



Special Section on Management of Feral Equids

Sage-Grouse Population Dynamics are Adversely Affected by Overabundant Feral Horses

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ABSTRACT In recent decades, feral horse (*Equus caballus*; horse) populations increased in sagebrush (*Artimesia* spp.) ecosystems, especially within the Great Basin, to the point of exceeding maximum appropriate management levels (AML_{max}), which were set by land administrators to balance resource use by feral horses, livestock, and wildlife. Concomitantly, greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are sagebrush obligates that have experienced population declines within these same arid environments as a result of steady and continued loss of seasonal habitats. Although a strong body of research indicates that overabundant populations of horses degrade sagebrush ecosystems, empirical evidence linking horse abundance to sage-grouse population dynamics is missing. Within a Bayesian framework, we employed state-space models to estimate population rate of change (λ) using 15 years (2005–2019) of count surveys of male sage-grouse at traditional breeding grounds (i.e., leks) as a function of horse abundance relative to AML_{max} and other environmental covariates (e.g., wildfire, precipitation, % sagebrush cover). Additionally, we employed a *post hoc* impact-control design to validate existing AML_{max} values as related to sage-grouse population responses, and to help control for environmental stochasticity and broad-scale oscillations in sage-grouse abundance. On average, for every 50% increase in horse abundance over AML_{max} , our model predicted an annual decline in sage-grouse abundance by 2.6%. Horse abundance at or below AML_{max} coincided with sage-grouse λ estimates that were consistent with trends at non-horse areas elsewhere in the study region. Thus, AML_{max} , as a whole, appeared to be set adequately in preventing adverse effects to sage-grouse populations. Results indicated 76%, 97%, and >99% probability of sage-grouse population decline relative to controls when horse numbers are 2, 2.5, and ≥ 3 times over AML_{max} , respectively. As of 2019, horse herds exceeded AML_{max} in Nevada, USA, by >4 times on average across all horse management areas. If feral horse populations continue to grow at current rates unabated, model projections indicate sage-grouse populations will be reduced within horse-occupied areas by >70.0% by 2034 (15-year projection), on average compared to 21.2% estimated for control sites. A monitoring framework that improves on estimating horse abundance and identifying responses of sage-grouse and other key indicator species (plant and animal) would be beneficial to guide management decisions that promote co-occurrence of horses with sensitive wildlife and livestock within landscapes subjected to multiple uses. Published 2021. This article is a U.S. Government work and is in the public domain in the USA. The Journal of Wildlife Management published by Wiley Periodicals LLC on behalf of the Wildlife Society.

KEY WORDS appropriate management level, *Centrocercus urophasianus*, *Equus caballus*, free-roaming, Herd Management Area, Nevada, sage-grouse, state-space model, wild horse.

Preserving the integrity of sagebrush (*Artimesia* spp.) ecosystems within the paradigm of multiple-use on public lands is a

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common goal of United States resource management agencies. Management of feral horses (*Equus caballus*; horse) within the western United States has been a topic of public debate (National Research Council 2013, Beever et al. 2018, Scasta et al. 2018), wherein litigation favored by animal advocacy groups often contrasts with reported ecological damage to semi-arid environments (Davies et al. 2014, Davies and Boyd 2019). In western landscapes, free-roaming feral horses occupy a

substantial proportion of public rangeland, and are primarily managed by the Bureau of Land Management (BLM) within Herd Management Areas (HMAs) designated to balance horse populations, cattle, and other livestock grazing with use by native wildlife and Herd Areas (HAs) that encompass the range of feral horses. Currently, the area of HMAs in the United States exceeds 12,500,000 ha (BLM 2020a) with the largest areas within the state of Nevada (6,340,696 ha), which consists of the most arid environments across feral horse distributional range (BLM 2020a). Additionally, horses occur within 53 Wild Horse and Burro (WHB) Territories managed by the United States Forest Service (USFS 2014). Other smaller areas with feral horses include lands managed by the National Park Service, the United States Fish and Wildlife Service, and the Department of Defense, and state, private, and tribal lands (Beever et al. 2018, Hennig et al. 2018). These animals, however, do not have the same federal protection under the Wild Free-Roaming Horses and Burros Act (1971) as those on lands managed by BLM and USFS. Although numbers of horses within HMAs vary annually, reported estimates have increased approximately 3 times from 2005 (27,369; BLM 2020a) to 2020 (79,568; BLM 2020a) with populations in Nevada representing the highest estimates (46,974 in 2020, representing ~59.0% of all horses; BLM 2020a).

A fundamental goal of the Wild Free-Roaming Horses and Burros Act (1971:649) is to manage herds within a range of population sizes that facilitate and protect “a thriving natural ecological balance.” Thus, BLM sets appropriate management levels for each HMA (BLM 2010) based on site-specific environmental analysis under the National Environmental Policy Act (1970). Appropriate management levels (AMLs) are established with the intention of balancing multiple-use mandates, including the protection of ecological processes, with the capacity of HMAs to support livestock and healthy horse and wildlife populations (BLM 2010). Although establishing and adjusting AMLs lacks specificity and consistency across HMAs (National Research Council 2013), maximum (AML_{max}) and lower limits are typically set according to a tiered approach that evaluates 4 habitat components: forage, water, cover, and space (BLM 2010).

Notably, the most influential habitat component is often the availability of forage, which is used to establish use rates and capacity (BLM 2010). The BLM recommends that forage-availability estimates are based on 3–5 years of data on forage use, accompanied by spatial use mapping products, while accounting for animal unit months (AUMs) for free-roaming horses and various domestic livestock (BLM 2010). Use in this context refers to the proportion of forage production consumed by herbivores (i.e., horses, burros, livestock, wildlife) on the range (BLM 2010). The AUM and desired level of use are then typically used to propose lower and maximum AMLs and allocate available forage between free-roaming equids, wildlife, and livestock (BLM 2010). Therefore, population estimates that exceed AML_{max} are taken as a sign that horses may be excessively damaging natural resources because forage use will exceed desired levels. Policies enacted in conjunction with the Wild

Free-Roaming Horses and Burros Act (as amended) permit removal of horses from the landscape using various tools, such as helicopter-assisted capture, and tools to manage removed animals, such as private care placements (e.g., adoptions) and permanent holding facilities (Garrott 2018). The BLM and USFS are not permitted to use lethal removal or sell horses to those who would kill otherwise healthy animals (Garrott 2018) as prescribed by annual Department of Interior appropriations acts (BLM 2020a). Despite permitted management actions occurring at HMAs range-wide (BLM 2020a), estimates have exceeded AML_{max} every year since 2005, which is largely influenced by population growth (Collins and Kasbohm 2017) that exceeds BLM's ability to pay for an adequate number of animal removals or fertility suppression (Garrott 2018). Horse population estimates, as a whole, are currently >1.97 times above AML_{max} across their range for every state except Arizona. The HMAs in Nevada are exceeding AML_{max} by >4 times, averaged across HMAs, and thousands of free-roaming horses occur in Nevada's HAs (BLM 2020a). If exceeding allowable use for all ungulates, collectively, defines overgrazing, and free-roaming horse populations exceed AML_{max} based on allowable use, then it is important to know the ecological effects of overgrazing to plant and animal communities that rely on sagebrush ecosystems.

Feral horses can severely affect ecological structure and function of semi-arid rangelands (Davies et al. 2014, Davies and Boyd 2019, Eldridge et al. 2020), particularly sagebrush ecosystems (Beever et al. 2018, Davies and Boyd 2019). For example, areas used by horses exhibit reduced herbaceous cover and biomass (Boyd et al. 2017, Baur et al. 2018, Kaweck et al. 2018), fragmented and reduced shrub cover (Beever and Brussard 2000, Beever et al. 2008, Boyd et al. 2017), and increased soil compaction (Beever and Herrick 2006, Davies et al. 2014) relative to areas where they are absent or excluded. Furthermore, recent evidence suggests that horses may contribute to the spread of harmful invasive grasses such as cheatgrass (*Bromus tectorum*; King et al. 2019) that facilitate increased frequency and severity of wildfire (Brooks et al. 2004, Chambers et al. 2014). Managed livestock, particularly cattle, are supplemented with salt, mineral, and water placement and graze during planned periods and locations, which allows direct management of land deferral and rest (Davies and Boyd 2019). Absent management action, where options are much more limited owing to the Wild Free-Roaming Horses and Burros Act (as amended), horses are not constrained to specific locations, often grazing continuously on preferred plant species and concentrating in riparian areas where ecological degradation is intensified (Kaweck et al. 2018). Collectively, the magnitude of these adverse effects is likely exacerbated as horse populations become increasingly overabundant relative to AML_{max} (i.e., exceed AML_{max}) and as horses move freely within the landscape uninhibited by fencing and other barriers. Additionally, previous research indicates that behavioral tendencies and interactions between horses and native ungulates can lead to displacement, even from the presence of a

single horse (Berger 1985), and exclusion from water sources (Gooch et al. 2017).

Overabundant horses will inevitably affect wildlife communities through modifications to their habitat (Davies et al. 2014, Hall et al. 2016), which is especially important to resource specialists that rely on specific habitat components during important life stages. One sagebrush-obligate species at the center of state and national land-use strategies (Stiver 2011), and potentially influenced by overabundant horse populations (Beever and Aldridge 2011), is the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse). Sage-grouse require specific seasonal habitats within sagebrush ecosystems during important life-history stages, such as nesting, brood-rearing, and wintering (Patterson 1952, Schroeder et al. 1999). Accordingly, population viability for sage-grouse largely depends on a diversity of habitat conditions that occur across broad spatial extents, such that resulting population trends can serve as an indicator for the ecological integrity of sagebrush ecosystems at large scales (Rowland et al. 2006, Hanser et al. 2011). Sage-grouse are experiencing long-term population declines in semi-arid environments (Garton et al. 2015) and are facing a myriad of threats that include wildfire and invasive grass cycles (Chambers et al. 2014, Coates et al. 2016b), expansion of pines (*Pinus* spp.) and junipers (*Juniperus* spp.;

Baruch-Mordo et al. 2013, Coates et al. 2017), anthropogenic development (Green et al. 2017), and increased drought (Coates et al. 2016b). Despite distributional overlap between sage-grouse and horses range-wide (Beever and Aldridge 2011), coupled with compelling evidence that most HMAs are exceeding set AML_{max} (BLM 2020a), studies that quantify relationships between horse abundance and sage-grouse population dynamics are notably missing. Such information can help validate and potentially refine setting and management of AMLs by estimating ecological thresholds of horse abundance that, when exceeded, have an additive negative influence on sage-grouse population dynamics.

