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ANALYSES OF SEXUAL SEGREGATION IN BISON AND THE PRODUCTIVITY
OF VEGETATION ON ANTELOPE ISLAND STATE PARK

By
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ABSTRACT

We examined two factors that directly affect population growth of American bison (*Bison bison*) on Antelope Island State Park, Utah. First, we studied patterns of social organization during times of sexual segregation and aggregation. We discovered that sexual segregation is driven primarily by ecological factors as opposed to social phenomenon. Males resided in areas characterized by high human activity and vegetative degradation. Females were located far from human activity, especially during parturition (birthing season) when females used high-elevation terrain. Social segregation hypotheses cannot explain those long-term differences in space-use between males and females. The predation hypothesis, a prominent hypothesis under ecological segregation, can explain that difference in space use throughout the study. Furthermore, factors from the gastrocentric hypothesis were evident because females frequently utilized areas of high forage quality, in particular high elevations and fields seeded with alfalfa mixtures. Understanding where and why females use habitat can greatly influence choices regarding habitat manipulation.

Second, we constructed a comprehensive index to forage productivity and examined changes in vegetative growth over time. Variables on local weather (average temperature and total precipitation), and vegetative growth (percent change in NDVI, and tree-ring width) were combined in a principal components analysis (PCA). Using the PCA, we clustered years into high and low vegetation productivity. Although we detected an increase in temperature, there was no corresponding change in growth of trees or total annual precipitation since 1950. Knowledge of short- and long-term patterns of vegetative productivity are critical for understanding variation in population growth of ungulates.

CHAPTER 1

Social Organization and Sexual Segregation in American Bison

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Abstract

Sexual segregation occurs commonly in sexually dimorphic ruminants. Factors underpinning this phenomenon, however, continue to be debated. We conducted research on spatial and social organization of American bison (*Bison bison*) on Antelope Island State Park, Utah, USA, to provide further insights into patterns and potential causes of sexual segregation. We examined the two prominent hypotheses associated with ecological segregation, the gastrocentric and predation hypotheses, and two hypotheses for social segregation: social-factors and activity-budget hypotheses. Results from multi-response permutation procedure (MRPP) and overlap analyses illustrated significant spatial and elevational separation between male and female groups throughout the year, which increased substantially during parturition (a period of strong sexual segregation), and decreased during the mating season (a time of pronounced sexual aggregation). Male-only groups commonly used habitat on the northern end of the island, which was characterized by low elevation and heavy recreational use by humans. Female bison used high elevations where vegetation was likely in an earlier phenology, and view of potential predators was unobstructed. Females also used areas on the

southern and eastern reaches of the island, where human recreational activity was low and fields with alfalfa were situated. Those outcomes provide evidence for both the predation and the gastrocentric hypotheses. Our results did not support social segregation as a cause of spatial differences between sexes. Indeed, if social factors and activity patterns were driving segregation of the sexes, the spatial distribution of single-sex groups should have remained the same between seasons and mixed groups should not have been observed during parturition—outcomes contradictory to our results. Further, those social hypotheses cannot explain the long periods over which sexual segregation occurred. This research can aid management of habitat and restoration of areas for bison and other wild ruminants by providing new insights into spatial use and social organization during two critical periods—parturition and rut.

Introduction

In gregarious and dimorphic mammals, social organization and patterns of spatial use can change drastically across seasons. Timing and synchrony of births and mating often define times of sexual segregation and aggregation, especially in northern populations of ungulates [1]. Segregation of sexes during parturition (birthing season) and aggregation during rut (mating season) is nearly ubiquitous among sexually dimorphic ruminants [1]. Although numerous studies of sexual segregation have been conducted [1–6], no operational definition of this phenomenon is widely accepted [6,7]. The literature offers two general hypotheses for defining and identifying sexual segregation—ecological (habitat, diet, or spatial) and social (activity patterns or other social behaviors) [8–11].

Ecological segregation can be understood through a niche-based framework [12], where males and females are treated as if they were coexisting species, each possessing a unique set of niche requirements. Although there may be substantial overlap on one niche axis (space, habitat, or diet), there often is partitioning on another axis [12–14]. Variation in niche dimensions between sexes typically varies seasonally during parturition and rut under hypotheses for ecological segregation.

Hypotheses forwarded to explain social segregation propose that differences in activity patterns or other social behaviors between the sexes result in the separation of social groups (male-only and female-only groups) [8,11,15]. This hypothesis is still relatively new compared with ecological segregation, which was first described by Darwin in 1859 [1] and formally articulated in 1871 [16]. Although changes in group composition and activity patterns during periods of segregation and aggregation have been well-documented [4,8,17], whether differences in social organization are causing or simply correlated with sexual segregation remains uncertain [1]. Moreover, not all research on this topic supports the role of activity patterns in causing sexual segregation [12,13,18]. Neuhaus et al. [19] further noted that activity patterns were unlikely to explain spatial segregation of the sexes. Indeed, those social hypotheses can cause differences in use of space over short intervals, but not long-term spatial separation [1].

Our aim was to examine factors capable of causing differential use of space by the sexes over periods of segregation and aggregation. The prevalent explanations for ecological (specifically spatial) segregation are the gastrocentric and predation hypotheses [1]. The gastrocentric hypothesis posits that males and females differ in diet and habitat use because of variation in digestive physiology and body size [7,20]. The large body size of males—and

thereby large rumen, liver, small intestines, and cecum—allows them to extract nutrients more efficiently from poor-quality high-fiber forage compared with females. Parturient females, however, remodel their digestive tract to allow them to more efficiently extract high-quality nutrients from forage [7,21,22]. Even with such modifications of the digestive tract, parturient females must seek high-quality forage to satisfy the heightened energetic costs associated with lactation [7]. Those differences in energetic demand and digestibility of forage are hypothesized to result in differential use of habitat or diet between the sexes of many ruminants. Moreover, nursing females often benefit from the use of high elevations because forage typically is in an earlier phenological state, and there is reduced risk of predation [23,24].

The predation hypothesis proposes that females preferentially select habitat that reduces the risk of predation, such as steep or rugged slopes [3], or aggregate in large groups to better detect danger or to confuse the predator and dilute the probability of becoming prey [25–28]. Moreover, humans can be perceived as predators by ungulates [29–31], and human alteration of landscapes can affect the behavior of ungulates [32]. Wiedmann and Bleich [33] demonstrated that areas with high human activity were avoided by parturient females, resulting in abandonment of birthing areas and subsequently a reduction in reproductive success of bighorn sheep (*Ovis canadensis*). For bison (*Bison bison*) on Antelope Island State Park, parturient females selected birthing habitat that was away from recreational trails, roads, and buildings [34].

Two hypotheses explaining social segregation are the social-preference and the activity- budget hypotheses. Those hypotheses posit that higher prevalence of same-sex groups outside the mating season are caused by differences in behavior, resulting from

patterns of interaction and levels of activity [35]. Males can benefit during rut by practicing fighting skills and establishing dominance hierarchies in advance, while females avoid aggressive interactions with males [15]. An outcome from those hypotheses, therefore, would predict substantial changes in the social organization and activity budget between parturition and rut. Likewise, same-sex groups (male-only and female-only) should not vary with respect to differences in spatial separation during parturition and rut—no mechanisms postulated by those hypotheses can explain that pattern of aggregation and segregation.

Although we do not test the gastrocentric and predation hypotheses directly, we use those hypotheses to help frame our research direction—others recently have used this approach effectively [14,36–38]. Bison are large, sexually dimorphic ruminants that are highly gregarious and inhabit large open expanses, making observations of social behavior and organization relatively easy. These iconic herbivores are an ideal species for investigating sexual segregation and its relation to life-history characteristics, such as parturition and rut.

We quantified the timing of parturition and rut, and used those benchmarks to test for differences in group size and social organization, and differences in use of elevation and space by the sexes of American bison. We hypothesized that the degree of sexual segregation differed between seasons, and predicted that male and female bison would segregate during parturition and aggregate during rut. If social factors primarily influenced segregation, then we predicted that the probability of overlap between single-sex groups would be similar during both sexual segregation and aggregation. If, however, sexual segregation of bison was because of ecological factors, we expected that there would be less overlap in use of space between the sexes during parturition. This outcome may be evidenced by geographic

differences in use of elevation [24] and overall greater distance between ranges commonly used by the sexes [37]. By conducting research at the interface of theory and application, we provide evidence to help better understand and disentangle the causes of sexual segregation, which should improve our understanding of how to manage habitat for the sexes of bison.

Materials and Methods

Study Site

Antelope Island State Park is located in the southeast corner of the Great Salt Lake, Utah, USA, approximately 34 km northwest of Salt Lake City. The island encompasses approximately 104 km² and is characterized by a north-south ridge with steep west-facing slopes, and gentler slopes facing eastward (Fig 1). The northern part of the island is influenced heavily by human recreational activities because of off-trail access by tourist, and the location of campsites, the visitor center, and park headquarters (Fig 1). Elevations on the island range from 1,278 m to 2,007 m, with the highest elevation ~700 m above lake level.

Antelope Island has a temperate-arid climate (Fig 2), with average maximum summer (Jun.–Aug.) temperatures of ~32°C and minimum winter (Dec.–Feb.) temperatures of ~ -6 °C. Annual precipitation averages 213 cm. Annual snowfall averages 25.4 cm and begins in October or November and ends in March or April.

The island is a sagebrush-steppe community. The principle vegetation on the island is sagebrush (*Artemisia tridentata*) and annual grasses including cheatgrass (*Bromus tectorum*) and threeawn (*Aristida* spp.). Isolated pockets of juniper (*Juniperus osteosperma*) and big tooth maple (*Acer grandidentatum*) also are scattered on the western side of the island, and on steeper slopes. Overall, however, habitat on the island is relatively uniform.

During the study, approximately 242 ha were planted with a mixture of other forbs and grasses on the flats just south of Garr ranch (Fig 1). Approximately 18% of the weight of the seed mixture was alfalfa (*Medicago sativa*). Additionally, about 100 ha of grass stands on the flats were mowed to “freshen” the grass. Of the 75 springs on the island, 37 are located on the east side [39], providing fresh water and green forage around the surrounding wetlands during the dry summer (Fig 2). Antelope Island was originally named for its pronghorn (*Antilocapra americana*) “antelope” population; however, populations of mule deer (*Odocoileus hemionus*) and bighorn sheep also exist on the island. Although these large herbivores inhabit the island, differential feeding styles and diets reduce the likelihood of competition for forage with bison [40–42]. Large mammalian predators are scarce on the island. Coyotes (*Canis latrans*) are present, yet pose little threat to mature bison. No attempt was made to control coyotes during our study.

A small bison herd ($n = 12$) was introduced to Antelope Island in 1893 [43]. Today, the herd has grown to approximately 700 individuals, and is one of the oldest and largest publicly owned herds in the United States. This herd acts as an important reservoir for genetic variation and purity, because these bison exhibit relatively low levels of cattle mitochondrial DNA, indicating limited historical crossbreeding with domestic cattle [44]. Bison on the island were free ranging during our study. Each year, employees and volunteers of Antelope Island State Park herded all bison—except mature bulls—into fenced pastures on the north end of the island to examine them for pregnancy and record weights [34]. Bison have been hunted on the island since 1987. The number of hunting permits issued has varied from 6 to 20 each year. From 2013 to present, seven permits have been issued each year. Across those years, all permits were only for mature bulls [34].

