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Social Organization and Decision Making In North American Bison: Implications For Management

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SOCIAL ORGANIZATION AND DECISION MAKING IN NORTH AMERICAN BISON:IMPLICATIONS FOR MANAGEMENT

by

Ryan A. Shaw

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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ABSTRACT

Social Organization and Decision Making in North American Bison:

Implications for Management

by

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Utah State University, 2012

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Social organization varies widely among herbivores, and the level of social organization in bison is widely debated. I hypothesized that when mother-daughter relationships are allowed to develop, bison form long-term associations. In my study, 25 treatment mothers were selected from a free-ranging herd and kept together with their calves, while 25 control females had their calves forcefully removed. Treatment mothers and offspring had by far the greatest number of associations with a greater percentage of individuals with a half weight index (HWI) > 0.50. The strongest associations (HWI > 0.31) were among treatment mothers and their offspring. Moreover, these associations persisted over multiple generations.

Group coordination requires group decisions and these can vary between extremes. I hypothesized bison utilized both democratic and despotic decisions. I examined movement initiation and direction decisions following rest periods. For direction decisions older cows repeatedly made decisions despotically for the group; in 93% of the choices, group directions were within 95% confidence intervals. For movement initiation, bison used a more democratic decision-making process; group movements did not begin until an average of 47% of adult cows exited the group. Interestingly, the oldest females led this final post-rest movement behavior in 81% of the decisions.

Presumably, living in properly functioning social groups has many benefits, including reduced stress. I hypothesized levels of stress was related to animal density. Consequently, yearling bison males were weaned and placed in either 1) tight confinement (TC), 2) loose (LC) confinement, or 3) free-ranging (FR, returned to herd). I measured fecal cortisol metabolites (FCM) as an index of stress. Fecal samples were collected in each group every 2 weeks from January to April 2009. Fecal cortisol levels were lowest for FR (23 ng/g DM), intermediate for LC (39 ng/g DM), and highest for TC (63 ng/g DM; $P<0.0001$). Fecal cortisol levels also varied by date ($P<0.0001$), and treatment and date interacted ($P<0.0001$).

These results indicate bison live in extended families. Also, older females strongly influenced the direction of group movements, but bison also used democratic decisions. Finally, confinement greatly increased stress in young male bison compared with allowing them to free-range.

(134 pages)

PUBLIC ABSTRACT

Social Organization and Decision Making in North American Bison:
Implications for Management

Ryan Shaw

Social organization varies widely among herbivores, depending in part on resource availability, habitat structure, and kinship. The level of social organization in bison is still widely debated. At the extremes, some believe bison live in extended families, while others believe their social interactions occur randomly. I hypothesized that when mother-daughter relationships are allowed to develop, bison form long-term associations among related individuals. In my studies, 25 mothers were randomly selected from a free-ranging herd and kept together with their calves, while 25 other females had their calves forcefully removed, a typical practice for this and most other bison operations in the United States. Animals were located on the Armendaris Ranch near Truth or Consequences, NM during spring, summer, and fall each year. On encounter, I recorded group composition, including ages, genders, and group member identification. Mothers kept with their offspring had by far both the greatest number of associations and the strongest associations. Moreover, these mothers and their offspring had close associations over multiple generations. Also, relationships were stronger among mothers and female offspring than mothers and male offspring.

Group coordination requires group decisions that can vary between two extremes: decisions made democratically, where a majority of individuals decides, and decisions made despotically, where a dominant member of the group decides. I hypothesized bison make decisions despotically and democratically, depending on activity. I observed behavior in a group of bison that originated from 15 cows and 2 bulls born in 2001. They were weaned in the fall of 2001, fitted with individual ear tags, and then moved to a part of the Armendaris Ranch separate from the main herd. Since their relocation, they have been managed without intervention. The original adults (RTC, red tag cows) can still be identified as a group by their red ear tags. This group numbered approximately 93 individuals, depending on the year of my study, and the offspring in this group were all related to the original 15 females and 2 males. I observed this group of bison from sunup to sundown for 4 days during each of the 6 trips to the field from May 2008 to September 2009. All animals occurred in one cohesive group that I followed until a rest period occurred. I examined movement initiation and direction following rest periods. During rest periods, I recorded individual female activity, location, age class, and compass bearing of the body axis. I assumed compass bearing was an expression of preferred direction. For direction of movement, RTC repeatedly made decisions despotically for the group; in 93% recorded choices, group directions were chosen by these individuals. These directions were significantly different from directions chosen by other group members in over half of the decisions. For movement initiation, bison used a more democratic decision-making process; group movements did not begin until an average of 47% of adult cows exited the group and waited for the near majority before moving. Interestingly, the oldest females led this final movement behavior in 81% of the decisions, again verifying their importance in the decision-making process.

Presumably, living in properly functioning social groups has many benefits, among them reduced stress on individuals. However, little is known about how management practices that disrupt social organization affect individuals. In the United States, male bison are typically weaned and placed in feedlots at a time when they would ordinarily be moving from matrilines into small bachelor groups. I assessed levels of stress for males under tight vs. loose confinement in feedlots and compared their levels of stress with males that remained under free-ranging conditions. I hypothesized levels of stress would increase as confinement size decreased and animal density increased. To examine this hypothesis, yearling bison males were weaned and placed in either tight (TC) or loose (LC) confinement. The free-ranging group (FR) was composed of males weaned from their mothers and then returned to the herd under free-ranging conditions. I measured fecal cortisol metabolites (FCM) as an index of stress. I calculated a pre-trial FCM baseline from samples taken prior calves being placed in confinement. Subsequently, fecal samples were collected from 20 different individuals in each group every 2 weeks. Fecal cortisol levels were lowest for FR (23 ng/g DM), intermediate for LC (39 ng/g DM), and highest for TC (63 ng/g DM; $P<0.0001$).

Collectively, these results support the hypothesis that bison live in extended families of mothers and their daughters. In my studies, as young males aged, they spent less time in extended families and more time in small bachelor groups. Older females strongly influenced the direction of group movements across landscapes, but bison used a more democratic decision-making process for initiation of movement than for direction choices. Finally, disruption of social organization due to confinement in large groups in drylots greatly increased stress in young male bison compared with allowing them to free-range.

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Finally, last but certainly not least, I acknowledge my wife, Elizabeth, and our troupe of girls. Thank you all for your endless support. It certainly wasn’t easy, but it was possible because of your selfless support and love. You let me chase my dreams, in this case literally, and for that and everything else, I love you.

Ryan Shaw

DEDICATION

To Samantha and Macie, thank you for teaching me the importance of the journey while not losing track of the destination.

And for making sure buffalo round-up had nothing on the adventure found walking through my own front door.

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CHAPTER 1

SOCIAL ORGANIZATION IN BISON

The influence of physical and social environments on the evolution and behavior of animals has long interested both researchers and managers (Flannery 2001). While many factors influence ungulates, including the availability of resources and predators, much research has focused on top-down influences on populations. Great emphasis is placed in landscape ecology on how the spatial structure and arrangements of habitats affect ecological patterns and processes (Bissonette & Storch 2003). In these attempts to understand evolution and behavior, the social environment -- and the role of the individual in it -- is only rarely considered and is viewed mostly as a factor modulated by biophysical and biochemical processes. This is unfortunate because social organization, behavior, and culture help explain why animals of the same species behave differently, even though they live in the same environments, and how animals of the same species can survive in environments that differ markedly in resources and predators (Provenza 1995b). Social behaviors lead to cultures that result in large individual variation in social and individual behaviors and demographic rates (Andersen 1991; Cam et al. 2002). Social interactions arising from individual behaviors cause population-level phenomena to vary in form and function (Lima & Zollner 1996; Sutherland 1996; Croft et al. 2008).

SOCIAL ORGANIZATION IN BISON

Herbivores display a wide range of organization from solitary to highly social (Wilson 1975). Social groups are comprised of non-random associations of related or unrelated individuals, which make them interesting evolutionarily, genetically, and behaviorally (Melnick 1987; Melnick et al. 1984; Uyenoyama & Feldman 1981). In polygynous mammals, social groups are typically composed of closely related philopatric females and their offspring and dispersal is male-based (Greenwood 1980; Dobson 1982). Retention of daughters within the maternal home range and male-based dispersal form the basis of sociality in many mammalian species (Armitage 1981). Social organization and fidelity to a landscape lead to culture, the collective knowledge and habits passed from one generation to the next about how to survive in a particular environment (De Waal 2001). A culture develops when practices that originate this way contribute to the group's success in solving problems, and cultures evolve as individuals in groups discover new ways of behaving -- as with finding new foods or habitats or better ways to select a nutritionally balanced diet (Skinner 1981).

Extended Families

Long-term mother-daughter associations lead to philopatric matrilines in species such as red deer (*Cervus elaphas*, Clutton-Brock et al. 1982), African elephants (*Loxodonta africana,* Douglas-Hamilton 1973; Moss & Poole 1983), and white-tailed deer (*Odocoileus virginianus*, Aycrigg & Porter 1997). The 4-year studies of bighorn sheep (*Ovis Canadensis*, Festa-Bianchet 1986), the 5-year studies of zebu cattle (*Bos primigenius*, Reinhardt & Reinhardt 1981), and the 14-year studies of water buffalo (*Bubalus bubalis*, Tulloch 1978) all indicate these animals live in extended matrilineal families.

With bison, however, the notion of philopatric matrilines is controversial. Ancestors of present-day Indians honored the social order they saw in bison by integrating it into their tribal organization. Buffalo hunters used social organization as the basis for successful hunting, and contrary to popular beliefs, their accounts state bison did not occur in vast herds; rather, they lived in matriarchal families of 10 to 25 animals in the arid southwest and 60 to 75 animals in the more fertile plains (Mayer & Roth 1995). In the 1870s, Colonel Dodge noted that only when amongst the huge herds did one realize they were actually comprised numerous smaller groups (Hornaday 1889). Some more recent observers also thought bison lived in extended families (Seton 1929; Soper 1941), but others felt kinship had little influence on group formation (McHugh 1958).

Research on social organization in bison is also equivocal. Some contend bison live in unstable groups of randomly associated individuals (Lott & Minta 1983; Van Vuren 1983), whereas others maintain bison live in stable groups of related individuals (Green et al. 1989; Brookshier 2000; Brookshier & Fairbanks 2003). Differences in methods of study and in bison-landscape interactions may help to account for these discrepancies. Some studies were inconclusive due to small sample sizes (3 pairs: see critique of Lott & Minta 1983 in Green et al. 1989), or biased due to the use of older, more recognizable mothers (see critique of Van Vuren 1983 in Green et al. 1989). More in-depth studies of associations among females and their offspring show extensive post-weaning associations between mothers and daughters (Green et al. 1989; Shaw & Carter 1990; Brookshier & Fairbanks 2003).

Differences in physical environments may influence social organization in bison. Stable groups of bison were not observed in steep, narrow canyons (Lott & Minta 1983) or forests (Van Vuren 1983), but they were observed in more open grasslands (Green et al. 1989). Lack of resources may encourage formation of smaller groups of individuals with similar nutritional needs (Lott & Minta 1983). Conversely, more open habitats with ample resources may support larger groups of bison (Shackleton 1968; Van Vuren 1983; Rutberg 1984), which may favor evolution of extended families. Differences in habitat preferences between females with or without calves, whether from limited ability to move long distances, threats of predation, or nutrient requirements, may also influence social organization in bison. African and Asian elephants that live in dense forests develop a more limited social organization that includes reduced group cohesion and less extensive family relationships compared with those that occupy more open habitats (Vidya & Sukumar 2005). While the ecological determinants for these differences are poorly understood, some believe forage availability and quality, social requirements, and threats of predation may help account for the differences (Vidya & Sukumar 2005).

Implications of Social Organization for use of Landscapes

People have stressed the importance of rotational grazing in managing livestock with the use of fences (Savory & Butterfield 1999; Gerrish 2004), but people have not thought about how social organization might cause rotational grazing in herbivores. Social organization may affect foraging behavior and lead to short-duration grazing without fences (Provenza 2003b). This notion is based on three assumptions: 1) social herbivores live in stable, cohesive groups, 2) maintaining the cohesiveness of these groups and their home ranges influences food and habitat selection, and 3) individuals within groups differ in their preferences for foods and habitats. If so, social interactions within groups may encourage animals to eat a broader array of plants and to forage in a greater variety of locations as individuals maintain group cohesion and respond to different preferences of individuals within the group by moving about a landscape. Interactions among extended families may further increase movements about landscapes as families avoid prolonged contact with one another by selecting spatially and temporally segregated foraging locations. Undoubtedly, there are critical densities of groups above which interactions can create rotational grazing without fences, but below which interactions are too few to create among-group dynamics. To date, classical theory and models make no attempt to address the behavioral complexities of diet and habitat selection under such conditions and there is no empirical data on the matter (Giraldeau & Caraco 2000, p. 331), despite its relevance to sustainable herbivore production and ecosystem management.

In sheep and cattle, social interactions within groups encourage animals to eat a broader array of foods (Scott et al. 1995), and to forage in a greater variety of locations (Howery et al. 1998), as individuals maintain the cohesiveness of the group and respond to ever-changing preferences of individuals within the group. Differences exist in how individuals are built morphologically and how they function physiologically, even within uniform groups, and marked variation is common even among closely related animals in needs for nutrients and abilities to cope with toxins (Provenza 2003b). Moreover, primary and secondary compounds in all foods cause animals to satiate, and excesses of nutrients, nutrient imbalances, and excess secondary compounds all limit food intake unless animals can eat a variety of foods (Freeland & Janzen 1974; Provenza 1995a, 1996; Critchley & Rolls 1996). The ability to choose among alternative forages best enables each individual to meet needs for nutrients, balance intake of different nutrients and toxins, and obtain medicinal benefits from lower doses of plant secondary compounds that at too high levels are toxic (Engel 2002; Burritt & Provenza 2000; Provenza 2003a). To do so, groups must move in ways that enable individuals to choose from an array of different forages to meet needs of individuals. Such socially and biochemically mediated interactions link cells, organs, individuals and social groups with landscapes (Provenza et al. 2011).

With increasing animal density, foraging in groups also may affect group interactions. With livestock, grazing at low stock densities can encourage selective grazing -- eat the best, leave the rest, and stay put -- inadvertently diminishing biodiversity and increasing less desirable plant species. Conversely, short-duration and management-intensive grazing at high stock densities can encourage animals to mix the best with the rest and move (Provenza 2003a,b). When herbivores learn to eat only the most preferred plants, they are not likely to learn to mix foods high in nutrients with foods that contain secondary compounds, whereas herbivores encouraged to eat all plants in an area are more likely to learn to eat mixes of plants that enhance nutrition and mitigate toxicity (Shaw et al. 2005, 2006). Such learned patterns of behavior are transmitted from mothers to their offspring (Thorhallsdottir et al. 1990; Mirza & Provenza 1990, 1992; Biquand & Biquand-Guyot 1992; Provenza 1994, 1995b; Wiedmeier et al. 2002), thereby creating a mechanism for social organization to affect patterns of landscape use.

In addition to the dynamics generated by interactions within stable cohesive groups, interactions among groups may cause bison to roam as groups maintain their unique identities by moving to avoid prolonged contact with other groups. Subgroups of free-ranging cattle (Lazo 1994), sheep (Hunter & Milner 1963), white-tailed deer (Hawkins & Montgomery 1969), and elephants (McComb et al. 2001) rarely integrate socially and typically remain spatially segregated. In feral cattle, the greater the size of a subgroup, and the poorer the quality of a subgroup's home range, the larger the size of the home range (Lazo 1995). When inter-group interactions occur, they are largely a passive process in which dominant groups displace subordinate groups, but high-ranking sub-groups can actively occupy preferred habitats and utilize preferred resources, and competition intensifies as the availability of resources diminishes (Mosley 1999).

From this, one could conclude that dominant groups would monopolize the “best” foods and habitats. However, the dynamics created by within-group social interactions described above -- individuality in food and habitat preferences, satiation on foods and habitats, high stock densities -- may instead cause stable groups to roam within their home range, rather than to monopolize resources. If maintaining group identity is important, groups may not set up home ranges in areas where they will encounter continual disruptions. If remaining with the group is more important to an individual than eating the “best” forage, then moving as a group is likely to mitigate the negative impact on “preferred” locations such as riparian areas.

