Weather and prairie grouse: dealing with effects beyond our control

by Bridgette L. Flanders-Wanner, Gary C. White, and Leonard L. McDaniel

Abstract We used multiple-linear-regression methods to simultaneously assess effects of vegetative disturbance and weather on the production of sharp-tailed grouse (*Tympanuchus phasianellus*) on Valentine National Wildlife Refuge (NWR) in Nebraska using a long-term data set of harvest-age ratios as production indices. After developing the model, we plotted the model-averaged predictions of sharp-tailed grouse production indices for Valentine NWR against actual sharp-tailed grouse production indices for our reference area, Samuel R. McKelvie National Forest (NF) in Nebraska. Model-averaged estimates of production provided reasonable predictions of actual production indices on Valentine NWR, although prediction intervals were large. The most useful predictor variables according to cumulative Akaike's Information Criterion weights were weather variables, emphasizing the significant influence of weather on sharp-tailed grouse production. As hypothesized a priori, "May Average Temperature," "June Average Temperature," and "Cumulative Precipitation from 1 January–31 July" were positively correlated with sharp-tailed grouse production, while "June Number of Heat Stress Days" and "June Number of Days of Precipitation >2.54 mm" were negatively correlated with sharp-tailed grouse production. The drought index, Cumulative Precipitation from 1 January–31 July, explained the most variability in sharp-tailed grouse production indices. The model developed on Valentine NWR overpredicted sharp-tailed grouse production indices on Samuel R. McKelvie NF by 0.77 juveniles per adult, when averaged across years. Further experimentation is needed to support our hypothesis that vegetative disturbance on Samuel R. McKelvie NF is negatively affecting sharp-tailed grouse production at its current levels.

Key Words brood survival, grouse, harvest-age ratios, nest success, precipitation, production, sharp-tailed grouse, temperature, *Tympanuchus*, weather

Production—the number of juveniles raised to independence per adult—is a key demographic parameter in the dynamics of any population. This parameter is influenced by percentage of hens nesting, clutch size, nesting success, and subsequent survival of juveniles to independence (Bergerud 1988). For prairie grouse species such as the greater prairie-chicken (*Tympanuchus cupido pinnatus*) and the sharp-tailed grouse (*T. phasianellus*)

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(hereafter sharptail), variation in production appears to be related to a number of factors. Of those factors, vegetative cover (Kirsch et al. 1978) and weather (Shelford and Yeatter 1955) are 2 of the foremost influencing production.

The first factor, vegetative cover, is partially influenced by disturbance. Newell (1987) found that greater prairie-chicken hens tended to avoid pastures with cattle and pastures that had been grazed earlier that year. Prairie-chicken females in disturbed habitats commonly are killed on the nest, and this type of depredation could be more frequent when cover is short and sparse or patchy (Bergerud 1988). Between 1980 and 2000, Valentine National Wildlife Refuge (NWR) in Nebraska reduced the number of hectares disturbed annually from 65% to 27% and also increased the periods of rest between disturbances.

There also is evidence that weather has a substantial influence on prairie grouse production (Shelford and Yeatter 1955, Yeatter 1963). Its importance has been suggested by regional trends in prairie grouse populations. A marked increase in the numbers of prairie chickens in Indiana, Illinois, Missouri, Kansas, and Nebraska in the late 1930s was reported by game technicians during a symposium in Urbana, Illinois, in 1940 (Yeatter 1963). Yeatter (1963) suggested that the marked population increase indicated that conditions favorable at that time to prairie chicken reproduction were regional in scope. Harvest data show a similar increase in prairie grouse numbers throughout the Nebraska Sandhills during the mid-1980s (L. L. McDaniel, United States Fish and Wildlife Service [USFWS], unpublished data).

However, investigators hold different opinions as to when weather is most important (Ritcey and Edwards 1963), partially because its direct and indirect effects are so multifaceted. Some of this inconsistency also may stem from attempts to draw simple linear relationships between a single weather variable and grouse production indices or lek counts. Such simple associations do not adequately represent the complex relationships between numerous weather factors that influence prairie grouse production.

The importance of both weather and vegetative disturbance suggests that these 2 factors may interact to influence prairie grouse production. Therefore, our goal was to use multiple-linear-regression methods to simultaneously assess the effects of both vegetative disturbance and weather on prairie grouse production on Valentine NWR. This approach would allow us to develop a model that could adequately represent the complex relationships between vegetative disturbance and numerous weather factors influencing prairie grouse production on the refuge. Our secondary goal was to assess how well our model could predict production indices on our reference area, Samuel R. McKelvie National Forest (NF) in Nebraska.

It is apparent that much of the variability in sharptail production from year to year was influenced by weather. Correlation between sharptail production and greater prairie-chicken production suggests that greater prairie-chicken production also may be broadly affected by weather.

Specific weather effects

We found limited information on specific effects of weather on prairie grouse production in the published literature. However, published literature on effects of weather on other species of Phasianidae may provide evidence as to how weather influences prairie grouse. However, some caution is needed when using literature on other species, for some of these weather effects may be more pronounced in species such as the willow grouse (*Lagopus lagopus*) that experience more extreme weather conditions than those faced by prairie grouse.

The nesting period in May could be an important period for prairie grouse production, as it is for several other grouse species. Dorney and Kabat (1960) found that ruffed grouse (*Bonasa umbellus*) production was above average following high average temperatures in May and below average following a cold May. Cold and wet conditions during incubation were associated with years of poor productivity in spruce grouse (*Dendragapus canadensis*) (Smyth and Boag 1984). Cold spring temperatures can delay gonadal recrudescence (Garbutt 1979) and inhibit nest initiation in ruffed grouse (Neave and Wright 1969). Such a delay in nest initiation could negatively impact production through reduced clutch size, as is suggested for spruce grouse by Ellison (1972), who found a decrease in numbers of females with broods as well as juveniles per brood in a year when nest initiation was delayed significantly. In addition, Smyth and Boag (1984) suggested that incubating females may increase the number and (or) length of feeding trips if they are energetically stressed by periods of cold and wet weather and thereby decrease nest attentiveness.