Sampling Procedures

We conducted surveys of bison on Antelope Island during parturition (birthing seasons in 2014 and 2015) and rut (mating season in 2014). All aspects of animal handling and sampling were approved by an Institutional Animal Care and Use Committee at Idaho State University, and were consistent with methods adopted by the American Society of Mammalogists for research on wild mammals [45]. All observations were made with a 20-60× spotting scope or 10× binoculars over distances of <1 km. Care was taken not to disturb bison; when our presence disturbed bison, we terminated observations on that particular group. Sex and age classes were identified primarily from body size and horn characteristics [46,47]. We assigned males to one of two age classes, 2-4, and ≥ 5 years old, because of similar behavior and size of horns and body [48]. Male and female yearlings were grouped together because many observations were made at distances too great to accurately identify sex of bison that were not reproductively mature [48]. We recorded the size and geographic location of all groups sampled. Distance and bearing for the groups allowed us to obtain the location of the bison herd relative to the observer with an accuracy of approximately 3 m. A group was defined as ≥ 1 individual that moved as a cohesive unit. That definition encompassed the complete range of sociality for bison. Individuals that were >100 m from one another were recorded as separate groups [48]. If a question arose as to whether a bison was part of a particular group, we observed that bison until it either joined the group or moved away. To examine aggregation and segregation of the sexes, we assigned all bison into one of three social categories: female-only, male-only, or mixed-sex groups. Mixed-sex groups included ≥ 1 female and at least one large male (≥ 5 years of age). All types of groups could include yearlings, and young could be present in female-only and mixed-sex groups.

We recorded timing and synchrony of births and copulations to more accurately identify times of sexual segregation and aggregation. During parturition, we either observed births of young or used a ratio of young to adult females in groups to estimate number of young born in a particular sampling interval. We identified neonates by the red-brown color of their pelage and small size [46]. We performed surveys three times per week, between mid-March and mid-May (Fig 2). During rut (mating season), copulations were determined through direct observations, or by noting the number of females with their tail held erect and exhibiting an enlarged vulva—reliable signs that mating had occurred within the past 6 h [46,48,49]. Female bison only copulate once per mating season [50], reducing the likelihood of resampling females. Because a second estrus is rare in bison [50] and reproduction is highly synchronous [48], surveys performed during July and August likely detected most copulations. Copulations early in rut were not detected because surveys started in July, near the peak of rut. We conducted surveys 5 days per week at the height of rut during July and August, and 2-3 days per week during September (Fig 2).

Statistical Analyses

We analyzed timing and synchrony of reproduction with a modification of Sheppard's correction using the Euler-Maclaurin procedure, a general method for correcting the bias of an estimator calculated from unequal sampling intervals (bins). That method provides the mean date of reproduction and a robust estimate of the standard deviation (synchrony) in timing of reproduction [51]. The 3 parameter logistic model [$f(x) = (a (x/c)^b) / (1 + (x/c)^b)$] was fitted to the cumulative proportions of young born during parturition.

During rut, surveys began near the peak of mating activity; therefore, the calculated mean date of copulation would have been skewed right (estimated later) compared with the

actual date. For that reason, we estimated the proportion of copulations that likely occurred prior to the first sampling period during rut. To create those estimates, we used the proportions calculated from surveys of parturition in 2015—births that resulted from the copulations observed during rut in 2014. The cumulative proportion of young born on the 8th week of surveys during parturition (47%) corresponded with the cumulative proportion of copulations observed during the first week surveyed in rut (45%). Therefore, using the sampling bins and proportions from parturition, we estimated the cumulative proportion of copulations that likely occurred 7 weeks prior to our first survey during rut. The 3 parameter logistic model $[f(x) = (a (x/c)^b) / (1 + (x/c)^b)]$ was fitted to the combined estimate and observed proportions of copulations during rut.

The composition of groups during parturition and rut were analyzed with confidence interval estimated for binomial parameters with the likelihood ratio method [52]. For this application we used the Bonferroni correction for simultaneous inference within group types (marginal significance level = $0.05/(2(3)) = 0.0083$) resulting in approximate 99% CIs for the true binomial probability of success [53].

We used GPS data to examine spatial patterns between the sexes during parturition and rut. We used multi-response permutation procedures (MRPP), including excess groups, to test if the spatial distribution within groups was significantly different from the spatial distribution between the groups (Blossom software,[54]). The excess-group command was used to determine if the spatial distribution of one group could be obtained from randomly drawn points from the joint distribution of all groups. MRPP are distribution-free statistics that use Euclidean distances and rely on permutations of data based on randomization theory [55,56]. The delta values represent the mean distances within a groups weighted by sample

size. To detect elevational differences between the sexes, we used a 10-m digital elevation model (DEM) in ArcMap 10.1. To further examine variation in the use of elevation; we partitioned parturition and rut into early, middle, and late (March, April, and May; July, August, and September, respectively). We calculated 95% confidence intervals (CI) around means. We estimated the degree of overlap of use for single-sex and mixed-sex groups with the kerneloverlap module in ADEHABITAT [57] in R.

We also estimated the size of core areas (50% fixed kernels) for male-only, female-only, and mixed-sex groups on Antelope Island during sexual aggregation and segregation. Mixed-sex groups were not included in analyses of parturition, because we observed too few of those groups. Fifty-percent volume kernel densities were estimated with program HoRAE [58], specifying the reference bandwidth, standard sextante biweight kernel, and a 100-m grid-cell size. This method is a 3-dimensional index that considers volumetric overlap among utilization distributions, and better quantifies overlap than traditional two-dimensional metrics [59]. Those maps were constructed in ArcMap 10.1.

Results

We observed approximately 400 groups of bison during parturition from the beginning of March through the end of May in 2014 and 2015. During rut, >1,000 groups were surveyed between the beginning of July through the middle of September 2014. We analyzed the timing and synchrony of births during parturition and copulations during rut to define periods in which sexual segregation and aggregation were likely to occur. Based on the timing of copulations and births, female bison on Antelope Island had a gestation length of approximately 292 days. The mean date of birth was highly synchronous between 2014 and 2015, occurring on April 28 (95% CI = ± 5.4 days) and 29 (± 6.9 days), respectively (Fig 3).

The mean date of mating in 2014 from the combined estimates (from timing of births) and observations was July 11 (± 5.7 days) (Fig 4). Within those defined periods of parturition and rut, we performed further analyzes to investigate whether sexual segregation was occurring, and if so, whether it was primarily driven by ecological or social factors.

A significant difference in the percent composition of groups occurred between parturition and rut (Fig 5B) for all group types. Female-only and male-only groups were more prevalent during parturition compared with rut. We observed mixed-sex groups most frequently when the sexes were aggregated during rut. The size of mixed-sex groups, however, was substantially smaller during rut, averaging 53 individuals, compared with 137 individuals during parturition (Fig 5A). Size of mixed-sex groups increased five-fold throughout parturition (Fig 6A). The size of mixed-sex groups decreased slightly throughout rut to the size they were in March (the beginning of parturition) (Fig 6). The size of female-only groups decreased slightly from an average of 25 individuals during parturition to 15 during rut (Fig 5A). The mean size of male-only groups remained the same throughout segregation and aggregation, with an average of two individuals (Fig 5A and 6).

Spatial distribution of the three types of groups (male-only, female-only, and mixed-sex) differed significantly during parturition (δ obs. = 5,292; $p < 0.0001$) and rut (δ obs. = 6,468; $p < 0.0001$) (Table 1). In addition, when each social group was included as an excess group in MRPP, that group was significantly different from the joint distribution of the two others (Table 1). Those results were significant during both parturition and rut (Table 1).

Elevational use by male-only and mixed-sex groups was not different between sexual segregation and aggregation (Fig 7A). Female groups, however, inhabited significantly higher elevations during parturition compared with rut, and higher elevations than other

group types during parturition (Fig 7A). Furthermore, when parturition was divided into periods (early, middle, and late), female-only groups during the late period congregated at significantly lower elevations compared with groups observed early or in the middle of parturition (Fig 7B).

When we examined overlap of groups, mixed-sex groups overlapped in areas used with female-only groups by approximately 90% during segregation and aggregation. The distribution of mixed-sex groups had far less overlap with male-only groups during parturition (61%) and rut (71%). Segregation between male-only and female-only groups was most dramatic during parturition, where only 42% of those groups overlapped in distribution. That percentage of overlap rose to 69% during rut. The 50% core areas, however, did not overlap for male-only and female-only groups (Figs 8 and 9). Moreover, core areas for each sex changed between parturition and rut. The range of female-only groups expanded from 15,623 km² to 24,787 km² as females began using more open, low-lying habitats along the eastern side of the island, where most springs were present. Furthermore, areas planted with alfalfa mixture were abundant south of Garr ranch (Fig 1), likely drawing females with young to those areas (Figs 8 and 9). Male-only groups, however, decreased the size of their core area from 18,735 km² during parturition to 13,335 km² during rut. Mixed-sex groups had the largest core area of 28,617 km² during rut (Fig 9).

Discussion

We used timing and synchrony of births and mating to help define times of sexual segregation and aggregation for bison on Antelope Island. From those results, we more closely examined patterns of spatial segregation from March to May and aggregation

between July and October for those ungulates. As we hypothesized, the degree of sexual segregation differed between seasons. In accordance with social segregation hypotheses, we did see single-sex groups significantly more during parturition compared with rut (Fig 5B). We also observed mixed-sex groups significantly less often during parturition (sexual segregation) (Fig 5B). Those outcomes are consistent with social segregation theory if, indeed, there were differences in social behavior and there were aggressive interactions between males and females [8,11,15]. Hypotheses regarding socially driven segregation cannot, however, explain changes in the distribution of single-sex groups between parturition and rut. No aspect of those hypotheses can account for long-term partitioning of space by the sexes—an outcome that we observed.

Our study supports previous research on ecological segregation, specifically those that demonstrated spatial segregation of the sexes in American bison [18] as well as other ungulates [3,13,60–63]. Male and female bison spatially segregated during parturition and aggregated during rut (Figs 8 and 9). Overall, males remained on the most northerly parts of the island, while female-only and mixed-sex groups resided on the southeasterly reaches of Antelope Island (Figs 8 and 9). We also documented significant differences in the use of higher elevations by female-only groups, especially during early and mid-parturition (Fig 7); a result that was consistent with other studies of bison during birthing on Antelope Island [34]. Those changes in spatial distribution and variation in overlap of ranges in male-only and female-only groups between seasons provide evidence against social segregation and for ecological segregation, in particular the gastrocentric and predation hypotheses.

Although we were not able to test the gastrocentric hypothesis directly, we believe that it influenced sexual segregation on Antelope Island. That hypothesis proposes that the

sexes should segregate based on differences in the ability to digest forages. Because of the high visitation rate on the northern, and more developed end of the island, soil degradation and invasion of noxious weeds are likely greater compared with the backcountry [64]. The larger size of mature male bison would allow them to digest forage in the northern part of the island more easily compared with females, which require high-quality diets [7,22,65]. Additionally, females with young were likely drawn to areas planted with alfalfa mixtures south of Garr Ranch, and to the reeds (*Phragmites australis*) that grows around springs on the shores of the island (Figs 8 and 9). Females also used areas of high elevation (Fig 7), where vegetation is often in an earlier phenological stage [23,24]. Indeed, Berger [24] observed that female-only groups occurred at elevations 100 m higher than males. We hypothesize that the gastrocentric model had some influence in the differential use of habitat between male-only and female-only groups.

There was strong support for the predation hypothesis when we examined the three major ways females reduce predation risk— seeking high elevation with steep and rugged slopes, aggregating in large groups, and avoiding areas of high human activity. During early and mid-parturition female-only groups resided at significantly higher elevations compared with other times of the year, and with other types of groups (male-only and mixed-sex) (Fig 7). Those elevational and social differences have been documented in bison and Yak (*Bos mutus*) [24].