DECISION MAKING IN GROUPS

In social species, group stability is compromised if members do not behave in unison and the advantages of group living are lost if decisions made by individuals do not scale up to group behaviors (Krause & Ruxton 2002; Couzin 2006). For group living to be sustainable, the group must benefit the individual, which in turn benefits the group.

Group living means some individuals may at times sacrifice their preferences for those of the group, but in general the benefits for the individual must outweigh the costs (Meunier et al. 2006). Group members often have conflicting motivations such as forage choices, activity patterns, or social agendas that force individuals to compromise their personal interests for those of the group. These choices may lead to additional costs if individual needs differ greatly from those of the group (Prins 1996; Conradt & Roper 2003). With respect to group movement, group stability is compromised if members chose different directions and the advantages associated with group living are lost (Terborgh, 1983; Sterck et al. 1997; Weimerskirch et al. 2001; Krause & Ruxton 2002).

Nonetheless, group stability and cohesion can remain intact as groups move across landscapes (Stewart & Harcourt 1994; Boinski & Campbell 1996; Boinski 2000; Byrne 2000; Parrish et al. 2002; Conradt & Roper 2003), particularly if the group moves across landscapes in ways that meet the nutritional needs of all of the individuals in the group, as discussed above (Provenza 2003a). If so, common decisions with regard to when and where to move can be reached by a collection of individual decisions among groups of animals throughout the day (Conradt & Roper 2005; Meunier et al. 2006). Decisions made collectively throughout the day enable group members to meet individual needs while maintaining the advantages associated with group membership.

Herders in France meet the needs of individual animals and fully use the range of plants in landscapes by moving livestock in grazing circuits designed to satisfy each animal's appetite for different nutrients and to regulate its intake of different secondary compounds (Meuret 2010). Social organization, whether in wild or domesticated herbivores, can enable individuality if species that live in groups forage in grazing circuits that enable individuals to meet their needs for nutrients and regulate their intake of secondary compounds as they move about the landscape each day (Provenza 2003a).

Various mechanisms are available for reaching decisions within groups. Two extremes are decisions made: 1) despotically, where one dominant animal decides, and 2) democratically, where a majority of group members decides (Conradt & Roper 2003; List

2004). On the one hand, mountain gorillas (Schaller 1967), horses (Waring 1983), and dwarf mongooses (Rasa 1987) behave despotically. On the other hand, African buffalo behave democratically: cows orientate in the direction they favor during periods of rest prior to movement, showing the direction of movement they favor and intentionally recruiting others (Prins 1996). Unfortunately, few studies have been conducted of decision-making processes in other animals and we do not know the degree to which animals within a social group may respond either despotically or democratically or both ways depending upon specific circumstances (Conradt & Roper 2005).

Decision making processes are influenced by group stability (Overdorff et al. 2005). The potential for despotism increases with stable relationships among individuals, as stability enables specific individuals to dominate group choices (Vehrencamp 1983; Chase et al. 2002; Beacham 2003; Robbins et al. 2005). Alternatively, the potential for democratic decision making increases when groups are characterized by fluid and relatively unstable relationships. The lack of stability allows individuals with the greatest immediate needs to influence group choice (Rands et al. 2003; Fischhoff et al. 2007). Ever-changing needs among individuals within a group -- influenced by nutrition and health due to differences in morphology and physiology among same-age/sex individuals within a group, as well as those related to differences in age, sex and reproductive status among individuals in the group (Fischoff et al. 2007) -- diminish the influence of any one individual on the behavior of the group and hence diminish the emergence of consistent leaders (Beacham 2003; Rands et al. 2003; Overdorff et al. 2005; Fischoff et al. 2007). While the fitness consequences of decision making are largely untested in the field, theoretical analyses suggest democratic decisions are more beneficial than despotic decisions as they can lead to more inclusive decisions (Conradt & Roper 2003).

FISSION AND FUSION SOCIAL BEHAVIORS

Many animal populations, including ungulates, primates, and cetaceans (Lott & Minta 1983; Whitehead et al. 1991; Henzi et al. 1997; Christal et al. 1998; Chilvers & Corkeron 2002), are classified as fission–fusion societies in which groups form and separate over time due to social interactions linked in part to the availability of resources (Cross et al. 2005). Fission-fusion societies exist along a continuum from highly fragmented groups where individuals move among groups at any time (Gittleman et al. 1989; Rodseth et al. 1991), to highly stable sub-groups that combine with other sub-groups such that groups, rather than individuals, control the fission-fusion process (Cross et al. 2005; Whittemyer et al. 2005). While some emphasize the importance of kinship in sub-group formation during fission-fusion episodes specifically and social organization generally (Douglas-Hamilton 1973; Moss & Poole 1983; Cross et al. 2005), others call attention to the importance of habitat structure and resource availability on fission-fusion processes (Wittemeyer et al. 2005; Fortin & Fortin 2009). Both are important.

The benefits derived from the propagation of kin by related individuals within extended families are a powerful force influencing social organization (Hamilton 1964; Emlen 1995). The amount of time relatives spend together influences how much time is available for kin selection to influence social behavior (Hamilton 1964; Maynard-Smith 1964; West-Eberhand 1975). Kin selection, however, is not the only force influencing social organization (Harcourt 1992). Fission-fusion societies are often composed of unrelated individuals that still reap the benefits of sociality (Archie et al. 2006). The benefits of sociality for related and unrelated individuals include obtaining protection from predators, enhancing reproductive success, learning traditional migratory routes, and knowledge of feeding sites and mineral licks to name a few.

While the formation of discreet groups of related or unrelated individuals is common (Greenwood 1980), resource availability also influences social organization (Wrangham et al. 1993; Chapman et al. 1995). The size and composition of social groups in fission-fusion societies is influenced by the availability of food, water, and cover (Devore & Washburn 1963; Kummer 1968; Wittemyer et al. 2005). In the short term, social groups typically aggregate into larger groups during times of resource abundance and segregate into smaller groups during times of resource scarcity. Over the longer term, resource availability within a home range influences group size and composition, and the lack of resources and agreement of individuals within a group on use of those resources may lead to the fission of groups into smaller sub-groups of related or unrelated individuals.

SOCIAL ORGANIZATION AND STRESS

Wild and domestic animals encounter a wide array of environmental and behavioral conditions that can threaten their survival. These varying ecological and social conditions often induce stress, leading to a surge of neurological, hormonal, and immunological responses within the animal (Sapolsky 1992). This cascade of responses, initiated by the introduction of stressors, starts with the activation of the hypothalamic-pituitary-adrenal (HPA) axis and the subsequent release of glucocorticoids (GCs; Sapolsky 1992; Wingfield et al. 1998; Koolhaas et al. 1999).

Physiological reactions to a disruption in homeostasis are characterized by a marked increase in GCs, which alter metabolic pathways aiding ATP production (Sapolsky 2002;

Mooring et al. 2006). This extra energy can enable survival by elevating heart rate, blood pressure, and breathing at times when these responses are necessary for endurance (Abbott et al. 2003; Muller & Wrangham 2004). However, the persistence of high levels of GCs for extended periods turns short-term benefits into long-term pathologies (Creel 2001; Wingfield & Sapolsky 2003).

People are increasingly appreciating the importance of stress in adversely affecting the behavior, well-being, and performance of domestic and wild animals. Disrupting social relationships increases stress. Forced weaning elevates stress in mothers and their offspring (Carter 1998; Gunnar 2000). Post-weaning interactions involving social organization and animal density are also potential sources of chronic stress. While bison males disperse into smaller bachelor groups after natural weaning, they typically are put in feedlots under crowded conditions in commercial bison operations. Aggressive interactions among members of gregarious species can be a source of chronic stress (Sands & Creel 2004), as can dominance rank though the nature of these relationships is unclear occurring at some times in some species but not in others (Holekamp & Smale 1998; Goymann et al. 2003; Muller & Wrangham 2004; Sannen et al. 2004).

Competition for food in feedlots can increase aggression, avoidance, and intimidation behaviors, ultimately increasing stress (Miller & Wood-Gush 1991), and decreasing production (Huzzey et al. 2006; González et al. 2008). Competition for food increases eating rate and decreases eating time which limit the body’s ability to manage digestive functions (González et al. 2008b), and increase rumen acidosis and liver abscesses (Stone 2004; Krause & Oetzel 2006). Collectively, all these factors decrease animal welfare and performance (Britton & Stock 1989; Schwartzkopf-Genswein et al. 2003).

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CHAPTER 2

OBJECTIVES AND GENERAL APPROACH

My objectives were to determine the degree to which: 1) female bison with and without forcibly weaned calves formed stable groups of related individuals, 2) the initiation and direction of movement following a rest period were despotic or democratic in bison, and 3) different types of confinement induced stress in yearling male bison. These objectives were addressed through three field studies.

MOTHER-DAUGHTER ASSOCIATIONS

In the first study, I investigated the influence of weaning on the formation of long-term mother-daughter associations and its implications on group composition and stability in bison. The treatment consisted of 25 adult female mothers paired with their female calves. Treatment mothers and daughters were fitted with unique ear tags and colored leather collars to facilitate in-field identification. The adult female control animals were randomly chosen and identified by ear tags and fitted with colored leather collars. Control animals had their calves removed from the herd during the weaning process.

Data were collected during eight periods: spring, summer, and fall of 2007 and 2008 and in the spring and fall of 2009. During each season, treatment and control animals were individually located a minimum of 3 times in the field with some animals located as many as 7 times. On encounter, group composition was recorded, including ages, genders, and individual identification (collars and ear tag numbers). Animals were considered part of the group when they were within 100m of one another. When large congregations consisting of multiple groups were together at waterholes, data were taken only when groups moved and acquired spatial autonomy.

DECISION MAKING

In the second study, I investigated the degree to which individual mature female bison made decisions regarding initiation and direction of group movement after resting or whether the decision was made by a consensus of individuals within the group. Data were collected from sunup to sundown for 4 days during each of the 6 trips to the field from May 2008 to September 2009. All animals occurred in one cohesive group, and I followed the group until a rest period occurred. A rest period, defined as at least half of the adult females lying down, continued until all group members were again up and engaged in a post-rest period behavior that involved choice of direction and behaviors such as foraging, traveling, and drinking.

During group rest periods, data were collected for animals within the group and those outside the group every 10 min using scan sampling (Altman 1974). Data collected included individual animal activity (laying or standing), location (within or outside group), age classes (juvenile- 2 years and younger; adult- adults without ear tags; and the original adult cows with distinctive red ear tags (RTC) from which the rest of the herd originated), and compass bearings of the body axis of adults and RTC adults. Compass bearings of the body axis of standing female adults and RTC individuals were considered an expression of preferred direction choices or individual “votes” (Prins 1996). This information allowed me to identify individuals possibly responsible for initiating movement and making direction choices. Finally, both pre- and post-rest period behavior as well as wind direction, was recorded.

INFLUENCE OF TYPE OF CONFINEMENT ON STRESS

In the final study, I determined if the production and excretion of fecal cortisol metabolites (FCM) was influenced by different types of confinement. Yearling bison males were weaned and separated into either the tight confinement treatment or the loose confinement treatment. The tight confinement group was composed of 90 yearling males while the loose confinement group had 100. The control group was composed of weaned yearling males left in free-ranging conditions in a mixed-age-and-sex herd composed of small groups that collectively totaled 599 animals.

Fecal samples were collected from the treatment and control animals every 2 weeks beginning January 15th 2009 and ending on April 30th 2009. Baseline FCM levels were established with the aid of 20 pre-study samples collected in November 2008. Twenty samples were collected from each group during each sampling period. As tight and loose confinement groups were composed only of treatment animals, samples were collected by locating and collecting fresh fecal matter. For free-ranging bulls, fecal samples were collected by finding yearling bulls and following them until defecation occurred and a fecal sample could be collected.

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CHAPTER 3

MOTHER-DAUGHTER ASSOCIATIONS IN BISON INFLUENCED BY WEANING[1]

ABSTRACT

Social organization among herbivores varies widely, depending on resource availability, habitat structure, and kinship. The level of social organization in bison is widely debated due to the ambiguous and confounding nature of most studies as they relate to resource availability, habitat structure, and kinship. With regard to the latter, some believe bison live in extended families, while others believe their social interactions occur randomly. I hypothesized that when mother-daughter relationships are allowed to develop, bison form long-term associations of related individuals. In this study, which occurred from 2007 through 2009, 25 treatment mothers were randomly selected from a free-ranging herd and kept together with their calves, while 25 control females had their calves forcibly removed, a typical practice for this and most other bison operations in the United States. This study was conducted on the privately owned Armendaris Ranch in Sierra County, NM. The ranch is 145,600 ha and has been owned and operated by Turner Enterprises since 1993. Animals were located during the spring, summer, and fall each year. On encounter, I recorded group composition, including ages, genders, and group member identification. Treatment mothers and offspring had a greater percentage of individuals with a half weight index (HWI) > 0.50, and the strongest associations (HWI> 0.31) were among treatment mothers and their offspring. The HWI is a measure of the amount of time two bison were observed together as a proportion of the total number of

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[1] Coauthored by Ryan A. Shaw, Fredrick D. Provenza, Kym Patison, and Dave Swain

times each animal was sighted within the sampling period. Further analysis revealed treatment mothers and their offspring had close associations over multiple generations. 5Relationships were stronger between mothers and female offspring than mothers and male offspring. At HWI > 0.50, there were more mother-female than mother-male offspring relationships: of 27 prominent kin relationships, only 5 involved males. In summary, my findings are consistent with the hypothesis that bison form long-term associations of related individuals when calves are not weaned and sold. Management practices influence the composition, cohesion, and productivity of social groups. As with domesticated livestock, bison managers typically remove older females that no longer produce offspring. The consequences for well-being and production of removing matriarchs and disrupting extended families are just now being appreciated by people who manage wild populations. The consequences of removing matriarchs for wild and domesticated animals are likely to be increasingly severe where animals must fend for themselves in ever harsher environments.

INTRODUCTION

The influence of biophysical environments on the evolution of animal behavior has long interested researchers and managers (Flannery 2001). While theories concerning the relationship between ecology and social behavior suggest large ruminants should be gregarious (Geist 1974; Jarman 1974), social organization varies due to habitat structure, food availability, predation risk and reproductive behavior (Lott 1989; Lazo 1994). Researchers place great emphasis on biophysical environments, but the social environment, and the role of the individual in it, is rarely considered or is viewed as a by-product of physical and biochemical processes. This is unfortunate because social organization and culture help explain why and how animals of the same species survive 55in markedly different environments, subsist on radically different diets, and behave differently even in the same environment (Provenza 1995b; Provenza et al. 2011).

Herbivores display a wide range of social organizations from solitary to highly social (Wilson 1975). In social species, the stability of groups varies by species. Stable associations among related females occur in water buffalo (Tulloch 1978), zebu cattle (Reinhardt & Reinhardt 1981), feral cattle (Lazo 1994), and domestic sheep (Hunter & Milner 1963), whereas unstable groups occur in species such as gaur (Schaller 1967). In polygynous mammals, social groups often are composed of closely related philopatric females (Greenwood 1980; Dobson 1982). Retention of daughters and young sons within the maternal home range, along with dispersal of older males, is the essence of sociality in many mammalian species (Armitage 1981). Long-term mother-daughter associations lead to philopatric matrilines, in red deer (Clutton-Brock et al. 1982), African elephants (Douglas-Hamilton 1973; Moss & Poole 1983), and white-tailed deer (Aycrigg & Porter 1997). The 4-year studies of bighorn sheep (Festa-Bianchet 1986), the 5-year studies of zebu cattle (Reinhardt & Reinhardt 1981), and the 15-year studies of water buffalo (Tulloch 1978) also suggest matrilines. Kinship is a primary determinant of sociality in elephants (Archie et al. 2006), and the matriarch, who is often the oldest adult female in the family, plays a critical role in the matriline (Vidya & Sukumar 2005). Elephant groups led by older more experienced matriarchs have a higher degree of reproductive success than groups led by younger matriarchs; older females' stature and knowledge of the biophysical and social environments benefits members of the group, thereby enhancing long-term survival and reproduction (Vidya & Sukumar 2005). Domestic animals learn and remember social companions and numerous vital landscape characteristics (add references). While we know little about how well wild animals learn and remember social companions and numerous vital landscape characteristics, the role of the matriarch as a repository of information is vitally important (McComb et al. 2001, Vidya & Sukumar 2005).

