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Corticosterone Metabolite Concentrations in Greater Sage-Grouse Are Positively Associated With the Presence of Cattle Grazing

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Abstract

The sagebrush biome in the western United States is home to the imperiled greater sage-grouse (*Centrocercus urophasianus*) and encompasses rangelands used for cattle production. Cattle grazing activities have been implicated in the range-wide decline of the sage-grouse, but no studies have investigated the relationship between the physiological condition of sage-grouse and the presence of grazing cattle. We sampled 329 sage-grouse across four sites (two grazed and two ungrazed) encompassing 13 600 km^2 during the spring and late summer–early autumn of 2005 to evaluate whether demographic factors, breeding status, plasma protein levels, and residence in a cattle-grazed habitat were associated with the stress hormone corticosterone. Corticosterone was measured in feces as immunoreactive corticosterone metabolites (ICM). Males captured during the lekking season exhibited higher ICM levels than all others. Prenesting female sage-grouse captured in a grazed site had higher ICM levels than those in ungrazed sites and prenesting female plasma protein levels were negatively correlated with ICM concentrations. With the use of a small-scale spatial model, we identified a positive correlation between cattle pat count and sage-grouse ICM levels. Our model indicated that ICM levels increased by 2.60 $ng \cdot g^{-1}$ dry feces for every increase in the number of cow pats found in the vicinity. Management practices will benefit from future research regarding the consistency and mechanism(s) responsible for this association and, importantly, how ICM levels and demographic rates are related in this species of conservation concern.

Key Words: bird, conservation physiology, corticosterone, endangered species, spatial statistics, stress

INTRODUCTION

The sagebrush biome is an expanse of semiarid rangeland dominated by sagebrush that is experiencing a range of anthropogenic disturbances, which are influencing species composition and native landscape heterogeneity (Connelly et al. 2004). This region is home to many avian species, but is perhaps most typified by the presence of the greater sage-grouse (*Centrocercus urophasianus*). The sage-grouse is a ground-dwelling sagebrush obligate that currently inhabits $\cong$56% of its former range (668 412 km^2 of 1 200 483 km^2 (Schroeder et al. 2004), with some population estimates indicating a 93% contraction from presettlement times (Braun 2006). Based on such population estimates, the US Fish and Wildlife Service classified the sage-grouse as a Candidate for Listing under the Endangered Species Act in 2010 (US Fish and Wildlife Service 2010).

Although native mammalian herbivores continue to inhabit the sagebrush biome, domestic cattle grazing is a recent phenomenon in this region, having been introduced during the mid-19th century (Young and Sparks 2002). In an evaluation of the association between land use, environmental and ecological factors, and sage-grouse population trends, Connelly and Braun (1997) identified weather patterns, fire, and livestock grazing as the three factors most likely accounting for the observed range-wide population decline. Although cattle function as keystone species in the sagebrush biome (Knick et al. 2011), and cattle grazing is the most pervasive land use in sage-grouse habitats (Knick et al. 2003), it is the least systematically studied (Knick et al. 2011; Wisdom et al. 2011). We focused our study on the effects of cattle grazing because of the potential negative effects on sage-grouse habitats and because cattle grazing practices can be influenced by management decisions.

Cattle feed on perennial grasses, especially focusing on riparian areas (Platts and Nelson 1985), whereas sage-grouse primarily select forbs and sagebrush (Crawford et al. 2004), yielding a limited potential for competition for specific

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nutritional resources between cattle and grouse (Gregg et al. 2008). Rather, it is the elimination, by cattle grazing, of proper upland vegetation structure for sage-grouse nesting and brood-rearing activities that may hamper sage-grouse productivity (Gregg et al. 1994; Kolada et al. 2009; Kirol et al. 2012). The effects of cattle on vegetation composition and structure depends on the timing and intensity of the grazing, but heavy grazing can decrease herbaceous understory and increase woody shrub coverage (Beck and Mitchell 2000). Reductions in perennial grass coverage and increases in shrub coverage can enhance nest predation (Gregg et al. 1994; Delong et al. 1995; Sveum et al. 1998; Watters et al. 2002; Coates and Delehanty 2010). Improperly managed domestic livestock grazing has also been associated with the invasion of exotic grasses and a reduction in native grasses and forbs important to sage-grouse (Beck and Mitchell 2000; Miller and Eddleman 2000). The substantial and complex impact of cattle-grazing on shrub-steppe makes it important, yet difficult, to decipher cattle grazing's impact on sage-grouse populations. It is puzzling that although cattle stocking rates have declined and rangeland condition has generally improved since the mid-1900s (Laycock et al. 1996), sage-grouse populations have not followed suit, reinforcing the interpretation that much remains unknown with regards to the relationship between cattle grazing, habitat condition, and sage-grouse viability.

Studies of sage-grouse nutritional condition have provided some insights concerning how habitat attributes and hen physiologic condition relate to demographic parameters (Barnett and Crawford 1994; Crawford et al. 2004; Dunbar et al. 2005; Gregg et al. 2006). However, nutritional condition is not the only means of assessing sage-grouse's physiological responses to habitat conditions, such as the presence of cattle grazing. Therefore, this study builds on a larger goal to develop a suite of physiological measurement capabilities associated with sage-grouse reproduction and survival to enable the early detection of local populations of concern. Herein, we present an assessment of fecal metabolites of the glucocorticoid hormone corticosterone (CORT) in sage-grouse as they relate to the presence of cattle grazing and breeding status.