In our study, females aggregated in large groups during parturition and rut. Females-only group were significantly larger than male-only groups during both parturition and rut, a finding similar to that of Berger (2014) who noted that females aggregated in groups 15 times larger than did male groups. Unexpectedly, however, mixed-sex groups were larger

during parturition compared with rut (Fig 5A). Most literature on bison documented that the largest groups in late parturition were nursery groups excluding large males (≥ 5 years old) [66–68]. In our study, however, those large groups of females and young often became mixed-sex groups with the addition of a single male ≥ 5 years of age. During parturition, male bison traversed greater distances compared with rut, because the delta values from MRPP were larger for male-only groups during parturition compared with rut, signifying larger within group distances (Table 1). That results likely increased the chance that males would encounter and temporarily joining female-only groups. Furthermore, as parturition ended and rut began 1 month later, male bison likely inspected the status of estrus in females as they moved about the island. Berger observed similar behavior, noting that males engaged in long-distance movements, likely in search for high-quality females [69].

The large female-only and mixed-sex groups during parturition mainly occurred on in open areas (i.e., salt flats or open meadows near the shore); a results demonstrated by others as well [66]. The collective vigilance of those large groups likely reduced the risk of predation by increasing detection rate of predators [26,27,66], especially in such open areas. Although ungulates that are naïve about predators fare poorly during initial attacks [70], ungulates respond to predation risk by engaging in behaviors that reduce the probability of being selected as prey, and those behaviors may persist for centuries, even when predators are no longer present [71].

Finally, we also demonstrated that female-only groups remained in areas of low human activity during parturition (Fig 7). Human recreational activity is higher on the open, low-elevation meadows along the east side of the island compared with the high-elevation and more rugged terrain on the central and western reaches of Antelope Island (Fig 1) [64].

Compared with the backcountry, human activity on the northern end of the island is four times greater because of off-trail access and the location of campsite, picnic areas, the visitor center, and park headquarters [64]. Humans can be perceived as predators [30,31], and bighorn sheep have abandoned particular habitat because of high human activity [33]. Taylor and Knight [72] demonstrated that on Antelope Island there was a 200 m “area of influence” around trails where human activity (e.g., hiking and mountain biking) frequently caused bison to flee. High levels of human activity likely deterred females and young more readily than males, resulting in a significantly greater abundance of male-only groups in those areas (Figs 8 and 9). We cannot determine, however, whether this shift in distributions resulted from perceived risk of predation, human disturbance, or both factors.

Outcomes from our study provide further evidence for ecologically driven segregation of the sexes in polygynous ruminants. Although we did not directly test the predation and gastrocentric hypotheses, we were able to provide valuable information in keeping with those hypotheses on the movement patterns and ranges of single-sex and mixed-sex groups during two critical periods—parturition and rut. Our observations provide evidence against social segregation in this population of bison because social factors (i.e. aggressive behavior) cannot explain changes in spatial patterns of the sexes between parturition and rut, or the long period of spatial segregation. Being able to identify how and why a population or species is sexually segregating can greatly improve management of wild ruminants. Habitat manipulation may inadvertently harm one sex while benefiting the other if differences in habitat selection between the sexes is not considered [38,73,74]. Indeed, Bowyer and Kie [13] suggested that the sexes should be managed as if they were separate species. If we can better understand the movement patterns and group dynamics of

gregarious and dimorphic herbivores during critical periods, we can make strides in the management of free-ranging populations and their habitat. Our study provides a deeper understanding of the principles underpinning sexual segregation, and helps us tease apart hypotheses for ecological and social segregation.

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Author Contributions

Conceived and designed the experiments: JCT, RTB, JCW. Performed the experiments: JCT. Analyzed data: JCT, RTB, KAA. Contributed analysis tools: JGK, KAA. Wrote the paper: JCT, RTB.

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Tables

Table 1. Delta values (m) from MRPP with excess groups.

Delta values represent the weighted means of the within groups distances. Data were from locations of bison groups on Antelope Island, Utah, USA, during rut in 2014 and parturition in 2015.

Excess group	δ of groups		δ observed	p -value
Parturition				
Mixed-sex	Male-only	4,287	5,292	<0.0001
	Female-only	7,177		
Male-only	Mixed-sex	4,647	4,212	<0.0001
	Female-only	4,127		
Female-only	Mixed-sex	4,647	6,040	<0.0001
	Male-only	6,238		
Rut				
Mixed-sex	Male-only	8,118	7,725	0.03
	Female-only	6,637		
Male-only	Mixed-sex	6,825	6,650	<0.0001
	Female-only	6,102		
Female-only	Mixed-sex	6,825	6,554	<0.0001
	Male-only	5,803		

Figures

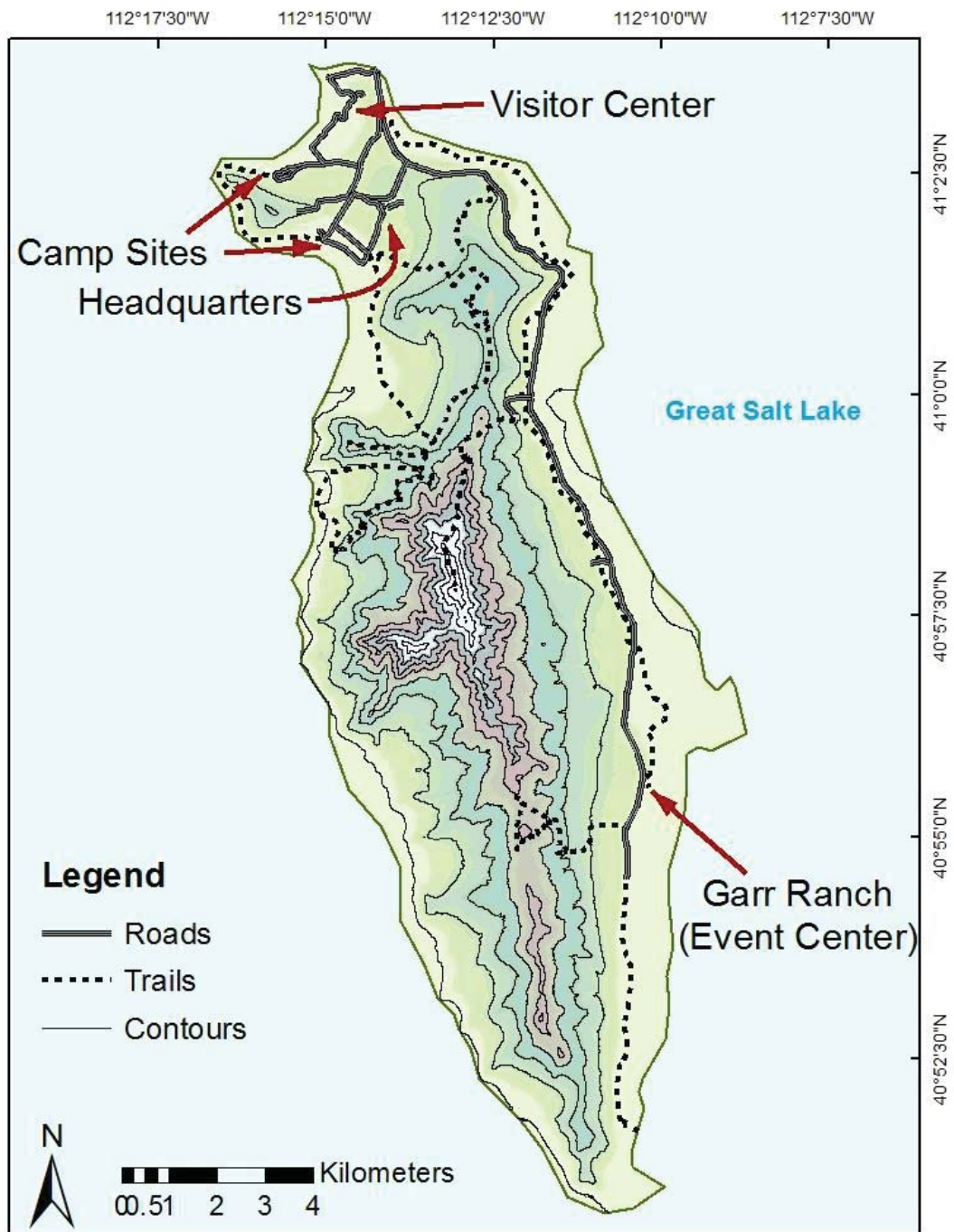


Fig 1. Map of Antelope Island State Park, Utah, USA. Elevation contour lines are indicating 80-m intervals. Places with high human activities are indicated with red arrows.

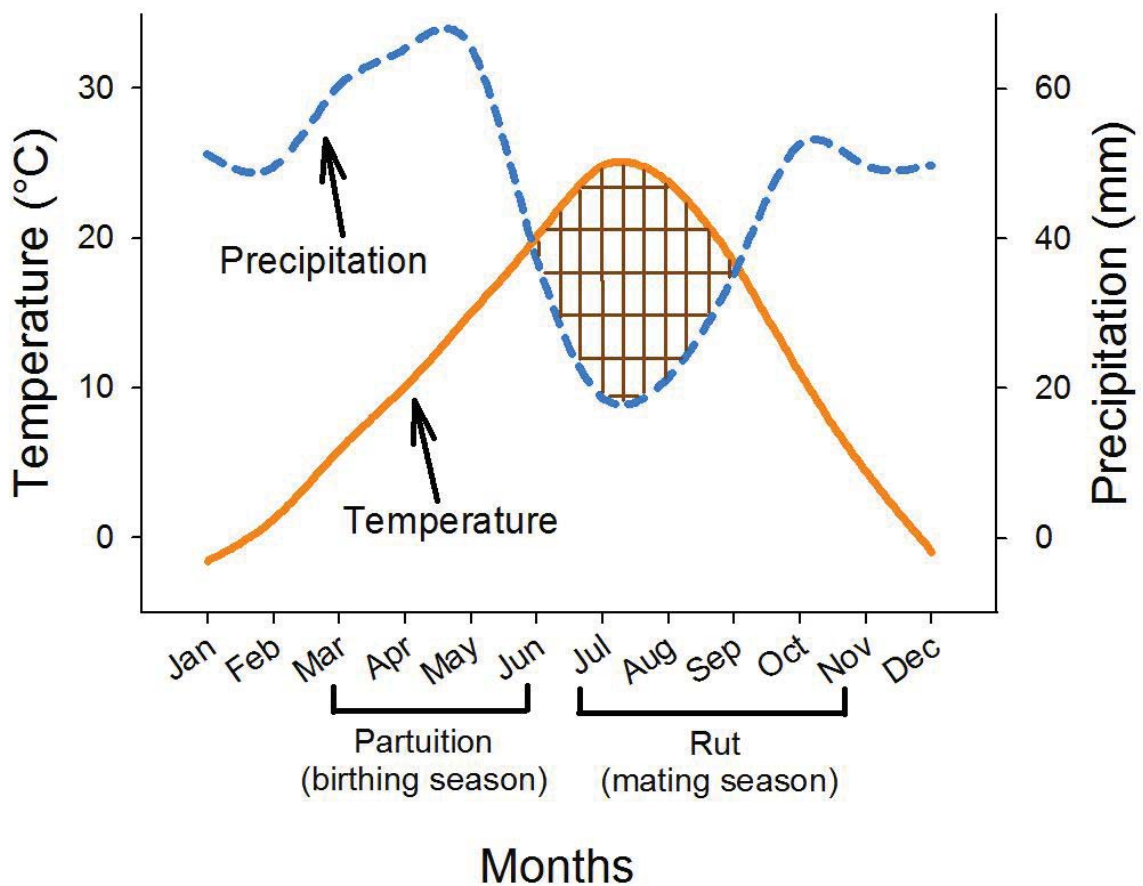


Fig 2. Walter climograph illustrating the relationship between average monthly temperature and average total monthly precipitation. Precipitation is indicated by the dashed line, whereas temperature is represented by the solid line. The cross-hatch area indicates times of water deficit where temperature (and thereby evapotranspiration) exceeds precipitation. Seasons of sexual segregation (parturition) and aggregation (rut) are identified for bison on Antelope Island State Park, Utah, USA. Data represent averages from 1948 to 2013 for Farmington, Utah, USA.