Recommendations published by the National Academy of Sciences (National Research Council 2013) recently called for research designs to validate and refine estimates of AML with a focus on response by plants or wildlife to manage horse populations effectively. We chose sage-grouse as the study species to serve as a surrogate for effects to other wildlife species that rely on sagebrush ecosystems. Additionally, management actions that benefit sage-grouse habitat can benefit other species with similar life-history requirements such as the pygmy rabbit (*Brachylagus idahoensis*; Rowland et al. 2006), though potential benefits to other species becomes reduced as the amount and similarity of habitat overlap declines (Carlisle et al. 2018).

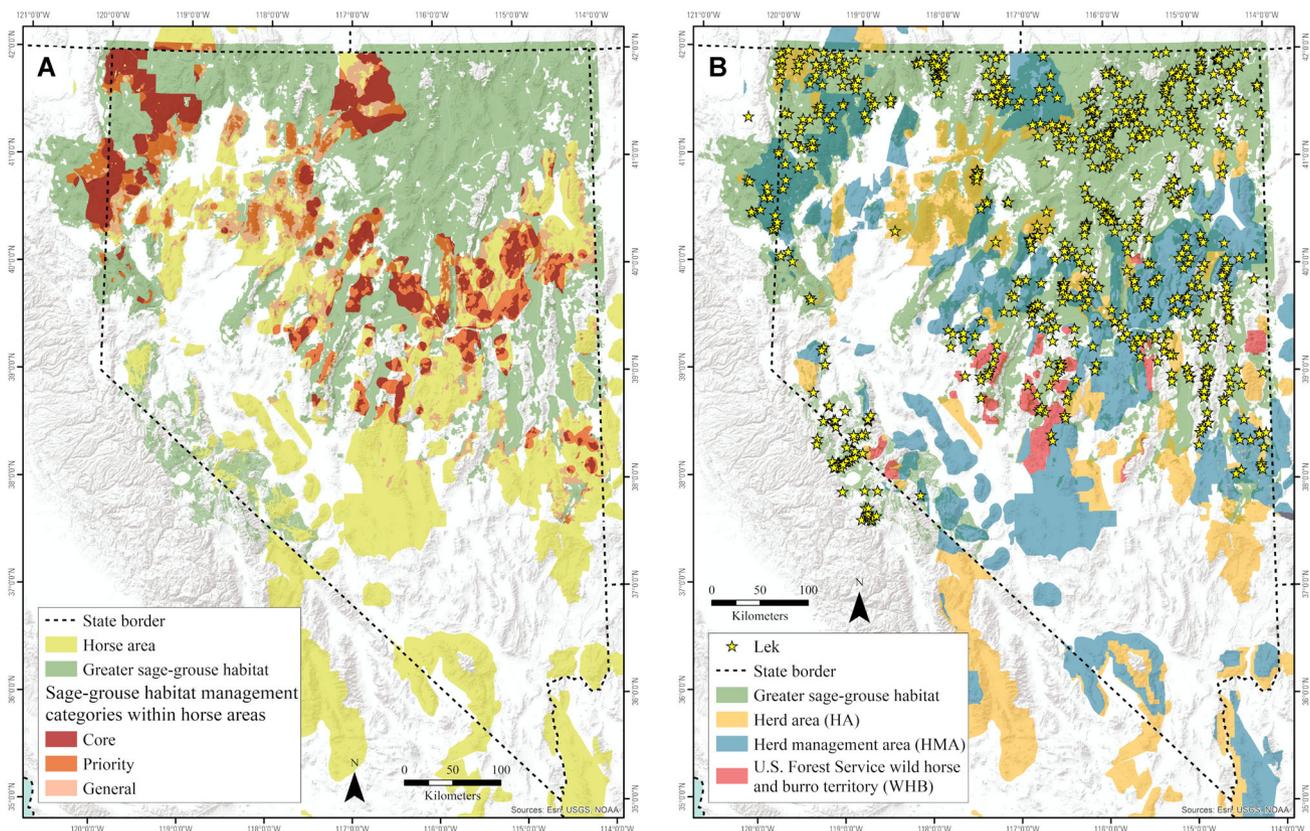


Figure 1. A) horse-occupied areas (i.e., Herd Management Areas, Herd Areas, and U.S. Forest Service Horse Territories) in relation to different habitat categories of greater sage-grouse (core, priority, and general; Coates et al. 2020a) and B) lek count locations used in Bayesian state-space models of greater sage-grouse rate of change in population abundance in relation to horse abundance and other environmental factors within sagebrush ecosystems of Nevada and California, USA, 2005–2019.

Importantly, in Nevada and northeastern California, increasing horse abundance represents a poorly quantified yet likely additional threat to sage-grouse populations because areas occupied by horses comprise $\geq 4,498,534$ ha of sage-grouse habitat (Fig. 1A), of which 1,648,807 ha is considered priority habitat (31%) from recent sage-grouse habitat mapping (Coates et al. 2016a, 2020a).

Our goal was to conduct research to assist with horse management decisions, with 3 primary objectives. First, we aimed to model sage-grouse population rate of change (λ) as a function of covariates that represented free-roaming horse abundance, specifically population size over AML_{max} ($\%AML_{max}$), while accounting for other known, potentially important environmental influences (i.e., wildfire, precipitation, $\%$ sagebrush, elevation). The second objective was to estimate changes in sage-grouse abundance over the next 15 years under 3 scenarios: horse population growth continues unabated, horse population rate of change is neutral (no growth) but current population abundance remains constant, and horse population numbers are reduced to current AML_{max} limits and maintained at those levels. Our third objective was to carry out an impact-control design by comparing estimates of sage-grouse population λ between areas occupied by horses (impact) relative to non-horse areas (controls). Impact areas included horse population sizes that were at or below AML_{max} and at different increments exceeding AML_{max} (exceeding by 1–3 times). We designed the last objective to validate the efficacy of AML_{max} as a whole, in sustaining healthy sage-grouse populations.

STUDY AREA

Our study area spans the current sage-grouse distribution across Nevada and northeastern California, which comprises approximately 12.6 million ha of the Great Basin (Fig. 1A) and includes varied sagebrush communities. The Great Basin is a cold desert characterized by 4 seasons (spring, Mar–May; summer, Jun–Aug; fall, Sep–Nov, and winter, Dec–Feb) with hot, dry summers and cold, snowy winters and is topographically diverse with elevations ranging 600–3,100 m (Snyder et al. 2019). Precipitation was generally low and varied by elevation but primarily occurred as snow during the winter and as rain during spring and early summer (Snyder et al. 2019). Snowmelt provided water for the remainder of the year. The mean elevation across 726 lek sites (Fig. 1B) was 1,910 m (range = 1,374–2,778 m). Mean maximum temperatures ranged from 31.4°C to 33.1°C (Jul) and mean minimum temperatures ranged from –7.2°C to 1.6°C (Jan; Western Regional Climate Center, <http://www.wrcc.dri.edu/>, accessed 1 Jun 2020).

At relatively low elevations (<2,100 m), vegetation was dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*; Cagney et al. 2010), black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*). Cheatgrass is an invasive annual grass that was interspersed with sagebrush in many low-elevation areas and often replaced sagebrush following major disturbances like wildfire, especially in more xeric environments (Chambers et al. 2014). Mountain big

sagebrush (*A. t. vaseyana*) dominated at higher elevations (>2,100 m). Single-leaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) are native conifers that were primarily present at mid to high elevations, but were expanding into sagebrush-dominated communities, likely because of a history of fire suppression over the last century in the Intermountain West (Miller and Rose 1999). Given the prevalence of sagebrush within the Great Basin, the faunal community was dominated by shrub-associated wildlife from various taxa including herptiles, raptors, passerines, and mammals (Rowland et al. 2006). Animals known to interact with sage-grouse or horses included common ravens (*Corvus corax*; Coates and Delehanty 2010), elk (*Cervus canadensis*; Perry et al. 2015), and pronghorn (*Antilocapra americana*; Gooch et al. 2017, Muñoz et al. 2021). Human enterprise including agriculture, energy development, mining, ranching, recreational activities, and transport infrastructure (e.g., roads, railways, water diversion) became commonplace following European settlement and have significantly altered Great Basin ecosystems (Morris and Rowe 2014).

