DOI: 10.1002/jwmg.22669



RESEARCH ARTICLE

Free-roaming horses exceeding appropriate management levels affect multiple vital rates in greater sage-grouse

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Abstract

Since the passage of the Wild Free-Roaming Horses and Burros Act of 1971, federal agencies have been responsible for managing free-roaming equids in the United States. Over the last 20 years, management has been hampered by direct opposition from advocacy groups, budget limitations, and a decline in the public's willingness to adopt free-roaming horses (Equus caballus). As a result, free-roaming equid numbers have increased to >3 times the targeted goal of 26,785 (horses and burros [E. asinus] combined), the cumulative sum of the appropriate management levels (AML) for all 177 designated herd management areas (HMA) managed by the Bureau of Land Management. This increase is one of the causes of greater sagegrouse (Centrocercus urophasianus) population declines, owing to habitat alteration from free-roaming equids exacerbated by ongoing drought. To evaluate potential demographic mechanisms influencing these declines, we compiled survival data from 4 studies in central Wyoming, USA, including 995 adult female (first-year breeders or older) sage-grouse during the breeding season, 1,075 nests, 372 broods, and 136 juveniles (i.e., overwinter survival for fledged young), from 2008-2022. During this period, we also obtained population information for free-

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Funding information

Wyoming Game and Fish Department; Wyoming Sage-Grouse Conservation Funds; Big Horn Basin, Southwest, South-Central and Wind River/Sweetwater River Local Sage-Grouse Working Groups; University of Wyoming-School of Energy Resources; Laramie Audubon Society; University of Wyoming Extension; U.S. Bureau of Land Management, Grant/Award Numbers: L16AC00156, L17AS00123, L19AC00090; U.S. Geological Survey Ecosystems Mission Area roaming horses from 9 HMAs used by individual grouse in our sample. Population estimates of free-roaming horses for these HMAs ranged from 59% to 7 times of the maximum appropriate management level (AML_{max}). Sage-grouse monitored outside of HMAs represented control populations and, because we assumed they were not exposed to populations of free-roaming horses, we set values of AML_{max} to zero for all grouse located outside of HMAs. To evaluate whether free-roaming horses were negatively affecting sage-grouse, we modeled daily survival of breeding age females, nest, broods, and juveniles. There was strong or moderate evidence that overabundant freeroaming horses negatively affected nest, brood, and juvenile survival. When horse abundance increased from AML_{max} to 3 times AML_{max}, survival was reduced 8.1%, 18.3%, 18.2%, and 18.2% for nests, early broods (≤20 days after hatch), late broods (>20 days to 35 days after hatch), and juveniles, respectively. These results indicate increasing free-roaming horse numbers affected vital rates for important life stages of sage-grouse, and that maintaining free-roaming horse numbers below AML_{max} would reduce negative effects to sage-grouse populations.

KEYWORDS

adult, and nest survival, brood, *Centrocercus urophasianus*, *Equus caballus*, feral equids, impacts of free-roaming ungulates, juvenile, Wyoming

Ancient wild horses (Equus spp.) became extinct in North America about 10,000 years ago (Luís et al. 2006, Ransom and Kaczensky 2016), but free-roaming horses (E. caballus) and burros (E. asinus) are currently on rangelands of western North America where they are descendants of escaped domesticated animals introduced by Europeans (Haines 1938). Free-roaming equids (collectively horses and burros) on some federal public lands in the western United States are protected under the Wild and Free-Roaming Horses and Burros Act of 1971 where their management is based upon a range-wide appropriate management level (AML) of 26,785; however, as of 1 March 2023 they exceeded that level by approximately 3.1 times (82,883; Scasta et al. 2018, Bureau of Land Management [BLM] 2023, Hennig et al. 2023a). The goal of the Wild and Free-Roaming Horses and Burros Act is "to maintain a thriving natural ecological balance on the public lands" (Public Law 92-195 1971). Managing free-roaming horse populations is challenging because annual growth rates can average 20% per year (Eberhardt et al. 1982) and freeroaming horse grazing on public lands, as compared to domestic livestock, is unmanaged and typically occurs on a continuous year-round basis (Davies and Boyd 2019). In addition, the ability of the BLM and United States Forest Service to manage burgeoning populations of free-roaming equids on federal lands is complex owing to issues including litigation that challenges federal enforcement of the Wild and Free-Roaming Horses and Burros Act, public emotions relative to the management of increasing populations, and increasing complexity in laws and amendments guiding free-roaming equid management policy (Scasta et al. 2018). Underlying the challenging issue of managing free-roaming equids on federal lands is the proper designation of these large ungulates as either livestock, pets, or wildlife; it is believed that such a designation would provide federal agencies clearer direction when writing plans and implementing practices to administer free-roaming horse and burro management programs (Hennig et al. 2023*a*). Nevertheless, proper management is important because uncontrolled grazing by free-roaming equids leads to adverse effects on soils, vegetation composition and structure, forage availability, and water sources, all of which have consequences to wildlife and wildlife habitats (Beever and Aldridge 2011, Davies and Boyd 2019). For instance, water sources accessible to free-roaming horses in the Great Basin had lower richness and diversity of native birds and mammals compared to water sources that excluded access to free-roaming horses (Hall et al. 2016). In addition, native species made fewer visits and spent less time at water sources accessible to horses than those where horses were excluded (Hall et al. 2016).