Measurements of physiological parameters such as corticosterone can reveal an animal's physiological reaction to habitat conditions on a shorter time scale than measurements of reproduction and survivorship (Ricklefs and Wikelski 2002; Wikelski and Cooke 2006), and thus provide a means to identify at-risk populations. Corticosterone is often used an index of an animal's physiological condition (Walker et al. 2005), because CORT provides an animal with a means to adjust its metabolic status based on both intrinsic and extrinsic stimuli (Carsia and Harvey 2000). Stimuli leading to CORT elevations lasting minutes to hours are referred to as *acute stressors*, whereas stimuli increasing CORT for days to weeks are termed *chronic stressors* (Wingfield et al. 1998). Acute elevations of CORT provide an animal with utilizable energy, cognitive acuity (Sapolsky et al. 2000), enhanced mucosal immunity (Dhabhar 2009), and can influence whether an animal delays reproduction for survival (Wilson and Holberton 2004). Chronic elevations of basal CORT, a form of allostatic overload (McEwen and Wingfield 2003), can lead to reduced mass, suppressed immunity (Sapolsky et al. 2000), and other maladaptive outcomes, including reduced fecundity (Greenberg and Wingfield 1987). Based on the above and other relevant literature, the CORT–fitness hypothesis has emerged and states that concentrations of CORT and fitness are negatively correlated because, although elevations of this hormone enable an animal to confront immediately challenging circumstances in the environment, resources for reproduction and long-term survival are sacrificed (Bonier, Martin et al. 2009).

Numerous published reports have identified relationships between CORT levels and habitat conditions in grouse, providing evidence for one key component of the CORT–fitness hypothesis in this species. For example, male sage-grouse that did not abandon experimentally treated noisy leks (Blickley, Blackwood et al. 2012) exhibited 16.7% higher levels of fecal corticosterone metabolites compared to males in control leks (Blickley, Word et al. 2012). Levels of CORT metabolites in male northern spotted owls (*Strix occidentalis caurina*) feces were higher when collected in closer proximity to logging roads in the Pacific Northwest (Wasser et al. 1997). In a study of CORT in the Western Capercaille (*Tetrao urogallus*), it was found that CORT metabolite concentrations were highest in fecal samples collected close to locations with winter recreational activity in a spruce forest (Thiel et al. 2011).

To understand the potential impacts of cattle grazing on sage-grouse physiological condition better, we measured fecal metabolites of CORT for two life-history stages of sage-grouse with respect to the presence of cattle grazing. In addition, we measured levels of plasma protein (PP) in a subset of females to aid in the interpretation of CORT levels. We measured PP specifically because past studies have demonstrated the importance of PP for a hen's reproductive effort (Gregg et al. 2006) and the relationship between dietary protein and plasma corticosterone is often negative (Carsia et al. 1988; Weber et al. 1990). Thus, we present findings on relationships to CORT at the physiological and ecological scales. Results are discussed for their biological plausibility and implications for the integration of physiological parameters into research and adaptive management activities.

METHODS

Study-Site Selection Process and Description

The study sites (all in UTM Zone 11N) were selected because of their known sage-grouse abundance and history of cattle grazing activities. The ungrazed sites, Sheldon National Wildlife Refuge (SR, centroid 301047E 4638487N) and Hart Mountain National Antelope Refuge (HR, centroid 284029E 4718394N), have been excluded from cattle grazing since 1994 and 1991, respectively, whereas the grazed sites Eureka (EU, centroid 563794E 4437106N) and Montana Mountains (MM, centroid 410777E 4636266N), have sustained cattle grazing activities since the late 19th century. Each site is located within the Great Basin physiographic area (Mozingo 1987), but according to Küchler (1970) the EU site is part of the Great Basin sagebrush vegetation class and the other three sites are part of the sagebrush steppe vegetation class. The four sites encompassed a total of 13 600 km^2 (Fig. S1; available online at http://dx.doi.org/10.2111/REM-D-13-00137.s1).

Grouse Sampling Procedures

We used spotlighting and netting techniques (Giesen et al. 1982) to capture sage-grouse for fecal sampling during the prenesting (March–April) and late brood-rearing (August–October) periods of 2005. We based the geographic extent of our sampling on the locations of previously known populations of sage-grouse for each site. During the prelaying (females) and lekking (males) periods, roosting sage-grouse were primarily found near known lekking grounds; nonbreeding birds distribute somewhat less predictably, so sample collection in the autumn involved road and foot searching for birds. To reduce the risk of measuring capture stress, we measured fecal metabolites of CORT, as these reflect an integrated and delayed measure of plasma concentrations (Goymann 2005), but see Legagneux et al. (2011). Within 10 min of capture, birds produced a fresh fecal sample (precise time between capture and sample collection is not available); this sample was collected, immediately preserved (up to 8 h on ice and frozen at ≤ -80°C until analysis), and analyzed by radioimmunoassay for immunoreactive corticosterone metabolites (ICM; Jankowski et al. 2009). Such preservation timing has been shown not to impact measured ICM levels (Jankowski et al. 2009). Briefly, frozen fecal samples were lyophilized, uric acid caps and undigested materials were removed, fecal samples were weighed to the nearest 0.0001 g, lipid-soluble metabolites were extracted into 80% methanol, and ICM were detected by their reactivity with a rabbit IgG anti-corticosterone-3-carboxymethyloxime antibody, per manufacturer's protocol (catalog no. 07–120103, MP Biomedicals, Costa Mesa, CA). Inter- and intra-assay coefficients of variation were 14.2% and 7.8%, respectively; therefore, samples were randomly distributed before chemical analysis. We distributed sampling events so that each site was sampled at least once during the early (March or mid August–September) and late (April or October) halves of both seasons to control for date of collection. We accounted for the effect of circadian rhythm (Carsia and Harvey 2000) by evenly distributing collection times across all four sites and by including time of sample collection in initial statistical models.