METHODS

Data Collection

Lek count surveys.—Nevada Department of Wildlife (NDOW) and the California Department of Fish and Wildlife (CDFW) along with numerous personnel from private, non-profit, and governmental agencies (state and federal) administered and led collection of lek data. Lek counts followed standardized established protocols approved by interagency collaboration (Connelly et al. 2003, Western Association of Fish and Wildlife Agencies [WAFWA] 2015, Blomberg and Hagen 2020). Briefly, observers counted sage-grouse each spring during maximum lek attendance periods (Mar–Apr; Wann et al. 2019) from 2005–2019. At each survey, ground observers used binoculars or spotting scopes to count male sage-grouse at locations with a full view of the lek. They conducted surveys from 30 minutes before to 90 minutes after sunrise (Monroe et al. 2016). They conducted 3 counts per survey, and recorded the highest count. We used maximum male counts for leks receiving multiple surveys within the spring season to represent peak attendance, which indexed annual abundance (Blomberg et al. 2013, Monroe et al. 2016, Green et al. 2017). All lek count data underwent validation and quality control. For example, we included only lek counts that followed the data collection protocols defined by NDOW and CDFW and eliminated records that indicated unfavorable lekking conditions, including the presence of precipitation and wind speeds ≥ 16 km/hour (Christiansen 2012, Monroe et al. 2016, Edmunds et al. 2018). We also excluded leks if their time series did not include ≥ 2 consecutive counts of ≥ 2 males (i.e., lek classified as inactive), if the majority (>66%) of the time series contained missing values (i.e., leks not regularly counted), or if they occurred on private lands. We established the latter condition because our objectives were to evaluate feral horse effects on sage-grouse, and information

on horse presence or absence on private lands was unavailable.

Lek and feral horse datasets.—We used multiple publicly available datasets to categorize lek overlap with horse-occupied areas (HOAs) and to develop covariates that indexed horse density. We then related horse density covariates to changes in sage-grouse population abundance at the lek level using the lek count data described above. We overlaid lek locations with BLM's Wild Horse and Burro Herd Area and Herd Management Area layer (BLM 2020*b*) and the USFS's Wild Horse and Burro Territory layer (USFS 2020) using ArcMap 10.7 (Esri, Redlands, CA, USA). We assigned each lek as overlapping none or 1 of 3 types of HOAs: BLM HMA, BLM HA, or USFS Wild Horse and Burro Territory. We consolidated these into 3 management groups for use in our analysis: active management—lek overlaps HOA with set values for AML_{max} and horse population estimate data (e.g., HMAs); passive management—lek overlaps HOA that lacks set values of AML_{max} and may or may not have available horse population estimates (e.g., HAs and USFS Territories); and none—lek does not overlap any HOA and horses are assumed to be functionally absent because population estimates are lacking. We classified leks that overlaid an HMA and an HA as HMA because HMAs are associated with AMLs and annual horse population estimates. We classified leks that overlapped an HA and a USFS Territory as HA because territories lacked publicly available annual estimates or AML. We manually recategorized a few leks ($n=7$) as overlapping an HMA rather than an HA when the lek fell on HA islands within HMAs. Burros (*Equus asinus*) are also present and populations monitored within some HOAs, but they are less widespread than horses within the Great Basin (Beever and Aldridge 2011). Additionally, few of the leks we monitored overlapped HOAs with burros and horses ($n=17$, 2% of total) and no leks overlapped management areas with only burro populations. Therefore we did not index burro density for this study.

We used R package *tabulizer* (Leeper 2018) to extract annual AML_{max} and horse population estimates (i.e., horse abundance) within HMAs and HAs from BLM annual data summaries (BLM 2020*a*) for 2005–2019. For each lek during each year, we tabulated the AML_{max} and horse abundance for the corresponding HOA, if available. Missing data within HOAs were rare; in these cases, we imputed values from existing data and modeled trends where they existed.

Feral horse abundance indices.—We calculated indices that represented temporal changes in horse abundance relative to AML_{max} (e.g., % AML_{max}) for each lek based on available BLM data. We consider these indices because true abundances were unknown, as numbers reported were not repeatable or corrected for imperfect detection (National Research Council 2013, Schoenecker et al. 2018). We calculated abundance relative to AML_{max} by dividing the BLM horse abundance estimate by the AML_{max} value for each year and multiplying by 100 to reflect a

percentage (% AML_{max}). To evaluate possible curvilinear pseudo-threshold relationships, we also considered log-transformed % AML_{max} . To accommodate delayed effects of horse abundance on sage-grouse response, we created an index to reflect 1-year time lag for % AML_{max} . Finally, we calculated the change (Δ) in % AML_{max} by dividing the index at time $t+1$ by the index at time t . As such, there were 6 candidate horse abundance indices considered in our models: % AML_{max} , $\ln(\%AML_{max})$, lagged % AML_{max} , lagged $\ln(\%AML_{max})$, $\Delta\%AML_{max}$, and $\Delta\ln(\%AML_{max})$.

Landscape covariates.—We considered several environmental predictors to account for landscape-scale habitat conditions explaining additional spatiotemporal variation in sage-grouse population rate of change. We modeled environmental predictors that accounted for sources of background variation in sage-grouse population trends along with estimation of any disturbance effects from horses to prevent potential confounding effects. We gathered these predictors from remotely sensed publicly available data sources typically developed with geographic information systems. We specified these predictors *a priori* based on environmental characteristics commonly known to explain distribution and population dynamics of sage-grouse. Predictors (Table S1, available online in Supporting Information) included sagebrush cover, sagebrush height, elevation, pinyon-juniper cover (Gustafson et al. 2018), proximity to water sources (water bodies, springs), cumulative burned area (Coates et al. 2016*b*), and precipitation indices (Palmer drought severity index [PDSI], Palmer Z index [PZI], standardized precipitation index [SPI], and standardized precipitation-evapotranspiration index [SPEI]; Kangas and Brown 2007, Daly et al. 2015, Abatzoglou et al. 2017).

We evaluated most predictors at 5- and 10-km radial buffers around each lek (Coates et al. 2016*b*), using zonal means to capture influences on sage-grouse population dynamics that are consistent with the spatial scale of sage-grouse breeding activity and space use across multiple life stages (Doherty et al. 2010, 2016). We modeled proximity to water sources as exponential distance-decay functions, $\exp(-d/\alpha)$, where d was the distance from each lek and candidate values for α were the 25th, 50th, and 75th percentile distances from all leks. Exponential decay functions allow a feature's influence to decline rapidly at large distances and we assumed they represented more biologically plausible relationships than if we treated distances as a continuous linear predictor (Coates et al. 2016*a*). To model precipitation influences, we evaluated 12 different precipitation indices characterized at both spatial scales (24; Table S1), ranging from immediate characterization of drought (e.g., PDSI, PZI) up to 2-year characterizations of precipitation patterns relative to long-term trends (e.g., 24-month SPI and SPEI; Abatzoglou et al. 2017). We treated vegetation predictors, water sources, and elevation as constant across the study's time series, whereas we updated cumulative burned area annually, and averaged precipitation indices for March–April of each annual breeding season when leks are counted (Table S1). Prior to modeling, we standardized all

candidate predictors to a common scale with mean = 0 and standard deviation = 1.

Statistical Analyses

State-space model.—We used Bayesian hierarchical state-space models (SSMs; Royle and Dorazio 2008, Kéry and Schaub 2011) to estimate lek-specific, interannual rate of change from lek count data gathered over the 15-year time series. The SSMs are advantageous over generalized linear models in this framework because they allow observation error to be modeled (i.e., detections are imperfect), and they are inherently Markovian, which is appropriate for modeling time series data (Kéry and Schaub 2011, Aeberhard et al. 2018). Thus, SSMs separate variance in the observation process from variance in the state process, which in this case is the change in abundance from year t to year $t+1$. We extended a general SSM framework, where the number of males (N) at each lek (lek = i), and for each year (time = t) was estimated as a function of the prior year N and intrinsic rate of change (r) in N with stochastic process error ($\sigma_{r_i}^2$) expressed as:

$$\log(N_{i,t+1}) = \log(N_{i,t}) + r_{i,t} \quad (1)$$

$$r_{i,t} \sim \text{Normal}(\mu_{r_{i,t}}, \sigma_{r_i}^2). \quad (2)$$

The observation component in our model was expressed as:

$$\log(y_{i,t}) = \log(N_{i,t}) + \varepsilon_i \quad (3)$$

$$\varepsilon_i \sim \text{Normal}(0, \sigma_{obs_i}^2). \quad (4)$$

We incorporated landscape covariates into the state process by modeling the mean rate of change ($\mu_{r_{i,t}}$) in N as a function of environmental predictors $x' = x_1, x_2, \dots, x_k$ that were described above and expected to influence variation in the intrinsic rate of change:

$$\mu_{r_{i,t}} = \beta_0 + x'_{i,t}\beta. \quad (5)$$

In this case, β_0 was the population-level intercept with $x'_{i,t}\beta$ representing covariates x' multiplied by the vector of linear predictor coefficients β .

Latent indicator variable selection.—To choose a subset of informative independent predictors from groups of similar type (e.g., predictors measured at multiple scales or time lags), we implemented Bayesian variable selection using reversible jump Markov chain Monte Carlo (MCMC) methods (O'Hara and Sillanpää 2009, Tenan et al. 2014) with Bayesian latent indicator scale selection (BLISS; Stuber et al. 2017). Our *a priori* set of candidate predictors included groups of correlated predictors that were initially characterized at different spatial scales (5-km and 10-km buffers; Table S1) or different time lags (e.g., precipitation indices; Table S1), and multiple representations of horse abundance within HAs or HMAs. For instance, sagebrush cover and sagebrush height were highly correlated, and both were measured at

2 spatial scales, providing 4 representations of sagebrush vegetation. Similarly, we had 24 candidate precipitation indices involving spatial scales and multiple time lags. We also applied variable selection to the horse abundance indices representing %AML_{max}.

We applied the BLISS method to identify a single predictor from each group based on probabilistic estimates from MCMC sampling. This method extends single-scale or single-variable approaches by introducing a latent categorical variable that is estimated along with the other quantities in a model (Stuber et al. 2017). For example, a single predictor variable x could have multiple candidate representations such as 2 spatial scales or 2 time lags, in which case $x_i \in \{x_{11}, x_{12}, x_{21}, x_{22}\}$, with sub-indices representing each unique combination of scale and time lag. A categorical distribution is then specified over all candidate representations with prior weights that sum to 1, $w_{i,1}, \dots, w_{i,n_i}; \sum_{m=1}^{n_i} w_{i,m}$. A non-informative prior distribution is specified by setting equal prior weights across categories: $w_{i,m} = 1/n_i$ (Stuber et al. 2017). The posterior distribution is then estimated for each candidate representation for each predictor using MCMC, thus facilitating probabilistic selection of the most informative representations across all predictor types.