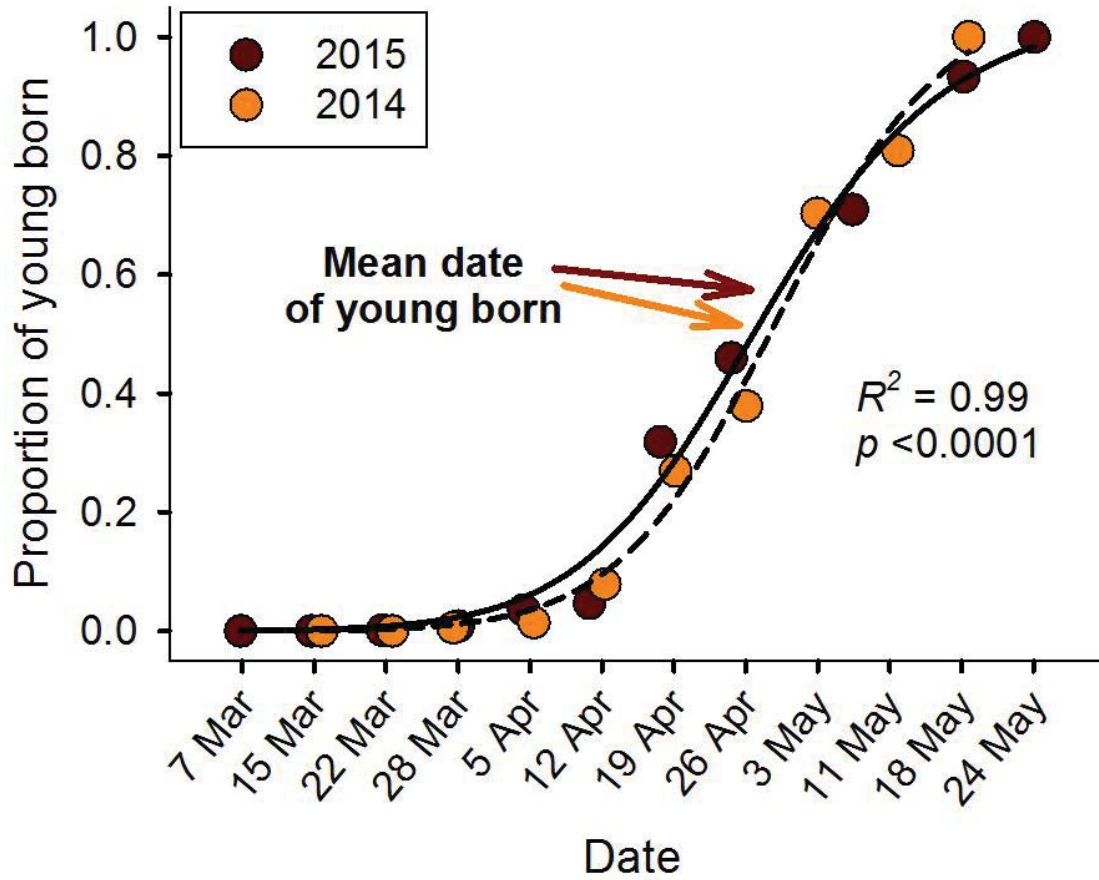


Fig 3. Cumulative proportion of births. Mean dates of birth were April 28 and 29 during 2014 (brown) and 2015 (orange). The R^2 and p -values shown are representative for both years. The model fitted for 2014 (dashed line) is $f(x) = (1.10 z)/(1+z)$, where $z = (x/119.9)^{14.34}$. The model fitted for 2015 (solid line) is $f(x) = (1.06 z)/(1+z)$, where $z = (x/117.7)^{12.78}$. Data were collected between the beginning of March through the end of May for bison on Antelope Island State Park, Utah, USA.

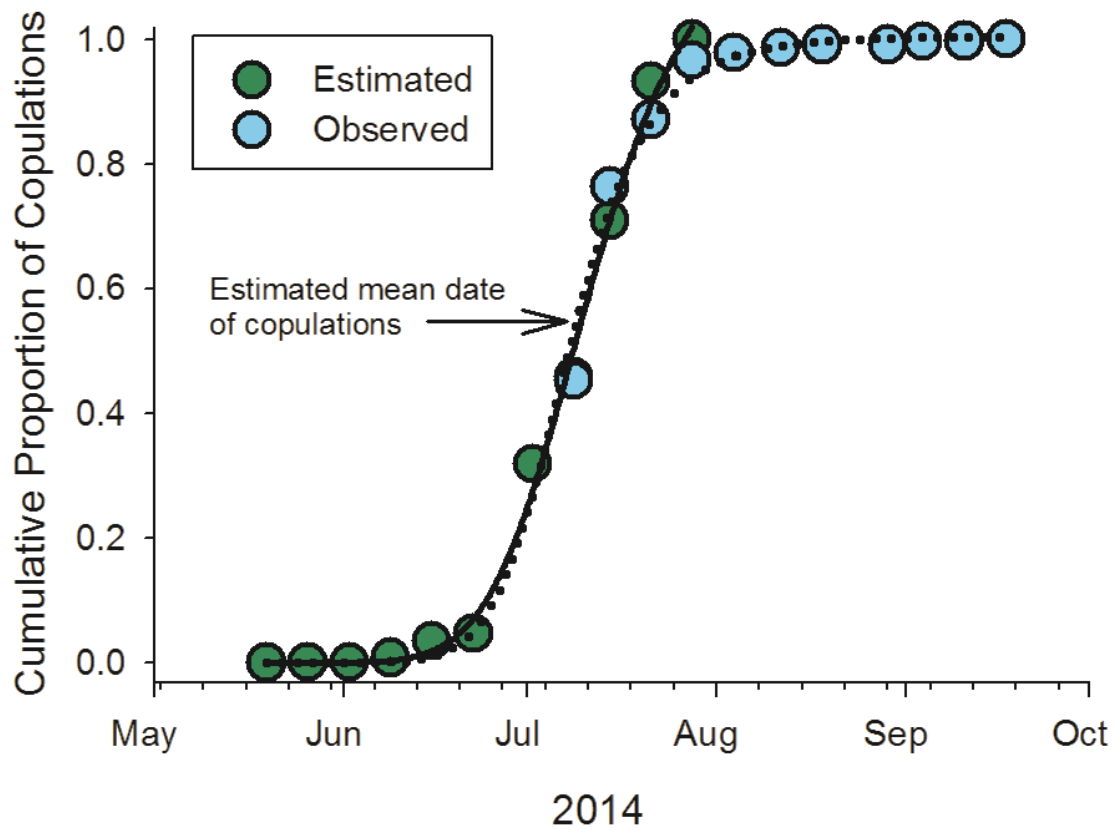


Fig 4. Estimated cumulative proportion of copulations during rut. The estimated mean date of copulation was July 11. The solid trendline represents the estimated proportions of copulations if they corresponded directly with the proportions of young born during parturition in 2015 ($f(x) = (1.21 z)/(1+z)$, where $z = (x/55.89)^{-6.30}$). The dashed trendline represents the observed cumulative proportions (blue points) are combined with the estimated proportions (first 7 points green points) ($f(x) = (1.01 z)/(1+z)$, where $z = (x/52.26)^{-7.89}$). Data were estimated from end of May through end of July. Observed data were collected between the beginning of July through the end of September bison on Antelope Island State Park, Utah, USA.

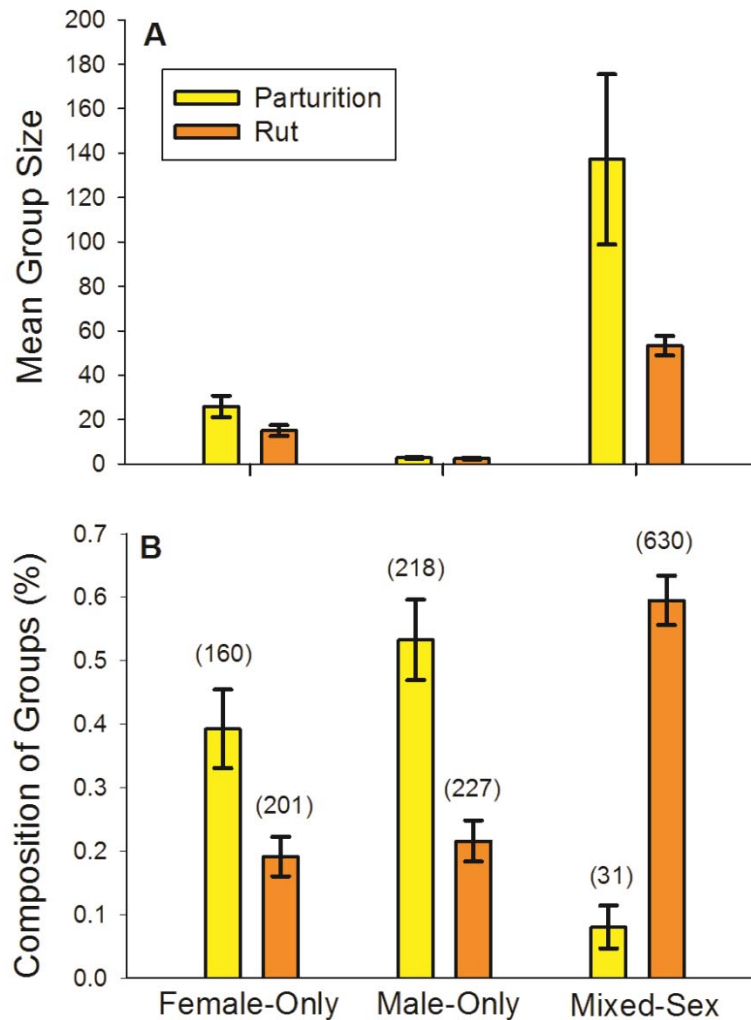


Fig 5. Average group size and percent composition of each type of group between parturition and rut. (A) Mean group size of bison during parturition (sexual segregation; yellow) and rut (sexual aggregation; orange) for each group type (female-only, male-only, and mixed-sex). The error bars depict $\pm 95\%$ CIs. (B) The percent composition of groups during parturition and rut among female-only, male-only, and mixed-sex groups. The error bars depict 99 % CIs for the true binomial proportion, to reflect Bonferroni correction for simultaneous inference within group types (marginal significance level = $0.05/(2(3)) = 0.0083$). Number of groups surveys is shown in the parentheses above the bars. Data were collected on Antelope Island, Utah, USA during 2014 and 2015.