The early post-hatching period in June is considered a sensitive period for prairie grouse (Shelford and Yeatter 1955). Greatest chick mortality tends to occur during

June because of the high vulnerability of chicks during early development. Myrberget (1972 as quoted in Erikstad 1985) reported that most mortality of willow grouse chicks occurred during the first 2 weeks after hatch and accounted for variation in chick production between years. Neave and Wright (1969) found that the greatest loss of juvenile ruffed grouse also occurred in June.

Newly hatched chicks still have poorly developed thermoregulation (Myhre et al. 1975, Aulie 1976, Allen et al. 1977) and are therefore more vulnerable to extreme weather conditions. Chilling occurs during cold and wet conditions. If heavy rains occur in June, many young chicks drown or get chilled and die (Horak and Applegate 1998). During cold summers, willow grouse mortality peaks at between 3 and 5 days of age (Erikstad unpublished as cited in Erikstad and Andersen 1983). Survival rates of gray partridge (*Perdix perdix*) chicks increased with mean temperatures and decreased with increasing numbers of rainy days in June (Panek 1992). When significant amounts of precipitation fell during the last 3 weeks of the hatching period, survival of blue grouse (*Dendragapus obscurus*) chicks was adversely affected (Cedarleaf et al. 1982).

To counteract the chilling effects of cold and wet conditions, chicks of Phasianidae must brood for longer durations (Boggs et al. 1977, Pedersen and Steen 1979, Erikstad and Spidsø 1982, Offerdahl and Fivizzani 1987). Increased brooding time results in decreased feeding time (Erikstad and Andersen 1983). Thus, food intake decreases and the chicks may starve to death if rain and low temperatures prevail for several days (Erikstad and Spidsø 1982).

Weather conditions during June also can influence the abundance and availability of insects that young chicks rely upon for nourishment (Green 1984, Potts 1986). Many studies provide evidence that survival of gray partridge chicks increases with abundance of their preferred insect prey (Southwood and Cross 1969, Potts 1986, Rands 1986, Enck 1987). Panek (1992) found that part of the variation in abundance of plant bugs (Hemoptera) was related to weather, with the number of Hemoptera increasing with temperature. Potts (1986) found reduced numbers of Hemoptera during cold and wet weather.

Extremely high temperatures may have negative impacts on chicks in the form of heat stress, as occurs in bobwhite quail (*Colinus virginianus*) (Forrester et al. 1998, Guthery et al. 2001) and willow ptarmigan (*Lagopus lagopus*) (Aulie and Moen 1975). Extremely high temperatures have the potential to harm chicks before they develop thermoregulation because it takes much less heat energy to increase a chick's body temperature to lethal levels (Calder 1974).

Finally, soil moisture indirectly influences prairie grouse production through its effect on vegetative growth. In especially dry years, soil moisture may be insufficient to produce grass and other food plants (Hamerstrom and Hamerstrom 1968) that are a requirement for good brood habitat. Sharptail production was positively correlated with a 23-month soil-moisture index in both North Dakota and South Dakota (Bergerud 1988).

Study area

Valentine NWR

Valentine NWR lies in the Sandhills of north-central Nebraska. The Sandhills region contains >49,000 km^2 of wind-blown, stabilized dune sand and is the largest sand-dune area in the Western Hemisphere (Bleed and Flowerday 1990). Physiographically, loose sandy soil is its chief characteristic, although hills and valleys are more sharply defined than are those of true prairie (Weaver 1965). In the uplands the hills rise 30–60 m above the valley floors. Elevations above sea level ranged from 867–954 m.

The 28,941-ha refuge has approximately 20,000 ha of grassy, undulating uplands (choppy sand and sand range sites), 5,000 ha of meadow (subirrigated and wetland range sites), and 4,000 ha of shallow lakes and marshes. Trees are infrequent, other than those found around the refuge headquarters and along the shorelines.

Annual precipitation on the refuge averaged 54.9 cm between 1945 and 1999 (USFWS 1999). Approximately 65% of that rainfall occurred between April and September (National Climatic Data Center 1996). The soil was fine sand and very porous. Therefore, rainfall was absorbed with little or no runoff. Much of the precipitation reached the water table, which can be just a few decimeters from the surface in the meadow areas. Tall grasses thrived on the dunes because the sand was efficient in absorbing rainfall without loss by runoff and in preventing evaporation from its surface (Weaver 1965).

The uplands consisted of sand and choppy sand range sites (USFWS 1999). Sand range sites consist of sands, loamy sands, and loamy fine sands on nearly level to gentle slopes. Typical vegetation included needle-and-thread (*Stipa comata*), prairie sandreed (*Calamovilfa longifolia*), little bluestem (*Schizachyrium scoparium*), sand bluestem (*Andropogon hallii*), sand lovegrass (*Eragrostis trichodes*), sand dropseed (*Sporobolus cryptandrus*), junegrass (*Koeleria pyramidata*), small soapweed (*Yucca glauca*), and poison ivy (*Rhus radicans*) (Weaver 1965). Choppy sand range sites consisted of sands on abrupt, irregular slopes of 20% or more. Vegetation was generally that of a sand range site, but was usually more sparse with patches of exposed sands.

Meadows consisted of wetland and subirrigated range sites. Wetland range sites were dominated by grass species that thrive in a moisture-saturated soil profile, such as prairie cordgrass (*Spartina pectinata*), northern reedgrass (*Calamagrostis stricta*), and sedges (*Carex* spp.) (USFWS 1999). Subirrigated range sites were meadows very close to groundwater level (USFWS 1999). Subirrigated meadows were dominated by tallgrass prairie species such as switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), and big bluestem (*Andropogon gerardii*) (Weaver 1965, USFWS 1999), as well as little bluestem on the drier portions of the meadows.