Density dependence.—We also investigated density-dependent influences on λ (Dennis et al. 2006, Hostetler and Chandler 2015) that have been described for sage-grouse population dynamics (Garton et al. 2015, Coates et al. 2016b, Edmunds et al. 2018). We specified density-dependent feedbacks with a 1-year time lag (Edmunds et al. 2018) that can yield cyclic patterns of λ displayed by sage-grouse in other areas (Fedy and Aldridge 2011, Coates et al. 2018). To prevent potential biases or overestimation of the density dependence term associated with substantial variation in lek size (counts ranging from <10 individuals to >250), we specified density for each lek as its count each year relative to an approximate maximum count after factoring in observation and process variance. The approximate maximum count is derived from the SSM structure itself rather than being calculated outside of the model and is included as a variable. Density dependence in this analysis thus took the form:

$$\frac{N_{i,t-1}}{k_i} = N_{i,t-1}/(\max(N_i) + \sigma_i), \quad (6)$$

where k_i represented maximum N per lek, and σ_i was the standard deviation of all lek counts. We then included this representation of density in the linear predictor of intrinsic rate of change in N (eq 6), along with other environmental predictors.

Priors and model implementation.—Using BLISS, we selected 1 predictor from each of the following groups during the initial modeling stage: sagebrush vegetative cover and height, pinyon-juniper cover, elevation, cumulative burned area, drought or precipitation, proximity to water body, proximity to spring, and free-roaming horse abundance %AML_{max} indices. We specified non-informative prior

weights corresponding to $w = 1/4, 1/2, 1/2, 1/24, 1/3,$ and $1/6$ for each of these groups, respectively. In addition, this model included whether a lek occurred outside of ($b = 0$) or within ($b = 1$) an HOA. Because horse estimates relative to AML_{max} were only available within HMAs, we included the horse abundance $\%AML_{max}$ index (Table S1) as a restricted interaction, such that its effect was conditioned on the subset of leks that overlapped HMAs. Under this constraint, we then selected the most informative horse abundance index from the set of candidate indices (Table S1).

In the second modeling stage, we selected the single predictor from each group that had the highest posterior probability of inclusion estimated from the model in stage 1. We carried each of these predictors forward into a new SSM with the selected predictor from each group. We used this method primarily so that each final predictor's posterior distribution was easily identified and interpretable. We obtained our final results from this second modeling stage, and based all inferences about free-roaming horse abundance influences on sage-grouse populations on this final model.

For both models, we specified Bayesian Lasso (double-exponential or Laplace) prior distributions for all predictor coefficients, $\beta_j \sim \text{Laplace}(0, \lambda)$, with an uninformative hyperparameter set for the tuning parameter, $\lambda \sim \text{Uniform}(0, 10)$. The Bayesian Lasso (Park and Casella 2008) protects against possible overfitting and predictor collinearity in a multivariate modeling framework by shrinking coefficient estimates toward zero when they are not well-supported by the data (Hooten and Hobbs 2015, Authier et al. 2017). A form of regularization (i.e., optimizing model fit by penalizing greater numbers of parameters), the Lasso results in better predictions and model stability in multiple regression models, particularly those with increasing numbers of candidate predictors (Tibshirani et al. 2012, Gerber and Northrup 2020).

We estimated model parameters in JAGS 4.2.0 (Plummer 2003) using packages `rjags` (Plummer 2018) and `jagsUI` (Kellner 2018) within R 3.6.3 (R Core Team 2019). We assigned vague prior and hyperprior distributions for the following parameters: process error $\sigma_{r_i} \sim \text{Uniform}(0, 1)$, $\tau_{r_i} = 1/\sigma_{r_i}^2$; observation error $\sigma_{obs_i} \sim \text{Uniform}(0, 2)$, $\tau_{obs_i} = 1/\sigma_{obs_i}^2$; and rate of change intercept $\sigma_{\beta_0}^2 \sim \text{Uniform}(0, 10)$, $\beta_0 \sim \text{Normal}(0, \sigma_{\beta_0}^2)$. We obtained 6,000 posterior samples from 3 independent chains (50,000 iterations) after a burn-in of 25,000 iterations, and thinned by a factor of 25. We determined convergence based on Gelman-Rubin $\hat{R} < 1.1$ for all model parameters (Brooks and Gelman 1998, Green et al. 2017), and assessed model fit using the Bayesian P -value (Kéry and Schaub 2011, Green et al. 2017). We evaluated predictor influence based on the proportion of the posterior distribution having the same sign as the mean (e.g., probability β_j greater or less than 0), and by graphically demonstrating the magnitude and uncertainty of predicted effects on the intrinsic rate of change parameter.

Future projections of sage-grouse population trends.—To help inform management decision and actions, we projected population trends over the next 15 years (i.e., 2020–2034) under 3 different simulated scenarios with the final SSM model: scenario 1 = horse abundance index continues at current rates of increase, scenario 2 = horse abundance index remains at values observed during the study (2005–2019), and scenario 3 = horse numbers are reduced to and maintained at AML_{max} for each HMA. We chose to project 15 years because this was the same number of years of which we acquired data to estimate parameters. We used the horse abundance index that garnered the most model support. For scenario 1, we fit a linear mixed model to estimate change in abundance index through time based on population and AML_{max} data from 2005 to 2019. The model took the form:

$$A = \zeta_j + \beta_j x_{j,t} + \varepsilon, \quad (7)$$

where we modeled the abundance index (A) as a linear function of random intercepts (ζ_j) for HMA j with a random slope coefficient per HMA (β_j) applied to a continuous covariate representing time ($x_{j,t}$, where t denotes years 2005–2019). Random slope coefficients were necessary because the trend in abundance varied by HMA, with a few decreasing and most increasing. We obtained an overall estimate of percent change in horse abundance by using model prediction for years 2005 and 2019 at each HMA and dividing the median difference by the median initial value. We calculated bootstrapped confidence intervals for this estimate by sampling with replacement among all HMAs 10,000 times. We derived posterior predictions of the abundance index at the HMA level for future years (2020–2034) by sampling from the posterior distribution of the linear mixed model for each HMA intercept and trend and projecting the trend over time.

To account for environmental stochasticity, for each iteration, we drew new precipitation values from a standard normal distribution (i.e., on the same scale as precipitation indices used in the model). This allowed for projections across a full range of future scenarios where climate conditions could range from low to high precipitation. We set burned area values to their last observed values, and held all other variables at their means for each lek. We then drew from posterior distributions of parameter estimates from the SSM to predict \hat{N} of sage-grouse for each year. This technique accounted for uncertainty in changes in horse abundance index and uncertainty in the estimated effect of horse abundance index on sage-grouse population \hat{N} . We obtained the starting population size for sage-grouse population projections by sampling from the 2019 lek estimates derived from the SSM, and subsequent annual changes in population size were expressed as a proportion of the population in 2005 (the max. observed sage-grouse population size). For scenario 2, we followed similar methods but instead projected the proportional changes in population size through time given no change in the abundance index. For example, model projections over the next 15 years were

based on current %AML_{max} held constant. For scenario 3, we reset horse populations that were above AML_{max} back to 100% and again projected sage-grouse population changes through time. For illustrative purposes, we developed spatial maps depicting percent decrease in population λ between 2019 and 2034 across all leks in our study area using \hat{N} from the SSM for each of the 3 scenarios.

Post hoc impact-control analysis.—In a final analysis, using predicted posterior distributions (pD) of sage-grouse population λ , we used our model to validate current AML_{max} settings and evaluate probability of sage-grouse population decline at different values of %AML_{max}. We estimated impact-control ratios based on methods modified from Conner et al. (2016). Specifically, we estimated predicted posterior distributions of population λ at HMA leks (e.g., impact leks) with %AML_{max} values of 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 times AML_{max}. These values corresponded to the majority observations of %AML_{max} at leks within our dataset, with the upper cutpoint coinciding with most recently observed %AML_{max} across Nevada. We also derived pD of λ at leks outside of HOAs (control leks). We developed distributions by averaging 5,000 iterations (MCMC samples) from the posterior probability distribution of each lek across all leks within and outside HOAs to account for uncertainty (variance) in the average λ at each percentile cutpoint. To estimate the probability of decrease in λ relative to controls at each cutpoint, we developed a distribution of ratios (impact:control), where 1.0 indicates an equivalent probability of increase or decrease relative to the control. After all iterations were completed, we then derived a predicted probability of decline under each defined threshold value by summing the number of iterations where the ratio was <1, divided by the number of iterations. These distributional ratios are advantageous as a post-processing technique to directly draw inference of effect size in terms of probability of declining λ at impact sites relative to controls (Conner et al. 2016). Additionally, full posterior predictions from MCMC sampling provide accurate estimates of variation for the ratios.

RESULTS

The lek count database (WAFWA 2015) contained 726 leks throughout Nevada (Fig. 1B). Of these leks, 213 (29%) overlapped with 59 HOAs and the remaining 513 (71%) did not overlap an HOA. Of the 213 leks that overlapped HOAs, 148 (69%) overlapped with 37 HMAs (63%), 61 (29%) with 19 HAs (32%), and 4 (2%) exclusively with 3 USFS WHB Territories (5%). We removed 65 leks from consideration because they occurred on private lands and horses could not be assumed present or absent. An additional 43 leks could not be used because of sparse information or lek inactivity during the study's time series. Our hierarchical SSMs thus incorporated 618 leks with usable count data, of which 193 (31%) overlapped with 55 HOAs and the remaining 425 (69%) did not. Of HOAs in modeled leks, 130 (67%) were designated as HMAs with set AML_{max}.