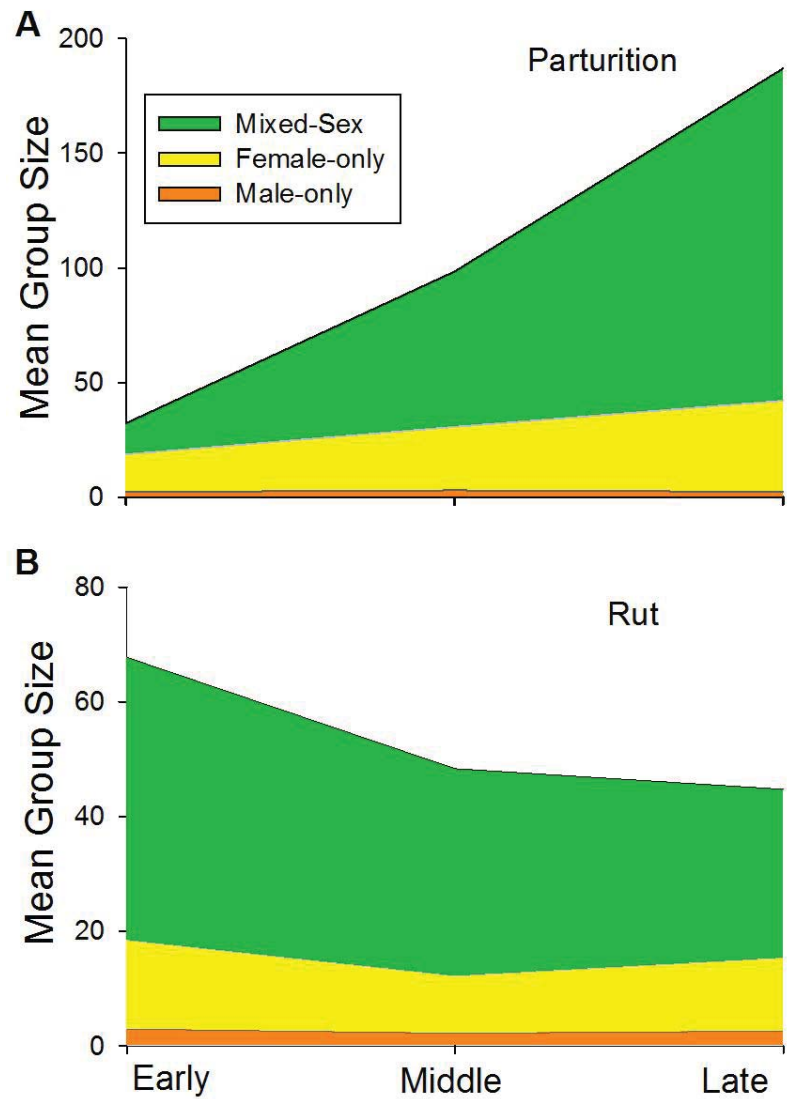


Fig 6. Mean group size through time for each type of group composition. (A) Group size during parturition (sexual segregation) divided into early (March), middle (April), and late (May) for 2014 and 2015. (B) Group size during rut (aggregation), divided into early (July), middle (August), and late (September) for 2014. Groups were separated by type of group composition (male-only, orange; female-only, yellow; mixed-sex, green). This graph does not depict stacked values. Data were collected for bison on Antelope Island, Utah, USA.

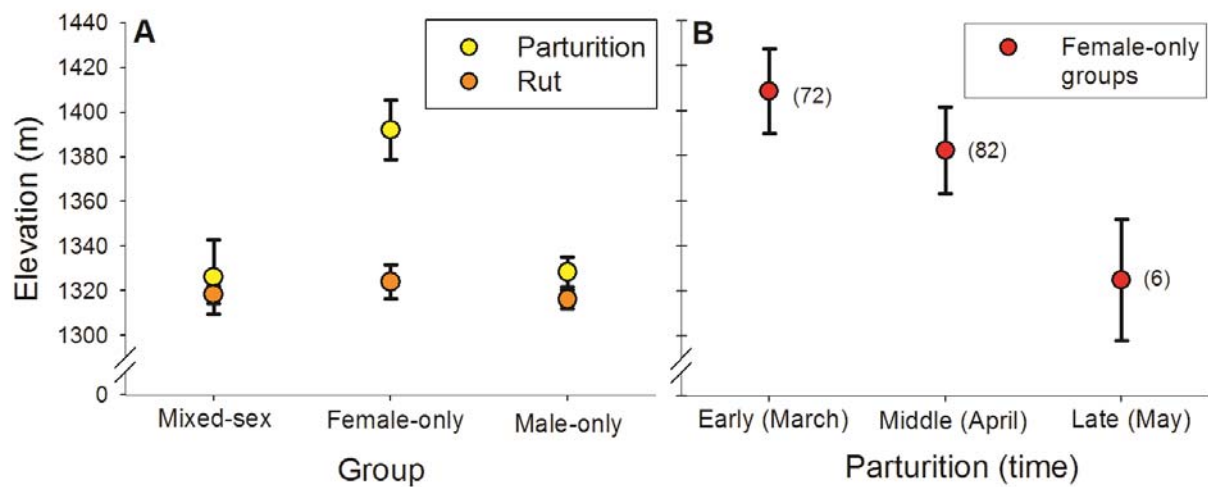


Fig 7. Mean elevation of groups. (A) Mean ($\pm$ 95% CI) elevational use among group types (male-only, female-only, and mixed-sex) and season (parturition in yellow and rut in orange). Sample sizes are the same as those depicted in Fig 5B. (B) Changes in elevation during parturition were divided into early, middle, and late. Sample sizes are shown in the parentheses. Data were collected during summer 2014 and spring 2014 and 2015 for bison on Antelope Island State Park, Utah, USA.

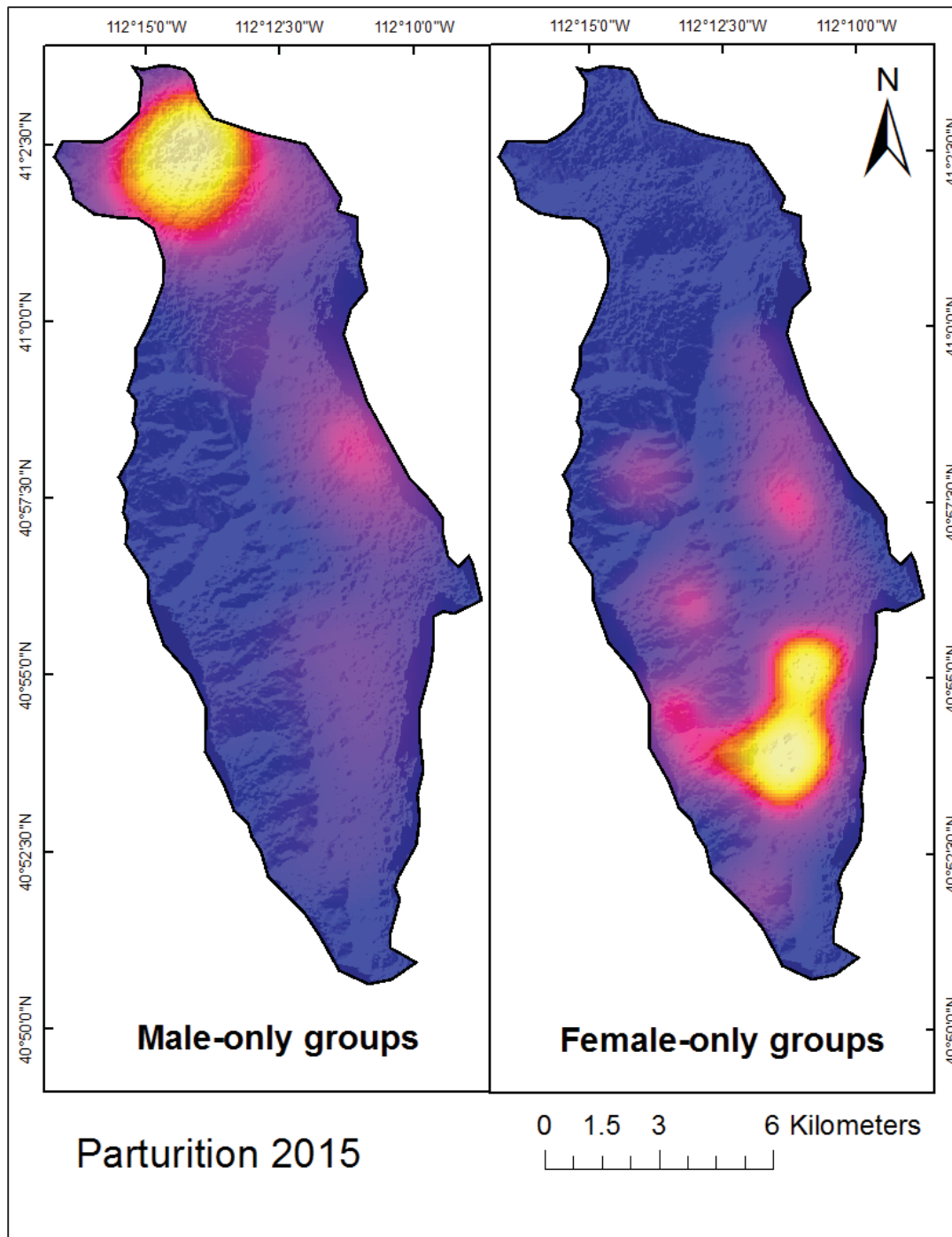


Fig 8. Kernel-density estimates for male-only and female-only groups of bison during sexual segregation (parturition). High density is represented in light yellow. Mixed-sex groups were not included because of small sample sizes. Data were collected from March to end of May in 2015 on Antelope Island State Park, Utah, USA.

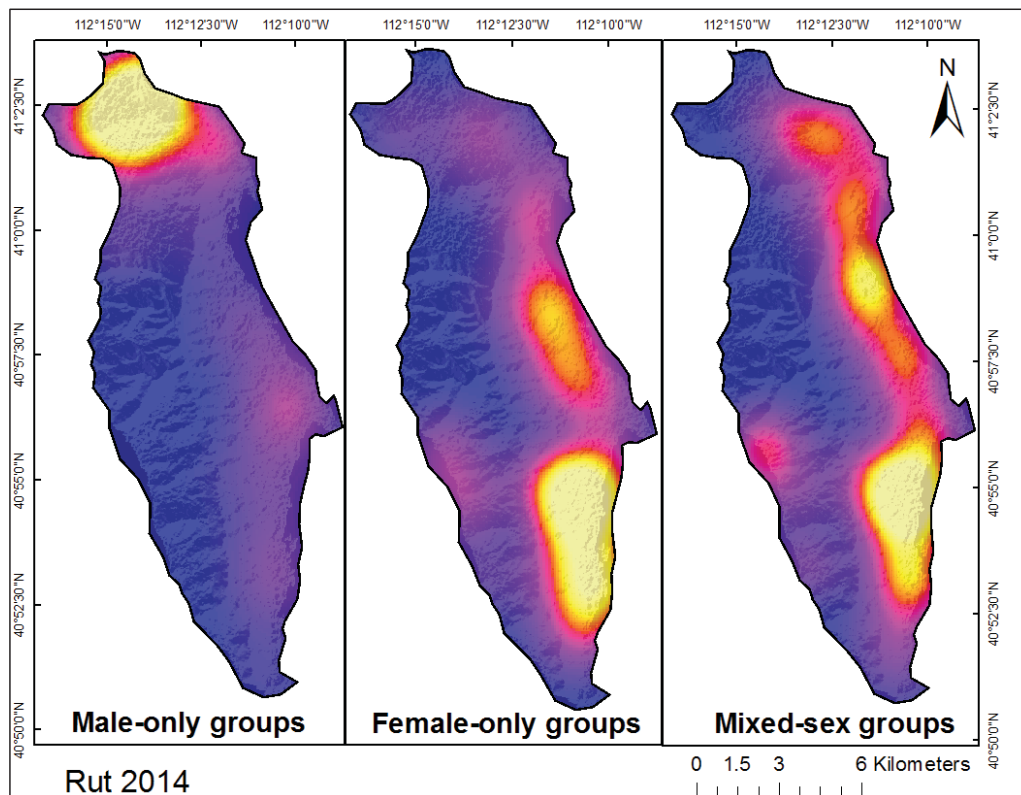


Fig 9. Kernel-density estimates for male-only, female-only, and mixed-sex groups of bison during sexual aggregation (rut). High density is represented as light yellow. Data were collected from July to end of September in 2014 on Antelope Island State Park, Utah, USA.