The land adjacent to the study area was used exclusively as rangeland for livestock grazing, with no cultivated cropland on or near the study area. Grasslands on the study area were managed using periodic rest, prescribed fire, and grazing treatments.

Samuel R. McKelvie National Forest

The 46,211-ha Samuel R. McKelvie National Forest was selected as a reference area because of its similarities to Valentine NWR. Located approximately 12 km northwest of Valentine NWR, its topography, climate, species of predators, and vegetative species were similar to those of the refuge. Predators were not controlled on either area, and both public land areas supported sharptail populations.

The major known difference in the 2 public land areas was the intensity and extent of vegetative disturbance. Cattle grazed almost 100% of Samuel R. McKelvie NF from 1980 to 2000. During the nesting season, less than 5% of McKelvie NF had not been burned or grazed by cattle within the past 12 months. Grazing treatments averaged about 1.24 animal-unit-months (AUMs)/ha between 1980 and 1990, and 0.74 AUMs/ha between 1991 and 2000. In comparison, 35% of Valentine NWR provided nesting cover undisturbed by cattle or fire within the past 12 months in 1980. Undisturbed nesting cover had steadily increased to 74% by 2000. Grazing treatments on Valentine NWR averaged about 0.57 AUMs/ha between 1985 and 2000.

Methods

Production indices

There is no known method for obtaining true estimates of prairie grouse production. An index of production can be developed using the ratio of juveniles to adults in the autumn harvest, or the harvest-age ratio. Annual harvest-age ratios were determined for Valentine NWR and McKelvie NF using wings removed from prairie grouse harvested within the public land areas. Every autumn, wing-donation boxes were placed along the roads in established locations throughout the 2 public land areas, to encourage hunters to donate wings and to ensure that a representative sample of the entire public land area was attained. Experienced biologists then identified age class and species of each wing. The number of juveniles and adults for each species was summed for each public land area, and the ratio was used as an index of production. These data were available for both public land areas between 1980 and 2000 through a cooperative effort by the USFWS, the United States Forest Service, and the Nebraska Game and Parks Commission.

Production data were available for both sharptails and greater prairie-chickens on Valentine NWR. An average of 60 (SE = 10) greater prairie-chicken wings was collected annually on Valentine NWR, as opposed to an average of 370 (SE = 26) sharptail wings. Marcström and Höglund (1980) concluded that a strong indication of the proportion of juveniles in the population within a restricted area could be ascertained within the first 70–75 grouse collected. Therefore, to avoid the large sampling variance associated with the small samples of greater prairie-chicken wings, we chose to use only the sharptail data for model development. We considered the sample sizes for McKelvie NF ($\bar{x}$ = 146, SE = 16) adequate for estimating harvest-age ratios, as those ratios were to be used in plots only and not for model development. Preliminary analyses of harvest data on both public land areas indicated there were no biases in the harvest-age ratios due to a changing ratio of juveniles to adults as the hunting season progressed (Flanders 2002). Thus, potential biases in the harvest-age ratios due to differential susceptibility to harvest or differential survival of juveniles and adults did not appear to be present (Flanders 2002).

It is important to note that as an index, harvest-age ratios can indicate only relative differences in production. To compare production indices, we assumed the ratio of juvenile to adult harvest rates was approximately constant across years and areas. To meet this assumption, potential influences on rate of harvest of juveniles and adults, such as early flocking of adult birds during years of poor production or late brood break-up during years of delayed nest initiation, must be minimal. In addition, production indices cannot be used as an index of recruitment or population size (Bergerud 1988). Nevertheless, production has the most influence on changes in breeding numbers of grouse (Bergerud 1988). Changes in breeding numbers were correlated with prior reproductive success in prairie chickens in Texas (Peterson and Silvy 1994), Kansas (Horak 1974), and South Dakota (Linde et al. 1978). Annual changes in density of sharptail males on leks have been correlated with production in Montana (Brown 1968), Minnesota (Berg 1977), South Dakota (Hillman and Jackson 1973), and North Dakota (Kobriger 1981). Therefore, long-term monitoring of harvest-age ratios can provide valuable information about the fitness of a population.

Vegetative disturbance data

Data on number of hectares within each habitat block and date of the last disturbance in each habitat block were available between 1980 and 2000. We managed habitat blocks on the refuge individually, with a rest treatment leaving the vegetation within a habitat block undisturbed. Grazing, prescribed fire, wildfire, and hail damage were considered disturbances within each habitat block. Calculated on 1 May, the number of hectares within each habitat block contributed to 1 of the 3 disturbance categories: "Disturbed," "1 Year Rest," and "2+ Years Rest." Disturbed referred to the percentage of refuge area that had been disturbed since the beginning of the previous growing season, 1 Year Rest referred to the percentage of refuge area that had received an entire growing season of rest, and 2+ Years Rest referred to the percentage of refuge area that had received ≥2 growing seasons of rest.

Weather data

We obtained precipitation data for 1980–2000 from the weather station located at the refuge headquarters. We obtained temperature data for 1980–2000 from the airport weather station, which provided more precise hourly temperature measurements, as opposed to the daily temperature measurements provided on the refuge. The National Oceanic and Atmospheric Administration supervised both weather stations.

Distance from the airport weather station to the farthest point of Valentine NWR and McKelvie NF was approximately 50 km and 60 km, respectively. In addition, the distances from the weather station at the refuge headquarters to the farthest point of Valentine NWR and McKelvie NF were approximately 30 km and 50 km, respectively. Thus, we felt that data from these 2 weather stations could represent weather conditions on both public land areas similarly.

