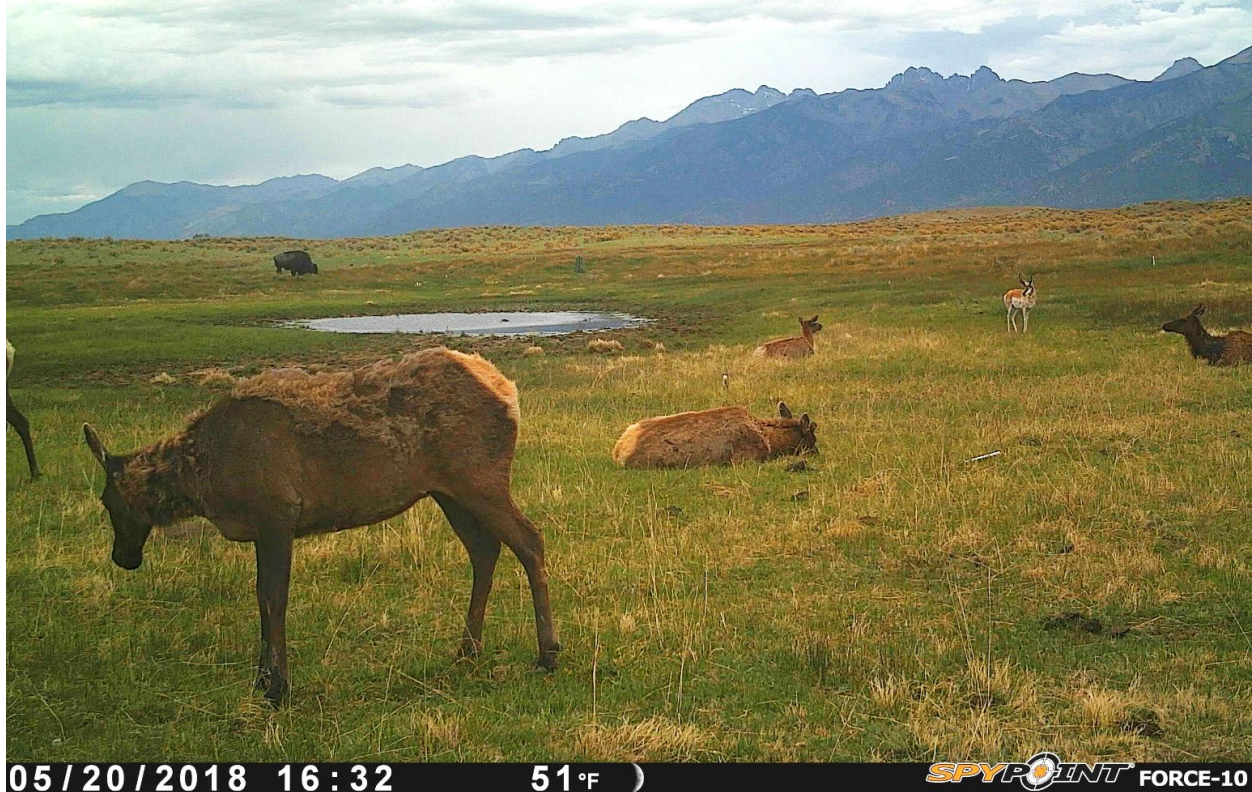


Wetland Habitat Use by Elk and Bison in Great Sand Dunes National Park



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Cover photo: Bison, elk and pronghorn graze an herbaceous wetland at Great Sand Dunes National Park and Preserve, 2018. NPS/WILDLIFE CAMERA

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Introduction

Ungulates, including native and introduced species, play an important role in the ecosystems of many protected wildlands of national and state parks, forests, and wildlife refuges in North America (Hobbs 1996; Singer et al. 1998; Singer and Schoenecker 2003). However, protection from hunting, lack of predation, and human-induced changes to vegetation composition and productivity in protected landscapes can also promote over-concentration of ungulates in certain habitats. When overconcentration of ungulates becomes too great, habitat degradation, including changes to plant species composition, productivity, soil physical and chemical properties, and water quality can follow. Ungulate use can vary both spatially and temporally over a landscape in response to a diverse suite of factors, such as forage and water availability, ambient temperature and precipitation, drought, inter- and intra-species competition, population demographics, species-specific behavior and feeding preferences, barriers to movement, and gradients in human disturbance (Schweiger et al. 2016). Effective management actions must consider seasonal variations in ungulate use as well as spatial distribution on a landscape.

Estimating the spatial and temporal distribution of ungulate use can prove challenging, time-consuming, and expensive. Some methods require multiple visits to sites within and across years, whereas other methods require constant monitoring of ungulates and habitats. Three methods are commonly used to gather information on ungulate density, behavior, and movement within and between habitats on a landscape: dung surveys, telemetry studies, and camera surveys. Each method has distinct advantages and challenges for determining the intensity, duration, and temporal variations in ungulate use of a site.

Surveys of animal fecal deposits (also called “dung pellet piles” or “dung pats”) have been a long-established method of relating dung deposition to habitat use, population trends, and population density (Eberhardt and Van Etten 1956; Neff 1968; White and Eberhardt 1980; Rowland et al. 1984; Edge and Marcum 1989; Marques et al. 2001; Webb et al. 2011; Brinkman et al. 2013; Griffin et al. 2014). The abundance of dung in an area is dependent on the number of animals using a specific area, the rate of dung production (defecation rate), and the rate at which dung piles/pats disappear due to decomposition, scattering, or concealment caused by vegetation growth or senescence, burial by loose soils moved by wind or water, or deposits of new dung piles on top of old ones. Dung counts are not perfect, and estimates may be biased because defecation rates vary by diet, season, and ungulate species, and because detectability of dung is affected by size, shape, and cohesiveness of the dung, animal activity at the site, climate, and habitat type. However, dung counts have been found to produce similar results for relative habitat use as results achieved from radio tracking and direct observation (Edge and Marcum 1989; Mänsson et al. 2011; Hema et al. 2017).

Dung counts offer benefits in that they can indicate animal presence at a location after the animals themselves have left the area; however, they may underestimate use if animals do not defecate during the time they use a site or they may overestimate use if dung persistence or detectability differs across habitat type and this is not accounted for (Campbell et al. 2004). Nevertheless, many studies have found positive relationships between known animal densities and indices derived from dung

pellet counts, such as total dung pellets, total pellet groups, and pellet frequency (Marques et al. 2001; Forsyth et al. 2007; deCalesta 2013; Hema et al. 2017), leading to the conclusion that dung surveys can be useful indices of animal abundance. Use indices derived from dung counts can also be used following management actions to assess the effectiveness of those actions at reducing ungulate use in target habitats.

Telemetry collars and tags have also long been used to identify movement patterns and habitat selection of wildlife species of interest (Mech 1967; Ables 1969; Sparrowe and Springer 1970). In recent decades, collars employing global positioning system (GPS) technology have provided researchers with the ability to obtain more detailed information on animal locations, including greater location accuracy and information about use patterns over shorter time scales by using satellites to obtain locations multiple times each day. This has improved how collar-based data is used in support of wildlife population management (Cleveland et al. 2012; Proffitt et al. 2013). For animals that move often over a 24-hour period and for small habitat patches, however, telemetry data may fail to capture habitat use if the time interval between acquisition of locations is too long. This issue can be resolved through analysis methods that interpolate point location data to create surfaces which have ungulate use values assigned across areas based on density of telemetry locations. Whereas modern GPS collars reduce the amount of time required for field work compared to earlier radiofrequency telemetry collars, there are still high costs associated with the capture and fitting of collars to animal subjects and costs of collars and data retrieval. This often leads to small sample size relative to overall population size for telemetry studies and the need for careful study design.

Over the past two decades, automated cameras have emerged as an important tool to detect elusive species, estimate occupancy and abundance of animals, and learn more about species' use of habitats as well as intra- and inter-specific interactions in particular habitats (Burton et al. 2015; Sollman 2018; Wearn and Glover-Kapfer 2019). Wildlife cameras can provide information that would otherwise require 24-hr monitoring of sites by observers, providing accurate data without an animal being captured or a researcher being present. Moreover, unlike data produce by live-trapping or observations, images from a camera trap can be reviewed by other researchers (O'Connell et al. 2011; Gooliaff and Hodges 2018, 2019). They produce results that may be less biased than methods that require a human presence, which can affect animal behavior and space use. They also allow site-specific data collection, which is important for habitat studies (Bowkett et al. 2007; Rovero et al. 2014). However, camera-trap studies must be carefully designed; there can be real problems with camera performance and often the amount of data produced and in need of quality assurance and analysis can be overwhelming (Hamel et al. 2013; Burton et al. 2015; Scotson et al. 2017; Sollman 2018; Kays et al. 2020).

In Great Sand Dunes National Park and Preserve (GRSA), park managers need information on the use of wetlands by elk (*Cervus elaphus*) and bison (*Bison bison*). GRSA and the National Park Service (NPS) Inventory and Monitoring Program's Rocky Mountain Network (ROMN) have been conducting a multi-year effort to determine the effects of ungulate use on GRSA wetlands as part of GRSA's Ungulate Management Plan (UMP) (Schweiger et al. 2017; NPS 2018). Data collected during this effort will be used to determine gradients in ungulate use that contribute to degradation

and loss of wetland habitats in the park. All three methods of quantifying ungulate use described above have been employed to quantify elk and bison use of GRSA wetlands. This report uses these data to describe the status of ungulate use in GRSA wetlands in both space and time. Ungulate use indices described in this report will be incorporated into models that will relate ungulate metrics to wetland habitat quality metrics developed by ROMN. These models could be used to help estimate thresholds in ungulate use–wetland condition relationships and determine factors that influence ungulate use of wetland sites, both of which will help target management to use at sites where it has the greatest impact. GRSA plans to implement elk management activities that will move elk away from sensitive and/or high use wetland areas in the park using hazing and culling. Information gathered using one of these methods (dung counts, cameras, and telemetry collars) may also be used to monitor response of animals to these management actions. Post-management-action values of ungulate use indices can be inputted into models to identify areas where management is succeeding at reducing ungulate use of wetlands and this success would be verified by improving wetland metrics.

Study Area and Context

Great Sand Dunes National Park and Preserve covers an area of 605 km² entirely within the San Luis Valley of south-central Colorado. The San Luis Valley is a high elevation desert and lies within the Great Basin Desert zone (Barbour and Billings 2000) and the Southern Rocky Mountains floristic zone (Daubenmire 1943). The park portion extends from the base of the foothills of the Sangre de Cristo Mountains in the east approximately 20 km across the valley floor to the west between the community of Baca Grande to the north and Alamosa County Lane 6 to the south. The park boundary includes lands on the Medano Ranch presently owned by The Nature Conservancy (Figure 1). The Baca National Wildlife Refuge (Baca NWR) bounds the park on the west. The preserve portion of GRSA extends eastward from the park to the crest of the Sangre de Cristo Mountains. The park portion is the focus of this study and is referenced by the term “GRSA.” Both GRSA and Baca NWR are entirely within Colorado Parks and Wildlife Game Management Unit (GMU) 82. The UMP study area used in these analyses includes approximately 31.4 km² of sandsheet wetlands within GRSA; however, analyses of elk home range extends to approximately 413 km² of all habitat types in Great Sand Dunes National Park below 2,744 m elevation, including the dune field and surrounding lands on the valley floor, as well as roughly 65% (10,482 ha) of the current fenced bison range (Zeigenfuss and Schoenecker 2015).

Precipitation, primarily in the form of rainfall, averages 28 cm annually and falls mostly during monsoonal rains in July through September. Summers are warm with average daytime temperatures ranging from 26.5 °C to 29.5 °C on the valley floor. Winters are cold and relatively dry with average valley daytime temperatures ranging from −9.5 °C to 1.5°C. Elevations on the valley floor range from 2,285 m to 2,744 m.

The valley landscape contains the highest sand dunes in North America (229 m). The sand dunes contain blowout grass (*Redfieldia flexuosa*) growing in low densities atop the most active dunes. A sand sheet surrounds the active dunes complex to the west, north, and south, and is dominated by greasewood (*Sarcobatus vermiculatus*) and rubber rabbitbrush (*Ericameria nauseosa*). Wetlands

within the sandsheet are either flooded ephemerally in the spring from mountain snowmelt or are watered from natural springs. Wetlands typically support dense ground cover of sedges (*Carex* spp.) and other wetland vegetation. Sixteen of the 48 vegetation types on the current park vegetation map occur on our study area (Salas et al. 2011).

GRSA is among the most ecologically diverse national parks in the world (NPS 2007), owing to a wide range of habitats and microclimates. Wetlands within the park are also diverse, ranging from alpine fens occurring above 3600 m, to montane riparian wetlands and seasonal wet meadows, to marsh and salt flat wetlands embedded in the sandsheet west of the main dunes (2290 m; Schweiger et al. 2017). Wetlands on the sandsheet are supported by several different water sources. One source is surface runoff flowing out of the adjacent Sangre de Cristo Mountains. Other sources are unique groundwater systems, many of which emerge from under the main dune field (Wurster et al. 2003). And finally, some are “introduced wetlands” (NPS 2007) created by human actions, including building ditches and other agricultural features, such as stock tanks, which have created wetland (Schweiger et al. 2017). Cottonwoods (primarily narrowleaf cottonwood, *Populus angustifolia*) and willows (primarily coyote willow, *Salix exigua*) grow atop some dunes, along Sand and Deadman Creeks, portions of Medano Creek, and near springs.

Wetland ecological integrity data were collected from 2010 to 2014 to determine baseline wetland condition and recent trends (Schweiger et al. 2017). Ungulate disturbance ranged widely across all sites in 2010, with 21% of the park wetlands experiencing major ungulate use, 33% experiencing moderate use, 33% experiencing minor use, and 13% of sites experiencing negligible ungulate use with no indication of overuse by ungulates. Riparian wetlands experienced higher ungulate use due to bison ranching operations that concentrated bison in areas with riparian wetlands and due to higher vegetation productivity in these sites. Trend models indicated that ungulate use increased 24% from 2010 to 2014 in sites along Big Spring Creek (Schweiger et al. 2017).

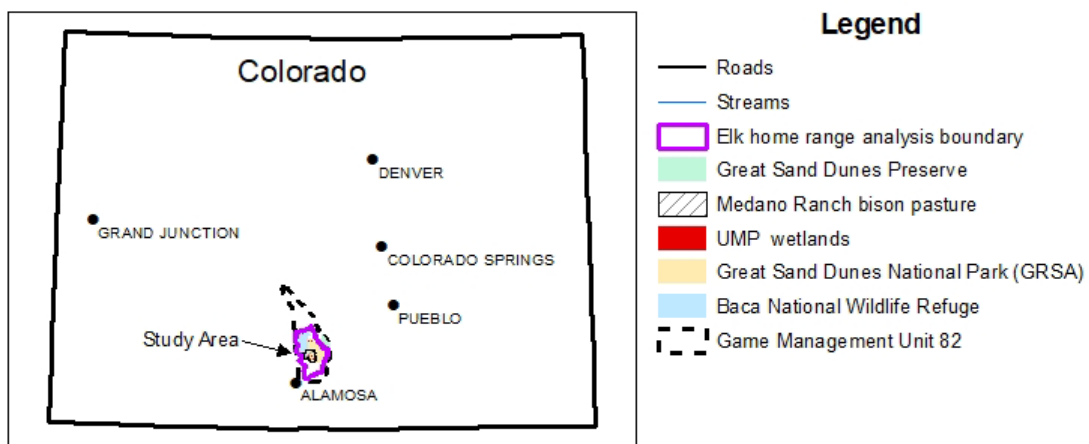
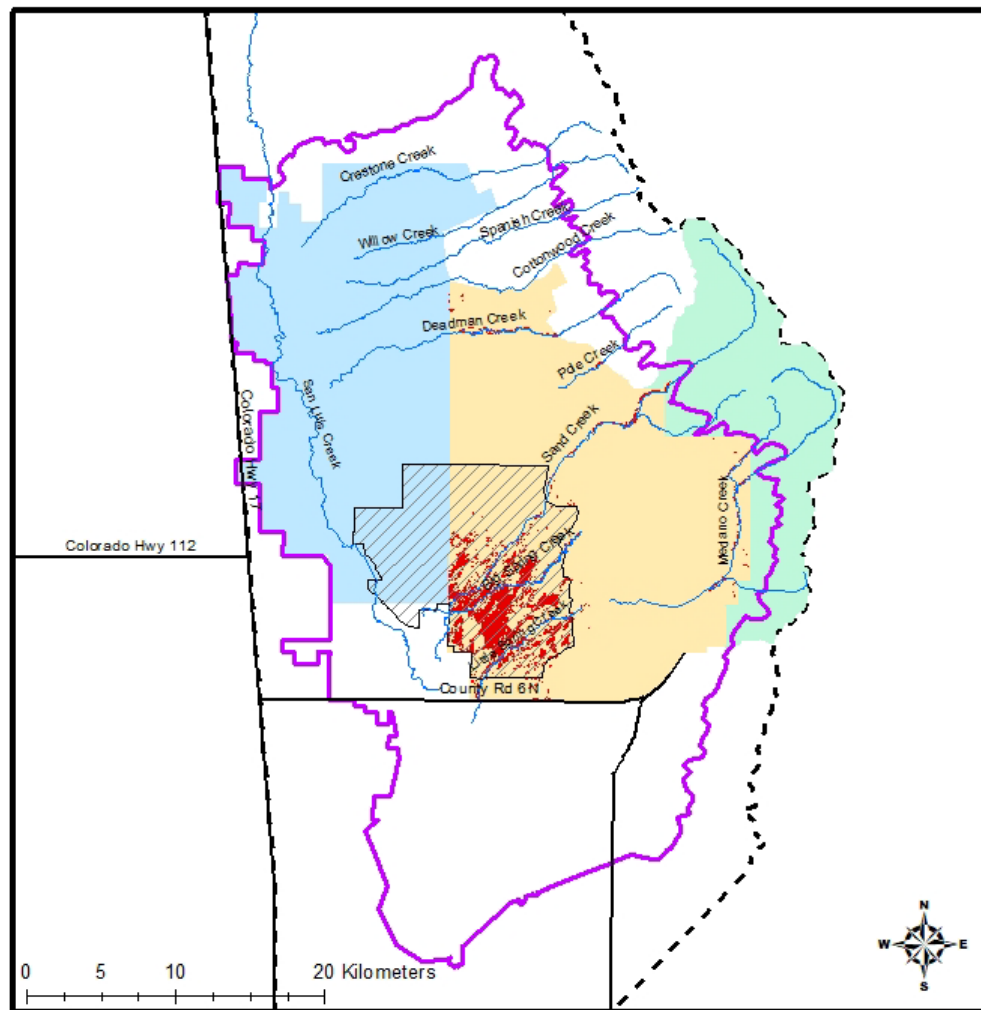


Figure 1. Location of analysis areas in relation to federal land boundaries and state wildlife management area around Great Sand Dunes National Park and Preserve, Colorado. Inset shows location within state of Colorado.

Ungulates in GRSA

Bison, elk, mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) were native to the area until about the turn of the 20th century when bison were extirpated and numbers of the other species were much reduced (Meany and Van Vuren 1993). Elk and pronghorn survived in small numbers (Warren 1910; Cary 1911; Swift 1945), and some animals likely moved back into the area from surrounding populations to the north and south, as well as from nearby animal releases by the Colorado Division of Wildlife (now known as Colorado Parks and Wildlife (CPW)) from the 1910s through the 1960s (Swift 1945; Colorado Division of Wildlife 2010). Elk were rarely noted in the study area prior to the late 1990s (Colorado Division Wildlife 2010). Elk roam freely throughout the study area, including the Medano Ranch bison pasture. In the late 1980s a commercial bison herd was established on private lands of the Medano Ranch. Bison are restricted by fencing to a 16,100 ha area on the Medano Ranch that lies about half within the boundary of GRSA and half within the boundary of the Baca National Wildlife Refuge. Ungulate populations in the valley are regulated by hunting, except for bison which are gathered and culled annually to maintain population levels. Finally, moose (*Alces alces*) have recently begun to expand their range into the study area but are present at low numbers.

Bison population data are collected by Zapata Partners and US Geological Survey (USGS) during annual roundup and culling of the bison herd each November. Schoenecker (2012) developed a state-space bison demographic model based on these data collected from 1993 to 2011 and has updated this model with data through 2018. State-space modeling is ideally suited for situations where there is uncertainty about the processes that affect population dynamics, and when observations of population size contain error. Model inputs include counts of adult female bison from 1993 to 2000 and counts for each of 4 age/sex classes (calves, female yearlings, adult females, males greater than 1 year old) after 2000. Estimated bison population size varied from 1993 to 2018 (Figure 2; Schoenecker 2012; Schoenecker et al. 2015), ranging from a low of roughly 1,000 animals to a high of about 2,500 animals. Estimated population size was held at approximately 2,000 animals from 1993 to 2001, when it dropped to an average of about 1,400 animals from 2002 to 2007. Bison population size was allowed to increase after 2007 and between 2008 and 2018 averaged closer to 2,150 animals, though a brief reduction in 2011 and 2012 dropped the herd size to ~1,750 (Figure 2). This reduction was followed by a return to a larger herd size.

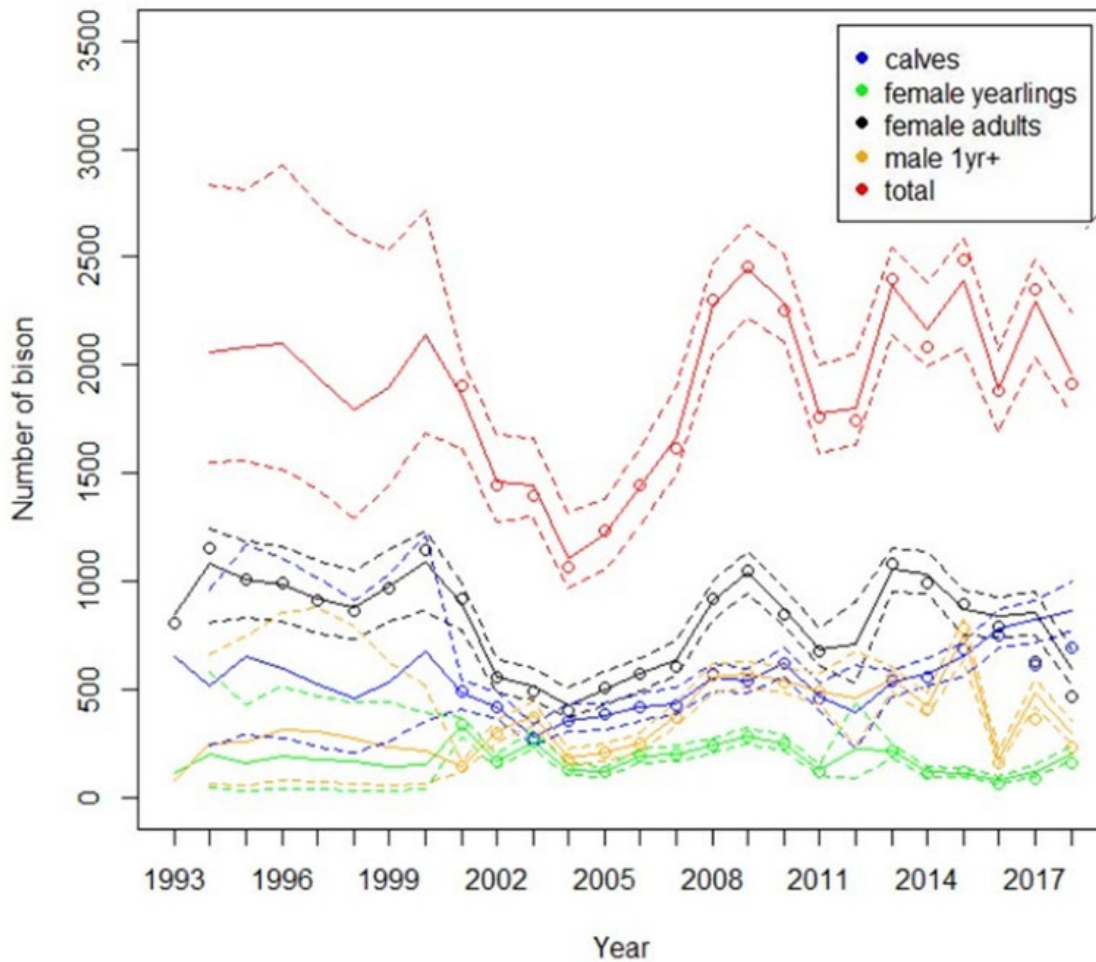


Figure 2. Raw counts (open circles) and modeled bison population size inside the bison pasture in Great Sand Dunes National Park and Preserve, Colorado, 1993-2018. Data provided by Kate Schoenecker, Research Ecologist, U.S. Geological Survey.

Post-hunt elk population estimates from Colorado Parks and Wildlife (CPW 2005-2020) from 2005 to present for GMU 82, which includes GRSA (Figure 1), suggest a general downward trend in elk population size on GMU 82 from 2005 to roughly 2015, but from 2016 to 2020, the elk population appeared to be increasing (Figure 3; CPW 2005-2020). These estimates are modeled based on biannual aerial game surveys and annual hunter harvest data. However, available data on elk population applies to the entirety of GMU 82 and cannot reliably be downscaled to a smaller reporting area such as the park.

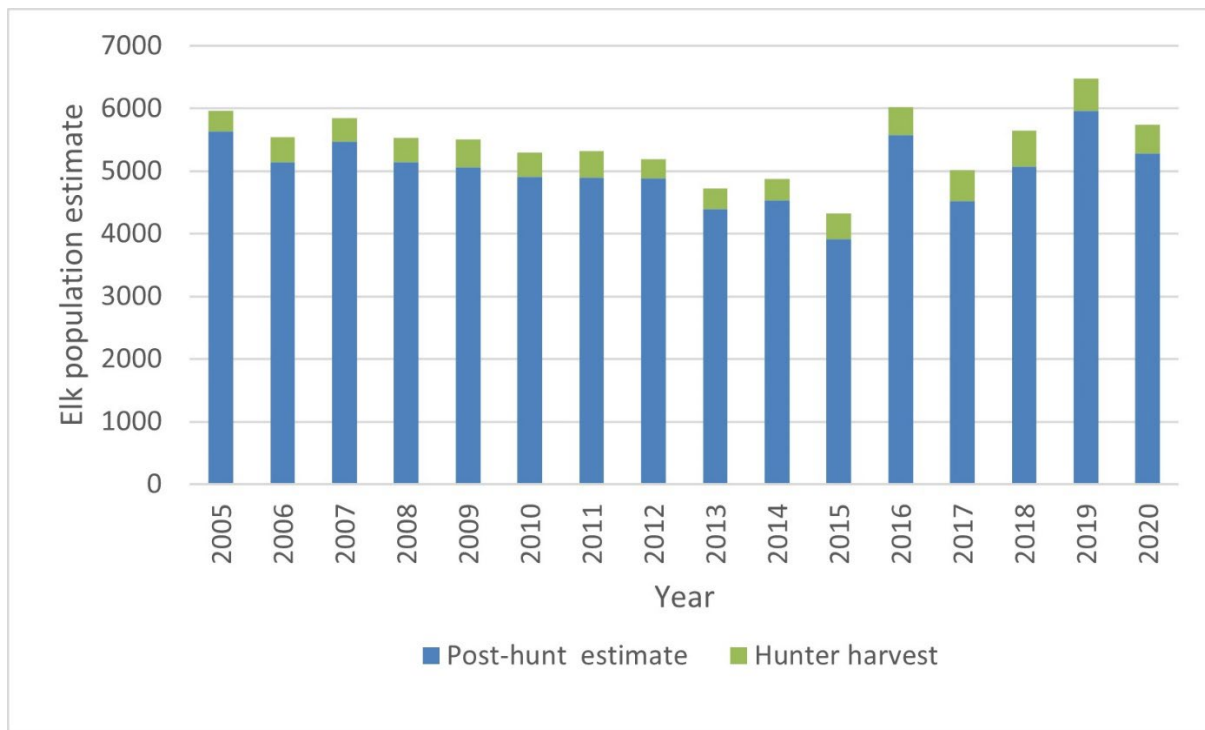


Figure 3. Post-hunt elk population estimates and hunter harvest estimates for Game Management Unit 82, Northern San Luis Valley, Colorado (Colorado Parks and Wildlife, 2005-2020).

Field Methods

Sites, Sample Events, and Plot Layout

A total of 74 sites were selected and sampled a total of 103 times for this study. These sites are collectively known as Ungulate Management Plan (UMP) sites. Twenty-nine sites were originally established in 2010 as part of the Wetland Ecological Integrity (WEI) Monitoring Program (Schweiger et al. 2017). UMP protocols were added to WEI protocols at 10 of these sites in 2016, 9 in 2017, 2 in 2018, and 8 in 2019. An additional 45 sites were established as UMP wetland sites between 2016 and 2019 (7 in 2016, 14 in 2017, 16 in 2018, 8 in 2019). UMP sites are wetland complexes with several plots established within the complex. ROMN ecologists used a classic approach to defining wetland boundaries based on vegetation, soils, and hydrology. Initial boundaries were defined using geospatial data and then refinements were made in the field based on observed wetland characteristics. In most cases GRSA wetlands are well-bounded. Ideal sites have one dominant wetland type, though small inclusions of other wetland types often occur within the complex. The maximum axis for a site was 100 m, thus maximum complex size is 100 m x 100 m or 1 ha. Some complexes were discontinuous (i.e., several patches that were clearly the same wetland but broken up by features like a stream). When hydrologic regime clearly varied and included several patches of different wetland types, then single, smaller patches were used to delineate the site. Most complexes contained a WEI or USGS legacy groundwater well or these were added to most sites as part of UMP sampling.

These sites fell into 2 distinct ungulate zones: areas inside the bison pasture where elk and bison (EB) both had access to wetland sites, and areas outside the bison fence where only elk had access to sites (E). However, after the study design was implemented, we discovered that bison were able to access wetlands in the area outside the northeast boundary of the pasture during times when the bison fence was in disrepair and that they were using many of these wetlands often and visiting in large groups. As a result, we identify a third ungulate zone where there are elk and some trespass bison (EsB).

We also classified each UMP site as 1 of 3 major wetland types following Schweiger and others (2017). Salty meadows include the continuum of wetlands from salt flats through wet meadows. Herbaceous riparian and woody riparian sites were located along riparian corridors and included typical, high gradient mountain streams as well as ephemeral and perennial spring-fed corridors on the sandsheet. Herbaceous riparian sites are dominated by herbaceous species, with high cover of graminoid species such as sedges, rushes (*Juncus* spp.), and various grasses. Woody riparian wetlands at GRSA are dominated by woody vegetation, especially willows and cottonwood.

At each site, a 10 m x 10 m (100 m²) “core” plot was established in the location that was most representative of the site as a whole. At these plots, vegetation composition and cover, woody vegetation height, soil characterization and chemistry, ground water depths, photos, and dung data (i.e., pellet counts) were collected. Between 1 and 5 additional 100 m² circular plots (11.2 m diameter) were established for both pellet counts and vegetation measures (PRW plots), or pellet counts only (P plots). The number of plots that measure both vegetation and pellet counts (PRW) was determined subjectively at the establishment of each site by the number of vegetation types observed

in the complex. The number of pellet count only plots (P) was similarly determined by dung density heterogeneity. If the range of observed dung density was adequately captured in the PRW plots, then no additional P plots were measured. Small sites with no variation in vegetation only had a “core” plot. Plots within a site did not overlap and were a minimum of 10 m from each other.

Dung Pellet Counts

Plots were divided into 4 equally-sized quadrants (to improve efficiency and accuracy of dung data collection) and counts of the number of dung piles in each quadrant were totaled by ungulate species (elk and bison) and age of dung pile (old or new). New dung deposits were defined as pellets or pats that were >5% green and wet, whereas old dung was defined as <5% green and wet. Individual deposition events were defined as 10-15 pellets in a group (winter elk) within a 30 cm diameter circle, or distinct dung pats (bison; summer elk). Single pellets or small patties that were not likely a distinct deposition event from the same animal were not counted. Elk dung pats >4.6 cm in diameter were also counted as distinct deposition event. All distinct pellet groups and pats within the quadrant, as well as those touching the plot edge, were counted. A second observer made an independent count of a subset of plots at several sites as time allowed.

Starting in 2018, we added methods to test the accuracy of definitions of new versus old dung, as well as to add to our understanding of seasonal ungulate use and fecal accumulation rates in wetlands. In 2018, four sites were cleared of all pellets and pats after an initial count in mid-June. These sites were revisited in mid-late July of 2018 and recounted but not cleared again. Visits were made to these 4 sites in mid-June 2019 as well as an additional site that was not cleared in 2018. June dung counts were performed at these 5 sites, and the sites were cleared of all pellets and pats after counting. The sites were revisited in mid-July 2019 and dung counts were performed again but no clearing took place after the July count. No sites were counted in 2020 due to field work restrictions related to the covid-19 pandemic.

2021-2023 Dung Disappearance Study

UMP methods measured fecal standing crop (FSC) and calculation of density from these data requires a known disappearance rate for dung or a fecal accumulation rate (FAR). To use a fecal accumulation rate, dung count plots must be revisited within a time period shorter than the disappearance time of the dung and plots must be cleared of dung after each count. The data collected in GRSA only measured FAR over a 1 month and 12-month period for 5 sites, thus limiting development of an index based on accumulation rates. Therefore, we decided that habitat-specific dung disappearance rates were needed to correct fecal standing crop counts to reflect ungulate use appropriately. Disappearance rate includes both decay of dung and the ability for crews to relocate dung, which is influenced by the detectability of any given dung pile. Jung and Kukka (2016) found that disappearance rates for elk dung in Canada were greatest in open and wet habitats and least in dry, forested habitats where dung pellets persisted for 3 growing seasons (28 months). Barber and others (2019) observed that bison dung pats lost 75% of their mass in as little as 1 week on restored and remnant tallgrass prairie in Illinois and nearly 100% of their mass after 5 weeks. However, we could find no estimates of decay or disappearance specific to elk or bison (or any large ungulate) in the unique, high desert (with important wetland inclusions) environment of GRSA.

To address this, ROMN and GRSA biologists began a study of habitat specific disappearance rates at 10 UMP sites in May 2021. Sites were selected to include the major wetland types (herbaceous riparian, woody riparian, and salty meadow) in each ungulate zone (elk, elk and bison, elk some bison). Seven of these sites were also monitored with wildlife cameras starting in 2016. Plots used in the disappearance study were set up in the same manner as described above for dung count plots but could not overlap existing plots. At each dung plot in the disappearance study, all bison and elk dung piles were counted and classified as fresh, completely dry, starting to decay with one or more pellets decomposing, 50% of the pile decomposed but still identifiable, or in a state of complete decay. All fresh piles were retained, all others were removed from the plot. Up to 10 of the fresh piles were marked with numbered tags. If fewer than 10 piles were found on the plot, then additional fresh piles were moved into the plot from nearby at the site and marked with a tag until a total of 10 marked fresh piles was reached. Sites were revisited at intervals throughout the following year (at roughly 45 days, 85 days, 300 days, 365 days) and the dung plot was searched for tagged piles and age/condition of the piles was reclassified. If a marked pile could not be found, it was recorded as missing and whether the ID tag associated with the pile was found. Pile diameter and approximate number of pellets in each marked dung pile were recorded at all visits. Final visits were made to all sites at approximately 2 years after dung study plots were established.

Telemetry Collar Data

Analyses of telemetry collar data were structured around 3 distinct areas of GRSA and surrounding lands where elk range. Data were first summarized in a region defined by the park vegetation map (Salas et al. 2011) but restricted to be below the high elevation boundary of the pinyon-juniper zone (Figure 1). This area encompasses the entirety of Great Sand Dunes National Park, Baca National Wildlife Refuge, and the Medano Ranch bison pasture. It also includes areas of Great Sand Dunes National Preserve, Rio Grande National Forest, and private lands to the north, east, and south of GRSA. The vegetation map was clipped along the eastern edge at the upper boundary of the pinyon-juniper zone to focus mainly on the area of the valley floor where UMP wetland sites were located. This region is referred to as the “elk home range analysis area” (Figure 1). Data were summarized within the National Park portion of the GRSA boundary. This region is owned by the NPS and is entirely on the sandsheet, below the high elevation boundary of the Pinyon-Juniper zone and does not include any part of the Great Sand Dunes National Preserve (Figure 1). This area is referred to as the “park analysis area” (Figure 1). Finally, a subset of results is reported at the scale of the Medano Ranch bison fenced area only. This area is referred to as the “Medano Ranch bison pasture” (Figure 1). Our analysis included historical data from radiotelemetry collars placed on elk and bison as part of research conducted by USGS/NPS/CPW in 2005-2007 (hereafter USGS dataset), and collars placed by NPS on elk (hereafter NPS dataset) in 2019-2020.