The scale of overlap between free-roaming equids and wildlife of conservation interest in the western United States is extensive. For example, a recent analysis reported that across 10 western states, free-roaming equids (horses, burros, or both) shared 7.7%, 4.3%, 5.8%, and 9.1% of habitat used by bighorn sheep (*Ovis canadensis*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*), respectively (Stoner et al. 2021). Across portions of their range, greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) also coexist with free-roaming equids, and about 12% of sage-grouse habitat is also managed for free-roaming equids within BLM herd management areas (HMAs; Beever and Aldridge 2011). The amount of overlap between free-roaming horses and sage-grouse varies among states, reaching a high of >99% overlap where free-roaming horses occur on BLM lands in Wyoming, USA (Beever and Aldridge 2011), which amounts to approximately 11% of the current sage-grouse distribution in the state. Yet only recently have free-roaming horses in the West been recognized as a potential threat to sage-grouse populations (Beever and Aldridge 2011, U.S. Fish and Wildlife Service 2013, Coates et al. 2021). Increased understanding of the potential impacts of free-roaming horses on sage-grouse is important owing to the recognition of sage-grouse as a potential umbrella species for about 350 other vertebrate species that use sagebrush (*Artemisia* spp.) ecosystems (Wisdom et al. 2005, Gamo et al. 2013) and the potential for free-roaming horses to degrade habitat for these species.

Multiple direct and indirect effects have been hypothesized regarding how free-roaming equids may influence sage-grouse life stages and habitat characteristics (Beever and Aldridge 2011). Research from the Great Basin documented free-roaming horses directly flushing sage-grouse from a lek and reported sage-grouse were least likely to be observed concurrently on leks with free-roaming horses or cattle (17.1% and 43.0% predicted probabilities, respectively) as compared with mule deer or pronghorn (~75.0% predicted probabilities for either native ungulate; Muñoz et al. 2021). Greater numbers of free-roaming horses have also increased stress hormones in sage-grouse in Nevada and Oregon, USA, which was intensified by drought conditions; notably this increase in stress levels was linked to reduced nest survival in sage-grouse (Behnke et al. 2022). Free-roaming horses also indirectly influence sage-grouse habitat by increasing bare-ground and reducing perennial grass height (Hennig et al. 2021*a*), propagating invasive exotic annual grasses, such as cheatgrass (*Bromus tectorum*), through their feces (King et al. 2019), decreasing native forb, grass, and shrub cover and overall vegetation height, and increasing dominance of unpalatable forbs (Beever and Aldridge 2011, Street et al. 2024). In addition, increasing abundance of free-roaming horses following years of low precipitation reduces the nesting propensity of sage-grouse (Behnke et al. 2023).

Recent research revealed adverse effects of overabundant free-roaming horses on sage-grouse population growth rates within the Great Basin, where sage-grouse abundance was predicted to decline by approximately 70% by 2034 if horse populations continue at current growth rates (Coates et al. 2021). Greater densities of cattle and free-roaming horses, quantified through indices of dung counts, were reported in another study to negatively affect sage-grouse nest survival (Behnke et al. 2022). Additional studies of free-roaming horses that evaluate different population vital rates as underlying demographic mechanisms of population-level impacts will allow managers options that take different sage-grouse life stages into consideration. For example, because sage-grouse use different vegetation communities within sagebrush ecosystems to meet their specific habitat requirements for each life-history phase (e.g., nesting, brood-rearing), demographic-specific information could assist land and wildlife managers with decisions on reducing species overlap in specific habitats. Meta-analyses of sage-grouse vital rates indicated that

changes in adult female survival resulted in the greatest changes to population growth (Taylor et al. 2012, Dahlgren et al. 2016); however, this vital rate is relatively constant from year to year when compared to other vital rates as predicted by life-history theory (Stearns 1989). In contrast, nest and brood survival are more variable from year to year, and account for more of the variation in population growth for greater sage-grouse (Taylor et al. 2012) and may be hypothesized as the demographic mechanism through which free-roaming horses affect sage-grouse populations. Understanding levels of free-roaming horses that influence vital rates of sage-grouse could be an impetus to remove horses exceeding the maximum AML in HMAs with declining sage-grouse populations.

Wyoming provides habitat to the largest sage-grouse (Western Association of Fish and Wildlife Agencies 2015) and second largest free-roaming horse populations on federally managed public lands in the United States (BLM 2023). Thus, understanding impacts of horses on sage-grouse is particularly important in Wyoming. The BLM sets AML at low and high (maximum) levels for each HMA, where equid numbers that exceed the maximum level are reasonably above numbers that may jeopardize a thriving natural ecological balance on public lands (Public Law 92-195 1971). Appropriate management levels account for animal unit months (AUMs) that have already been delegated to wildlife and livestock within grazing allotments that overlap HMAs (BLM 2010); thus, forage used by all wild and free-roaming ungulates are inherently incorporated into population estimates calculated as a percent of the AML (% AML). This method is more appropriate than other metrics of horse use, such as density or simple abundance, when analyzing effects on other species because %AML provides a broader perspective of herbivory impacts within an HMA. Recent research has shown that maintaining free-roaming horses at or below maximum AML (AML_{max}) was consistent with maintaining sage-grouse populations, as assessed by male lek counts, at levels similar to areas where sage-grouse do not co-occur with free-roaming horses (Coates et al. 2021). In south-central Wyoming, free-roaming horses and sage-grouse that shared habitat overlapped most in summer (Jul-Oct) when habitat selection by both species was tied to proximity to water and secondarily during spring (Apr-Jun) when sage-grouse were selecting flatter areas with greater herbaceous cover, similar to areas preferred by horses (Hennig et al. 2023b). As a result, high numbers of horses most likely will affect demographic parameters associated with reproduction for sage-grouse, but it is important to evaluate the effects on multiple vital rates (and compounding negative effects) to investigate the demographic mechanisms behind demonstrated impacts on population growth rates.

