**Title**

Non-native grazers affect physiological and demographic responses of Greater Sage-grouse

**Authors**

Tessa L. Behnke1,2\*, Phillip A. Street2, Scott Davies3, Jenny Q. Ouyang1, James S. Sedinger2

1 Program in Ecology, Evolution, and Conservation Biology, University of Nevada – Reno, Reno, Nevada

2Department of Natural Resources and Environmental Science, University of Nevada – Reno, Reno, Nevada

3Department of Biological Sciences, Quinnipiac University, Hamden, Connecticut

\*Corresponding Author: Tessa L. Behnke, [tlbehnke@gmail.com](mailto:tlbehnke@gmail.com)

**Acknowledgements**

Funding for this project was provided by the Greater Hart-Sheldon Conservation Fund, Nevada Department of Wildlife, Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, and the Nevada Chukar Foundation. Additional thanks to the Hart-Sheldon National Wildlife Refuge staff and the Applegate Office of the BLM for logistical support. Thank you to the dozens of technicians that collected the field data.

**Conflict of Interest**

The authors declare no commercial or financial relationships generating a conflict of interest in this work.

**Authors’ contributions**

TB, JO, JS, and PS conceived the ideas and designed the methods; TB and PS collected the field data; SD conducted the laboratory work; TB and PS analyzed the data; TB led writing of the manuscript. All authors contributed significantly to revision of the manuscript and gave final publication approval.

**Data Availability**

Data and R code will be archived in Dryad after acceptance.

## Abstract

1. Non-native ungulate grazing has negatively impacted native species across the globe, leading to massive loss of biodiversity and ecosystem services. Despite their pervasiveness, interactions between non-native grazers and native species are not fully understood. We often observe declines in demography or survival of these native species, but lack understanding about the mechanisms underlying these declines. Physiological stress represents one mechanism of (mal)adaptation but data are sparse.
2. We investigated glucocorticoid levels in a native avian herbivore exposed to different intensities of non-native grazing in the cold desert Great Basin ecosystem, USA. We measured corticosterone, a glucocorticoid in feathers for a large sample (n = 280) of female Greater Sage-grouse (*Centrocercus urophasianus*) from three study areas in Northern Nevada and Southern Oregon with different grazing regimes of livestock and feral horses.
3. We found greater feral horse density was associated with higher corticosterone levels, and this effect was exacerbated by drought conditions. Livestock grazing produced similar results; however there was more model uncertainty about the livestock effect. Subsequent nesting success was lower with increased feather corticosterone, but corticosterone levels were not predictive of other vital rates.
4. Our results indicate a physiological response by sage-grouse to grazing pressure from non-native grazers. We found substantial among-individual variation in the strength of the response. These adverse effects were intensified during unfavorable weather events, highlighting the need to reevaluate management strategies in the face of climate change.

## Key Words

Greater Sage-grouse, Centrocercus urophasianus, corticosterone, grazing, avian physiology, non-native ungulate, drought

## Introduction

Glucocorticoid hormones (GCs) link a vertebrate’s internal condition and its external environment (Sapolsky et al., 2000). Baseline levels of GCs have been related to components of fitness in several species (Bonier et al., 2009; Cyr & Romero, 2007; Hau et al., 2010; Henderson et al., 2017; Madliger & Love, 2016; Sorenson et al., 2017; Wingfield & Sapolsky, 2003). The Cort-Fitness Hypothesis, proposed by Bonier et al. (2009), suggests that elevated baseline levels of GCs reflect a physiological response to environmental or social resource limitation that in turn results in lower reproductive investment or survival, thereby lowering fitness. Alternatively, Bonier et al. (2009) also propose the Cort-Adaptation Hypothesis, in which elevated GCs help direct resources towards reproduction. Existing data are conflicting as to the nature of this relationship (Injaian et al., 2020; Madliger & Love, 2016; Sorenson et al., 2017), leaving us with no consensus on the interplay between GCs and fitness. Understanding is poor in part due to lack of context (Romero, 2004; Vera et al., 2017) about the specific environment as experienced by wild individuals.

Invasive or introducted species serve as novel stressors that can detrimentally increase physiological stress in co-occurring native species, impacting survival and/or reproduction (Graham et al., 2012; Narayan et al., 2015; Santicchia et al., 2018; Van Zwol et al., 2012). Introduced non-native ungulates, both domestic and wild, are known to degrade habitats for native species across numerous ecosystems (Dettenmaier et al., 2017; Eldridge et al., 2020; Spear & Chown, 2009; Volery et al., 2021), thereby having the potential to chronically elevate GC levels. Grazing by domestic cattle (*Bos bos*) has been a prominent land use in the western U.S for more than a century (Bureau of Land Management, 2020b). Feral horses (*Equus ferus caballus*) have increased dramatically over the past two decades, largely associated with sociopolitical resistance to removing horses from rangelands (Garrott, 2018). Both livestock and horses graze plants that are preferred by native herbivores because of their higher nutritional content (Hanley & Hanley, 1982; Scasta et al., 2016; Veblen et al., 2015). Livestock and horses also cause physical damage to riparian areas (Batchelor et al., 2015; Beever & Herrick, 2006; Beschta et al., 2014; Boyd et al., 2017; Dobkin et al., 1998), that provide essential foods and water during dry periods in the cold deserts of western North America (Batzer & Baldwin, 2012; Donnelly et al., 2018). Such impacts are likely to be exacerbated when seasonal moisture is reduced because primary productivity is lower under such conditions in already dry environments (Chambers et al., 1999; Donnelly et al., 2018; Zeigenfuss et al., 2014).

Greater Sage-grouse (*Centrocercus urophasianus*; hereafter, “sage-grouse”; Figure 1) are herbivorous birds that are sympatric with feral horses and/or livestock throughout their range in the western United States (Schroeder et al., 2020). They rely on sagebrush as their main food source outside the breeding season but expand their diet during breeding to include insects and other plants (Rowland et al., 2006). Sage-grouse are highly selective of specific sagebrush plants because individual shrubs can vary in nutrient content and anti-herbivore secondary compounds (Frye et al., 2013; Remington & Braun, 1985).

Following nesting in early spring, adult female sage-grouse and their offspring feed on forbs and associated invertebrates (Casazza et al., 2011; Gregg et al., 2008; Gregg & Crawford, 2009). As the offspring age the days get longer, temperature increases, precipitation decreases, and by early summer (June) these critical foods are available primarily in higher elevation sites or riparian areas. Such areas represent as little as 2% of the landscape (Atamian et al., 2010; Donnelly et al., 2016). Growth rate of young, which influences both prefledging and postfledging survival (Blomberg et al., 2014; Gibson et al., 2016) is directly dependent on the quality and quantity of food (Blomberg, Poulson, et al., 2013; Smith et al., 2019). It seems likely that adult females also restore some depleted nutrient reserves during this period because forbs represent the highest protein content foods females encounter (Gregg et al., 2008) and protein is a limiting nutrient for herbivorous birds (Sedinger, 1997). These high-quality foods potentially regulate individual fitness and population dynamics of sage-grouse (Kane et al., 2017). Consequently, non-native ungulates have the potential to negatively influence sage-grouse through their influence on key food plants (e.g., sagebrush and forbaceous vegetation) and seasonal habitats used by sage-grouse. In fact, recent analyses by Coates et al. (2021) demonstrates that abundance of feral horses is negatively correlated with the rate of growth of local sage-grouse populations.