CHAPTER 2

Combining the old and new: climate change and an index to vegetation productivity in a semi-arid environment

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Abstract

The ability to predict future population dynamics of flora and fauna within an ecosystem is critical to improving management decisions in response to increasing climatic- and anthropogenic-induced changes. Our aims were to investigate changes in vegetative growth since 1951, and to develop an index to vegetative productivity in a sage-steppe ecosystem, using Antelope Island State Park, Utah, USA as a model. We compiled data on local weather (average monthly temperature, total monthly precipitation, and growing-degree days [GDD]), vegetative productivity (percent change in Normalized Difference Vegetation Index [NDVI] and ring-width increment of Utah juniper [*Juniperus osteosperma* (Torr.) Little]), and regional climate (Southern Oscillation Index [SOI], and Palmer Drought Severity Index [PDSI]). Since 1951, there has been a significant increase in average temperature and tree-ring width. No change occurred in total annual precipitation. We performed a principal component analysis with temperature, precipitation, NDVI, and tree-ring data. The first principal component represented a simple metric of vegetative productivity, explaining 46%

of the variation among years. The second component was predominantly a temperature axis, explaining an additional 29% of variation. The PDSI was significantly related to the PCA when years were clustered into times of high and low productivity. We demonstrate that vegetation in a semi-arid environment may not be as susceptible to an increase in temperature compared with more mesic ecosystems. We also offer a simple metric for vegetative productivity that likely relates to quality of forage for herbivores, which can benefit modeling efforts by replacing multiple parameters with a single yet comprehensive index.

Keywords climate, index, semi-arid, Utah, vegetation, management of ungulates

1 Introduction

Climate change is expected to alter patterns of local weather and, consequently, ecological processes (Overpeck et al. 1990; Cramer et al. 2001; Meehl et al. 2007). Europe, Africa, and the Americas already have reported changes in seasonal patterns of climate (Pachauri and Reisinger 2007). Overwhelming evidence from long-term research indicates that phenology in plants and animals responds to climate change (Post and Stenseth 1999; Stenseth et al. 2002; Badeck et al. 2004; Gordo and Sanz 2005; Monteith et al. 2011). Those climatically induced changes in the phenology and biomass of vegetation influences reproductive success of large herbivores by altering the body mass of females (Sadleir 1987; Langvatn et al. 1996; Pettorelli et al. 2007). Minor changes in quality and availability of forage result in relatively large fluctuations in rate of parturition and recruitment of young, because of the high energetic requirements necessary for gestation and lactation (White 1983; Stearns 1992; Cameron and Ver Hoef 1994; Cook et al. 2001; Monteith et al. 2013; Monteith et al. 2014a).

In addition to an increase in mean annual temperature, frequencies of extreme climatic events are expected to increase around the world (Pachauri and Reisinger 2007). Annual consistency and seasonal predictability of climatic conditions can have profound ramifications for reproductive success in large herbivores (Bowyer 1991; Hewison and Gaillard 2001; Loe et al. 2005; Monteith et al. 2013). Knowledge about which areas experience the most pronounced changes in climate may aid future management and conservation efforts for the flora and fauna of a particular region. Consequently, creating an index to vegetative productivity is crucial for comparing the present with the past, and predicting the future.

Records of temperature and precipitation have been recorded for centuries, and are highly correlated with vegetative growth (He and Shao 2006). Patterns of growth and productivity of vegetation, however, also are influenced by a multitude of factors, including wind (Wilson 1959), composition of soil (Xiong and Nilsson 1999; Rustad et al. 2001), and effects of animals (McNaughton 1983; Molvar et al. 1993; Scheu 2003). Simultaneously accounting for all of those variables can be challenging, leading many scientists to prefer direct measures of plant productivity over use of indices to vegetative growth. Obtaining direct measures, however, often can be costly, time-consuming, and only captures vegetative productivity for a small area and time period (Cook and Stubbendieck 1986). For that reason, obtaining a single comprehensive index is an ideal approach, especially if that metric can be related to forage of herbivores.

Tree-ring data have been used successfully as a direct measure of past net primary productivity (Graumlich et al. 1989), and allow scientists to assess historic patterns of vegetative growth. Nonetheless, the use of tree-rings when analyzing forage availability has limitations. For example, acquiring tree cores can be labor intensive and costly, especially in

remote locations. Moreover, large trees are more resistant to short-term droughts compared with grasses and forbs because of their extensive root systems (Walter et al. 1971; Sala et al. 1989), consequently, tree-ring data may not be the best approach for examining the productivity of grass-dominated landscapes. Annual ring width, however, has been associated previously with net primary productivity and the Normalized Difference Vegetation Index (NDVI) (D'arrigo et al. 2000; Wang et al. 2004; Liang, Shao, and He 2005).

Today, satellite-based estimates of vegetative productivity are easily accessible via NDVI. Substantial literature involving the use of NDVI has demonstrated that this index is highly correlated with measure of vegetative biomass, phenology, and net primary productivity for most ecosystems (Myneni and Hall 1995; Buermann et al. 2002; Hicke et al. 2002; Kawamura et al. 2003; Lendrum et al. 2014; Stoner et al. 2016). In particular, net primary productivity in the sagebrush steppe has been related to NDVI directly through fluxes in CO₂ (Wylie et al. 2003). Remote sensing has become a key component for analyzing vegetation around the globe; however, uses of those methods are limited during times of cloud-cover or for analyses prior to the 1980s (Pettorelli et al. 2005).

We aimed to create a simple index to plant productivity that overcomes the limitations associated with individual measures described previously. Specifically, we used Antelope Island State Park, Utah, as a test-case for developing a general model for vegetation productivity for a sage steppe environment. We hypothesized that in concert, tree-rings, NDVI, and local weather will represent a more reliable index to the quality and quantity of plants than when those variables were considered individually. We predicted that there would be an increase in temperature and corresponding decline in growth of trees over the past 65

years. We also postulated that tree-ring data and NDVI would be positively correlated, allowing us to assess the historical potential productivity of grasses and forbs. Results of our study will provide new insights into factors affecting plant productivity, and examine how climate change may be affecting growth of vegetation in a semi-arid environment. We also hoped to obtain an index that would reflect the value of vegetation to herbivores. Our study, therefore, can aid current efforts to understand how life-history events of large herbivores will be affected by climatic variability.

2 Methodology

2.1 Study area

Antelope Island State Park is located in the southeast corner of the Great Salt Lake, Utah, USA (40.9581° N, 112.2072° W), and is about 34 km northwest of Salt Lake City. The island encompasses approximately 104 km² and is characterized by a north-south ridge (maximum elevation above lake level = 600 m) with steep west-facing slopes, and gentler slopes facing east. Antelope Island has a temperate-arid climate (Fig. 1), with average maximum summer (Jun.–Aug.) temperatures of ~32° C and minimum winter (Dec.–Feb.) temperatures of ~ -6° C. Annual precipitation averages 213 cm. Annual snowfall averages 25.4 cm and begins in October or November and ends in March or April. Vegetation on the island consists primarily of a sage steppe community. The principle vegetation on the island is sagebrush (*Artemisia tridentate wyomingensis*); annual grasses include cheatgrass (*Bromus tectorum*) and threeawn (*Aristida* spp.). Isolated pockets of Utah juniper (*Juniperus osteosperma*) and big tooth maple (*Acer grandidentatum*) also are scattered on the western

side of the island, and on steep slopes. Portions of the island have been re-seeded with perennial grasses and grass-legume mixtures. Approximately 40% of the soil on the Island is loamy-skeletal missed mesic Typic Argixerolls with rocky outcrops. The lower elevations are predominantly gravelly sandy loam, making up another 30% of the soil types (<http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx>).

2.2 Data collection

Historical records of climate from both regional and local weather stations were assembled for the water-year (October through September). Local weather variables of interest included total monthly precipitation and average monthly temperature collected at the Salt Lake City Airport from 1950 to 2014. In addition, we calculated growing-degree days [GDD] as another metric of potential plant growth throughout the year (Chapin 1983; Davidson and Campbell 1983; Rachlow and Bowyer 1994). Many aspects of plant phenology (e.g., emergence, bud burst, flowering) have been linked with GDD, because plants are not able to photosynthesize when air temperatures are $<5^{\circ}\text{C}$. The Southern Oscillation Index [SOI] was used to characterize regional patterns of climate, because that index reflects the development and intensity of El Niño or la Niña events in the Pacific Ocean, which dramatically affect precipitation in the western United States (Ropelewski and Halpert 1986; Ropelewski and Halpert 1987). We also collected data on drought conditions using the Palmer Drought Severity Index (PDSI), a commonly used index of regional drought (Palmer 1965; Keyantash and Dracup 2002). Data on GDD, PDSI, and SOI were collected from 1990 through 2011. All data were retrieved from online archives from NOAA (National Oceanic and Atmospheric Administration: <http://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>, <http://w2.weather.gov/climate/xmacis.php?wfo=slc>, [43](http://www.ncdc.noaa.gov/temp-and-</p></div><div data-bbox=)

[precip/drought/nadm/indices/palmer/stn#select-form, http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/](http://www.ncdc.noaa.gov/temp-and-precip/drought/nadm/indices/palmer/stn#select-form)).

Normalized difference vegetation index (NDVI) was calculated monthly from 250-m² resolution satellite imagery of Antelope Island. We restricted analyses to between 1990 and 2011 so that all data for NDVI were retrieved from the same satellite (LS5), reducing potential issues with switching satellites during our study. No images were used for November through February because of recurrent cloud cover. Additionally, the average daily temperatures during those months were frequently <5°C, resulting in extended periods of vegetative dormancy (Chapin 1983; Monteith et al. 2011). Percent change in mean NDVI was used because frequent cloud-cover reduced the number of images we were able to acquire over a short time interval during the growing season. NDVI is an instantaneous measure that is calculated from the percent reflectance of incident near infrared and red visible light wavelengths. Consequently, NDVI provides a simple index to plant productivity via measures of greenness and biomass (Myneni and Hall 1995). We calculated the percent change in NDVI by subtracting the maximum from minimum values to reflect change during the growing season (March through October). Studies have demonstrated that percent change in NDVI is an accurate indicator of phenology and productivity of vegetation (Pettorelli et al. 2005; Lendrum et al. 2014).

To gain a more complete understanding of changes in vegetative growth as a result of climate, we also collected increment cores from 30 randomly selected junipers (>3 m tall) dispersed across the Island. Increment cores were taken at stump height (Meeuwig and Cooper 1981) from trees with a diameter of >30 cm. Cores were air-dried and prepared with progressively finer sandpaper at *ca.* 600 grit. We cross-dated the tree-ring series, assigning a

year to each ring. The rings were measured to 0.001 mm, and examined for dating accuracy with the program COFECHA (Grissino-Mayer 2001; Deroose et al. 2016). We developed a ‘standard’ tree-ring index for analysis. That index was created by detrending each series with its mean, a method especially appropriate for Utah juniper (DeRose et al. 2016), before series were averaged with a biweight robust mean. By using the standard chronology, we retained the inherent autocorrelation in the ring-width data, which likely is related to biological and climatic variability (Woodhouse et al. 2006). For examining change over time, the standardized tree-ring widths were analyzed with a weighted least-squares regression to reduce the influence of outliers.