Along this spectrum of solitary to highly social, many ungulates, primates, and cetaceans can be classified as fission-fusion societies, whereby groups form and separate over time (Cross et al. 2005; Whitehead et al. 1991; Henzi et al. 1997; Christal et al. 1998; Chilvers & Corkeron 2002). The most complex are classified as flexible fission-fusion societies with a hierarchical structure (Kummer 1995; Conner 2000; Wittemyer et al. 2005). They consist of stable social units that change in size and composition frequently over time as individuals join (fusion) and break away (fission) from other stable subgroups belonging to the larger social unit (Wittemyer et al. 2005). Fission-fusion societies exist along a continuum. At one extreme, individuals are free to move among groups at any time; at the other, individuals only move among groups as a member of a subgroup without any one individual controlling the fission-fusion process (Cross et al. 2005). Such societies limit within-group competition through fission events during periods of high competition for resources (Dunbar 1992; Kummer 1995); conversely, they enhance cooperative through fusion events when resources are abundant (Takahata et al. 1994; van Schaik 1999). While some emphasize the importance of habitat structure and resource availability on fission-fusion processes (Wittemeyer et al. 2005; Fortin & Fortin 2009), others call attention to the importance of kinship in sub-group formation during fission-fusion episodes specifically and social organization more generally (Douglas-Hamilton 1973; Moss & Poole 1983; Cross et al. 2005).

With bison, for reasons noted above, the notion of group stability is controversial. Buffalo hunters used social organization and the influence of the matriarch on group dynamics as the basis for successful hunting during the 1800s (Mayer & Roth 1995). While some more recent observers thought bison lived in extended families (Seton 1929; Soper 1941), others felt kinship had little influence on group formation (McHugh 1958). Research on bison is also equivocal. Some contend bison live in unstable groups of randomly associated individuals (Lott & Minta 1983; Van Vuren 1983), whereas others maintain bison live in stable groups of related individuals (Green et al. 1989; Brookshier 2000; Brookshier & Fairbanks 2003).

Given these controversies, my objective was to determine the degree to which bison with and without forcibly removed calves formed stable groups composed of related individuals. I was interested in whether long-term mother-daughter associations formed when female calves were not removed from the herd. I hypothesized that when long-term mother-daughter relationships were allowed to form, mothers and their offspring would spend more time together, leading to the formation of groups composed of related individuals. Based on this hypothesis I predicted that mothers and their related female offspring would be in the same groups more often than allocated by chance.

STUDY AREA

This study was conducted on the privately owned Armendaris ranch in Sierra County, NM, a former land grant now managed by Turner Enterprises. The ranch is 145,600 ha and has been owned and operated by Turner Enterprises since 1993. The climate is warm-temperate, with an average of 213 frost-free days per year recorded for nearby

Truth or Consequences, NM. The mean annual precipitation is 250 mm. Approximately 105,220 ha of the ranch are classified as semi-desert grassland (Brown 1994) characterized by grasses and shrubs such as black grama (*Bouteloua eriopoda*), palmilla (*Yucca elata*), and Mormon tea (*Ephedra torreyana*). Most of the remaining vegetation is classified as Chihuahuan desert scrub, which is composed of shrubs such as mesquite (*Prosopis spp.*), saltbrush (*Atriplex spp*.), and creosote bush (*Larrea tridentate*).

Bison (*Bison bison*) and other wild herbivores including gemsbok (*Oryx gazella*), mule deer (*Odocoileus hemionus*), desert bighorn sheep (*Ovis canadensis*), and pronghorn antelope (*Antilocapra americana*) are the only permitted grazing animals. Bison were introduced to the ranch in 1993 and they currently number approximately 900 females and 150 males. Other than during the annual roundup in January, when the calves are weaned and the females are tested for pregnancy, the bison are managed without intervention.

METHODS

I hypothesized that if long-term relationships developed, bison would form mother-daughter lineages or matrilines and these mother-daughter relationships would persist beyond natural weaning. To test this hypothesis, 25 mothers with female calves were located and marked in the field in December 2006. Pairs were chosen at random from groups scattered around the ranch. While mothers were identified by unique ear tags, calves were marked with oil-based paintballs to facilitate recognition of treatment animals during roundup. All identified mother-daughter treatment pairs were moved through the entire roundup process together in January 2007 to ensure no prolonged separation occurred. Each calf was given a unique ear tag during this process while mothers were fitted with a yellow leather collar to facilitate in-field identification of mothers and calves. Following roundup, treatment pairs were held together as a group for 2 days to allow me to verify that all 25 calves were still strongly paired with their respective mothers; the group was then released and allowed to roam with the rest of the herd throughout the year.

I also identified 25 control animals. The controls allowed me to evaluate fidelity of individuals to a group, without the presence of related offspring, and to compare their fidelity with that of mothers and their offspring. The 25 control animals were chosen during the same roundup. Every 20th female that came through the squeeze chute was identified by ear tag and fit with a green leather collar. The calves of control females were weaned and sold.

In December 2007 treatment animals were again located in the field and their current year's calves, which lacked any type of permanent identification, were marked with oil-based paintballs. During January 2008 roundup, mothers and marked calves were again kept together. In 2007, 20 of the 25 treatment adult females produced offspring. Following their release from this roundup the treatment group consisted of 25 adult females, 20 yearling heifers, 9 female calves and 11 male calves. Calves were weaned from the 25 control animals as in the previous year.

Data Collection

Data were collected during eight periods: spring, summer, and fall of 2007 and 2008 and in the spring and fall of 2009. During each season both treatment and control animals were located a minimum of 3 times in the field with some animals located as many as 7 times. On encounter, group composition was recorded, including ages, genders, individual identification (collars and ear tag numbers), as was the group's general location. Animals were considered part of the group when they were within 100m of other group members (Archie et al. 2006). When large congregations consisting of multiple groups were together at waterholes, I recorded data only when a group containing a target individual broke away and remained spatially autonomous.

Data Analysis

Before I conducted analyses of associations, the data were first summarized and then restricted to include only adults observed in every season over the 3 years. All treatment offspring were included in the analyses. The resultant data are shown in Table 1.

Table 1
Descriptive information on the number of observations and the portion of the population analysed seasonally each year.

Sample of population:				
	No. observations all treatments	**Treatment mothers: Treatment offspring**	**Control mothers: Treatment offspring**	**Treatment mothers: Control mothers**
Total:	137	78	78	52
Per treatment:				
No treatment	33			
Control mothers	26		26	26
Treatment mothers	26	26		26
Treatment offspring	52	52	52	
Total:	2620	1392	1376	1456
Per season per year:				
Spring 2007	355	180	175	199
Summer 2007	327	169	165	206
Fall 2007	318	161	166	195
Spring 2008	368	213	209	184
Summer 2008	315	184	180	168
Fall 2008	317	172	172	172
Spring 2009	325	167	166	173
Fall 2009	295	146	143	159

To investigate associations among individuals and group composition, I calculated association indices for each pair of animals. Specifically, the analyses focused on the differences in association between 1) treatment mothers and their offspring, 2) control mothers and treatment offspring, and 3) treatment mothers and control mothers. Finally, I also recorded the number of groups and their size observed in each season to identify seasonal trends in fidelity of individuals to groups within years.

To calculate the association indices for each pair of animals, I used a computer program called SOCPROG 2.4 designed specifically to analyse animal associations (Whitehead 2009). Observational data from excel were imported into SCORPROG based on season, group identification, and animal identification. A supplementary excel file containing data on the age, origin (location of birth), gender and treatment category of each individual was also imported into SOCPROG. The data were collected on a seasonal basis each year (sampling period) and restricted to allow analyses of two separate groups within the population at one time: treatment mothers and their offspring, control mothers and offspring of treatment mothers, and treatment mothers and control mothers.

Associations between individuals were calculated using the half weight index (HWI). The HWI provides a measure of the amount of time two bison were observed together as a proportion of the total number of times each animal was sighted within the sampling period. The HWI values range from 0 (two individuals never seen together) to 1 (two individuals always seen together). To compare associations between the three treatment comparisons, HWI values were divided into 10 categories and the total numbers of associations per category were expressed as a percent of the total associations per comparison. To visualise the association networks between female bison and offspring within the population, the HWI for each pair of individuals in the restricted populations was imported into NETDRAW (Borgatti 2002). Based on the distributions of association indices between treatments, only HWI ≥ 0.50 were displayed in the network diagrams. The 0.50 value was chosen to accent strength of associations, as only 5% of bison had HWI ≥ 0.50.

RESULTS

The number of groups identified per season and the average group size per season is shown in Table 2. Over all 3 years, the greatest number of sightings of groups occurred during spring. The average number of bison per group (±s.d.) varied between seasons, ranging from a minimum of 11.7 ± 5.4 in summer of 2007 to a maximum of 17.6 ± 7.3 in spring of 2008 (Table 2). The distributions presented in Figure 1 show the differences between the numbers of individuals sighted per group each season.

Table 2
The number of groups of bison and the average group size (± s.d.) observed in spring (March and April), summer (July and August), and fall (October and November) from 2007 to 2009.

Season		Number of groups	Mean group size
Spring	2007	120	15 (6)
Summer	2007	107	12 (5)
Fall	2007	86	15 (5)
Spring	2008	94	18 (7)
Summer	2008	75	15 (6)
Fall	2008	84	17 (6)
Spring	2009	77	16 (7)
Fall	2009	77	16 (7)

Association Indices

Bison associations varied by group. The strongest associations were among treatment mothers and their offspring (HWI > 0.31). Treatment mothers and their offspring had the greatest number of associations with a HWI > 0.50. Control mothers and treatment offspring had only 2 associations with an HWI > 0.50 (Fig. 3). Treatment and control mothers had the weakest association (HWI from 0.21 to 0.30).

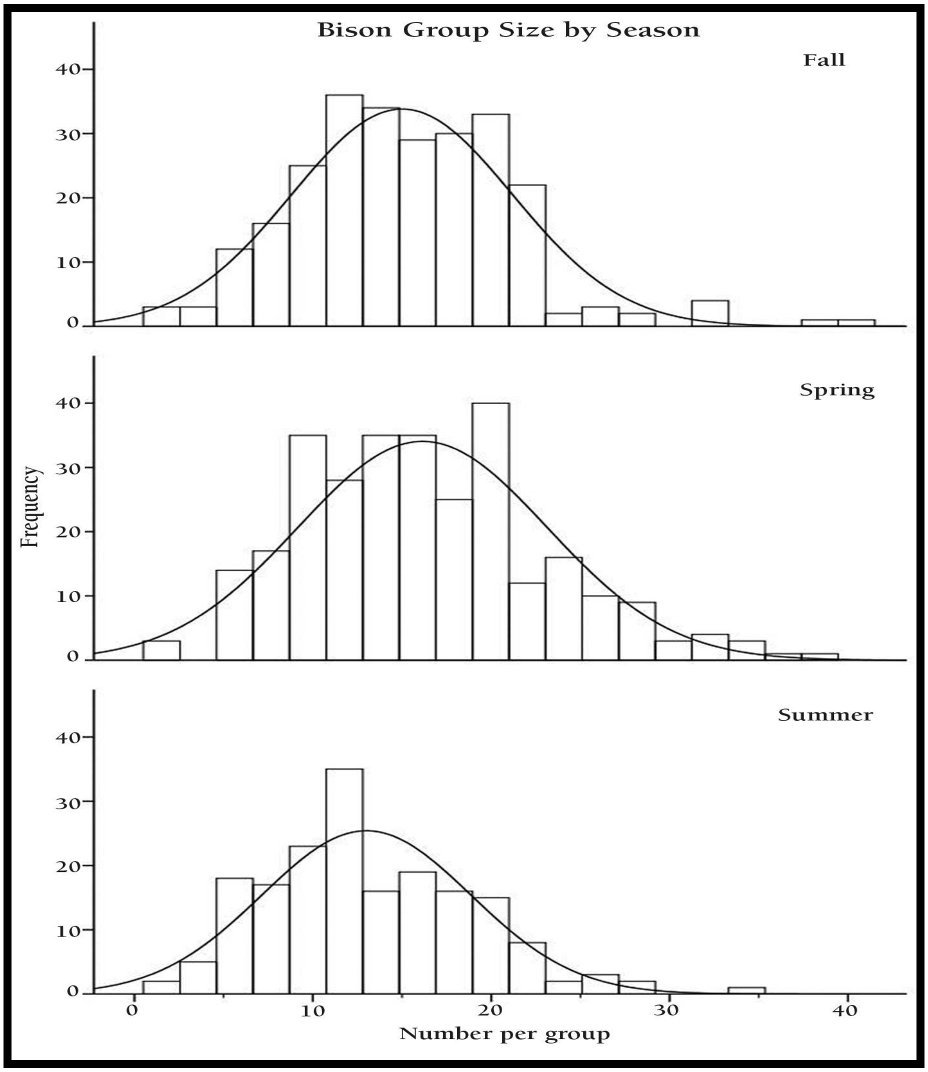

Figure 1. Bison group size by season.

I observed many weak associations (HWI from 0.11 to 0.30) and very few strong associations among unrelated individuals.

The network diagrams, which provide detail on the differences in associations between treatments, also make a compelling case for mother-offspring relationships (Fig. 2). Based on this association network, mother-offspring relationships within the herd were identifiable even without prior knowledge of maternal relationships.

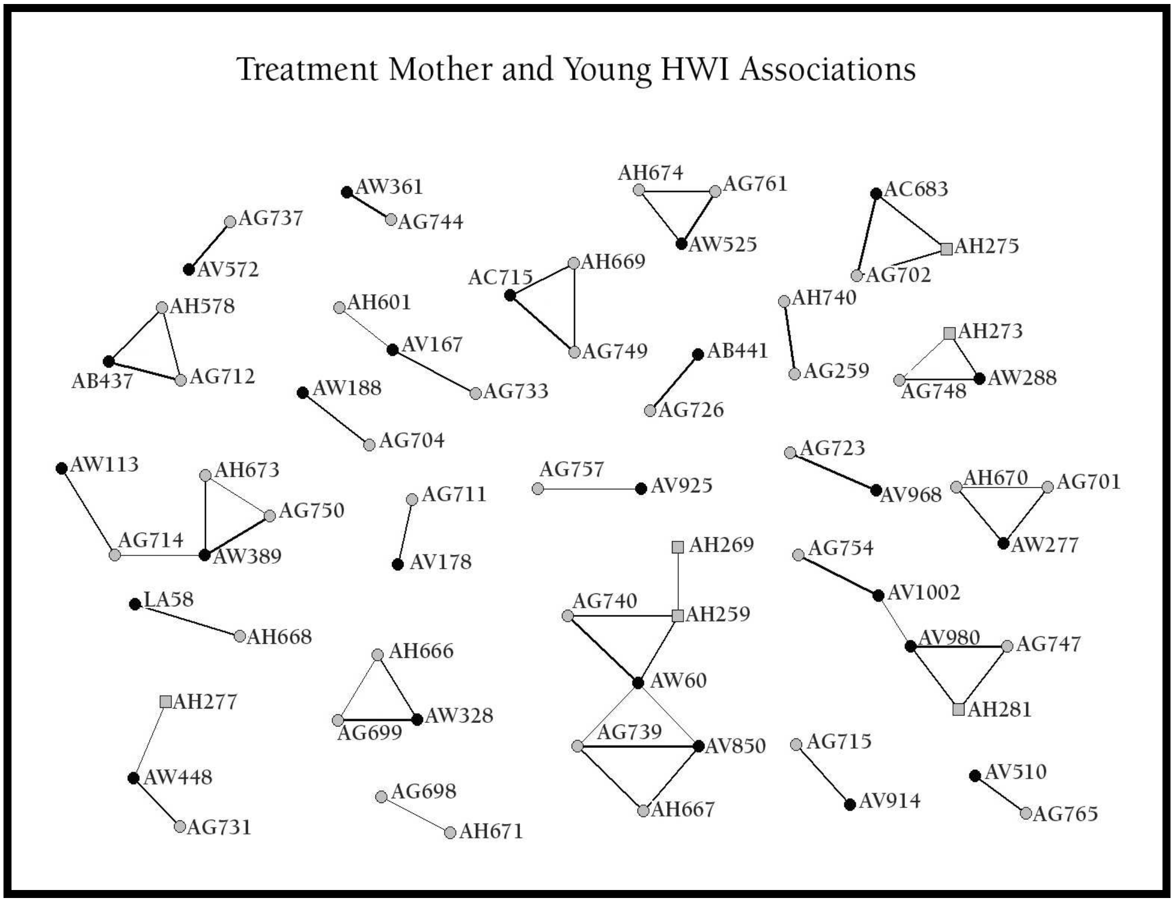

Figure 2
Associations between treatment mothers and their offspring for HWI > 0.50. Shapes represent sexes: circles = females; squares = males. Colors represent treatments: black = treatment mothers; grey = treatment young. Thicknesses of lines represent association strength.