Assessment of the potential effects of domestic cattle and feral horses on sage-grouse has primarily been through the lens of habitat modification or behavioral disturbance (Beck & Mitchell, 2000; Boyd et al., 2014; Dahlgren et al., 2015; Dettenmaier et al., 2017; Williamson et al., 2020). Direct assessment of the effects of livestock or horses on fitness, demography, and population dynamics of sage-grouse is lacking. Possible physiological mechanisms for demographic effects resulting from coexistence with these non-native ungulates are also largely unaddressed (Monroe et al., 2017).

We measured variation in corticosterone levels, the predominant GC in birds, in feathers of female sage-grouse across a gradient of livestock and feral horse densities in multiple years that varied in precipitation to assess the elevation of GC levels in relation to the abundance of livestock and feral horses under variable climatic conditions. Feather corticosterone (fCort) is an indicator of chronic stress, which may alter an individual’s ability to allocate resources to reproduction or survival over time. In house sparrows (*Passer domesticus*) and Eurasian Sparrowhawks (*Accipiter nisus)* higher fCort levels in feathers were associated with lower survival in the following season (Koren et al., 2012; Monclus et al., 2017). High GC concentrations in feathers led to a higher likelihood of skipping breeding in the following breeding season for harlequin ducks (*Histrionicus histrionicus*) (Hansen et al., 2016) and successfully breeding giant petrels (*Macronectes* spp.) had 1.5 times higher fCort than non-breeders (Crossin et al., 2013), indicating some cost to reproduction. Other studies have found no support for links between fCort and fitness (Henderson et al., 2017; Madliger & Love, 2016), which suggests that these relationships may be context dependent.

We assessed potential sources of chronic stress and the demographic consequences for female sage-grouse by testing the relationships between fCort and important demographic rates, including adult survival, probability of initiating breeding, nest success, and probability of producing fledged young. We utilized on-going management actions, e.g. feral horse removals, and grazing regimes as quasi-experimental treatments across a large area of sage-grouse habitat. Under the Cort-Fitness Hypothesis, we predicted horse and cow densities would be related to increases in fCort, followed by declines in survival and breeding of sage-grouse.

## Materials and Methods

### Study Areas

We studied sage-grouse in three study regions in the northern Great Basin, USA (Figure 2). Hart Mountain National Antelope Refuge (hereafter Hart Mountain) in southcentral Oregon encompasses over 112,500 hectares and ranges in elevation from 1,360 to just over 2,445 m at the top of Warner Peak (U.S. Fish and Wildlife Service). Domestic livestock grazing ceased on Hart Mountain in 1991 and feral horses occur only in very low numbers outside areas where we studied sage-grouse. Sheldon National Wildlife Refuge (hereafter Sheldon) in northern Nevada includes over 231,840 hectares (U.S. Fish and Wildlife Service). The lowest elevation is approximately 1,300 m at the bottom of the Thousand Creek Gorge and the highest peak is Catnip Mountain, which reaches just over 2,220 m. Domestic livestock were removed from Sheldon in 1994. Feral horses were abundant but nearly all feral horses were removed in 2014-2015. The Bureau of Land Management (BLM)-managed portion of our study is delineated by the Vya and Massacre Sage-grouse Population Management Units (hereafter Vya-Massacre) which encompass approximately 711,200 hectares in northwestern Nevada and northeastern California (Nevada Department of Wildlife). There are 22 grazing allotments for domestic cattle, as well as 7 Herd Management Areas (HMAs) for feral horses which overlap in the BLM portion of our study area (Figure 2).

### Field methods

We trapped yearling (ca. 10 months old at the time of capture) and adult female sage-grouse near active breeding leks (Gibson & Bradbury, 1987) during March of 2013 to 2017. We captured birds at night using spotlights (Giesen et al., 1982) and handheld nets. Once captured, we banded females with unique metal bands (National Band and Tag, Newport, KY; size 14) and fit them with 22g very high-frequency necklace-style radio-collars (VHF; Advanced Telemetry Systems, Isanti, MN, USA). We measured culmen using dial calipers (±1 mm), tarsus using dial calipers (±1 mm), flat wing using a board (±1 mm), and weighed each individual (±1 g). We aged birds as yearlings or adults based on plumage characteristics (Crunden, 1963). During capture, we plucked 2 breast feathers, which are thought to be grown in fall (Clait Braun, personal comm.) from each individual. We labeled feathers by individual and stored them frozen in small plastic storage bags (2013-2016) or dry in small paper coin envelopes (2017-2019). For this analysis, we used feathers collected from Hart Mountain (2013-2015), Sheldon (2013-2017), and Vya-Massacre (2013-2017).

We monitored females every 2-3 days via ground telemetry during the early nesting period, to document nesting and success or failure of nests. For females that had successful nests, we began monitoring their broods within the first 2-3 days after chicks hatched (Street et al. in press). We performed weekly checks of these broods, to count the surviving chicks up to 42-49 days of age. For the remaining months of the year, we employed aerial telemetry, approximately monthly, to assess live/dead status and location.

### Additional Data

We used reported data to assess horse and cow usage across our study region (Figure 2). For cows, we used BLM data for each allotment, which included the number of cows present and the amount of time spent in the allotment (BLM Applegate Field Office unpublished data). To account for variation in the number of days cows were actually on each allotment, we multiplied the number of cows by number of days they were on an allotment, then divided by the size of the area to produce a variable reflecting cow use days per unit area. For horses, we used annual population estimates reported for each Herd Management Area (HMA; (Bureau of Land Management, 2020a). Because horses are on the landscape year-round, we multiplied number of horses by 365 days and divided by the size of the HMA. Thus, our variables for analysis were horse and cow use days per square kilometer.

Our study region experienced significant variation in precipitation among years (150 – 410 mm). We used cumulative precipitation from October to September, referred to as the ‘northern water year’, as a measure of annual drought conditions (Huntington et al., 2017; PRISM Climate Group, 2011). Because invasive annual grasses displace native vegetation and can be detrimental to sage-grouse fitness and population dynamics (Blomberg et al., 2012), we included invasive annual grass cover as an explanatory variable in some candidate models of fCort levels. We used year-specific layers of estimated invasive annual grass percent cover created by Boyte et al., 2019, which in this area is primarily cheatgrass (*Bromus tectorum*), for this purpose.

Because feathers were collected at the time of capture, in late winter or early spring, the exact geographic locations of the birds during feather growth was unknown. Site fidelity of sage-grouse for specific seasonal habitats is high (Fischer et al., 1993), thus we used locations collected after capture as an index of where the female was the prior season. We extracted values for horse and cow density, drought, and annual grass cover for each individual sage-grouse at each location and averaged the covariate values across all locations. We used the locations for the year corresponding to feather growth, rather than the year the bird was captured for these estimates.

We calculated body condition as residuals of body mass regressed on female structural size, a principal components score of wing and tarsus lengths (Blomberg, Gibson, et al., 2014; Freeman & Jackson, 1990). When measurements were missing (n = 16), we assigned the individual the mean condition value. As noted above, measurements were conducted at the time of capture so our analyses of condition assessed whether fCort was predictive of body condition a few months after feather growth.