USGS Collars, 2004-2006

USGS deployed 47 very high frequency (VHF) and 18 global positioning system (GPS) collars on 65 elk captured from across GMU 82 (Figure 1) beginning in February 2005 and on 18 Medano Ranch bison (14 VHF and 4 GPS) in mid-November 2004 (the VHF collars) and in mid-November 2006 (the GPS collars). A total of 23 times (13 VHF, 10 GPS) during the study, these researchers placed collars on new individual elk mid-study when the original collar was removed due to malfunction or

mortality, resulting in a total of 88 (60 VHF and 28 GPS) collared elk. The purpose of these collars was to collect data to be used in determining population demography, habitat selection, and movements of the elk and bison in this area.

Bison VHF and GPS collars in the USGS dataset were active for varying lengths of time from November 2005 to December 2007 (VHF) and from November 2006 to November 2007 (GPS). Every VHF collared bison was visually located once every 1-2 weeks by ground search. GPS collar location times varied from once per day to once per hour, depending on the animal. No data on the distribution of bison within the bison pasture have been collected since the end of the 2007 study. However, because the bison herd is confined to their habitat by the bison fence, USGS bison location data were used to approximate current bison range use.

Elk GPS collars in the USGS dataset were active for varying lengths of time (7 to 21 months) between February 2005 and December 2007, but most were only active for 12 months. These collars varied in the number of locations acquired daily, with some collars collecting hourly data, while others collected locations once every 4 hours and others once every 5 hours. Elk VHF collars were active for varying lengths of time from 1 to 33 months. Both VHF and GPS collars were located by aerial surveys and/or targeted ground surveys at least once every 2 weeks.

The USGS data were used by R. Boone, Natural Resources Ecology Lab, Colorado State University to develop a range map for elk as part of a carrying capacity modeling exercise (Wockner et al. 2015). Boone developed kernel density home ranges for each collared elk and then developed a map of overlapping home ranges (based on 90% isopleths) by “stacking” these home range maps to determine density of use for elk in the study area. Data from GPS fixes and aerial survey data for all 88 elk collars were used to develop the final home range overlap map. Data and finalized maps were provided to B. Schweiger, Rocky Mountain Network, NPS Inventory and Monitoring Program, in 2014.

NPS Collars, 2019-2020

In March 2019, NPS researchers fitted 35 female elk located in the elk home range analysis area with Globalstar (n=33) and Iridium (n=2) GPS collars. The dataset analyzed here extended from late March 2019 through April 1, 2020. The Globalstar collars collected 2 locations each day at 6 am and 6 pm local standard time. The Iridium collars collected 6 locations each day at 2 am, 6 am, 10 am, 2 pm, 6 pm, and 10 pm.

Harmonizing Historical and Current Telemetry Data

Several key differences between the USGS and NPS datasets required reconstruction of the overlapping USGS elk and bison home range maps following R. Boone’s methods. The USGS range maps were constructed from daily GPS fixes as well as those developed from aerial surveys and ground tracking of VHF collars. Aerial survey and ground tracking data were not available for the NPS data. Elk captures for the USGS dataset occurred over a much larger area, well beyond the GRSA boundary where captures for the NPS study occurred. Deconstruction of the bison range density map included in Wockner et al. (2015) indicated that the map was created by overlaying maps of buffered locations for each collared bison, instead of overlapping kernel density home

ranges. As a result of these differences, the current analysis required construction of new 90% kernel density home ranges for bison and elk, so that elk and bison distribution and habitat use could be compared in a similar manner across datasets. As a result, maps presented here may differ from those found in Wockner and others' (2015) analysis.

For each individual collar in the NPS dataset, the first 5 days of locations after the collar was put on the animal were removed to eliminate any influence the capture event may have had on the animal's movements. Locations with a GPS horizontal error (a measure of positional accuracy) greater than 55 m (Globalstar collars) or a dilution of precision (DOP) greater than 10 (Iridium/USGS collars) were also removed. DOP is a location error related to the distribution of satellites in space and their geometry (Langley 1999). Low DOP values usually represent better GPS location accuracy because of wider angular separation between the satellites (Langley 1999). The decision to remove locations with a horizontal error greater than 55 m was based on examination of the data and consultation with Dewane Mosher, GRSA biologist, and typically resulted in the removal of 2-3% of locations from the dataset. Removal of DOP values greater than 10 was based upon general recommendations and practices found in the literature (Moen et al. 1996, 1997; Lewis et al. 2007) and resulted in removal of roughly 2% of locations as well.

To make the data between the two time periods as comparable as possible, elk that were not captured on GRSA or Baca NWR were removed from the USGS dataset. Additional examination of the USGS collar data and the original home range overlap map revealed several individuals with a large number of locations at GRSA Headquarters and at a location to the west of GRSA, which were assumed to be another office where collars were kept prior to deployment. Most of these locations were dated at the very beginning of the deployment as well, which further supports the assumption that these were collars that were transmitting prior to deployment on elk. All these locations were removed from the dataset, as well as locations recorded during the first 5 days following deployment and locations with DOP values greater than or equal to 10 as was done for the NPS dataset. The USGS elk collars varied in the number of locations acquired daily, with some collars collecting hourly data, while others collected locations every 4 hours and others every 5 hours. Two locations each day that were collected at times closest to those in the NPS dataset were used in the USGS collar datasets. The final USGS elk data (trimmed as described above) included 16 individuals; however, some individuals did not have enough data available to calculate seasonal home ranges for all seasons because of collar malfunctions or animal mortality, which shortened the data collection period to less than a full year.

The bison GPS collar data were limited to 4 individuals, one having only 3 months of location data, so it was necessary to include the VHF collar data to expand the set of data points that contributed to the final seasonal and year-round overlapping home range maps. Location data were trimmed to remove early locations after animals were collared and null locations when the collar was transmitting data but not attached to a bison. VHF collar data were collected only during the daytime, likely resulting in biased location data that favored open areas accessible by road where the bison spend their daylight hours and are easiest to locate. These locations were acquired once every 1-2 weeks, with fewer locations acquired during the late fall through winter. To estimate bison movements and distribution relative to various habitat throughout day and night, bison GPS location

data were trimmed to remove only locations with high DOP values and early and null locations as described previously. In the absence of collar-based data on bison distribution in 2016 to 2019, it was necessary to assume that bison distribution and habitat use had not meaningfully changed over the past 13-15 years. These assumptions may not be entirely valid given the change in bison population size between 2005-2007 and 2016-2020 (Figure 2) and the ability of bison to access areas outside the bison pasture due to fence failures.

Home Ranges

The Home Range Tools® (HRT) for ArcGIS v.1.1 (Rogers and Kie 2011) was used to create kernel home ranges for both current/historical elk and historical bison telemetry data following R. Boone's methods provided in written communication with B. Schweiger in 2014. HRT settings files from Boone's analysis were used to parameterize the HRT tool. For each collared individual, all locations in the trimmed dataset were used to create a year-round home range. These home range maps are titled "year-round" instead of "annual" because few collars aligned with January-December dates within a single year. Trimmed location data for each collared individual were subsetted into those locations collected in fall (September-November), winter (December-February), spring (March-May), and summer (June-August) to create seasonal home range maps for that animal. Kernel density utilization distributions were estimated using an adaptive kernel method and a smoothing parameter determined by least-squares-cross-validation (Rogers and Kie 2011). Kernel analysis is a nonparametric statistical method for estimating probability densities from a set of points and the resulting utilization surface describes the probability of finding an animal in any one place (Worton 1989; Rogers and Kie 2011). Home ranges were derived by summing the volumes of the kernels at grid intersections and then producing isopleths that define home range polygons at different probability levels (Figure 4). Following methods used by R. Boone, 90% probability contours (isopleths) were created for each home range in HRT and then converted to raster files reclassified to values of 0 (outside individual home range) and 1 (inside individual home range).

After development of seasonal and year-round 90% kernel density home ranges for each animal, all home range files were summed for each species for both USGS and NPS datasets by season and over all locations to create seasonal and year-round "density of use" maps using the Raster Calculator function in ArcMap (Figure 4). These raster maps had integer values that reflected the number of overlapping home ranges at any given cell. Because of differences in the number of collared animals whose home ranges contributed to any seasonal or year-round map, these numbers were standardized by estimating the proportion of total home ranges that overlapped at that spot. This was done to allow for comparison between NPS and USGS datasets, and between seasons. Even though the distribution of bison home ranges is bounded by the bison fence, incidents of bison trespass outside the fence have occurred in recent years. Estimated home ranges were allowed to extend beyond the bison fence to project where high density use might occur when bison are able to cross the fence based on observed use levels on adjacent areas inside the fence. Elk home ranges were clipped to the elk home range analysis area described above and in Figure 1. HRT was also used to calculate distance moved between locations over a 12-hour time period (the minimum standard time between GPS fixes for the GPS telemetry collars) for each elk in the NPS dataset and the result used to determine a buffer that could be applied to UMP wetland sites to estimate a likely distance from which elk and bison might

be considered to potentially use these sampled wetland areas. Only GPS collar data could be used for these distance estimates due to the shorter temporal scale compared to the VHF data. Because of differences in number of locations gathered per day, and the limited total number of days that some collars were deployed, the estimates of average bison distance moved every 12 hours could only be based on 2 animals—a number unlikely to reflect average movement distances across the bison population.

The original analysis (Schweiger et al. 2017) of ungulate use in wetlands in the park used data provided as Wockner and others' (2015) overlapping “home ranges.” We discovered that these home range polygons were, in fact, created by joining polygons of buffered (300 m) location points for each collared animal and overlaying these polygons rather than overlaying true kernel density home ranges. Because this metric was used to index ungulate use in earlier reports (Schweiger et al. 2017), we decided to test similar metrics. We created “concentrated use” ranges for each collared animal by buffering each location to several distances: 100 m, 200 m, 300 m, 500 m, 1000 m (Figure 5). Because we are only interested in developing one set of metrics for each species, we only performed this analysis on the USGS bison (2005-2007) dataset and the NPS elk (2019-2020) dataset. We examined simple bivariate correlations between each buffer distance index and dung indices for each species to determine which distance appeared to best correlate with dung data.

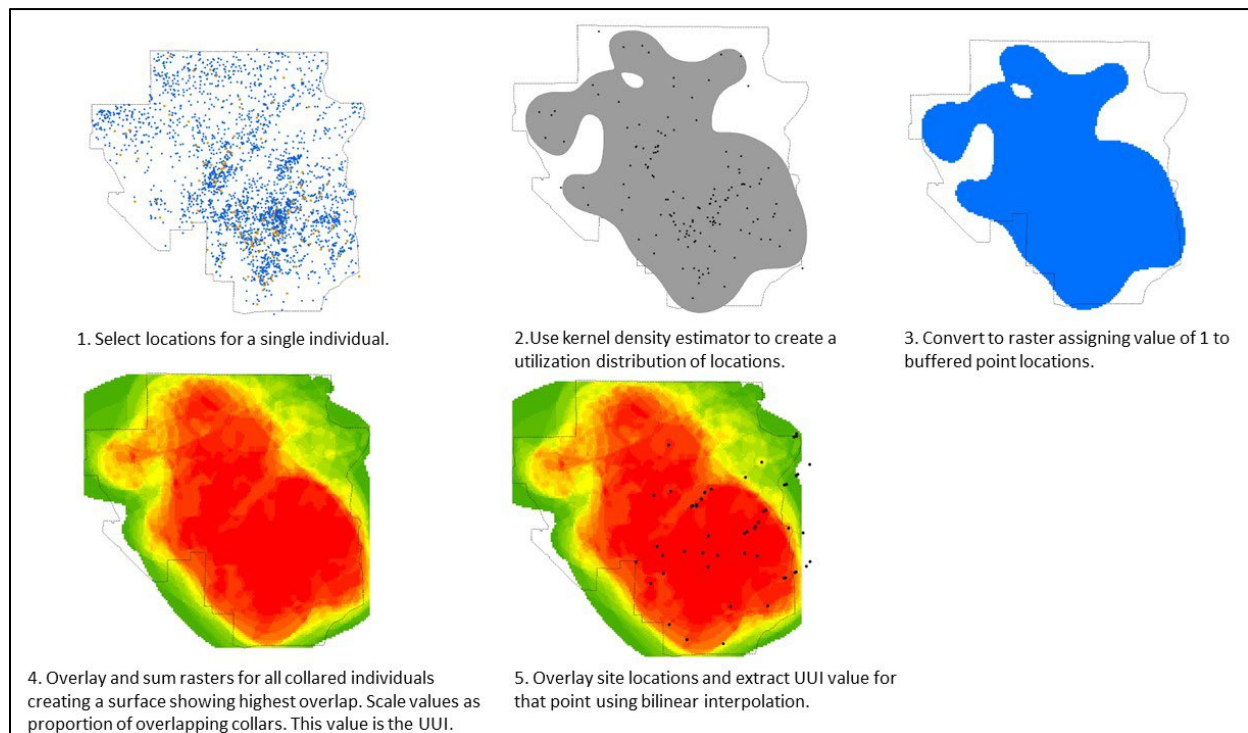


Figure 4. Summary of the steps used to create telemetry collar-based ungulate use indices (UUI) based on proportion of overlapping kernel density home range. Example is for bison on the Medano Ranch, but the same methods were used for elk in Great Sand Dunes National Park, Colorado.

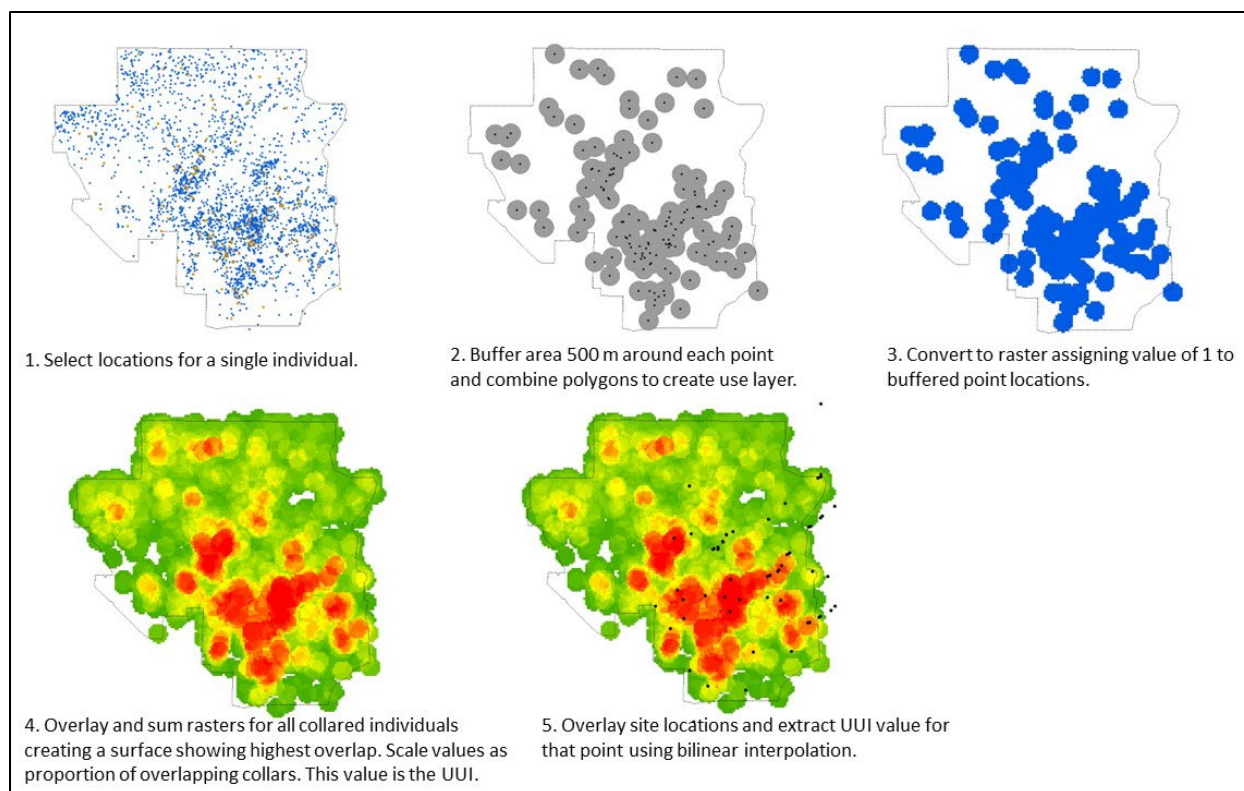


Figure 5. Summary of the steps used to create telemetry collar-based ungulate use indices (UUI) based on proportion of overlapping buffered location home range. Example is for bison on the Medano Ranch, but the same methods were used for elk in Great Sand Dunes National Park, Colorado.

Camera Traps

Field Placement of Cameras

Beginning in July 2016, Spypoint Force 10 automated trail cameras were placed at 10 wetland sites in Great Sand Dunes National Park by ROMN and GRSA scientists (Table 1). Camera data analyzed in this report includes data from late June 2016 through June 2020. Sites selected for camera deployment covered all wetland habitat types and were both inside and outside the bison fence. We attempted to place cameras in each of the important habitat and ungulate type classes, but the small number of cameras we could deploy and analyze limited this. Camera deployment was limited by costs and personnel availability associated with maintenance of cameras (replacement of photo cards and batteries) and processing of image data. Six camera sites were located outside the bison fence and 4 sites inside. Some sites were located outside the bison pasture but were very close to the fence and were used by bison when the fence was not functioning. Four sites had dual deployment of cameras in one or more years, with one camera triggered by motion and the second camera programmed to take pictures at designated intervals ranging from 1 minute to 1 hour. However, it was determined that for the purposes of developing dung metrics consistently across all sites, only camera surveys based on motion-trigger activation of cameras would be used.

Cameras were pointed towards one or more dung sample plots and were assumed to record ungulate activity associated with measured dung plots. Cameras were mounted on exclosures or other pre-

existing structures where available, or on t-posts driven into the ground. The detection range of the cameras was 60 ft (18.3 m). To maintain consistent photo coverage, cameras were visited regularly to change batteries and remove and replace photo cards; however, full cards and dead batteries were encountered during some visits. Cameras were also subject to malfunctions of time/date stamps and abuse by wildlife, which led to camera malfunctions and changes in camera viewscape mid-survey.

In addition to the 10 cameras deployed by ROMN, Dr. Kate Schoenecker of U.S. Geological Survey also had 12 cameras deployed in the sandsheet region of GRSA. Only 4 USGS camera sites, however, coincided with wetland sample sites being used by ROMN. A further examination of the 4 USGS sites found that only one of them had cameras pointed in the direction of the delineated wetland plot that was being measured for vegetation and dung, while the remaining 3 cameras captured only a small portion or none of the wetland plot. The single USGS camera that was a good match to the ROMN site location, however, was only deployed during 2.5 weeks during the month of November preceding a June dung count and the few photos were of poor quality. We determined that sufficient USGS camera data were not available to increase the sample size of camera sites.

Table 1. Site characteristics and camera deployment time for wetland sites in Great Sand Dunes National Park, Colorado, 2016-2019. EB=sites accessible to both elk-bison; EsB=sites accessible to elk and some limited bison use; E=sites accessible only to elk.

Site	General Location	Habitat Type	Ungulate Type	Deployment Days by Year				
				2016	2017	2018	2019	2020
GRSA_108	Medano Ranch House	Salty meadow	EB	145.5	302.2	204.5	30	0
GRSA_215	Big Spring Creek Terminus	Salty meadow	EB	139.9	276.3	364.8	285.6	66.6
GRSA_204	Elk Springs North	Salty meadow	EsB	45.0	118.4	269.2	66.1	0
GRSA_302	Little Spring Creek swale	Salty meadow	EsB	46.4	365.0	204.4	1.7	26.4
GRSA_306	Indian Spring	Salty meadow	EsB	147.0	168.2	287.8	210	182.0
GRSA_211	Big Spring Creek	Herbaceous riparian	EB	63.9	207.9	303.3	90.5	182.0
GRSA_404	Little Spring Creek	Herbaceous riparian	EsB	184.4	365.0	324.8	141.6	0
GRSA_416	Deadman Creek	Herbaceous riparian	E	182.0	268.3	161.5	226.8	0
GRSA_406	Middle Sand Creek	Woody riparian	EB	146.8	265.2	329.8	300.5	156.6
GRSA_252	Medano-Mosca Creek confluence	Woody riparian	E	163.4	364.9	116.5	0	0

Image Processing and Quality Control

Camera surveys were manually processed by ROMN technicians following protocols laid out in the Rocky Mountain Network’s Wildlife Photo Processing Standard Operating Procedure version 1 (Eschler and Sherrill 2018). Wildlife photos were viewed and processed using Camera Base v. 1.7 (Tobler 2015). Camera Base uses a Microsoft Access database and interactive tools to identify and manage camera survey data. Images containing wildlife were identified with the species of animal, how many animals were located within the wetland boundary of the photo frame, and the activity of most animals in the photo. Individual images that were classified as having animals were saved and copied to a separate folder and a record for each image was stored in a table in the Camera Base database.

The “capture” dataset—those images which captured animals—was checked for anomalies and quality assurance by the ROMN database manager and ecologists and a subset was checked by L. Zeigenfuss (consultant). Images containing bison or elk and other non-target species (e.g., birds, humans, ungulates other than elk and bison) were coded to identify only the primary species of interest. Images containing only non-target species were identified by the majority non-target species observed in the image and not further processed. Surveys where date-time stamps had malfunctioned were flagged for removal from the dataset. The final dataset used for development of ungulate use metrics only contained images with elk and/or bison.

A dataset of 2,500 images was provided by the ROMN data manager for quality control (QC) analysis by an independent technician (L. Zeigenfuss staff member). The independent analyst was provided the same protocols and similar training as ROMN analysts. Original analyst records were extracted from the overall dataset based on image date-time stamp. The two datasets (original and QC) were merged based on date-time stamps on the photos and analyzed for key differences in classification (species, group size, activity) between ROMN and independent QC analysts. Factors other than individual analyst that might affect classification were examined.

Ungulate Use Indices (UUI)

The development of metrics that described intensity of ungulate use for elk and bison as individual species as well as combined intensity of ungulate use was the primary objective of the work described here. A suite of metrics was developed for each data collection method that estimated ungulate use and these metrics were used to describe spatial and temporal patterns in ungulate use on GRSA wetlands. These metrics were also examined for correlations across the 3 methods described above so that detail of ungulate use available through one method might be correlated to metrics developed using the one or both of the other 2 methods.

Dung UUI

A single site-scale ungulate use index was derived from dung counts (DI). This metric was calculated at the site level rather than treating individual dung count plots as independent data points.

Delineation of wetland sites was based on wetland complexes that shared characteristics and usually had defined boundaries; therefore, dung count data at the plot scale were not statistically independent of each other and many defining characteristics (e.g., wetland type, distance to landscape features, elevation, etc.) are the same (or nearly so) for all dung count plots within a site. Sampling across a site can account for variance in dung counts across the site and result in a single value for the site that reflects a “homogenized” assessment of dung deposition for the whole site. This should result in reduced variance across all sites within a given category, such as wetland habitat type or ungulate strata (areas with no bison vs. areas used by both elk and bison).

Dung pellet group density (D_{pg}) for a site was derived from physical counts of total (old and new) dung pellet piles (elk) or dung pats (bison) (Equation 1). All dung pellet groups/pats counted within a single visit were summed over all pellet plots at a site and then divided by the total area surveyed (n plots $\times 100 \text{ m}^2/\text{plot}$).

$$D_{pg} = \frac{\sum_{i=1}^n pg}{n \times A} \quad (1)$$

where pg is the number of pellet groups/pats counted in a plot, n = the total number of plots counted in a site, and A = the area of an individual plot.

Dung index (DI_x) was calculated for each species based on a method for estimating animal population density first proposed by Eberhardt and Van Etten (1959) based on dung counts (Härkönen and Heikkilä 1999; deCalesta 2013) using equation 2. These types of density estimates require an estimated number of days over which dung piles are deposited or an estimated disappearance rate for calculation of the index (Campbell et al. 2004).

$$DI_x = \frac{D_{pg}}{T * F} \quad (2)$$

where x =species [b = bison, e = elk, and t = bison+elk], T = persistence time for dung pellets (i.e., the amount of time it takes for dung to either decay, scatter, or otherwise disappear to the point it is no longer detected by observers as a unique defecation event; Laing et al. 2003), and F = species-specific defecation rate.

A defecation rate of 9 defecations per day for bison, and 18.8 defecations per day for elk were used based on observations conducted on the National Bison Refuge in Montana (Belovsky and Slade 1986). Lower defecation rates of 12.5 defecations/day have been recorded for elk (Neff 1968; Overton and Davis 1969) when data included both winter and summer, but Collins and Urness (1979) observed defecation rates for elk as high as 24 per day in lodgepole pine habitats and 30 per day in aspen habitats during summer. The rate of 18.8 defecations per day is likely a good reflection of the high nutritive quality and moisture of forage (especially in wetland habitats; Baker and Hobbs 1982) in June/July in GRSA while still accounting for lower winter deposition rates. Few defecation rates were available for American bison, though rates of 7.5 defecations per day were reported for European bison (*Bison bonasus*) in summer (Eycott et al. 2013). This metric could be adjusted if data on species-specific defecation rates for GRSA elk and bison were determined in the future.

Telemetry UUI

Year-round and seasonal (spring, summer, fall, and winter) ungulate use indices were developed based on estimates of spatial and temporal distribution of elk and bison from telemetry collar data (Table 2). Historical bison collar data collected from 2005 to 2007 were used as a proxy for current bison use based on the assumption that the bison pasture fence and ranch management operations effectively constrain bison use to a limited area at present that is roughly similar to the 2005-2007 time period. However, changes in wetland community composition, irrigation practices, ranching practices, and/or competition with elk may affect bison use of wetlands. Correlations between telemetry data and camera and dung pellet data were used to investigate whether these assumptions about current bison distribution appear to hold true.

Telemetry based UUI are continuous grids of values (Table 2) at a cell size of 100 m. The UUI for both years and seasons within the one-year time period from March 2019 through March 2020 values was extracted at individual UMP plots using bilinear interpolation of all adjacent cell values to a plot (Figures 4 and 5). These values apply to all subplots in a UMP wetland site. Telemetry-based UUI values ranged from 0 to 1, though in many cases for elk, 100% of the collared elk home ranges did not overlap, resulting in maximum values below 1. For bison, which were restricted in their distribution (for the most part) by the bison fence, areas of 100% overlap were common, resulting in maximum telemetry UUI values of 1. An additional index combined the year-round UUI for both elk and bison, weighting bison use to account for the larger body size and consumption rates of bison. Average body weights for elk (227 kg) and bison (453 kg) were based on the Wockner et al. (2015) carrying capacity model of the GRSA region and used to determine a weighting factor (roughly 2x)

for bison. Importantly, weighted UIIs and bison UIIs assumed that bison distribution and density of use did not change substantially since the USGS data were collected in 2005-2007.

Table 2. Ungulate use indices (UII) derived from elk and bison telemetry collar data.

Metric	Description/Range
Year-Round Bison Home Range Density	Proportion of overlapping 90% kernel density home range estimates based on all locations from 18 collared bison (2005-2007)
Year-Round Elk Home Range Density	Proportion of overlapping 90% kernel density home range estimates based on all locations from 34 collared elk (2019-2020)
Seasonal (4) Bison Home Range Density	Proportion of overlapping 90% kernel density home range estimates based on seasonal locations from 18 collared bison (2005-2007)
Seasonal (4) Elk Home Range Density	Proportion of overlapping 90% kernel density home range estimates based on seasonal locations from 34 collared elk (2019-2020)
Body Size Weighted Year-Round Home Range Density Index	Year-round elk home range density + (Year-round bison home range density * 2)
Body Size Weighted Spring and Summer Home Range Density Index	Seasonal elk home range density + (Seasonal bison home range density * 2). This metric was developed for spring and summer, the seasons most likely to reflect high intensity use by both species.
Year-Round Bison Concentrated Use Index	Proportion of overlapping buffered telemetry collar locations based on all locations from 18 collared bison (2005-2007)
Year-Round Elk Concentrated Use Index	Proportion of overlapping buffered telemetry collar locations based on all locations from 34 collared elk (2019-2020)
Seasonal Bison Concentrated Use Index	Proportion of overlapping buffered telemetry collar estimates based on seasonal locations from 18 collared bison (2005-2007)
Seasonal (4) Elk Concentrated Use Index	Proportion of overlapping buffered telemetry collar estimates based on seasonal locations from 34 collared elk (2019-2020)
Body Size Weighted Spring and Summer Concentrated Use Index	Seasonal elk concentrated use index + (Seasonal bison concentrated use index * 2). This metric was developed for spring and summer, the seasons most likely to reflect high intensity use by both species.

Camera Trap UUI

Three site-specific (at a subset of sites) UUI (daily presence index, relative index of activity by photo event, and relative index of activity by capture event) were developed to describe ungulate use for 10 UMP wetland sites with cameras (Table 3). These metrics were based on those commonly found in the literature (Sollman et al. 2013; Burton et al. 2015; Palmer et al. 2018; Sollman 2018). All camera-based UUI were calculated for a variety of time periods detailed in Table 3.

Table 3. Ungulate use indices (UUI) derived from camera trap data.

Metric	Description	Time Frame
Annual Deployment	All camera data available within a particular year	2016, 2017, 2018, 2019
Seasonal Deployment		
Spring	Traditional spring months	March 1–May 31 each year
Summer	Traditional summer months	Summer: June 1–August 31 each year
Fall	Traditional fall months	Fall: September 1–November 30 each year
Winter	Traditional winter months	Winter: December 1–February 28-29 each year
Pellet Growing Season (PGS)	The part of the growing season likely represented by the dung pellet samples in any given year	April 3 through the date when dung counts conducted at that site ^a
Growing Season	Growing season was defined as that time when plants are likely to be actively growing	April 3 (see above) through October 10 ^{ab}
Bison Breeding Season	Season when most active bison breeding occurs	July and August (Meagher 1986).
Elk Breeding/Elk Hunting Season	Approximate dates of elk breeding and hunting season.	September 1 through November 15 each year (CPW 2014, 2019)
Bison Gather	The time period that includes the length of the bison gather, processing, and culling operations on Medano Ranch plus one week prior and one week following the processing dates	Dates of gathers were supplied by Kate Schoenecker, Research Ecologist, U.S. Geological Survey
Monthly deployments	Each calendar month when a camera was deployed at a site	January, February, March, April, May, June, July, August, September, October, November, December

^aStart date determined by estimating the mean earliest date (2016-2019) that mean daily temperature was above 0 °C without a subsequent return to below zero temperatures for more than a day based on DAYMET version 3 randomized points from across the GRSA sandsheet.

^bAverage date of first severe killing freeze (air temperature <-4.4°C), which would cause heavy damage to most plants (Thom 1959; Vestal 1971).

We calculated a variety of metrics in an attempt to identify those that best described ungulate use in our sites. The simplest camera-based metric was the daily presence index (DPI), which calculated the proportion of days (out of the total deployment time) when a species group (bison, elk, or both species) was present at a site (Equation 3).

$$DPI = d_p / d_t \quad (3)$$

where d_p = number of days (defined as 24-hr period starting at midnight) the species was present at a site and d_t = total days of camera deployment at site. This metric is a general indicator of use per year, season, or month.

The second camera-based metric estimated was the Relative Index of Activity_Photos (RIA_p). This metric (Figure 6) is based on relative abundance indices (RAI) commonly used for camera trap studies (O'Brien et al. 2003; O'Brien 2011; Sollman et al. 2013; Palmer et al. 2018). However, the design of our camera data was not intended to determine animal abundance over the landscape, but rather intensity of use at an individual point within a wetland site, therefore we changed the name associated with this metric to better reflect how we are using to index intensity of elk and bison activity at these sites. The index is derived using the total number of photos capturing bison, elk, both species, or either species at a site to estimate use, and similar to DPI, was standardized by the number of days of camera deployment (Equation 4).

$$RIA_p = p_t / d_t \quad (4)$$

where p_t = total number of photographs and d_t = total days of camera deployment at site. RIA_p treats cumulative number of photos as an indicator of the amount of animal activity under the presumption that larger numbers and longer visit duration to a site will result in a greater number of photos. This metric is standardized to account for length of camera deployment by dividing the total number of photos by the deployment time (days per year, season, or month). This metric does not, however, account for the number of animals that are captured in a photo, thus treating photos with only 1 animal equally with photos capturing 100 animals. To incorporate group size into the RIA metric, 2 weighting metrics were created. RIA_{p_wtd} uses the total number of individuals counted in all the photos instead of the total number of photos to calculate RIA_p. RIA_{p_w2} uses both the number of photos and the number of animals adjusting the RIA_p by multiplying it by the total number of animals and resulting in a much larger value that reflects duration of visit as well as total number of animals (Figure 6).

The third camera-based metric was also a relative index of activity; however, this metric accounts for lack of independence of individual photos. Relative Index of Activity_CaptureEvent (RIA_c), defines “capture events” that we assume subset data into independent sets of animals at a site and then uses the total number of these events to estimate ungulate activity (Figure 6; Equation 5) standardized by the number of days of camera deployment.

$$RIA_c = c_t / d_t \quad (5)$$

where c_t = total number of capture events and d_t = total days of camera deployment at site. A capture event was defined as a series of photos where the time between individual photo frames was less than 5 minutes. This interval length between events was based on density distribution plots of “time since last photo” for all intervals between photos containing elk or bison that were less than one day (Figure 7). It appears that for all sites, there is a major change in slope between 0.002 days (2.9 minutes) and 0.004 days (5.76 minutes). This estimate was generalized to 5 minutes for ease of subsequent calculation. A search of the published literature found interval lengths for determining single capture events that ranged from 1 min to 1 day and few studies gave a reason behind these selections (Bowkett et al. 2007; Karanth et al. 2017; Palmer et al. 2018). Capture event-based metrics were weighted to account for group size with the mean, median, and maximum group size (Figure 6). Weighted values were summed across the time period of interest (year, season, month, etc.) and divided by d_t to create the final mean-weighted metric (RIAc_m), median-weighted metric (RIAc_d), and maximum-weighted metric (RIAc_x).



Relative Index of Activity_Photos (RIA_p): Total number of **photos** capturing bison, elk, both species, or either species at a site.

$$RIA_p = p_t / d_t \quad RIA_{p_wtd} = p_i / d_t \quad RIA_{pw2} = (p_t / d_t) * p_i$$

p_t = total number of photographs

p_i = total number of animals in all photographs

d_t = total days of camera deployment at site

$RIA_p = 11 \text{ photos} \div 2 \text{ days camera deployment} = 5.5$

$RIA_{p_wtd} = 56 \text{ animals counted} \div 2 \text{ days camera deployment} = 28$

$RIA_{pw2} = RIA_p (5.5) * \text{total animals counted} (56) = 308$

1 event
mean # animals=2.5
median # animals=2.5
maximum # animals=4



1 event
mean # animals=10
median # animals=10.5
maximum # animals=12



1 event
mean # animals=1
median # animals=1
maximum # animals=1



Relative Index of Activity_CaptureEvent (RIA_c): Total number of **events** (photo series of same species with less than 5 minutes between successive photos) capturing bison, elk, both species, or either species at a site.

$$RIA_c = c_t / d_t \quad RIA_{c_mean} = \sum c_m / d_t \quad RIA_{c_median} = \sum c_d / d_t \quad RIA_{c_maximum} = \sum c_x / d_t$$

c_t = total number of capture events

c_m = sum mean # animals per capture event

c_d = sum median # animals per capture event

c_x = sum maximum # animals per capture event

d_t = total days of camera deployment at site

$RIA_c = 3 \text{ capture events} \div 2 \text{ days camera deployment} = 1.5$

$RIA_{c_mean} = \text{sum mean \# animals each event (13.5)} \div 2 \text{ days camera deployment} = 6.75$

$RIA_{c_median} = \text{sum median \# animals each event (14)} \div 2 \text{ days camera deployment} = 7$

$RIA_{c_maximum} = \text{sum maximum \# animals each event (17)} \div 2 \text{ days camera deployment} = 8.5$

Figure 6. Depiction of how relative index of activity (RIA) was calculated using individual photos and capture events.