Plasma Protein Analysis

We sampled 61 of the 74 prenesting females at SR and MM for both ICM and total PP levels during the prebreeding season. After fecal sample collection, blood was collected from the brachial vein with a 22-gauge needle and placed into Microtainer7 ethylendiamintetraacetic acid (EDTA) tubes (Beckton Dickinson and Company, Franklin Lakes, NJ). Blood was held on ice ($\cong$4°C) overnight until it was centrifuged (1 500 $\times$ g); plasma was collected then frozen until analysis by a refractometer as in Gregg et al. (2006).

Estimation of Cattle Presence

We evaluated the capacity for permitted animal unit month (AUM, the amount of forage required to feed one 454-kg cow and her calf for 1 mo), actual cattle use data by allotment or pasture, and cattle fecal pat counts to quantify relative cattle presence on grazed sites. We used only fecal pat counts for statistical analyses because these provided information on actual previous cattle presence, whereas AUM data are more spatially coarse and do not represent actual cattle use. Additionally, the more spatially resolved pasture-scale data were not fully available for our sites.

We obtained permitted AUM and actual cattle use (timing and cattle number) data by both allotment and pasture from the US Department of Interior, Bureau of Land Management (BLM). Records were obtained for 2003–2005, so that all cattle data were roughly comparable to each other, as intact fecal pats remain on the landscape for up to 3 yr in the semiarid western USA (Mueggler 1965). The numbers of cattle permitted, actual numbers of cattle grazed, and the season of grazing were collated into a Gantt chart (Fig. S2; available online at http://dx.doi.org/10.2111/REM-D-13-00137.s2). Cattle-months were estimated for a pasture or allotment, depending on data availability, by multiplying the number of months grazed by the actual number of cattle grazed in a given unit.

We determined fecal pat counts by strip transects in the autumn of 2005 and spring of 2006. We used 1 $\times$ 100-m strip transects to quantify relative cattle presence across our study sites. With the use of ArcGIS 9 (Esri, Redlands, CA), we created a 2-km buffer around the most exterior sage-grouse captures for each study site, calculated total area (km^2), and created transects such that 10% of the study area would be directly measured for fecal pats. To select the location of each strip within a study site, we generated random points along road networks. Roads were identified with the use of US Geological Survey (USGS) topographic maps as well as through satellite imagery. Thus, all roads (gravel or dirt) traversing the sites were used. From these points, we produced a right triangle with individual legs of 750, 1 000, and 1 250 m long, and extracted the coordinates (xy) for all vertices. There was no apparent relationship between distance from a road and fecal pat counts. We randomly determined the spatial orientation of each triangle and excluded the potential for triangle overlap. As we traversed a triangle leg, we totaled intact fecal pats (diameter greater than $\cong$3 in.) that fell in the 1-m strip and recorded these data every 100 m. Next, we used ArcGIS 9.3 (Esri) to designate the 100-m^2 strips and assign the centroid of each strip as the location for the fecal pat count for use in spatial kriging models.

We used the spatial kriging function spatial.exp in WinBUGS (Lunn et al. 2000; Thomas et al. 2004) to estimate pat counts at uncounted (grouse capture) locations. We formulated estimates of fecal pat counts as Poisson random variables $C_j \sim \text{Pois}(\lambda_j)$, where C was the observed count, and C was unknown for grouse capture locations. We log-transformed λ_j to assist with convergence in WinBUGS and modeled our response variable as $\log(\lambda_j) = \alpha + W_j + \beta X_i$; where W_j is the spatial term or between area correlation, X_j is a row vector of covariate values for each fecal pat count j, and β is the column vector of regression effects (the estimated effects of each covariate on the predicted fecal pat count). W_j is defined by the spatial.exp function as $\exp[-(\Phi d_{i,j})\kappa]$, where $d_{i,j}$ = distance between areas i and j (the locations where the fecal pats were sampled), Φ controls the rate of decline of correlation with distance, and κ controls the smoothing function. Separate models were run for each of the two grazed sites because of the large distance between the sites (which would make the model run much more slowly), the possibility that different factors at each site would contribute to cattle grazing activity, and the fact that the

parameters of the kriging function (Φ and κ) were different for each site. We assigned noninformative priors for α and β as $\sim$N(0,0.001). For all analyses, convergence of the Markov chains was assessed visually and by the Brooks-Gelman-Rubin statistic (Gelman and Rubin 1992). We summarized the posterior distribution by the Bayesian 95% credible interval (BCI, the 2.5th and 97.5th percentile) and the median. Best models of cattle pat counts among a suite of candidate models were selected for each site with the use of the deviance information criterion (DIC; Spiegelhalter et al. 2002). Models within 2 DIC values are generally considered competitive with each other.

The covariates that we included in spatial models of fecal pat counts were chosen because they influence vegetation patterns and therefore may have influenced cattle grazing patterns (Connelly et al. 2004). The chosen variables were normalized difference vegetation index (NDVI), aspect, slope, elevation, AUMs, soil characteristics (rock depth, water capacity, pH, and salinity). ArcGIS 9.3 was used to calculate aspect and slope and to determine the value of each covariate for each strip transect's centroid.