The identified relationships (Table 3) show that relationships were retained by treatment mothers and their offspring over two generations. Relationships were stronger between a mother and female offspring than a mother and male offspring. For HWI > 0.50, there were more female than male offspring relationships: of the 27 prominent kin relationships, only 5 involved males (Table 3).

Table 3
The maternal linkages between mothers and offspring over two generations, identified by HWI > 0.50.

Mother ID	Offspring 1			Offspring 2		
	ID	Year Born	Sex	ID	Year Born	Sex
AB437	AG712	2006	Female	AH578	2007	Female
AB441	AG726	2006	Female			Male
AC683	AG702	2006	Female	AH275	2007	Male
AC715	AG749	2006	Female	AH669	2007	Female
AV1002	AG754	2006	Female	n/a	n/a	n/a
AV167	AG733	2006	Female	AH601	2007	Female
AV178	AG711	2006	Female			Male
AV510	AG765	2006	Female			Male
AV572	AG737	2006	Female			Male
AV850	AG739	2006	Female	AH667	2007	Female
AV914	AG715	2006	Female	n/a	n/a	n/a
AV925	AG757	2006	Female	n/a	n/a	n/a
AV968	AG723	2006	Female			Male
AV980	AG747	2006	Female	AH281	2007	Male
AW113	AG714	2006	Female	n/a	n/a	n/a
AW188	AG704	2006	Female	n/a	n/a	n/a
AW277	AG701	2006	Female	AH670	2007	Female
AW288	AG748	2006	Female	AH273	2007	Male
AW328	AG699	2006	Female	AH666	2007	Female
AW361	AG744	2006	Female	n/a	n/a	n/a
AW389	AG750	2006	Female			Female
AW389	AG714	2006	Female	AH673	2007	Female
AW448	AG731	2006	Female	AH277	2007	Male
AW525	AG761	2006	Female	AH674	2007	Female
AW60	AG740	2006	Female	AH259	2007	Male
LA58	AH668	2007	Female	n/a	n/a	n/a

The network diagrams also highlight some highly social adult female bison. For example, treatment mothers AW60 and AW389 were strongly connected to other adult females and their offspring, though less so than to their own offspring. The associations were weaker for control mothers and treatment offspring.

Only eight strong associations existed between treatment mothers and control mothers (Fig. 3). Two cases of cross-mothering may have occurred between control mother AV362 and offspring AH665, and control mother AV591 and offspring AH269 (Fig. 3).

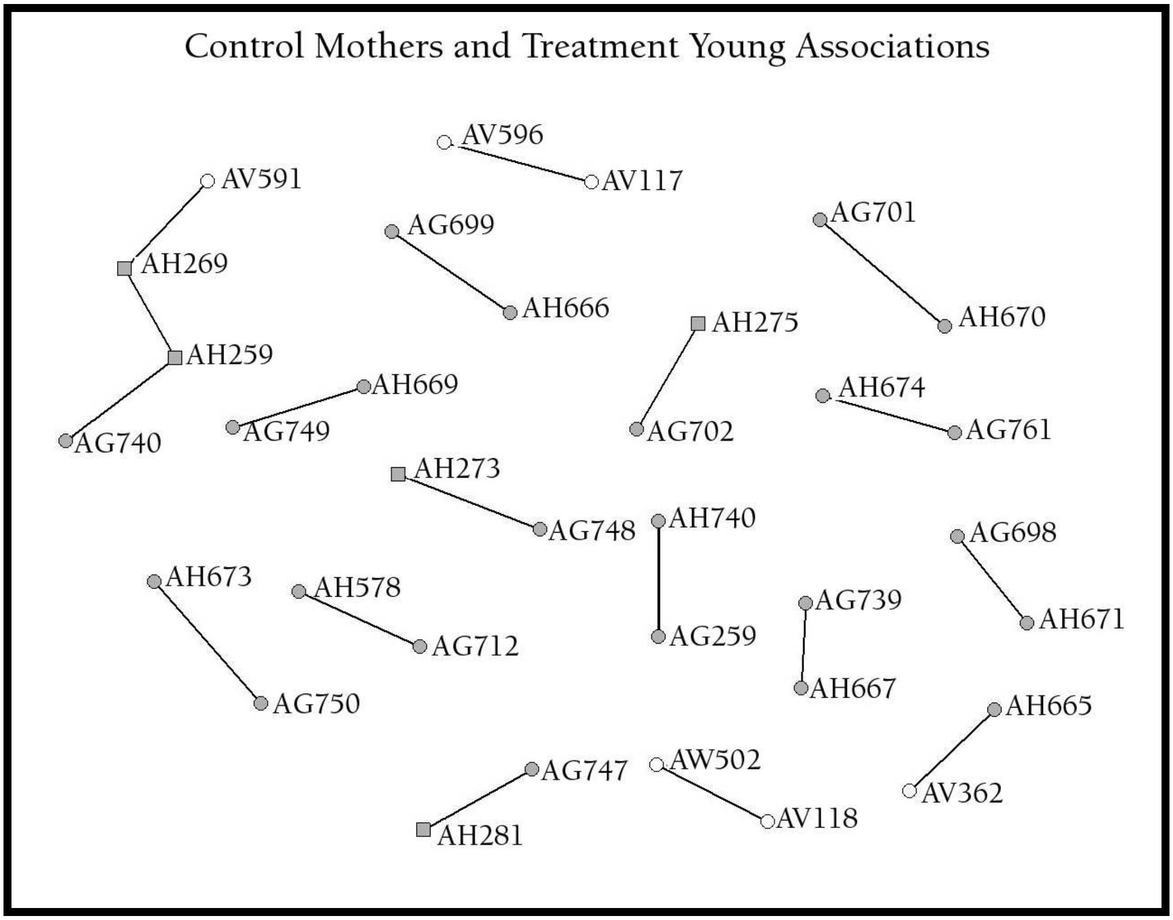

Figure 3
Associations between control mothers and treatment offspring greater than HWI > 0.50. Shapes represent sexes: circles = females; squares = males. Colors represent treatments: white = control mothers; grey = treatment young. Thicknesses of lines represent association strength.

DISCUSSION

Sociality and Kinship

Mother-daughter associations over generations lead to philopatric matrilines in many species, but this notion is controversial with bison. I found that mother-daughter relationships developed when calves were left with their mother and these relationships persisted through successive generations. The association indices showed treatment mother-daughter comparisons had the greatest percentage of individuals with a HWI > 0.50 (Table 3). Association networks, which provided further evidence of long-term mother-daughter relationships, illustrated that associations and linkages persisted over three generations (2-year old offspring, yearling offspring, and new calf). Relationships were stronger for mother-female than mother-male offspring. For a HWI > 0.50, there were many more mother-female than mother-male offspring relationships (Table 3). These data, coupled with the few significant relationships found among either control group members or the hundreds of other group members repeatedly associating with treatment and control animals during the 3-year study, show that relatedness influences bison group composition.

Differences in methods of study may partially account for the discrepancies between my studies and those of others. Some studies were inconclusive due to small sample sizes (3 pairs: see critique of Lott & Minta 1983 in Green et al. 1989), or biased due to the use of older, more recognizable mothers (see critique of Van Vuren 1983 in Green et al. 1989). More in-depth studies of associations among females and their offspring show extensive post-weaning associations between mothers and daughters (Green et al. 1989; Brookshier & Fairbanks 2003).

Bison-landscape interactions may also help account for these discrepancies. Stable groups of bison were not observed in steep, narrow canyons (Lott & Minta 1983) or forests (Van Vuren 1983), but they were observed in open grasslands (Green et al. 1989). Lack of resources may encourage formation of smaller groups of individuals with similar nutritional needs (Lott & Minta 1983). Conversely, open habitats with ample resources may support larger groups of bison (Van Vuren 1983; Rutberg 1984), favoring development of extended families. Differences in habitat preferences -- between females with or without calves due to limited ability to move long distances, threats of predation, and nutrient requirements -- may also influence social organization in bison. In my study, bison roamed over open desert grasslands that provide sufficient resources in most seasons. These conditions likely facilitated group formation and cohesion among family members.

Non-related Individuals and Group Dynamics

At the Armendaris Ranch, bison groups were composed primarily of unrelated individuals. Extended families cannot form due to forced weaning and removal of yearlings from the herd. With these practices group members are not likely to accrue substantial benefits from long-term associations. The only known maternal relationships in the herd were those in our treatment group.

Sociality is a function of the cost and benefits associated with aggregations of related and unrelated individuals (Hughes 1998; Clutton-Brock 2002; Lukas et al. 2005; Metheny et al. 2008; Wittemeyer et al. 2009). Genetic relatedness increases fitness through kin selection (Hamilton 1964; Alexander 1974), while non-kin-based groups experience benefits derived from predator vigilance, cooperative defense, resource defense, increased foraging efficiency, and parental assistance (Trivers 1971; Axelrod & Hamilton 1981; McComb et al. 2001; Foley 2002; Sukumar 2003). The amount of time relatives spend together influences how much time is available for kin selection to influence social behavior (Hamilton 1964; Maynard-Smith 1964; West-Eberhand 1975). Fission-fusion societies, however, are often composed of unrelated individuals, attenuating opportunities for kin selection (Archie et al. 2006). Inclusive fitness benefits derived from kin survival are a cohesive force in many social organizations (Hamilton 1964; Emlen 1995), though not necessarily the only force (Harcourt 1992).

Whittemyer et al. (2009) found that 2nd tier social groups (groups composed of multiple breeding females and their calves) were related individuals of matrilineal descent in 80% of elephant groups. However, 20% of the groups were unrelated, demonstrating that kinship was not a prerequisite for social affiliation or group membership. So while we found relatedness a key parameter of group composition among bison, it may not be the only parameter dictating group membership in bison.

My in-field observations support this idea. The oldest members of the Armendaris herd were brought to the ranch from different ranches as yearlings in 1993. They can still be identified by ear-tag numbers. While I did not identify specific associations based on ranch of origin, I commonly saw individuals from various ranches in the same groups, often composed of a majority of individuals with a common location of origin. These individuals often separated together during fission events, and then fused with others groups sharing members with a common origin. Relationships forged as yearlings in this unfamiliar Armendaris environment in 1993 thus may still be affecting group associations. While domestic calves prefer to associate with their mother even after weaning, in the absence of mother, strong social bonds were formed among peers (Veissier & Le Neindre 1989). Individuals may base their group fusion decisions on relatedness and associations formed at the location of origin. These peer associations may be an attempt to compensate for the absence of mother (Veissier et al. 1990b), and minimize aggression as their nearest neighbors are familiar or less dominant females (Rutberg 1984; Green et al. 1989; Weckerly 1999).

Seasonality

Seasonality influences sociality (Altman 1974; Jarman 1974), and socio-ecological models predict seasonality should influence group dynamics, including levels of disassociation (Wrangham 1980; Isbell 1991; Wittemyer et al. 2005). Typically, as resource quality and quantity decrease, intergroup competition increases and animals disperse when they are able to do so. Nonetheless, I found no differences in group sizes during seasons of low or high resource availability.

Precipitation and forage production were mostly confined to the summer monsoon season with the majority of precipitation coming between July and September. I would expect group size to increase then, but differences in resource availability may have been mitigated by the size of the ranch. While precipitation and ensuing forage production differences existed, localized precipitation events that occurred throughout the ranch apparently minimized the differences. Small groups of bison often traveled upwards of 30 km in response to rainfall and remained in these areas for days foraging on new growth. While rain seldom fell in large quantities outside of the monsoon season, these localized events may have enabled group size to remain stable from season to season.

The slight increases in group sizes observed during spring may have been a result of calving. One possible explanation is that females with calves less than 1 year old increase their levels of aggregation and group size as an anti-predation defense. At the same time, these results discount the idea that bison with calves less than 1 year old may be more vulnerable to intra-group competition because of greater nutritional requirements and as a result decrease group cohesion (Wittemyer et al. 2005).

Group Dynamics and Management

Management practices influence sociality, including the composition and cohesion of social groups. As with domesticated livestock, bison managers typically remove older females that no longer produce offspring. The consequences of the removal of matriarchs are only now being considered by managers, as illustrated by the Amboseli and Samburu herds of African elephants (Archie et al. 2006; Wittemyer et al. 2009). While the Samburu elephants experience extremely high rates of illegal poaching, including 85% population decline and death of many older females (Poole et al. 1992), the Amboseli population is generally undisturbed (Moss 1988, 2001). Amboseli groups show strong evidence of kin-based structuring (Archie et al. 2006), whereas Samburu groups have much higher levels of non-relatives comprising groups (Wittemyer et al. 2009). Very few livestock producers have considered the implications of sociality for their herds (Bray 2011). The consequences of removing matriarchs and breaking down extended families in livestock herds are likely to be increasingly severe where animals must fend for themselves in harsher environments (Zimmerman 1980).

Social learning is important in many species as the store of environmental and social knowledge accumulated by older females is transmitted to conspecifics (Moss & Lee 1999; McComb et al. 2001; Foley 2002). This local knowledge is lost from groups when older females are removed, a common practice when they no longer produce offspring. Age of matriarch is positively correlated with group size and with the reproductive success of other group members (McComb et al. 2001; Vidya & Sukumar 2005). The productivity of social groups deprived of this knowledge thus can be seriously disadvantaged due to a lack of environmental and social knowledge.

Foraging in groups can decrease uncertainty regarding fluctuations in environmental quality as information is gained and shared among group members, as is the case with cattle ranching in the desert environments of Nevada (Zimmerman 1980). Information regarding the spatial structure and function of variable environment may be more readily learned by all age classes depending on its complexity, however, knowledge of some ecological variants that occur or are encountered only rarely may exist only among the senior members of the group. While bison face higher foraging costs in larger than in smaller groups (Fortin & Fortin 2009), the accumulated knowledge of older matriarchs appears to offset the costs of species utilizing lower-quality forage due to larger group size (Freeland & Choquenot 1990; McLoughlin et al. 2006). This matriarchical knowledge can increase foraging efficiency and thus provide incentives for group formation and cohesion (Fernández-Juricic et al. 2006).

Many studies highlight the important role of mother as a transgenerational link to the foods and habitats her offspring are likely to eat and inhabit (Green et al. 1984; Distel & Provenza 1991; Provenza 1995a,b; Wiedmeier et al. 2002; Chadwick et al. 2009a,b,c; Tzack et al. 2009). Offspring learn what to eat (e.g., Mirza & Provenza 1990, 1992; Thorhallsdottir et al. 1990) and where to go (e.g., Key & MacIver 1980; Howery et al., 1998) from mother. Exposures to foods for as little as a few days early in life have lifelong influences on what an animal eats. Experiences in utero and early in life cause a suite of neurological (e.g., Coppersmith & Leon 1986; LeDoux 2002; Doidge 2007), morphological (e.g., Schlichting & Pigliucci 1998), and physiological (e.g., Duffy et al. 2002) changes that in turn affect behavior in ways that enable animals to continually adapt in a world of change (Provenza & Villalba 2006). By interacting with the genome during growth and development, social and biophysical environments can influence gene expression and behavioral responses, as the emerging field of epigenetics is highlighting, and over generations they create animals locally adapted to landscapes (Provenza 2008). These processes, which enable animals to adapt to diets and habitats available locally and to changes in those diets and habitats over time, imply that what constitutes a “high quality diet or habitat” will differ for herbivores reared in different environments at different points in space-time. More generally, social interactions and locally adapted cultures are an essential part of the collective memory of a population, whereby individuals learn from their ancestors through their mothers. That knowledge, locally inflected, adds uniquely to the biodiversity of landscapes for species and has implications for conservation (Davis & Stamps 2004; Laiolo & Tella 2007).