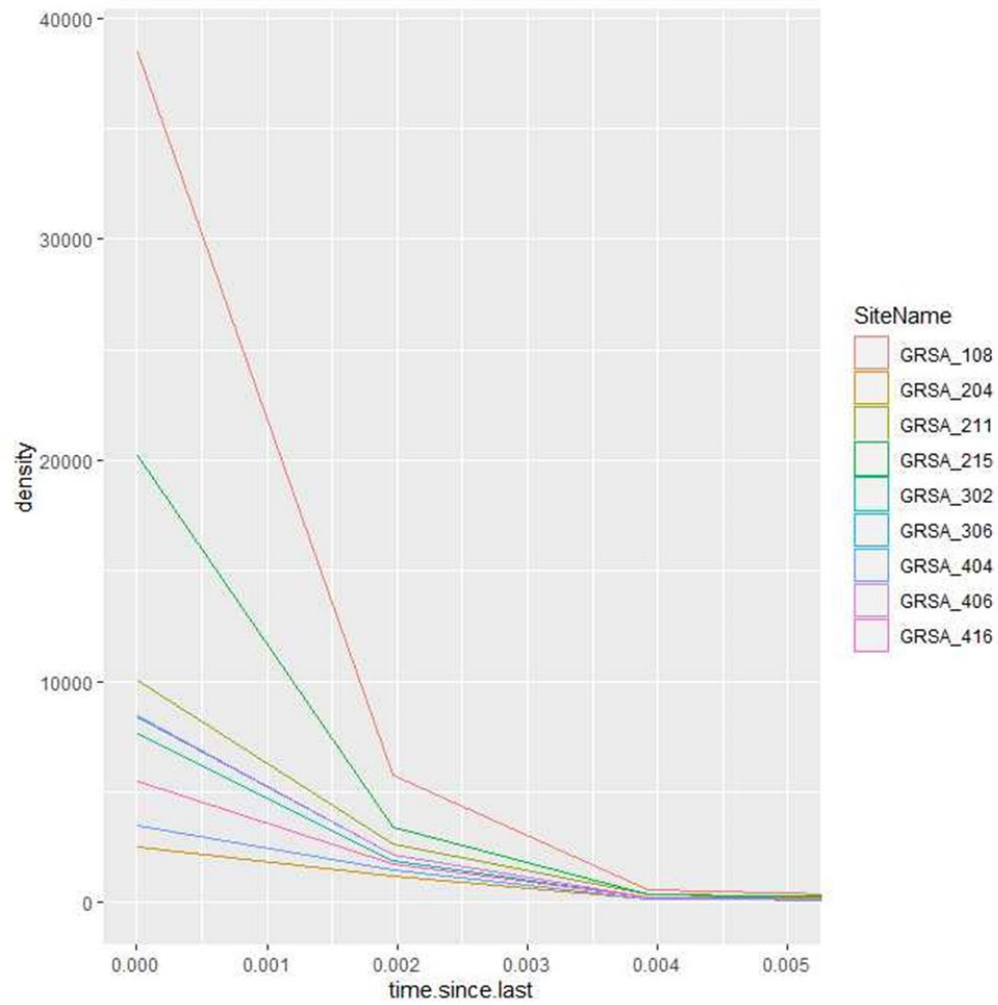


Figure 7. Density distribution plot of time since last photo for all photo intervals less than one day at Great Sand Dunes wetland sites. Curves flatten at a point slightly less than 0.004 days (5.76 minutes).

Statistical Analyses

We conducted a series of analyses to better understand spatial and temporal patterns in each UUI. Understanding how a given UUI varies across space and time facilitates 2 important needs of the UMP project: 1) selection of a subset of UUI that are most informative, and 2) models of relationships among ungulate use and wetland habitat response and how these relationships might relate to ungulate management actions conducted by GRSA (Mosher et al. 2018).

We began with a variety of exploratory data analyses (EDA) and visualizations. EDA included maps of a subset of UUI, standard box plots, histograms, scatter plots and various descriptive statistics. We then tested for differences across habitat type, ungulate use classes and year using methods specific to each UUI type and presented below. Importantly, all of our interpretations must only be applied to specific sites – our data cannot make inference to unsampled areas. All statistical analyses were conducted using R statistical computing package v. 4.0.3 with a variety of functions and libraries as detailed below. All R code and detailed results are available upon request from the Rocky Mountain Network. All GIS analysis was done in ArcMap 10.8.1 using Geospatial Processing Tools, Spatial Analyst (ESRI 2020), and Home Range Tools (Rogers and Kie 2011).

Dung UUI

Due to the highly non-normal nature of the dung-based UUI and the unbalanced sampling design, we used nonparametric methods to test for differences across habitat types and year. We used an analysis of variance of aligned rank transformed (ART) data to investigate interactions between habitat type and year. ART is a nonparametric factorial data analysis that relies on a preprocessing step that “aligns” data before applying averaged ranks, after which point common ANOVA procedures can be used (Wobbrock et al. 2011, 2018). We used the ARTool package in R for these analyses. We also used a Kruskal-Wallis test to look for differences between ungulate zones. We could not look at interactions between habitat type and ungulate zone because the habitat types were not distributed across all 3 ungulate zones (e.g., there was no woody riparian in the EsB zone). Therefore, we only treated these as main effects.

Telemetry UUI

We compared telemetry-based UUI for differences between habitat types and ungulate zones using nonparametric Kruskal-Wallis test. We could not look at interactions between these variables because the habitat types were not distributed across all three ungulate zones.

Camera Trap UUI

Sample size was too small to compare between habitat type, ungulate zone, and year for the camera data. Data were therefore only analyzed qualitatively for patterns across habitat type, ungulate class, and various temporal intervals.

Patterns Across UUI

Finally, we examined patterns across indices using simple correlations and scatter plots. We explored all possible comparisons across variants of UUI. At least one dung pellet count was conducted at all 74 ROMN UMP sites from 2016 to 2021. We used Spearman’s correlation coefficient to determine

strength of relationship between variables. For comparisons between dung and camera UUI we use only data from the 10 camera sites and matched by year ($n = 4$). For comparisons between dung and telemetry data we use site-scale extracted telemetry based UUI matched to dung UUI for each site and year. We also estimate correlations between telemetry and camera UUI by collapsing across sites and various time periods (year, season).

Future models will estimate an adjusted synoptic UUI (from dung counts) using the finer scale and more nuanced camera based UUI. The dung disappearance rate data being collected in 2021 and 2023 and the additional camera and dung counts are required to build these models.

Results

Dung UUI

A total of 258 dung pellet plots were established and counted at 74 sites from 2016 through 2019. Number of pellet plots at each site ranged from 1 to 5. Sixty-three sites were only visited once from 2016 through 2019. Of the remaining 11 sites, 7 were sampled 2 years and 4 were sampled 3 years (not counting revisits for dung deposition estimates in 2021 and 2022) for a total of 95 site visits for dung sampling.

General Spatial Patterns

Many bison dung piles were observed at sites immediately outside the bison fence, including site 306 (located at Indian Spring, approximately 850 m outside of the bison fence), site 439 (located 300 m outside of the bison fence on Big Spring Creek), and site 204 (located at Elk Springs, less than 100 m outside of the bison fence). These observations led to examination of dung data from several other sites outside but further from the bison fence. Eight of 12 sites located within 1 km outside the bison fence contained bison dung pats. Because it was obvious that bison were accessing sites within 1 km of the fence, a third ungulate zone was designated as “elk-some bison.” In previous work (Schoenecker 2012; Schoenecker et al. 2022), areas outside the bison fence were considered an elk only zone.

All dung counted in July at plots cleared in June were assumed to have been deposited in the previous month, whether characterized as fresh or old during the recount. Both elk and bison dung were observed in 4 of the 5 sites cleared and remeasured within a month. This suggests that “new” dung piles appear fresh for a shorter time period (likely just a single season) than was originally expected.

Dung Disappearance

Dung count data collected in 11 UMP sites located inside intact ungulate research exclosures were examined to determine how long detectable dung might persist in the study area. These exclosures were built in 2005 as part of an earlier study (Schoenecker 2012; Schoenecker et al. 2022) and were only located in woody riparian and herbaceous riparian habitats as an artifact of the original study design. Elk dung was present in 2 of 4 exclosures located outside the bison pasture. In 2 exclosures located >2 km from the bison fence, a few old bison dung piles were observed; however, it is likely these were misidentified summer elk dung. Elk dung was present in 3 of the exclosures inside the bison pasture. All the exclosures located in woody riparian habitat inside the bison fence had at least a small number of dung piles identified as elk and bison. All bison dung and most elk dung in these exclosures were categorized as “old,” but a few elk dung piles were categorized as “new.” In contrast, 3 of the 4 exclosures located in herbaceous riparian habitat inside the bison pasture had no elk dung, and bison dung was not found inside any of these herbaceous riparian exclosures either. This may suggest that decay and disappearance of dung is greater in wetter herbaceous riparian habitats compared to woody riparian habitats. It also may indicate that these exclosures are not presently successful at excluding elk, though they may still be effective for excluding bison.

The data collected on dung disappearance appears to support species-specific differences in the length of time that a given dung pile could be identified, and therefore would be likely to be included in a count (Table 4). The fastest disappearance occurred in salty meadow sites, with 100% of dung piles no longer identifiable after one year and elk dung disappearing 4.5 months earlier than bison dung. Bison dung disappeared faster than elk dung in herbaceous riparian sites, with 100% of bison piles disappearing after one year (Table 4), indicating that dung on these sites may be visible well into a second growing season. However, 25% of elk piles were still evident at about 16 months. In woody riparian sites, both bison and elk dung disappeared more slowly (Table 4). After 24–26 months, only 60% of marked elk piles had disappeared, and none of the marked bison dung piles had disappeared. Because we could not estimate a mean disappearance rate for bison dung in woody riparian habitats, we applied the minimum disappearance rate from our disappearance study. This potentially could overestimate bison use in woody riparian habitats; however, given the much lower bison dung counts in woody riparian sites, we believe that our method will be able to appropriately reflect marked increases in bison use.

Table 4. Estimated days to dung disappearance for elk and bison dung in wetland habitats in Great Sand Dunes National Park, Colorado, 2021-2023.

Species	Vegetation type	Proportion of marked dung piles that disappeared (A)	Mean interval between dung creation and recorded disappearance (B)	Disappearance rate (A/B)	Estimated days for dung to disappear (1/disappearance rate)
Bison	Overall	0.87	346.4	0.00251	398.2
Bison	Herbaceous riparian	1.00	355.1	0.00282	355.1
Bison	Salty meadow	1.00	339.2	0.00295	339.2
Bison	Woody riparian	0	Unknown	0.00105 ^a	955.3
Elk	Overall	0.77	386.4	0.00200	499.1
Elk	Herbaceous riparian	0.73	506.2	0.00145	690.2
Elk	Salty meadow	1.00	199.1	0.00502	199.1
Elk	Woody riparian	0.60	573.2	0.00105	955.3

^a No bison dung in woody riparian habitats disappeared in the 725-day study period. Therefore, the mean interval to disappearance is unknown. We used the minimum disappearance rate available in our data to determine days to disappearance.

Patterns in Dung Density Across Habitat Type and Ungulate Use Zone

Bison use based on dung index (DI) was greater in 2018 compared to 2016 and 2017 (Figure 8) and this was mainly due to increased use in salty meadow habitats (Figure 9) both inside the bison pasture (EB) and in the zone about 1 km outside the bison fence (EsB)—possibly due to discovery and exploitation of the Indian Spring and Elk Spring areas when the fence fell into disrepair. We found that the dung index (DI) was able to successfully discriminate use between ungulate zones for bison use and combined (elk + bison) use, and between habitat types for bison, elk, and combined ungulate use (Figures 10 and 11). Even though our bison dung index may overestimate woody riparian use as a result of using the elk-derived days to disappearance, estimated bison use was

consistently greater in salty meadows and herbaceous riparian sites compared to woody riparian sites which received the least bison use (Table 5; Fig. 9). Unsurprisingly, the greatest bison use was inside the bison pasture (EB), followed by the area within 1 km outside of the pasture (EsB), with little to no use at sites beyond 1 km from the bison fence (E). There were no significant ($P > 0.05$) interactions between year and habitat type for any DI (Table 5). Patterns in combined elk/bison use were similar to bison alone (Table 5, Figures 8-11), indicating that bison are the main driver of use where they are present.

Elk DI values indicated no differences in use between years or ungulate zones (Figures 12 and 13), but similar to bison, elk used salty meadows more than either herbaceous riparian or woody riparian types (Table 5; Figure 13).

Table 5. Results of Kruskal-Wallis nonparametric test for dung index for bison, elk, and both species combined in Great Sand Dunes National Park, Colorado. Test statistic for ungulate zone is Kruskal-Wallis chi-square. Test statistic for all other variables and interactions is the F-statistic associated with aligned ranks transformation (ART) analysis of variance.

Species	Variable	Test statistic	Degrees of freedom	P-value
Bison (DI_B)	Year	12.87	3	0.0049
Bison (DI_B)	Habitat type	21.68	2	<0.0001
Bison (DI_B)	Year*Habitat	2.17	6	0.0542
Bison (DI_B)	Ungulate zone	39.90	2	<0.0001
Elk (DI_E)	Year	3.93	3	0.2688
Elk (DI_E)	Habitat type	20.89	2	<0.0001
Elk (DI_E)	Year*Habitat	1.99	6	0.0767
Elk (DI_E)	Ungulate zone	2.88	2	0.2375
Bison + Elk (DI_T)	Year	10.69	3	0.0136
Bison + Elk (DI_T)	Habitat type	28.26	2	<0.0001
Bison + Elk (DI_T)	Year*Habitat	1.97	6	0.0792
Bison + Elk (DI_T)	Ungulate zone	25.54	2	<0.0001

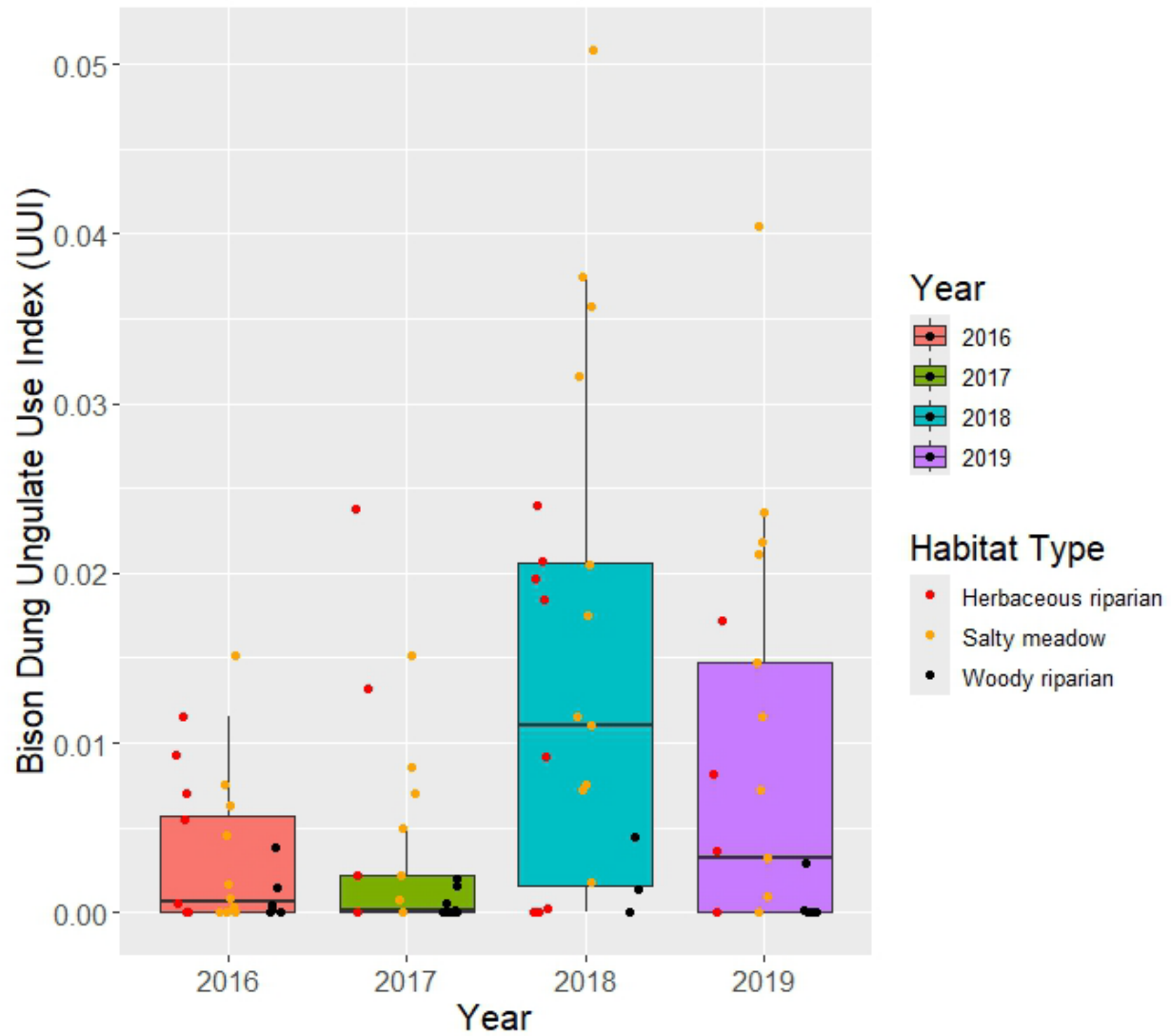


Figure 8. Box plots showing variation in bison dung index (DI) between years and habitat types at Great Sand Dunes National Park, Colorado.

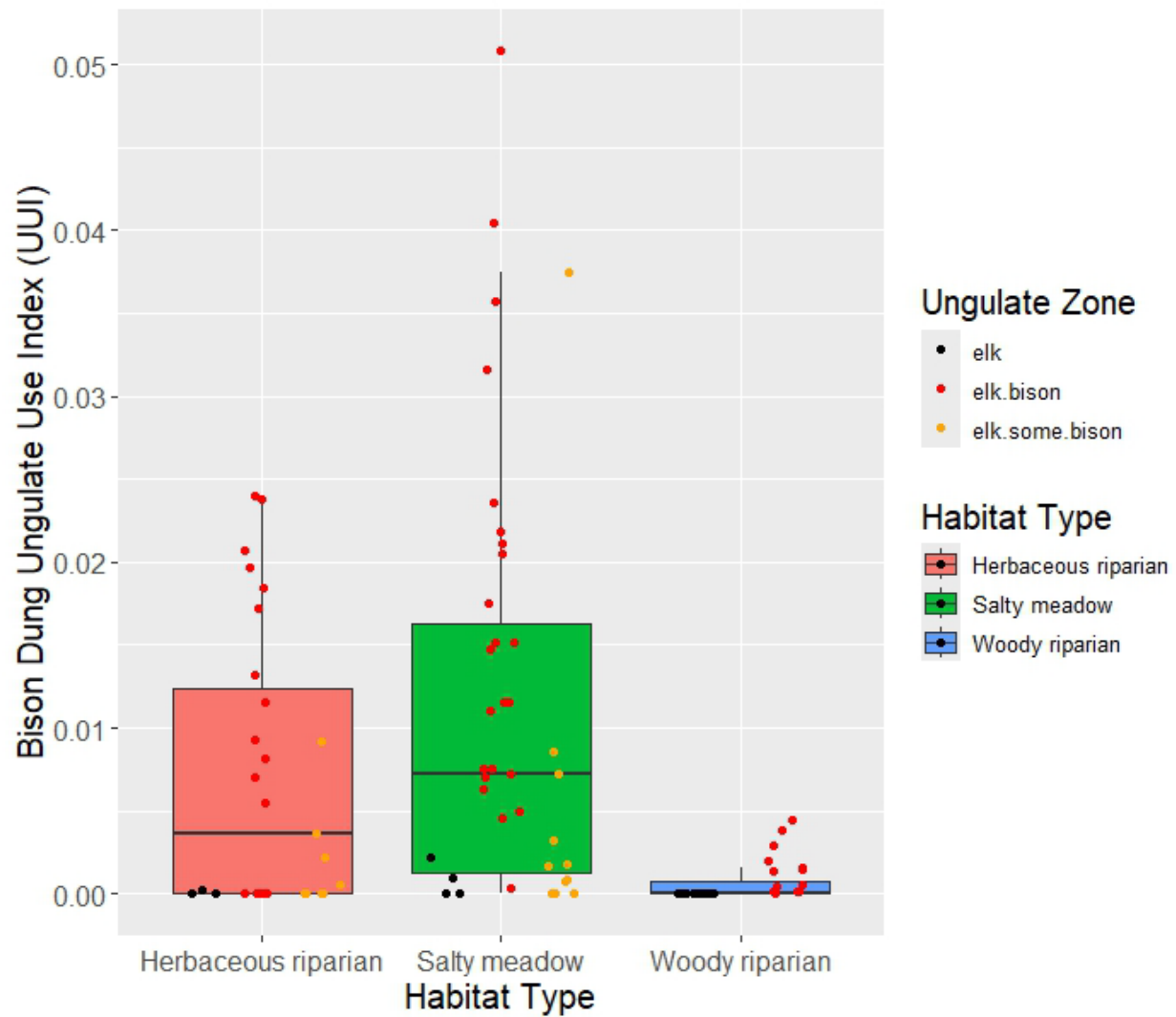


Figure 9. Box plots showing variation in bison dung index (DI) between habitat types and sorted by ungulate zone, at Great Sand Dunes National Park, Colorado.

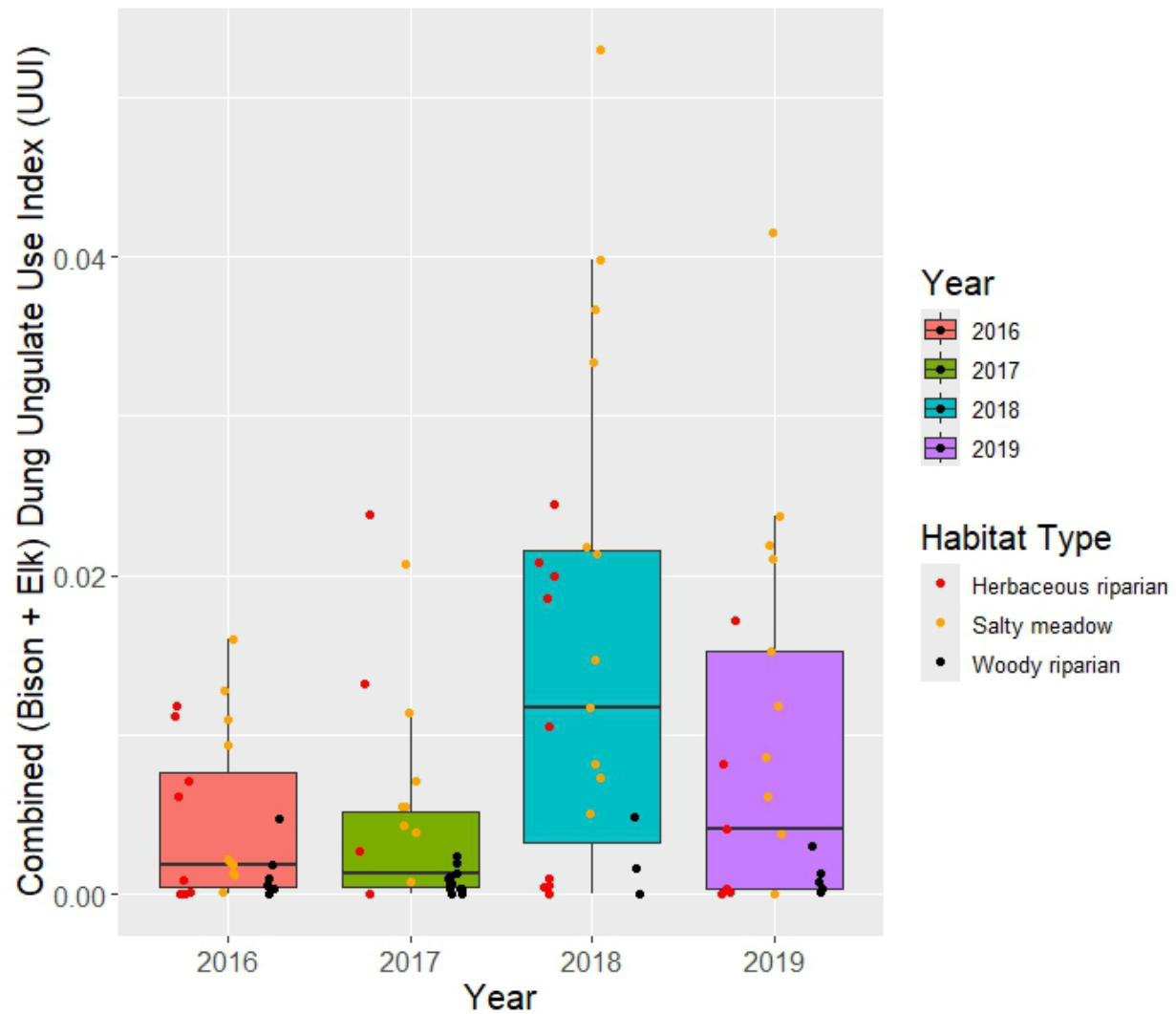


Figure 10. Box plots showing variation in combined bison and elk dung index (DI) between years and habitat types at Great Sand Dunes National Park, Colorado.

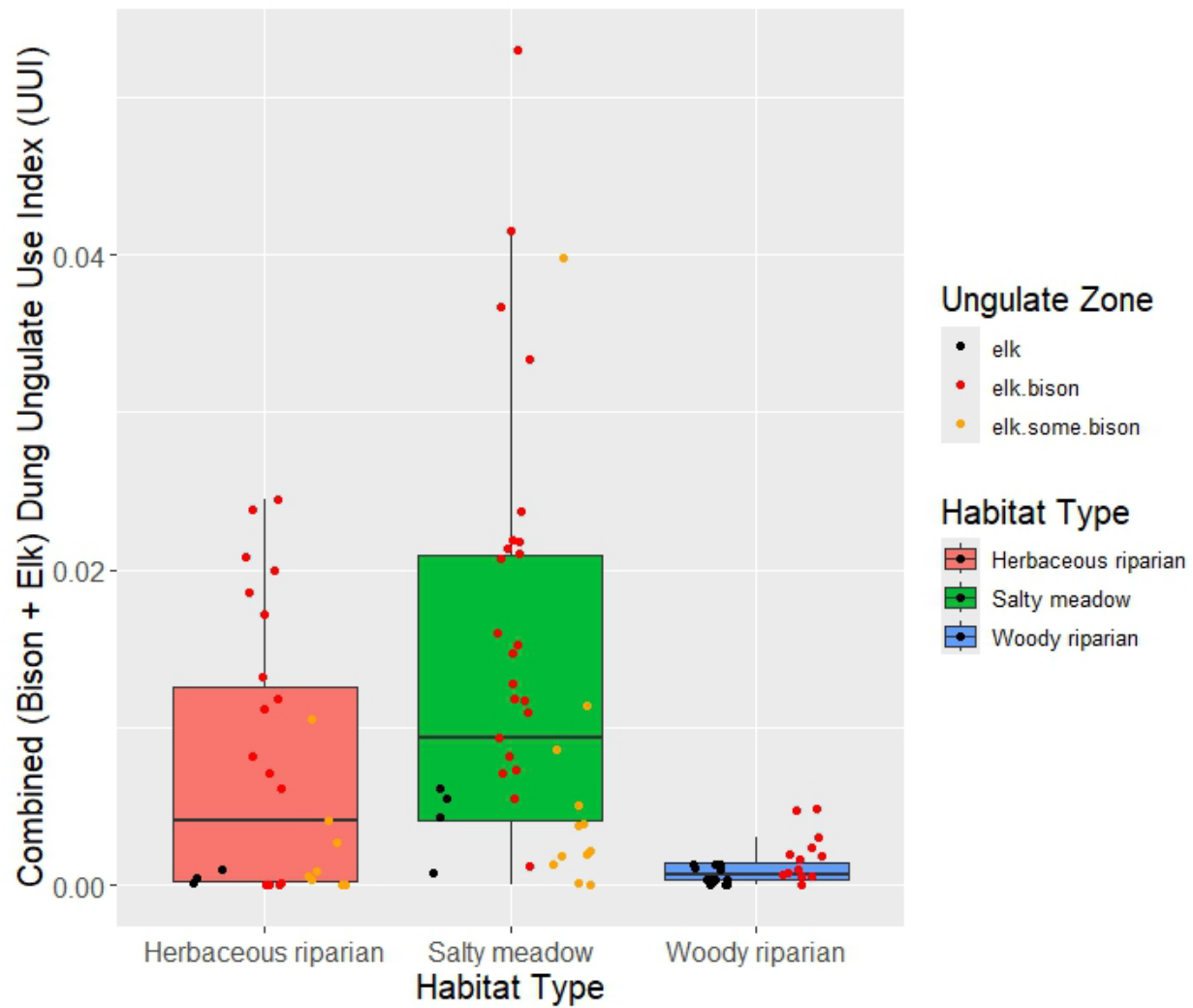


Figure 11. Box plots showing variation in combined bison and elk dung index (DI) between habitat types and sorted by ungulate zone, at Great Sand Dunes National Park, Colorado.

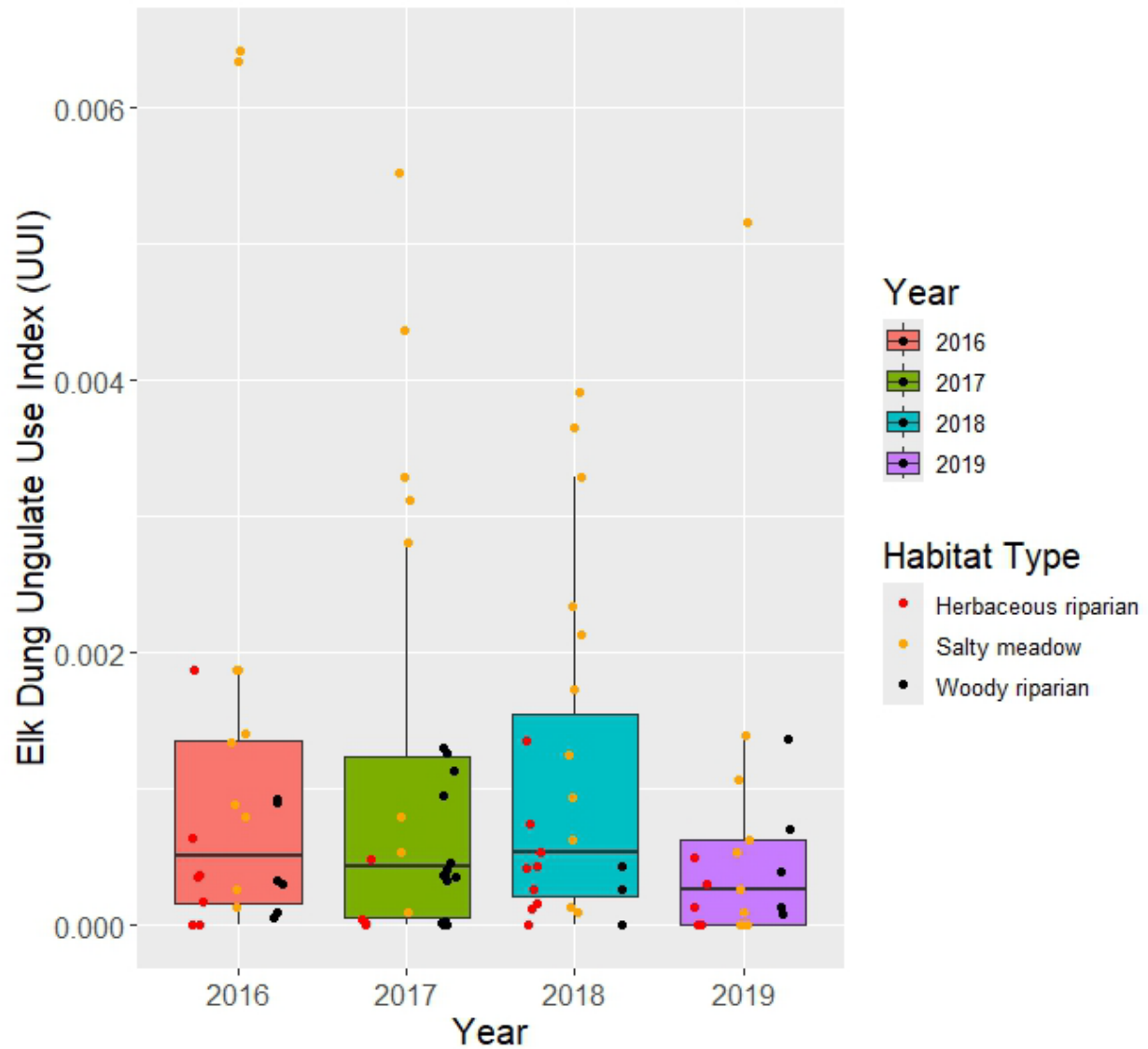


Figure 12. Box plots showing variation in elk dung index (DI) between years and habitat types at Great Sand Dunes National Park, Colorado.

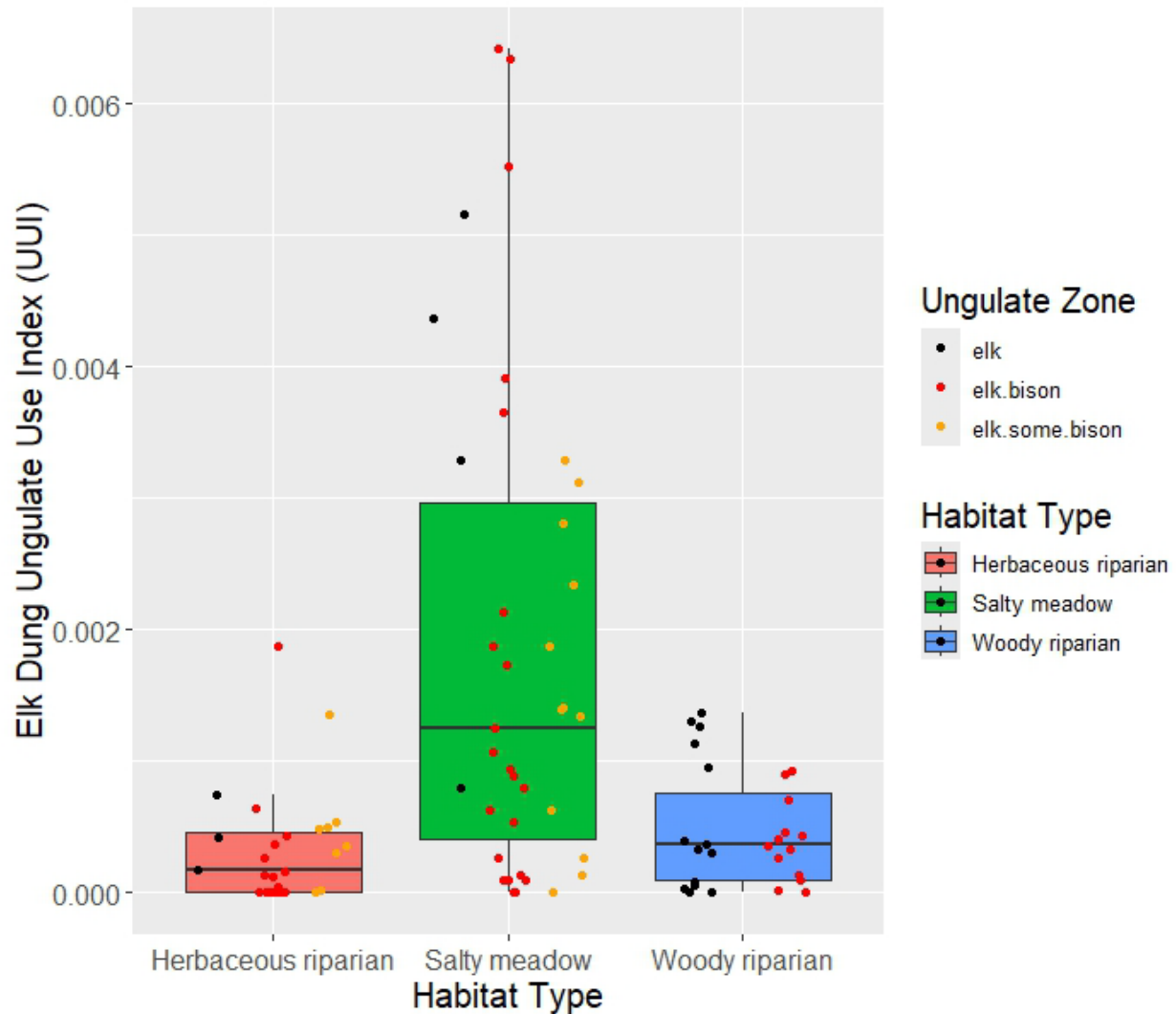


Figure 13. Box plots showing variation in elk dung index (DI) between habitat types and sorted by ungulate zone, at Great Sand Dunes National Park, Colorado.

