Inc., Cary, NC U.S.A.). For each weather variable that was significantly related to occupancy and fail-

ure (one temperature variable and one precipitation variable per each reproductive outcome), we regressed year against the temperature or precipitation variable.

RESULTS

We initially located 27 nesting territories in 1992, and found five, five, and four additional nesting territories in 1993, 1994, and 1996, respectively. We monitored a mean of 32.5 \pm 4.7 ($\bar{x} \pm SD$) nesting territories annually (Table 1). Goshawks occupied an average of 20.3 ± 6.7 of these nesting territories each year. The odds of nesting territory occupancy by breeding pairs increased by 55.8% with each 1°C increase in combined February and March mean daily temperature (odds ratio = 1.558, P =0.018; Table 2). The odds of occupancy of a nesting territory increased by 7.7% for every cm increase in cumulative April precipitation (odds ratio = 1.077, P = 0.03). We detected a significant cooling trend in combined February and March mean daily temperature in our study area ($r^2 = 0.41$, P = 0.04), but we found no trend in cumulative April precipitation ($r^2 < 0.0002, P = 0.97$).

Goshawk breeding pairs fledged a mean of 2.27 \pm 0.76 young annually. Mean productivity per breeding pair increased 10.5% for every 1°C increase in the mean daily April temperature (Table 3; percent change in mean = 1.105, P < 0.0001). Mean productivity per breeding pair decreased by 1.9% for every 1 cm increase in combined April and May precipitation (percent change in mean = 0.981, P < 0.0003).

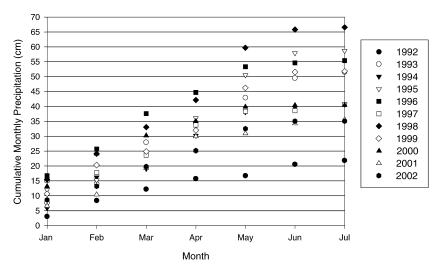


Figure 2. Monthly precipitation in the Independence and Bull Run Mountains, Nevada, for 1992–2002, expressed as cumulative monthly totals for January–July.

On average, 13.5% of breeding attempts failed. The odds of failure decreased by 40.5% with every 1°C increase in mean daily April temperature (Table 2; odds ratio = 0.595, P < 0.0007) and increased by 8.7% with each cumulative 1 cm increase in combined May and June cumulative precipitation (odds ratio = 1.087, P < 0.006). We found no trends in April ($r^2 = 0.094$, P = 0.39) or combined May and June ($r^2 = 0.007$, P = 0.80) temperatures.

Successful pairs produced a mean of 2.64 ± 0.57 young. For each 1°C increase in mean daily April temperature, we found a 6.4% increase in mean productivity per successful pair (Table 3; percent change in mean = 1.064, P < 0.0001). Mean productivity per successful pair decreased by 3.2% for each cumulative cm of combined June and July precipitation (percent change in mean = 0.978, P = 0.042).

DISCUSSION

Long-term trends in goshawk reproduction were significantly related to weather, with a stronger influence of temperature than of precipitation. Although late winter temperatures decreased in the study area from 1992–2002, our results suggested that warmer late winter temperatures favored goshawk breeding. Decreased productivity has been related to colder and wetter spring weather (Kostrzewa and Kostrzewa 1990, Patla 1997, Penteriani 1997, Bloxton 2002). Colder temperatures increase

energetic stresses and increase dietary demands on raptors and can result in non-laying (Newton 1979). Studies correlating winter temperatures with North American goshawk reproduction are lacking, but in European goshawks winter temperatures were not related to occupancy by breeding pairs (Kostrzewa and Kostrzewa 1991). However, the larger size of European goshawks may make them more robust to temperature and energetic demands early in the breeding season than the smaller North American subspecies (Kendleigh 1970).

Our finding of increased April precipitation favoring occupancy by breeding pairs was unusual, and we found no previous studies to support this result. Moreover, increased precipitation early in the breeding season is typically associated with reduced numbers of breeding pairs (Kostrzewa and Kostrzewa 1990, Ingraldi 1998, Bloxton 2002). Perhaps our finding of statistical significance does not necessarily relate to biological relevance, and the significant result is spurious.