Selection of variables

The dependent variable for all analyses was sharptail juveniles per sharptail adult harvested. From the 3 disturbance categories, we selected the 2 extreme categories, Disturbed and 2+ Years Rest, as vegetative disturbance variables for our model. These 2 highly correlated variables were not included with the expectation that both variables would be selected for the final model(s). Instead, we included both variables because we were uncertain whether the amount of disturbed cover or the amount of cover in extended rest would have greater influence on sharptail production. Including both variables allowed us to objectively select the more important variable. We hypothesized that Disturbed would be negatively correlated with sharptail production and that 2+ Years Rest would be positively correlated with sharptail production.

We then selected weather variables we believed would have the greatest influence on sharptail production based on the published literature. We identified the nesting period in May and the early post-hatch period in June as 2 important periods for sharptail production.

For the nesting period, we included the variable "May Average Temperature" and hypothesized it would be positively correlated with sharptail production. Since both the timing and amount of precipitation have the potential to affect sharptail production, we included 2 May precipitation variables, "May Total Precipitation" and "May Number of Days with Precipitation >2.54 mm," and hypothesized that both would be negatively correlated with sharptail production. Days with precipitation <2.54 mm did not contribute a significant amount of precipitation and therefore were not included in the calculation of the second May precipitation variable.

For the early post-hatch period in June, we selected several important weather variables, including a heat-stress variable. However, we found no literature specific to thermoregulation in North American prairie grouse chicks. Yet, some extrapolation was reasonable, since a bird's thermoneutral zone is dependent upon its size, independent of the species (Calder 1974). Based on this premise, we used research on willow grouse chicks of similar size to extrapolate a sharptail chick's response to heat stress.

One-day-old willow ptarmigan chicks placed inside a climatic chamber with ambient temperatures of 38.9°C experienced an increase in body temperature to 41.5°C after 20 minutes of exposure, causing them to "[try] desperately to get away from the heat" (Aulie and Moen 1975:606). Unlike the air temperature in a natural environment, ambient temperature in a climatic chamber provides an accurate measure of a chick's microclimate. Air temperature is not an accurate measure of a chick's microclimate because it does not take into account the heating effects of solar radiation near the ground. Consequently, a chick's microclimate near the ground could potentially be 3°C to 4°C higher than the measured air temperature because of the additional heat created by solar radiation (F. S. Guthery, Oklahoma State University, personal communication). Therefore, an air temperature of 35°C could correspond to Aulie and Moen's (1975) ambient temperature of 38.9°C, because the solar radiation not accounted for by air temperature could compensate for the difference in the 2 values. To account for this disparity, we used the number of days with air temperatures ≥35°C as an indicator of potential heat stress in sharptail chicks. We hypothesized that the variable "June Number of Heat Stress Days" would be negatively correlated with sharptail production if heat stress impacted chick survival.

As long as temperatures in June are not extremely hot, June temperatures generally have a positive influence on sharptail chick survival. Therefore, we selected the variable "June Average Temperature" and hypothesized that it would be positively correlated with sharptail production.

As with May precipitation, both the timing and amount of precipitation in June have the potential to affect sharptail production. For instance, a large amount of precipitation in one day may be more detrimental to the survival of sharptail chicks than the same amount of precipitation spread out over the course of several weeks. Therefore, we selected the variables "June Total Precipitation" and "June Number of Days with Precipitation >2.54 mm" and hypothesized that both would be negatively correlated with sharptail production.

In addition to the nesting period in May and the early post-hatch period in June, drought also may have a large effect on sharptail production. We chose "Cumulative Precipitation from 1 January–31 July" as an index of drought because we preferred values that could be easily calculated for future use and because precipitation tends to be the overriding predictor of drought conditions (M. D. Svoboda, National Drought Mitigation Center, personal communication). We hypothesized that Cumulative Precipitation from 1 January–31 July would be positively correlated with sharptail production.

In summary, we chose 8 weather variables and 2 vegetative disturbance variables to use as main effects in our production model. We also suspected that temperature and precipitation interactions could be useful in explaining some of the variability in sharptail production, but waited to select the most important main effects before incorporating any specific interactions.

Statistical procedures

We broke down the analysis into several steps to avoid over-parameterizing the model. First, we sought to explain some of the variability in the sharptail production indices with the weather variables. We used multiple-linear-regression methods (SAS Institute 1989) to fit the dependent variable, sharptail juveniles per sharptail adults harvested, to the independent weather variables. The sampling unit was years, with a total of 21 data points. We chose not to split our data for cross-validation purposes because we did not want to further reduce the small sample size and because the observations within a year could not be split. The full model included all 8 weather variables, an intercept, and an estimate of MSE, for a total of 10 parameters. Our suite of candidate models included all possible combinations of weather variables for a total of $2^8 = 256$ models. We included all possible combinations because we felt all 8 weather variables were justified in the final model and we had no way of knowing which variables were more likely to appear together in the most plausible models.

We used Akaike's Information Criterion with a small-sample bias adjustment (AICc) model selection (Burnham and Anderson 1998) to objectively select the most parsimonious model(s). We then calculated the cumulative AICc weights for each weather variable by summing the AICc model weights of every model containing that variable. We could then objectively select variables with the greatest cumulative AICc weights as the most biologically important weather variables with which to continue our model development.

In the final analysis, we sought to explain additional variability in the data by including the 2 vegetative disturbance variables, Disturbed and 2+ Years Rest. Although no obvious relationship existed between annual sharptail production indices and the vegetative disturbance variables (Figure 1), we wanted to evaluate whether the 2 vegetative disturbance variables could be used as predictors of sharptail production indices now that some of the variability in the data had been explained by weather variables. We also included an interaction term for 2 of the retained variables, June Average Temperature and June Total Precipitation. Thus, the full model included the 5 best weather variables, 2 vegetative disturbance variables, an interaction term, an intercept, and an estimate of MSE, for a total of 10 parameters. Our suite of candidate models included all possible combinations of weather variables for a total of $2^8 = 256$ models. Once again, we used AICc model selection to select the most parsimonious model(s).