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CHAPTER 4

INITIATION AND DIRECTION OF MOVEMENT CHOICES IN BISION FOLLOWING REST[1]

Abstract

To reap the benefits of living in groups, individual decisions must scale up to group behaviors for groups to remain intact. Group coordination requires group decisions that can vary between decisions made democratically, where a majority of individuals decides, and decisions made despotically, where a dominant member of the group decides. How these decisions are reached and transmitted is poorly understood. I hypothesized that for bison decisions about direction of movement are more despotic while those concerning when to move are more democratic. I evaluated this hypothesis by examining movement initiation and direction following rest periods in a group of bison that originated from 15 cows and 2 bulls born in 2001. They were weaned in the fall of 2001, fitted with individual ear tags, and then moved to a part of the Armendaris Ranch separate from the main herd. Since their relocation, they have been managed without intervention and free-range over 2,800 ha. The original adults (RTC, red tag cows) can still be identified as a group by their red ear tags, although individual identification can no longer be achieved due to faded tag numbers. This group numbered approximately 93 individuals, depending on the year of my study, and the offspring in this group are all related to the original 15 females and 2 males. I observed this group of bison from sunup to sundown for 4 days during each of the 6 trips to the field from May

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2008 (24 days) to September 2009. I collected data for 12 decisions in 2008 and for 19 decisions in 2009. All animals occurred in one cohesive group that I followed until a rest period occurred. I observed movement initiation and direction following rest periods. During rest periods, I recorded individual female activity, location, age class, and compass bearings of the body axis, which I considered an expression of preferred direction or individual “votes.” For direction of movement, select older females made despotic decisions in 93% of the 31 recorded choices. These directions were different ($P < 0.01$) from directions chosen by other group members in 52% of decisions. For movement initiation, bison used a more democratic decision-making process: group movements did not begin until an average of 47% of adult cows departed the group and waited for the near majority to join them. Interestingly, the oldest females led this final post-rest movement behavior in 81% of the decisions, again verifying their importance in the decision-making process.

1. Introduction

In species such as bison that live in social groups, movements across landscapes, foraging, sentinel behavior, and babysitting are continually coordinated among individuals such that complex social organizations and behaviors emerge (Whitehead, 1996; Clutton-Brock, et al., 1999; Wilson, 2000; Franks et al., 2002; Couzin and Krause, 2003; Couzin, 2006). When animals change activity and/or location, and the group remains intact, that outcome implies a consensus has been achieved through a group decision (Conradt and Roper, 2005; Ramseyer et al., 2009). The cohesiveness of the group is compromised if members do not behave in unison, and the advantages of group living are lost if decisions made by individuals do not scale up to group behaviors

(Krause and Ruxton, 2002; Couzin, 2006). If and how individuals know which choices others will make, whether or not they know if their decision is in the majority or minority, or even how the information they possess compares with that of other members is largely a mystery (Couzin et al., 2005). The recruitment of others, vital in the decision making process (Ramseyer et al., 2009), can happen in three ways: 1) Communicative recruitment occurs when displayed behaviors induce other group members to follow (e.g., primates, Sueur and Petit, 2008, Meunier et al., 2008; geese, Ramseyer, et al., 2009). 2) Active recruitment occurs when individuals forcefully act on others (e.g., equids, Waring, 1983). 3) Passive recruitment occurs when the location or movement of an animal prompts others to follow (e.g., black-headed gulls, de Schutter, 1997; geese, Ramseyer et al., 2009).

Group coordination requires group decisions that vary between two extremes: one in which decisions are made democratically, where a majority of individuals decides, and the other in which decisions are made despotically, where a dominant member of the group decides (Conradt and Roper, 2003; 2005; List, 2004). Societies vary in how consistently particular individuals lead group decisions (Leca et al., 2003). On the one hand, studies of cattle (Dumont et al., 2005), sheep (Rameseyer et al., 2009), zebras (Fischhoff et al., 2007), and zebu (Reinhardt, 1983) illustrate the importance of multiple versus single individuals in decision making. African buffalo cows orientate their body axis in the direction they favor during rest periods prior to movement (Prins, 1996), which suggests individuals indicate their preferred path and intentionally recruit others. On the other hand, several species of social mammals appear to behave despotically, including mountain gorillas (Schaller, 1963), horses (Waring, 1983), and dwarf mongooses (Rasa, 1987). In these species, dominant males lead group movements of related females which often form long-term dominance hierarchies (Robbins et al., 2005). While the fitness consequences of decision making are largely untested in the field, theoretical analyses suggest democratic decisions are more beneficial than despotic decisions as they lead to more inclusive decisions (Conradt and Roper, 2003). Many authors who question the feasibility of democratic decision-making ascribe despotism to species without determining if that is actually the case (Norton, 1986, Byrne, 2000).

Different types of social organization can also influence decisions and some contend that group stability determines whether or not certain individuals are consistent leaders of group movements (Overdorff et al., 2005). Along a spectrum from solitary to highly social (Wilson, 1975), many species live in fission-fusion societies, wherein groups form and separate over time as commonly occurs in ungulates, primates, and cetaceans (Cross et al., 2005; Whitehead et al., 1991; Henzi et al., 1997; Christal et al., 1998; Chilvers and Corkeron, 2002). The potential for despotism increases with stable relationships among individuals, as stability enables individuals to dominate group choices (Vehrencamp, 1983; Chase et al., 2002; Robbins et al., 2005). Conversely, the potential for democratic decision making increases when groups are characterized by fluid and relatively unstable relationships, as the lack of stability allows individuals with the greatest immediate needs to influence group choice (Rands et al., 2003; Fischhoff et al., 2007).

Given so little is known about decision making in groups, my objective was to determine the degree to which the initiation and direction of movement following rest was despotic or democratic in bison. I determined the degree to which the behavior of mature females affected the timing and direction of group movement after resting or if the outcome was made by a consensus of individuals within the group. The specialized and often unique knowledge that exists in matriarchs of some species (McComb et al., 2001; Vidya and Sukumar, 2005), coupled with the matriarchal bonds formed among bison (Shaw et al., 2012), led me to hypothesize that decisions about direction of movement would be despotic while those concerning when to move would be democratic. Matriarchal knowledge thus would be used to make decisions about direction while the cohesive nature of bison groups composed of related individuals would ensure decisions on when to move would be made by the group. Based on this hypothesis I predicted that decisions on when to move would be made by group consensus while decisions on the direction of movement would be made by adult females, though not necessarily the same ones each time.

2. Study Area

This study was conducted on the privately owned Armendaris ranch in Sierra County, New Mexico, a former land grant now managed by Turner Enterprises. The ranch is 145,600 ha and has been owned and operated by Turner Enterprises since 1993. The climate is warm-temperate, with an average of 213 frost-free days per year recorded for nearby Truth or Consequences, New Mexico. The mean annual precipitation is 250 mm. Approximately 105,220 ha of the ranch are classified as semi-desert grassland (Brown, 1994) characterized by grasses and shrubs such as black grama (*Bouteloua eriopoda*), palmilla (*Yucca elata*), and Mormon tea (*Ephedra torreyana*). Most of the remaining vegetation is classified as Chihuahuan desert scrub, which is composed of shrubs such as mesquite (*Prosopis spp.*), saltbrush (*Atriplex spp.*), and creosote bush (*Larrea tridentate*).

Bison (*Bison bison*) were introduced to the ranch in 1993 and they currently number approximately 1,000 females and 150 males. Aside from the main herd of bison, another small group of bison (Quail Herd) lives at the Armendaris ranch. This group originated from 15 cows and 2 bulls born in 2001 to mothers in the main herd. As calves, they were weaned in the fall of 2001, fitted with individual ear tags, and then moved to a separate part of the Armendaris Ranch. This group now numbers approximately 93 individuals, and the offspring in this group are all related to the original 15 cows and 2 bulls, which are still in the herd. Since their relocation, they have been managed without intervention and free-range over 2,800 ha. The original adults (RTC, red tag cows) can still be identified as a group by their red ear tags, although individual identification can no longer be achieved due to faded tag numbers. During the 2008 field season the Quail herd numbered 13 RTC cows, 27 additional adult females (3 and older), 10 female yearlings and 2 year olds, and 16 calves. In 2009 the herd contained 13 RTC cows, 37 additional adult cows, 16 female yearlings and 2 year olds, and 27 calves. This herd also contained adult males that only occasionally occurred with the females; as a result, they were not included in the study. I used the Quail Herd for this study because repeated observations by me and ranch personnel indicate these animals, excluding mature bulls, are always together in a cohesive group.

3. Methods

3.1. Data Collection

Data were collected from sunup to sundown for 4 days during each of the 6 trips to the field from May 2008 to September 2009. During this period, data for 12 decisions were recorded in 2008 and for 19 decisions in 2009. All animals occurred in one cohesive group that I followed until a rest period occurred. A rest period, defined as at least half of the adult females lying down, continued until all group members were again up and engaged in a post-rest behavior that involved choice of direction and behaviors such as foraging, traveling, and drinking.

During group rest periods, data were obtained for animals within and outside the group every 10 min using scan sampling of every individual within the group using binoculars (Altman, 1974). I recorded individual animal activity (laying or standing), location (within or outside group), age class (juvenile 2 years of age and younger; adults without ear tags, and original RTC adults), and compass bearings of the body axis of adults and RTC adults. I considered compass bearings of the body axis of standing female adults and RTC individuals an expression of preferred direction choices or individual “votes” (Prins, 1996). Data were collected from inside a vehicle at a minimum distance of 200m from the group and once in position, the vehicle did not move until the rest period was concluded to minimize body-orientation bias.

Votes were recorded as either within-group votes or outside-group votes. Individuals were considered outside the group if they occurred more than 50m from the group or if they moved away from the remaining members of the group by at least 50m, otherwise they were considered within the group. Additional data for within-group animals included individual differentiation in standing and moving activities, as well as the compass bearing for the first individual moving and for the final group movement. This information allowed me to identify individuals possibly responsible for initiating movement and making direction choices. Finally, I recorded both pre- and post-rest period behavior (drinking, grazing and traveling), as well as wind direction.

I calculated the mean heading and **r**-values for within-group body axis orientations (votes), outside-group votes, and RTC votes both within and outside the group. Mean headings were calculated as mean directions -- expressed as degrees where north is 0° which is identical to 360°, east is 90°, south is 180°, and west is 270° -- chosen by individuals (within the group, outside the group, and RTC). Vector lengths or **r**-values were calculated as a means to evaluate vote distribution and varied between 0 (every animal orients in a different direction) and 1 (all animals orient the same direction).

3.2. Statistical Analysis

Orientation data were analyzed using procedures for circular data (Batschelet, 1981). I calculated the mean heading, **r**-values, and confidence intervals for within-group body orientations (votes), outside-group votes, and RTC votes. The 95% confidence intervals were used to determine whether the mean direction, as determined by the compass bearings of the body orientations, were different from the final direction chosen by the group (Stapput and Wiltschko, 2005).

Within-group votes were analyzed in three ways: 1) total within-group votes, 2) within-group votes prior to animal(s) moving outside the group, and 3) within-group votes after animal(s) moved outside the group. This allowed me to measure the influence of animal(s) moving outside the group on within-group votes. For each decision-making event, distributions were analyzed using the V-test to determine whether the body orientation mean directions were significantly different from randomness. I used the Mardia–Watson–Wheeler test (Batschelet, 1981) to determine if differences existed for within group, outside group, and RTC body orientation comparisons. Differences in confidence intervals and **r**-values between groups were calculated with t-tests. I considered $P < 0.10$ significant.

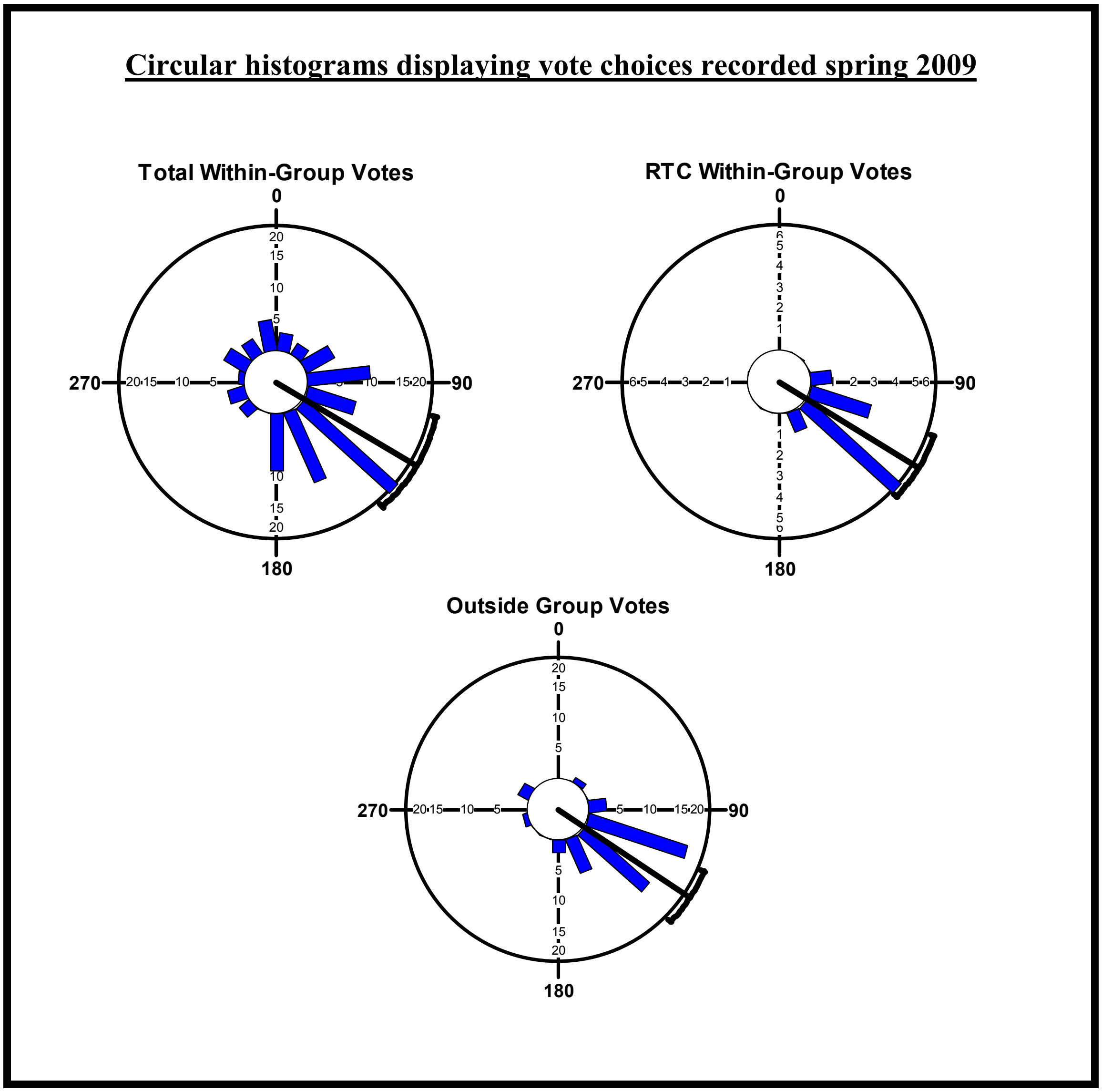
4. Results

4.1. Within-Group Votes

Total within-group votes were non-randomly distributed in 97% of the decisions. Non-random distribution of within-group votes was 65% before animals left the group and increased to 100% after animal(s) left the group, which illustrates the influence of animals leaving the group on animal votes (Fig. 4). Within-group animals orientated themselves in accord with individuals that left the group, which ultimately influenced group distribution. This is further illustrated by the Mardia–Watson–Wheeler tests which show that within-group votes before animal(s) left the group were different ($P < 0.05$) from within-group votes after animal(s) left the group in 94% of the decisions.