The primary objective of our study was to evaluate the relative degree by which free-roaming horse numbers above AML_{max} influence multiple greater sage-grouse vital rates including survival of adult females during the breeding season, nest survival, early and late brood survival, and overwinter juvenile survival. We hypothesized that free-roaming horses would have the greatest effect on survival during the earliest life stages (nesting, early brood-rearing, and late brood-rearing), when habitat overlap with sage-grouse was highest.

STUDY AREA

Our study included demographic data for sage-grouse and AML_{max} data for free-roaming horses collected from 2008–2022 within central Wyoming (Table 1; Figure 1). We obtained sage-grouse data from 4 studies. The Atlantic Rim study area included an initial study from 2008–2011 and a second study combined with a study in the Red Desert, where there was considerable temporal and spatial overlap among marked sage-grouse from 2018–2022 with grouse located in the 2008–2011 study. Each study, except for the Red Desert study (Hennig et al. 2023*b*), was designed to answer research questions outside the effects of free-roaming horses on sage-grouse. Our study areas were classified as cold arid steppe (Kottek et al. 2006), characterized by hot, dry summers from May–September, and cold, snowy winters from November–March. Each study area was dominated by Wyoming big sagebrush (A. *tridentata wyomingensis*) at lower elevations and mountain big sagebrush (A. *t. va-seyana*) at higher elevations. See Kirol et al. (2012) for the Atlantic Rim and Stewart Creek study areas, Smith et al. (2023) for the Jeffrey City study area, and Hennig et al. (2023*b*) for the Red Desert study area for detailed descriptions.

FABLE 1 Su	mary of sample sizes (n) of adult females, nests, early broods (≤20 days after hatch), late broods
>20 days to 35	ays after hatch), and juveniles (7 months from Sep until recruitment into the adult population the
ollowing Mar) ι	ed to evaluate the influence of free-roaming horses within Bureau of Land Management (BLM)
Herd Manageme	t Areas (HMAs) on greater sage-grouse vital rates in central Wyoming, USA, 2008–2022.

			n				
		BLM	Adult		Early	Late	
Study area	Years	HMAs ^a	females	Nests	broods	broods	Juveniles
Atlantic Rim	2008-2011	AT, SWC	129	118	35	27	N/A ^b
Atlantic Rim, Red Desert	2018-2022	AT, SWC	165	201	44	31	50
Jeffrey City	2011-2019	CC, CM, DPB, MB, RC	663	706	270	192	86
Stewart Creek	2008-2011	GM, SC	38	50	23	22	N/A
Totals			995	1,075	372	272	136

^aAT = Adobe Town; CC = Conant Creek; CM = Crooks Mountain; DPB = Dishpan Butte; GM = Green Mountain;

MB = Muskrat Basin; RC = Rock Creek; SWC = Salt Wells Creek; and SC = Stewart Creek.

 ${}^{b}N/A$ = no data available.

METHODS

Field methods

We captured female sage-grouse in 2008–2021 using multiple capture methods, primarily through spotlighting and hoop-netting (Wakkinen et al. 1992), and less frequently by rocket-netting (Giesen et al. 1982), and a mobile CODA© net launcher (Sutphin et al. 2018). We aged females to first-year breeders or older (Eng 1955, Dalke et al. 1963) and outfitted them with very high frequency (VHF)-necklace transmitters (22-g A4060, Advanced Telemetry Systems, Isanti, MN, USA or 17.5-g RI-2D, Holohil Systems, Carp, ON, Canada) or global positioning system (GPS) transmitters (22-g Solar Argos/GPS platform transmitter terminal, Microwave Telemetry, Columbia, MD, USA; GeoTrak, Apex, NC, USA; Bird Solar 15-g, e-obs GmbH, Gruenwald, Germany). We attached ancillary VHF transmitters (3.5-g PD-2 or 6-g RI-2C, Holohil Systems) to GPS transmitters to aid in locating these female sage-grouse from the air and ground if necessary. We attached GPS transmitters with rump-mount harnesses. For all individuals fitted with either VHF-necklace transmitters or rump-mounted GPS transmitters, we ensured that transmitters did not exceed a recommended 3% of body mass (Phillips et al. 2003) to reduce risk of mortality to sage-grouse associated with transmitter mass (Severson et al. 2019).

We monitored radio-marked female sage-grouse weekly from mid-April through the end of the breeding season in mid-August. For females equipped with VHF transmitters, we assumed females were nesting if we found them in the same location for 2 visits and we monitored nests from ≥ 20 m to minimize disturbance and nest abandonment. For GPS-equipped females, we visually inspected potential nests after the female left a location of clustered GPS points. We considered a nest attempt successful if ≥ 1 egg hatched as determined by examining the nest site and any remaining eggshells. The mean exposure period was slightly lower for GPS-marked female sage-grouse than VHF-marked females on nests, but modeled exposure for nesting GPS-marked female grouse was within the range of variation in the data (i.e., the standard deviation for GPS-marked females overlapped the mean for VHF-marked females). We monitored females that successfully hatched chicks weekly through mid-August to record brood fate. During each visit, we attempted to determine if the brood was still active by visually locating chicks or observing brooding behavior by the female. We considered a brood successful if ≥ 1 chick survived to 35–40 days post hatch and we conducted night-time spotlight counts between 35–40 days post hatch to verify brood fate (Dahlgren et al. 2010). We captured juvenile sage-grouse in late summer when they were 5–7 weeks old



FIGURE 1 Study areas in central Wyoming, USA, where greater sage-grouse survival was monitored from 2008–2022. Herd management areas (HMAs) managed by the Bureau of Land Management are labeled and shown in gray. This map shows the 9 HMAs that included sage-grouse locations, which are shown in dark gray in the inset map. Salt Wells Creek HMA was used by adult grouse but did not contain nests of marked birds.

using spotlighting techniques, equipped them with VHF-necklace transmitters (10-g or 15-g RI-2B, Holohil Systems; 12-g model A3950 or 15-g model A3960, Advanced Telemetry Systems) and monitored them with monthly telemetry flights from September until the following March (Smith et al. 2024).