To address model uncertainty, we used model-averaging as a formal way to base inference on more than a single model. All models within 2 units of the minimum AICc model were considered plausible (Burnham and Anderson 1998). Using the annual predictions of sharp-

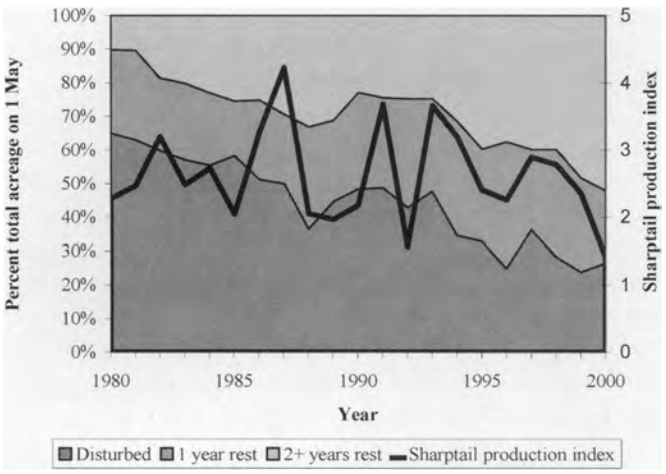

Figure 1. Annual plains sharp-tailed grouse (Sharptail) production indices plotted against vegetation disturbance categories on Valentine National Wildlife Refuge, Nebraska, 1980–2000. Disturbed = the percentage of refuge area on 1 May that had been disturbed since the beginning of the previous growing season, 1 year rest = the percentage of refuge area on 1 May that had received an entire growing season of rest, 2+ years rest = percentage of refuge area on 1 May that had received ≥2 growing seasons of rest, and Sharptail production index = ratio of juveniles to adult sharptails in the autumn harvest.

tail production indices from all plausible models, we calculated a weighted average using the equation,

$$\hat{\theta}_a = \sum_{i=1}^{R} \hat{w}_i \hat{\theta}_i,$$

where $\hat{\theta}_a$ = weighted average of predicted annual production indices, R = number of models considered, $\hat{w}_i$ = scaled AICc weight for model i (scaled to sum to 1) (Burnham and Anderson 2002), and $\hat{\theta}_i$ = prediction of the production index according to the year for model i. To account for both sampling variance and model selection uncertainty, we used the adjusted standard error ($\widehat{\text{ase}}$) estimator (Buckland et al. 1997),

$$\widehat{\text{ase}}\left(\hat{\theta}_a\right) = \sum_{i=1}^{R} \hat{w}_i \sqrt{\widehat{\text{var}}\left(\hat{\theta}_i \middle| M_i\right) + \left(\hat{\theta}_i - \hat{\theta}_a\right)^2},$$

where M_i = model i. We then used the adjusted standard errors to develop unconditional 95% confidence intervals (CI).

Finally, we plotted the model-averaged predictions of sharptail production indices for Valentine NWR against the actual sharptail production indices for our reference area, McKelvie NF. Since vegetative disturbance was the only known influence on sharptail production that was notably different between the 2 public land areas, we hypothesized that the model-averaged predictions developed on Valentine NWR would over-predict sharptail production indices on McKelvie NF if the increased vegetative disturbance on McKelvie NF was negatively influencing sharptail production.

Results

All models within 2 units of the minimum AICc value have substantial support and should receive consideration in making inferences (Burnham and Anderson 1998). Using that criterion, at least 5 models were especially useful in our first iterative analysis (Table 1). Cumulative AICc weights indicate the percent of weight attributable to models containing that particular variable (Table 2).

Following our final analysis, 7 models were highly plausible based on their AICc values (Table 3). None of the most plausible models contained a vegetation variable. We included all 5 weather variables in the top models and correlated each with sharptail production as hypothesized a priori.

Cumulative Precipitation from 1 January–31 July (JulCumPr) was positively correlated with sharptail production. We attributed 75% of the AICc weight to models that included JulCumPr. According to the coefficients for the top 7 models, every additional centimeter of cumulative precipitation as of 31 July would result in a 0.05 (95% CI = 0.02, 0.08) to 0.03 (95% CI = –0.002, 0.06) increase in the juvenile-to-adult harvest ratio of sharptails, when holding all other variables constant.

June Number of Heat Stress Days (JunDay35) was negatively correlated with sharptail production. We attributed 55% of the AICc weight to models that included JunDay35. According to the JunDay35 coefficients for the top models, every day in June with air temperatures ≥35°C would result in a 0.20 (95% CI = –0.33, –0.07) to 0.16 (95% CI = –0.29, -0.03) decrease in the juvenile-to-adult harvest ratio when holding all other variables constant.

May Average Temperature (MayAveTe) was positively correlated with sharptail production. We attributed 44% of the AICc weight to models that included MayAveTe. According to the MayAveTe coefficients for the top models, every increase in May average temperature of 1°C would result in a 0.19 (95% CI = (0.02, 0.36) to 0.12 (95% CI = -0.07, 0.31) increase in the juvenile-to-adult harvest ratio of sharptails, when holding all other variables constant.

June Average Temperature (JunAveTe) was positively correlated with sharptail production. We attributed 35% of the AICc weight to models that included JunAveTe. According to the JunAveTe coefficients for the top models, every increase in June average temperature of 1°C

Table 1. Candidate models[a] used to fit the dependent variable, annual sharp-tailed grouse production index[b] on Valentine National Wildlife Refuge, Nebraska, to the independent weather variables, 1980–2000.

Variables in model	No. of parameters	AICc [c]	Delta AICc	AICc weight [d]	R^2
JulCumPr [e]	3	−13.50	0.00	0.08	0.16
MayAveTe [f], JunAveTe [g], JunTotPr [h], JunDay35 [i], JulCumPr	7	−12.41	1.09	0.05	0.57
MayAveTe, JulCumPr	4	−12.32	1.17	0.05	0.24
MayAveTe, JunAveTe, JunDay35, JulCumPr	6	−12.10	1.40	0.04	0.46
JunTotPr, JulCumPr	4	−11.61	1.89	0.03	0.21

[a] Models may be compared by AICc values to models in Table 3.