Dung Density Spatial Pattern

Maps of dung index (DI_x) reveal patterns of use across the landscape (Figure 14). Bison DI was greatest along Big and Little Spring Creeks, Elk Springs, meadows to the west of Sand Creek, and meadows between Sand and Little Spring creeks. The highest densities of bison dung were found inside the bison fence, except for the Elk Springs site. Elk DI was greatest along Sand Creek, both inside and outside the bison fence, along Big Spring Creek outside the bison fence, Deadman Creek, and some meadows near Big and Little Spring Creek that were also used by bison (Figure 14).

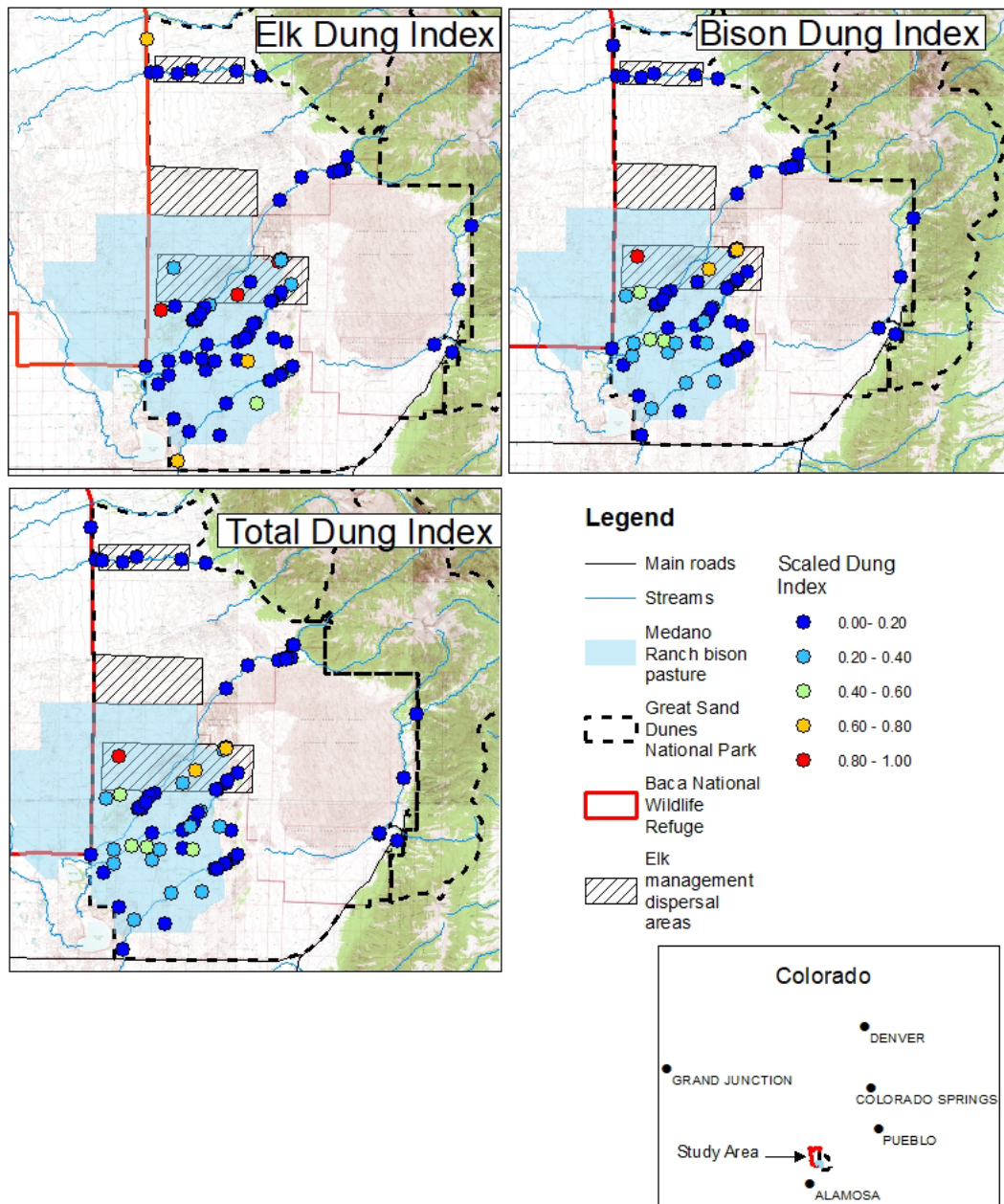


Figure 14. Scaled values of dung ungulate use index (UII) for elk, bison, and both across Ungulate Management Plan sites in Great Sand Dunes National Park. Inset shows location within state of Colorado.

Telemetry UUI

Bison Spatial and Temporal (2005-2007) Distribution

The year-round spatial distribution (in 2005–2007) of bison as derived from the proportional overlap of year-round home ranges for 18 collared bison suggested bison concentrate use in the central areas of the bison pasture between Sand Creek and Little Spring Creek (Figure 15). This area of the bison pasture has a diversity of vegetation types, with several productive wetland areas, especially in herbaceous riparian habitat along the stream corridors. Based on the high proportional overlap of home ranges, the area of the bison pasture along the GRSA-Baca NWR boundary north of Sand Creek also appears to be used heavily year-round. The vegetation in this area includes salty meadow wetlands as well as areas of greasewood. Proportion of bison use dropped off at the extreme western edge of the bison pasture, though a pocket of higher use was located in the northwest corner of the bison pasture where there are areas of xeric grasslands. Bison use also appears lower along the northeastern corner of the bison pasture, an area dominated by shrubby vegetation, such as rabbitbrush and greasewood.

When we created maps of proportional overlap based on buffering individual animal locations to 500 m, the resulting map showed a much finer pattern of animal use (Figure 16). Areas of greatest bison concentrated use on a year-round basis appeared to be sandwiched between Big and Little Spring Creeks and the areas along the boundary between Baca NWR and NPS lands (Figure 16). The resulting UUI values for each UMP wetland site had greater variation using this method, which resulted in higher correlations to dung UUI as noted in later sections of this report. This level of detail will also make these maps better for identifying areas of high ungulate use that might be targeted for ungulate management activities.

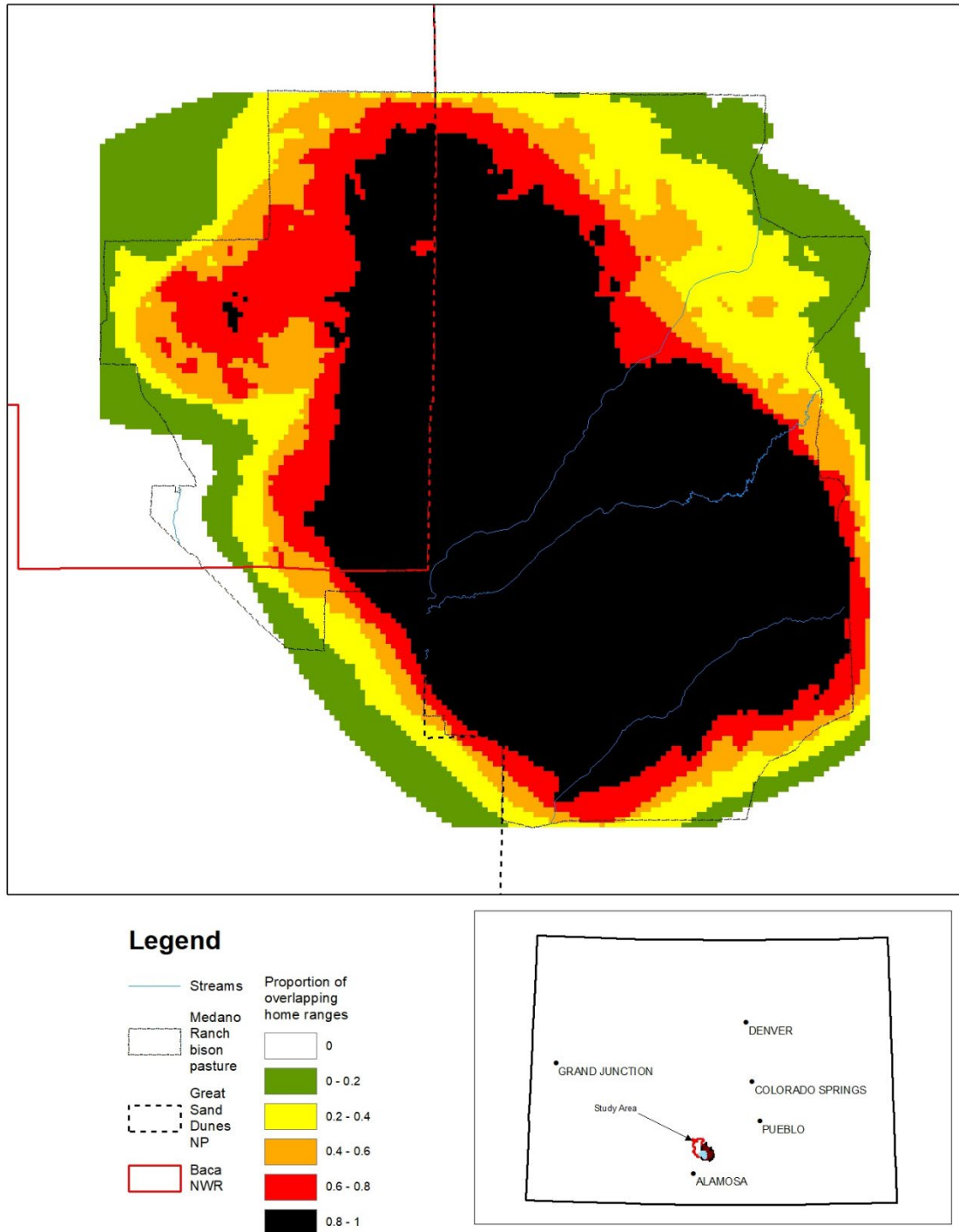


Figure 15. Bison year-round home range density of use based on proportion of overlapping 90% kernel density home ranges of 18 collared animals (4 GPS collars and 14 VHF collars) in Great Sand Dunes National Park (GRSA), Colorado, 2005-2007. The number of overlapping home ranges used to standardize the metric was 0 to 18. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

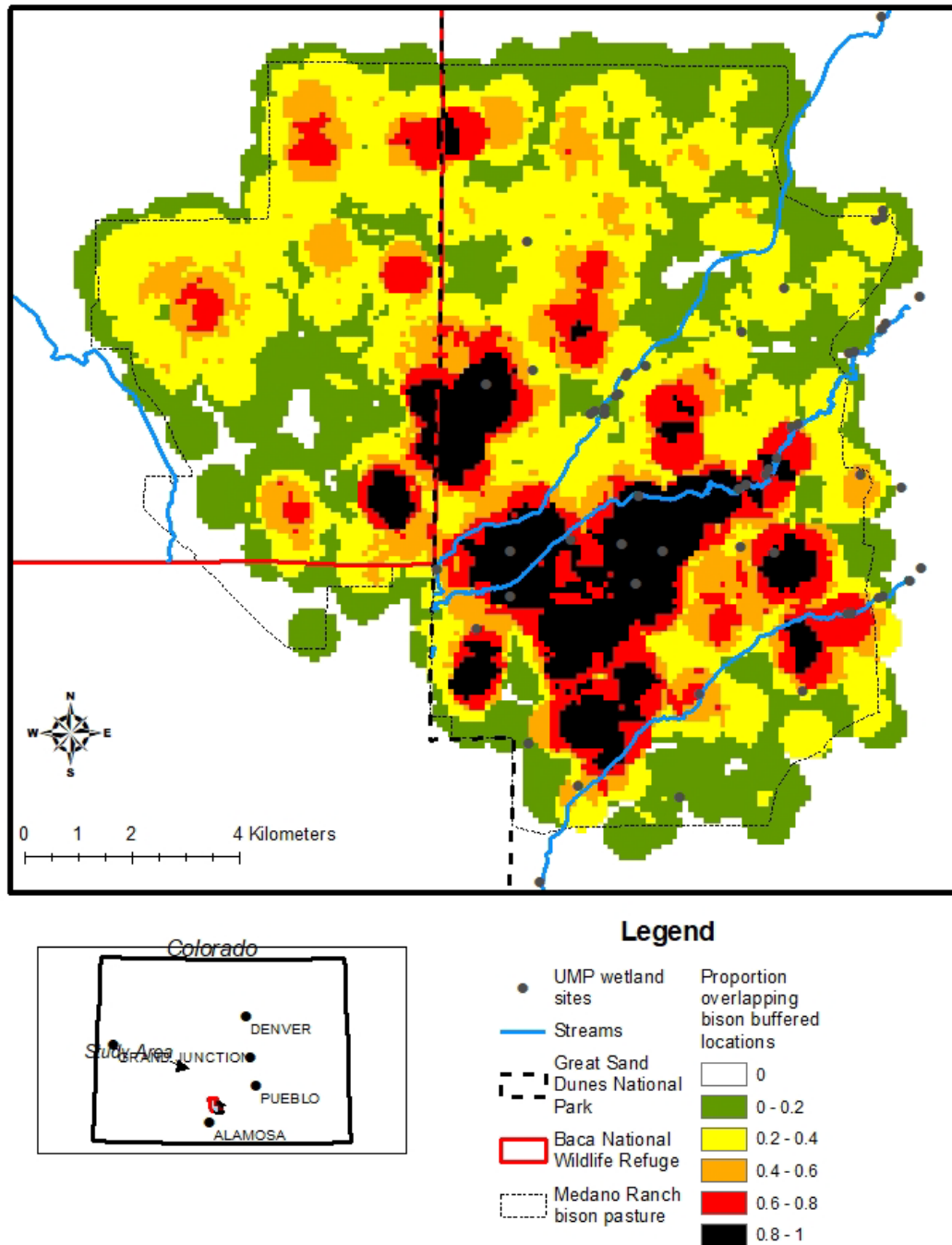


Figure 16. Bison year-round ungulate use index (UII) based on proportion of overlapping concentrated use polygons of 18 collared animals (4 GPS collars and 14 VHF collars) in Great Sand Dunes National Park (GRSA), Colorado, 2005-2007. The number of overlapping home ranges used to standardize the metric was 0 to 18. Concentrated home ranges were created by buffering an individual animal's collar locations to 500 m. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

Bison appeared to spread out more during fall and winter as evidenced by the smaller area of 80-100% home range overlap (Figure 17a,b). Spring and summer bison distributions (Figure 17c,d) were similar to the year-round pattern, with higher proportional range overlap in and around the central region of the bison pasture. However, in the summers, distribution was more concentrated in the highly productive wetland areas on Sand, Big Spring, and Little Spring Creeks. Fall use patterns may reflect the influence of the movement of bison to pastures in the south-central part of the bison pasture in conjunction with annual roundup and culling of the herd in early November. Bison were attracted to pastures near the bison barn prior to roundup by the placement of supplemental feed.

As was evident with the year-round results, maps of concentrated use areas based on 500 m buffered animal locations had much finer detail. “Hot spots” where many of the collared animals spend time during each season become particularly evident (Figure 18). The greatest use of the western half of the bison pasture occurs in winter (Figure 18, top right panel) and this area receives virtually no use in summer (Figure 18, bottom right panel) when more productive grasslands and wetlands between the creeks draw highest use. The area between Big and Little Spring Creeks has concentrated use in all seasons; however, that use becomes greatest during spring and summer (Figure 18, lower left and right panels). Use of the northwest corner of the bison pasture is lower in summer than all other seasons.

Given the better discrimination in UUI values for the buffered location maps compared to the 90% kernel density home range maps, we decided to use the UUI based on buffered locations to analyze for differences in UUI based on habitat type and ungulate zone. We could not test for interaction effects between habitat type and ungulate zone because all habitats were not represented in all ungulate zones.

We found differences in bison collar UUI for all ungulate zones over all seasons (Table 6; Figure 19). Unsurprisingly, bison use was greatest inside the bison pasture (EB), followed by the zone right outside the bison fence (EsB), then areas further outside the bison fence (E). However, we point out that the collar data used for this comparison was from a time when the fence was a functional barrier and we had no data points that could accurately identify use beyond the bison pasture except for where UUI extended beyond the fence lines as result of buffering locations inside the bison pasture that were near the fence. Wetland habitat use by bison only differed significantly ($P < 0.05$) year-round, and seasonally in winter and spring when salty meadow and herbaceous riparian habitats were used to a much greater extent than woody riparian habitats. Results were nearly significant ($P < 0.10$) for summer and fall and showed a similar pattern of lower use of woody riparian areas.

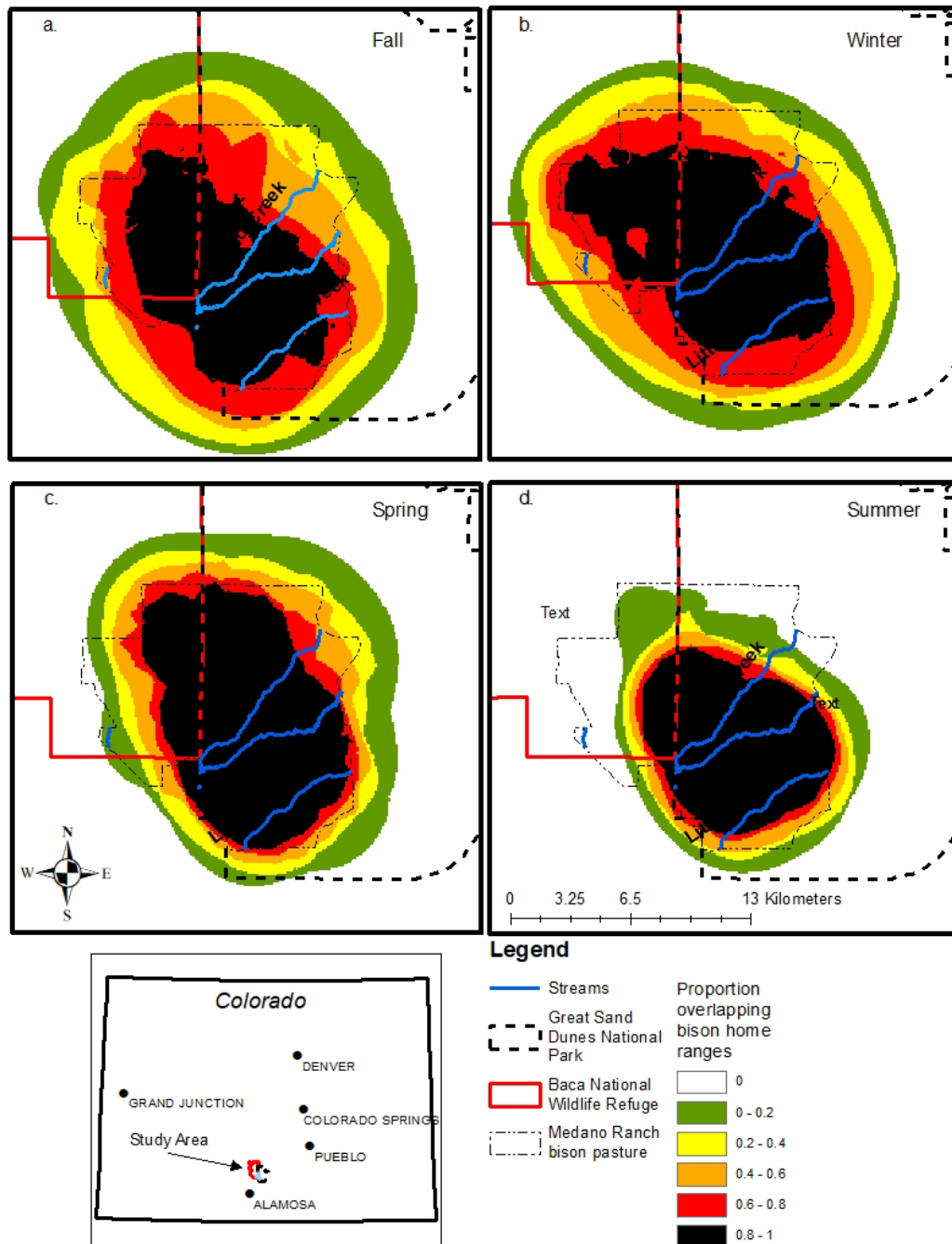


Figure 17. Seasonal bison density of use maps based on the proportion of overlapping 90% kernel density home ranges for 18 radio collared bison (4 GPS and 14 VHF) inside the bison pasture at Great Sand Dunes National Park (GRSA), Colorado, 2005-2007. Minimum overlapping home ranges (used to scale the indices) were 0 for all seasons except fall where the minimum was 3. Maximum overlapping home ranges were 17 for spring and summer, and 18 for fall and winter. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

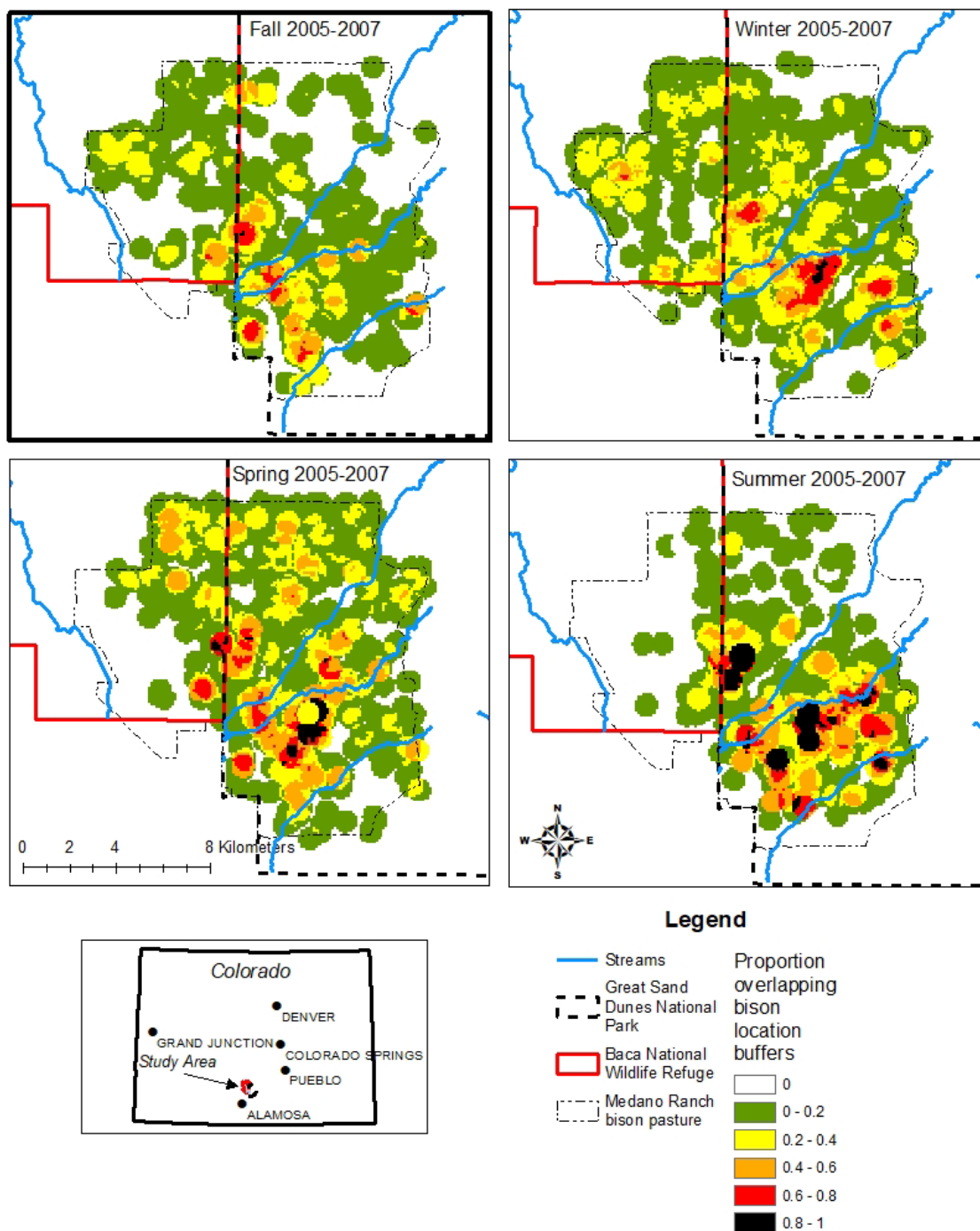


Figure 18. Bison seasonal ungulate use index (UII) based on proportion of overlapping concentrated use polygons of 18 collared animals (4 GPS collars and 14 VHF collars) inside the bison pasture at Great Sand Dunes National Park (GRSA), Colorado, 2005-2007. Concentrated home ranges were created by buffering an individual animal's collar locations to 500 m. Maximum overlapping home ranges were 17 for spring and summer, and 18 for fall and winter. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

Table 6. Results of Kruskal-Wallis nonparametric test for telemetry based indices (overlapping ranges of buffered animal locations) for bison, elk, and both species combined in Great Sand Dunes National Park, Colorado.

Collar UUI	Variable	Chi-square	Degrees of freedom	P-value
Bison Year-round	Habitat type	16.171	2	0.0003
Bison Year-round	Ungulate zone	62.975	2	<0.0001
Bison Fall	Habitat type	4.8236	2	0.0896
Bison Fall	Ungulate zone	47.304	2	<0.0001
Bison Winter	Habitat type	9.7413	2	0.0077
Bison Winter	Ungulate zone	59.924	2	<0.0001
Bison Spring	Habitat type	15.369	2	0.0005
Bison Spring	Ungulate zone	59.143	2	<0.0001
Bison Summer	Habitat type	5.181	2	0.0750
Bison Summer	Ungulate zone	55.375	2	<0.0001
Elk Year-round	Habitat type	6.5586	2	0.0376
Elk Year-round	Ungulate zone	33.633	2	<0.0001
Elk Fall	Habitat type	1.7670	2	0.4133
Elk Fall	Ungulate zone	25.351	2	<0.0001
Elk Winter	Habitat type	0.0733	2	0.964
Elk Winter	Ungulate zone	4.7245	2	0.0942
Elk Spring	Habitat type	24.231	2	<0.0001
Elk Spring	Ungulate zone	29.084	2	<0.0001
Elk Summer	Habitat type	0.6030	2	0.7397
Elk Summer	Ungulate zone	20.492	2	<0.0001
Bison + Elk Year-round	Habitat type	22.015	2	<0.0001
Bison + Elk Year-round	Ungulate zone	62.781	2	<0.0001
Bison + Elk Spring	Habitat type	32.282	2	<0.0001
Bison + Elk Spring	Ungulate zone	53.725	2	<0.0001
Bison + Elk Summer	Habitat type	16.603	2	0.0002
Bison + Elk Summer	Ungulate zone	47.043	2	<0.0001

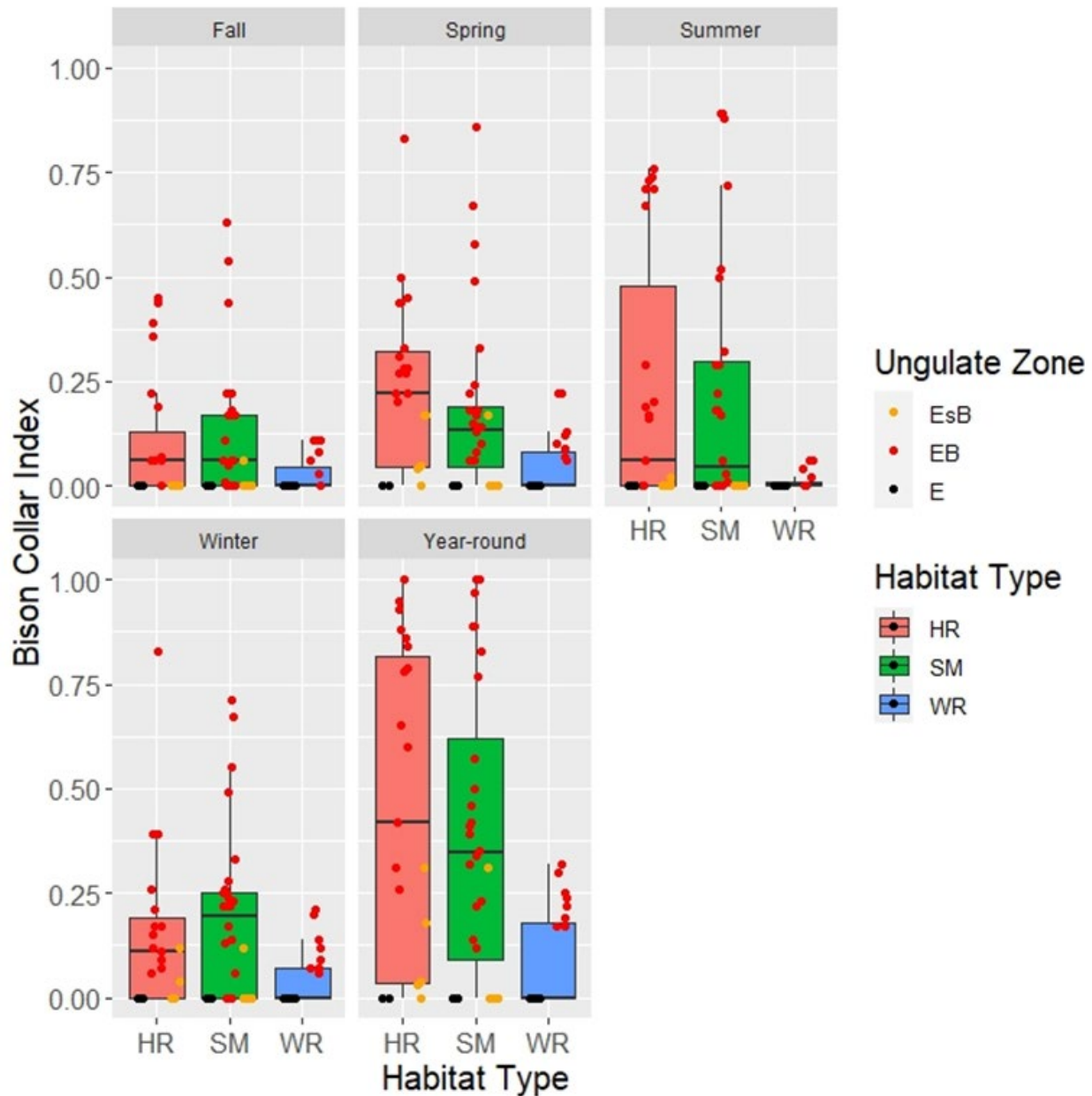


Figure 19. Box plots of telemetry collar UUI based on overlapping maps of buffered animal locations for bison use in Great Sand Dunes National Park, Colorado. Habitat types are herbaceous riparian (HR), salty meadow (SM), and woody riparian (WR). Ungulate zones: EsB= elk some bison zone within 1km outside the bison fence, EB = bison pasture that both elk and bison can roam freely, E = elk only zone more than 1 km outside the bison fence.

Elk Spatial and Temporal Distribution

Based on the UUI developed from overlapping 90% kernel density home ranges, year-round elk spatial distribution appears to have shifted between 2005-2007 and 2019-2020 (Figure 20). During 2005-2007, year-round elk spatial distribution was largely north of the bison pasture, concentrated in the area between Deadman Creek and the northern boundary of the bison pasture and extended across

the western park boundary onto the Baca NWR (Figure 20a). In 2019-2020, elk distribution appeared to have shifted south and was concentrated on either side of the northern boundary fence of the bison pasture (both in GRSA and Baca NWR), along the upper reaches of Big Spring Creek along the eastern boundary of the ranch, and outside the bison fence along the SE edge (Figure 20b). Elk use of the central and SW corner inside the bison pasture was only moderate in both time periods (Figure 20). Bison tend to use this area heavily and many wetlands are located here.

We found that maps of overlapping concentrated use areas based on buffered individual 2019-2020 elk locations had more defined patterns compared to those based on kernel density home ranges (Figure 21). Areas of highest year-round use fell within the 3 areas that the park has targeted for elk dispersal management actions (Mosher et al. 2018), but additional high use areas exist in the southeast corner of the study area just outside the bison fence. Elk year-round use was also higher to the west of the Baca NWR/NPS boundary just north of the bison pasture. Year-round elk use was concentrated between Sand and Big Spring Creeks, and south of Little Spring Creeks—areas that are less frequented by bison. Outside the bison pasture, use was high along Deadman Creek (north of the bison pasture), and immediately north of the bison fence (Figure 21).

Elk distribution observed year-round north of the bison fence in 2005-2007 was mainly driven by fall and winter distribution (Figure 22a,b). Spring and summer distributions appeared much more spread out throughout the area (Figure 22c,d) and some elk moved completely off the analysis area during these seasons. In 2019-2020, elk proportional home range overlap inside the bison pasture increased spring through fall (Figure 22e-h), with higher range overlap north of Sand Creek and in the central wetland areas. These wetlands have high numbers of bison during summer (based on the 2005-2007 bison collar data and direct observation of current bison use patterns; Figure 18).