NDVI data were collected for two date ranges including from 9 May 2006 to 24 May 2006 and from 30 September 2005 to 15 October 2005 (i.e., the periods during which fecal pats were counted) as moderate resolution imaging spectroradiometer data (250-m grid size) then processed and distributed by the Global Land Cover Facility (University of Maryland, College Park, MD). Aspect, slope, elevation (30-m grid size) were attained via The National Map (USGS 2013). AUM data were gathered as described above. Soil characteristics data were from the State Soil Geographic Database (140-m grid size) from the Natural Resources Conservation Service, US Department of Agriculture, and processed and distributed by the Sagebrush and Grassland Ecosystem Map Assessment Project of the USGS Forest and Rangeland Ecosystem Science Center. Precipitation data (e.g., Parameter–Elevation Relationships on Independent Slopes Model; Oregon State University 2013) were not used for this study because 1) they were too coarse (800-m grid size), and 2) the data types above are strongly related to precipitation (Connelly et al. 2004). For EU, rock depth, pH, and salinity were confounded with each other and therefore categorized as soil_type with a value of 0 or 1. Soil_type 1 included soils with pH $\geq$ 6.9, salinity $\geq$ 0.5, and rock depth $\geq$ 40 cm; all other soils were designated as soil_type 0. For MM, we found no variation across the study site in these soil characteristics (pH=7.4, water capacity=6.65, salinity=4.24, and rock depth=60 cm) and so they were not included in the analysis for this site. AUMs were categorized as two discrete variables (high=25 000; low=9 000) rather than included in models as continuous covariates because the sites were located within only two to four different AUM levels, and the sample sizes for four levels were small.

Statistical Analysis of ICM

Grouse ICM levels were analyzed in two ways. First, linear mixed models were executed in Systat (version 13.1, Chicago, IL) to determine whether the fixed effects of grazing treatment (n = 2), bird sex and age, season of capture, and the season by sex interaction were associated with ICM levels. For this analysis, bird mass and time of sample collection were included as covariates. We treated site of capture as a random effect with birds nested in site. Individual birds were not treated as random effects because birds were only sampled once. No spatial autocorrelation of individual sage-grouse ICM levels was found (Moran's I, results not shown). Because PP was collected in only a subset of captured grouse (n=61 of 329) at two of four sites, separate linear models were produced to test the correlation between PP and ICM levels in prenesting female sage-grouse captured at SR and MM using the 'stats' package in R (R Core Team 2012). Second, to evaluate the cumulative effect of past cattle presence further ($\cong$ 3 yr) on contemporary grouse ICM levels, ICM levels were modeled as a function of the derived fecal pat counts (0 for ungrazed sites), grouse mass (g), grouse age and sex, time of sample collection, season of capture (breeding or nonbreeding), and the season by sex interaction. ICM levels were modeled as a normally distributed variable ICM $\sim$ N(μ_{ij},τ) with mean μ, precision τ, and standard deviation σ. In this formulation, $\mu_{i,j}=\alpha+\beta X_{ij}$; $\tau=1/\sigma^2$, where the prior on σ=U(0,1); X_{ij} is a row vector of covariate values for each individual animal j at location i; and β is the column vector of regression effects. ICM levels were standardized prior to this analysis. We conducted our analysis in R (2012) with the use of the 'R2WinBUGS' package (Sturtz et al. 2005). All models were checked for convergence with the use of the Gelman-Rubin diagnostics function (gelman.diag) in the R package 'coda' (Plummer et al. 2006). Best models were selected with the use of the deviance information criterion (DIC; Spiegelhalter et al. 2002).

Grouse Lek Counts

Data from lek surveys conducted from 1990–2012 by the States of Nevada and Oregon were assembled to provide a general idea of lek counts at each of the four sites. Lek count methods, timing, survey effort, and number of leks counted varied over year and site and thus cannot be quantitatively compared. The use of lek-count data to estimate population levels requires rigorous standardization (Walsh et al. 2004), but can still provide a qualitative view (up or down) of population trends (Fig. S3; available online at http://dx.doi.org/10.2111/REM-D-13-00137.s3).

RESULTS

Cattle Presence

We sampled a total of 606 and 614 strip transects at EU and MM, respectively. Fecal pat counts 100 m^{-2} were 0–93 (mean 7.0 $\pm$ 0.4 SEM) in EU and 0–112 (mean 13.0 $\pm$ 0.6 SEM) at MM. Models including only the spatial covariate were the best models of fecal pat count for both sites (Table 1). Records from the BLM indicated that cattle use was in general more intensive at MM than EU, but full data sets were not available for the EU site. The average number of cattle-months was higher at MM ($\cong$ 1 440) than at EU ($\cong$ 600). This trend followed the overall pattern found with the use of fecal pat counts reported above. Turnout dates for MM ($\cong$ June) were later than at EU ($\cong$ May) but dates varied (see Fig. S2, available online at http://dx.doi.org/10.2111/REM-D-13-00137.s2).

Table 1. Model selection results for cattle fecal pat kriging models at Eureka and Montana Mountains study sites. DIC = deviance information criterion and ΔDIC is the difference between the DIC for a model and the minimum DIC for a suite of models. Results presented are top five models.

	Eureka		Montana Mountains	
Model	DIC	ΔDIC	DIC	ΔDIC
Null model	2 756	0	3 514	0
Slope	2 787	31	3 568	54
Elevation	—	—	3 566	52
Aspect	2 807	51	—	—
May 2006 NDVI[1]	2 809	53	3 562	48
October 2005 NDVI	2 825	69	3 558	44

[1]NDVI indicates normalized difference vegetation index.