### Hormone Assays

We extracted corticosterone from feathers following Bortolotti et al. (2008), with some modifications. We first removed the calamus before measuring the length of each feather. We cut each feather into pieces < 5 mm2, mixed the pieces with 7 mL of HPLC grade methanol, and incubated the samples in a sonicating water bath at room temperature for 30 min. After sonication, we incubated the samples overnight in a shaking water bath at 50 °C. To separate the feather pieces and methanol, we used vacuum filtration with grade 4 filter paper (Whatman, Little Chalfont, United Kingdom). We also washed the sample tube, feather pieces, and filter apparatus twice with 2 mL of methanol, with washes added to the methanol extract. We dried the methanol extracts under air in a 50 °C heat block, reconstituted the extracts in assay buffer provided with the assay kit (see below), and froze them until assay.

We quantified corticosterone using enzyme-linked immunoassay according to the manufacturer’s instructions (Enzo Life Sciences, Farmingdale, NY, USA). To validate this assay, we verified that a serially diluted sample was parallel with the corticosterone standard curve. The average intra- and inter-assay coefficients of variation were 4.7% and 16.9%, respectively. The average assay sensitivity was 8.3 pg/mL. Because hormone deposition occurs in a time-dependent fashion during feather growth over several days to weeks (Bortolotti et al., 2009; Bortolotti et al., 2008), we normalized all final corticosterone values by feather length.

Corticosterone Model

We analyzed fCort levels in a Bayesian framework using JAGS UI (Kellner, 2015; Plummer, 2003) in Program R (R Core Team, 2019). We modeled fCort rounded to the nearest pg/mm for each bird *i*, with negative binomial variation approximated by a mean fCort level (µ), and shape term (r) to account for the highly skewed distribution. For all models we considered r to be constant. We modeled individual variation among µ with covariates of age (yearling or adult) and body condition. We included horse and cow densities, precipitation, and annual grass cover to assess the potential for impacts of grazing by non-native ungulates on fCort. We included interaction terms for horses x precipitation, cows x precipitation, and horses x annual grass to allow for spatial-temporal variation in the effects of non-native grazers in response to variation in climate or ecological conditions. Continuous covariates were z-standardized so that the estimates of each beta value are comparable to each other. Thus, our full model, for each individual female, , was,

We calculated the mean absolute prediction error (MAPE) from an 8-fold cross-validation as a measure of the predictive ability of our model (Hooten & Hobbs, 2015). We divided the dataset into 8 clusters. We then withheld one data cluster from each model run and compared the predicted values from the model to the recorded data values of the withheld data. We used normal priors centered on 0 for all of our beta coefficients. The prior for had a variance of 10. For all other beta coefficients, we used Bayesian regularization to optimize the variance on the priors to minimize the MAPE (Hooten & Hobbs, 2015). We performed an iterative search, fitting the model with variances of 0.001, 0.01, 0.05, 0.1, 0.15, 0.2, 0.5, and 1. This allowed for selection of the variance with the minimum MAPE across model runs (Appendix 1: Figure 1). We then ran the model with the whole dataset, using the best optimized variance for the priors. For the shape parameter of the negative binomial, we used a uniform prior from 0 to 500. The model was run with a burn-in of 5,000 iterations followed by additional 10,000 iterations.

fCort and Demographic Rates

We included additional data collected from radio-marked birds to estimate the effects of fCort on adult survival, breeding propensity, nest success, and overall breeding success using a Bayesian framework. For adult female survival, we used a known fate binomial survival model with a weekly interval (Royle & Dorazio, 2008). We also included seasonal offsets, a 1 or 0 assigned for that occasion, on survival for the spring (March 1 – May 31), summer (June 1 – July 31), fall (August 1 – October 31), and winter (November 1 – February 28/29). We only modeled survival during the first year following collection of a feather sample. We modeled probability of survival for each individual female, , at time, , as:

.

The winter season served as the intercept. Birds were assigned a 1 for age if first sampled as adults, or a 0 if sampled as yearlings, thus reflects the difference between adults and yearlings.

For each female,, we investigated whether fCort affected different components of the recruitment process. Breeding propensity () was recorded as a 1 if we observed a female on a nest, and a 0 if we never observed a nesting attempt. Similarly, nest success () was recorded as a 1 if birds successfully hatched a nest, and a 0 otherwise. We modeled the probability of success for each component of the recruitment process (d) as , where,

.

Overall breeding success () was considered to be a 1 if the bird fledged, raised to 42 days, at least one chick. To estimate the number of chicks that each female successfully fledged ), we modeled ~ where µ was the mean and variance of the number of chicks fledged, based on,

.

## Results

###### Corticosterone Model

We estimated fCort for 280 female sage-grouse. We detected substantial among-individual variation in fCort levels, with 65% of the sample having fCort levels < 10 pg/mm, while 20% of the sample had fCort levels > 100 pg/mm feather. There was no effect of age, and body condition only had a small negative effect on mean fCort (Table 1). In contrast, horse and cow densities interacted with precipitation to influence fCort levels. Increasing numbers of horses were associated with higher fCort in drought years (Figure 3; Table 1). This interaction was similarly positive but the effect was not as large for cows (Figure 4; Table 1). FCort levels were also positively associated with the interaction between horse density and percent cover of annual grasses (Figure 5; Table 1). Despite substantial among-individual variation, fCort levels tended to be highest in grazing allotments or horse management areas containing the largest numbers of cows and horses, respectively.

###### Demographic Model

Mean fCort was not strongly predictive of future survival or reproductive success (Table 2). The posterior distribution for the beta estimate for nest success, however, suggested the potential for a negative relationship between fCort and nest success (Figure 6; Table 2).

## Discussion

Mean fCort levels in female sage-grouse were higher when density of non-native ungulates was higher under drought conditions. Ungulates in arid environments can remove a high percentage of primary productivity (Baur et al., 2018; Veblen et al., 2015), an effect that is exacerbated under drought conditions when primary production is reduced (Donnelly et al., 2018; Zeigenfuss et al., 2014). Our findings are, therefore, consistent with the hypothesis that grazing by ungulates, likely through a reduction in late summer food availability for sage-grouse (Street, 2020), acts as a chronic stressor for a significant number of female sage-grouse. Horses in particular remove vegetation closer to the ground than other ungulates and consume upwards of 20% more plant matter than cows (Hanley & Hanley, 1982). This may explain the stronger effect found with horses than with cows, in spite of the higher density of cows on the landscape. The increase in fCort correlated with the combined effect of horses and annual grass cover is not suprising, given that horses can help spread cheatgrass (King et al., 2019) and sage-grouse recruitment suffers in areas with higher cheatgrass cover (Blomberg et al., 2012), as cheatgrass expansion displaces critical native perennial grasses and forbs (Williamson et al. 2020).