Spatial covariates

To evaluate the effect of horse abundance on sage-grouse demographic rates, we first compiled horse data from the BLM Wild Horse and Burro Program. There were no free-roaming burros in our study areas. We included data from BLM on AML_{max} and the estimated horse population size (\hat{N}) for each HMA in each year of the study (https://www.blm.gov/programs/wild-horse-and-burro/about-the-program/program-data, accessed 29 Dec 2023). We used these data to calculate an index of horse abundance (% AML_{max}) because this best explained population growth for sage-grouse in Coates et al. (2021) as:

$$\% \text{AML}_{\max,j,k} = \frac{\hat{N}_{j,k}}{\text{AML}_{\max,j,k}} \times 100,$$

where *j* and *k* represent HMA and year, respectively. The BLM reports AML_{max} as the maximum number of freeroaming horses on a yearlong basis that is consistent with a healthy ecosystem after accounting for vegetation and soil characteristics, wildlife populations, and other grazing animals including cattle. The AML for each HMA ranges between a minimum and a maximum level; thus, 100% of %AML_{max} represents the upper limit of AML, which if surpassed will lead to rangeland degradation (BLM 2010). Therefore, we hypothesized that higher values of % AML_{max} would have negative effects on sage-grouse demographic rates. Sage-grouse monitored outside of HMAs represented control populations and we set values of %AML_{max} to zero for all locations outside of HMAs because we assumed they were not exposed to populations of free-roaming horses. During our study period, all HMAs had horses present. Therefore, estimates of effects on demographic rates where %AML_{max} equaled zero represented estimates for sage-grouse monitored outside of HMAs.

We also estimated sagebrush cover associated with sage-grouse locations, which we included in our analyses to account for this important environmental factor. To characterize sagebrush cover, we used time-varying estimates of cover from the Rangeland Condition Monitoring Assessment and Projection time-series layers (Rigge et al. 2021). We evaluated the effect of sagebrush cover at 2 spatial scales (205 m and 1,071 m), which represented averages of the mean and maximum daily distances traveled by sage-grouse in our study. We also included a smaller radius (75 m) that approximated the minimum distance traveled by sage-grouse, while minimizing error based on the available resolution of remotely sensed layers. We first evaluated if sagebrush cover was an important predictor for each individual vital rate (described below) using univariate models and calculated the probability of direction (P($|\beta|$ >0)) to evaluate variable importance (Makowski et al. 2019). If the probability of direction was >0.80, we included the most predictive scale in the full model described below.

Analysis

We evaluated survival for 4 different life stages: nesting, brood-rearing, juvenile, and adult. We evaluated nest survival for an exposure period from the first day of incubation to hatch and assumed a 28-day incubation period. We excluded exposure during the laying period because of difficulty finding nests prior to incubation. We divided the brood-rearing life stage into 0–3 weeks post hatch (≤20 days after hatch) and 3–5 weeks post hatch (>20 days to 35 days after hatch), where we considered the early brood-rearing period to be transitional between nesting and the late brood-rearing period (Blomberg et al. 2014). We defined the juvenile life stage as the 7-month period (Sep–Mar) after chicks are more

capable of independence in fall until they were recruited into the breeding population the following spring. We evaluated adult survival only during the breeding season (15 Apr-15 Aug) because of data limitations. For brood, juvenile, and adult survival, we used models that accounted for exposure time in a Bayesian framework (Shaffer 2004). Because there was uncertainty in the exact day nest incubation and hatch occurred due to the monitoring interval, we modeled nest survival with a multistate model that explicitly modeled the transition probabilities between non-nesting, nesting, and failed states (Behnke et al. 2023). We assumed all females started in a non-nesting phase but could survive and transition to a nesting state, and we then modeled nest survival as a function of environmental covariates described below. The exposure and multistate frameworks modeled daily survival as a binomial response. We assessed the effects of covariates on each vital rate (*h*), using the following equations:

 $y_h \sim \text{Bernoulli}(\theta_h)$

$$\theta_h = DS^{t_{h,i}}$$

$$logit(DS_h) = \gamma_{h,0} + X\beta_h + \kappa_h$$

We modeled the survival probability of an individual, nest, or brood over interval i with a Bernoulli distribution where $y_h = 1$ if the individual or brood survived the interval and θ_h was the probability of the individual, nest, or brood surviving the interval; θ_h equaled the daily survival probability (DS) raised to the length (time = t) of interval i. We modeled daily survival (DS) as a combination of the baseline survival rate (γ), a vector of selection coefficients β multiplied by fixed covariates X, described below for each analysis, and a random effect for site-year (k; see Appendix for estimates of random effects; Figures A1-A4). We structured encounter histories to represent the interval between successful relocations of an individual, nest, or brood, with habitat features measured at the beginning of each interval. All analyses included a fixed effect of horse abundance (%AML_{max}) and, if there was support based on the univariate models described above, sagebrush cover at the most predictive scale. The nest survival analysis also included an effect of nest age, the nest and adult survival analyses included an effect of transmitter type (VHF vs. GPS), the brood survival analysis included an effect of brood age as an indicator variable for early vs. late brood-rearing (i.e., binary variable [0 or 1]) in interaction with % AML_{max}, and the juvenile survival analysis included an effect of sex. We included a random effect for the combination of site (HMA or control population) and year to capture differences in other factors such as annual precipitation not explicitly included in our analysis. Because horse abundance was only available at the level of the HMA, we were unable to explicitly incorporate additional factors such as precipitation that were also only available at a coarse spatial resolution because of high correlations and low sample sizes.