2.2 Analyses

We examined change in local weather (average monthly temperature and total monthly precipitation) and vegetative growth (tree-ring chronology) since 1951. To model annual vegetative productivity we performed a principal component analysis (PCA) on local weather during the wet-season (October through September), standard tree-ring chronology (Cook and Peters 1997), and the percent change in NDVI (Bhatt et al. 2010) from 1990 through 2010. We conducted a cluster analysis on PC1 and PC2 using the k-means method, which separates points into groups where the sum of squares from the points to the allocated cluster are minimized (Hartigan and Wong 1979). We then compared those clusters with respect to growing-degree days, the Palmer Drought Severity Index (PDSI), and the Southern Oscillation Index (SOI) using 95% confidence intervals. In addition, changes in NDVI were then compared with Utah juniper ring-width increment, temperature, and precipitation with multiple regression (Neter et al. 1985), which allowed us to identify an index that best represented growth of grasses and forbs when assessing historic patterns of productivity.

3 Results

Summary statistics for local weather (average monthly temperature and total monthly precipitation), vegetative productivity (tree-ring width, Normalized Difference Vegetation Index [NDVI], and growing-degree days [GDD]), and regional climate (Palmer Drought Severity Index [PDSI] and Southern Oscillation Index [SOI]) were compiled for 1990 through 2010 (Table 1). Contrary to our prediction, tree-rings and change in NDVI were not related ($y = -5E^{-16} + 0.2686x$, $r^2 = 0.07$, $p = 0.74$); therefore, productivity of grasses and forbs is unknown prior to 1990 when we incorporated data from NDVI. When we examined changes in temperature from 1951 to 2014, we identified a significant positive increase (Fig. 2A, $CV = 7.15\%$). The tree-ring data were even more variable over time ($CV = 34.2\%$). The transformed tree-ring widths increased over time (Fig. 2B). Analyses of variance, however, demonstrated that temperature did not have a significant influence on vegetative productivity of trees (tree-ring data) or grasses and forbs (NDVI data) ($F_{1,18} = 0.159$, $p = 0.70$; $F_{1,18} = 0.487$, $p = 0.49$, respectively). Instead, precipitation was the main variable affecting growth of junipers (tree-ring data), and grasses and forbs (NDVI data) in this semi-arid ecosystem ($F_{1,18} = 6.614$, $p = 0.02$; $F_{1,18} = 10.625$, $p = 0.004$, respectively).

When local weather, change in NDVI, and tree-ring data from the standard chronology were combined in a principal components analysis, a productivity vector (PC1) resulted, explaining 46% of the variation among years (Fig. 3). The addition of the second principal component increased the variance explained among years to 75%. Principal component two (PC2) was primarily a temperature axis with negative values representing years of high temperature and positive values years of low temperature (Fig. 3).

The k-means cluster analysis of PC1 and PC2 resulted in two groupings that explained 48% of the variation among years. Those clusters represented years of high and low productivity. The Palmer Drought Severity Index had significantly higher values (times of water surplus) during years of high vegetative production compared with low-productivity years (Fig. 4). Growing degree-days and the Southern Oscillation Index were not significantly related to our index of plant productivity (Fig.4).

4 Discussion and conclusions

We created a simple index to forage productivity using the principal components analysis. That index was comprehensive because we included variables representing local weather (average temperature and total precipitation), and vegetative growth (percent change in NDVI, and tree-ring width). Contrary to our predication, however, there was no significant relationship between tree ring width and change in NDVI. Other studies have demonstrated associations between annual ring width and NDVI (Franklin et al. 1997; D'arrigo et al. 2000; Wang et al. 2004; Liang et al. 2005), however, the sparse distribution of junipers on Antelope Island likely contributed to the lack of correlation between those variables. Data on NDVI in our study, therefore, represented mainly the quality and quantity of grasses and forbs, bringing additional information to our study that was not detectable with only tree-ring data. This relationship, however, did hinder our ability to draw conclusions about historic growth of grasses and forbs on Antelope Island.

We demonstrated an increase in temperature over the last 65 years (1950-2015) (Fig. 2A)— similar to other current literature describing climatic shifts around the world (Swetnam and Betancourt 2010). Contrary to our prediction, however, we did not observe a

corresponding decline in the growth of Utah juniper on Antelope Island. Instead, we identified an increase in growth (Fig 2B). Indeed, studies of western juniper (*J. occidentalis*) in east Oregon, USA, offered similar results to ours, indicating no obvious decline in vegetative growth through time (Miller and Rose 1995). An increase in temperature could have aided overall annual tree growth by extending the growing season in late autumn and early spring, times when water availability is high (Lloyd et al. 2001; Fig. 1)). Moreover, compared with grasses and forbs, trees are better buffered against short-term drought and high summer temperatures, because extensive root systems enable them to reach underground sources of water (Walter et al. 1971; Sala et al. 1989).

In some studies, high temperatures and variable precipitation during the growing season have resulted in reduced growth of vegetation because of increased water stress (Bowyer et al. 1998; Lenart et al. 2002; Andreu et al. 2007; Gea-Izquierdo et al. 2011). One explanation for the lack of observable decline in plant productivity with increasing temperature is that flora of arid environments are more highly adapted to high temperatures and drought compared with vegetation in temperate zones (Fischer and Turner 1978; Morgan 1984; DeLucia and Schlesinger 1991; Mueller et al. 2005; Rivero et al. 2007). Consequently, plants in semi-arid ecosystems may be more resistant to a warming climate than other species in more mesic environments.

Although the productivity of vegetation in semi-arid regions may be more resilient to increased temperature, hotter weather is not the only stress on plants in changing climates. The combination of increasing temperatures with an increase in evapo-transpiration of plants might be what ultimately hinders plant growth (Eamus et al. 2013). Indeed, vegetative growth on Antelope Island was significantly related to the Palmer Drought Severity Index

(PDSI). Although total annual precipitation has not changed dramatically in the past 65 years, Gillies et al. (2012), noted that winter precipitation is becoming more variable in northern Utah. Differences in the amount and timing of rainfall can greatly affect levels of soil moisture (indexed by PDSI), leading to variation in patterns of plant growth.

Large-scale weather patterns can drastically influence rainfall patterns across the globe. In our study, however, the Southern Oscillation Index (SOI) (a proxy of regional climate) did not relate to the quality and quantity of vegetation on Antelope Island—a pattern also demonstrated by (Wood and Werner 2011) for the Colorado River Basin. Indeed, effects of regional climate on the growth of trees have been identified across central Utah, yet those effects have fluctuated in the past (Hidalgo and Dracup 2003; Brown and Comrie 2004). A better understanding of the complex interactions of local weather and regional climate on plant productivity will become crucial for determine the next course of action in a changing climate.

Outcomes from our principal component analyses aid efforts to more accurately identify effects of a changing climate on plant productivity without the use of costly or disruptive methods for obtaining direct measures of vegetative growth. The cluster analysis on PC1 and PC2 offered a simple and basic measure of vegetative productivity. This index is concise, comprehensive, and overcomes many of the complications associated with the individual variables. The first principal component alone explained almost 50% of the annual variability in the quality and quantity of vegetation on Antelope Island. The combination of the first and second principal components explained 75% of the variability among years. Using just those two variables, scientists can greatly improve the statistical significance of models by reducing over parameterization, while maintaining high levels of information and

interpretation. Modeling effects of climate on the plants and animals for an ecosystem only will become more valuable as the environment changes ever more rapidly.

Considerable effort currently is being devoted to understanding how life-history events of large herbivores will be affected by climatic variability (Stearns 1992; Bowyer et al. 1998; Lenart et al. 2002; Stenseth and Mysterud 2002; Winkler et al. 2002; Monteith et al. 2011; Monteith et al. 2013; Monteith et al. 2014b; Thalmann et al. 2015). Recently, a comprehensive report discussing potential effects of climate change on big game species in North America was released by The National Wildlife Federation (Berman 2014). The wide distribution of large herbivores across varying landscapes, however, makes broad conclusions difficult. A simple index to vegetative productivity, therefore, could aid the understanding and management of populations of large herbivores at local scales, because the availability of forage can influence body mass necessary for reproduction in adults (Monteith et al. 2014b) and winter survival of juveniles (Hurley et al. 2014). Outcomes from our study, therefore, can greatly aid our understanding of the effect of climate change on the patterns of productivity of vegetation and, consequently, the herbivores that rely on those plants.

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Tables

Table 1 Summary statistics for data on climate and plant productivity collected between 1990 and 2011 for the water-year (October through September) on Antelope Island State Park, Utah, USA.

Variable	$\bar{x}$	SD	Range
Average Temperature (°C)	11.7	0.74	10.0 – 12.8
Total Precipitation (mm)	386.4	90.59	262.2 – 579.2
Standardized Tree-Ring Width (mm)	1.1	0.44	0.2 – 1.9
Percent Change in NDVI	58.0	15.52	38.0 – 93.6
Total Growing-Degree Days	4949.4	282.3	4442.7 – 5405.1
Average Palmer Drought Severity Index	0.1	2.65	-3.8 – 4.2
Average Southern Oscillation Index	0.1	0.65	-0.9 – 1.5

Figures

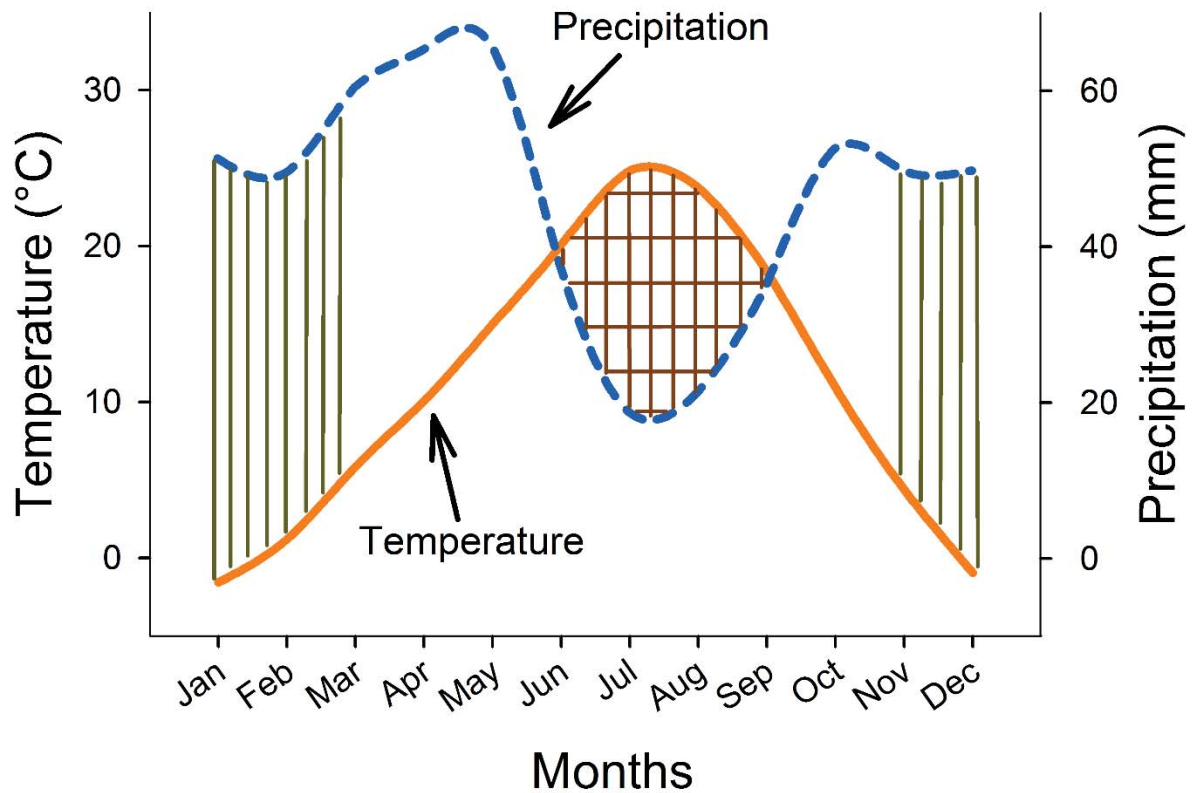


Fig. 1 The relationship between average monthly temperature and average total monthly precipitation illustrated as a Walter climograph. Precipitation is indicated by the dashed blue line, whereas temperature is represented by the solid orange line. The cross-hatch area indicates times of water deficit where temperature (and thereby evapotranspiration) exceeds precipitation. Vertical lines represent months when the average daily temperature is $<5^{\circ}\text{C}$ (times of vegetative dormancy). Data represent mean values from 1950 to 2014 for Salt Lake City, Utah, USA.