Our findings are consistent with other research demonstrating that environmental or social restrictions on energy or nutrient intake can produce chronic physiological stress (Fairhurst et al., 2017; Johns et al., 2018; Will et al., 2015; Wingfield et al., 1997; Wingfield et al., 2017; Wingfield & Sapolsky, 2003). Drought conditions are known to reduce reproductive investment by female sage-grouse (Blomberg et al., 2017; Blomberg et al., 2012; Blomberg, Sedinger, et al., 2013b) and male sage-grouse were less likely to attend leks during drought, especially at higher population densities (Blomberg, Sedinger, et al., 2013a), indicating that factors reducing food availability between breeding seasons constrain reproductive activities in sage-grouse. The fact that grazing by ungulates under drought conditions was associated with increased fCort levels is consistent with the general linkage between nutrient intake and elevated GCs, and elevated GC levels and reduced breeding investment (Hansen et al., 2016; Harms et al., 2015; Williams et al., 2008). We caution that our results, while consistent with the hypothesis that habitat degradation and food restriction elevate GCs in some females, should not be used to establish a direct linkage between a chronic physiological stress and reproductive investment because we assessed the GC levels several months before breeding began. Delayed impacts on current breeding and survival (carry-over effects) have been demonstrated for other variables in various avian species, such as previous breeding experience (Souchay et al., 2014; Warren et al., 2014) and population density (Blomberg et al., 2017).

Our data suggest that not all individuals responded the same way to grazing impacts (Figures 2 & 3). This could result from underlying intrinsic differences in reactivity to stressors (Cockrem, 2007, 2013) or other aspects of individual quality. Unknown circumstantial influences during the period of feather growth such as a predator attack, prior breeding effort, or disease status could also contribute to variation in response (Wingfield et al., 2017). Females that attended a brood during the summer delay molt of their primary feathers (Braun et al., 2020). If replacement of body feathers is also delayed, the timing of fCort deposition could differ by previous reproductive state. However, we found no effect of age on fCort, thus adults showed similar levels to yearlings who had no previous reproductive experience.

We found weak support that fCort was related to decreased nesting success, in line with the Cort-Fitness Hypothesis, but fCort was not otherwise predictive of vital rates. The time interval between the elevated GCs and nesting, however, suggests that both reflect nutritional condition, rather than the GC elevation causing lower nest success in some females. Because we captured females in spring of the year following feather growth, our sample only contains those females who survived from fall to spring. If high fCort levels had more immediate survival consequences, we would have been unable to detect them in this analysis because mortality would have occurred before females entered our demographic samples. The associations we have detected are, thus, likely a conservative measure of these relationships.

Using Bayesian methods to address the uncertainty in our estimates, we were able to identify the variation in female responses to stressors. We likely would have missed this important pattern with traditional methods used for comparing hormone levels. We observed a significant amount of variation in fCort among females. We modeled variation in the mean of the negative binomial distribution and allowed the rate (variance term) to be constant.  We also attempted to model variation in the rate term of the negative binomial and with a Poisson distribution, but observed poorer fit. Jankoski et al. (2014) standardized fecal corticosterone so that they could fit a linear model with a normal distribution. The highly skewed distribution of fCort levels we found could have influenced conclusions in studies that assumed a normal distribution for the residual variance. We emphasize that this variation is important to our understanding of the physiological response of chronic stressors. Our results suggest that there will likely be females with elevated fCort levels even when chronic stress is low, and there will likely be females with low fCort levels when chronic stress is high. Yet, the proportion of birds with high GC levels is higher when chronic stress is higher, and that adverse weather conditions combined with higher levels of either livestock of feral horses represent one source of chronic stress in our system.

Climate projections for the Great Basin indicate more frequent and longer lasting drought (Bradford et al., 2020; Snyder et al., 2019). Our results suggest that these conditions, along with unchecked increases in feral horse populations, will contribute to chronic stress in a substantial proportion of sage-grouse. Birds may acclimate to grazing pressure during wet or average years, but such responses are insufficient under drought conditions when resources become scarce. While short-term spikes in GCs facilitate survival and onset of breeding, chronic stress can lead to suppression of immune response, reproduction, and growth. Downregulation of the stress response system due to chronic stress can impede an individual’s ability to respond to acute stressors when needed (Rich & Romero, 2005). Our results suggest that under increased drought, female sage-grouse could experience an increased frequency of physiological stress under current grazing regimes.

Our study used a large dataset of feather corticosterone across a key sage-grouse habitat region of over 1 million hectares. This allowed us to assess both individual variation and effects of a gradient of biotic and abiotic environmental variables. Declines of sage-grouse populations have continued (Coates et al., 2021) despite intensive conservation efforts over the last few decades. Investigating the physiological links between the birds, their habitat, and the threats to both is important for informing future conservation actions.

## References

Atamian, M. T., Sedinger, J. S., Heaton, J. S., & Blomberg, E. J. (2010). Landscape-level assessment of brood rearing habitat for Greater Sage-grouse in Nevada. *Journal of Wildlife Management*, *74*(7), 1533-1543. https://doi.org/10.2193/2009-226

Batchelor, J. L., Ripple, W. J., Wilson, T. M., & Painter, L. E. (2015). Restoration of riparian areas following the removal of cattle in the Northwestern Great Basin. *Environmental Management*, *55*(4), 930-942. https://doi.org/10.1007/s00267-014-0436-2

Batzer, D. P., & Baldwin, A. H. (2012). *Wetland Habitats of North America: Ecology and Conservation Concerns*. University of California Press.

Baur, L. E., Schoenecker, K. A., & Smith, M. D. (2018). Effects of feral horse herds on rangeland plant communities across a precipitation gradient. *Western North American Naturalist*, *77*(4), 526-540. <https://doi.org/10.3398/064.077.0412>

Beck, J. L., & Mitchell, D. L. (2000). Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin*, 993-1002. http://www.jstor.org/stable/3783858

Beever, E. A., & Herrick, J. E. (2006). Effects of feral horses in Great Basin landscapes on soils and ants: direct and indirect mechanisms. *Journal of Arid Environments*, *66*(1), 96-112. <https://doi.org/10.1016/j.jaridenv.2005.11.006>

Beschta, R. L., Kauffman, J. B., Dobkin, D. S., & Ellsworth, L. M. (2014). Long-term livestock grazing alters aspen age structure in the northwestern Great Basin. *Forest Ecology And Management*, *329*, 30-36. <https://doi.org/10.1016/j.foreco.2014.06.017>

Blomberg, E. J., Gibson, D., Atamian, M. T., & Sedinger, J. S. (2014). Individual and environmental effects on egg allocations of female Greater Sage-Grouse. *The Auk*, *131*(4), 507-523. https://doi.org/10.1642/auk-14-32.1

Blomberg, E. J., Gibson, D., Atamian, M. T., & Sedinger, J. S. (2017). Variable drivers of primary versus secondary nesting; density-dependence and drought effects on greater sage-grouse. *Journal of Avian Biology*, *48*(6), 827-836. https://doi.org/10.1111/jav.00988

Blomberg, E. J., Poulson, S. R., Sedinger, J. S., & Gibson, D. (2013). Prefledging diet is correlated with individual growth in Greater Sage-Grouse (Centrocercus urophasianus). *The Auk*, *130*(4), 715-724. <https://doi.org/10.1525/auk.2013.12188>

Blomberg, E. J., Sedinger, J. S., Atamian, M. T., & Nonne, D. V. (2012). Characteristics of climate and landscape disturbance influence the dynamics of Greater Sage-grouse populations. *Ecosphere*, *3*(6), 20. https://doi.org/10.1890/es11-00304.1

Blomberg, E. J., Sedinger, J. S., Gibson, D., Coates, P. S., & Casazza, M. L. (2014). Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. *Ecology and Evolution*, *4*(23), 4488-4499. https://doi.org/10.1002/ece3.1139