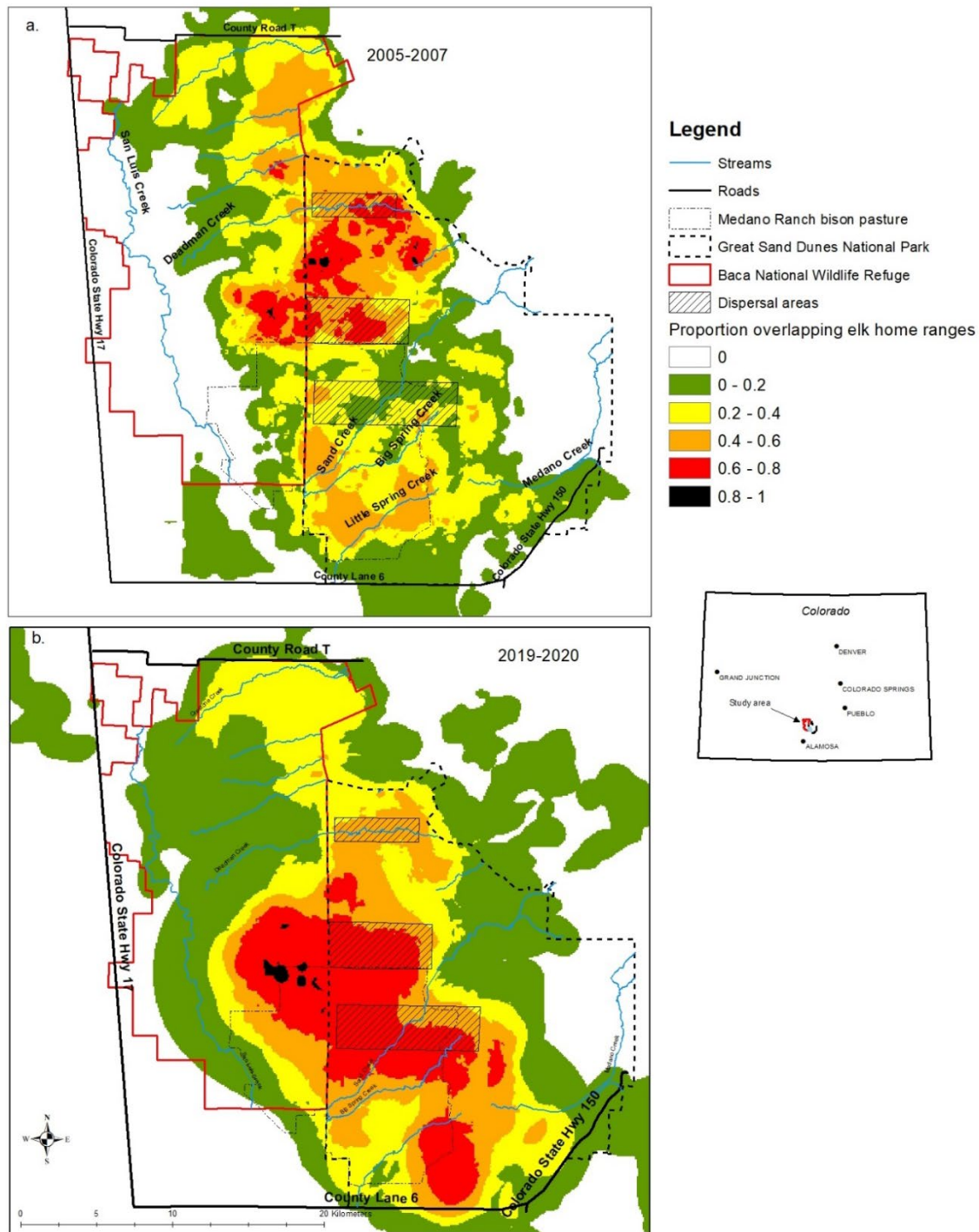


Figure 20. Comparison of 2005-2007 (a) and 2019-2020 (b) year-round home range density based on proportion of overlapping home ranges of GPS collared elk ($n=16$ for 2005-2007, $n=35$ for 2019-2020) in Great Sand Dunes National Park (GRSA). Maximum number of overlapping ranges for 2005-2007 was 16 and for 2019-2020 was 34. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

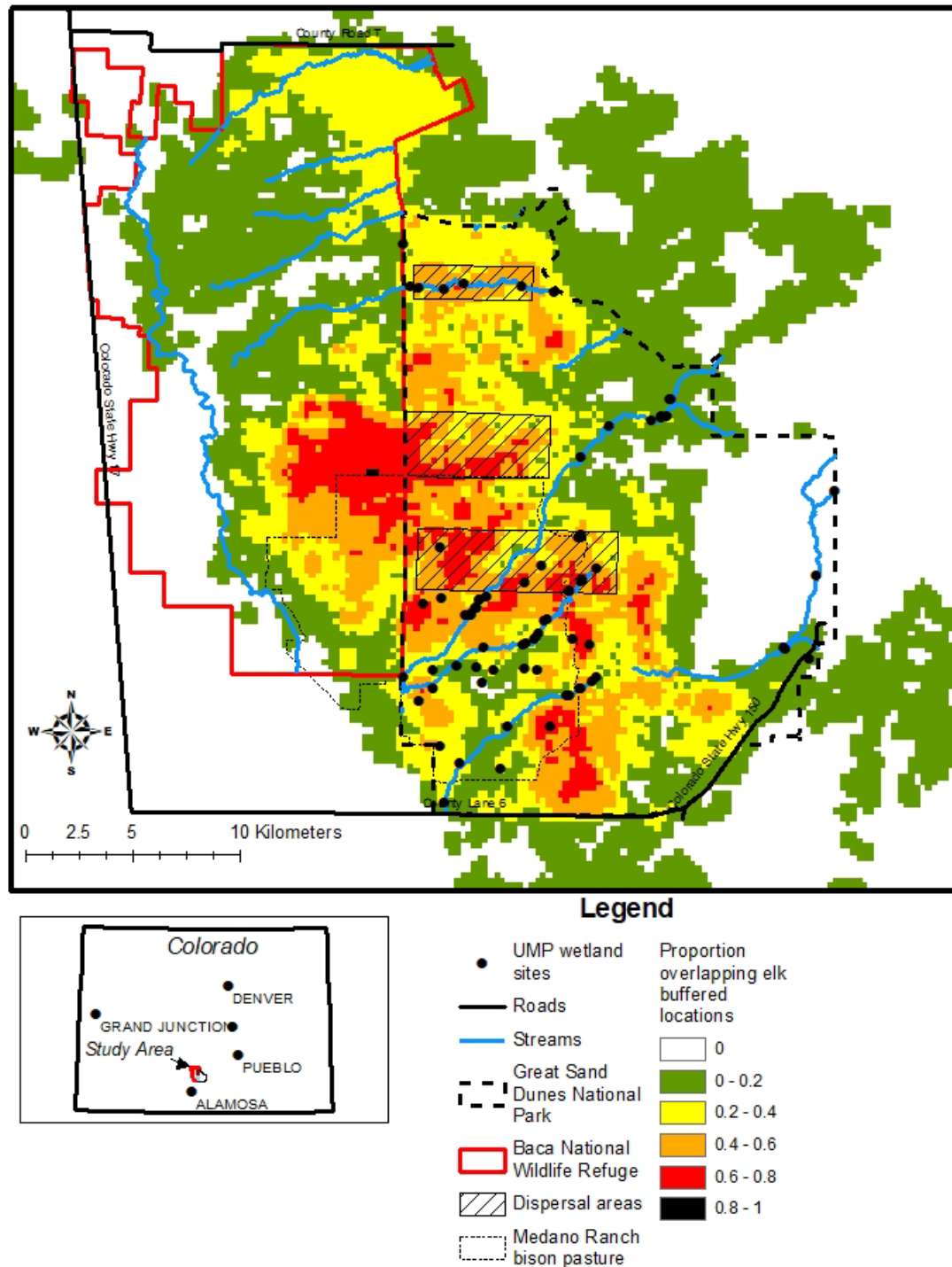


Figure 21. Elk year-round ungulate use index (UII) based on proportion of overlapping concentrated use polygons of 35 GPS collared animals in Great Sand Dunes National Park (GRSA), Colorado, 2019-2020. The number of overlapping home ranges used to standardize the metric was 0 to 34. Concentrated home ranges were created by buffering an individual animal's collar locations to 500 m. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

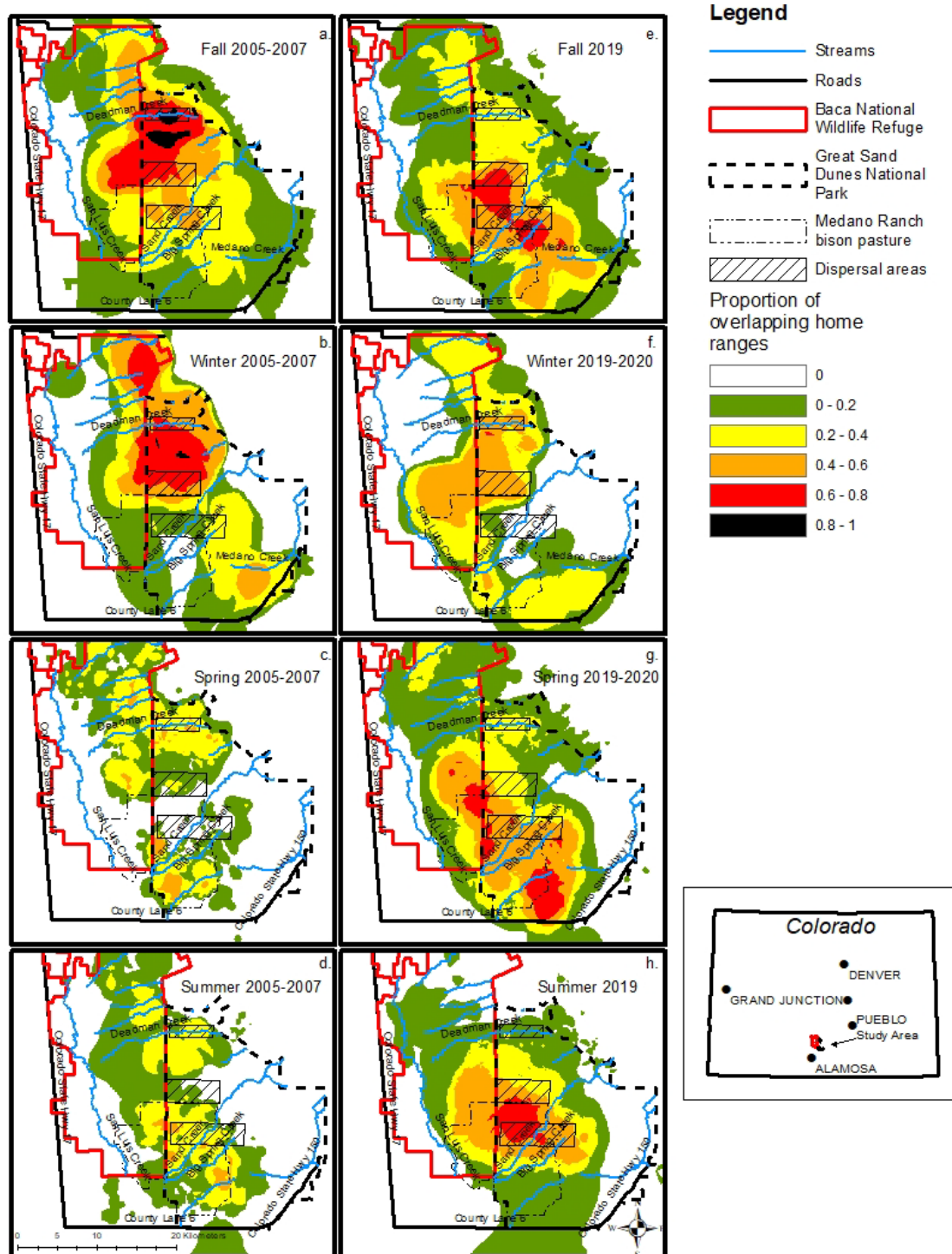


Figure 22. Seasonal density of elk use at Great Sand Dunes National Park (GRSA), Colorado, based on proportion of overlapping home ranges for 16 elk fitted with radiocollars 2005-2007 (only 15 elk had available data for fall and summer, and 14 elk for winter) and 34 elk fitted with GPS collars in 2019-2020 (33 in fall and winter, 34 in spring and summer). Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

When we used buffered elk location data to create seasonal maps of concentrated elk use, we observed greater use of the area within the elk management dispersal area on Sand Creek in the bison pasture, particularly in summer and fall (Figure 23a,d). During spring elk appeared to use wetlands near Dollar Lake in the southwest corner of the bison pasture, salty meadow/playa areas in the southeast corner of the bison pasture both inside and outside the fence, and the area to the northwest of the bison pasture (Figure 23c) the most heavily. Use of the dispersal area north of the bison pasture is highest in winter (Figure 23b), but also has substantial use in summer and fall (Figure 23a,d) compared to spring (Figure 23c). The greatest concentration of use in the Deadman Creek dispersal area appears to be in winter (Figure 23b). In winter and spring, elk use appears to be concentrated on the Baca NWR just outside the northwest corner of the bison pasture.

We found that UUI based on overlapping concentrated use areas showed differences in elk use of ungulate zones in all seasons except winter. Elk collar UUI was greatest in the EsB zone, followed by areas within the bison pasture (EB), with elk only (E) areas used the least (Figure 24). This is likely driven, at least in part, by the larger area of productive wetlands in the EsB and EB zones. Elk collar UUI indicate that elk use was only significantly different ($P < 0.05$) between wetland habitat types in spring and when calculated year-round, with elk using salty meadow and herbaceous riparian habitats to a much greater extent than woody riparian areas over these time frames (Figure 24).

On average, collared elk moved 1,873 ($\pm$ a standard error of 129) m over a 12-hour period, therefore, a 2 km buffer around wetlands would likely be a relevant and conservative area for examining elk influences on a wetland site. We could not estimate a buffer for bison given limited telemetry data.

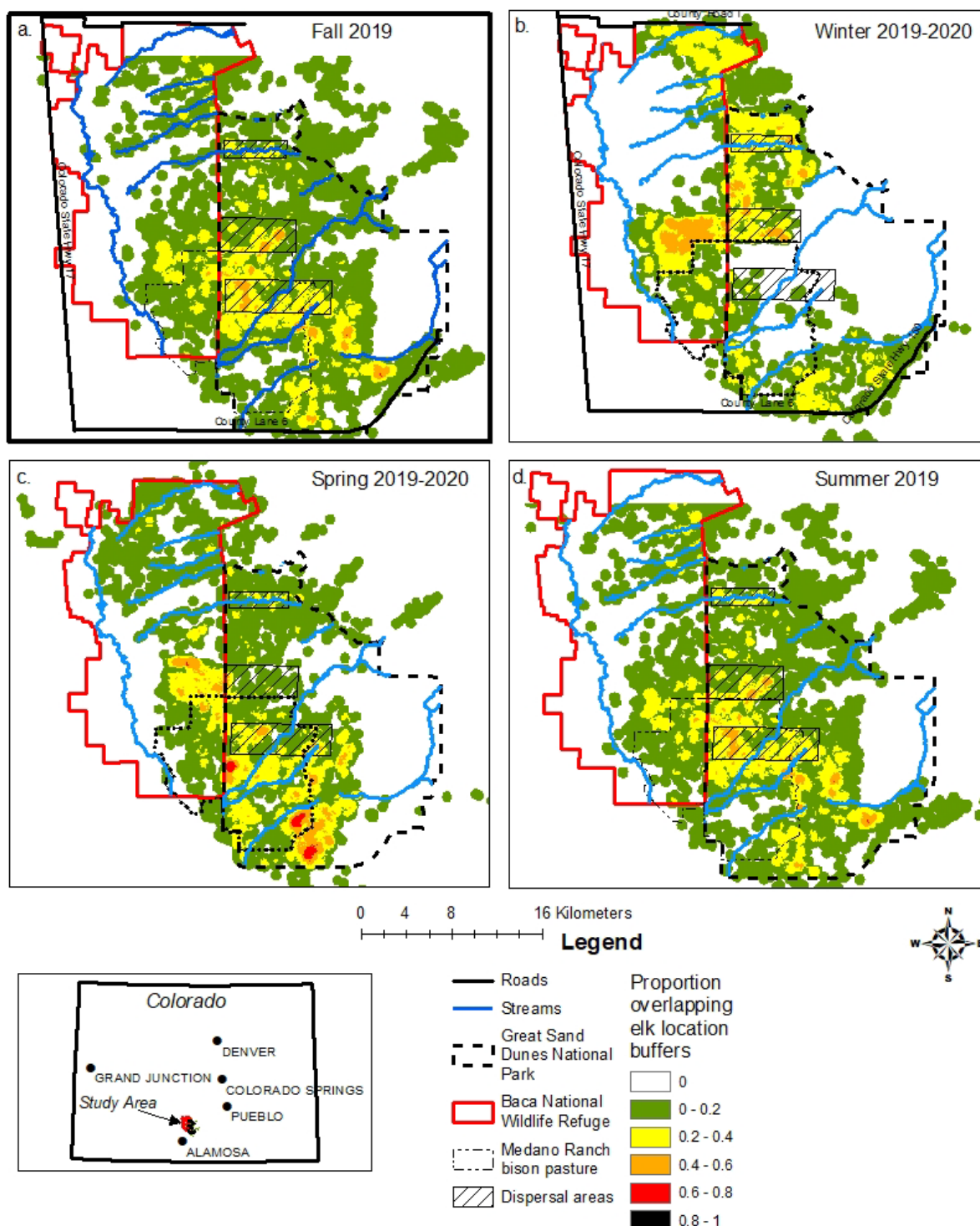


Figure 23. Elk seasonal ungulate use index (UII) based on proportion of overlapping concentrated use polygons of 35 GPS collared animals in Great Sand Dunes National Park, Colorado, 2019-2020. The number of overlapping home ranges used to standardize the metric was 0 to 33 in fall and winter and 0 to 34 in spring and summer. Concentrated home ranges were created by buffering an individual animal's collar locations to 500 m. Inset shows location of study area in state of Colorado. See Figure 1 for location of the bison pasture relative to GRSA boundary.

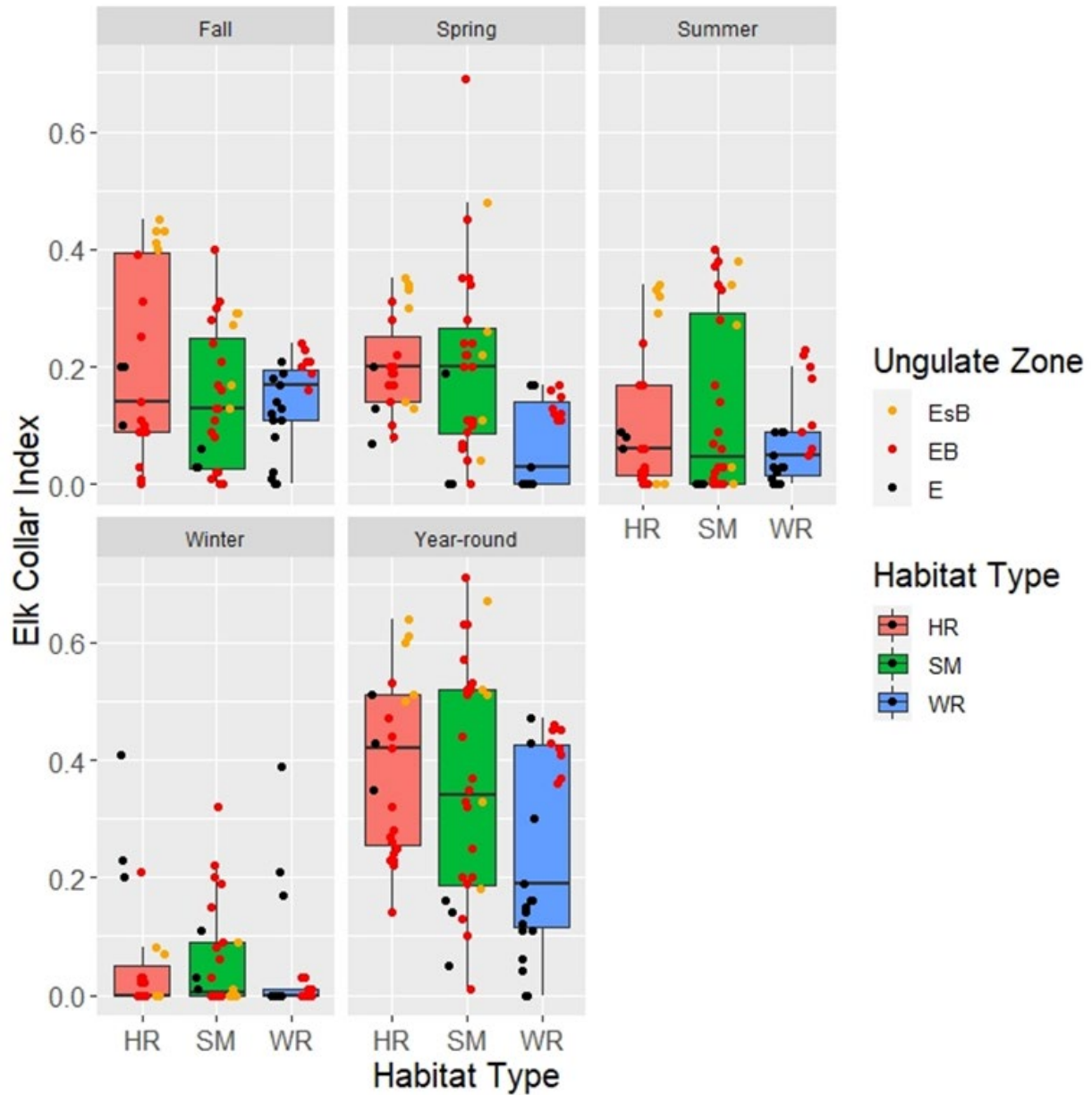


Figure 24. Box plots of telemetry collar UUI based on overlapping maps of buffered animal locations for elk use in Great Sand Dunes National Park, Colorado. Habitat types are herbaceous riparian (HR), salty meadow (SM), and woody riparian (WR). Ungulate zones: EsB= elk some bison zone within 1 km outside the bison fence, EB = bison pasture which both elk and bison can roam freely, E = elk only zone more than 1 km outside the bison fence.

Camera Trap UUI

A total of 111 surveys from 10 sites from July 28, 2016, to July 1, 2020, were included in the photo capture dataset used in our analysis. A total of 103,892 images from the 111 surveys were classified as containing an animal. Elk and/or bison were identified in 101,798 (98%) of accepted classified images. Images containing only bison accounted for 55% of the total elk/bison images, while images containing only elk accounted for 44%. The majority (68%) of bison images were at sites inside the bison pasture, whereas only 16% of elk images were inside the bison pasture. Only 818 (<1%) images had both elk and bison in the image, and 97% of these images were taken at sites outside the bison fence, with 69% from a single site (Elk Springs) and an additional 25% from a second site outside the bison fence along Little Spring Creek. Both of these sites were <1 km outside the bison fence (EsB zone). Most images were captured during daylight hours (73% overall), but bison were more often captured during the daytime (81% of bison images) than elk (63% of elk images).

Classified images of elk and bison spanned nearly the entire camera deployment period (July 2, 2016, to June 28, 2020), but no site had continuous camera coverage for the entire time. Total camera deployment time for the 10 sites ranged from 518 days to 1,277 days (Table 7), with a mean of 838 days (Table 7). Length of deployment varied by year, with the longest deployments occurring in 2017 and 2018 (Table 1). The mid-summer start of camera deployment in 2016 shortened the deployment days for that year. Camera malfunctions also impacted the duration of many deployments – we removed all photos from periods when cameras were not functioning properly, or an image could not be placed in time.

Other species observed in photos included birds (American wigeon, green-winged teal, Canada goose, magpies, and various raptors), small mammals (porcupine, rabbits, prairie dogs), predators (black bear, bobcat, coyote), ungulates (pronghorn, mule deer), horses, and humans. Mule deer images accounted for roughly 0.5% of all images, pronghorn for 0.1%. Roughly 70% of the mule deer images were captured at site 252 located along Medano Creek. The camera at this site captured only a single image of elk. Lower elk use at this site may be a consequence of its location near the areas of greatest human use in the park (campground, visitor center, and dunes recreation area) and less preferred pinyon-juniper habitats nearby.

Table 7. Deployment time in days by habitat types and seasonal categories for wildlife cameras at Ungulate Management Plan sites in Great Sand Dunes National Park by season, 2016 to 2019. See text for definitions of the 5 custom intervals over which photos were analyzed. PGS=pellet growing season.

Habitat Type	Site #	Total Days	Summer Days	Fall Days	Winter Days	Spring Days	PGS Days	Growing Season Days	Bison Breed Days	Bison Gather Days	Elk Breed/Hunt Days
Salty meadow	108 ^a	682.3	232.1	89.1	172.4	188.6	58.3	428.2	159.5	0.2	73.6
Salty meadow	215 ^a	1224.1	248.2	257.5	180.0	236.7	19.4	535.6	185.8	53.0	222.0
Salty meadow	204 ^b	518.6	257.8	84.8	84.3	91.7	112.5	401.3	224.4	0.0	84.8
Salty meadow	302 ^b	615.8	145.4	106.4	180.0	184.0	0.0	303.4	85.4	19.0	74.0
Salty meadow	306 ^b	805.6	316.5	193.6	83.3	212.2	300.5	550.7	226.7	34.0	168.0
Woody riparian	406 ^a	880.9	247.6	269.3	180.0	184.0	174.4	485.6	185.4	53.0	222.0
Woody riparian	252 ^c	644.8	133.4	182.0	180.0	149.5	0.0	296.9	103.4	37.0	148.0
Herbaceous riparian	211 ^a	575.5	213.3	115.6	84.4	162.3	205.0	405.6	153.3	13.8	104.2
Herbaceous riparian	404 ^b	1277.7	207.9	271.4	270.0	266.5	1.4	493.8	147.5	53.0	220.4
Herbaceous riparian	416 ^c	1156.6	317.5	293.0	270.0	276.0	9.4	633.6	227.5	53.0	241.0
Mean	–	838.2	232.0	186.3	168.4	195.2	88.1	453.5	169.9	31.6	155.8

^aEB=sites accessible to both elk-bison

^bEsB=sites accessible to elk and some limited bison use

^cE=sites accessible only to elk

Quality Control of Photo Dataset

The classification error rate in the images independently analyzed for quality control (QC) was 3.2% in terms of determining if an animal was present in an image. Of the 2,500 images, both analyst groups agreed on classification of 2,420 images (1,253 with an animal present and 1,167 with no animals present). The original analyst identified 1,303 images as having an animal present, whereas the independent analyst identified 1,283 images having an animal.

Of the 1,253 QC images with animals, the classification error rate for species identification was 4.0% (50/1253). Classification error in species identification was not greater for one species compared to another, with classification error of 4.0% (29/730) for bison photos and 3.8% for elk photos (19/499). When both elk and bison were present in an image, classification error increased to 15.4% (2/13 images). For species identifications other than elk and bison (coyote, pronghorn, horseback riders, mule deer, humans, bison, bird), the analysts had 100% agreement on classification, although these

images comprised <1% of the QC images. Disagreement in species identification may have been affected by time of day. Only 25% of all photos in the QC dataset were taken during nighttime hours, but analysts disagreed on classification for 42% of these photos compared to only 3% disagreement for photos taken during daylight hours. For images where animals were close to the camera (“wall of fur”) or photo series taken under poor lighting conditions, the lack of preceding and succeeding photos in a series in which an identification could be confirmed may have put the QC analyst at a disadvantage for identifying the correct species.

There was a greater difference in agreement between analysts regarding group size. One-third of the images classified by both ROMN and independent analysts as having at least one animal, disagreed regarding the group size category (1, 2-10, 11-15 or >15 individuals). Agreement between analysts was greatest (91%) when group size was 1 individual but considerably lower when the ROMN analyst determined that group size was between 2 and 10 individuals (54%). With the largest group sizes, only 11-12% agreement was found between analysts. However, because group size categories could be affected by a counting difference of only one individual, we feel the QC of raw count number is more relevant. Analysis of actual counts of individuals found a 68% agreement between observers. For counts where the observers did not agree, 48% of counts disagreed by only 1 animal, 66% by 1 or 2 animals, and 75% by 1-3 animals. Count differences >3 animals between analysts were overwhelming bison photos (>90%) and most were in sites where the wetland boundary was less discernable. Differences between observers in group counts did not appear to be affected greatly by day vs. night, or by partial obstruction of the photo/poor image.

Ungulate Use Across Years and Months

We first present camera-based UUI with habitat type lumped to focus on general patterns across time. This assumes that there are not important differences across habitat type nor any interaction between time and habitat type. Given sample size constraints we do not estimate any model of patterns in the camera-based UUI, so we cannot test these assumptions. Importantly, all of our interpretations must only be applied to these specific 10 sites – our data cannot make inference to unsampled areas. That said, we suspect our interpretations are generalizable.

Patterns were relatively similar across all camera UUI (Figures 25 and 26). Bison and elk daily presence index (DPI) values at the 10 UMP sites with cameras were visually similar across years from 2016 to 2020, but bison presence appeared to increase from 2016 to 2018 then decreased (Figure 25a). This pattern was also evident in the capture-based relative indices of activity (RIA_c) and individual photo-based indices (RIA_p), both weighted by group size (Figure 26) and unweighted (Figure 25), but when the index was based on the total number of photos (Figure 26) the pattern was less discernable.

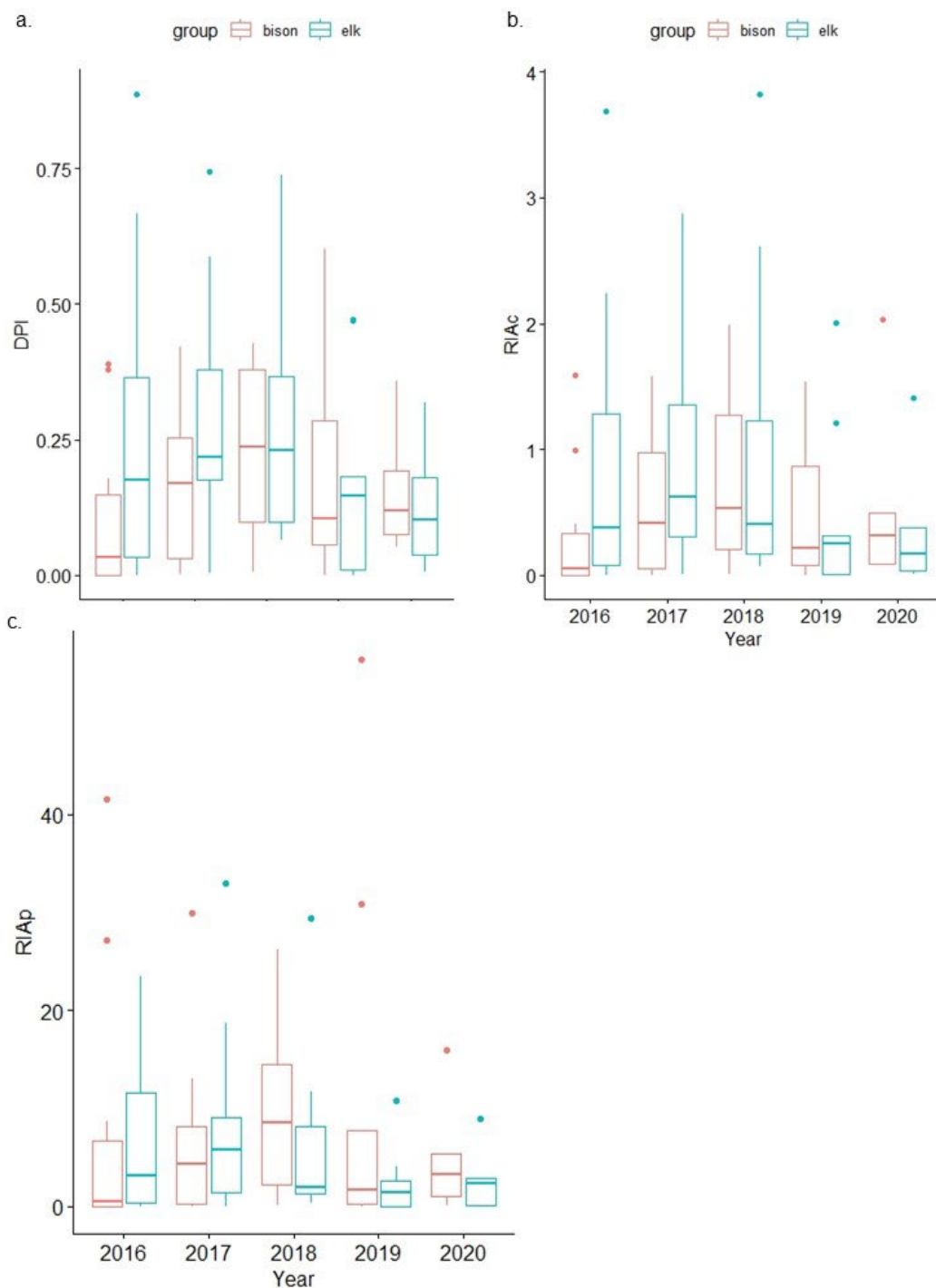


Figure 25. Boxplots depicting various ungulate use indices (UII) for elk and bison developed from trail camera data at wetlands in Great Sand Dunes National Park, Colorado. DPI (a) is an index based on days animals were present. Relative Index of Activity was based on b) capture events (all photos with less than a 5 minute gap between photos) per days camera deployment, both unweighted (RIA_c), or c) total number of individual photos per days of camera deployment (RIA_p).

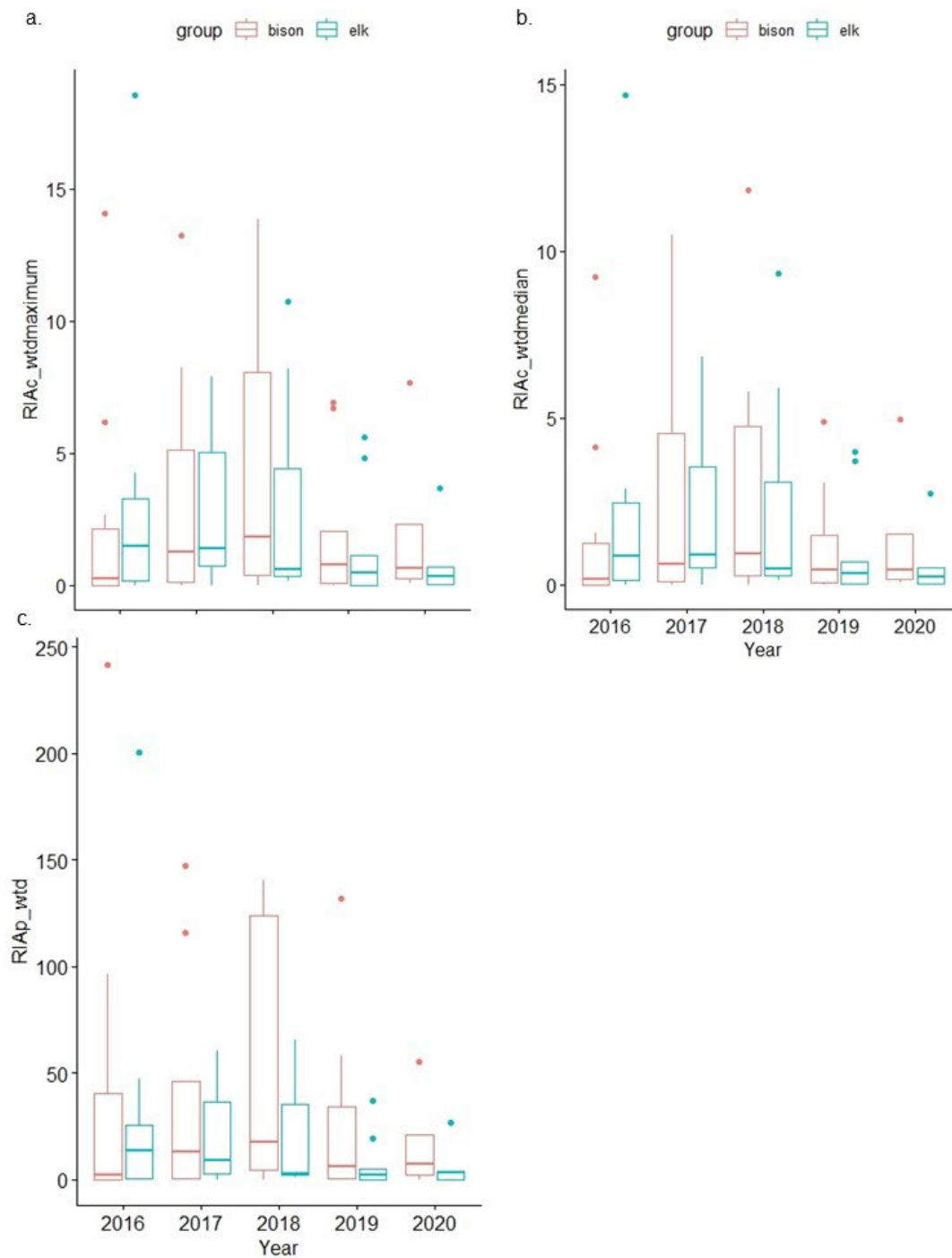


Figure 26. Boxplots depicting various ungulate use indices (UII) for elk and bison developed from trail camera data at wetlands in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5 minute gap between photos) per days camera deployment weighted by a) maximum ($RIA_{c_wtdmaximum}$) and b) median ($RIA_{c_wtdmedian}$) group size during

capture event, or c) total number of individual photos per days of camera deployment and weighted by total number of photos (RIA_{p_wtd}).

Because there was so little variation in patterns for year among the various UUI, we chose to present only one representative index for the remaining graphics in this report section. We selected the Relative Index of Activity based on capture event and weighted by median group size observed during the capture event ($RIA_{c_wtdmedian}$) because we believe it to be the most conservative estimate that describes ungulate use of these sites without overestimating (due to the multiple photos of the same animal) but also accounting for how many animals in a group are using the site during a given “capture event.”