[b] Annual sharp-tailed grouse production index = sharp-tailed grouse juveniles per sharp-tailed grouse adults in the fall harvest on Valentine National Wildlife Refuge.

[c] AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

[d] AICc weight = percent of total weight from all 256 models that can be attributed to the specified model.

[e] JulCumPr = cumulative precipitation from 1 January–31 July.

[f] MayAveTe = May average temperature.

[g] JunAveTe = June average temperature.

[h] JunTotPr = June total precipitation.

[i] JunDay35 = No. of heat stress days in June (air temperatures ≥35°C).

would result in a 0.21 (95% CI = 0.03, 0.39) to 0.18 (95% CI = –0.01, 0.37) increase in the juvenile-to-adult harvest ratio of sharptails, when holding all other variables constant.

June Total Precipitation (JunTotPr) was negatively correlated with sharptail production. We attributed 34% of the weight to models that included JunTotPr. According to the JunTotPr coefficients for the top models, an increase in June total precipitation of 1 cm would result in a 0.44 (95% CI = –0.79, –0.08) to 0.04 (95% CI = –0.11, 0.04) decrease in the juvenile-to-adult harvest ratio of sharptails, when holding all other variables constant. The effect of JunTotPr was more variable than any of the previous 4 weather variables.

Thirty percent of the weight was attributed to models that included the June Average Temperature × June Total Precipitation interaction (Interact). The interaction effect was small, and the correlation varied unpredictably according to the other variables in the model. Interact coefficients for the top models varied between 0.020 (95% CI = 0.002, 0.039) and –0.003 (95% CI = –0.007, 0.0003).

Averaged across years, the model-averaged predictions of sharptail production indices for Valentine NWR overpredicted actual sharptail production indices on McKelvie NF by 0.77 juveniles per adult (Figure 2). Thirteen of the 21 sharptail production indices for McKelvie NF were not included in the 95% unconditional CI around the prediction estimates. However, the trend in predicted sharptail production indices generally followed that of the actual production indices on McKelvie NF.

Table 2. Cumulative AICc [a] weights for all 8 weather variables hypothesized to influence annual sharp-tailed grouse production on Valentine National Wildlife Refuge, Nebraska, 1980–2000.

Variable	Cumulative AICc weight [b]
July Cumulative Precipitation	0.72
June No. of heat stress days [c]	0.46
May average temperature	0.41
June average temperature	0.34
June total precipitation	0.30
May No. of days of precipitation [d]	0.17
June No. of days of precipitation [d]	0.16
May total precipitation	0.16

[a] AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

[b] Cumulative AICc weight of a variable = the percent of weight attributable to models containing that particular variable and is calculated by summing the AICc model weights of every model containing that variable.

[c] A heat stress day = a day with air temperatures ≥35 °C.

[d] Days with insignificant precipitation events <2.54 mm not included.

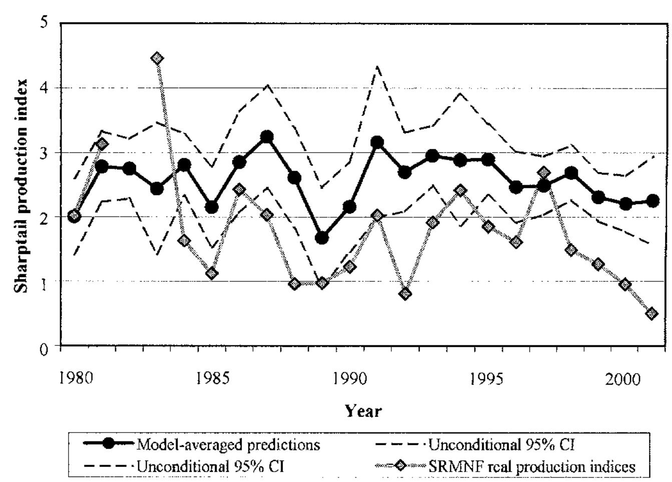

Figure 2. Actual sharp-tailed grouse (Sharptail) production indices for Samuel R. McKelvie National Forest, Nebraska, (SRMNF real production indices) plotted against model-averaged, predicted sharptail production indices (Model-averaged predictions) for Valentine National Wildlife Refuge, 1980–2001. Production indices were attained from juvenile to adult harvest-age ratios. CI = 95% confidence interval.

Table 3. Top 7 candidate models [a] in final model selection procedure used to fit the dependent variable, annual sharp-tailed grouse production index [b] on Valentine National Wildlife Refuge, Nebraska, to the independent weather and vegetation variables, 1980–2000.

Variables in model	No. of parameters	AICc [c]	Delta AICc	AICc weight [d]	R^2
JulCumPr [e]	3	−13.50	0.00	0.06	0.16
MayAveTe [f], JunTotPr [g], JunDay35 [h], JulCumPr, Interact [i]	7	−12.74	0.75	0.04	0.58
MayAveTe, JunAveTe [j], JunTotPr, JunDay35, JulCumPr	7	−12.41	1.09	0.04	0.57
MayAveTe, JulCumPr	4	−12.32	1.17	0.03	0.24
MayAveTe, JunAveTe, JunDay35, JulCumPr, Interact	7	−12.23	1.26	0.03	0.57
MayAveTe, JunAveTe, JunDay35, JulCumPr	6	−12.10	1.40	0.03	0.46
JunTotPr, JulCumPr	4	−11.61	1.89	0.02	0.21

[a] Models may be compared by AICc values to models in Table 1.

[b] Annual sharp-tailed grouse production index = sharp-tailed grouse juveniles per sharp-tailed grouse adults in the fall harvest on Valentine National Wildlife Refuge.

[c] AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

[d] AICc weight = percent of total weight from all 256 models that can be attributed to the specified model.