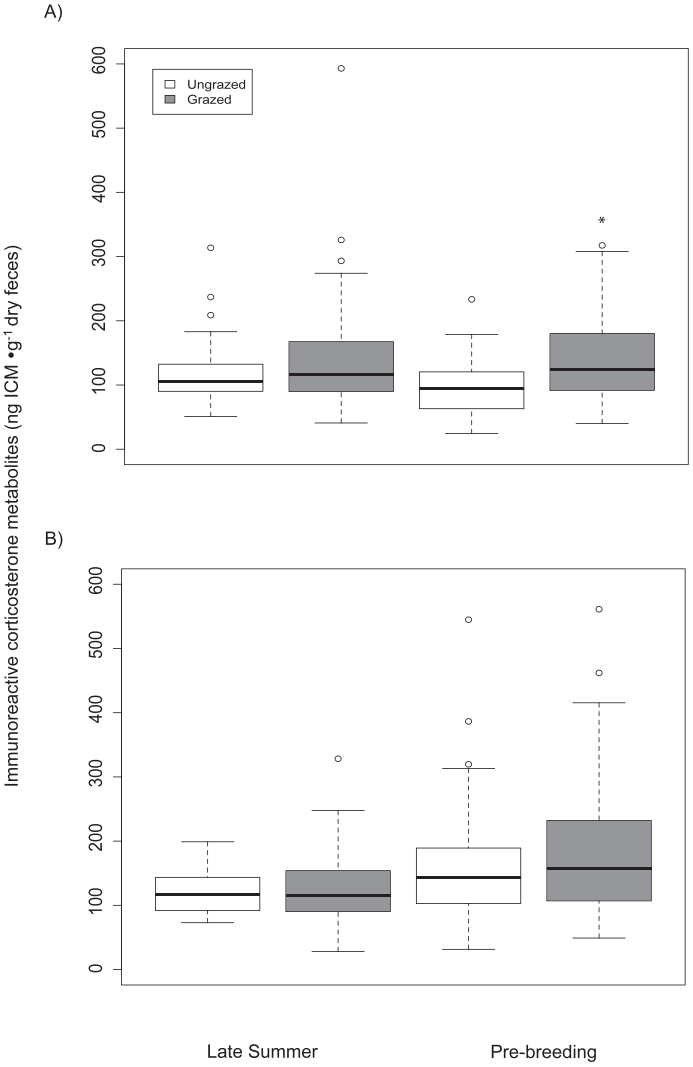

Figure 1. Box plots showing concentrations of immunoreactive corticosterone metabolite (ICM) concentrations ($ng \cdot g^{-1}$) in fecal samples collected from (**A**) female and (**B**) male greater sage-grouse. "Pre-breeding" on the *x*-axis indicates that grouse sampling occurred in March and April, and "late summer" indicates results from August–October sampling. Means represented by plots tipped with asterisks were significantly different from directly adjacent plots ($P < 0.05$).

Table 2. Model selection results for models of immunoreactive corticosterone metabolite concentrations ($ng \cdot g^{-1}$) in the feces of all sampled greater sage-grouse. Results presented are top five models.

Model	DIC	ΔDIC
Cow pats	7 020	0
Null model	7 118	98
Season (breeding, nonbreeding)	7 121	101
Season and cow pats	7 500	480
Cow pats and sex of grouse	9 307	2 287
Cow pats, season, sex	9 348	2 328

ICM Levels

We sampled a total of 329 sage-grouse, 160 from grazed sites and 169 from ungrazed sites. Fifty-three grouse were sampled at EU, 105 at MM, 64 at HR, and 107 at SR. The relationship between ICM levels and bird sex ($F = 9.72$, $P = 0.002$, df = 322), season by sex interaction ($F = 11.850$, $P = 0.001$, df = 322), and grazing treatment ($F = 4.006$, $P = 0.046$, df = 322) were statistically significant (Fig. 1). Males captured during the lekking season exhibited the highest ICM levels, but the effect of sex on ICM levels was not present in birds captured during the late summer (i.e., late summer to early autumn). ICM levels of males captured during the lekking season were 168.6 ± 8.5 SEM and 123.9 ± 6.5 SEM $ng \cdot g$ dry $feces^{-1}$ in the late summer period. Prenesting females captured in grazed sites had higher ICM levels than those captured in ungrazed sites (138.1 ± 11.5 SEM versus 98.8 ± 7.6 SEM $ng \cdot g$ dry $feces^{-1}$, respectively; Fig. 1). Without respect to grazing treatment, ICM levels for prenesting females were 119.5 ± 7.4 SEM and 138.3 ± 10.8 SEM $ng \cdot g$ dry $feces^{-1}$ for females captured in the late summer. There was no detected effect of site on ICM levels ($F = 2.149$, $P = 0.094$, df = 3), but birds captured in the MMs tended to have the highest ICM levels. Mean ICM levels (95% CI) at ungrazed sites were SR 139.8 (125.1–154.6) and HR 119.0 (107.5–130.5) $ng \cdot g$ dry $feces^{-1}$, and at grazed sites ICM levels were MM 156.9 (138.3–175.5), and EU 147.5 (119.5–175.6) $ng \cdot g$ dry $feces^{-1}$.

We further analyzed the data for a relationship between ICM levels and cattle presence and found that the best models of ICM levels included only the predicted fecal pat counts at sage-grouse capture locations (Table 2). Parameter estimates indicated an increase of sage-grouse ICM levels corresponding to an increase in fecal pat counts (Table 3). For every additional fecal pat in a 100-m^2 strip transect, predicted sage-grouse ICM levels increased an average of 2.60 $ng \cdot g^{-1}$ (95% credible interval [1.30, 4.20]; Fig. 2). Male sage-grouse captured in all sites during the breeding season tended to exhibit higher ICM concentrations than all other birds (Table 4).

Plasma Protein Levels

PP values were measured in 61 out of the 74 prelaying hens for which ICM values were obtained at SR and MM. Given this incomplete data set, impacts of residence in a cattle grazed habitat on PP levels could not be appropriately tested; thus, models were specifically constructed to assess the correlation between PP and ICM. In this subset of birds, we observed a negative correlation ($F = 17.77$, $R^2 = 0.231$, $\beta_1 = -15.70$,

Table 3. Parameter estimates for the best model of immunoreactive corticosterone metabolite (ICM) concentrations ($ng \cdot g^{-1}$) in greater sage-grouse fecal samples collected at Eureka and Montana Mountains. Separate kriging models (one for each site) were run to estimate cattle pat counts at grouse capture locations, for use as a covariate in ICM models. ICM values were standardized prior to analysis.