Latent Indicator Variable Selection

The BLISS approach identified the following predictor variables from each candidate group that we then used in our second stage SSM of sage-grouse population growth: percent sagebrush (5-km buffer), percent pinyon-juniper (5-km buffer), elevation (10-km buffer), cumulative burned area (10-km buffer), and standardized precipitation index (SPI; 12-month time lag, 10-km buffer). The horse abundance index that best explained sage-grouse population growth was abundance divided by AML_{max} (termed %AML_{max}). In addition, exponential decay functions representing proximity to springs ($\alpha = 1.28$ km, 25th percentile) and water bodies ($\alpha = 2.70$ km, 50th percentile), density dependence, and HOA (i.e., lek overlaps with any defined horse area) were included in the final model (Table S2).

State-Space Model

We obtained convergence on all model parameters ($\hat{R} < 1.1$), and the Bayesian P -value indicated strong goodness of fit ($P = 0.56$). Our final SSM suggested a declining population on average across all leks and years ($\hat{\lambda}$ [interquartile range] = 0.961 [0.730, 1.272]). Environmental predictors indicating strong evidence of positive influence on sage-grouse population growth (e.g., increasing λ with increasing predictor values) included elevation ($\hat{\beta} = 0.053$, $P > 0 = 1$; Fig. 2), previous 12-month precipitation at the lek (SPI; $\hat{\beta} = 0.029$, $P > 0 = 1$), and percent sagebrush ($\hat{\beta} = 0.019$, $P > 0 = 0.997$). Predictors evidencing strong negative influences (e.g., decreasing λ with increasing predictor values) included proximity to water body ($\hat{\beta} = -0.018$, $P < 0 = 0.997$) and horse %AML_{max} (effect given presence within HMA; $\hat{\beta} = -0.090$, $P < 0 = 1$). Notably, the proximity to water body effect implied reduced λ closer to water bodies because of the exponential decay transformation. Percent pinyon-juniper cover and cumulative burned area were also negatively associated with λ , with less evidence of effects ($\hat{\beta} = -0.006$, $P < 0 = 0.792$; and $\hat{\beta} = -0.002$, $P < 0 = 0.616$, respectively). We observed strong evidence for negative density-dependent feedback effects where counts were likely to decline when closer to their relative maximums, resulting in a negative influence on λ ($\hat{\beta} = -0.135$, $P < 0 = 1$). There was minimal evidence for influences of springs ($\hat{\beta} = -0.003$, $P < 0 = 0.632$), and weak evidence for an overall HOA effect after %AML_{max} was accounted for ($\hat{\beta} = -0.009$, $P < 0 = 0.762$).

Predicted λ was generally lower in HOAs ($\hat{\lambda} = 0.948$ [0.732, 1.241]), and declined further when summarized within HMAs ($\hat{\lambda} = 0.942$ [0.734, 1.225]). These declines were attributed to observed horse population sizes within HMAs being approximately 2 times AML_{max} on average during the time series ($\bar{x} = 2.30$, median = 1.92, 95% CI = 0.65–5.52), and increasing to 4.13 times AML_{max} (median = 3.61, 95% CI = 0.51–11.15) by the end of the study. Estimates from the linear mixed model of horse abundances reflected the trend across the time series for all HMAs but slightly underpredicted horse abundance for the

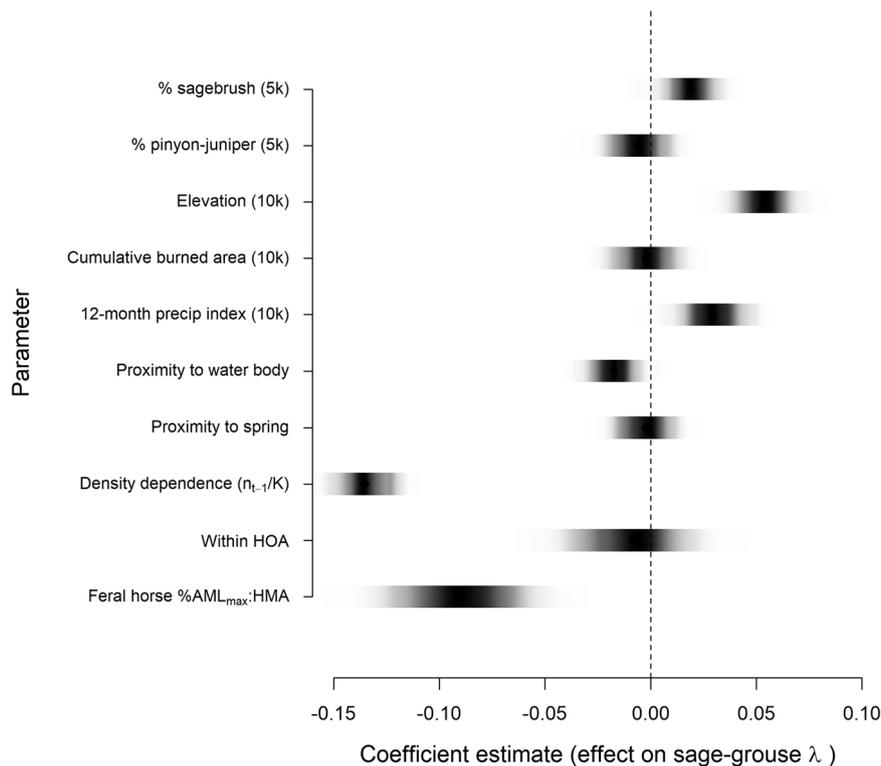


Figure 2. Estimated effects of environmental covariates with shaded 95% credible intervals used in Bayesian state-space models on annual greater sage-grouse rate of change (λ) in population abundance within Nevada and California, USA, 2005–2019. We selected scales and representations of environmental covariates using a latent indicator variable selection approach, and final representations included percent sagebrush (5-km buffer [5k]), percent pinyon-juniper (5-km buffer), elevation (10-km buffer [10k]), cumulative burned area (10-km buffer), standardized precipitation (precip) index (12-month time lag, 10-km buffer), proximity to water bodies, proximity to spring, prior year density-dependence effects (where K represents an estimate of maximum carrying capacity at each sage-grouse lek), within horse-occupied area (HOA) effect, and percent feral horse abundance relative to current maximum appropriate management level (AML_{max}) set by the Bureau of Land Management based on use rate and ecological capacity within horse management areas (HMAs).

last year (2019; Fig. 3A). Model estimates indicated that sage-grouse population $\hat{\lambda}$ decreased approximately 2.6% for every 50% increase in %AML_{max} (Fig. 3B).

Future Projections of Sage-Grouse Population Trends

Under scenario 1, we sampled from posterior probability distributions of the %AML_{max} trend model parameters to extrapolate future %AML_{max} over 15 more years. Sage-grouse populations were projected to decline by 70.9% (95% CI = 65.3–77.5%, precipitation at median; 95% CI = 45.4–90.9%, precipitation varied randomly) with 100% probability of decline by 2034 within HOAs under scenario 1 (Fig. 4). For scenario 2, in which horses reflected %AML_{max} observed in the study, our model predicted a 56.9% decrease (95% CI = 54.5–69.5%, precipitation at median; 95% CI = 11.2–87.5%, precipitation varied randomly) within HOAs, with 98% probability of decline. For scenario 3, with horses held to their current AML_{max}, we predicted an increase of 12.2% (95% CI = –25.9–1.8%, precipitation at median; 95% CI = –80.7–48.6%, precipitation varied randomly) within HMAs, with 62% probability of increase. For control areas, outside of HOAs, predictions indicated declines over 15 years of 21.2% (95% CI = 41.2–90.4%, precipitation at median; 95% CI = –45.0–65.6%, precipitation varied randomly), with 75% probability of decline.

Post Hoc Impact-Control Analysis

Our *post hoc* impact-control analysis revealed that current AML_{max} (e.g., horse abundance equal to established AML_{max}) resulted in little evidence that sage-grouse population λ for leks within HMAs was lower than control leks (outside HOA) when free-roaming horse populations were set at AML_{max} (i.e., 100% AML_{max}; Fig. 5A). Specifically, models predicted a 21% probability of population λ decline relative to controls at AML_{max} under this condition. At 1.5 times AML_{max}, the probability of decline increased to 46%. When horse populations were set to 2 times the AML_{max}, the probability of sage-grouse population λ decline was predicted to be 76% relative to controls, and at 2.5 and 3 times the relative AML_{max}, probabilities of decline increased to 97% and nearly 100%, respectively (Fig. 5).