We fit all models using Markov chain Monte Carlo (MCMC) simulations with JAGS (version 4.3.0, mcmc-jags. sourceforge.net, accessed Mar 2021) implemented via the rjags package (Plummer 2018). We used vague normal priors for random effects and their measures of error ($\mu = 0$, $\sigma^2 =$ Uniform [0,100]; Kéry 2010) and, to prevent overfitting, we specified lasso (i.e., Laplace) prior distributions for each fixed effect, with an uninformative hyperprior specified for the tuning parameter lambda (Uniform [0.001,10]; Park and Casella 2008, Hooten and Hobbs 2015). Each model ran for 50,000 iterations thinned by a factor of 5, with the first 25,000 samples discarded and inferences made based on the remaining 15,000 samples from 3 independent MCMC chains. We assessed convergence and MCMC chain mixing visually and based on Gelman-Rubin convergence statistics (<1.1; Gelman and Hill 2006). To evaluate a variable's importance, we calculated the probability of direction ($P(|\beta|>0)$) and considered probabilities ≥ 0.85 and ≥ 0.95 to represent moderate and strong effects, respectively (Makowski et al. 2019).

To compare demographic rates between areas not affected by free-roaming horses (i.e., outside of HMAs where %AML_{max} was assumed to be zero) to areas where horse abundance was assumed to be sustainable (i.e., %AML_{max} = 100), we calculated the relative change in each predicted demographic rate when %AML_{max} increased from 0 to 100. We calculated the relative change for demographic rate *h* as $\frac{\text{survival rate}_{h,AMLmax=0} - \text{survival rate}_{h,AMLmax=100}}{\text{survival rate}_{h,AMLmax=0}} \times 100$.

Calculating relative changes allowed us to compare differences across demographic rates while allowing for differences in the absolute value of those rates. We calculated absolute changes (i.e., just the numerator of the above equation) as well for reference (Table A1). We also calculated the relative change in demographic rates between areas where horse abundance was assumed to be sustainable (i.e., %AML_{max} = 100) and where horse abundance was 3 times over sustainable levels (i.e., %AML_{max} = 300) using the following equation for demographic rate h: $\frac{\text{survival rate}_{h,\text{AML max}=100} - \text{survival rate}_{h,\text{AML max}=300} \times 100$.

survival rateh,AMLmax=100

RESULTS

We monitored 995 female sage-grouse between 2008–2022, 535 of whom used 9 HMAs (Figure 1). Over this period, population estimates of free-roaming horses for these HMAs ranged from 59–700% of the maximum appropriate management level (AML_{max}). Of the 70 HMA × year combinations in our analyses, 49 (70.0%) exceeded AML_{max}, 20 (28.6%) were below AML_{max}, and 1 (1.4%) was at AML_{max}. Average breeding season (123-day) survival for adult females was 0.81 (95% credible interval [CRI] = 0.76–0.86) based on VHF-marked birds. There was evidence of a negative effect of GPS transmitters on adult survival (β = –0.34, 95% CRI = –0.80 – 0.10, P(| β |>0) = 0.93), with GPS-marked sage-grouse predicted to have lower survival (breeding season survival = 0.75; 95% CRI = 0.66–0.82) than VHF-marked sage-grouse. There was no evidence for an effect of increasing abundance of horses above AML_{max} on adult survival (β = –0.0005, 95% CRI = –0.002 – 0.001, P(| β |>0) = 0.76; Figure 2A; Table 2). Because there was no evidence for an effect of sagebrush cover (P(| β |>0) = 0.66), we did not include this variable at any scale in the final model.

We monitored 1,075 nests from 714 unique females between 2008 and 2021, with 600 nests within 8 HMAs and the remaining nests in control areas outside of HMAs that were not exposed to free-roaming horses. Overall nest survival from start of incubation to hatch at 28 days for VHF-marked birds was estimated as 0.52 (95% CRI = 0.49 – 0.56). Daily nest survival increased with nest age (β = 0.05, 95% CRI = 0.046 – 0.060, P(| β |>0) = 1). We found evidence for a negative effect of transmitter type on daily nest survival (β = -0.19, 95% CRI = -0.41 – 0.03, P(| β |>0) = 0.95), with GPS-marked birds having lower overall nest survival (0.45; 95% CRI = 0.39 – 0.53). There was no evidence for an effect of sagebrush cover at any scale (P(| β |>0) = 0.57) and so it was not included in the final model. We found strong evidence that increasing free-roaming horse abundance (%AML_{max}) decreased daily nest survival (β = -0.09, 95% CRI = -0.17– 0.002, P(| β |>0) = 0.97; Figure 2B; Table 2). Overall nest survival was reduced 3.9% when horse abundance was increased from 0% (i.e., outside HMAs) to 100% and 8.1% when horse abundance increased from 100% to 300% of AML_{max} (Table 2).