[e] JulCumPr = cumulative precipitation from 1 January–31 July.

[f] MayAveTe = May average temperature.

[g] JunTotPr = June total precipitation.

[h] JunDay35 = No. of heat stress days in June (air temperatures ≥35°C).

[i] Interact = June average temperature × June total precipitation

[j] JunAveTe = June average temperature.

Discussion

Model fit

Model-averaged prediction estimates predicted general trends in sharptail production indices well (Figure 3). However, the model-averaged predictions tended to be more conservative than the real sharptail production indices in most years. In addition, large confidence intervals reflect the amount of variability in data that cannot be explained by model-averaged predictions.

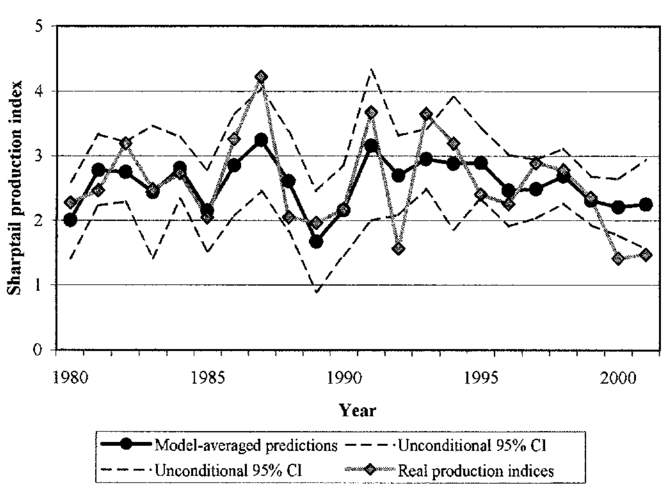

Figure 3. Actual sharp-tailed grouse (Sharptail) production indices for Valentine National Wildlife Refuge, Nebraska, (Real production indices) plotted against model-averaged, predicted sharptail production indices (Model-averaged predictions) for Valentine National Wildlife Refuge, 1980–2001. Production indices were calculated from juvenile to adult harvest-age ratios. CI = 95% confidence interval.

Some of this additional variability could be due to single, extreme weather events. For instance, extreme amounts of precipitation or extremely high temperatures late in the hatching period could have significant effects on production. However, extreme weather events cannot be distinguished by monthly averages or cumulative values, which are too coarse to detect such singular occurrences. Additionally, there are a multitude of finer factors and minute interactions that each explain a small proportion of the data. To maintain parsimony, not all of these factors and interactions can be included in the model. As a result, "We can rarely hope to uncover the true model; rather the objective must be to select the simplest, biologically meaningful model that is fully supported by the specific dataset" (Burnham and Anderson 1992:18).

Model variables

All 5 weather main effects retained in the suite of most-plausible models were correlated with sharptail production as we hypothesized a priori. Consequently, the probability that these effects are spurious is diminished.

The most valuable predictor of sharptail production was the drought index, Cumulative Precipitation from 1 January–31 July (JulCumPr). Seventy-five percent of the AICc weight was attributed to models that included JulCumPr, which was positively correlated with sharptail production. Lack of soil moisture may be indirectly restricting sharptail production by limiting the availability of food plants and vegetative cover (Hamerstrom and Hamerstrom 1968). Without adequate vegetative cover, sharptail chicks may be more vulnerable to predators (Bergerud 1988).

Some models include 2 precipitation variables, suggesting that not just the amount of precipitation but also the timing of precipitation can influence sharptail production. To illustrate, sharptail production is positively correlated with Cumulative Precipitation from 1 January 1–31 July, but negatively correlated with June Total

Precipitation. Thus, it seems that adequate soil moisture on a season-long basis results in increased sharptail production. However, if too much of that total rainfall occurs in June, sharptail production may be lower. This may be due to excessive precipitation during the peak hatch causing chilling and drowning.

Some models include 2 different June temperature variables that are correlated with sharptail production in opposite directions. In these models, June Average Temperature is positively correlated with sharptail production, while June Number of Heat Stress Days is negatively correlated with sharptail production. This may seem incongruous, but together these variables may suggest a nonlinear relationship between temperature and sharptail production. More specifically, warmer weather in June benefits sharptail production to a point. After that point, an upper temperature threshold may begin to generate heat stress that may be detrimental to chick survival.

The suggestion of an important heat-stress effect on chick survival is a valuable finding, as we found no literature on negative impacts of heat stress on sharptail production. More research would be needed to show a definite relationship between heat stress and sharptail production, especially in the southern portion of their range.

The interaction effect is small and explains only 0.07% more variability in the data than the model with 5 main weather effects. It would appear that the interaction effect adds no new information to the model.

Only 23% and 18% of the weight were attributed to models that included the vegetation variables, Disturbed and 2+ Years Rest, respectively. Subsequently, we did not include them in any of the most-plausible models, as the penalty for over-fitting the data is too large to include any mediocre predictors.

There may be several reasons vegetation disturbance variables were not more useful for modeling sharptail production on the refuge. First, the vegetation disturbance variables may not provide a comprehensive enough representation of vegetative structure. Height and density of vegetation at the refuge scale is simultaneously dependent upon vegetation species composition, annual precipitation, the percent of the refuge annually disturbed, the timing of the disturbance, and the intensity of the disturbance. Thus, there is confounding between these variables that prevents any of these elements from being a good measure of vegetative structure. In the future, visual obstruction readings (VOR) within randomly selected, permanently marked transects might provide a better estimate of the vegetative structure on the refuge, provided the sample size is adequate to represent the structure of vegetation on the entire refuge.

Second, Valentine NWR provides more than 24,300 contiguous ha of grassland that has been managed largely for upland-nesting birds for the last 2 decades. Therefore, vegetative cover may not have limited sharptail production on the refuge during the last 21 years. This would concur with Lutz and Silvy (1980), who suggested that vegetative cover could be a limiting factor for prairie grouse only if it were below some critical level.