Parameter	Mean	2.50%	Median	97.50%	Interpretation
α_1	0.945	0.758	0.939	1.135	Intercept for cattle pat model at Eureka
α_2	1.962	1.857	1.961	2.060	Intercept for cattle pat model at Montanas
α_3	−0.192	−0.296	−0.191	−0.086	Intercept for ICM model
β_4	0.025	0.011	0.022	0.038	Estimate for effect of cattle pats

$P < 0.0001$, df$=59$) between PP and ICM levels taken at the same sampling event. Site of capture did not affect mean PP levels (one-way analysis of variance, $P=0.4073$), but PP levels in hens captured in the MM exhibited a higher maximum PP value (95% CI, 6.43–8.58 $g \cdot dl^{-1}$) than hens in SR (95% CI, 6.48–7.43 $g \cdot dl^{-1}$).

DISCUSSION

The presence of cattle grazing, bird sex, breeding stage, and plasma protein levels were associated with ICM levels in sage-grouse. Cattle fecal pat counts and ICM levels were positively correlated. Males captured during the lekking season exhibited the highest ICM levels irrespective of the site of capture, and prenesting females captured in grazed sites had higher ICM levels than those captured in ungrazed sites. Plasma protein concentrations were negatively correlated with ICM in prenesting females. Below we provide a contextual evaluation of these findings.

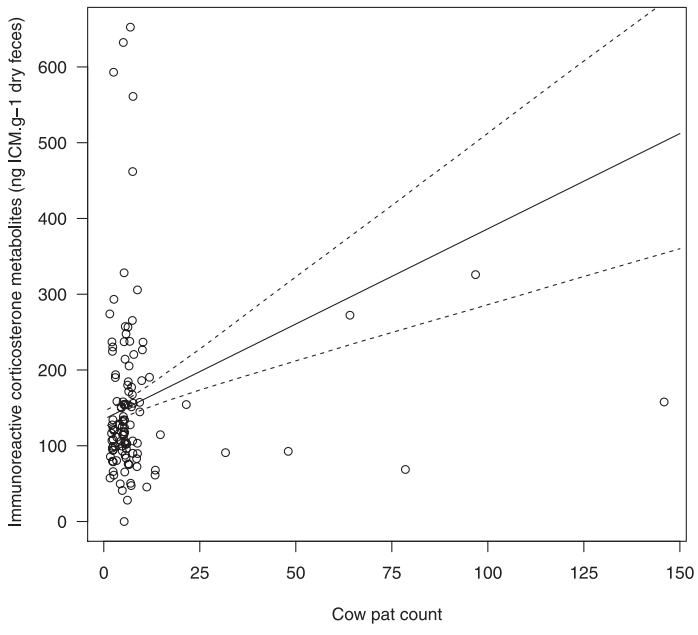

Figure 2. Observed and predicted immunoreactive corticosterone metabolite (ICM) concentrations ($ng \cdot g^{-1}$) as a function of cattle fecal pat counts (100 m^{-2}) for Eureka and Montana Mountains.

Table 4. Ranges of greater sage-grouse immunoreactive corticosterone metabolite concentrations ($ng \cdot g^{-1}$) in fecal samples by breeding status based on data from nongrazed sites. Mean, 95% confidence interval, and percentiles are shown.

Season	Sex	Mean	Lower 95%	Upper 95%	0%	25%	50%	75%	100%
Late summer	Both	119.3	108.1	130.4	51.1	91.3	108.8	142.2	313.7
Prenesting	Female	98.8	83.4	114.2	24.5	60.7	94.6	122.7	233.5
Lekking	Male	160.1	140.6	179.6	31.5	102.8	144.1	189.5	544.8

Information Provided by Cattle Fecal Pat Counts

Cattle produce fecal pats at a rate of 11–12 per day per animal (Johnstone-Wallace and Kennedy 1944; Julander 1955). Cow pats are an index of cattle presence, distribution, defecation patterns, and the relative use of an area (Cook 1966) within their home range (Bailey et al. 1996) over a period of up to three years (Mueggler 1965). The presence of fecal pats does not indicate the consumption of local palatable plants (Johnstone-Wallace and Kennedy 1944; Julander 1955). Rather, fecal pat distribution has been associated with % slope, % of high palatability forage, and the % of grasses on slopes adjacent to water (Cook 1966); pats have also been found to be associated with salting, watering, and bedding grounds (Julander 1955). Cattle prefer meadows (Gillen et al. 1984) and slopes of less than 10% (Mueggler 1965; Cook 1966; Gillen et al. 1984) in areas near water sources and to a lesser degree salt deposits (Cook 1966). This information suggests that cattle select and defecate in areas with the potential for high forage production. It is therefore not surprising that previous research of cattle foraging patterns has found that cattle preferred riparian vegetation over upland vegetation at a ratio of up to 2:1 in semiarid sites (Platts and Nelson 1985), and that this preference increases as upland vegetation desiccates during the summer months (Kinch 1989). Our fecal pat counts seemed to reflect this pattern, as pats were most concentrated in riparian areas.

In our analysis of the distribution of fecal pat counts at EU and MM, the spatial covariate was the only term included in the best model of fecal pat counts at sage-grouse capture locations. This finding potentially reflects the social nature of cattle (Bailey et al. 1996), the similarity of directly adjacent environments, or that the spatial scale of fecal pat counts (100 m^2) was lower than the resolution of the environmental covariate data (30–250 m^2). Alternatively, this result may reflect the nature of the spatial models themselves. Research has found that fixed effects such as slope can "drop" out of models with the inclusion of a spatial effect; the interpretation of this result is ambiguous (Hodges and Reich 2010). We conclude that areas with higher fecal pat counts reflected a higher number of cattle, a similar number of cattle with a more concentrated pattern of defecation, or the interaction thereof, likely in accordance with the distribution of cattle-preferred vegetation as discussed above.