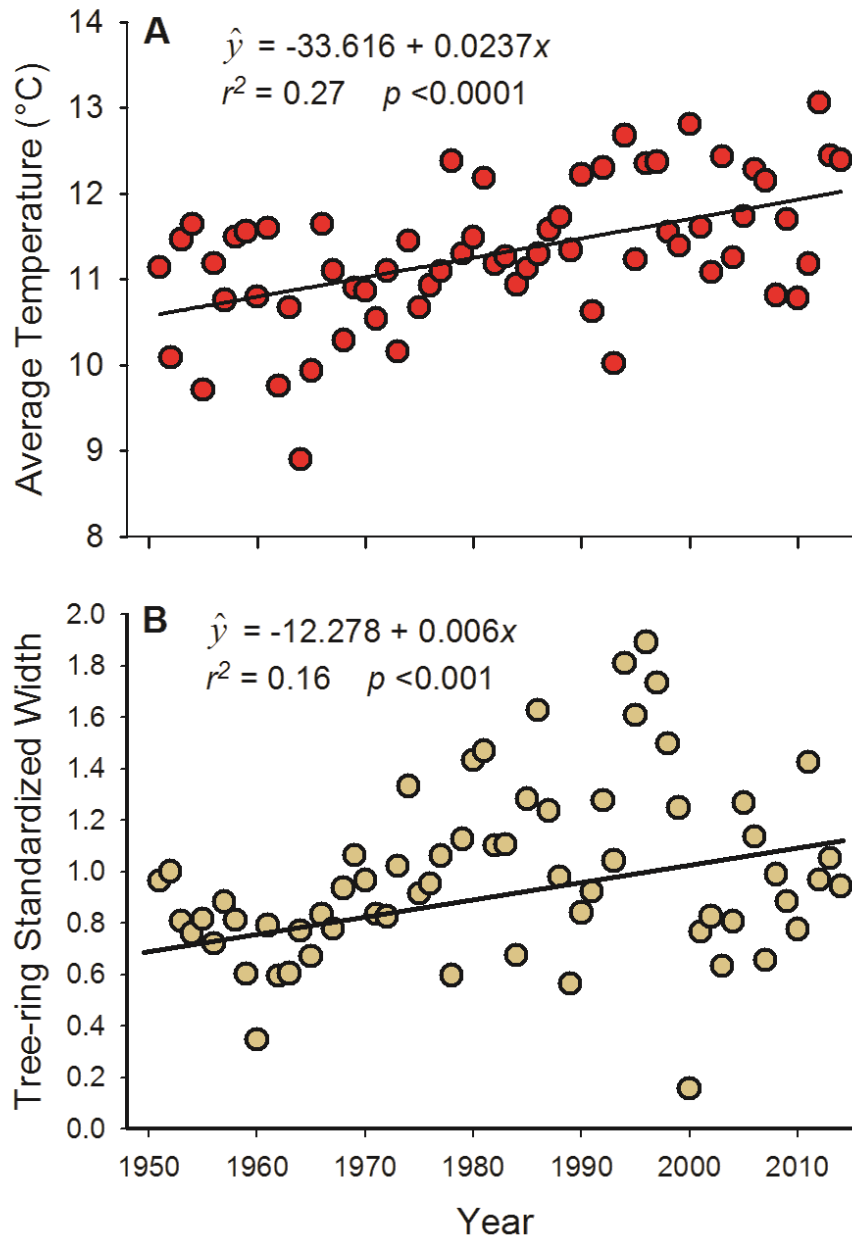


Fig. 2 (A) Change in average annual temperature (°C) through time. (B) Standardized tree-ring width through time. The trendline and associated r^2 and p -value are all from the transformed data using weighted least squares. Data were collected from 1950 to 2014 at Salt Lake City, Utah, USA.

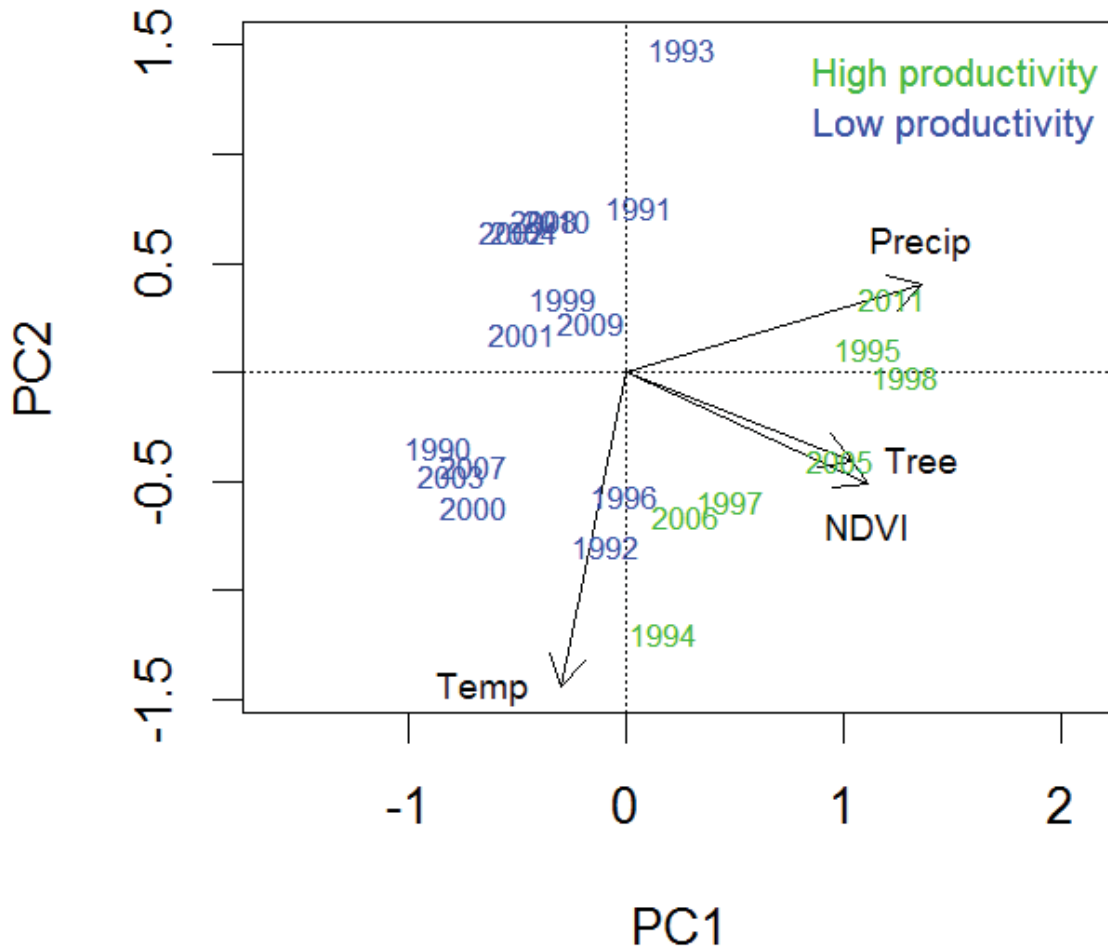


Fig. 3 Principal components analysis for local weather data (total precipitation and average temperature) for Salt Lake City, Utah, USA, and metrics for vegetative productivity (change in NDVI and standardized tree-ring widths) for Antelope Island, Utah, USA. The proportion of variance explained by each principal component is 46% for PC1 and 29% for PC2. Arrows point in the direction of the greatest value. A k-means cluster analysis divided years into two groups: high (green) and low (blue) productivity. Data were collected from 1990 through 2010.

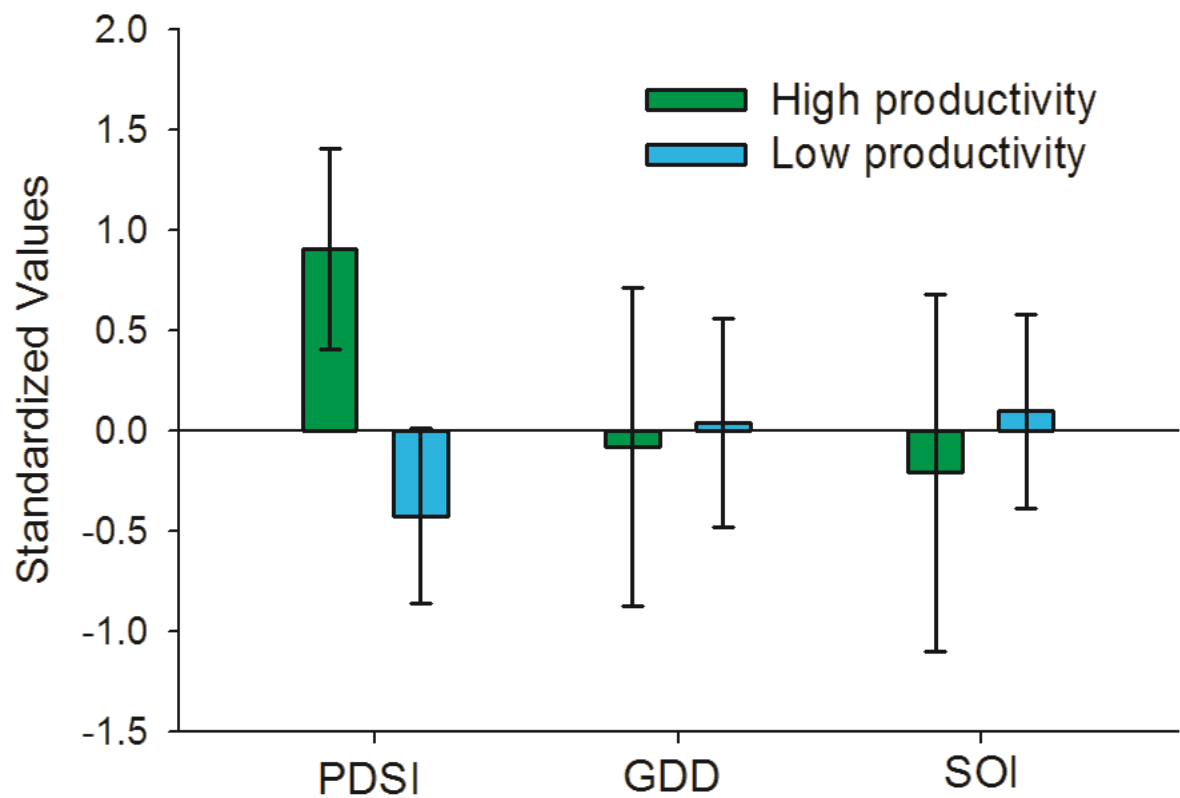


Fig. 4 A comparison of principal component one (PC1) with Growing-Degree Days (GDD), the Palmer Drought Severity Index (PDSI), and the Southern Oscillation Index (SOI). Years were divided into levels of vegetative productivity based on the k-means cluster analysis. Error bars represent 95% CIs. Those data were collected annually from 1990 to 2010 for North-central Utah, USA.