Blomberg, E. J., Sedinger, J. S., Nonne, D. V., & Atamian, M. T. (2013a). Annual male lek attendance influences count-based population indices of Greater Sage-grouse. *Journal of Wildlife Management*, *77*(8), 1583-1592. https://doi.org/10.1002/jwmg.615

Blomberg, E. J., Sedinger, J. S., Nonne, D. V., & Atamian, M. T. (2013b). Seasonal reproductive costs contribute to reduced survival of female Greater Sage-grouse. *Journal of Avian Biology*, *44*(2), 149-158. https://doi.org/10.1111/j.1600-048X.2012.00013.x

Bonier, F., Moore, I. T., Martin, P. R., & Robertson, R. J. (2009). The relationship between fitness and baseline glucocorticoids in a passerine bird. *General and Comparative Endocrinology*, *163*(1-2), 208-213. https://doi.org/10.1016/j.ygcen.2008.12.013

Bortolotti, G. R., Marchant, T., Blas, J., & Cabezas, S. (2009). Tracking stress: localisation, deposition and stability of corticosterone in feathers. *Journal of Experimental Biology*, *212*(10), 1477-1482. https://doi.org/10.1242/jeb.022152

Bortolotti, G. R., Marchant, T. A., Blas, J., & German, T. (2008). Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Functional Ecology*, *22*(3), 494-500. https://doi.org/10.1111/j.1365-2435.2008.01387.x

Boyd, C. S., Beck, J. L., & Tanaka, J. A. (2014). Livestock grazing and sage-grouse habitat: impacts and opportunities. *Journal of Rangeland Applications*, *1*, 58-77. https://thejra.nkn.uidaho.edu/index.php/jra/article/view/24

Boyd, C. S., Davies, K. W., & Collins, G. H. (2017). Impacts of feral horse use on herbaceous riparian vegetation within a sagebrush steppe ecosystem. *Rangeland Ecology & Management*, *70*(4), 411-417. <https://doi.org/10.1016/j.rama.2017.02.001>

Boyte, S. P., Wylie, B. K., & Major, D. J. (2019). Validating a time series of annual grass percent cover in the sagebrush ecosystem. *Rangeland Ecology & Management*, *72*(2), 347-359. <https://doi.org/10.1016/j.rama.2018.09.004>

Bradford, J. B., Schlaepfer, D. R., Lauenroth, W. K., & Palmquist, K. A. (2020). Robust ecological drought projections for drylands in the 21st century. *Global Change Biology*, *26*(7), 3906-3919. <https://doi.org/10.1111/gcb.15075>

Braun, C. E., Dunn, P. O., Wann, G. T., Schroeder, M. A., & Hupp, J. W. (2020). Body mass and primary molt patterns of Greater Sage-grouse in Colorado. *Western North American Naturalist*, *80*(3), 330-336, 337. https://doi.org/10.3398/064.080.0304

Bureau of Land Management. (2020a). *BLM National Wild Horse and Burro Herd Area and Herd Management Area*. https://catalog.data.gov/dataset/blm-national-wild-horse-and-burro-herd-area-and-herd-management-area

Bureau of Land Management. (2020b). *Livestock Grazing on Public Lands*. https://www.blm.gov/programs/natural-resources/rangelands-and-grazing/livestock-grazing

Casazza, M. L., Coates, P. S., & Overton, C. T. (2011). Linking habitat selection and brood success in Greater Sage-grouse. *Ecology, conservation, and management of grouse. .Studies in Avian Biology*, *39*, 151-167. <https://doi.org/10.1525/9780520950573>

Chambers, J. C., Blank, R. R., Zamudio, D. C., & Tausch, R. J. (1999). Central Nevada riparian areas: Physical and chemical properties of meadow soils. *Journal of Range Management*, *52*(1), 92-99. https://doi.org/10.2307/4003497

Coates, P. S., Prochazka, B. G., O'Donnell, M. S., Aldridge, C. L., Edmunds, D. R., Monroe, A. P., . . . Wiechman, L. A. (2021). *Range-wide greater sage-grouse hierarchical monitoring framework—Implications for defining population boundaries, trend estimation, and a targeted annual warning system* (2331-1258). US Geological Survey.

https://doi.org/10.3133/ofr20201154

Cockrem, J. F. (2007). Stress, corticosterone responses and avian personalities. *Journal of Ornithology*, *148*(2), 169-178. https://doi.org/10.1007/s10336-007-0175-8

Cockrem, J. F. (2013). Corticosterone responses and personality in birds: individual variation and the ability to cope with environmental changes due to climate change. *General and Comparative Endocrinology*, *190*, 156-163. <https://doi.org/10.1016/j.ygcen.2013.02.021>

Crossin, G. T., Phillips, R. A., Lattin, C. R., Romero, L. M., & Williams, T. D. (2013). Corticosterone mediated costs of reproduction link current to future breeding. *General and Comparative Endocrinology*, *193*, 112-120. <https://doi.org/10.1016/j.ygcen.2013.07.011>

Crunden, C. W. (1963). Age and sex of sage grouse from wings. *Journal of Wildlife Management*, *27*, 846-850. https://doi.org/10.2307/3798498

Cyr, N. E., & Romero, L. M. (2007). Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *General and Comparative Endocrinology*, *151*(1), 82-89. <https://doi.org/10.1016/j.ygcen.2006.12.003>

Dahlgren, D. K., Larsen, R. T., Danvir, R., Wilson, G., Thacker, E. T., Black, T. A., . . . Messmer, T. A. (2015). Greater sage-grouse and range management: Insights from a 25-year case study in Utah and Wyoming. *Rangeland Ecology & Management*, *68*(5), 375-382. <https://doi.org/10.1016/j.rama.2015.07.003>

Dettenmaier, S. J., Messmer, T. A., Hovick, T. J., & Dahlgren, D. K. (2017). Effects of livestock grazing on rangeland biodiversity: A meta‐analysis of grouse populations. *Ecology and Evolution*, *7*(19), 7620-7627. https://doi.org/10.1002/ece3.3287

Dobkin, D. S., Rich, A. C., & Pyle, W. H. (1998). Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. *Conservation Biology*, *12*(1), 209-221. https://doi.org/10.1046/j.1523-1739.1998.96349.x

Donnelly, J. P., Allred, B. W., Perret, D., Silverman, N. L., Tack, J. D., Dreitz, V. J., . . . Naugle, D. E. (2018a). Seasonal drought in North America’s sagebrush biome structures dynamic mesic resources for sage-grouse. *Ecology and Evolution*, *8*(24), 12492-12505. https://doi.org/https://doi.org/10.1002/ece3.4614

Donnelly, J. P., Naugle, D. E., Hagen, C. A., & Maestas, J. D. (2016). Public lands and private waters: scarce mesic resources structure land tenure and sage‐grouse distributions. *Ecosphere*, *7*(1), e01208. https://doi.org/10.1002/ecs2.1208

Eldridge, D. J., Ding, J., & Travers, S. K. (2020). Feral horse activity reduces environmental quality in ecosystems globally. *Biological Conservation*, *241*, 108367. <https://doi.org/10.1016/j.biocon.2019.108367>