We monitored 372 broods from 318 unique females between 2008 and 2021, with 372 broods monitored during the early brood-rearing period (\leq 20 days after hatch) and 272 broods monitored during the late brood-rearing period (\geq 20 days to 35 days after hatch). During the early and late brood-rearing periods, 222 and 140 broods, respectively, used 7 HMAs. Survival for the entire 35-day brood-rearing period was estimated as 0.42 (95% CRI = 0.18 - 0.66). We found strong evidence for a positive effect of both brood age (β = 0.07, 95% CRI = 0.04 - 0.10, P(| β |>0) = 1) and sagebrush cover within 205 m (β = 0.04, 95% CRI = -0.004 - 0.08, P(| β |>0) = 0.96) on brood survival. We found moderate evidence that increasing horse abundance (%AML_{max}) had a negative effect on daily brood survival during the early (β = -0.002, 95% CRI = -0.004 - 0.0005, P(| β |>0) = 0.93; Figure 3A) and late (β = -0.002, 95% CRI = -0.004 - 0.001, P(| β |>0) = 0.91; Figure 3B; Table 2) brood-rearing periods. Early brood survival was reduced by 8.1% over 20 days and late brood survival was reduced by 7.3% over 15 days when horse abundance increased from 0% to 100% of AML_{max}. When horse abundance increased from 100% to 300% AML_{max}, early brood survival was reduced 18.3% and late brood survival was reduced 18.2%.

We monitored 136 juvenile sage-grouse (63 males and 73 females) between 2017 and 2022, with 65 using 8 HMAs. Seven-month survival for juveniles from September until birds were recruited into the adult population the following March was estimated as 0.61 (95% CRI = 0.41 - 0.79). Juvenile survival did not differ between the sexes ($\beta = -0.24$, 95% CRI = -0.88 - 0.41, P($|\beta| > 0$) = 0.76) or relative to sagebrush cover within 205 m ($\beta = -0.03$, 95%



FIGURE 2 Effect of the abundance of horses (%AML_{max}) on adult female (A) and nest (B) survival of greater sage-grouse in central Wyoming, USA, 2008–2022. The vertical line indicates a sustainable abundance of horses based on the upper limit of the appropriate management levels (AMLs) set by the Bureau of Land Management. Gray shading represents 95% credible intervals.

CRI = -0.09 - 0.03, P($|\beta| > 0$) = 0.80), but increasing horse abundance (%AML_{max}) had a moderate negative effect on juvenile daily survival (β = -0.002, 95% CRI = -0.004 - 0.0006, P($|\beta| > 0$) = 0.94; Figure 3C; Table 2). Juvenile survival was reduced by 7.9% when horse abundance increased from 0% to 100% of AML_{max} and by 18.2% when horse abundance increased from 100% to 300% of AML_{max} (Table 2).

DISCUSSION

We designed our study to evaluate the influence of free-roaming horses exceeding AML_{max} on multiple vital rates obtained from individually marked sage-grouse across a 15-year window. We found strong or moderate evidence for negative effects on nest survival and both early and late brood survival. In addition, our results suggested there

TABLE 2 Predicted overall survival probabilities (95% credible intervals [CRI]) of greater sage-grouse adult females, nests, early broods (\leq 20 days after hatch), late broods (>20 days to 35 days after hatch), and juveniles (7 months from Sep until recruitment into the adult population the following Mar) at different levels of horse abundance (%AML_{max}) in central Wyoming, USA, 2008–2022, where 100 equals the sustainable abundance of horses based on the upper limit of the appropriate management levels (AMLs) set by the Bureau of Land Management.

	Predicted survival (95% CRI)							
AML_{max}	Adults	Nests	Early broods	Late broods	Juveniles			
0	0.813 (0.76-0.862)	0.542 (0.496-0.585)	0.606 (0.372-0.788)	0.686 (0.476-0.837)	0.608 (0.405-0.792)			
50	0.808 (0.762-0.854)	0.528 (0.489-0.565)	0.582 (0.353-0.766)	0.661 (0.445-0.819)	0.584 (0.398-0.765)			
100	0.804 (0.760-0.848)	0.521 (0.485-0.556)	0.557 (0.330-0.747)	0.636 (0.405-0.806)	0.560 (0.383-0.741)			
150	0.799 (0.753-0.845)	0.509 (0.472-0.544)	0.532 (0.299-0.728)	0.609 (0.357-0.798)	0.536 (0.363-0.712)			
200	0.794 (0.742-0.846)	0.497 (0.457-0.538)	0.507 (0.266-0.712)	0.582 (0.301-0.793)	0.510 (0.338-0.69)			
250	0.789 (0.727-0.848)	0.489 (0.444-0.535)	0.481 (0.229-0.701)	0.551 (0.242-0.790)	0.484 (0.302-0.672)			
300	0.783 (0.708-0.853)	0.479 (0.428-0.531)	0.455 (0.189-0.690)	0.520 (0.185-0.794)	0.458 (0.264-0.661)			

was moderate evidence of a negative effect on juvenile daily survival but no evidence of an effect on adult survival. Predicted declines in survival ranged from 8.1% (nest survival) to 18.3% (early brood survival) when horse abundance increased from 100% of AML_{max} , a level of ecologically sustainable abundance in horse numbers, to 300% of AML_{max} . The effects on sage-grouse vital rates relative to free-roaming horse abundance above AML_{max} are particularly important because they encompass survival rates during key life stages including over winter for juveniles and reproductive life stages (Taylor et al. 2012, Dahlgren et al. 2016).

The negative effects of increasing free-roaming horse abundance on important vital rates provide evidence of a demographic mechanism through which free-roaming horses affect population growth of sage-grouse populations where these species co-occur. Recent research from California and Nevada evaluating the response of sage-grouse lek trends relative to free-roaming horse numbers in HMAs reported that when horse numbers were 2, 2.5, and ≥ 3 times over AML_{max}, the probability of sage-grouse population decline relative to control areas with no horses was 76%, 97%, and >99%, respectively (Coates et al. 2021). Similarly, our results indicate that vital rates for most life stages declined with increasing levels of %AML_{max}. These findings indicate that managing free-roaming horse numbers at low levels of %AML_{max} may be harmonious with maintaining sage-grouse populations where the 2 species share space. Moreover, %AML_{max} was a reliable predictor of the influence of overabundant free-roaming equid populations on sage-grouse populations.