DISCUSSION

Our study revealed new findings about adverse effects of horses on sage-grouse populations, especially where horse population estimates exceeded AML_{max}. Free-roaming horse populations have continued to grow (~20% annually; BLM 2020a) and have exceeded AML_{max} settings across most managed HMAs. Our models predicted a 70.9% reduction in sage-grouse numbers within HOAs by 2034 across approximately 4,500,000 ha of sage-grouse habitat in Nevada and north-eastern California, assuming horse populations continue to

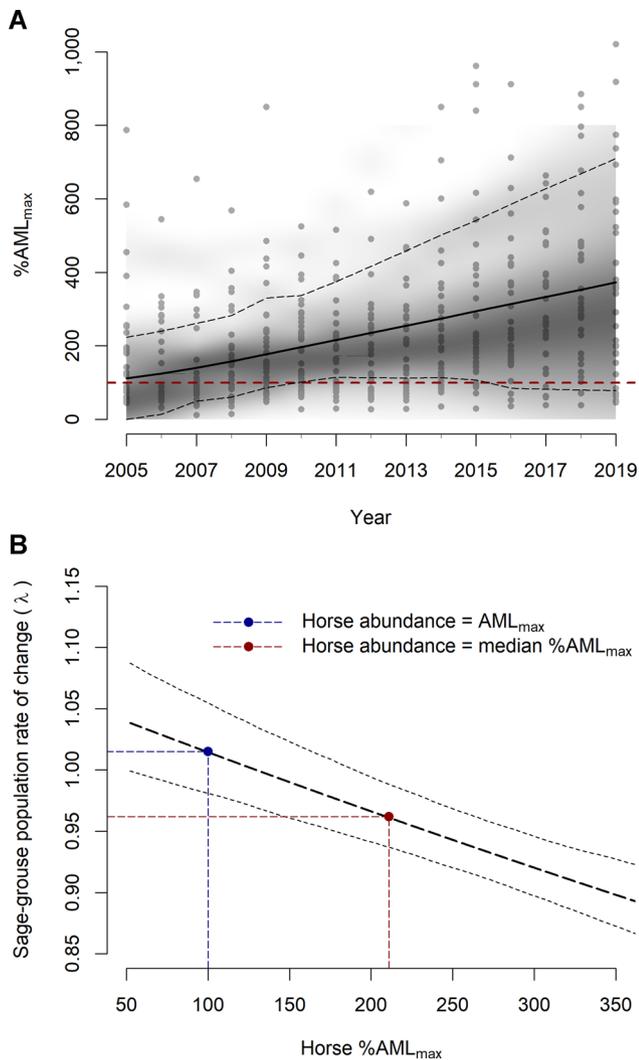


Figure 3. A) Trends in horse abundance relative to maximum appropriate management level (%AML_{max}) estimated from a linear mixed model at Horse Management Areas (HMAs) intersecting sage-grouse leks in Nevada and California, USA. The red dashed line indicates the defined maximum AML (100% AML_{max}), and black dotted lines above and below the main trend line show the 2.5th and 97.5th percentiles of the observed horse abundances relative to AML_{max}. B) Estimated effect of percent horse abundance over AML (%AML_{max}) with 95% credible intervals (black dotted lines) used in Bayesian state-space models on annual greater sage-grouse population rate of change (λ) within Nevada and California, USA, 2005–2019. The standardized linear effect is transformed to the original scale of %AML_{max}. Dashed vertical lines represent λ when horse population estimates are predicted to be at AML_{max} (blue), as compared to the median estimated AML_{max} across HMAs during the study (red).

increase at their current rates. If horse population growth was halted entirely, and numbers remained close to those observed during the previous 15 years, our model predicts a reduction in sage-grouse populations by 56.9% in areas affected by horses. Steep declines in sage-grouse populations are projected in this scenario because, as of 2020, horse populations were well above AML_{max}. Thus, sage-grouse populations are likely to experience continued decline in areas with overabundant horses. If horse herd sizes could be maintained at AML_{max}, an increase of 12.2% was predicted, suggesting there is a potential for rebound where sage-grouse populations have previously declined.

As recommended by the National Research Council (2013), we provide a novel example of using sage-grouse as an indicator species within sagebrush ecosystems (Hanser et al. 2011) to validate AML_{max}, which could help assist with an adaptive management framework that consists of multiple-use mandates intended to balance the presence of free-roaming horses with managed livestock and native sagebrush-dependent species. Successful adaptive management is contingent on the ability to evaluate outcomes that help validate management actions and suggest adjustments to management decisions (Schreiber et al. 2004). Although our study lends support to current AML_{max} settings as a whole, well-designed local monitoring programs of other ecological responses such as the functionality of riparian systems, or the abundance and trends of plants or other key wildlife indicator species, will help ensure adequate rigor is built into validating and adjusting management decisions.

Spatiotemporal variation in %AML_{max}, including substantial increases within HMAs over 15 years, provided an opportunity to establish empirical links between variation in sage-grouse population λ and horse abundance relative to AML_{max}, and also facilitated evaluation of ecological thresholds based on modeled predictions. Model support for %AML_{max} as a covariate for sage-grouse population λ indicated a decline in λ as horse abundance increased above AML_{max}. Current values set for AML_{max} seemed adequate, as predicted sage-grouse population λ was similar within treatments and controls when horse population estimates were equal to or below AML_{max}, and also because λ was lower in treatments than controls when AML_{max} was exceeded. The metric of %AML_{max} was an informative predictor of sage-grouse population trends, which can likely be attributed to the establishment of AML_{max} from information concerning the capacity of rangelands to meet target utilization rates and other factors (BLM 2010). For the purposes of this study, %AML_{max} may be considered an overgrazing index under the assumption that AUMs of cattle did not change as horses increased within HMAs.

Previous research on ecological effects of horses has largely focused on vegetation and soils (Davies and Boyd 2019), but few studies have addressed effects on wildlife (Eldridge et al. 2020). Although interactions between horses and other ungulates have been investigated (Berger 1985, Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017, Hall et al. 2018), the effects to sensitive species are not well-understood (Cherubin et al. 2019). Our study corroborates hypothesized links between horses and sage-grouse populations (Beever and Aldridge 2011) by demonstrating reductions in sage-grouse population λ in response to increases in horse abundances relative to AML_{max} settings. It is important to recognize that our response variable λ was largely a product of multiple population demographic rates related to reproduction (e.g., nest and chick survival) and adult survival (Taylor et al. 2012). Thus, it is logical to expect negative effects on sage-grouse population dynamics through indirect pathways associated with degradation of sage-grouse habitat across different demographic rates (Beever and Aldridge 2011, Davies

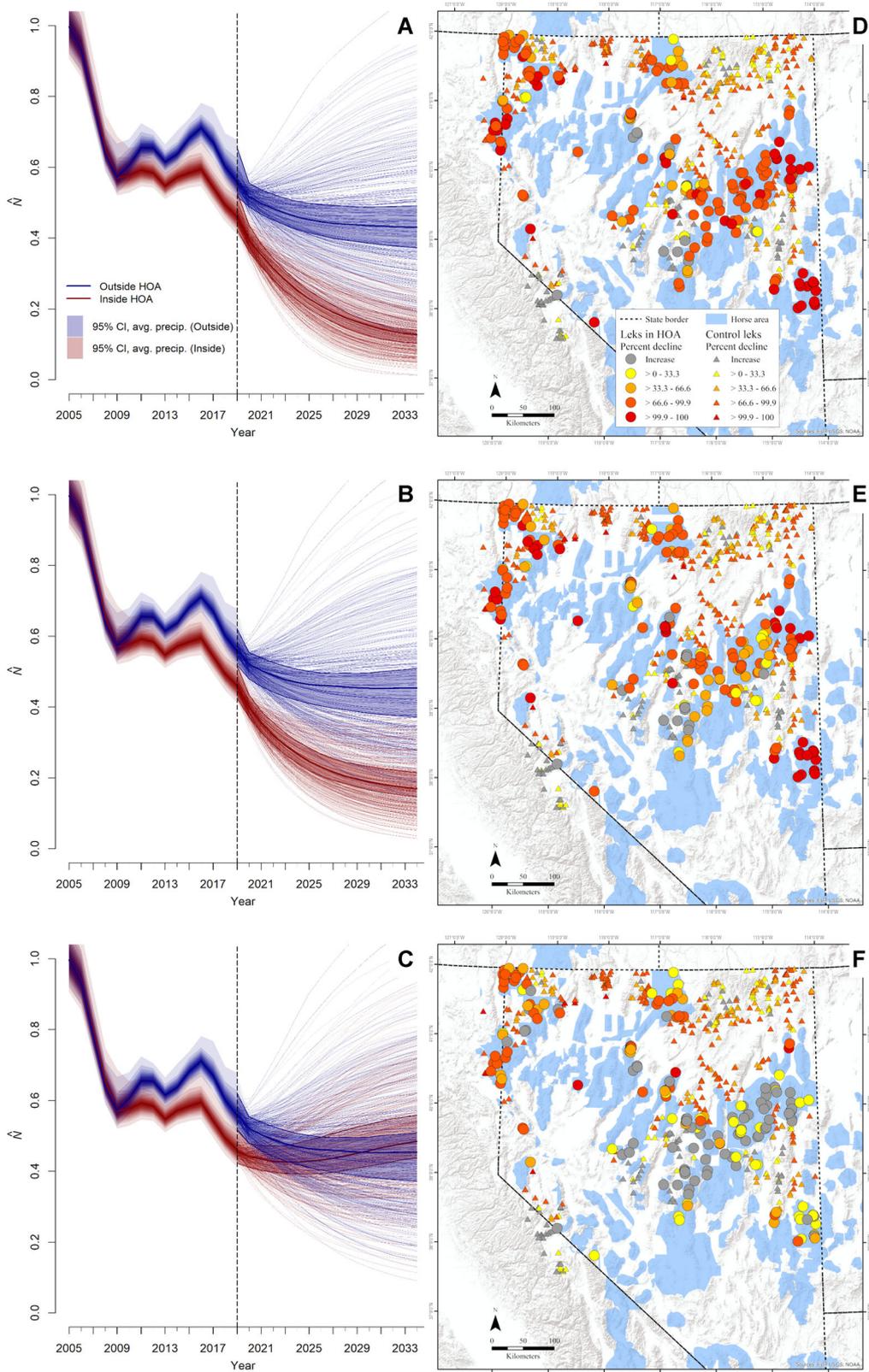


Figure 4. Bayesian state-space modeled estimates of annual predicted apparent abundance (\hat{N}) for greater sage-grouse populations within and outside horse-occupied areas (HOAs) in Nevada and California, USA, 2005–2019 (shaded areas represent samples from posterior distribution). We derived predictions of \hat{N} during 2020–2035 from estimated parameters based on 3 scenarios: A) growth rate of horses continues unabated, B) growth rate of horses is neutralized but numbers remain constant, and C) numbers of horses are held at maximum appropriate management levels (AML_{max}). Shaded areas in 2020–2034 represented \hat{N} under median (avg.) precipitation (precip.; e.g., $\%AML_{max}$ effect) and thin lines represented variation in precipitation sampled from its full distribution (e.g., $\%AML_{max}$ effect + environmental stochasticity), while other model parameters were held constant. Maps D–F illustrate spatial predictions of percent change in \hat{N} (median precipitation) for sage-grouse under the same 3 scenarios, respectively.