Ungulate Use Across Seasons, Habitats and Ungulate Classes

We next present camera based UUI with interpretations of patterns across season, habitat type, and ungulate classes. Seasons include all subsets (traditional, growing, breeding, etc.). Sample size for these comparisons is constrained and we do not estimate any models. Our interpretations must be applied to specific sites only (we suspect our interpretations are generalizable).

Traditional Climate Seasons

Seasonal use of our 10 camera sites by bison (Figure 27 and 28) was concentrated in herbaceous riparian and salty meadow sites inside the bison pasture (EB) and was highest during spring through fall. Cameras in the “elk some bison” (EsB) ungulate zone (area ~1 km outside the bison fence) suggest even greater bison activity in these areas but mainly during winter and spring (Figure 27). Cameras at sites in the “elk” (E) zone further outside the bison fence recorded no bison, indicating that bison did not venture long distances from the productive wetlands in and near the bison pasture during times when the fence was in disrepair.

Elk use of our wetland camera sites was greatest at the sites in the EsB zone (Figure 27). Moderate levels of elk activity were recorded in all seasons except winter in the E and EB zones. Only very rare occurrences of elk use were captured by the cameras during winter in areas inside the bison pasture (EB) or areas more than 1 km outside the bison fence (E)(Figure 27).

Bison activity was concentrated in herbaceous riparian and salty meadow camera sites overall and was greatest in herbaceous riparian habitats in the spring, followed by salty meadows in winter and spring (Figure 28). Summer and fall bison activity was also relatively high in both herbaceous riparian and salty meadow sites, but bison use of woody riparian areas was low across all seasons (Figure 28).

Elk seasonal use of the 10 wetland sites with cameras was also greatest in the spring, summer, and fall across all habitat types with lower use in the winter (Figure 28). Spring and summer elk activity was greatest on salty meadow habitats, followed by fall in both herbaceous riparian and salty meadow habitats. Although elk use of woody riparian camera sites was low compared to the other 2 wetland types, it was much greater than bison activity in the same sites and elk activity peaked in woody riparian camera sites in summer. This may be due to elk using shaded areas under cottonwood

to escape summer heat. The single woody riparian site outside the bison pasture received very little use from elk and none by bison; however, this site did record mule deer use.

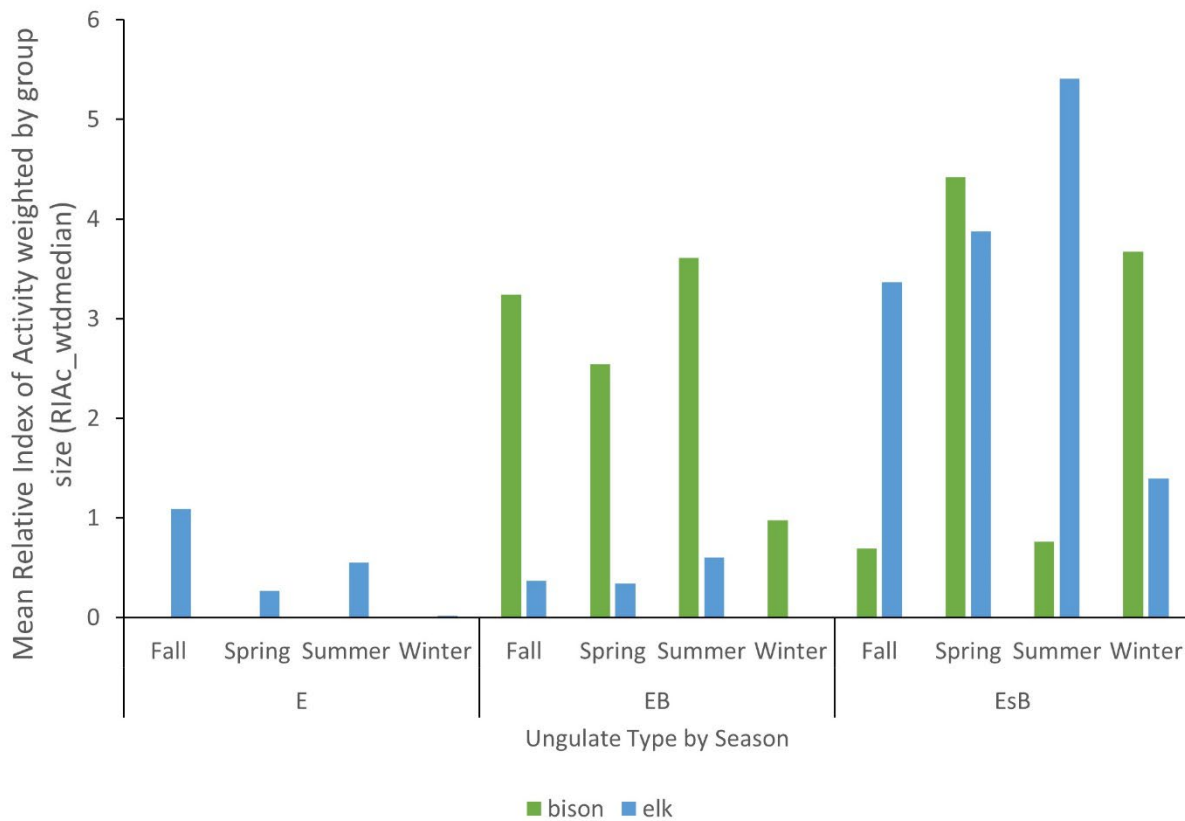


Figure 27. Seasonal (traditional seasons) bison and elk activity by ungulate zone at wetland sites fitted with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median ($RIAc_{wtdmedian}$). E=elk only zone, EB=elk and bison (Medano Ranch bison pasture), EsB=elk some bison (area outside bison pasture fence but within 1 km of fence).

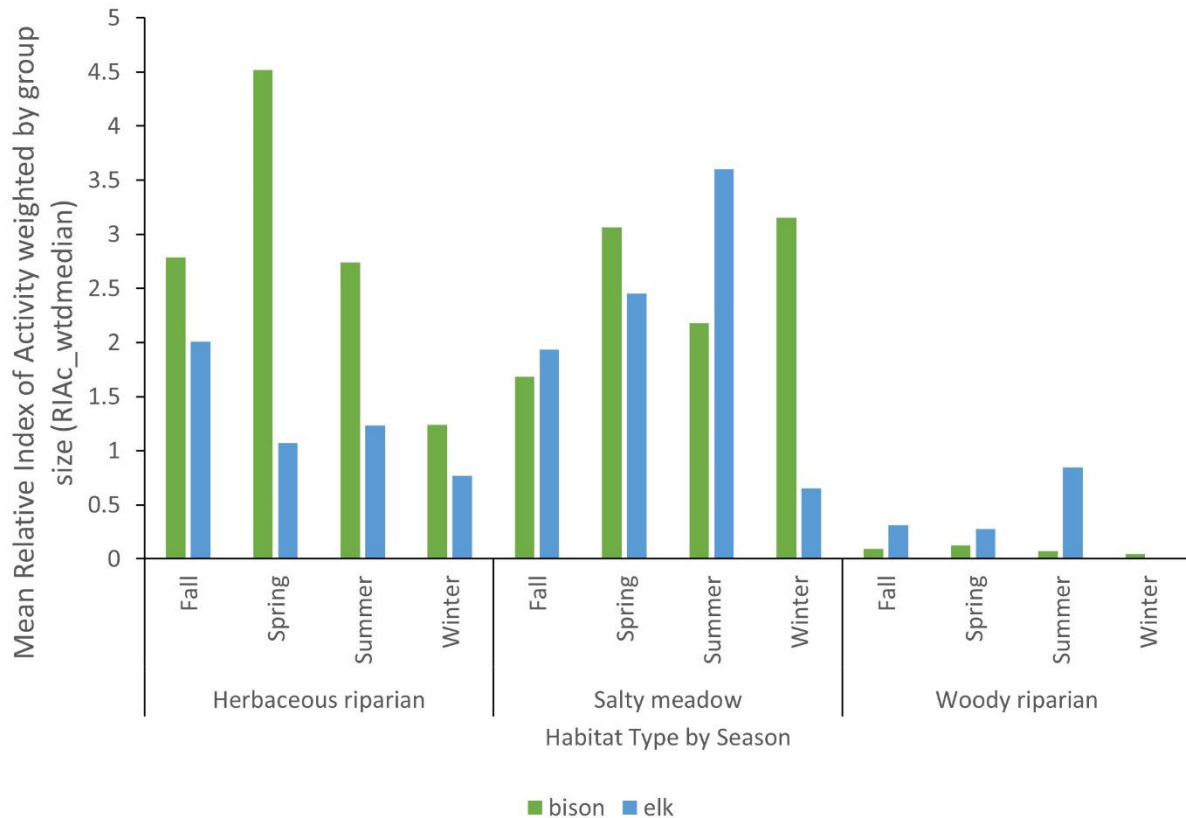


Figure 28. Seasonal (traditional seasons) bison and elk activity by wetland habitat type at wetland sites fitted with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median (RIAc_wtdmedian).

Plant Growing Seasons and Animal Management Seasons

We observed that the bison breeding season camera UII was very similar to summer season UII. Similarly, elk breeding/hunting seasons were very similar to fall season UII. To limit the number of seasons that we compare here, we decided to only use growing season, pellet growing season (PGS; because of its very specific relationship to the dung counts), and bison gather season. Definitions of each of these seasons can be found in Table 3. Camera UII did appear sensitive to expected use changes. Bison activity in herbaceous riparian and salty meadow camera sites was lowest during the bison gather season, as would be expected during the time when animals are being rounded up and moved to holding facilities (Figure 29). Elk did not appear to exploit the movement of bison away from sites in the EsB zone as their use of both salty meadow and herbaceous riparian camera sites did not appear to increase substantially during the bison gather compared to the growing season (Figure 29).

Both elk and bison activity were comparatively greater during PGS compared to the full growing season. The PGS is calculated over a smaller time span than the full growing season, indicating use for both species during the growing season tends to be weighted by springtime use (Figure 28). The

ability of the camera UUI to detect changes in this type of use indicates good potential for use of these indices to measure effects of elk management actions on elk activity in wetlands at GRSA. Bison activity in the early growing season (PGS) was greater in the herbaceous riparian areas, whereas elk activity is greater in salty meadows during this time.

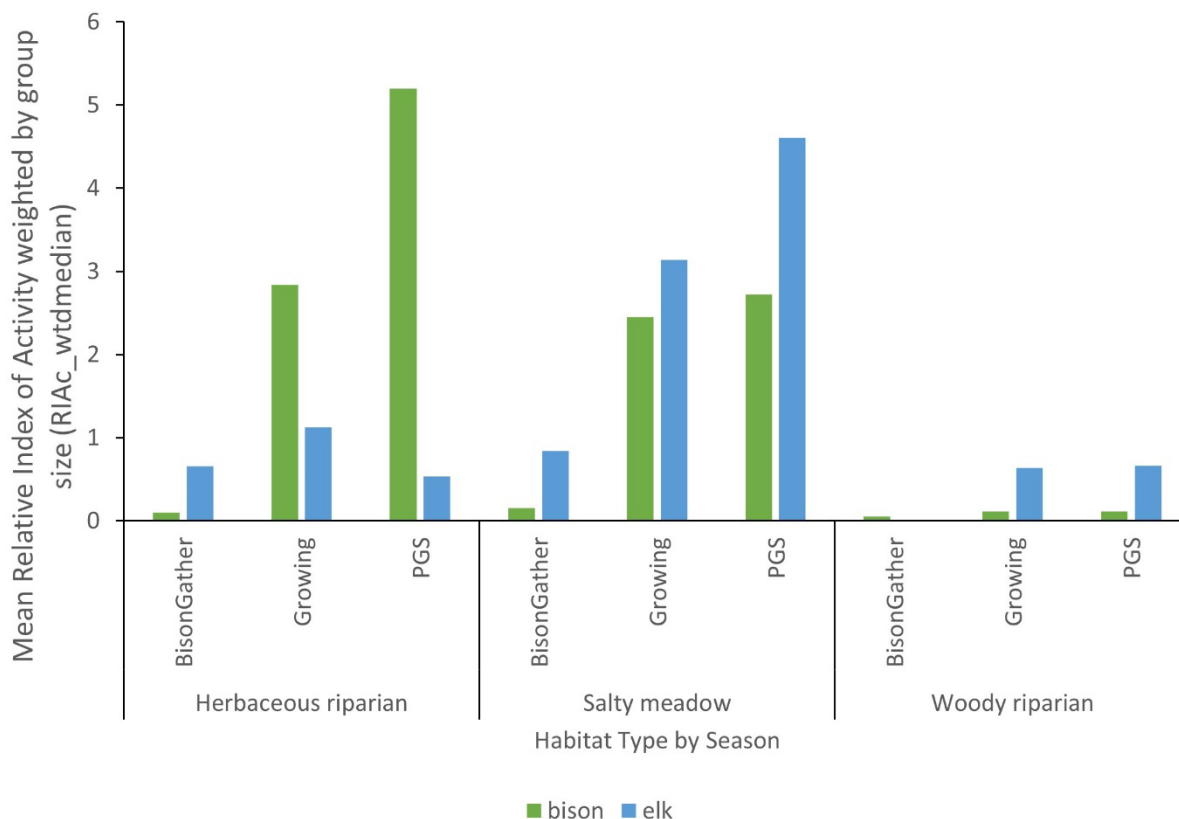


Figure 29. Seasonal bison and elk activity at wetland sites fitted with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median (RIA_{c_wtdmedian}).

Ungulate Use by Month

Monthly activity patterns tracked with those observed for traditional climate-based seasons (see previous section), and therefore we present limited data on monthly use by habitat type and ungulate zone. Monthly activity by bison at wetland camera sites showed greater activity in late winter (February), slightly lower activity March-September, and lowest activity October-January (Figure 30). Lowest level of activity at the camera sites in November is likely attributable to the annual bison gather operation when bison are moved to the south end of the bison pasture for culling of the herd. Elk, on the other hand had a steady increase in activity at these sites March through September with

only a slight drop in October through December (Figure 30). Lowest use of these sites by elk was in January and February.

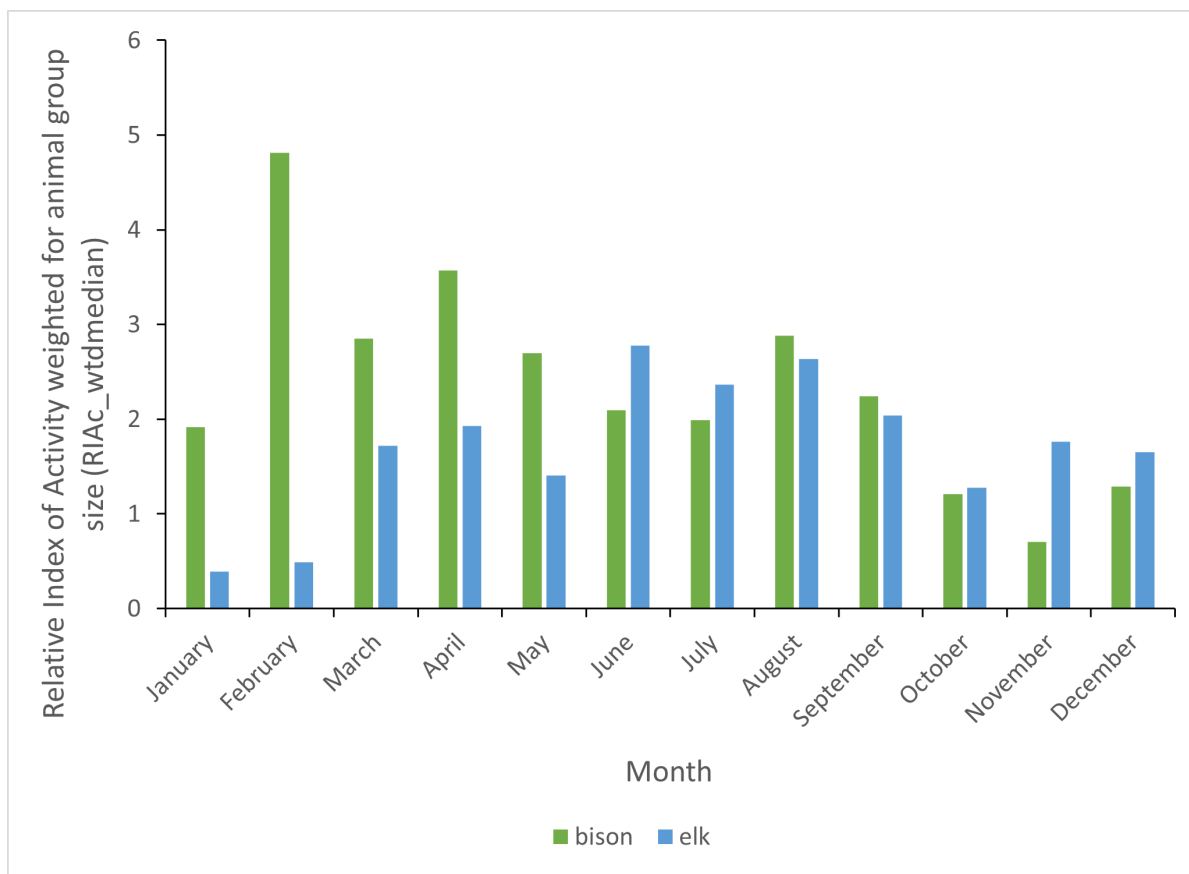


Figure 30. Monthly bison and elk activity at wetland sites fitted with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median (RIA_{c_wtdmedian}).

Ungulate Use: Day vs. Night

Primary use of UMP wetland camera sites by both species was during the day (Figure 31). However, elk activity at night on wetlands is much greater than bison night use and concentrated during the summer months, possibly due to the same separation between the two species that is evidenced by the low number of photos (<1%) that have both species using a site at the same time. Daytime bison activity on these wetland sites appeared to drop October-January (Figure 31a), whereas nighttime bison activity was relatively stable and low throughout the year. In contrast, elk appeared to show an increasing trend in daytime use of the wetland camera sites starting in March and continuing through September, and their nighttime use, while lower, showed a similar pattern (Figure 31b). Greatest night activity by elk appeared to be occurring on the salty meadow types (Figure 32), though its ratio of day to night use was similar across habitat types.

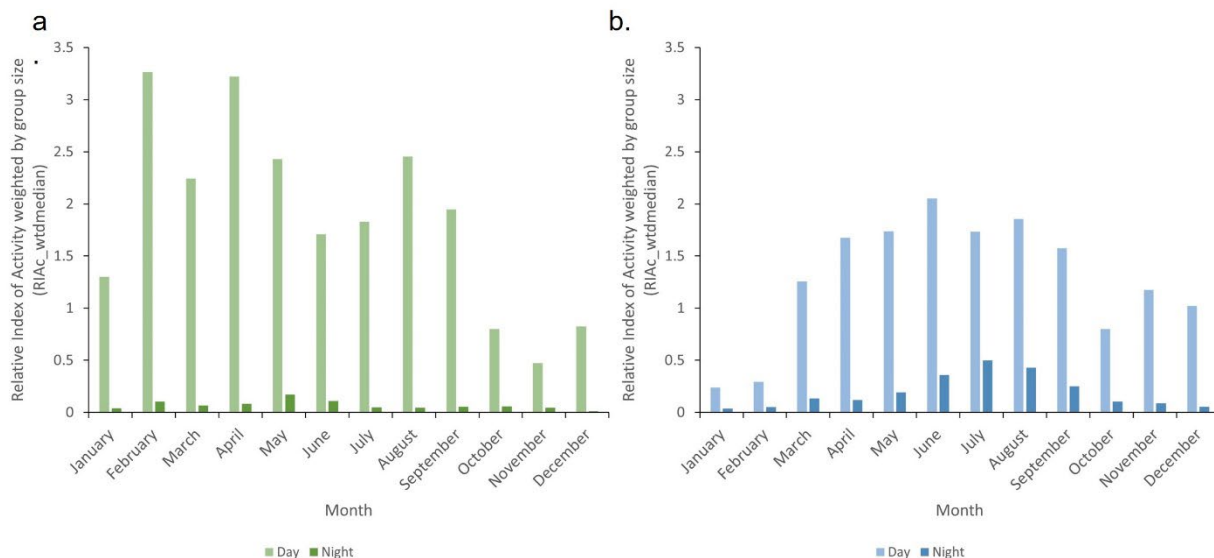


Figure 31. Monthly bison (a) and elk (b) daytime activity compared to nighttime activity at wetland sites fitted with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median ($RIA_{c_wtdmedian}$).

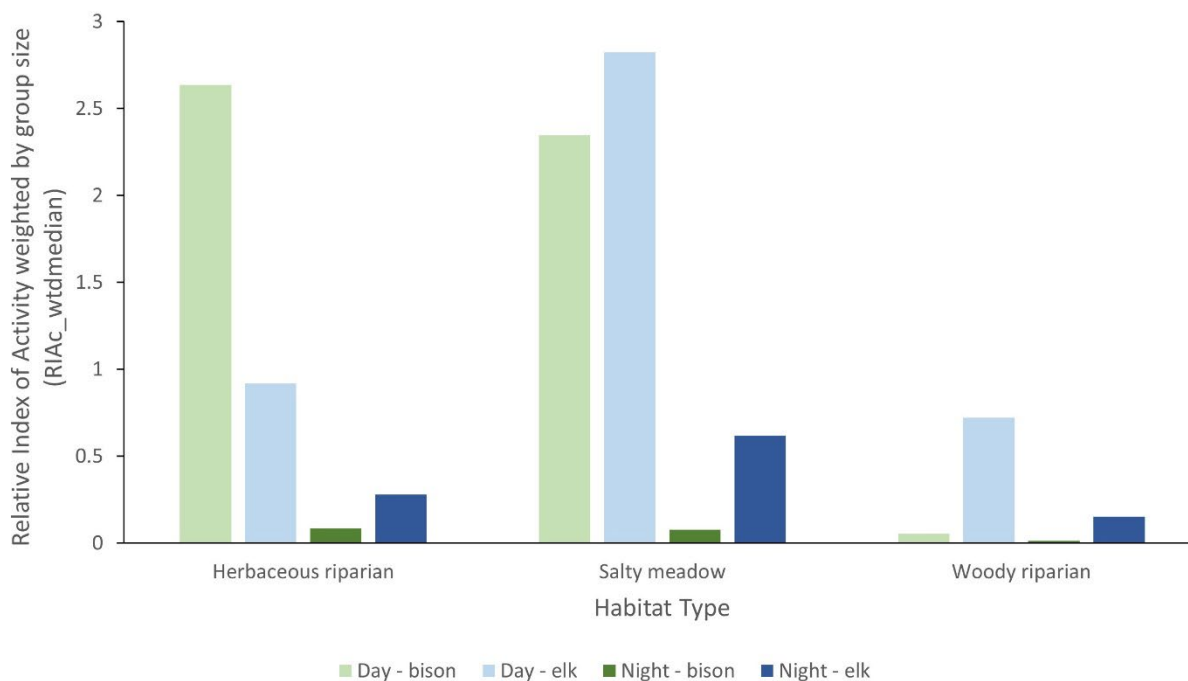


Figure 32. Bison and elk daytime activity compared to nighttime activity by wetland habitat type at sites with remote cameras in Great Sand Dunes National Park, Colorado. Relative Index of Activity was based on capture events (all photos with less than a 5-minute gap between photos) per days camera deployment, weighted by median ($RIA_{c_wtdmedian}$).

Comparisons of Ungulate Use Indices

Each UUI likely captures different aspects of how elk and bison use habitat due to innate differences in each method and the precision and accuracy in how use is approximated by each. There is not likely a single perfect approach to estimating UUI – or at least a perfect method given constraints in our budget and other practical concerns. Dung-based metrics, when corrected for defecation and disappearance rates, are relatively simple and were deployed at all UMP sites. However, we still must make assumptions about structural relationships amongst use and pattern in fecal deposition and the efficiency of dung counts disappears when counts are collected more frequently. As a result, our current data are restricted to synoptic mid-late summer.

Telemetry-based UUI capture animal movements across the entire study area, and especially with GPS collars, provide rich data. However, collars are expensive, heavily biased to individual animals, and twice daily samples may not capture the use of rare habitats on the landscape unless those habitats are visited a disproportionate amount of time.

Camera data are very fine-grained and open a window to amazing detail on what animals are doing. However, the data are very expensive to collect and process and there are real issues with cameras failing.

Ideally, ungulate use indices derived from all 3 methods (dung counts, telemetry collars, and cameras) would be positively correlated, although given differences in methodology, by definition the strength of these correlations will vary. We ran simple bivariate correlations across all possible contrasts. Based on these results, we selected a subset of “best” UUI correlations to present here. We see the strongest correlations in UUI within a method as would be expected.

The most synchronous match for correlating dung-based indices with camera-based indices was for the “pellet growing season (PGS),” and sample size was very small ($n=13$, Figures 33–35). However, for this limited sample, correlation coefficient for DI_B (bison dung index) and bison RIA_c was $R=0.78$, though we found that weighting RIA_c only improved correlation coefficient slightly (Figure 33). Correlations between DI_E (elk dung index) and elk RIA_c was $R=0.56$ and weighting did not improve correlation coefficient (Figure 34). When we matched annual dung index values to annual camera indices for growing season, the sample size increased and the resulting correlation coefficients improved for elk ($R=0.82$) but were relatively similar for bison ($R=0.76$) and lower for combined bison and elk indices (Figures 36–38). Summer season camera indices were also highly correlated with dung indices for each species individually, but not for the combined elk and bison indices (Figure 39–41). The RIA_c seasonal index generally performed well across all correlations for bison and elk individually, but RIA_p and RIA_{p_wtd} had better correlations to combined bison + elk dung index (Figures 35–41).

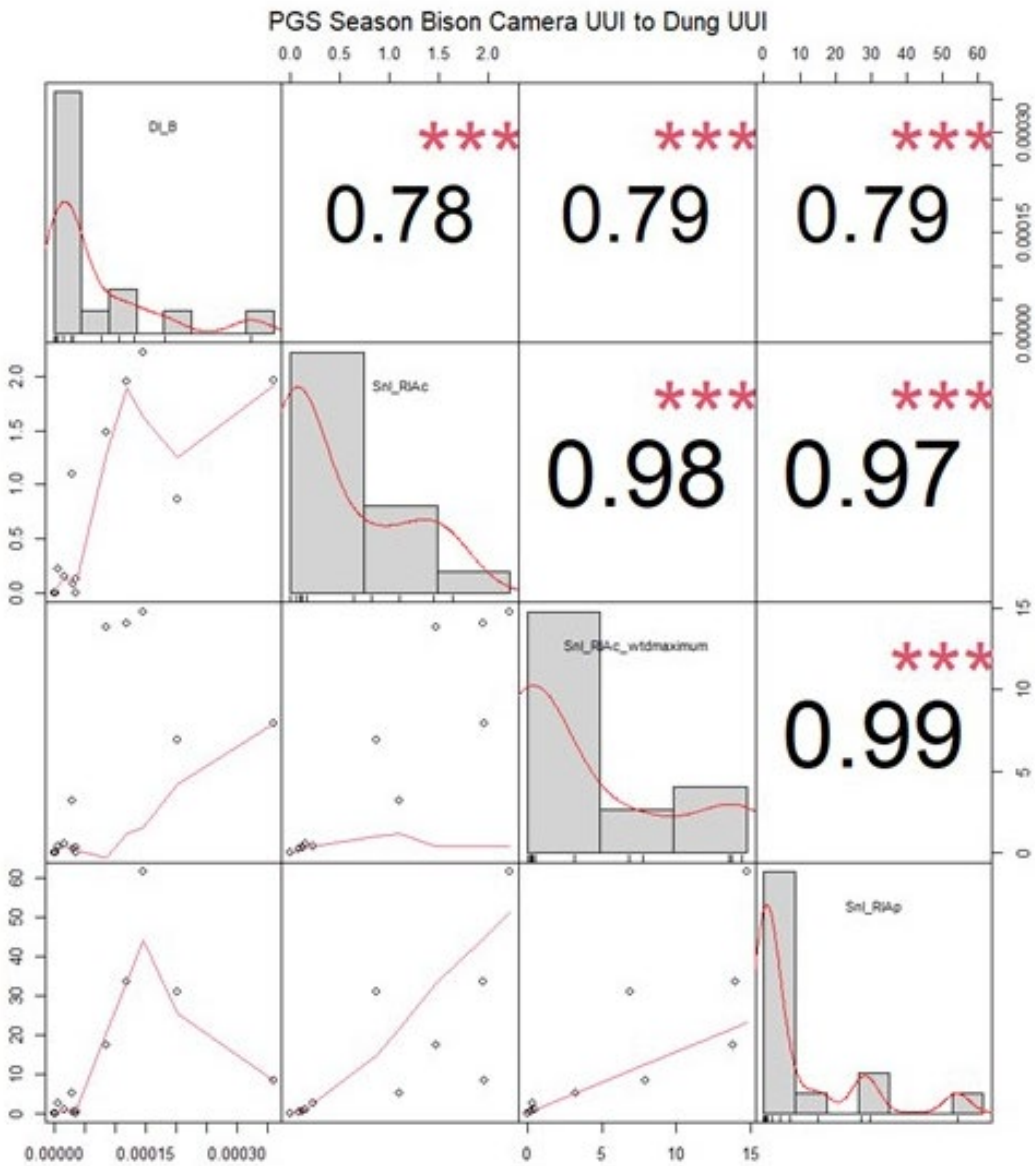


Figure 33. Correlation matrices for pellet growing season (PGS) camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_B denotes dung index for bison. Sni_RIAc, Sni_RIAc_wtdmaximum, and Sni_RIAp denote seasonal relative index of activity for photo capture events, capture events weighted by maximum group size, and total photos, respectively.

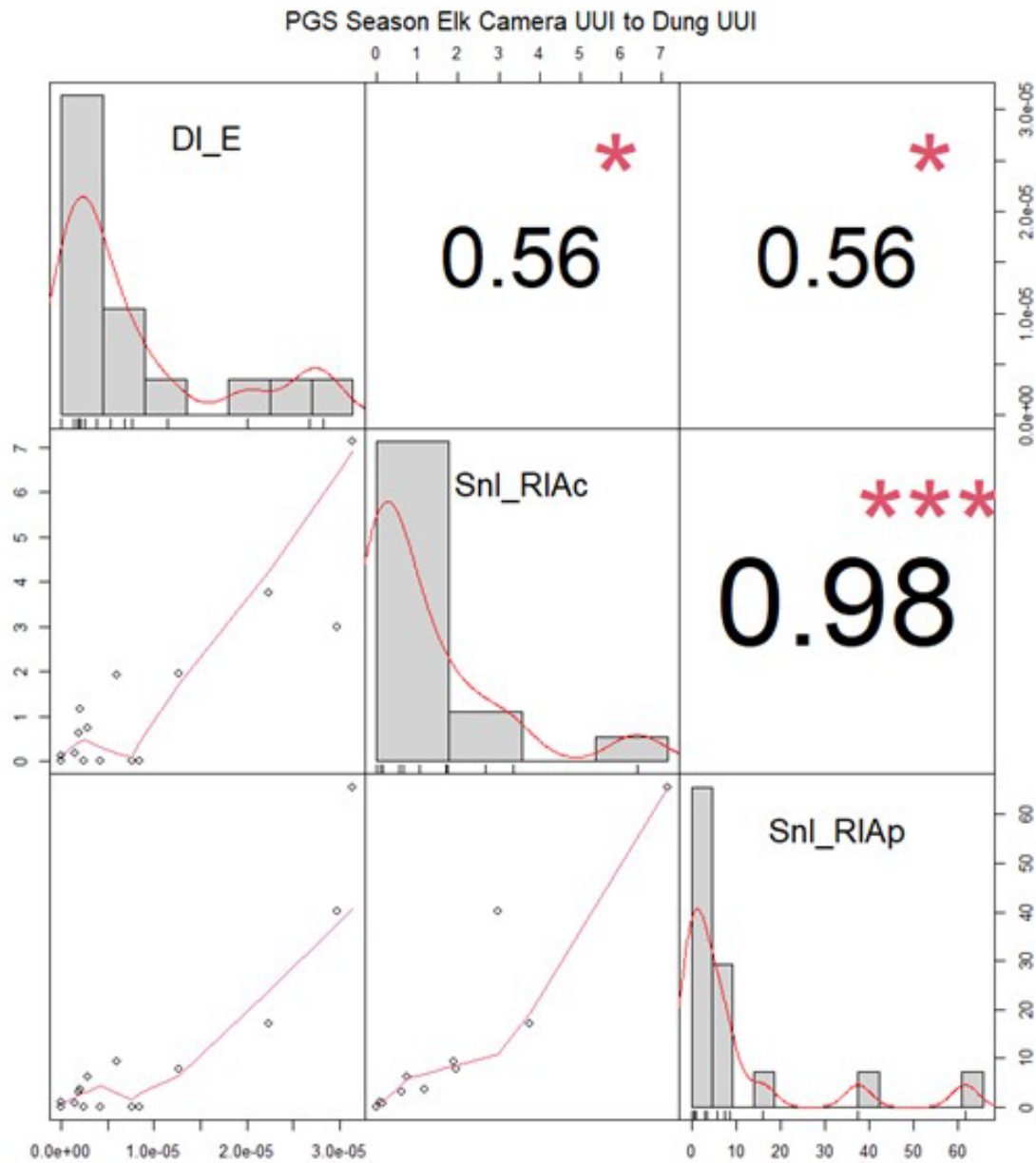


Figure 34. Correlation matrices for pellet growing season (PGS) camera ungulate use indices (UUI) with dung UUI for wetland sites at Great Sand Dunes National Park, Colorado. DI_E denotes dung index for elk. Sni_RIAc and Sni_RIAp denote seasonal relative index of activity for photo capture events and total photos, respectively.

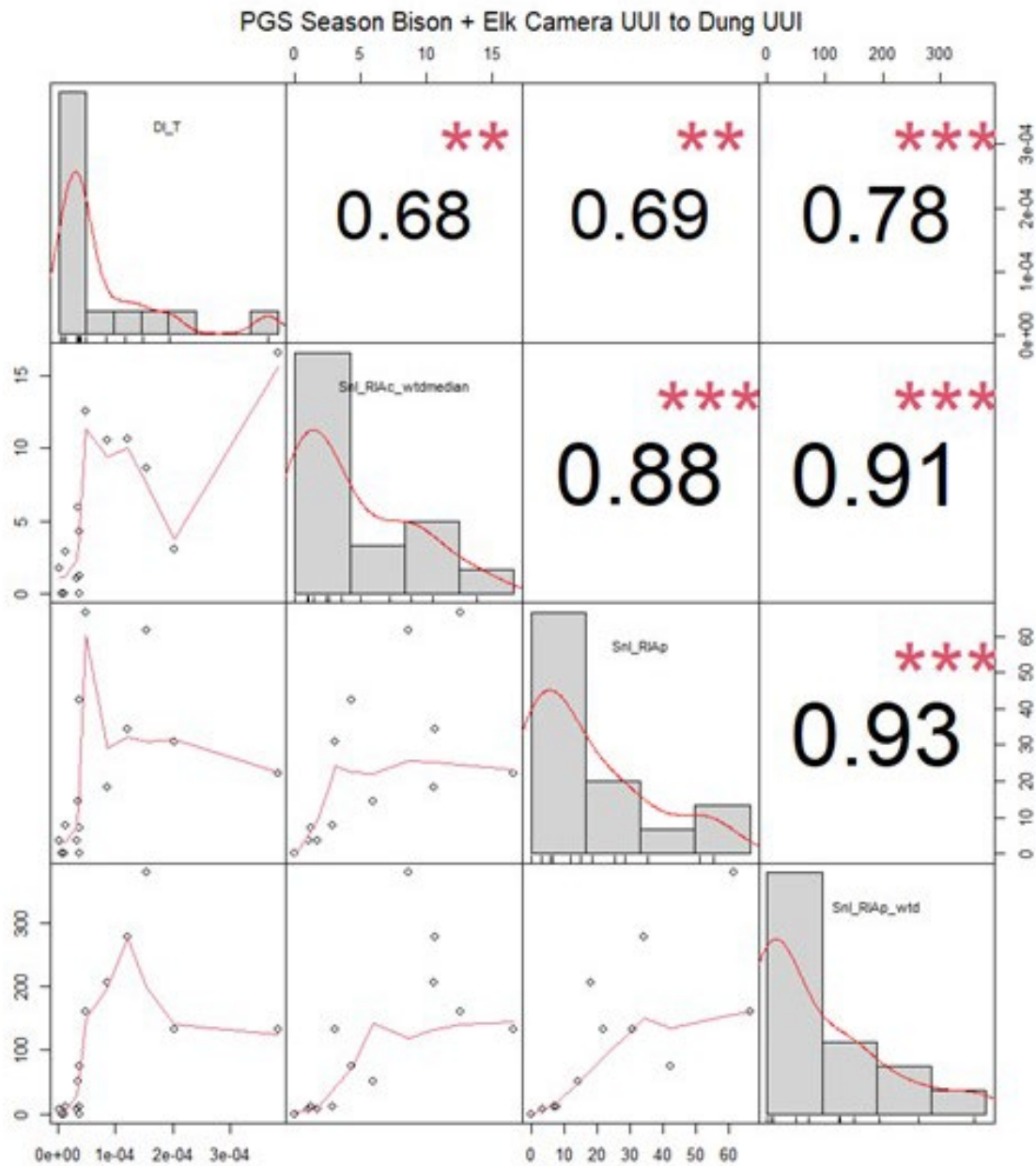


Figure 35. Correlation matrices for pellet growing season (PGS) camera ungulate use indices (UUI) with dung UUI for wetland sites at Great Sand Dunes National Park, Colorado. DI_T denotes dung index for bison and elk combined. Sni_RIAc_wtdmedian, Sni_RIAp, and Sni_RIAp_wtd denote seasonal relative index of activity for photo capture events, capture events weighted by median animal group size, total photos, and total photos weighted by animal group size, respectively.