Investigating the effects of free-roaming horses on multiple key vital rates allowed us to develop a more complete picture of the potential impacts on sage-grouse populations. By evaluating multiple vital rates, we can better understand the potential for compounding or compensatory effects across different life-history stages (Doak and Morris 2010). For example, an individual's risk from disturbance, such as that caused by overabundant free-roaming horses, can vary depending on life stage and whether such effects either demonstrate demographic compensation that can ameliorate overall risk or are cumulative over an individual's lifetime to contribute to population-level effects (Doak and Morris 2010, Kissel et al. 2018). Based on our results, predicted effects on individual vital rates varied depending on life stage, but they were consistently negative and thus even small effects can compound over an individual's lifetime, particularly with regards to reproduction. Therefore, our study provides initial findings of horse overabundance as an important demographic mechanism that influences sage-grouse survival and subsequently population growth, where even small effects on reproduction can compound across nests, early broods, and late broods to significantly depress reproductive success of sage-grouse populations (Kissel et al. 2018).



FIGURE 3 Effect of the abundance of horses (%AML_{max}) on the survival of early broods (A; \leq 20 days after hatch), late broods (B; >20 days to 35 days after hatch), and juvenile (C; 7 months from Sep until recruitment into the adult population the following Mar) greater sage-grouse in central Wyoming, USA, 2008–2022. The vertical line indicates a sustainable abundance of horses based on the upper limit of the appropriate management levels (AMLs) set by the Bureau of Land Management. Gray shading represents 95% credible intervals.

The main mechanism by which free-roaming horses influence sage-grouse populations is through indirect effects on habitat characteristics (Beever and Aldridge 2011, Davies et al. 2014, Coates et al. 2021, Street et al. 2024). Indirect effects of high numbers of horses, interacting with drought, compromised habitat for sagegrouse in Nevada and southern Oregon, increased stress in nesting sage-grouse, and led to reduced nest survival (Behnke et al. 2022). Grazing by horses can directly reduce shrub density, reduce overall vegetation concealment cover, reduce key forbs, and increase bare ground (Beever and Brussard 2000, Beever and Aldridge 2011, Davies et al. 2014, Hennig et al. 2021a, Street et al. 2024). This can negatively affect nest survival, in part by increasing the ability of visual predators, such as common ravens (Corvus corax), to find sage-grouse nests (Kolada et al. 2009, Coates and Delehanty 2010, O'Neil et al. 2020). Horse grazing also reduces herbaceous understory, reduces heights of perennial grasses, and promotes invasive plants such as cheatgrass (Beever and Aldridge 2011, King et al. 2019, Street 2020, Hennig et al. 2021a). This change in food and cover resources leads to indirect effects on sage-grouse, particularly during late summer (Street 2020, Street et al. 2024). For example, mesic areas, including wet meadows, temporary wetlands, and irrigated pastures, can provide numerous benefits to wildlife, particularly during late summer (Donnelly et al. 2016) and are important for sage-grouse during the late brood-rearing season (Atamian et al. 2010, Casazza et al. 2011, Lundblad et al. 2022, Severson et al. 2022), despite often only occupying a small fraction of the landscape (Atamian et al. 2010, Donnelly et al. 2016). Horses also tend to congregate in mesic areas, particularly during summer, and can alter riparian vegetation by reducing the height of herbaceous cover and increasing bare ground (Hall et al. 2016, Boyd et al. 2017, Kaweck et al. 2018), all of which can degrade these resources for sage-grouse and depress brood success, which was the most influenced vital rate among those studied here.

Direct effects of increased horse abundance on sage-grouse vital rates are also possible but are less likely to be the primary factors affecting the population. For example, it is unknown whether free-roaming horses depredate sage-grouse eggs or chicks. Historically high numbers of cattle and domestic sheep in north-central Utah, USA, trampled eggs and led to nest desertions by sage-grouse (Rasmussen and Griner 1938), suggesting that high numbers of other grazers including free-roaming horses could have similar effects on sage-grouse nests. Interference competition may be a more plausible mechanism whereby free-roaming horses directly affect wildlife use of scarce resources in sagebrush ecosystems. For instance, recent research has documented horses disrupting male sage-grouse displaying on leks (Muñoz et al. 2021) and similar habitat requirements by sage-grouse and freeroaming horses for perennial grass cover and riparian areas during nesting and brood-rearing, respectively, could provide opportunities for interference competition during these life stages. As an additional example, pronghorn encountering free-roaming horses at water sources increase vigilance, are excluded from water, and reduce time spent foraging and drinking, and larger group sizes of free-roaming horses increased the time pronghorn spent at water sources (Gooch et al. 2017, Hennig et al. 2021b). Research from the northwestern Great Basin reported nesting propensity for sage-grouse was higher in areas with higher densities of free-roaming horses, indicating potential for co-occurrence of horses and nesting sage-grouse in similar habitats (Behnke et al. 2023); this similar pattern of habitat selection during the sage-grouse nesting period was recently documented in Wyoming (Hennig et al. 2023b). Areas with higher densities of free-roaming horses following years of low precipitation reduced nesting propensity of sage-grouse in the northwestern Great Basin, suggesting horses reduced the suitability of nesting habitat during dry years (Behnke et al. 2023).

Free-roaming horse population estimates based on %AML_{max} provided a metric to predict the impact of increasing horse numbers on sage-grouse populations. Vital rates estimated from individually marked animals provide the best information to parameterize population growth models (Frederiksen et al. 2014). Future research could link declines in specific vital rates to population growth rates of sage-grouse within a population modeling framework and extend these analyses using %AML_{max} as a predictor variable to other species including mammals, birds, and herpetofauna. Managing free-roaming equids on federal lands is challenging and greater investments in education have been called for to better educate the public about proper management to solve increasing impacts of these iconic animals on wildlife habitats (Frey et al. 2022).