The temporal trend in the failure of breeding attempts was strongly related to April temperature and cumulative May and June precipitation. Increased precipitation and decreased temperatures during the egg-laying and early nestling periods can increase egg and nestling mortality rates (Hoglund 1964, Zachel 1985) and affect nestling development (Kostrzewa and Kostrzewa 1990).

Table 1. Annual reproductive performance of Northern Goshawk nesting territories based on surveys conducted May-June 1992-2002 in the Independence and Bull Run Mountains, Nevada. All data previously reported in Bechard et al. (in press).

	No.								No.
	NESTING	NESTING NO. NESTING		No.	No.			No.	YOUNG PER
	Territories	TERRITORIES	OCCUPANCY	BREEDING	SUCCESSFUL	FAILURE	TOTAL NO.	YOUNG PER	SUCCESSFUL
YEAR	SURVEYED	OCCUPIED	(%)	$PAIRS^a$	$PAIRS^b$	(%) _c	$ m YOUNG^d$	Breeding Pair	PAIR
1992	27	22	81.5	22	21	4.5	61	2.77 ± 0.92	2.90 ± 0.70
1993	32	25	78.1	24	22	12.5	20	2.08 ± 1.14	2.38 ± 0.86
1994	37	26	70.3	19	24	10.5	47	2.47 ± 1.22	2.76 ± 0.90
1995	37	27	73.0	25	20	28.0	46	1.84 ± 1.40	2.56 ± 0.92
1996	41	30	73.2	30	28	6.7	73	2.43 ± 0.94	2.61 ± 0.68
1997	24	20	83.3	19	19	5.3	39	2.05 ± 0.85	2.17 ± 0.71
1998	33	18	54.6	18	15	16.7	40	2.22 ± 1.17	2.67 ± 0.62
1999	33	17	51.5	17	12	29.4	26	1.53 ± 1.33	2.17 ± 1.03
2000	33	18	54.6	18	18	0.0	61	3.39 ± 0.78	3.39 ± 0.78
2001	30	13	43.3	13	10	23.1	25	1.92 ± 1.55	2.50 ± 1.27
2002	31	7	22.6	7	4	42.9	10	1.43 ± 1.40	2.50 ± 0.58
Total	358	223	I	212	193	I	478	I	I
Mean	32.5 ± 4.7	20.3 ± 6.7	$62.4 \pm 18.8\%$	19.3 ± 6.1	17.5 ± 6.8	13.5	43.5 ± 18.3	2.27 ± 0.76	2.64 ± 0.57

^a Reflects number of pairs for which productivity was determined.

^b Success defined as raising at least one young to ≥21 d post-hatching.

^c Percent of breeding pairs that were successful; includes pairs where productivity was not determined.

d The number of young reaching ≥21 d post-hatching.

Table 2. Odds ratios, confidence intervals (CI), and significance of weather variables related to Northern Goshawk nesting territory occupancy in the Independence and Bull Run Mountains, Nevada, for 1992–2002.

Model Term	Odds Ratio	95% CI ^a	P -value $^{\mathrm{b}}$
Occupancy by breeding pairs			
Year ^c	0.785	0.701 - 0.880	< 0.0002
Mean daily combined February and March			
temperature	1.558	1.135-2.138	0.018
Cumulative April precipitation	1.077	1.014-1.143	0.03
Failure			
Year	1.157	1.021-1.312	0.044
Mean daily April temperature	0.595	0.455 - 0.780	< 0.0007
Cumulative combined May and June			
precipitation	1.087	1.031-1.146	< 0.006

^a Odds ratios are nonsignificant if confidence interval covers 1.0 (even odds).

Despite evidence that weather can directly affect goshawk breeding, it is unlikely that direct weather effects are solely responsible for our reported trends in reproduction (Newton 1998). We found no significant temporal trends in weather related to nest failure, suggesting changes in that reproductive variable were due to other factors such as reduced hunting and food provisioning due to continued rainfall (Zachel 1985, Bloxton 2002). Also, depredation of goshawk nests can result in nest failures. Because our nest visits were several weeks apart, and we could not determine the exact cause of nest failure in all cases, we included all

failures in our analysis, possibly biasing our results. Nevertheless, we found no direct evidence indicating that other factors unrelated to weather, such as depredation by Great Horned Owls (*Bubo virginianus*), played a significant role in the breeding failures we observed.