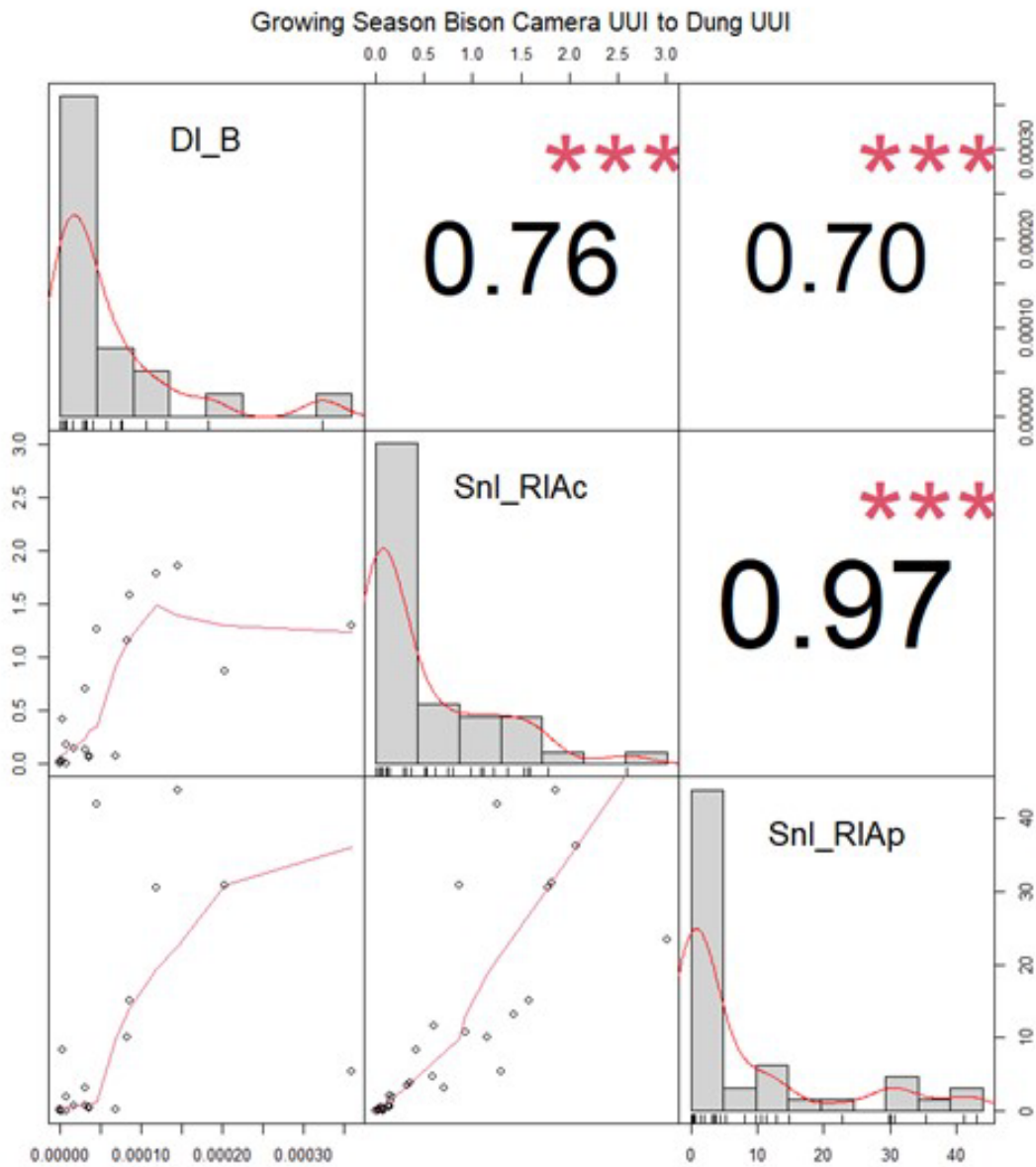


Figure 36. Correlation matrices for growing season (roughly April-September) camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_B denotes dung index for bison. Sni_RIAc, Sni_RIAp, denote seasonal relative index of activity for photo capture events, total photos, and total photos weighted by animal group size, respectively.

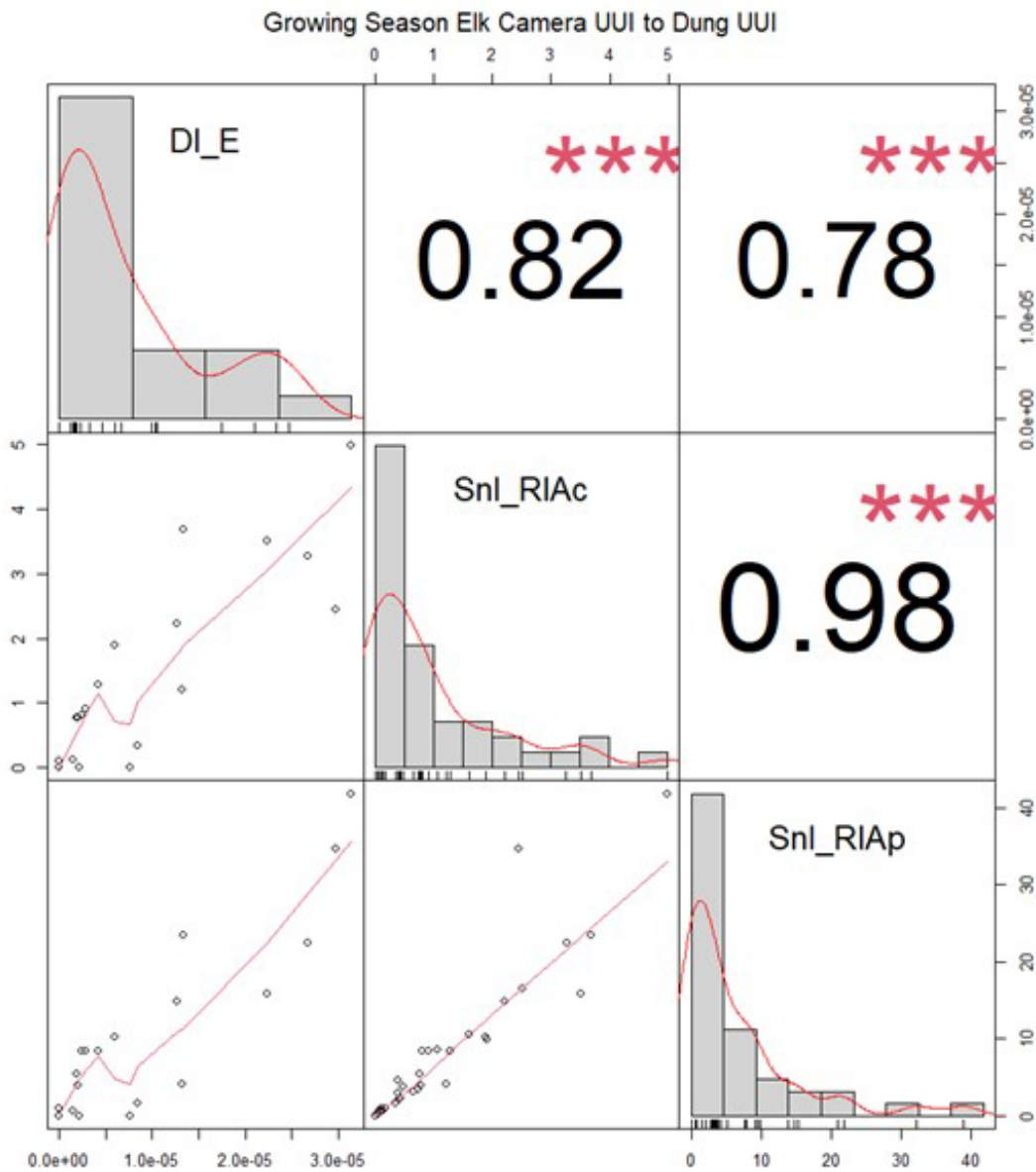


Figure 37. Correlation matrices for growing season (roughly April-September) camera ungulate use indices (UUI) with dung UUI for wetland sites at Great Sand Dunes National Park, Colorado. DI_E denotes dung index for elk. Sni_RIAc, and Sni_RIAp denote seasonal relative index of activity for photo capture events, total photos, and total photos weighted by animal group size, respectively.

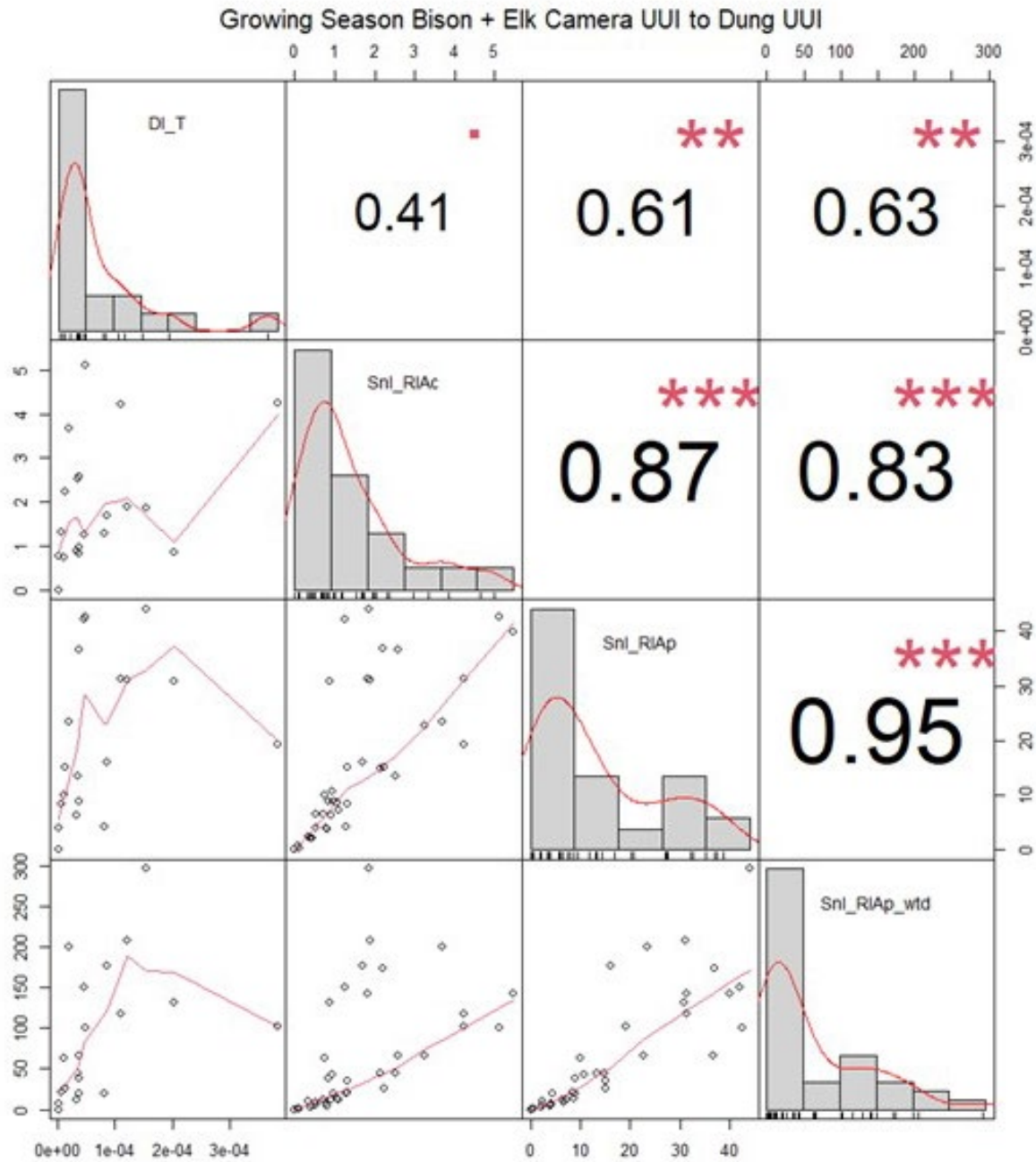


Figure 38. Correlation matrices for growing season (roughly April-September) camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_T denotes dung index for bison and elk combined. Sni_RIAc, Sni_RIAp, Sni_RIAp_wtd denote seasonal relative index of activity for photo capture events, total photos, and total photos weighted by animal group size, respectively.

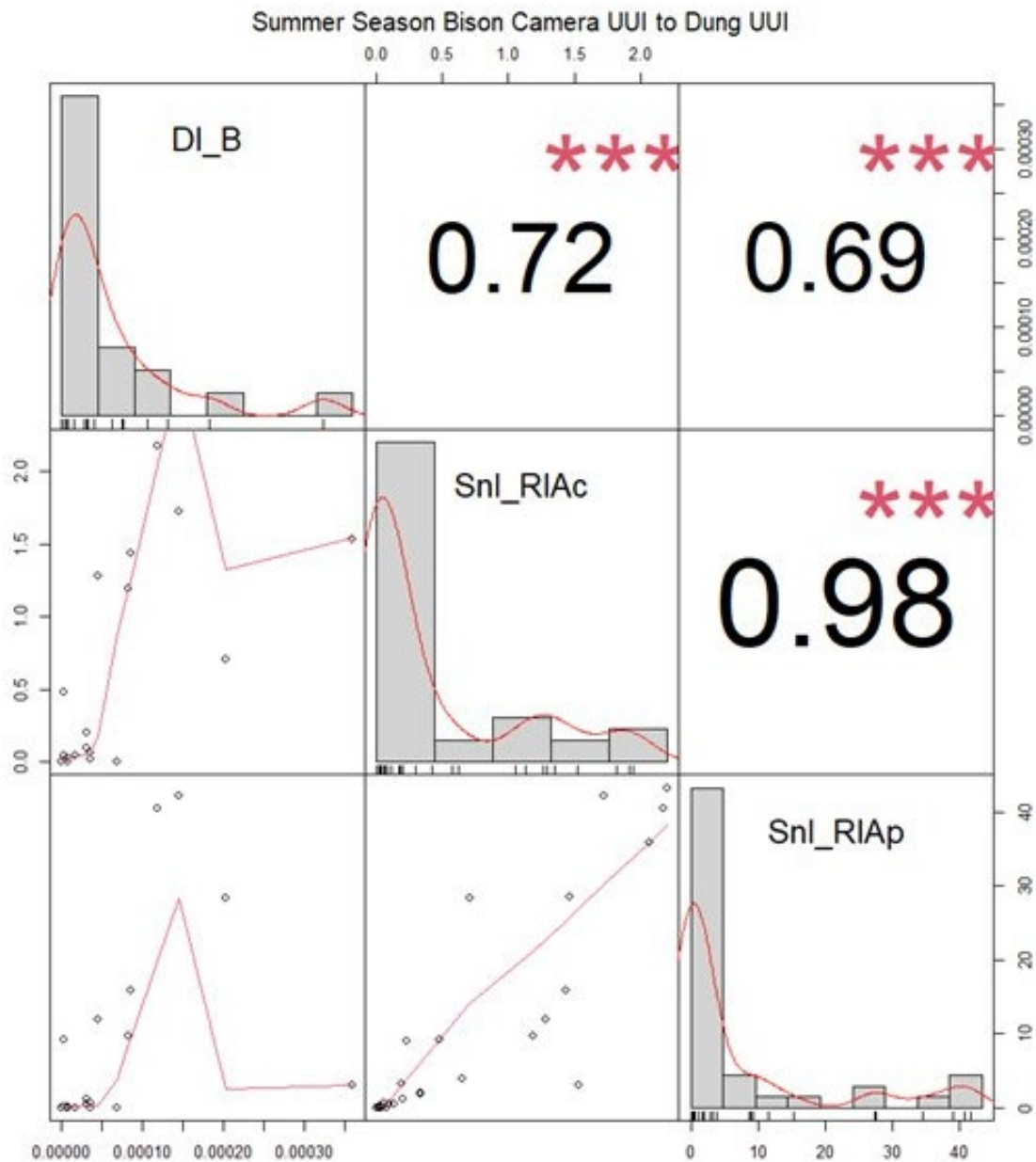


Figure 39. Correlation matrices for summer (June-Aug) season camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_B denotes dung index for bison. Sni_RIAc and Sni_RIAp denote seasonal relative index of activity for photo capture events and total photos, respectively.

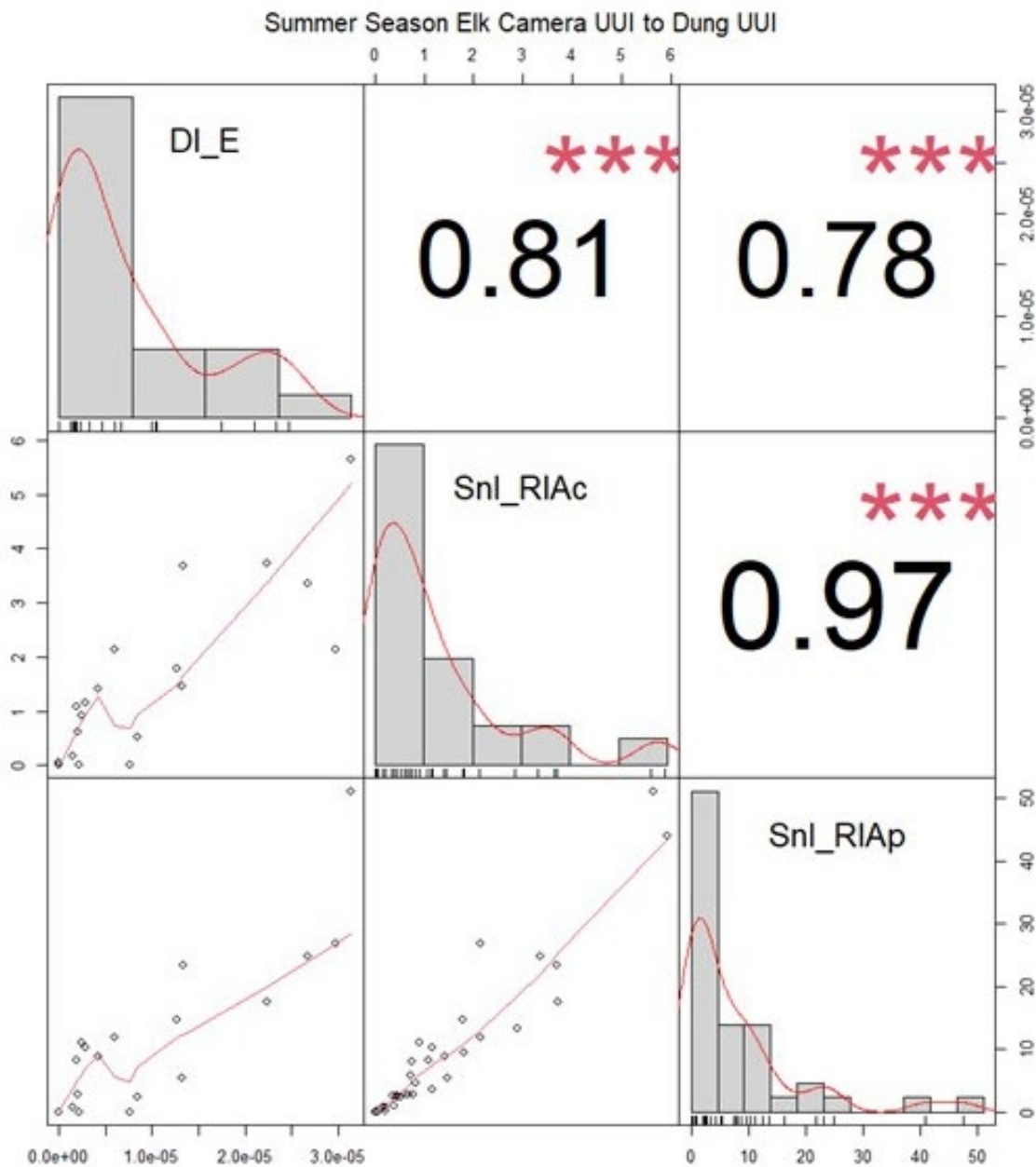


Figure 40. Correlation matrices for summer (June-Aug) season camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_E denotes dung index for elk. Sni_RIAc and Sni_RIAp denote seasonal relative index of activity for photo capture events and total photos, respectively.

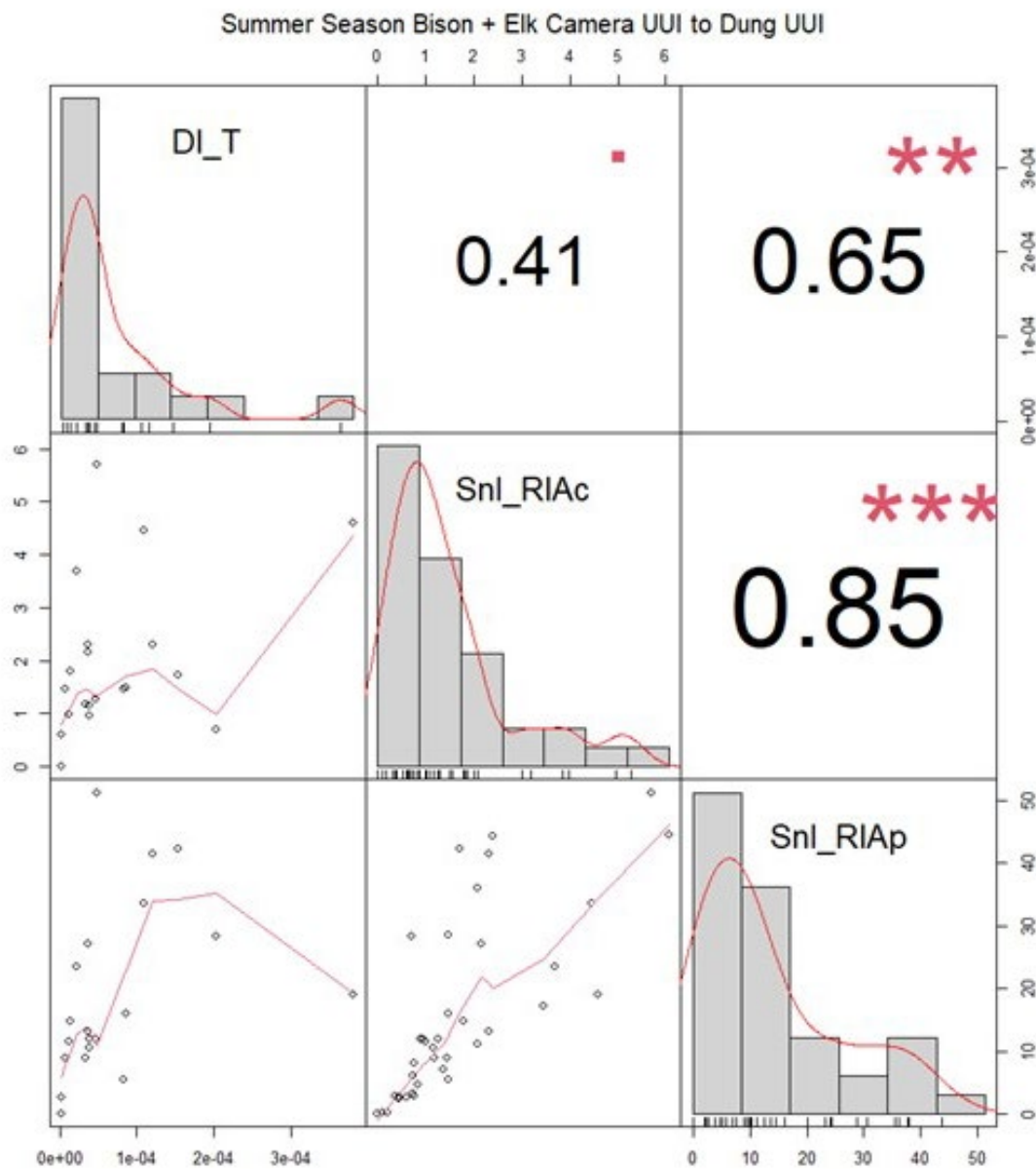


Figure 41. Correlation matrices for summer (June-Aug) season camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_T denotes dung index for bison and elk combined. Sni_RIAc and Sni_RIAp denote seasonal relative index of activity for photo capture events and total photos, respectively.

We also found that annual camera index RIA_c could be reasonably well correlated with the dung indices for both species and combined (Figures 42–44); however, correlation coefficient improved when weighted by median animal group size for each capture event ($RIA_{c_wtdmedian}$). We also found a relatively simple index that indicates the proportion of days a species was present (DPI) was highly correlated with elk dung index (Figure 43, $R=0.80$), though it did not correlate well for combined bison and elk ($R=0.20$, Figure 44).

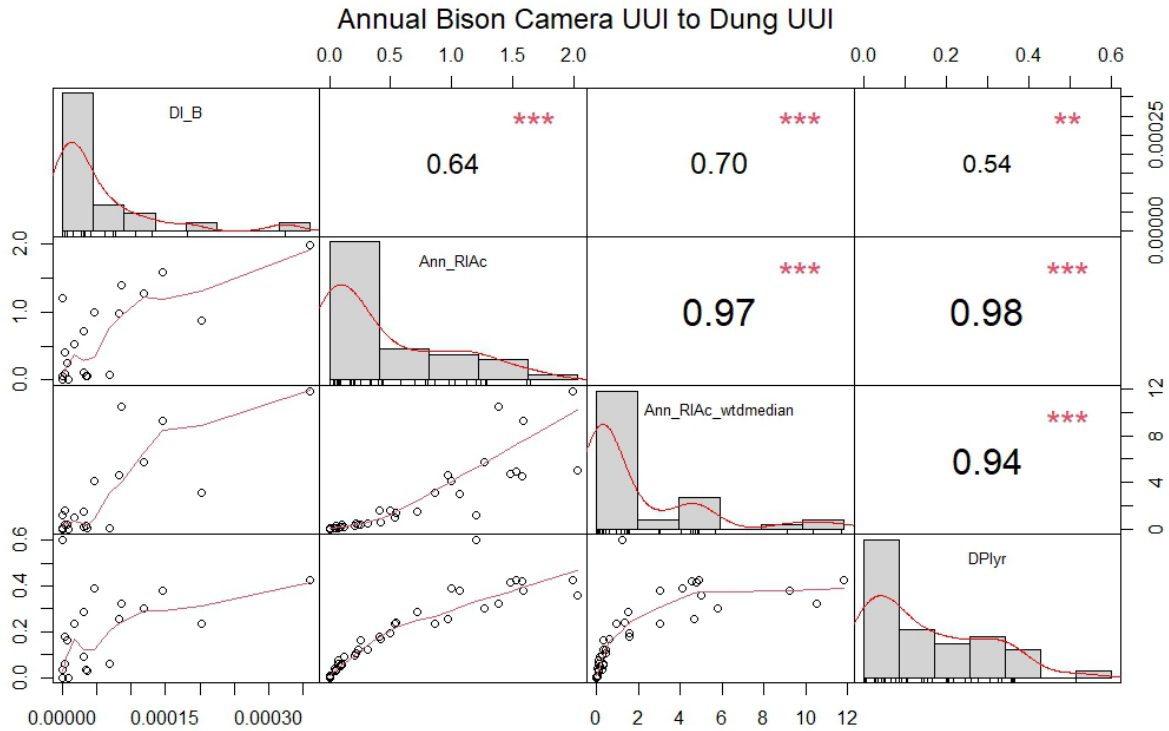


Figure 42. Correlation matrices for annual camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_B denotes dung index for bison. Ann_RIAc, Ann_RIAc_wtdmedian, and DPlyr denote annual relative index of activity for photo capture events, capture events weighted by median animal group size, and days present, respectively.

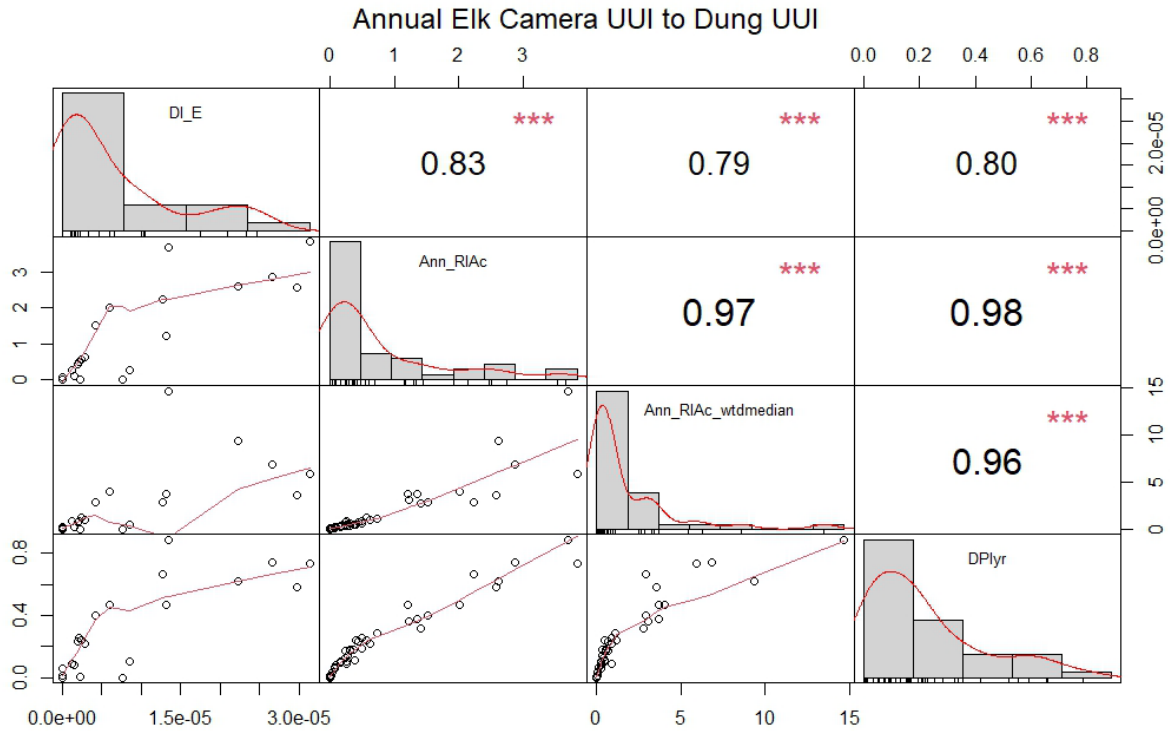


Figure 43. Correlation matrices for annual camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_E denotes dung index for elk. Ann_RIAc, Ann_RIAc_wtdmedian, and DPlyr denote annual relative index of activity for photo capture events, capture events weighted by median animal group size, and days present, respectively.

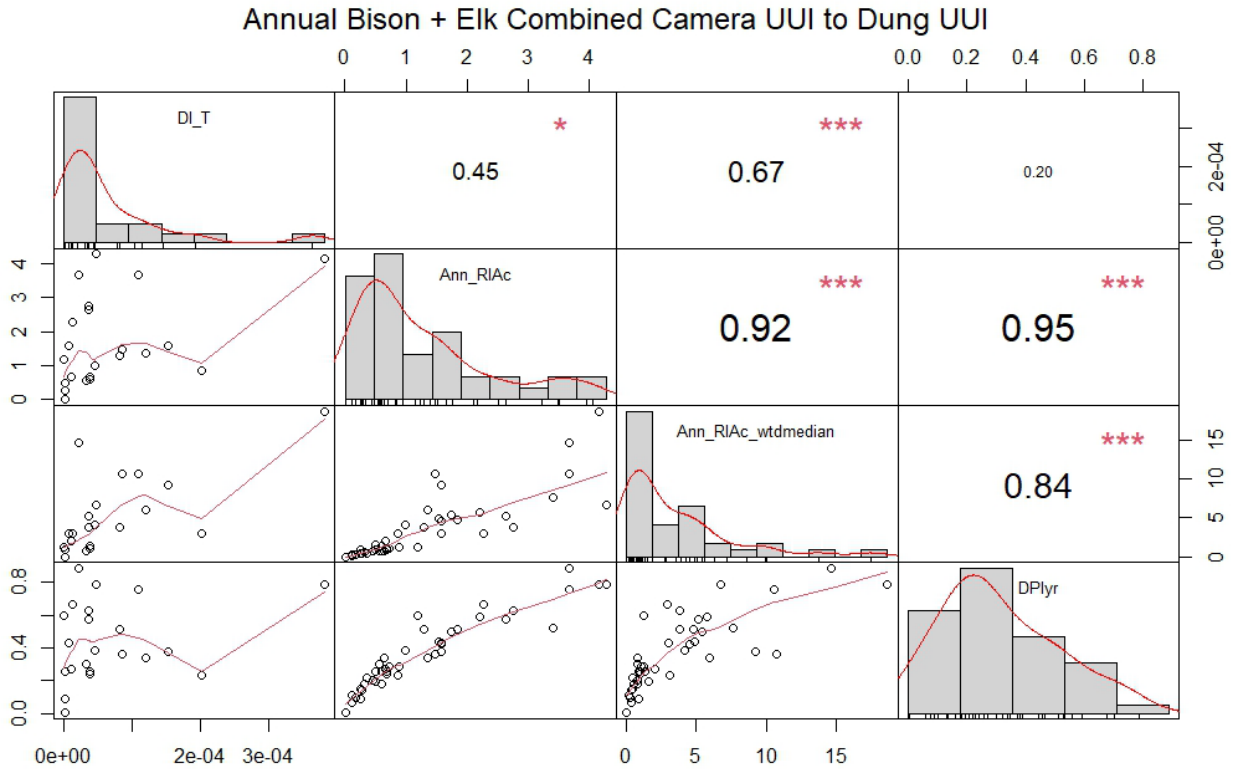


Figure 44. Correlation matrices for annual camera ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. DI_T denotes dung index for both elk and bison combined. Ann_RIAc, Ann_RIAc_wtdmedian, and DPlyr denote annual relative index of activity for photo capture events, capture events weighted by median animal group size, and days present, respectively.

Correlation between telemetry-based UII and camera UII when collapsed to year or season varied (Figures 45-47). Given the difference in sample periods for bison collars (2005-2007) and cameras (2016-2020), correlation coefficients between RIAc_wtdmaximum and concentrated use areas were greater than expected, ranging from 0.47 to 0.65 for bison in all seasons and were most strongly correlated with spring concentrated use. Correlations for elk camera and collar UII were higher, with best correlation between RIAc and year-round concentrated use ($R=0.82$).

Simple correlations between dung-based use indices and collar-based use indices varied and were significant for both species, but correlation coefficients were much greater for bison than elk (Figures 48-50). We hadn't necessarily expected bison collar data to match well with dung data because bison were using areas outside the bison pasture during our dung sampling years, but we had no collar data that reflected this use. Thus, the results for all seasons, as well as year-round collar UII with bison dung UII indicate that bison distribution has not likely changed substantially since 2005-2007.