Significance of Measuring Immunoreactive Corticosterone Metabolites in Feces

The current work represents an initial effort to determine if habitat conditions influenced by cattle grazing affected CORT levels (i.e., a component of the CORT–fitness hypothesis; Bonier, Martin et al. 2009) in sage-grouse. However, it is important to understand how the timing and method of CORT measurement can influence detected concentrations.

Although measurements of metabolites of CORT in feces can provide an integrated noninvasive assessment of CORT status in animals (Möstl et al. 2005), CORT concentrations in feces are affected by a number of factors. These include diet, sex, metabolic rate, bacterial degradation of fecal metabolites (Goymann 2012), and capture stress (Legagneux et al. 2011).

Diet can influence detected ICM concentrations through differences in fecal mass and gut transit time. ICM concentrations are normalized by fecal mass; therefore, faster transit times and larger fecal mass production would both effectively dilute hormone concentrations. Sage-grouse diets are known to vary between and within season based on available vegetation and life-history stage with a large bias in both sexes toward nutritionally rich forbs over sagebrush when available (Braun et al. 1977; Barnett and Crawford 1994; Connelly et al. 2004; Gregg et al. 2008). If some grouse in the current study were consuming more sagebrush than others, this difference may have diluted effective ICM concentrations between birds, but further study is needed to determine if fecal mass is affected by diet variations in sage-grouse. As site was not a significant effect in models of ICM, any diet variation affecting ICM levels must have been within site rather than between sites. We did identify a season by sex interaction effect on ICM levels, suggesting that either ICM levels differed because of seasonal differences in hormone concentrations based on unique life history strategies between the sexes, on diet differences between the sexes that vary by season, or both of these issues. We suggest that the reported ICM levels were impacted by intrinsic hormonal variation rather than by differences in diet and fecal mass, as both males and females prefer forbs to sagebrush, when available. We further note that although PP (an index of dietary protein) and ICM were negatively correlated (R^2=–0.231), the relationship was not strong, indicating that factors other than protein (e.g., from forbs) consumption were stronger drivers of ICM levels.

In addition to diet, metabolic rate can also affect fecal mass excretion, so it is advised to account for issues that influence metabolic rate such as ambient temperature (Goymann et al. 2006); we performed this assessment and found no effect of ambient temperature on ICM levels (data not shown). Sex of the individual may affect the chemical structure of the metabolites that are excreted (Goymann 2012), but previous work has found no difference in ICM responses between the sexes in a capture and ACTH experiment with sage-grouse (Jankowski et al. 2009).

The impact of capture stress on sage-grouse ICM levels was evaluated previously and found that ICM peak $\cong$2 h postcapture, but rise rapidly upon capture (Jankowski et al. 2009); a similar rapid response to capture was found in snow geese (*Chen caerulescens*; Legagneux et al. 2011). However, we conclude that capture-stress bias was avoided because most samples were collected within 10 min of capture and the time between capture and collection was effectively randomly distributed across the 329 sampled birds. Further, as birds were sampled only while roosting after daily breeding and feeding activities were completed, ICM levels likely integrated CORT metabolite levels indicative of a sustained excretion rate rather than reflecting an immediate response to a stressor. However, the time period for CORT metabolite integration is not known in sage-grouse and should be examined. We conclude that our reported ICM levels primarily reflect an integrated index of circulating hormone concentrations rather than capture stress or artifacts of hormone normalization to fecal sample mass.

The Correlation Between Sage-Grouse ICM Levels and the Presence of Cattle Grazing

In both ecological and epidemiological research, the identification of a correlation often stimulates skepticism whilst spurring further research into causation. Such projects often involve statistically but not experimentally controlled variables, but may not account for some variables altogether. Thus, standard practice states that hypothesized and identified correlations should first be evaluated for biological plausibility before the development of experiments to understand causation and mechanism. Above, we have evaluated our explanatory (grazing and fecal pat count) and response variables (ICM concentration) to aid in the interpretation of the currently identified correlation between these measured factors.

Of all explanatory variables tested in the models including fecal pat count, estimated cattle pat count was the only term included in the best model of sage-grouse ICM. Specifically, mean estimated ICM values with a fecal pat count of zero were 115 $ng \cdot g^{-1}$. Estimated fecal pat counts 100 m^{-2} at sage-grouse capture locations at EU ranged from 3.2 to 49.7, and 6.6 to 155.6 at MM. The estimated maximum rise in ICM associated with fecal pat counts was thus 129 $ng \cdot g^{-1}$ above the mean value at EU and 403 $ng \cdot g^{-1}$ above the mean values at MM. Previous studies of ICM in the sage-grouse suggest that the high end of these ranges, if sustained, may be of concern because the acute stress of capture resulted in an increase of $\approx$400 $ng \cdot g^{-1}$ (Jankowski et al. 2009). In another study, male sage-grouse in noise-treated leks had fecal ICM concentrations of 119 versus 103.2 $ng \cdot g^{-1}$ in controls (Blickley, Word et al. 2012).

Higher ICM levels in cattle-grazed sites and the positive correlation with cattle fecal pat count may have been a result of a physiological response to the direct visual presence of cattle on the landscape (although turn-out dates occurred after prenesting birds were sampled), infrastructure associated with cattle grazing, the use of degraded habitats (e.g., reductions in perennial grasses or trampled riparian areas), or how sage-grouse populations with different ICM levels may distribute across habitats of differing quality based on social status (Creel 2001). Interestingly, the MM site exhibited higher fecal pat counts and cattle-use months than the EU site, and higher (but not statistically significant) ICM estimates in the former site. Much research remains to determine if the reported correlation is persistent and if so, what specifically accounts for it. For instance, studies could be conducted to investigate whether specific habitat use and interaction with high cattle use areas is more impactful to grouse ICM than an average use of cattle-

grazed habitats. The advantage of measuring ICM and other physiological parameters is that they are detectable before changes in demographic rates can be observed. Intensive studies of fecundity and survivorship would be advised if the ICM ~ fecal pat correlation is persistent and mechanistically supported.