Fairhurst, G. D., Champoux, L., Hobson, K. A., Rail, J. F., Verreault, J., Guillemette, M., . . . Soos, C. (2017). Feather corticosterone during non-breeding correlates with multiple measures of physiology during subsequent breeding in a migratory seabird. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, *208*, 1-13. https://doi.org/10.1016/j.cbpa.2017.02.024

Fischer, R. A., Apa, A. D., Wakkinen, W. L., Reese, K. P., & Connelly, J. W. (1993). Nesting-area fidelity of sage grouse in southeastern Idaho. *The Condor*, *95*(4), 1038-1041. https://doi.org/10.2307/1369442

Freeman, S., & Jackson, W. M. (1990). Univariate metrics are not adequate to measure avian body size. *The Auk*, *107*(1), 69-74. <https://doi.org/10.1093/auk/107.1.69>

Frye, G. G., Connelly, J. W., Musil, D. D., & Forbey, J. S. (2013). Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. *Ecology*, *94*(2), 308-314. https://doi.org/10.1890/12-1313.1

Garrott, R. A. (2018). Wild horse demography: implications for sustainable management within economic constraints. *Human–Wildlife Interactions*, *12*(1), 7. <https://doi.org/10.26077/z7w0-0w34>

Gibson, D., Blomberg, E. J., Atamian, M. T., & Sedinger, J. S. (2016). Nesting habitat selection influences nest and early offspring survival in Greater Sage-Grouse. *The Condor*, *118*(4), 689-702. https://doi.org/10.1650/condor-16-62.1

Gibson, R. M., & Bradbury, J. W. (1987). Lek organization in sage grouse: variations on a territorial theme. *The Auk*, *104*(1), 77-84. https://doi.org/10.2307/4087236

Giesen, K. M., Schoenberg, T. J., & Braun, C. E. (1982). Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin*, 224-231. http://www.jstor.org/stable/3781009

Gooch, A. M., Petersen, S. L., Collins, G. H., Smith, T. S., McMillan, B. R., & Eggett, D. L. (2017). The impact of feral horses on pronghorn behavior at water sources. *Journal of Arid Environments*, *138*, 38-43. https://doi.org/10.1016/j.jaridenv.2016.11.012

Graham, S. P., Freidenfelds, N. A., McCormick, G. L., & Langkilde, T. (2012). The impacts of invaders: basal and acute stress glucocorticoid profiles and immune function in native lizards threatened by invasive ants. *General and Comparative Endocrinology*, *176*(3), 400-408. [https://doi.org/https://doi.org/10.1016/j.ygcen.2011.12.027](https://doi.org/https:/doi.org/10.1016/j.ygcen.2011.12.027)

Gregg, M. A., Barnett, J. K., & Crawford, J. A. (2008). Temporal variation in diet and nutrition of preincubating Greater Sage-grouse. *Rangeland Ecology & Management*, *61*(5), 535-542. https://doi.org/10.2111/08-037.1

Gregg, M. A., & Crawford, J. A. (2009). Survival of Greater Sage-Grouse chicks and broods in the Northern Great Basin. *Journal of Wildlife Management*, *73*(6), 904-913. https://doi.org/10.2193/2007-410

Hall, L. K., Larsen, R. T., Knight, R. N., & McMillan, B. R. (2018). Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi‐arid environment. *Ecosphere*, *9*(1), e02096. https://doi.org/10.1002/ecs2.2096

Hanley, T. A., & Hanley, K. A. (1982). Food resource partitioning by sympatric ungulates on Great Basin rangeland. *Rangeland Ecology & Management, 35*(2), 152-158.

Hansen, W. K., Bate, L. J., Landry, D. W., Chastel, O., Parenteau, C., & Breuner, C. W. (2016). Feather and faecal corticosterone concentrations predict future reproductive decisions in harlequin ducks (Histrionicus histrionicus). *Conservation Physiology*, *4*, Article cow015. https://doi.org/10.1093/conphys/cow015

Harms, N. J., Legagneux, P., Gilchrist, H. G., Bêty, J., Love, O. P., Forbes, M. R., . . . Soos, C. (2015). Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1800), 20142085. <https://doi.org/10.1098/rspb.2014.2085>

Hau, M., Ricklefs, R. E., Wikelski, M., Lee, K. A., & Brawn, J. D. (2010). Corticosterone, testosterone and life-history strategies of birds. *Proceedings of the Royal Society B-Biological Sciences*, *277*(1697), 3203-3212. https://doi.org/10.1098/rspb.2010.0673

Henderson, L. J., Evans, N. P., Heidinger, B. J., Herborn, K. A., & Arnold, K. E. (2017). Do glucocorticoids predict fitness? Linking environmental conditions, corticosterone and reproductive success in the blue tit, Cyanistes caeruleus. *Royal Society Open Science*, *4*(10), 11, Article 170875. https://doi.org/10.1098/rsos.170875

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*(1), 3-28. <https://doi.org/10.1890/14-0661.1>

Huntington, J. L., Hegewisch, K. C., Daudert, B., Morton, C. G., Abatzoglou, J. T., McEvoy, D. J., & Erickson, T. (2017). Climate Engine: cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. *Bulletin of the American Meteorological Society*, *98*(11), 2397-2410.

<https://doi.org/10.1175/BAMS-D-15-00324.1>

Injaian, A. S., Francis, C. D., Ouyang, J. Q., Dominoni, D. M., Donald, J. W., Fuxjager, M. J., . . . Johnson, M. A. (2020). Baseline and stress-induced corticosterone levels across birds and reptiles do not reflect urbanication levels. *Conservation Physiology*, *8*(1), coz110. [https://doi.org/https://doi.org/10.1093/conphys/coz110](https://doi.org/https:/doi.org/10.1093/conphys/coz110){Injaian, 2020, Baseline and stress-induced corticosterone levels across birds and reptiles do not reflect urbanication levels}{Injaian, 2020, Baseline and stress-induced corticosterone levels across birds and reptiles do not reflect urbanication levels}

Jankowski, M. D., Russell, R. E., Franson, J. C., Dusek, R. J., Hines, M. K., Gregg, M., & Hofmeister, E. K. (2014). Corticosterone metabolite concentrations in Greater Sage-grouse are positively associated with the presence of cattle grazing. *Rangeland Ecology & Management*, *67*(3), 237-246. https://doi.org/10.2111/rem-d-13-00137.1

Johns, D. W., Marchant, T. A., Fairhurst, G. D., Speakman, J. R., & Clark, R. G. (2018). Biomarker of burden: Feather corticosterone reflects energetic expenditure and allostatic overload in captive waterfowl. *Functional Ecology*, *32*(2), 345-357. <https://doi.org/10.1111/1365-2435.12988>

Kane, K., Sedinger, J. S., Gibson, D., Blomberg, E. J., & Atamian M. T. (2017). Fitness landscapes and life table response experiments predict the importance of local areas to population dynamics. *Ecosphere 8*:e01869.

Kellner, K. (2015). jagsUI: a wrapper around rjags to streamline JAGS analyses. *R package version*, *1*(1), 2015.