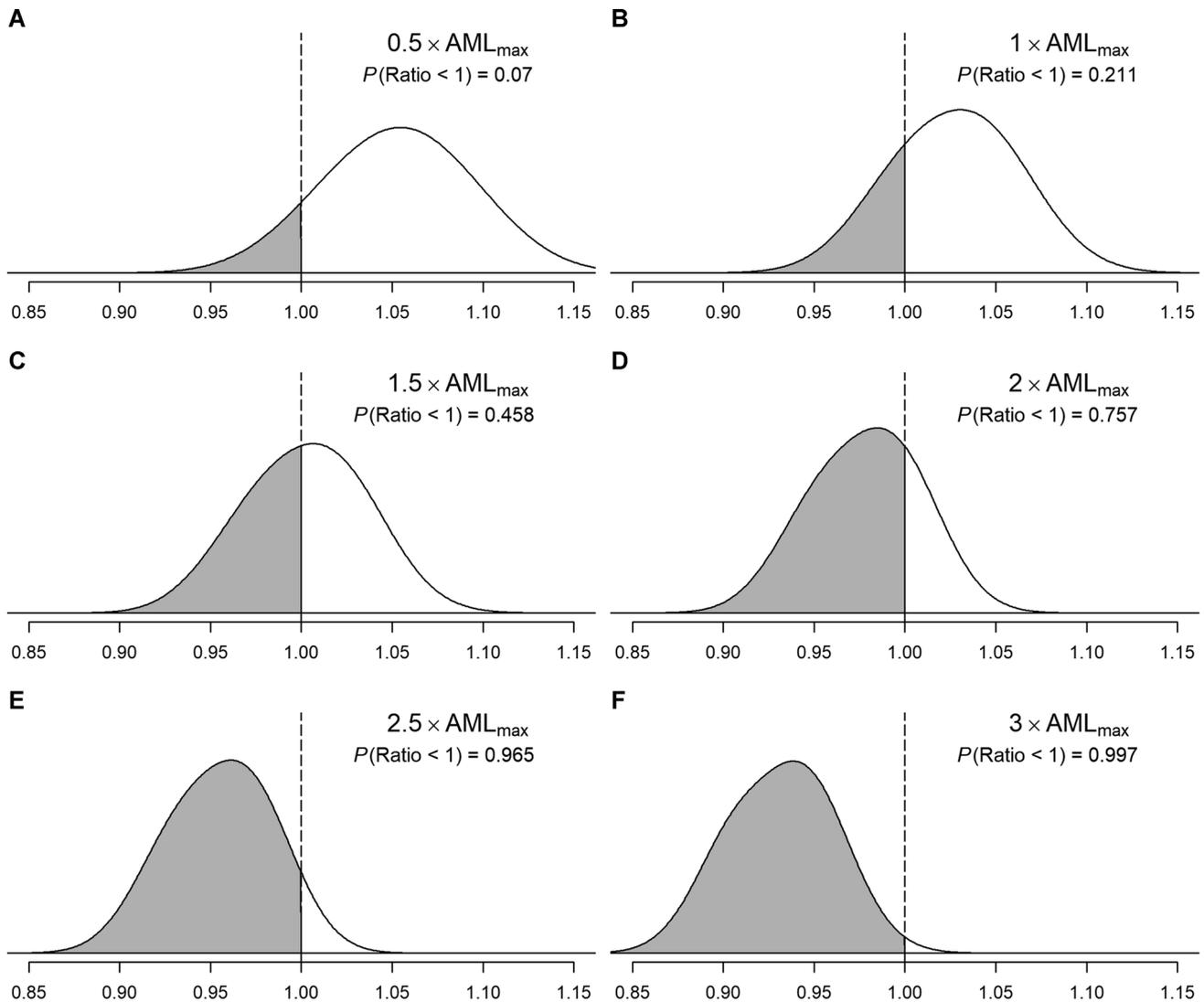


Figure 5. Ratio of greater sage-grouse population rate of change between impact (horse-occupied areas) and control (outside horse-occupied) leks in Nevada and California, USA, 2005–2019. Ratios were estimated at 6 levels of horse abundance relative to maximum appropriate management level (AML_{max}): A) 50% of current AML_{max} , B) AML_{max} (100%), C) 1.5 times AML_{max} , D) 2.0 times AML_{max} , E) 2.5 times AML_{max} , and F) 3.0 times AML_{max} . The area under the curve below a ratio of 1.0 represented the probability of sage-grouse reduced population growth relative to control areas, which were assumed to have very few or no horses.

et al. 2014). Although identification of specific demographic mechanisms influencing changes in sage-grouse λ was beyond the scope of our study, horses likely affect multiple population vital rates such as nest and chick survival, leading to cumulative effects across life stages that can lead to reduced sage-grouse population growth and, ultimately, population viability (Taylor et al. 2012).

The importance of overstory shrub cover and density for sage-grouse is arguably the most consistent habitat component to influence nest survival in semi-arid environments of the Great Basin (Gregg et al. 1994, Kolada et al. 2009, Coates and Delehanty 2010, Coates et al. 2017). This habitat component provides concealment from nest predators (Schroeder and Baydack 2001, Coates and Delehanty 2010), which are responsible for the majority of nest failures (Moynahan et al. 2007, Lockyer et al. 2015). Grazing by free-roaming horses directly reduces shrub density (Davies et al. 2014, Beever

and Brussard 2000) and continuity of shrub canopy (Beever et al. 2008). In one study, shrub canopy cover was 1.1–1.9 times greater in exclosures where free-roaming horses were removed (Beever et al. 2008), and this loss of shrub cover was attributed mainly to rubbing and trampling. Decreased shrub cover likely increases the ability of visually cued predators such as common ravens to find sage-grouse nests (Coates and Delehanty 2010), which is concerning given that raven abundance has also been increasing precipitously within the Great Basin since the 1970s (Sauer et al. 2017). A study in northeastern Nevada reported that a 1% decrease in shrub cover increased the probability of nest predation by ravens by 7.5% (Coates and Delehanty 2010). This may not be unique to the western United States because researchers of ground-nesting birds in Argentina reported that horse-grazed areas exhibited higher egg predation rates than horse-excluded areas (Zalba and Cozzani 2004).

Another important nest habitat component is structure and composition of herbaceous understory cover (Gregg et al. 1994, Doherty et al. 2010). Although the effects of herbaceous understory on nest survival may vary across sage-grouse range (Smith et al. 2020), the role of perennial grasses and forbs may be contingent on variation in primary productivity across the landscape (Coates et al. 2017). For example, grass height becomes more important in drier and warmer sagebrush environments where grasses are typically shorter and sagebrush shape is columnar (Coates et al. 2017). Additionally, relatively tall grasses and forbs immediately near the nest and within the shrub interspace might help conceal females from predators as they move to and from their nests during incubation recesses (Coates et al. 2008). Feral horse diet consists primarily of graminoids (80–95%; Hanley and Hanley 1982, Scasta et al. 2016) and areas occupied by horses have shorter perennial grasses with reduced cover relative to exclosures (Beever et al. 2008, Baur et al. 2018). Furthermore, sage-grouse tend to avoid nesting in areas with annual invasive grasses (Lockyer et al. 2015), and propagation and dispersal of invasive grasses by horses through intake and subsequent excretion of seeds (King et al. 2019) may decrease habitat suitability for nesting. Site-level mechanistic research that focuses on interactions among free-roaming horses, vegetation degradation, and nest predation by ravens is needed to identify proximate and ultimate causes of nest failure.

During the sage-grouse brood-rearing period, specifically later months in summer, riparian vegetation communities are important resources for chicks (Casazza et al. 2011, Gibson et al. 2016). These areas constitute a small proportion of western lands, but are some of the most productive and ecologically important areas of sagebrush ecosystems (Svejcar 1997, Donnelly et al. 2018). Feral horses within the Great Basin often relocate to higher elevations during the brood-rearing period from late spring to early fall (Pellegrini 1971, McInnis 1985) seeking riparian areas (Crane et al. 1997) because of the relatively higher water intake needs of horses compared to other ungulates (Groenendyk et al. 1988). They often concentrate at these sites throughout the day, especially during periods of high ambient temperatures and low precipitation (Hall et al. 2016). Grazing by horses can have severe effects on upland riparian areas (Boyd et al. 2017, Kaweck et al. 2018) by reducing the height of herbaceous cover, increasing bare ground, selective consumption, trampling of plants and soil, and the redistribution of nutrients and seeds on the landscape (King et al. 2019). In xeric regions of the Great Basin, sage-grouse select sites with greater perennial forb cover, also favoring taller forbs, increasing survival rates (Coates et al. 2017). These plants meet dietary needs (Sveum et al. 1998) and help to conceal chicks from predators while foraging (Casazza et al. 2011). Furthermore, detrimental effects of horses on hydrologic cycles of springs and riparian areas (Kaweck et al. 2018) limit water availability for sage-grouse, particularly chicks in late-summer habitat (Casazza et al. 2011). A recent study indicated that equids can dig wells to groundwater in arid environments to access water

and, thereby, increase density of water features on the landscape for other wildlife species, and stimulate growth of riparian trees (Lundgren et al. 2021). But any benefits from well-digging by horses likely do not compensate for the substantial adverse effects of horses on riparian areas (Boyd et al. 2017, Kaweck et al. 2018), and such wells likely provide negligible to no benefit to sage-grouse. For example, water bodies included in our models were largely stock ponds and impoundments. Predicted negative effects of these features may be related to such areas attracting horses, livestock, and other species that might disturb or prey on sage-grouse, which likely also pertains to groundwater wells created by horses.