Final directions chosen by groups following rest periods were captured by the 95% confidence intervals calculated for total within-group votes in 50% of the decisions. This percentage varied from 36% for within-group votes prior to animal(s) leaving the group to 60% for within-group votes after individual(s) left the group. So while there was a correlation between within-group votes and direction of movement, these votes did not always account for the final direction of movement chosen by the group.

Total within-group vote confidence intervals were different ($P = 0.07$) when comparing the ensuing behaviors -- foraging or traveling to water -- indicating that group votes differed depending on the behavior chosen following the rest period. Variation among votes decreased when the group chose water as opposed to foraging. The diverse forage options available, compared to the limited sources of water, likely increased variation among individuals that differed in morphology, physiology, and preferences for forages and hence subsequent votes for foraging preferences.



Circular histograms displaying vote choices recorded spring 2009

Fig 4. Sample of circular histograms from spring 2009 showing body axis alignments (votes) of total within-group females, RTC cow's within-group, and votes of animals outside the group prior to the initiation of the final behavior. Blue bars represent votes and black line and bracket represents the 95% confidence interval of analyzed votes.

Neither wind direction nor time of day influenced within-group votes. Wind direction was within the confidence intervals generated by with within-group vote for 9.6% (against the wind; 3 out of 31 decisions) and 16% (with the wind; 5 out of 31 decisions) of the decisions, while the time of day (morning vs. afternoon) confidence intervals were not significantly different (P = 0.4).

4.2. RTC Votes

Votes by older RTC cows from within-group were non-randomly distributed in 100% of the decision events. Final directions were captured by the RTC 95% confidence intervals in 93% of the decisions; this is in contrast to the total within-group votes which were 50% (Fig. 5). Older RTC females clearly influenced group decision-making processes. Further analysis showed that RTC within-group votes (directions) were different from other within-group votes in 52% of the decisions (Mardia–Watson–Wheeler, P < 0.01). Vector lengths (**r**-values) were different (P < 0.001) when comparing within-group (minus RTC votes) votes and RTC votes, again indicating the importance of RTC on movements. Pre-rest period group movement directions were within the confidence intervals generated by RTC within-group votes (collected during the rest period) in only 25% of the decisions and only 11% for total (all adult females minus RTC votes) within-group votes. This illustrates that post-rest movement directions changed in most cases and that rest periods did not just serve as a delay in behaviors already determined but instead as a period when decisions were made.

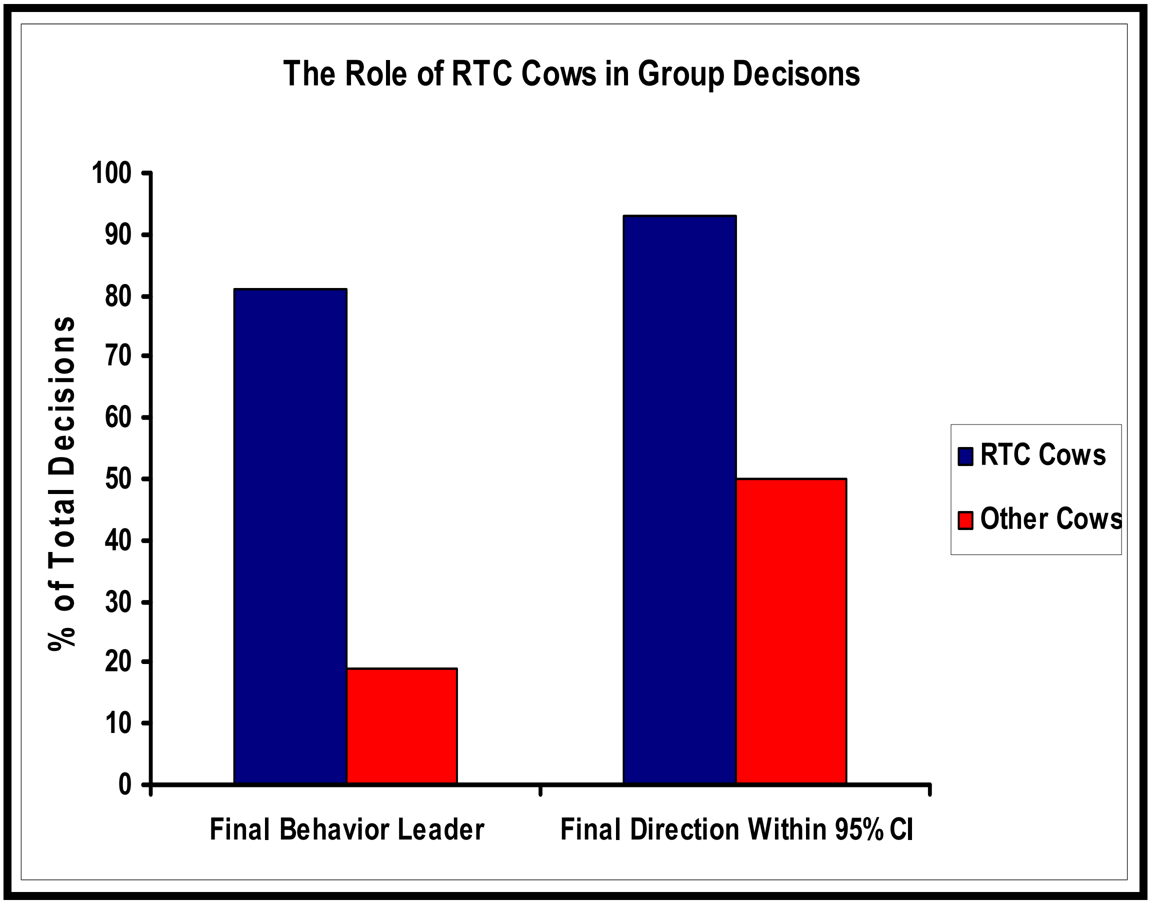


Fig. 5. Comparison of RTC cows versus other adult cows with regard to final direction and leadership of post-rest final direction behaviors.

4.3. Outside Group Votes

Votes recorded for individuals outside the group were non-randomly distributed in 96% of the decisions, and when an adult female(s) left the group the rest of the group went that same direction in 83% of the decisions. In every decision, adult females that left the group never went further than 100 m from the group where they waited until an average of 47% of the adult cows also left the group before continuing to move (Fig. 6). RTC animals, which were the oldest females with the most experience in this environment, led this final post-rest movement behavior in 81% of the decisions.

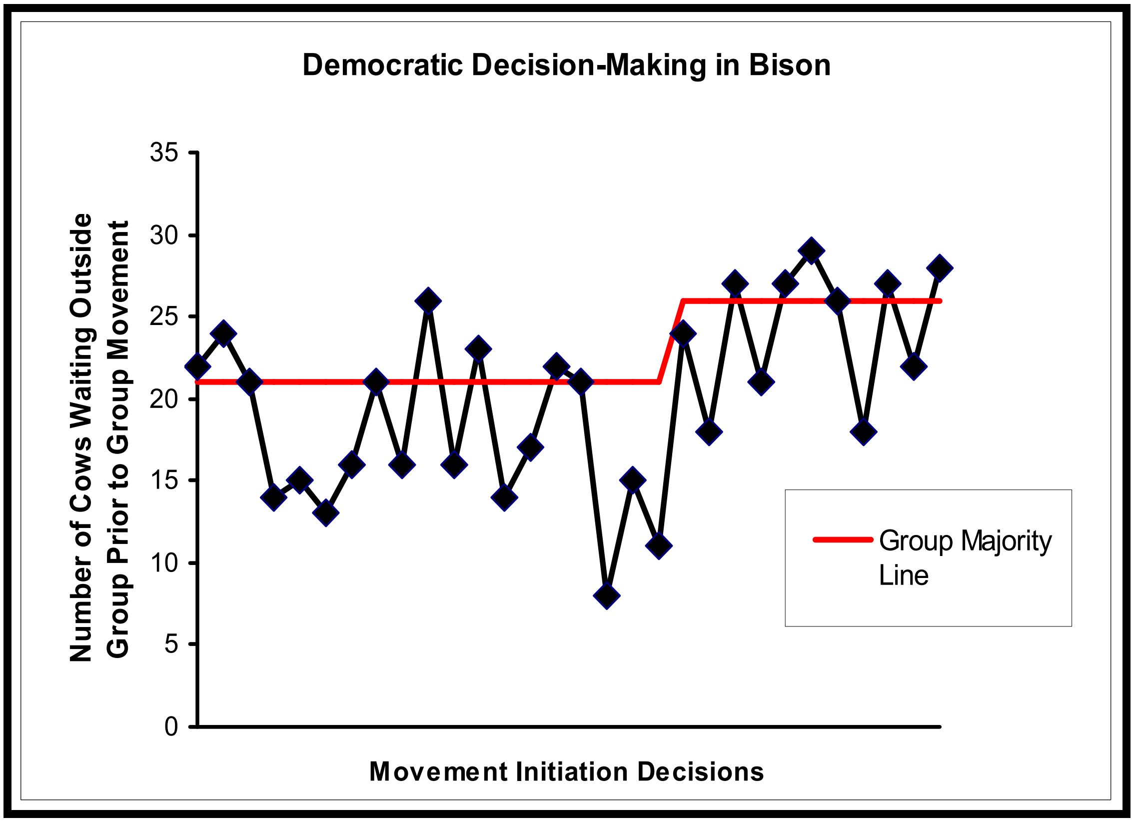


Fig. 6. Number of adult cows waiting outside of the group when movement initiation decisions were reached on 30 different occasions.

5. Discussion

I determined the degree to which the initiation and direction of movement following a rest period were despotic or democratic. I hypothesized bison use both types of decision making, as a result of the specialized and often unique knowledge that exists in matriarchs (McComb et al., 2001; Vidya and Sukumar, 2005), and the matriarchal bonds formed among bison (Shaw et al., 2012). I predicted decisions about direction would be despotic while those on group departure would be democratic. My results suggest bison make decisions despotically and democratically.

5.1. Despotic Decisions

In decisions regarding the choice of direction, bison did not exclusively use a democratic decision-making process. Instead, specific individuals appeared to influence the group. When an adult female left the group, other individuals watched her activity, which in turn affected their orientations or "votes." The Mardia-Watson-Wheeler test showed a significant difference between within-group votes before animal(s) left the group and within-group votes after animal(s) left the group in 94% of the decisions ($P < 0.05$). These differences illustrate that remaining group members responded to the departing individual(s) by altering their votes.

While total within-group votes were non-randomly distributed in 97% of the decisions, the final directions chosen by the group following rest were captured by the within-group vote confidence intervals in only 50% of the decisions. So while votes were not random they accounted for only half of the final directions chosen in this study, indicating that the direction was not chosen by the body axis orientation (votes) of all adult females in the group. This result is contrary to the democratic decision making process of African buffalo, where group members' body axis orientation determine choice of direction following rest in 85% of the voting episodes (Prins, 1996).

The RTC cows strongly influenced decisions, consistent with the role of matriarchs in group decisions (Vidya and Sukumar, 2005). Their influence was seen most easily in decisions regarding direction of movement. These apparently despotic decisions were led by RTC animals in 81% of the group decisions. Moreover, the final direction of the group was captured by 95% confidence intervals generated by RTC votes (93%, Fig. 5). The RTC animals were the original members of the group and thus had the most experience in this environment; all other group members were descendents of the RTC cows. The RTC cows' ability to recruit other group members adds further evidence of intentional recruitment (primates, Kummer, 1968; Leca et al., 2003; African buffalo, Prins, 1996; geese, Ramseyer et al., 2009). As with geese (Ramseyer et al., 2009), the first animal to move appeared to be especially influential in the recruitment process. Observations of group movements to feeding sites suggest leaders are often older animals (Reinhardt 1983; Réale and Festa-Bianchet, 2003). Despite initial skepticism, people now accept leading as an active behavior that occurs when individuals consistently initiate changes in activity and direction of movement (Dumont et al., 2005).

Matrilineal relationships along with age/size dominance interactions help account for the role RTC cows played in the decision-making process. The RTC were the dominant individuals with the most accumulated experience. Their knowledge and age, coupled with stability of the Quail herd, increased the likelihood of despotic decision-making. In elephants, older, larger females consistently dominate younger females, where the reduction of uncertainty concerning social interactions increases the likelihood of age/size dominance hierarchies (Archie et al., 2006). Hierarchies are common where the risk of injury is high even in mildly aggressive interactions (Crowley, 2001).

Group decision making processes are influenced by group stability. Leader-follower relationships and despotism are more likely to emerge from more cohesive groups. Conversely, the less stable the group, the higher the likelihood of democratic decision making instigated by individuals with the strongest need for change. Less stable groups are characterized by loose aggregations likely to be dominated by individuals with the strongest needs (Rands et al., 2003, Fischhoff et al., 2007), influenced by physiological and morphological factors including nutrition, health, age, and reproductive state (Fischoff et al., 2007). Ever-changing needs among individuals within the group diminish the influence of particular individuals and hence the emergence of consistent leaders (Beacham, 2003; Rands et al., 2003; Overdorff et al., 2005; Fischoff et al., 2007), and may have caused different RTC to initiate movement at different times in my study.

Variation among bison votes was much less when the group chose water as opposed to foraging (P = 0.07). This may relate to morphological and physiological differences among individuals and their subsequent impact on foraging preferences. Morphological and physiological differences exist even among group members of similar age and sex thus creating different needs for and abilities to use primary and secondary compounds (Provenza, 2003). Nonetheless, groups can remain intact if individuals have appropriate forage choices. Choice and ability to choose is one of the most important benefits that occurs as groups encounter different forages and environments while they move across landscapes, and one of the most important factors influencing the nutrition and health of individuals (Provenza et al., 2011). Choice enables individuality and allows group members to learn to maximize nutrient intake while retaining the advantages associated with group membership. The diverse forage options available compared to the single choice of water may have increased variation among votes.

5.2. Democratic Decisions

Bison appeared to be democratic with respect to decisions regarding when to move. When an adult cow left the group she never moved more than 100 m from the rest of the group before waiting either for other animals to join her or to move back into the group.

The cows that left the group and waited for other animals to join them waited until an average of 47% of the other adult cows also left the group before proceeding (Fig. 6).

Tradeoffs can result between choice of direction and group cohesion. On the one hand, individuals within a group may differ in their preferred direction of movement due to differences in needs (Krause and Ruxton, 2002; Franks et al. 2002; Couzin et al., 2005). On the other hand, the benefits of sociality -- obtaining protection from predators, enhancing reproductive success, learning about feeding sites and mineral licks, and learning migratory routes to name a few – are lost if animals do not stick with the herd.

Living in stable groups and extended families thus means individuals may at times sacrifice their preferences for those of the group (Meunier et al., 2006), though that will depend to great extent on how groups interact and move across landscapes. Individuals may compromise their personal interests for those of the group if individual needs differ greatly from those of the group (Prins, 1996; Conradt and Roper, 2003), unless the group moves across landscapes in ways that meet the needs of all individuals (Provenza, 2003). Living in extended families may encourage movement about landscapes influenced by cellular processes that cause animals to satiate on foods and habitats, by differences among individuals within families in preferences for foods and habitats, and by social interactions among families (Provenza, 2003). The patterns that emerge from these interactions may lead to movements *within* and *among* families: interactions *within* families cause movement to meet the needs of everybody in the group; interactions *among* families cause movement to maintain the autonomy of the family unit. In sheep and cattle, social interactions *within* groups encourage animals to eat a broader array of foods (Scott et al., 1995), and to forage in a greater variety of locations (Howery et al., 1998), as individuals maintain the cohesiveness of the group *and* respond to ever-changing preferences of individuals within the group. Species that live in groups may thus meet the nutritional needs of the group, and reap the benefits of sociality – obtaining protection from predators, enhancing social status and reproductive success, learning traditional routes, and sharing feeding sites – by roaming (Provenza, 2003).