Biologically Plausible Sources of Causation

Although this study was focused on investigating whether sage-grouse ICM and the presence of cattle grazing were correlated, we evaluated other factors predicted to influence hormone status. We found that total plasma protein concentration, bird sex, and season were each associated with ICM levels.

Effect of Plasma Protein on ICM Concentrations. To understand whether an index of a component of nutritional condition (total plasma protein) may have partly driven ICM concentrations, we sampled a subset of prelaying females for both of these parameters. We predicted that ICM and PP would be negatively correlated because elevated glucocorticoid secretion results in the release of amino acids from skeletal muscle as a way of providing a substrate for ATP production in nutritionally deprived individuals (Smith et al. 1990; Sapolsky et al. 2000). For example, the relationship between dietary protein and plasma corticosterone levels has been found to be negative in chickens (*Gallus gallus*; Carsia et al. 1988; Weber et al. 1990), and food restriction (65% of ad lib diet) elevated basal CORT levels in western scrub jays (*Aphelocoma californica*; Pravosudov and Kitaysky 2006). Plasma protein was positively associated with body condition in American kestrels (*Falco sparverius*; Dawson and Bortolotti 1997) and reproductive effort in sage-grouse hens (Gregg et al. 2006). Although we found a biologically plausible negative relationship between PP and ICM, the relationship was not strong (R^2=–0.231), suggesting other physiological, social, habitat, or environmental factors also related to ICM. If protein deprivation was the primary factor driving differences in ICM, bird weights would have been expected to be lower in birds with high ICM levels; however, the best model of ICM did not include bird mass (Table 2). Site of capture did not significantly affect bird mass, again suggesting that ICM levels were influenced by something other than reduced body condition in grazed sites. Given this observation, it is plausible that the ICM levels were not high enough in enough birds to lead to muscle wasting and mass loss, which occurs only in the high stress range (Smith et al. 1990; Sapolsky et al. 2000). However, it should be noted that mass was recorded for ≈ 50% of the birds.

Effect of Being Male on ICM Concentrations. Capture location did not affect ICM levels in males. However, ICM levels were higher in males captured during the lekking season compared to all others. The lack of a site-dependent difference in ICM levels in males caught during the lekking season might reflect an interseasonal dependence on contemporary and wintering habitat conditions. Males can catabolize lipid stores gained during the winter to supplement reductions in exogenous energy acquisition (Hupp and Braun 1989), and a sustained elevation of corticosterone would stimulate the catabolism of fat or protein (Carsia and Harvey 2000). However, bird mass was not correlated with ICM, suggesting an alternative mechanism to the above. For instance, the psychosocial effects of breeding may have more directly affected ICM than habitat factors (Creel et al. 2013). It should also be considered that ICM and breeding success may be positively correlated in lekking male sage-grouse because CORT is a metabolic hormone, and male sage-grouse with the highest metabolic rates were thought to be the most successful males because of elevated strutting rates (Vehrencamp et al. 1989).

Effect of Being Female on ICM Concentrations. ICM levels were lowest in prelaying females, a finding that is biologically plausible given that CORT levels in preincubating females and reproductive success can be negatively related (Bonier, Moore et al. 2009). Prelaying females captured in grazed sites exhibited higher ICM levels than the same category of females in nongrazed sites, which is perhaps reflective of a higher sensitivity of prelaying females than lekking males to differences in factors in the habitat. For instance, a reduction in perennial grasses by cattle grazing may reduce available nesting sites, leading to enhanced predation pressure or competition for fewer high-quality nesting sites and elevations of ICM. As differences between the sexes and sites appear to have been driven primarily by samples collected during the prebreeding season, further research is warranted to determine whether the differences in detected ICM may impact reproductive success.

IMPLICATIONS

Several other studies have reported relationships between anthropogenic factors in the habitat and levels of plasma corticosterone or fecal metabolites of corticosterone in birds (Wasser et al. 1997; Thiel et al. 2011; Blickley, Word et al. 2012; Strasser and Heath 2013). The current study provides evidence for a positive association between ICM levels and the presence of cattle grazing. Although we detected a difference in sage-grouse ICM levels based on indices of cattle grazing presence, it is not clear how the current findings might be associated with population parameters. Although recognizing that lek counts are a suboptimal means to compare population trends between locations and years (Walsh et al. 2004), we note that lek counts reveal no obvious trends between sites. This observation suggests that if ICM levels were associated with differences in lek attendance (or demographic rates), this variation has occurred at a spatial scale smaller than site level.

Assessments of physiological status provide an opportunity to understand a more proximal response of sage-grouse to habitat conditions than do measurements of fecundity, survivorship, and population metrics. Further studies are recommended to determine the persistence and the mechanism of the identified correlation, including whether cattle grazing regime (temporal–spatial variability of stocking rates, e.g.), vegetation characteristics (e.g., grass height), and current management guidelines (Connelly et al. 2000; Hagen et al. 2007) are associated with ICM, and critically, how ICM levels in breeding hens relate to reproductive success. The scaling of suborganismal-level observations such as hormone values to organismal and population attributes remains a challenge. However, if assessments of physiological condition are performed in deference to each organism's life-history traits, management

actions to enhance sage-grouse productivity or survival might be made more swiftly compared to current approaches.

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