Our study had several limitations. First, our study was limited to a subset of HMAs in Wyoming and so may not be representative of other portions of the sage-grouse range across the West. Expanding the study to encompass the entire sage-grouse range could provide results that are more broadly representative and increase the sample size of HMAs, which necessarily influences the variation in %AML_{max} and would improve the power of the study. Our results complement similar findings in the Great Basin where lek counts were affected by horse numbers on BLM lands in California and Nevada (Coates et al. 2021). Furthermore, the effects we report on nesting and brood survival of sagegrouse as affected by high horse numbers in Wyoming indicates a process explaining the pattern in lek counts observed in California and Nevada, which is likely generalizable to other areas that support free-roaming horses and sage-grouse. These results provide a strength of support to our study and the study of Coates et al. (2021). Second, available estimates of free-roaming horse abundance are aggregated at the level of HMA and so do not represent fine-scale estimates of horse abundance or use (but see Street et al. 2024 for information on density effects of freeroaming horses on fine-scale vegetation and bare ground attributes in sage-grouse nesting and brood-rearing habitats). Nevertheless, we were able to identify important effects of free-roaming horse abundance on key vital rates despite the coarse resolution of available data, suggesting that fine-scale data may only further refine our understanding of these relationships. Third, we did not evaluate any lag effects associated with removing free-roaming horses and future work could evaluate long-term impacts of the overabundance of horse populations because improving habitat quality following reductions in horse abundance may take years. Finally, we did not explicitly incorporate estimates of cattle grazing and abundance; however, our estimate of horse abundance (%AML_{max}) accounts for animal unit months (AUMs) that have already been delegated to livestock and wildlife within allotments that overlap HMAs (BLM 2010), so in practice overgrazing in these areas is a result of overabundant free-roaming horses. In addition, horses and cattle graze and use the landscape in fundamentally different ways (Menard et al. 2002, Scasta et al. 2016) such that exceeding AML_{max} may have more impact than allowing too many AUMs.

MANAGEMENT IMPLICATIONS

Our research identified the conservation value of maintaining free-roaming horse numbers at low levels of maximum AMLs, which is a key factor in sage-grouse conservation that appropriate rangeland management can rectify to reduce further declines of this imperiled species. Our study helps validate the process of setting AMLs, which is based on a landscape's capacity to support free-roaming equids after accounting for vegetation and soil characteristics, wildlife populations, environmental quality, and other grazing animals including cattle. Our results indicate that vital rates for adult female sage-grouse were similar in areas outside of HMAs, where exposure to freeroaming horses was assumed to be zero, and in areas where horse abundance did not exceed AML_{max}, but that vital rates declined with increasing AML_{max} for most life stages. Collectively, this information will aid in future management of horses at levels that alleviate potential impacts to sage-grouse. This is particularly important considering the burgeoning number of free-roaming horses on public lands where sage-grouse occur and the heightened conservation status of sage-grouse populations that are declining rangewide. Managing free-roaming horses at appropriate levels would be highly beneficial to sage-grouse populations, and other species that rely on functioning sagebrush ecosystems. This situation is amplified because >80% of HMAs exceed AML_{max} (BLM 2018).

ACKNOWLEDGMENTS

The findings and conclusions in this article do not necessarily represent the views of the United States Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank the Bureau of Land Management and Wyoming Game and Fish Department for logistical support. We thank J. Lautenbach, J. Leonard, J. LeVan, H. North, and countless technicians who assisted with field data collection. We also thank J. S. Sedinger and an anonymous reviewer for their comments that markedly improved our paper. Our research was funded through grants from Anadarko

Petroleum Company, Bureau of Land Management (agreement numbers L16AC00156, L17AS00123, L19AC00090, L19AS00013, L20AS00049), Laramie Audubon Society, Wyoming Sage-Grouse Conservation Funds, Wyoming Game and Fish Department, Big Horn Basin, Southwest, South-Central and Wind River/Sweetwater River Local Sage-Grouse Working Groups, and University of Wyoming-School of Energy Resources. Additional support was provided by University of Wyoming Extension and the United States Geological Survey Ecosystems Mission Area.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All sage-grouse were captured, marked, processed, and monitored in adherence with approved protocols for the 2008–2011 Atlantic Rim and Stewart Creek studies (Wyoming Game and Fish Department [WGFD] Chapter 33 permits 572 and 699, University of Wyoming Institutional Animal Care and Use Committee [UW IACUC] protocol 03032009, WGFD and Chapter 33 permit 657, Utah State University IACUC protocol 33-1357), the 2020–2022 Atlantic Rim and 2018–2022 Red Desert studies (Chapter 33-1303 and Chapter 33-1160 permits, UW IACUC protocols 20200317JB00413 and 20170324AP00266), and the Jeffrey City study (WGFD Chapter 33-801 permit, UW IACUC protocols 03132011, 20140128JB0059, and 20170322JL00266).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Associate Editor: Andrew Gregory.

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How to cite this article: Beck, J. L., M. C. Milligan, K. T. Smith, P. A. Street, A. C. Pratt, C. P. Kirol, C. P. Wanner, J. D. Hennig, J. B. Dinkins, J. Derek Scasta, and P. S. Coates. 2024. Free-roaming horses exceeding appropriate management levels affect multiple vital rates in greater sage-grouse. Journal of Wildlife Management 88:e22669. https://doi.org/10.1002/jwmg.22669