6. Conclusions

Bison used despotic decisions when choosing a direction to travel or forage following rest periods and democratic decisions when choosing when to move following rest periods. Adult females did not vote by aligning their body axis with their desired direction, instead the oldest females (RTC) chose a direction by moving to the edge of the group and waiting for a majority of adults to join her before beginning post-rest foraging or watering behaviors (Fig. 6). Older RTC cows strongly influenced the decision making process, verifying the important role of older matriarchs in social group dynamics in bison as in other species. Using both ends of the decision-making spectrum may help group members benefit from the social and environmental knowledge accrued by older RTC individuals while also allowing them to reap the benefits of collective decisions and group cohesion. Foraging in groups decreases uncertainty regarding habitat quality as information is shared among group members. Information regarding the spatial structure of the environment may be readily learned by all age classes depending on its complexity, however, knowledge of some ecological variants that occur or are encountered only rarely may only exist only among senior members of the group. While bison may face higher foraging costs in large than in small groups (Fortin and Fortin, 2009), the accumulated knowledge of older matriarchs may offset the potential costs of decreased individual selectivity as a function of larger group sizes (Freeland and Choquenot, 1990; McLoughlin et al., 2006). Goats (*Capra hircus)* use information gathered from conspecifics to increase foraging gains as group sizes increase to up to four members (Shrader et al., 2007). This can increase foraging efficiency and thus provide incentives for group formation and cohesion (Fernández-Juricic et al., 2006).

More generally, social interactions and locally adapted cultures are an essential part of the collective memory of locally-adapted populations, whereby individuals learn from their ancestors through their mothers. That knowledge, locally inflected, adds uniquely to the biodiversity of landscapes for species and has implications for conservation (Davis and Stamps, 2004; Laiolo and Tella, 2007).

These findings also have implications for rotational grazing in bison and livestock. People have stressed the importance of rotational grazing at high stock densities and the use of electric fences to manage livestock (Savory and Butterfield, 1999; Gerrish, 2004). We have not thought about how social organization might cause rotational grazing without fences (Provenza, 2003). This notion is based on three assumptions: 1) social herbivores live in stable, cohesive groups, 2) maintaining the cohesiveness of these groups and their home ranges influences food and habitat selection, and 3) individuals within groups differ in their preferences for foods and habitats. If so, social interactions within groups may encourage animals to eat a broader array of plants and to forage in a greater variety of locations as individuals maintain group cohesion and respond to different preferences of individuals within the group by moving about a landscape. Interactions among extended families may further increase movements about landscapes as families avoid prolonged contact with one another by selecting spatially and temporally segregated foraging locations. Social interactions encourage sheep and cattle to eat a broader array of foods (Scott et al., 1995), and to forage in a greater variety of locations (Howery et al., 1998), as individuals maintain the cohesiveness of the group and respond to ever-changing preferences of individuals within the group.

Differences exist in how individuals are built morphologically and how they function physiologically, even within uniform groups, and marked variation is common even among closely related animals in needs for nutrients and abilities to cope with toxins (Provenza, 2003). Moreover, primary and secondary compounds in all foods cause animals to satiate, and excesses of nutrients, nutrient imbalances, and excess secondary compounds all limit food intake unless animals can eat a variety of foods (Freeland and Janzen, 1974; Provenza 1995; 1996). The ability to choose among alternative forages best enables each individual to meet needs for nutrients, balance intake of different nutrients and toxins, and obtain medicinal benefits from lower doses of plant secondary compounds that at too high levels are toxic (Engel 2002; Burritt and Provenza 2000; Provenza, 2003). To do so, groups must move in ways that enable individuals to choose from an array of different forages to meet needs of individuals. Such socially and biochemically mediated interactions link cells, organs, individuals, and social groups with landscapes (Provenza, 2008). Ever-changing needs among individuals within the group diminish the influence of particular individuals and hence the emergence of consistent leaders (Beacham, 2003; Rands et al., 2003; Overdorff et al., 2005; Fischoff et al., 2007), and may have caused different RTC to initiate movement at different times in my study.

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CHAPTER 5

STRESS RESPONSES OF BISON TO THREE DIFFERENT FINISHING REGIMES[1]

Abstract

Living in properly functioning social groups presumably reduces stress on individuals, though little is known about how management practices that disrupt social organization affect levels of stress in individuals. In the United States, male bison are typically weaned and placed in feedlots at a time when they would ordinarily be moving from matrilines into small bachelor groups. I assessed levels of stress for males under tight vs. loose confinement in feedlots and compared their levels of stress with males that remained under free-ranging conditions. I hypothesized levels of stress would increase as confinement size decreased and animal density increased. To examine this hypothesis, yearling bison males were weaned and placed in either tight (TC) or loose (LC) confinement. The free-ranging group (FR) was composed of males weaned from their mothers and then returned to the herd under free-ranging conditions. I assessed fecal cortisol metabolites (FCM) as a measure of stress. A pre-trial FCM baseline (PTB) was calculated from samples taken prior to treatment application. Fecal samples were collected from 20 different individuals in each group every 2 weeks beginning 15 January 2009 and ending on 30 April 2009. Fecal cortisol levels varied by date ($P<0.0001$), and treatment and date interacted ($P<0.0001$) because pre-trial FCM levels increased dramatically from Period 1 to Periods 2-8 for TC and LC, but not for FR. Averaged

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[1] Coauthored by Ryan A. Shaw, Fredrick D. Provenza, and Xavier Manteca.

throughout the study, fecal cortisol levels were lowest for FR (23 ng/g DM), intermediate for LC (39 ng/g DM), and highest for TC (63 ng/g DM; P<0.0001). Thus, my results show that bison finished in free-ranging conditions experience the lowest stress levels while those finished in confinement experienced stress apparently due to social disruptions and aggressive interactions. Such stress may adversely affect animal welfare leading to decreases animal performance and increased costs of production.

Introduction

Wild and domestic animals encounter an array of social and biophysical situations that can threaten their survival and that in turn induce stress, leading to a surge of neurological, hormonal, and immunological responses (Sapolsky, 1992). This cascade of responses begins when the hypothalamic-pituitary-adrenal axis is stimulated and glucocorticoids (GCs; cortisol in large mammals) are released from the adrenal cortex (Sapolsky, 1992; Wingfield et al., 1998). These physiological responses enhance production of ATP (Nelson, 2000; Sapolsky, 2002; Mooring et al., 2006), and increase carbohydrate metabolism resulting in elevated levels of glucose in the bloodstream (Sapolsky, 2002). Energy mobilization accompanied by elevated heart rate, blood pressure, and breathing enhance an animal's ability to 'fight or flee' a stressful situation (Abbott et al., 2003; Muller and Wrangham, 2004). High levels of GCs for extended periods, however, have deleterious consequences including the loss of muscle mass, immuno-suppression, reproductive failure, shorter life span, and gastric ulcers (Creel, 2001; Sapolsky, 2002; Wingfield and Sapolsky, 2003; Sands and Creel, 2004). Producers and consumers are increasingly concerned about the welfare of animals raised for human consumption. To the degree that we do not appreciate the social and biophysical needs of animals, we can induce stresses that adversely affect their welfare and ours (Patison, 2011). With bison, for instance, both the density of animals and the social conditions under which they are reared are potential sources of chronic stress. Bison live in social groups composed of mature females and their offspring; females often remain in the groups but males typically leave matrilineal groups at around 2 years of age to live in small bachelor groups (Shaw et al., 2012). Production systems that appreciate these behavioral changes may reduce stress, enhance performance, and reduce costs of production, whereas those that do not may adversely affect welfare and profits.

Turner Enterprises, Inc. manages approximately 2 million acres and 50,000 bison on ranches throughout the United States. An integral part of their management involves examining different ways to finish bison. In some of their herds, young bulls are weaned from the cow herd as calves, supplemented on winter pasture, summered on grass, and then placed in commercial feedlots as long yearlings (17 to 22 months old). Grain-finished bulls (24 to 30 months old) are then supplied to high-end retail markets, providing fresh meat 365 days per year. In other herds, bison are allowed to free-range until the time of slaughter.

My objective was to determine if these different finishing techniques influenced levels of stress for males under tight vs. loose confinement in feedlots compared with males that remained under free-ranging conditions. I hypothesized that levels of stress would increase as confinement size decreased and animal density increased. Based on this hypothesis I predicted young males would have higher levels of stress in tight than in loose confinement and that free-ranging bison would have the lowest levels of stress.

Study Area

This study was conducted on the Flying D ranch owned and operated by Turner Enterprises. The ranch is approximately 680 km^2 and has 1800 bison. It is located in southwest Montana's Madison Range of the Rocky Mountains and is bordered on the east by the Gallatin River, on the west by the Madison River, and on the south by the Spanish Peaks of the Gallatin National Forest. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain. The vegetation is dominated by shrub/steppe habitat but also includes coniferous forest. Vegetation varies from dry grassland/juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines and are predominantly mountain big sage (*Artemesia vaseyana*) /grassland mosaics. Temperatures range from highs of 21-32°C in the summer months to lows of -34°C in the winter months. Large mammals on the ranch include grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), gray wolves (*Canis lupus*), elk (*Cervus elaphus*), mule deer (*Odocoileus heminonus*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*).

Methods

Measuring levels of stress

Concentrations of GCs in plasma are an index of stress (Levine and Treiman, 1964; Licht et al., 1983; Morton et al. 1995; Romero, 2002; Romero et al., 2008). As the process of blood withdrawal induces stress (Beehner and McCann, 2008), researchers have developed non-invasive alternatives for measuring GC in saliva (Granger et al., 1996; Tiefenbacher et al., 2003), urine (van Schaik et al., 1991; Carlstead et al., 1992), and feces (Palme and Möstl, 1997; Wasser et al., 2000). These methods alleviate observer-induced bias in measurements of stress.

One of these techniques, measurement of fecal cortisol metabolites (FCM), provides an integrated measure of cortisol secretion over the previous 1 to 2 days, which better accounts for short-term fluctuations and diurnal variations (Monfort et al., 1998; Palme et al., 1999). This improved sensitivity allows researchers to better distinguish between baseline GC release and legitimate physiological stress reactions occurring in response to the stressors of interest (Palme et al., 2005; Beehner and McCann, 2008). Thus, FCM is considered one of the most reliable noninvasive measurements of chronic stress in animals because it does not interfere with the stress response itself (Lane, 2006).

The use of FCM as an indicator of stress has been used in numerous studies of wild and domestic ungulates including Alpine chamois (Thaller et al., 2004), American bison (Mooring et al., 2006), Pere David's deer stag (Li et al., 2007), and cattle (González et al., 2008a). Studies of captive animals show that cage size and animal density are primary factors elevating GC levels, with deleterious consequences (Koontz and Roush, 1996; Crockett et al., 2000; Wells et al., 2004; Weingrill et al., 2004; Carlstead and Brown, 2005; Li et al., 2007). The increased GC levels are caused in part by increases in aggression, avoidance, and intimidation behaviors, due to increasing animal density (Miller and Wood-Gush, 1991; González et al., 2008a).

Bison groups

Males, approximately 9 months old, were weaned and placed in either tight (TC) or loose (LC) confinement pastures. The TC group had 90 males confined to a 2.5 ha (5 acre) pasture while the LC group had 100 males confined to a 10.8 ha (27 acre) pasture. Animals in both groups were fed ad libitum diets of grass hay and whole oats. The TC and LC diets were identical and consisted of 1st and 2nd cutting hay and whole oats. The free-ranging group (FR) was composed of males weaned from their mothers and then returned to the herd of 599 animals under free-ranging conditions. These animals occurred in small social groups that roamed about the ranch where they had access to a variety of dried grasses and forbs as well as shrubs. The FR animals were weaned, as were TC and LC animals, to minimize the confounding effect of weaning on stress and to highlight confinement method as the variable of interest.

Fecal sample collection

Fecal samples were collected from the treatment and control animals every 2 weeks beginning 10 January 2009 and ending on 26 April 2009. Baseline FCM levels were established with 10 pre-study samples collected from the free-ranging herd in November 2008 just prior to weaning. On each subsequent sample date, fecal samples were collected from 20 animals in each of the three groups. As TC and LC were composed of treatment animals only, samples were collected by locating and collecting fresh fecal matter. Fecal samples from FR were collected by finding free-ranging yearling bulls (identified by unique ear tags) and following them until 20 different males defecated and each of their fecal samples could be collected. Fecal samples were collected from different animals in each of the three treatment groups at each sample date.

Fecal samples were frozen immediately and they remained frozen until they were freeze-dried for analysis. After mixing to obtain homogeneous samples, 0.5 g of lyophilized feces were extracted with 4 ml methanol + 1 ml H_2O for 45 min with agitation. After centrifugation at 3000 rpm for 20 min, extracted samples were diluted 1:10 in the assay buffer to avoid methanol interference. Corticosterone was determined in the supernatants with the corticosterone ^{125}I-Radioimmunoassay (Rats and Mice Corticosterone kit, ICN Pharmaceuticals), according to the manufacturer's instructions. The extraction efficiency, determined by spiking fecal samples with ^{125}I – corticosterone before extraction, was calculated as 51.6%. Assay precision, assessed by calculating intra and inter-assay coefficients of variation, was 8.36 % (intra-assay) and 19.5 % (inter-assay).

Statistical Analysis

The statistical design for the analysis of variance (ANOVA) was a two-way ANOVA (criteria of classification: treatment and date). Animals (subsamples) were considered different for each treatment and date. The covariance structure variance component was used, as it yielded the lowest BIC values. ANOVA was performed using the MIXED procedure in SAS (SAS; Littell et al., 1996). When F values were significant ($P < 0.05$), differences in means were analyzed with the least significant difference test.

As this is a case study, conducted with bison under production conditions in confinement in feedlots and free-ranging, we were unable to spatially replicate the three treatments (TC, LC, and FR). Rather, we obtained baseline values for FCM under free-ranging conditions prior to weaning and allotting bison to the three treatments and then compared those values across time for different treatments.

Results

Fecal cortisol levels varied by date ($P<0.0001$), and treatment and date interacted

(P<0.0001) (Fig. 7). Pre-trial FCM levels for Sampling Period 1 increased dramatically for Sampling Periods 2-8 for TC and LC, but not for FR. Averaged throughout the study, fecal cortisol levels were lowest for FR (23 ng/g DM), intermediate for LC (39 ng/g DM), and highest for TC (63 ng/g DM; P<0.0001).

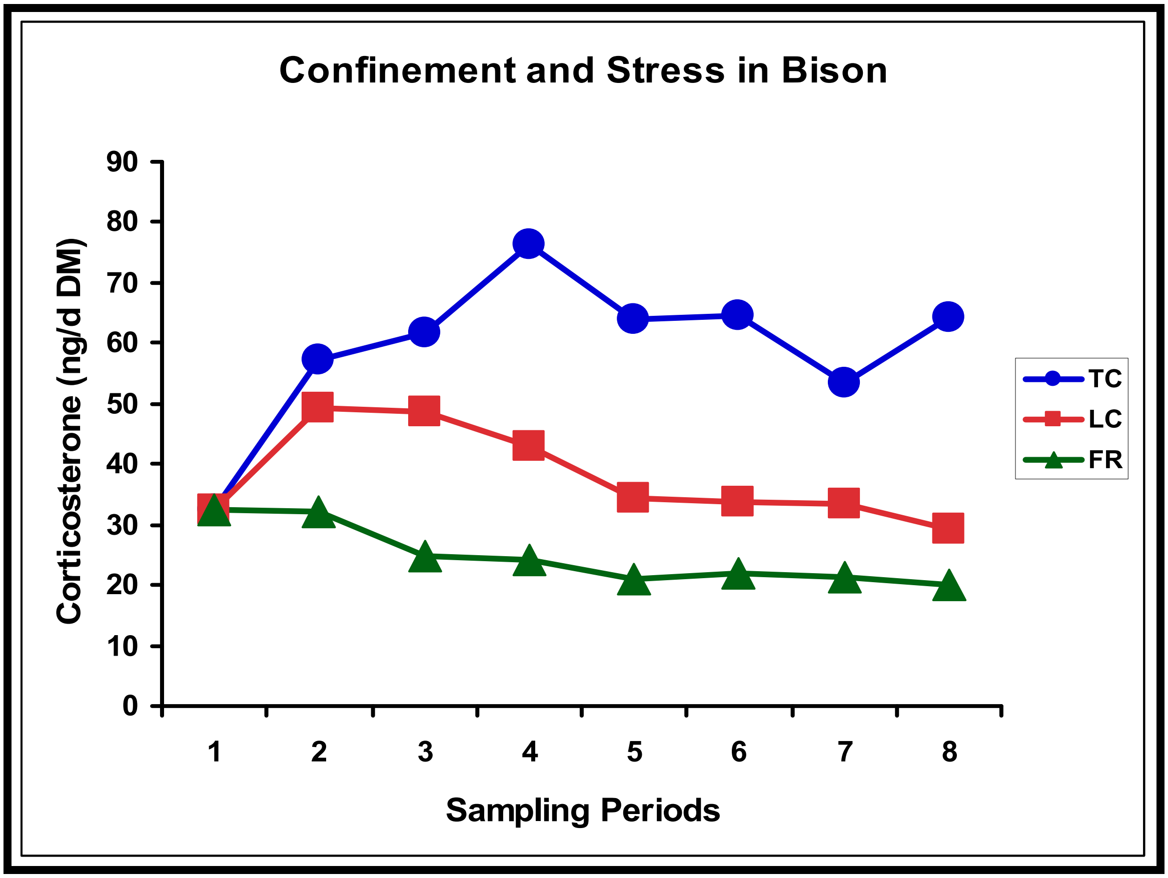

Fig. 7. Fecal corticosterone levels for bison under loose confinement (LC), tight confinement (TC), and free ranging (FR). The pre-trial corticosterone baseline is Sampling Period 1; treatment Sampling Periods are 2-8. Sampling periods are at 2-week intervals.