Although indirect effects from habitat degradation to specific vital rates offer the most logical explanation for reduced sage-grouse population λ , recent evidence also indicates that horses directly disrupt sage-grouse breeding behavior at lek sites (Muñoz et al. 2021). Specifically, the probability of sage-grouse being absent from lek sites was greatest (75.4%) when horses were present on leks relative to cattle and native ungulates. Because sage-grouse mating success is partly determined by the amount of time they spend displaying on the lek (Gibson and Bradbury 1985), disruption by feral horses potentially reduces reproductive activity. The frequency and scale at which this effect occurs is not well known, and research that disentangles potential bias in lek counts from effects on demographic rates related to disturbance would be beneficial.

In addition to strong evidence of negative horse effects, other covariates in our model corroborate a growing body of literature that sage-grouse population declines are attributed to cumulative and concomitant effects. Horses serve as another factor that can negatively influence sage-grouse populations, adding to other correlates of sage-grouse decline in this study region. For example, sagebrush habitat within the Great Basin has been declining since European settlement, and many native bunchgrasses and forbs have been replaced by introduced perennial and invasive annual grasses (Morris and Rowe 2014). Further exacerbating the loss of sagebrush and native vegetation components, wildfire destroys sagebrush and facilitates invasion of annual grasses that provide fine fuels such as cheatgrass (Chambers et al. 2014), which leads to an accelerated feedback loop of larger and more frequent fires (Brooks et al. 2015), with potentially negative responses by sage-grouse to wildfire (Coates et al. 2016b, Foster et al. 2019). Additionally, our model supported the conclusion that population λ was reduced when pinyon-juniper increased close to leks. One feasible explanation is that pinyon-juniper leads to greater movements by sage-grouse, which increases risk of predation (Prochazka et al. 2017) and leads to lower survival rates (Coates et al. 2017). Consequently, declines in sage-grouse population λ within and outside of HOAs were likely influenced by a combination of cumulative effects between several factors and the degree to which feral horses were above AML_{max} .

There were positive effects on sage-grouse λ in response to increased sagebrush cover, increasing elevation, and

increasing precipitation expressed as standardized precipitation index with a 12-month time lag. As expected, sage-grouse population λ was closely linked to sagebrush cover within 5 km of leks, which corroborates results from habitat suitability models for leks (Knick et al. 2013) and across individual sage-grouse at life stages in the Great Basin (Coates et al. 2017). Sage-grouse move to mesic areas at higher elevations during summer to access increased forb availability (Patterson 1952, Klebenow and Gray 1968, Connelly et al. 2004) that is directly linked to brood survival (Casazza et al. 2011, Coates et al. 2017). Lower elevation regions are more susceptible to invasion by cheatgrass (Chambers et al. 2007), are more readily grazed by cattle (Ganskopp and Vavra 1987), and often have greater raven occupancy and density (O'Neil et al. 2018, Coates et al. 2020). Lastly, independent of other environmental factors, precipitation can be a major influence of sage-grouse demographic rates by promoting plant production (Blomberg et al. 2012, Guttery et al. 2013). Because feral horse effects appear greatest in more arid environments where water is scarce (Eldridge et al. 2020), years with greater annual precipitation may mitigate the effects of horses on sage-grouse by diluting horse visitation to higher elevations and riparian areas used by sage-grouse or by masking the effects of horse herbivory through increased plant productivity. Additionally, our models corroborate findings of others that rate of change in sage-grouse populations exhibits strong negative density dependence (Garton et al. 2015, Coates et al. 2016*b*, Edmunds et al. 2018).

Our analysis did not explicitly model livestock (e.g., cattle) and large native ungulates as covariates, primarily because of challenges associated with compiling quality spatial data. We assumed that the amount of grazing pressure by these animals, particularly cattle, arises from the same distribution inside and outside areas occupied by free-roaming horses. We surmise that this assumption was met considering approximately 82.0% and 83.3% of leks within areas occupied by horses and those not occupied, respectively, were located within grazing allotments. We only expected competition for forage between cattle and horses, which primarily consume graminoids year-round, whereas smaller native ungulates such as pronghorn and mule deer (*Odocoileus hemionus*) primarily consume, browse, and move more freely across the landscape (Hanley and Hanley 1982, Scasta et al. 2016, King and Schoenecker 2019). Thus, our results should be interpreted as influences of %AML_{max} given current AUMs allocated to cattle. Research that investigates the influences of reducing cattle AUMs (e.g., lessening cattle grazing pressure) on estimated changes in the effects of %AML_{max} would be helpful. Cattle-induced effects on the landscape likely differ from horse-induced effects because of fundamental differences in physiology and behavior between the species (Beever 2003) and the year-round grazing pressure that free-roaming horses apply (Kaweck et al. 2018).

Multiple obstacles restricted our ability to compile precise information on horse occupancy and spatial distribution throughout our study area. For example, the horse

abundance estimates we used for HMAs were likely underestimated because of failure to account for imperfect detection (National Research Council 2013, Schoenecker et al. 2018). If true, this should not influence estimated effects of %AML_{max} because this variable was an index of abundance above a set capacity point (AML_{max}). Because methodology used to determine AML_{max} does not consider imperfect detection, then estimates of %AML_{max} may in fact be lower than true values. For this reason, it would be valuable to know the extent to which true horse abundance exceeds estimated horse abundance to provide better calibration between AML_{max} and horse abundance estimates, but this should have little or no influence on the outcomes of this research. Survey methods that BLM has adopted since the report from the National Research Council (2013) appear to have relatively low bias in estimated herd sizes (Lubow and Ransom 2016). Additionally, lack of spatial movement data for free-roaming horses (Collins et al. 2014) meant that we could not account for horses moving outside of HOAs and into nearby control areas, which could introduce estimation error. Given the broad-scale scope of our study, potential error associated with movement of horses and horses occupying areas outside of HOAs was likely negligible. Finally, we had to exclude leks on tribal and private lands to reduce error in areas where horse data were not available, so inferences about horses and the influence of private and tribal lands is limited. In Nevada, because these lands account for a relatively small proportion of the entire study area, such error is likely negligible.

Interpretation of model projections is not without important considerations. First, because model projections did not consider sage-grouse habitat recovery times with simulated reductions in horses, and explicitly model mechanistic effects of horses to sage-grouse habitat, it is likely that predictions of immediate projected improvements in sage-grouse numbers derived from scenario 3 (i.e., horse numbers are reduced to and maintained at AML_{max} for each HMA) were optimistic. For example, sage-grouse habitat degradation attributed to overabundant horses, such as detrimental effects to riparian areas (Boyd et al. 2017, Kaweck et al. 2018), will likely require multiple years to recover following reduction in herd sizes and ultimately reverse negative effects on sage-grouse populations. Additionally, projected increases of sage-grouse numbers under the third scenario did not account for changes in other environmental factors influencing sage-grouse populations. For example, sage-grouse will likely still decline with additional losses of sagebrush as a result of continued increase in cumulative burned area associated with acceleration in wildfire-invasive grass cycles (Chambers et al. 2014, Coates et al. 2016*b*) and elevated nest predation from growing populations of ravens (Sauer et al. 2017, Coates et al. 2020*b*). Lastly, sage-grouse population abundance fluctuates with precipitation (Coates et al. 2018) and, thus, our predictive posterior distributions broaden as years progress to fully account for this environmental stochasticity.

In conclusion, we found sage-grouse populations in Nevada and northeastern California are declining at a rate

of approximately 3.9% annually ($\hat{\lambda}=0.961$) with strong evidence that declines are associated with horse abundances that exceed the established AML_{max} for HMAs. These data garnered substantially more support for $\%AML_{max}$ as a predictor variable than other types of horse abundance indices on sage-grouse population λ , which suggests that effects are a likely result of overgrazing by horses that damage sage-grouse habitat. Exceeding current AML_{max} , or adjusting AML_{max} to higher values within the model, resulted in clear evidence of negative effects to sage-grouse population λ . In contrast, model predictions indicated that when horse populations did not exceed current AML_{max} values, there was no significant evidence of declines in sage-grouse population λ when compared to areas where horses were assumed absent. Sagebrush ecosystems are dynamic, undergoing changes in vegetation function, composition, and structure based on a variety of disturbances (e.g., wildfire, invasive plants) and different climatic conditions (e.g., drought), which affect the ecosystem's resilience (ability to recover) and resistance to invasive plants (Chambers et al. 2014). These processes necessitate periodic re-evaluation and modifications to AML_{max} to help prevent horses from exceeding the capacity of the ecosystem under these varying conditions. Our results indicate a need for appropriate science-based calculations of AML_{max} with continuous validation as additional ecological information is obtained. Studies that focus on disentangling use rates between horses and livestock, while linking grazing patterns to sage-grouse seasonal habitat and population vital rates, would provide valuable mechanistic pathways to help refine AML_{max} settings. Recent developments in telemetry of free-roaming horses have set the stage for investigations on movement patterns, habitat preferences, and resource uses that can address important research questions and help management and policy decisions at finer spatial scales (Collins et al. 2014, Schoenecker et al. 2020).

MANAGEMENT IMPLICATIONS

Effective management strategies for multiple-use landscapes with feral horse populations are likely to be those that target, reach, and hold horse abundance below or at AML_{max} . According to our models, this would neutralize negative effects of overabundant horses to sage-grouse populations, allowing for potential positive growth rates of sage-grouse assuming other threats were not increasing. Sage-grouse lek count data can be a useful environmental indicator for validation of AML_{max} . State-space population modeling frameworks can be periodically replicated by leveraging existing collaborations for lek data collection by state and federal agencies, universities, and private organizations. Although this SSM framework can be improved to help guide management decisions at finer spatial scales, it may not encompass the requirements of other key indicator species that may exhibit different responses to horse densities. Improved monitoring and information that helps to capture the broader community-level effects of horses will be key to validating and refining the designation of horse

AML_{max} for the purpose of balancing multi-use landscape needs.

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