The confounding influences of unmeasured, but plausible, factors that may have changed during the study period complicated the analysis. Obvious among these was a possible trend in prey populations. Goshawks respond numerically to changes in numbers of prey (McGowan 1975, Doyle and Smith 1994). In our study area, they relied heavily on

Table 3. Percent change in mean, confidence intervals (CI), and significance of weather variables related to Northern Goshawk productivity in the Independence and Bull Run Mountains, Nevada, for 1992–2002.

	PERCENT CHANGE		
Model Term	IN MEAN	95% CI ^a	P -VALUE $^{ m b}$
Productivity per breeding pair			
Year ^c	0.985	0.963 - 1.008	0.20
Mean daily April temperature	1.105	1.070-1.140	< 0.0001
Cumulative combined April and May			
precipitation	0.981	0.971 - 0.990	< 0.0003
Productivity per successful pair			
Year	1.003	0.989 - 1.017	>0.90
Mean daily April temperature	1.064	1.040-1.089	< 0.0001
Cumulative combined June and July			
precipitation	0.978	0.962 - 0.994	0.042

^a Percent changes in the means are nonsignificant if confidence interval covers 1.0 (even odds).

^b Significance of terms assessed using a step-down Bonferroni adjustment (Holm 1979).

^c Data for year model terms taken from Bechard et al. (in press).

^b Significance of terms assessed using a step-down Bonferroni adjustment (Holm 1979).

^c Data for year model terms taken from Bechard et al. (in press).

Belding's ground squirrels (*Spermophilus beldingi*) for food (Younk and Bechard 1994, Younk 1996), but because we did not census ground squirrels, we could not determine what effect change in ground squirrel populations had on goshawk reproduction.

Further, interactions of weather and prey abundance may affect raptor reproduction (Gargett et al. 1995, Steenhof et al. 1997, Bloxton 2002). Weather has been shown to affect ground squirrel populations in other parts of the northern Great Basin (Van Horne et al. 1997). Bloxton (2002) attributed increased breeding failure and significantly lower productivity to reduced abundances of goshawk prey species following the wet and cold winter and spring of a La Niña weather event in western Washington. He noted that goshawks did not breed if weather had affected prey populations. Although the climate of the northern Great Basin differs markedly from western Washington, the interactive effects of weather and prey may not.

ACKNOWLEDGMENTS

This project was supported by the Nevada Department of Wildlife, U.S. Department of Agriculture Forest Service (Humboldt-Toiyabe National Forest), Independence Mining Company (now AngloGold-Meridian Jerritt Canyon Joint Venture), and Boise State University. We would like to thank P. Bradley of the Nevada Department of Wildlife for his foresight in initiating this much-needed study of goshawks in an unusual habitat. We are deeply grateful to Forest Service biologists W. Amy, S. Anderson, P. Jelinek, J. Warder, and B. Whalen for all their efforts through the years to help with this project. Without the support of Independence Mining Company this project would never have been possible. We would like to especially thank J. Bokich, J. Campbell, L. Gionet-Sheffield, G. Goodrich, M. Jones, S. Lewis, K. McAdoo, and J. Parks at the mine for their support. G. Fairhurst was supported by a Dan Montgomery Graduate Research Fellowship while at Boise State University. We are indebted to J. Younk, M. Shipman, and H. Smith for their substantial contributions to this project, and to L. Bond for her statistical help. We would like to thank all the field assistants who contributed to this project. We are grateful to reviewers P. Beier, C. Boal, and M. Goldstein for providing valuable comments and suggestions. Finally, we would like to thank the organizers of the goshawk symposium, Editors C. Boal and J. Bednarz for their hard work.

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Received 2 February 2004; accepted 9 March 2005 Associate Editor: Michael I. Goldstein