Discussion

Our findings and those of others suggest bison live in extended families composed of females and young males, who leave the family around 2 years of age to live in small bachelor groups (Green et al., 1989; Berger and Cunningham, 1994; Shaw et al., 2012).

Production systems that confine young bulls at a time when they are naturally breaking up into smaller bachelor groups may increase stress, diminish performance, and increase the costs of production. Levels of FMCs increased in both TC and FC from Sample Period 1 (baseline) to 2 (Fig. 1), likely due both to social disruptions and confinement. Between Sample Periods 1 and 2, all bison claves were weaned and then TC and LC were placed in confinement, all of which cause stress.

Disruption of social bonds among individuals has severe behavioral and physiological effects, especially mother-infant separation (Carter, 1998; Gunnar, 2000; Patison, 2011). Aggressive interactions among individuals that are re-establishing social dominance as well as competition for resources lead to conflicts that are exacerbated in confinement (Koontz and Roush, 1996; Sands and Creel, 2004). Competition and conflict, amplified by confinement, induce a vicious cycle where increased FCM secretion leads to ever increasing levels of aggression (Sapolsky, 1992; Möstl and Palme, 2002). Prolonged aggressive interactions adversely affect food intake, are energetically demanding, and are thus potent stressors (Fletcher, 1978; Li et al., 2001; Patton et al., 2001; Sapolsky, 2002; Sands and Creel, 2004; Mooring et al., 2006).

Changes in diet and competition for food in confinement interact to increase stress. Stress increases when animals are confined and offered only a few, highly processed, unfamiliar foods (Villalba et al., 2011). Competition among dairy cows increases aggression, avoidance, and intimidation behaviors, which increase stress (Miller and Wood-Gush, 1991), and decrease welfare and production (Huzzey et al., 2006; González et al., 2008b). Confinement can also increase eating rate and decrease eating time (Harb et al., 1985), which adversely affect digestive functions (González et al., 2008b). The resultant decrease in animal welfare can increase the risk of ruminal acidosis and liver abscesses (Stone 2004; Krause and Oetzel, 2006), all of which decrease performance (Britton and Stocks, 1989; Schwartzkopf-Genswein et al., 2003). Animals experiencing increased competition for food also decrease time resting and increase time standing. These changes in foraging behaviors and ruminating patterns are sensitive indicators of physiological states and ultimately indicate changes in animal welfare.

Conclusions

These findings are consistent with analyses that show the most profitable way to finish bison is to let them free-range with their mothers. While bison require more time to finish under free-ranging than confined conditions, the input costs are much lower under free-ranging conditions and hence profitability is higher (Mark Kossler and Dave Hunter, unpublished data). Finishing bison on pasture also takes advantages of seasonal cycles of production in grass and bison and increases the quality of meat for human consumption.

Food intake decreases with decreasing photoperiod during fall and winter and increases with longer day lengths in spring and summer (reviewed by Rhinde et al., 2002). While animals of all species and breeds exhibit these cycles, the magnitude is greater in wild than in domestic species. Seasonal variations in food intake result from physiological changes that are not due to reduced forage availability. This phenomenon, considered to have evolved as an adaptation to reduce energy expenditure during winter, causes animals to spend less time and energy searching for food less when forage availability is low. While animals can lose more than 10% of body mass during winter, when spring arrives and forage availability and quality increase, animals quickly make compensatory gains. To increase food intake year-round, some bison producers are attempting to select breeding stock from the rare individuals that gain weight year-round, while others are increasing the amount of light in feedlots during winter (Robinson, 2007).Nonetheless, if we appreciate the evolved social and biophysical needs of animals, we can reduce stresses that adversely affect their welfare thereby improving their health and ours. Production systems that confine young bulls when they normally form small bachelor groups increase stress, diminish performance, and increase the costs of production. This is important for producers and consumers increasingly concerned with animal welfare and the health benefits of meat and milk from grass-fed ruminants including bison (Robinson, 2007). As with domesticated animals reared on grass, meat from pasture-reared bison is better for human health (Robinson, 2007). Meat from pasture-reared bison has less fat and cholesterol, fewer omega-6 fatty acids, and more omega-3 fatty acids and conjugated linoleic acid than meat from grain-fed bison. Meat from grass-fed bison thus has a much healthier ratio of omega-6 to omega-3 fatty acids (2 to 1) than bison that are penned and fed grain in feedlots (7 to 1) (Rule et al., 2002).

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CHAPTER 6

CONCLUSIONS

My studies enhance understanding of social organization in North American bison by showing mothers and daughters form matriarchical relationships that influence group composition. When calves were not weaned from their mothers, mothers and daughters showed high levels of associations throughout my 4-year study, while control animals and other members of the bison herd lacked any significant associations. Mother-daughter associations illustrate that bison social organization is influenced by relatedness and that they may influence social group dynamics including fission-fusion process.

My study of group decisions following rest illustrate bison movements are both democratic and despotic. When bison move following rest they do so democratically while decisions regarding direction are made despotically. Within bison groups, some individuals may at times sacrifice their food and habitat preferences for those of the group in an effort to retain group cohesiveness. Group stability may or may not be compromised if individual decisions scale up to group movement decisions.

Finally, my studies of stress show that as confinement size decreases stress increases. Additionally, calves that are left in free-ranging conditions with their mothers experience significantly less stress than calves removed from their mothers and placed in confinement.

Controversies Regarding Social Organization in Bison

In polygynous mammals, social groups often are composed of closely related philopatric females (Dobson 1982). Retention of daughters and young sons within the maternal home range, along with dispersal of older males, is the essence of sociality in many mammalian species. Such kinship is a primary determinant of sociality in elephants (Archie et al. 2006), and the matriarch, who is often the oldest adult female in the family, plays a critical role in a matriline.

Research on bison social organization is equivocal. Some contend bison live in unstable groups of randomly associated individuals (Lott & Minta 1983), whereas others maintain bison live in stable groups of related individuals (Green et al. 1989; Brookshier & Fairbanks 2003). Different conclusions regarding bison social organization have arisen, in part, due to contradictory observations (Green et al. 1989, Brookshier & Fairbanks 2003). While some contend the fission-fusion nature and lack of persistent associations of bison are a response to seasonal variation in competition for forage (Wittemyer et al. 2005), others contend differences in physiological needs among individuals necessitate repeated fission events (Fortin & Fortin 2009). Evolutionarily, the diverse and fluctuating Great Plains environment where bison evolved may also have encouraged exploratory behavior, including increased propensity to disperse (Lott 1991).

My research helps clarify these issues regarding social organization in bison. My results illustrate mother-daughter associations developed when calves were left with their mother and these relationships persisted through multiple generations. The association indices showed that the treatment mother-daughter comparisons produced the greatest percentage of individuals with a HWI greater than 0.50 (Chapter 3, Table 3). Network diagrams of treatment mothers and daughters clearly illustrated that retained associations and linkages present during three generations (2-year old offspring, yearling offspring, and new calf; Chapter 3). These data coupled with the fact few other significant relationships were found among either control group members or the hundreds of other group members repeatedly associating with treatment and control animals shows the importance of relatedness in bison group composition. Non-random associations develop among bison groups and mother-daughter relationships are an important part of group dynamics. One of the primary challenges I faced in conducting a study of social organization in bison was finding a location, be that publically or privately administered, that left bison families intact as most do not. In the end, I worked at the Armendaris Ranch where they allowed me to study the influence of not weaning bison calves on the development of family groups.

Social Organization and Decision Making

In species such as bison that live in social groups, movements across landscapes are continually coordinated among individuals such that complex social structures and behaviors emerge (Whitehead 1996). Group stability and composition is compromised if members do not behave in unison, and the advantages of group living are lost if decisions made by individuals do not scale up to group behaviors (Couzin 2006). Living in stable groups and extended families thus means individuals may at times sacrifice their preferences for those of the group (Meunier et al. 2006), though that will depend to great extent on how groups interact and move across landscapes. Individuals may compromise their personal interests for those of the group if individual needs differ greatly from those of the group (Prins 1996; Conradt & Roper 2003), unless the group moves across landscapes in ways that meet the needs of all individuals (Provenza 2003a,b).

Group coordination requires group decisions that can vary between decisions made democratically, where a majority of individuals decides, and decisions made despotically, where a dominant member of the group decides (Conradt & Roper 2003; 2005). Use of both ends of the decision-making spectrum, as was the case with bison, may help group members benefit from the social and environmental knowledge accrued by older individuals while also allowing them to reap the benefits of collective decisions and group cohesion. Foraging in groups can also decrease uncertainty regarding environmental quality as information is gained and shared among group members. Many authors who question the feasibility of democratic decision making ascribe despotism to species without determining if that is actually the case (Byrne 2000).

My study of group decisions following rest illustrate bison movements are both democratic and despotic. When bison move following rest they do so democratically while decisions regarding direction are made despotically. Within bison groups, some individuals may at times sacrifice their food and habitat preferences for those of the group in an effort to retain group cohesiveness. Group stability may or may not be compromised if individual decisions scale up to group movement decisions.

Group decision making processes are influenced by group stability. Leader-follower relationships and despotism are more likely to emerge from more cohesive groups. Conversely, the less stable the group, the higher the likelihood of democratic decision making instigated by individuals with the strongest need for change. Less stable groups are characterized by loose aggregations likely to be dominated by individuals with the strongest needs, influenced by physiological and morphological variables, including general health, age, and reproductive state (Fischoff et al. 2007). Ever-changing needs among individuals within the group diminish the influence of particular individuals and ultimately the emergence of consistent leaders.

These differences were apparent comparing the main herd and the quail herd. The main herd consisted of only a few known related individuals (treatment mothers and young) whose social dynamics was characterized by temporary associations among members in small groups of 15 to 20 animals (Chapter 3). These less stable associations were often fragmented at key decision making junctures, such as when to move following rest periods, where to forage following rest periods and during foraging events, and during interactions with other individuals or groups. In these cases individual needs apparently dominated group dynamics leading to fragmentation and democratic decision–making. Social dynamics of the quail herd were considerably different. This herd consisted of related individuals with a much more stable group composition (Chapter 4). This stability allowed for a small group of individuals (RTC cows) to despotically lead activities of the entire group of 90 individuals following rest periods.

Social Organization and Management

Producers and consumers are increasingly concerned about the welfare of animals raised for human consumption. To the degree that we do not appreciate the social and biophysical needs of animals, we can induce stresses that adversely affect their welfare and ours. With bison, for instance, both the density of animals and the social conditions under which they are reared are potential sources of chronic stress. Bison live in social groups composed of mature females and their offspring; females often remain in the groups but males typically leave matrilineal groups at around 2 years of age to live in small bachelor groups (Shaw et al. 2012). Production systems that appreciate these behavioral changes may reduce stress, enhance performance, and reduce costs of production, whereas those that do not may adversely affect welfare and profits.

Bison finished in free-ranging conditions experience the lowest levels of stress while those finished in confinement experienced stress, apparently due to social disruptions and aggressive interactions (Chapter 5). This stress likely decreases animal performance, while increasing costs of production, and may raise concerns about animal welfare.

Conclusions

Management practices influence sociality, including the composition and cohesion of social groups. As with domesticated livestock, bison managers typically remove older females whose value is measured only by the yearly production of offspring. If bison form long-term matrilines, as our findings suggests, the role of matriarchs in these groups needs to be better understood. Under natural conditions, the social and environmental knowledge they posses could be vital in reproductive success and survival. Likewise, in managed systems their presence could affect production by influencing forage and habitat use, as well as the reproductive success of other group members. Their value may thus extend beyond their capacity to produce offspring.

The consequences of the removal of matriarchs are only now being considered by managers. The loss of matriarchs can have far reaching implications for the health of individuals that comprise family groups derived both from companionship and from knowledge of biophysical environments. Social learning is important in many species as the store of environmental and social knowledge accumulated by older females is transmitted to conspecifics (McComb et al. 2001; Foley 2002). This local knowledge is lost from groups when older females are removed, which can decrease production and survival in both natural and production systems. Social groups deprived of this knowledge can be seriously disadvantaged due to this missing environmental and social knowledge (McComb et al. 2001; Vidya & Sukumar 2005).

Appreciating social organization has the potential to increase production efficiencies, and hence commercial value, at all stages of converting bison to meat – including handling, grazing, feeding, growing to slaughter size on grass, feedlots – and to enable managers to more readily establish new herds. It also provides insights into weaning practices and the use of landscapes and long-term productivity of animals. Bison reared as families may be more economical to produce and they may graze in ways that do not degrade landscapes. The lack of social organization and culture, as a result of current management practices, may help explain why commercial operations often have difficulty getting bison to graze in ways that do not damage riparian areas and uplands (Mark Kossler, personal communication). If bison families graze rotationally, in ways that maintain the integrity of land, this study is a first step in learning how to manage lands grazed by bison and cattle in environmentally friendly ways (Provenza 2003a,b). This knowledge is invaluable for those who aspire to manage wild and domestic animals in ways that maintain the integrity of ecosystems.

Regarding use of landscapes, resource availability and use determines the land area needed to support a given number of animals, which might be expressed as a formula based on multiples of families or groups in bison and cattle. At a minimum, livestock producers might begin culling animals in ways that reflect understanding of how social organization affects use of landscapes, rather than culling based merely on which cows have calves; in so doing, they could encourage the development of sub-groups of animals that use different parts of allotments, thereby better distributing foraging across landscapes. At best, producers may eventually begin to develop and manage based on families – which is not a difficult step if they keep replacement heifers from their herds and cull in ways that encourage development of extended families – and benefit from lower costs due to less fencing and labor and higher prices for people willing to pay a premium for pasture-reared bison (see Bray 2011).

With North American livestock production, some people are increasingly emphasizing reducing costs by managing animals in more natural ways that reduce inputs and stress (Darrell Emmick, Grazing Lands Specialist, NRCS, New York; Dave Pratt, Director Ranch Management Consultants, Inc., Bud Williams, Bud Williams Stockmanship School, Bowie TX, personal communication). For much of the past 50 years, prices have lagged behind inflation, input costs have ballooned, and producers have turned to technology and economies of scale to remain profitable. Increased dependence on high-tech "solutions" such as anthelmintics, antibiotics, and vaccines, for health and nutrition have enormous ecological repercussions – including soil sterility, antibiotic resistant bacteria, and ecological imbalances – and cost enormous amounts of money annually. These pursuits are increasingly unpopular and rapidly becoming a political impossibility. Modern animal husbandry, which emphasizes productivity of individuals, as opposed to well-being of extended families and culture, must face the realization that animals without social order foraging in biochemically monotonous environments likely experience chronic stress. Management systems that encourage social organization may improve animal performance. Such systems are also likely to reduce susceptibility to pathogen and nutrition-related diseases and physical dangers. Basic research of this nature will provide some insight into social processes that influence animal performance, land productivity and the economics of operating a land enterprise.

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APPENDIX

March 10, 2012

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