King, S. R., Schoenecker, K. A., & Manier, D. J. (2019). Potential spread of cheatgrass and other invasive species by feral horses in western colorado. *Rangeland Ecology & Management*, *72*(4), 706-710. https://doi.org/10.1016/j.rama.2019.02.006

Koren, L., Nakagawa, S., Burke, T., Soma, K. K., Wynne-Edwards, K. E., & Geffen, E. (2012). Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1733), 1560-1566. <https://doi.org/10.1098/rspb.2011.2062>

Madliger, C. L., & Love, O. P. (2016). Conservation implications of a lack of relationship between baseline glucocorticoids and fitness in a wild passerine. *Ecological Applications*, *26*(8), 2730-2743. https://doi.org/10.1002/eap.1401

Monclus, L., Carbajal, A., Tallo-Parra, O., Sabes-Alsina, M., Darwich, L., Molina-Lopez, R. A., & Lopez-Bejar, M. (2017). Relationship between feather corticosterone and subsequent health status and survival in wild Eurasian Sparrowhawk. *Journal of Ornithology*, *158*(3), 773-783. https://doi.org/10.1007/s10336-016-1424-5

Monroe, A. P., Aldridge, C. L., Assal, T. J., Veblen, K. E., Pyke, D. A., & Casazza, M. L. (2017). Patterns in Greater Sage-grouse population dynamics correspond with public grazing records at broad scales. *Ecological Applications*, *27*(4), 1096-1107. https://doi.org/10.1002/eap.1512

Narayan, E. J., Jessop, T. S., & Hero, J. (2015). Invasive cane toad triggers chronic physiological stress and decreased reproductive success in an island endemic. *Functional Ecology*, *29*(11), 1435-1444. [https://doi.org/https://doi.org/10.1111/1365-2435.12446](https://doi.org/https:/doi.org/10.1111/1365-2435.12446)

Nevada Department of Wildlife. *Sage Grouse Conservation Plans*. Retrieved August 4, 2020 from http://www.ndow.org/Nevada\_Wildlife/Sage\_Grouse/Conservation\_Plans/

Ostermann-Kelm, S., Atwill, E. R., Rubin, E. S., Jorgensen, M. C., & Boyce, W. M. (2008). Interactions between feral horses and desert bighorn sheep at water. *Journal of Mammalogy*, *89*(2), 459-466.

https://doi.org/10.1644/07-MAMM-A-075R1.1

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* (Vol. 124, No. 125.10, pp. 1-10).

PRISM Climate Group. (2011). *PRISM climate data*. http://www.prism.oregonstate.edu/

R Core Team. (2019). R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria.

Remington, T. E., & Braun, C. E. (1985). Sage grouse food selection in winter, North Park, Colorado. *Journal of Wildlife Management*, 1055-1061.

https://doi.org/10.2307/3801395

Rich, E. L., & Romero, L. M. (2005). Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *288*(6), R1628-R1636. <https://doi.org/10.1152/ajpregu.00484.2004>

Romero, L. M. (2004). Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*, *19*(5), 249-255. <https://doi.org/10.1016/j.tree.2004.03.008>

Rowland, M. M., Wisdom, M. J., Suring, L. H., & Meinke, C. W. (2006). Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation*, *129*(3), 323-335. <https://doi.org/10.1016/j.biocon.2005.10.048>

Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Elsevier Science.

Santicchia, F., Dantzer, B., van Kesteren, F., Palme, R., Martinoli, A., Ferrari, N., & Wauters, L. A. (2018). Stress in biological invasions: Introduced invasive grey squirrels increase physiological stress in native Eurasian red squirrels. *Journal of Animal Ecology*, *87*(5), 1342-1352. [https://doi.org/https://doi.org/10.1111/1365-2656.12853](https://doi.org/https:/doi.org/10.1111/1365-2656.12853)

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, *21*(1), 55-89. <https://doi.org/10.1210/edrv.21.1.0389>

Scasta, J. D., Beck, J. L., & Angwin, C. J. (2016). Meta-analysis of diet composition and potential conflict of wild horses with livestock and wild ungulates on western rangelands of North America. *Rangeland Ecology & Management*, *69*(4), 310-318. <https://doi.org/10.1016/j.rama.2016.01.001>

Schroeder, M. A., Young, J. R., & Braun, C. E. (2020). Greater Sage-Grouse (Ce*ntrocercus urophasianus)*. In A. F. Poole & F. B. Gill (Eds.), *Birds of the World* (version 1.0 ed.). Ithaca, NY, USA: Cornell Lab of Ornithology.

Sedinger, J. S. (1997). Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *The Condor*, *99*(2), 314-326. <https://doi.org/10.2307/1369937>

Smith, K. T., Pratt, A. C., LeVan, J. R., Rhea, A. M., & Beck, J. L. (2019). Reconstructing Greater Sage-Grouse chick diets: Diet selection, body condition, and food availability at brood-rearing sites. *The Condor: Ornithological Applications*, *121*(1), duy012.

https://doi.org/10.1093/condor/duy012

Snyder, K. A., Evers, L., Chambers, J. C., Dunham, J., Bradford, J. B., & Loik, M. E. (2019). Effects of changing climate on the hydrological cycle in cold desert ecosystems of the Great Basin and Columbia Plateau. *Rangeland Ecology & Management*, *72*(1), 1-12.

https://doi.org/10.1016/j.rama.2018.07.007

Sorenson, G. H., Dey, C. J., Madliger, C. L., & Love, O. P. (2017). Effectiveness of baseline corticosterone as a monitoring tool for fitness: a meta-analysis in seabirds. *Oecologia*, *183*(2), 353-365. https://doi.org/10.1007/s00442-016-3774-3

Souchay, G., Gauthier, G., & Pradel, R. (2014). To breed or not: a novel approach to estimate breeding propensity and potential trade‐offs in an Arctic‐nesting species. *Ecology*, *95*(10), 2745-2756. https://doi.org/10.1890/13-1277.1

Spear, D., & Chown, S. L. (2009). Non‐indigenous ungulates as a threat to biodiversity. *Journal of Zoology*, *279*(1), 1-17. https://doi.org/10.1111/j.1469-7998.2009.00604.x

Street, P.A., Riecke, T.V., Williams, P.J., Behnke, T.L., & Sedinger, J.S. (in press). Estimating survival and adoption rates of dependent juveniles. *Ecology and Evolution.*

Street, P. A. (2020). *Greater Sage-grouse habitat and demographic response to grazing by non-native ungulates.* [DoctoralDissertation, University of Nevada, Reno].

U.S. Fish and Wildlife Service. *Hart Mountain National Antelope Refuge*. Retrieved June 6, 2021 from https://www.fws.gov/refuge/Hart\_Mountain/

U.S. Fish and Wildlife Service. *Sheldon National Wildlife Refuge*. Retrieved June 6, 2021 from https://www.fws.gov/refuge/Sheldon/

Van Zwol, J. A., Neff, B. D., & Wilson, C. C. (2012). The influence of non-native salmonids on circulating hormone concentrations in juvenile Atlantic salmon. *Animal Behaviour*, *83*(1), 119-129. [https://doi.org/https://doi.org/10.1016/j.anbehav.2011.10.015](https://doi.org/https:/doi.org/10.1016/j.anbehav.2011.10.015)

Veblen, K. E., Nehring, K. C., McGlone, C. M., & Ritchie, M. E. (2015). Contrasting effects of different mammalian herbivores on sagebrush plant communities. *PLoS One*, *10*(2), e0118016. <https://doi.org/10.1371/journal.pone.0118016>