Area effects

Although we did not find vegetative disturbance to be an important variable in our final models, the striking contrast in vegetative disturbance between the 2 public land areas provided us with another opportunity to evaluate the effects of vegetation disturbance on sharptail production. The majority of sharptail production indices on McKelvie NF are below the 95% unconditional CI around the predicted indices of sharptail production on Valentine NWR (Figure 2). This result adds support to our hypothesis, "Model-averaged predictions developed on Valentine NWR will over-predict sharptail production indices on McKelvie NF if the increased vegetative disturbance on McKelvie is negatively influencing sharptail production." However, we admit that the lack of replication and random application of treatments between public land areas weaken the strength of our result.

Nonetheless, the literature provides additional support for our hypothesis. Newell (1987) found that vegetation in deferred pastures and prairie hay (undisturbed vegetation) had superior height and density compared to grazed pastures. Broods used lowlands and midlands more than uplands both day and night because of the superior cover provided, avoiding areas of sparse vegetation (Horak 1985). Newell (1987) recognized the need for undisturbed cover after finding that hens with broods utilized vegetation which provided visual screening in excess of 2.5 dm throughout the summer and that hens appeared to avoid shorter vegetation, especially as the growing season progressed and taller vegetation became more available. Lack of residual herbaceous vegetation has been cited as the most limiting factor for the sharptail (Pepper 1972, Hillman and Jackson 1973, Sisson 1976, Grosz 1988) throughout its range. Without adequate vegetative cover, sharptail chicks may be more vulnerable to predators (Bergerud 1988).

Therefore, we suspect that the difference in production indices between the 2 areas was at least partially influenced by the longer grazing periods and the greater total number of hectares grazed annually on McKelvie NF during the last 22 years compared to Valentine NWR. However, it is possible that other unknown factors also are negatively impacting sharptail production on

McKelvie NF. For instance, population estimates of the major sharptail predators were not available for either area, although we do know that the same species of predators inhabit both areas and that predators are not controlled on either area. Nonetheless, a greater total number of predators per ha could at least partially account for the lower production indices, although greater numbers of predators per ha has never been confirmed on McKelvie NF. Higher disease prevalence, also never verified in the sharptail population on McKelvie, also could have negative impacts on production if it did exist in the population.

To further decipher which factors may be suppressing sharptail production on McKelvie NF, we propose a pseudo-experiment in which lengths of grazing periods and particularly number of annually disturbed hectares on McKelvie NF are reduced to levels similar to those on Valentine NWR. Once a vegetation structure similar to that on Valentine NWR has been achieved, we hypothesize that sharptail production indices on McKelvie NF will increase to levels similar to those on Valentine NWR. Should no increase in production indices occur on McKelvie, other factors such as predators and disease may need to be considered.

Regional effects

Aside from the within-year differences in sharptail production between Valentine NWR and McKelvie NF, considerable parallelism in sharptail production indices can be noticed between the 2 areas when comparing across years (Figure 2). This further suggests that regional factors such as weather may be influencing fluctuations in sharptail production on a broader scale than the public land area.

Applicability to the greater prairie-chicken

Greater prairie-chicken production indices tend to follow trends similar to sharptail production indices on Valentine NWR (Figure 4). Therefore, although these analyses were limited to sharptail data, it may be reasonable to assume there may be similarities between the factors affecting production of sharptail and those affecting the production of the greater prairie-chicken in the Nebraska Sandhills.

Management implications

It is apparent that much of the variability in sharptail production from year to year was influenced by weather. Correlation between sharptail production and greater prairie-chicken production suggests that greater prairie-chicken production also may be broadly affected by weather. Although the impacts of weather on prairie grouse production are beyond management control, nutrition and temperatures at ground level may be mediated through cover management, as has been suggested for Gambel's quail (*Callipepla gambelii*) (Heffelinger et al. 1999).

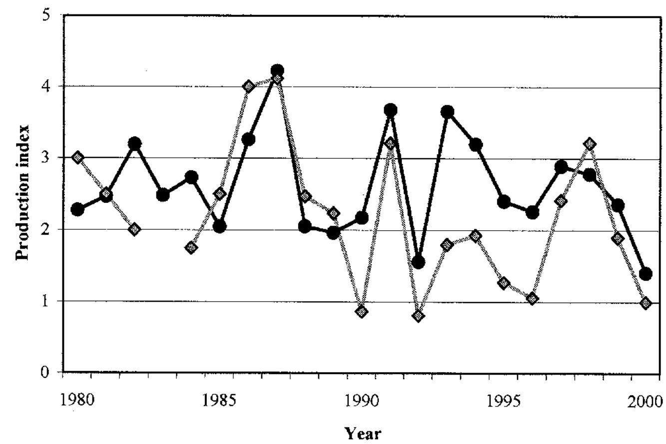

Figure 4. Sharp-tailed grouse and greater prairie-chicken production indices for Valentine National Wildlife Refuge, Nebraska, 1980–2000. Production indices were calculated from juvenile to adult harvest-age ratios.

For example, the intensity of solar radiation decays rapidly as it passes through the plant canopy, thereby nullifying a potential source of heat stress (Guthery 2002). In a similar fashion, an ample plant canopy may help insulate young chicks against the negative effects of heavy rainfall. In years with adequate soil moisture, the current year's growth may be sufficient in providing such shelter. However, in drought years, there may not be enough vegetative growth to provide adequate shelter. Since vegetation in deferred pastures and prairie hay (undisturbed vegetation) was found to have superior height and density compared to grazed pastures (Newell 1987), reductions in both the length of grazing periods and the proportion of hectares grazed annually should result in vegetation of increased height and density. Therefore, by minimizing vegetative disturbance to that necessary for the maintenance of healthy, productive grasslands with desirable species compositions, managers provide extra insurance that prairie grouse chicks will have sufficient shelter in all years.

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