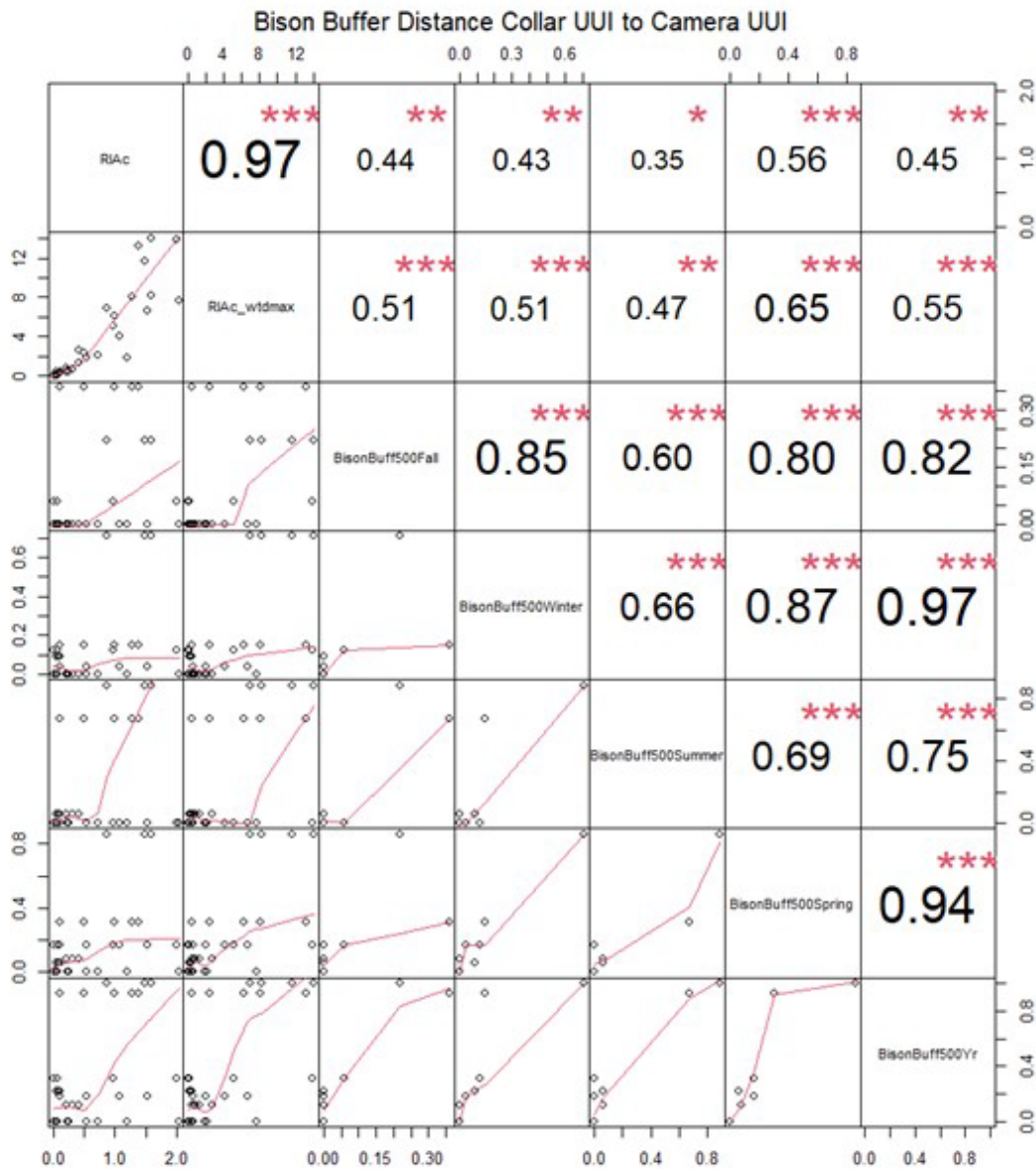


Figure 45. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UUI) with camera UUI for wetland sites at Great Sand Dunes National Park, Colorado. Collar UUI are for bison use (BisonBuff500xx) for each season and over a full year. Ann_RIAC and Ann_RIAC_wtdmaximum denote annual relative index of activity for photo capture events and capture events weighted by maximum animal group size, respectively.

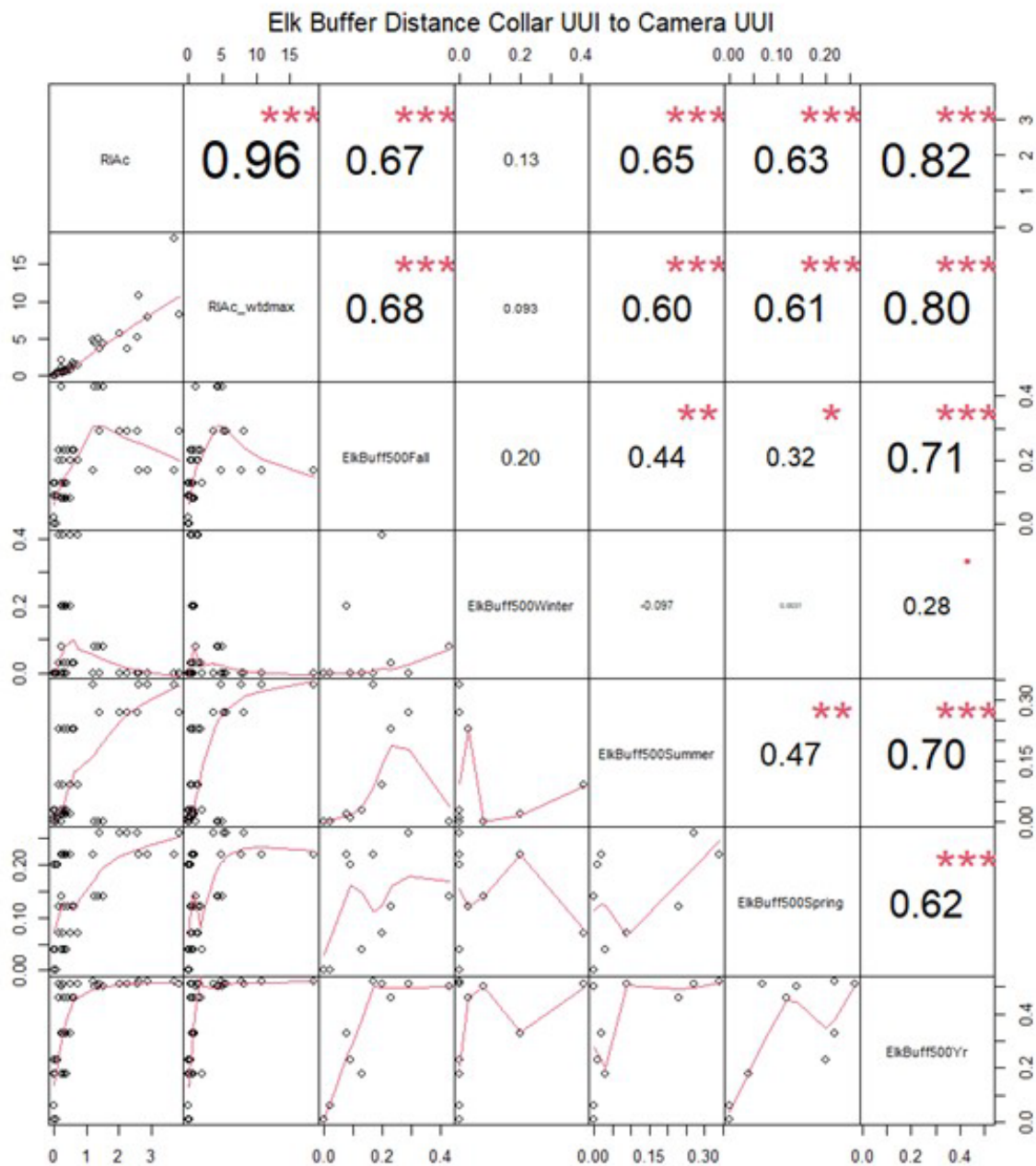


Figure 46. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UII) with camera UII for wetland sites at Great Sand Dunes National Park, Colorado. Collar UII are for elk use (ElkBuff500xx) for each season and over a full year. Ann_RIAC and Ann_RIAC_wtdmaximum denote annual relative index of activity for photo capture events and capture events weighted by maximum animal group size, respectively.

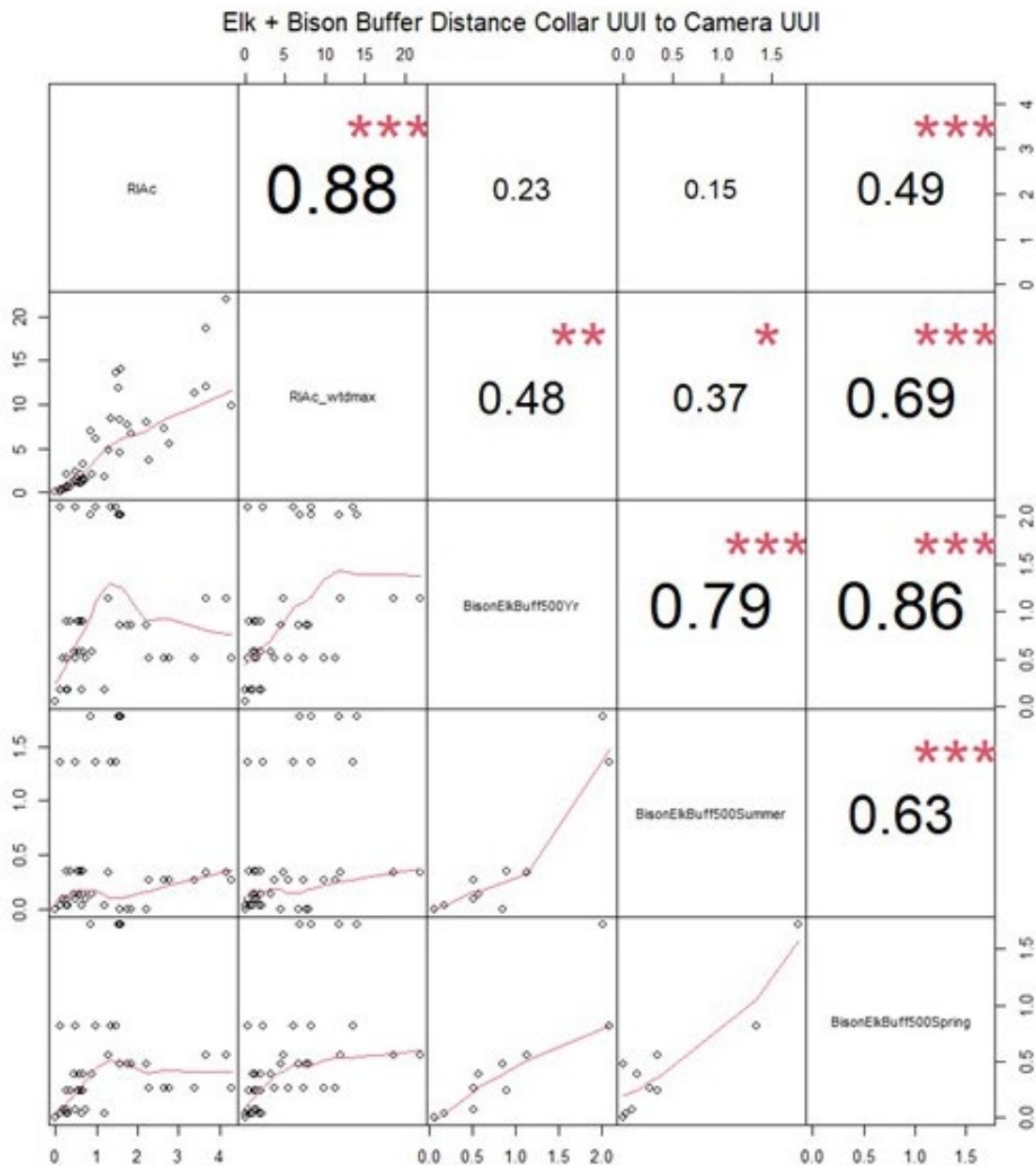


Figure 47. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UUI) with camera UUI for wetland sites at Great Sand Dunes National Park, Colorado. Collar UUI are for combined elk and bison (BisonElkBuff500xx) use for summer and spring and over a full year. Ann_RIAC and Ann_RIAC_wtdmaximum denote annual relative index of activity for photo capture events and capture events weighted by maximum animal group size, respectively.

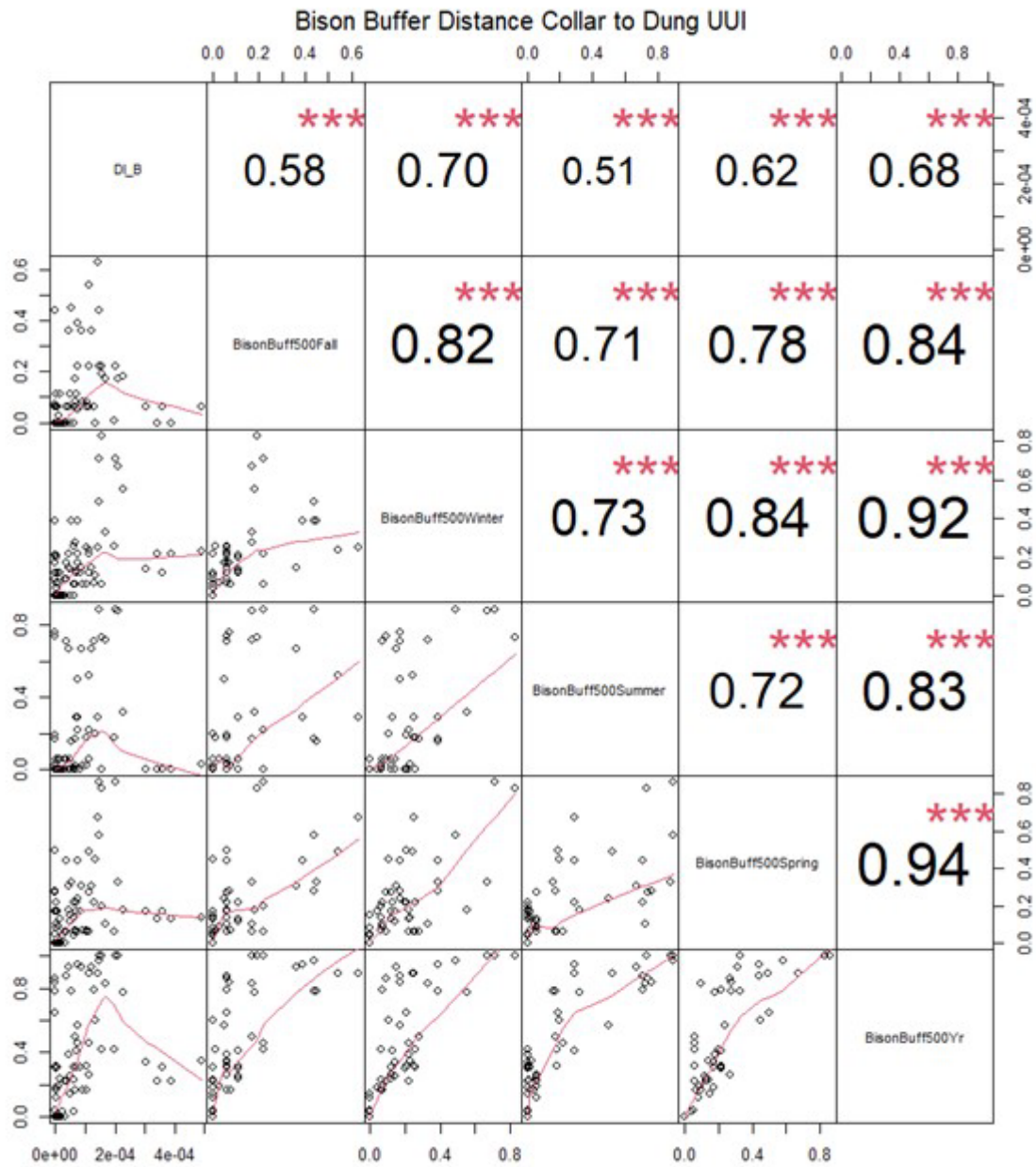


Figure 48. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UII) with dung UII for wetland sites at Great Sand Dunes National Park, Colorado. Collar UII are for bison (BisonBuff500xx) use for each season and over a full year. DI_B denotes dung index for bison.

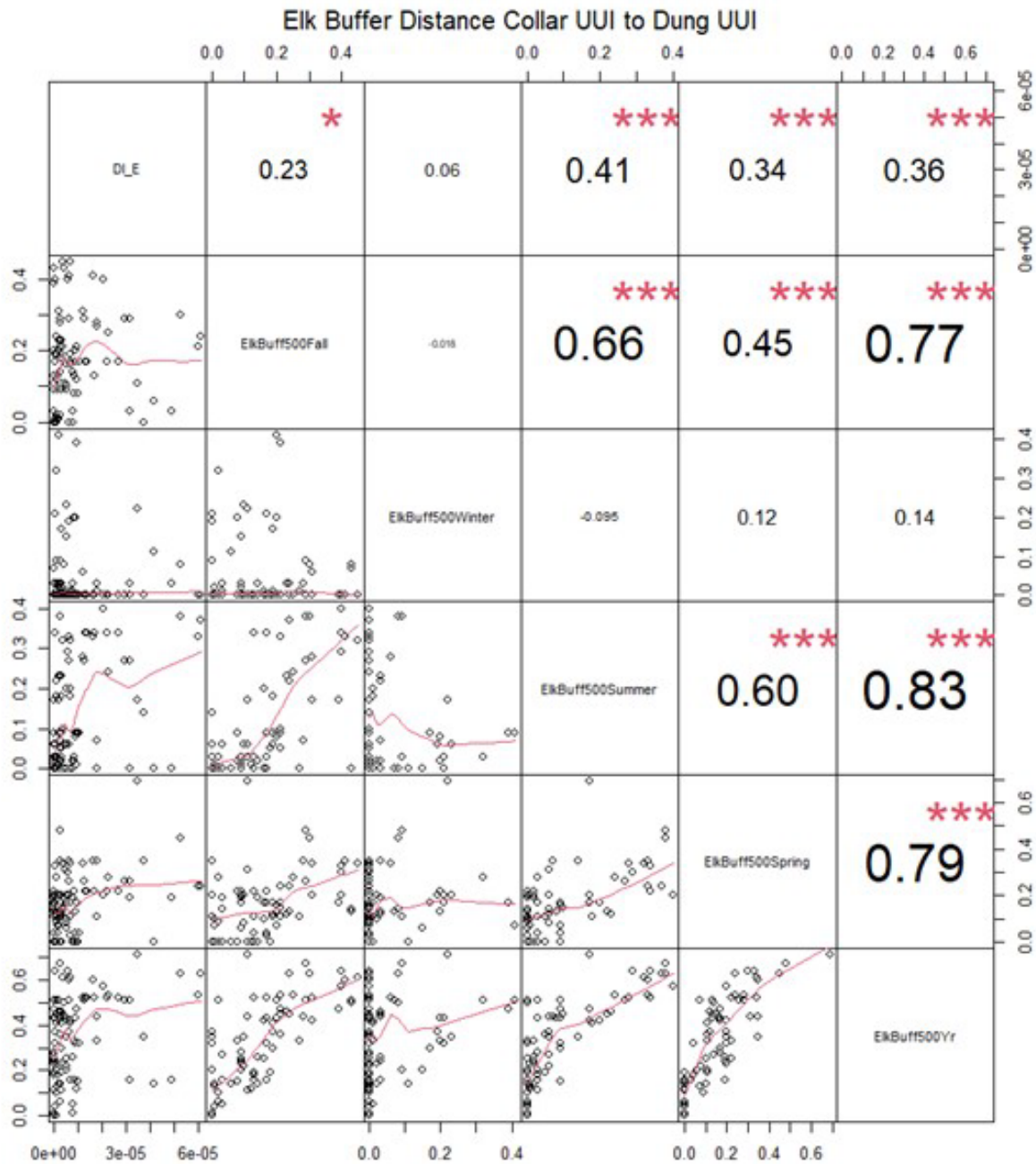


Figure 49. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UUI) with dung UUI for wetland sites at Great Sand Dunes National Park, Colorado. Collar UUI are for elk (ElkBuff500xx) use for each season and over a full year. DI_E denotes dung index for elk.

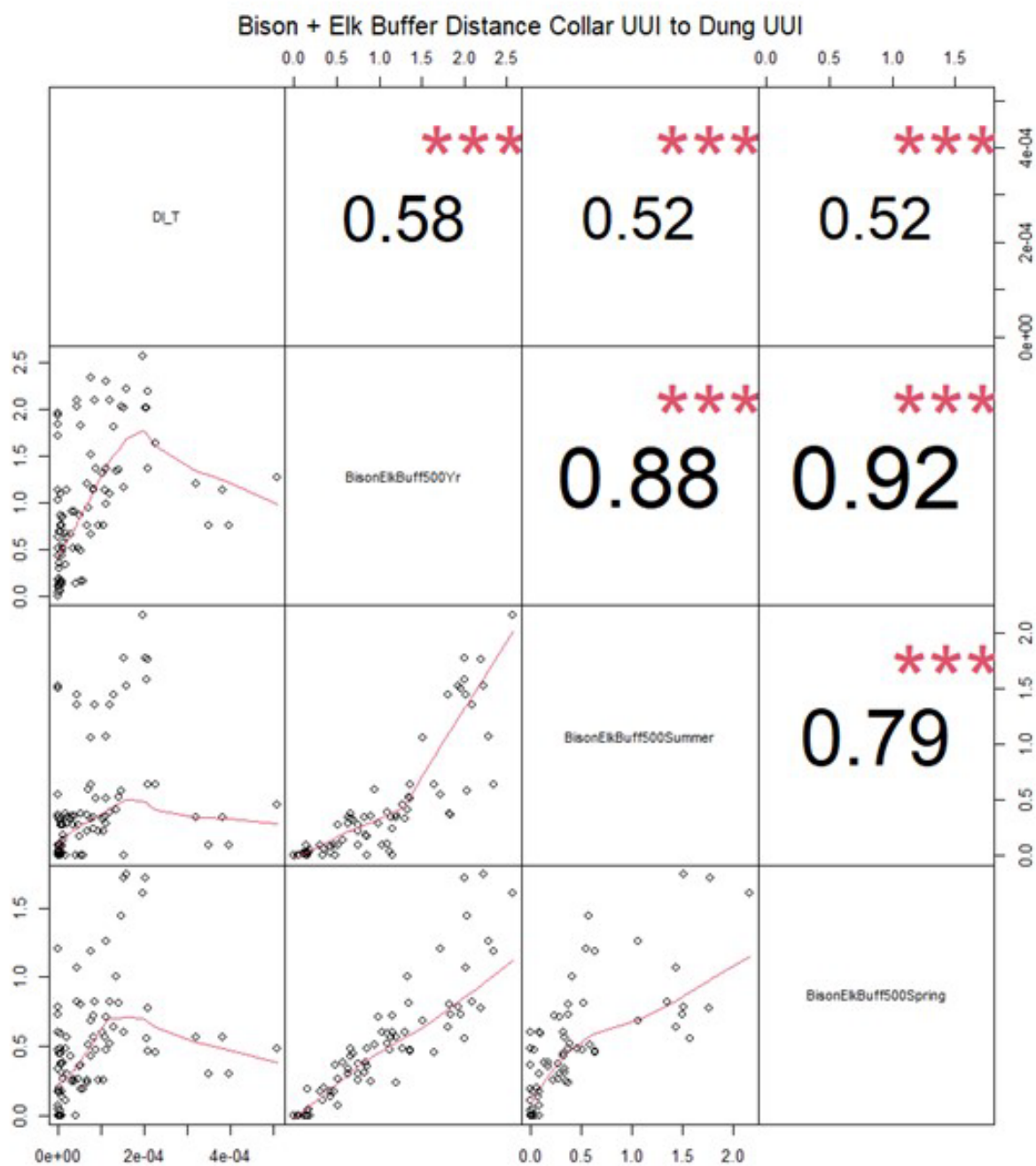


Figure 50. Correlation matrices for year-round and seasonal telemetry collar ungulate use indices (UUI) with dung UUI for wetland sites at Great Sand Dunes National Park, Colorado. Collar UUI are for combined elk and bison (BisonElkBuff500xx) use for summer and spring and over a full year. DI_T denotes dung index for combined elk and bison use.

Discussion

General Elk and Bison Population Dynamics and Change in Wetland Use

Elk and bison populations in and around GRSA have experienced changes over the past two decades. Overall, when comparing 2005-2007 data with 2016-2019 data, elk population size at the scale of the Game Management Unit (GMU) differs little, but in the intervening years, elk population size declined by as much as 20% (Figure 3). However, depending on how these changes scale to the distribution of the elk in the Ungulate Management Plan (UMP) study area, the downward trend in elk numbers at the scale of the GMU in the intervening years may have had little effect on changes in elk use and subsequent impacts to wetland condition within the park. Hunter harvest in the GMU has remained fairly steady during that time (Figure 3), suggesting that the number of elk inside the park has also remained stable over the years, but more elk use areas inside the park than areas outside the park, especially during hunting season.

It is possible that the larger bison population size from 2008 to 2020 influenced wetland habitat differently than in 2005-2007. However, at the time of the USGS study, Schoenecker (2012) and Schoenecker et al. (2022) found that wetland communities were able to compensate in terms of plant productivity and nitrogen yield for bison grazing levels being experienced at that time. It may be that the wetlands in GRSA have the capacity to absorb the impacts of higher levels of herbivory with little consequent impact on plant productivity. Also, higher bison populations 2008 to 2020 may have influenced elk distribution and the subsequent use of wetland habitat, perhaps pushing them to less-used wetlands, less favored wetland subtypes, or non-wetland vegetation types. If the larger bison herd in 2016-2020 did have qualitatively greater impacts on wetlands, then we should consider estimates of use based on the telemetry collars deployed during a time of lower bison population size as a best-case scenario.

Shifts in elk distribution to the south into the area near and inside the bison pasture in 2019-2020 relative to 2005-2007 may have been influenced by several factors. In the earlier period, cattle had been recently removed from the northern portions of GRSA and Baca NWR, and elk may have moved into these areas as they were newly free of competition with cattle. In April 2010, the NPS capped all wells in GRSA outside the bison pasture (Garza 2013), which may have influenced movement of elk closer to water sources in the bison pasture. Finally, Baca NWR now allows hunting of elk on refuge lands. Hunting areas are located on the northern two-thirds of the refuge to the west of the GRSA/Baca NWR boundary. Elk may be moving to the east and south of these hunting areas into the area of Baca NWR just north of the bison fence, into the bison pasture, and into the area of GRSA north of the bison fence and east of the GRSA/Baca NWR boundary. Fall and winter elk concentrated use overlap is greatest in these areas (Figures 22 and 23), though elk use recorded on wildlife cameras did not reflect trends toward increased use during hunting (fall) season compared to growing season.

Elk and Bison Use of Wetlands, 2016–2019

Elk and bison use of wetland sites in GRSA varied greatly in space and time. Generally, both species used most of the wetland sites they had access to, but rarely at the same time as evidenced by the lack

of images (<1%) from wildlife cameras with both species using a site at the same time. Elk appeared to use productive wetland sites that lie just beyond the bison pasture fence around Sand, Big Spring, and Little Spring Creeks, including Elk Spring and Indian Spring. Bison also use these sites when they have access due to breaks in the fence.

While elk do use wetland areas inside the bison pasture, their use of the highly productive herbaceous riparian and salty meadow wetland sites are limited by the large bison presence in these wetlands. Elk appear to concentrate their use inside the bison pasture (EB zone) on the woody riparian wetland sites where bison spend very little time. Zeigenfuss and Schoenecker (2021) found that elk in GRSA consumed cottonwood at a much higher rate than bison, and Schoenecker and others (2015) observed that bison avoided willow and cottonwood areas (i.e., woody riparian) in most seasons. There may be important implications for elk habitat use in the absence of bison that will require close monitoring and fast action if bison populations decrease substantially.

Bison use at sites appears to drive the majority of patterns in wetland habitat use at sites inside the bison pasture (EB), but in the EsB zone, where there are productive wetlands near but outside the bison fence (Elk Spring, Indian Spring, upper end of Little Spring Creek), both species appear to influence overall use of sites. The bison fence was repaired in 2020 to prevent future bison access to these sites. It will be interesting to see how elk use may change at these wetlands if bison no longer use them. Changes in elk use that may occur in response to the fence repair may prove a good predictor of how elk may use herbaceous riparian and salty meadow wetlands inside the bison pasture if bison are removed or herd size is reduced. Continued emphasis on monitoring these sites over the next 5 years may be warranted.

Seasonal migration patterns were observed using telemetry collars in studies collected by USGS during 2005-2007 (K. Schoenecker, USGS, unpublished data). In Rocky Mountain National Park, elk regularly spend summer at alpine and subalpine areas, descending to lower elevations in the fall where winter snow depths are consistently shallower (Bear 1989; Larkins 1997). Our data are not clear on whether seasonal migration continues to occur to any great extent, but collar and camera ungulate use indices (UUI) indicate elk presence throughout the year, leading us to conclude that there is only a minimal level of seasonal migration from these wetland sites. However, as more elk telemetry data become available, patterns of seasonal migration can be further investigated.

Schweiger and others (2017) suggest that wetland vegetation composition and overall condition did respond to ungulate use at the levels present in 2010, despite enhanced plant production (Schoenecker 2012; Schoenecker et al. 2022), which may be unaffected or even positively impacted by ungulate use. Future models will examine this same relationship in UMP data using the most informative UUI.

Selection of UUI for Linking Ungulate Use to Wetland Ecological Integrity

A good ungulate use index should be able to reflect the patterns in ungulate use imposed by the bison fence. Bison are concentrated at sites inside the bison pasture (EB zone), but the fence is permeable, leading to bison use of wetlands outside the fence, but typically within 1 km of the fence (EsB zone). Sites outside the bison pasture, but further than 1 km from the fence, typically see use by only elk (E

zone). UUI derived from all 3 methods (camera, dung, and collars) appear to perform well at describing relative ungulate use and are able, to varying degrees, to discriminate between different habitat types, indicating their utility for further analysis of factors influencing wetland health and to assess effectiveness of management actions. However, using a single metric, such as dung counts, to discern future temporal changes in ungulate use, particularly changes in seasonal use, will likely be insufficient. This may limit the ability to determine success of management actions in reducing ungulate use if the measured ungulate response cannot discriminate between seasons of ungulate use. The development of a combined metric using 1 or more UUI from each method may perform much better than any single UUI (e.g., summer bison collar UUI + spring elk collar UUI + elk dung UUI + bison dung UUI). But this will be best determined in conjunction with the vegetation metrics. We suggest that there are several UUI that will likely provide the best associations with wetland metrics (Table 8). It is improbable that any single metric will adequately describe these relationships, but rather a combination of best UUI.

Table 8. Rankings of top candidate ungulate use indices (UUI) for linking ungulate use to wetland ecological integrity metrics at Great Sand Dunes National Park, Colorado. Rationale for selecting each UUI is provided.

Ungulate Use Measurement Method	Rank	Ungulate Use Index	Reason
Dung	1	DI_E/DI_B/DI_T	Dung index for elk and bison and both species combined. DI_T is a combined metric across both species. It is driven by bison in areas where both species are using the habitats. Simplicity of data collection makes it a likely candidate for continued field data collection.
Photo	2	Growing Season RIA _c / Pellet Growing Season (PGS) RIA _{c_wtdmedian}	These photo metrics capture time of highest use and have the best correlation to bison and elk dung indices and are well matched to vegetation data collection season.
Photo	3	Annual RIA _{c_wtdmedian}	Good correlations to dung indices.
Photo	4	Annual RIA _c	Good correlations to both dung and collars indices.
Photo	4	Growing season RIA _p	Correlates well to combined bison + elk dung indices and is well matched to vegetation data collection season.
Photo	4	Annual RIA _{c_maximum}	These photo metrics correlate well to individual species as well as combined dung indices and year-round 500 m buffered location indices.
Collar	5	BisonElkBuff500yr BisonBuff500yr ElkBuff500yr	These collar indices correlate well to bison and combined species annual RIA _{c_wtdmaximum} bison and to elk dung index.
Collar	6	ElkBuff500spring ElkBuff500summer BisonBuff500spring	Spring and summer fit better for elk; spring was better for bison. Well matched to vegetation data collection season.
Photo	7	DPI	Very simple days present index (DPI) had a very good fit to both bison and elk dung indices, though was poor fit to combined dung index.

All methods of measuring ungulate use have disadvantages. Dung counts may underestimate use if animals do not defecate in the habitat of interest. Collins and Urness (1979) found that defecations by elk only occurred during grazing or travel, but that distribution of dung pellets by elk was quite different from distribution of grazing activity in lodgepole pine and aspen habitats. They observed that 40% of defecations occurred while animals were traveling even though traveling represented a small portion (<6%) of elk activity during a day. Animals that move more while they are grazing will be likely to deposit feces over a larger area than those that can graze more “in place.” Elk may be moving more than bison and their use may be greater than is reflected in dung counts because they are depositing dung over a wider area and outside of wetland habitats. Conversely, elk use might be overestimated if their dung persists longer because of diet differences compared to bison (more woody material, which may cause the dung to decay more slowly) or if they use habitats that are drier and prone to slower disappearance of dung due to slower decomposition or faster disappearance due to sand burial in dry sites with highly mobile sand. While it would be difficult to account for lower dung deposition due to movement patterns, current field work focused on determining species-specific dung disappearance rates in different wetland habitats is providing important information in reducing over- or underestimation of use due to a lack of data on disappearance rates.

Telemetry collars are expensive in terms of time and labor costs to place collars on animals. There is also always the risk of potential injury to animals and humans during collaring operations. However, once collars have been placed, data collection is relatively low-cost. Collars are subject to loss due to animal mortalities and malfunction. Due to the initial costs of collaring operations, often only a limited number of animals will be fitted with collars, therefore mortality or collar malfunction of even a few individuals can have an outsized influence on the data acquired. GPS collars can provide very fine-scale temporal and spatial data, but increases in temporal detail come at the cost of battery life, and thus can limit overall length of collar deployment. Additionally, collar data cannot provide information on size of animal groups using a particular area and may result in UUI that underestimate actual use at a site. Data capture does not distinguish the amount of time an animal spends in a habitat, which can also lead to over- or underestimation of ungulate use.

Camera-based UUI are ideal for resolving many of the potential problems with dung count and collar-based UUI. Cameras not only detect animal presence, but also type of activity, group size, and duration of visit to a site. Like collars, partitioning of animal use by season can be determined and cameras are better than collars for tying use to a particular location on a landscape. Camera-based UUI capture use at a site whether the animal defecates or not during their visit and are thus likely to better estimate use than dung counts. However, cameras are subject to malfunction, limited battery life, and data collection is limited by size of the data card. Gathering data without large gaps requires regular maintenance visits, potentially limiting the number of sites that can be surveyed. Malfunction is highly likely because curious animals are often drawn to camera noise and like to rub on posts holding cameras in place.

Applying UUI to GRSA Ungulate Management

The UUI described here are presented as a baseline for ungulate use of UMP wetland sites. Ideally, select UUI should be able to provide GRSA biologists and managers with a simple means to translate

ungulate monitoring data into changes in ungulate wetland use. Changes in ungulate wetland use may occur in response to animal management actions (hunting and dispersal actions), land management actions (e.g., changes to irrigation regimes), changes to herd population size, climate conditions (e.g., drought, hard winters), or even competitive interactions between ungulate species. As was demonstrated with the collar data, changes in elk distribution and use over the last 2 decades can be identified and linked to management actions that have taken place, such as hunting on the Baca NWR. This baseline UUI can be used to determine where and when (season/time of day) to employ management actions so that areas of greatest ungulate use are targeted and so that resources, in terms of time and money, are directed in the wisest and most efficient manner. Both camera and collars can be used after management actions take place to track whether, for example, elk dispersal actions are effective at moving animals away from wetland sites and for how long. Cameras can also monitor whether there are changes in animal activity in response to dispersal/harassment actions, such as animals moving through habitats instead of grazing and loafing in them, or animals changing their temporal use to avoid management actions (e.g., changing use of wetlands from day to night to avoid dispersal/harassment activities).

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