Vera, F., Zenuto, R., & Antenucci, C. D. (2017). Expanding the actions of cortisol and corticosterone in wild vertebrates: A necessary step to overcome the emerging challenges. *General and Comparative Endocrinology*, *246*, 337-353. https://doi.org/10.1016/j.ygcen.2017.01.010

Volery, L., Jatavallabhula, D., Scillitani, L., Bertolino, S., & Bacher, S. (2021). Ranking alien species based on their risks of causing environmental impacts: A global assessment of alien ungulates. *Global Change Biology*, *27*(5), 1003-1016. https://doi.org/10.1111/gcb.15467

Warren, J. M., Cutting, K. A., Takekawa, J. Y., De La Cruz, S. E., Williams, T. D., & Koons, D. N. (2014). Previous success and current body condition determine breeding propensity in lesser scaup: evidence for the individual heterogeneity hypothesis. *The Auk: Ornithological Advances*, *131*(3), 287-297. <https://doi.org/10.1642/AUK-13-236.1>

Will, A., Watanuki, Y., Kikuchi, D. M., Sato, N., Ito, M., Callahan, M., . . . Kitaysky, A. (2015). Feather corticosterone reveals stress associated with dietary changes in a breeding seabird. *Ecology and Evolution*, *5*(19), 4221-4232. https://doi.org/10.1002/ece3.1694

Williams, C. T., Kitaysky, A. S., Kettle, A. B., & Buck, C. L. (2008). Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *General and Comparative Endocrinology*, *158*(1), 29-35. <https://doi.org/10.1016/j.ygcen.2008.04.018>

Williamson, M. A., Fleishman, E., Mac Nally, R. C., Chambers, J. C., Bradley, B. A., Dobkin, D. S., . . . Leu, M. (2020). Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass (Bromus tectorum) in the central Great Basin, USA. *Biological Invasions*, *22*(2), 663-680. https://doi.org/10.1007/s10530-019-02120-8

Wingfield, J. C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G. S., Freed, L., & Lepson, J. (1997). Environmental stress, field endocrinology, and conservation biology. In: J.R. Clemmons & R. Buchholz (Eds.). *Behavioral Approaches to Conservation in the Wild*. 95-131. Cambridge University Press.

Wingfield, J. C., Perez, J. H., Krause, J. S., Word, K. R., Gonzalez-Gomez, P. L., Lisovski, S., & Chmura, H. E. (2017). How birds cope physiologically and behaviourally with extreme climatic events. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *372*(1723), Article 20160140. https://doi.org/10.1098/rstb.2016.0140

Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: when and how. *Journal of Neuroendocrinology*, *15*(8), 711-724. <https://doi.org/10.1046/j.1365-2826.2003.01033.x>

Zeigenfuss, L. C., Schoenecker, K. A., Ransom, J. I., Ignizio, D. A., & Mask, T. (2014). Influence of nonnative and native ungulate biomass and seasonal precipitation on vegetation production in a Great Basin Ecosystem. *Western North American Naturalist*, *74*(3), 286-298. http://www.jstor.org/stable/24644405

## Figures Legends

Figure 1. Photo of female Greater Sage-grouse with brood in dry late summer habitat, northwestern Nevada.

Figure 2. Study area map showing areas with horses, cows, or both during the course of the study. Bird locations include all known locations of the birds with fCort measurements. Hart Mountain was the northern-most area, while Sheldon was the approximately rectnaangular area on the Oregon border. BLM managed lands containing cattle allotments and horse management areas were the remainder of the area. Note- Hart Mountain did have a few horses (<31) in 2012-2013, but these were not in the same areas as monitored sage-grouse.

Figure 3. Interaction effects of horses (horse use days per km2) and annual precipitation (mm) on fCort (pg/mm feather), at the mean of all other covariates. Grid surface represents the estimated interaction of effects from the full model. Points are observed values of fCort with lines to corresponding location on the grid surface; right color bar represents these fCort measurements in pg/mm.

Figure 4. Interaction effects of cows (cow use days per km2) and annual precipitation (mm) on fCort (pg/mm feather), at the mean of all other covariates. Grid surface represents the estimated interaction of effects from the full model. Points are observed values of fCort with lines to corresponding location on the grid surface; right color bar represents these fCort measurements in pg/mm.

Figure 5. Interaction effects of horses (horse use days per km2) and annual grass cover (% cover) on fCort (pg/mm feather), at the mean of all other covariates. Grid surface represents the estimated interaction of effects from the full model. Points are observed values of fCort with lines to corresponding location on the grid surface; right color bar represents these fCort measurements in pg/mm.

##### Figure 6. Posterior distributions for parameters from the models using fCort as a predictor of demographic rates – adult survival (known-fate binomial), breeding propensity (Bernoulli), nest success (Bernoulli), and overall breeding success (zero-inflated Poisson and Bernoulli) in the breeding year following fCort deposition (Table 2).

##### Appendix l: Figure 1. Sigma optimization. Upper plot shows the mean absolute prediction error assessed for sigma values from 0.001 to 1. Lower plot shows the range of beta estimates associated with each sigma in different colors for each beta value. Sigma = 0.1 minimized the absolute prediction error of the beta estimates for the covariates and was used for the main model.

## Tables

Table 1. Model estimates for the full fCort model with covariates. LCI and UCI represent lower and upper 95% credible intervals, respectively. Pr < 0 and Pr >0 were the proportions of the posterior distribution below and above zero, respectively.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Term | Estimate | SD | LCI | UCI | Pr <0 | Pr >0 |
| Intercept | 3.779 | 0.107 | 3.574 | 3.99 | 0 | 1 |
| Cows | 0.016 | 0.064 | -0.107 | 0.143 | 0.405 | 0.595 |
| Horses | -0.056 | 0.077 | -0.206 | 0.096 | 0.764 | 0.236 |
| Body Condition | -0.037 | 0.061 | -0.159 | 0.081 | 0.726 | 0.274 |
| Age | -0.004 | 0.087 | -0.174 | 0.168 | 0.517 | 0.483 |
| Annual Grass | -0.078 | 0.073 | -0.219 | 0.065 | 0.86 | 0.14 |
| Annual Precipitation | -0.125 | 0.068 | -0.258 | 0.008 | 0.967 | 0.033 |
| Horses \* Precipitation | -0.125 | 0.069 | -0.261 | 0.01 | 0.965 | 0.035 |
| Horses \* Annual Grass | 0.075 | 0.086 | -0.095 | 0.243 | 0.19 | 0.81 |
| Cows\* Precipitation | -0.043 | 0.06 | -0.161 | 0.073 | 0.759 | 0.241 |

Table 2. Estimated effects of fCort on each demographic rate. LCI and UCI represent lower and upper 95% credible intervals, respectively. Pr < 0 and Pr >0 were the proportions of the posterior distribution below and above zero, respectively.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Demographic rate | Estimate | SD | LCI | UCI | Pr < 0 | Pr > 0 |
| Adult Survival | 0.001 | 0.001 | -0.002 | 0.004 | 0.252 | 0.748 |
| Breeding Probability | 0 | 0.002 | -0.003 | 0.003 | 0.435 | 0.565 |
| Nest Success | -0.002 | 0.002 | -0.006 | 0.001 | 0.873 | 0.127 |
| Breeding Success | -0.001 | 0.001 | -0.004 | 0.002 | 0.691 | 0.309 |