

# Impact of Spatial Memory on Habitat Use

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## Abstract

**Spatial memory allows animals to remember where they have foraged and use that information to determine where they will travel and forage. Spatial abilities likely evolved as a survival mechanism to allow herbivores to forage more efficiently and safely. Spatial memory can be inferred when behavior can be predicted from an animal's prior experiences. Maze and arena studies have been used to demonstrate spatial memory in various livestock species. Anecdotal observations suggest that spatial memory plays an important role in grazing distributions of both wild and domestic ungulates. By examining how animals remember areas with abundant and scarce resources, researchers are discovering more about the behavioral mechanisms that determine grazing distribution patterns of large herbivores. The challenge is to use knowledge about spatial memory to predict grazing patterns and to manipulate grazing distribution through management. In this paper we review basic concepts and evidence for spatial memory in ungulates and other species, discuss working hypotheses regarding how land managers and livestock producers might manipulate grazing distribution and behavior using our current knowledge of spatial memory, and identify gaps in our understanding of spatial memory and propose hypotheses to address these gaps.**

## Introduction

The key to developing innovative management practices to solve animal distribution problems is to understand the behavioral processes that animals invoke during grazing (Bailey et al. 1996). Recent studies of spatial memory in large herbivores have improved our understanding of grazing distribution (Bailey et al. 1996, Edwards et al. 1996, 1997, Laca 1998). Other research

and modeling efforts that incorporate spatial memory and other cognitive processes have also improved our understanding of grazing processes (Coughenour 1991).

In a grazing behavior context, spatial memory is the ability of an animal to remember where it has foraged and use that information to determine where it will travel and forage. Spatial memory, the memory of locations in space, can be inferred when behavior can be predicted from an animal's prior experiences (Domjan and Burkhard 1982). By examining how animals remember areas with abundant and scarce resources, researchers are discovering more about the behavioral mechanisms that determine grazing distribution patterns of large herbivores. The challenge is to use knowledge about spatial memory to predict grazing patterns or to manipulate grazing distribution through management. The objectives of this paper are to: 1) describe basic concepts of and evidence for spatial memory in ungulates and other species, 2) discuss working hypotheses regarding how land managers and livestock producers might manipulate grazing distribution and behavior of large ungulates using our current knowledge of spatial memory, and 3) identify gaps in our understanding of spatial memory and propose approaches to address these gaps.

## Basic Concepts

### Working and reference memory

Spatial memory has been represented as a two-part code, working (short-term) memory and reference (long-term) memory (Honig 1978, Olton 1978, Staddon 1983). *Working memory* is retained only long enough to complete a particular task, after which the information is discarded because it is no longer needed, or because it may interfere with the successful completion of the next task. In contrast, *reference memory* is retained for longer periods because it is needed to complete successive tasks. Working and reference memory have been evaluated in mazes for a number of species where the animal's "objective" is to retrieve food without reentering any arms of the maze. Working memory is used *within* trials to remember which arms have been visited, whereas reference memory is used *between* trials to store the maze's spatial configuration and food availability and quality.

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## The importance of scale

Senft et al. (1987) and Bailey et al. (1996) identified discretionary spatial hierarchies to describe grazing behavior. For grazing herbivores, temporal and spatial scales of forage and habitat availability probably determine the functional value of working and reference memory (Laca and Ortega 1996). Knowledge of how working and reference memory interact across hierarchical levels is incomplete, but the following discussion provides a framework for our current level of understanding.

A *bite* is defined by a sequence of prehension, jaw and tongue movements, and severance by head movement (Laca et al. 1994). Diet selection of individual plants and plant parts is determined by animal decisions made at this level. Because livestock consume thousands of bites a day, it is unlikely that spatial memory plays a significant role at this level.

A *feeding station* is defined as an array of plants available to an animal for grazing without moving its front feet (Novellie 1978). Working memory may affect behaviors at this hierarchical level as animals may remember and avoid recently grazed areas.

A *patch* is a cluster of feeding stations separated from others by a break in the foraging sequence when animals reorient to a new location (Jiang and Hudson 1993). Working memory operates at the patch level *within* grazing bouts (i.e., grazing periods that are separated by non-grazing activities such as resting or ruminating) so that animals avoid depleted or poor areas and stay within preferred and ungrazed patches. Reference memory may also be used at the patch level *between* grazing bouts because patches vary in levels of nutrients and may be routinely visited or avoided on a daily basis (Bailey 1995, Ruyle and Rice 1996).

A *feeding site* is a collection of patches in a contiguous foraging area that animals use within a grazing bout. Animals may use working memory to return to or avoid feeding sites that were visited during the preceding grazing bout. Animals may also use reference memory to remember important abiotic and biotic characteristics of feeding sites from one day to the next.

A *camp* is a set of feeding sites with a common focus where animals drink, rest, or seek cover between grazing bouts within their home range area. Reference memory is probably used at this level to store the location(s) of water, cover, and the relative value of feeding sites within a camp. This information may be stored for periods of weeks to months.

Finally, *home range areas* are collections of camps defined by fences, natural barriers, and extent of migration or transhumance. Reference memory is used to remember the relative value of several camps within a home range area for months, even years.

## Incorporating spatial memory into other grazing behavior models

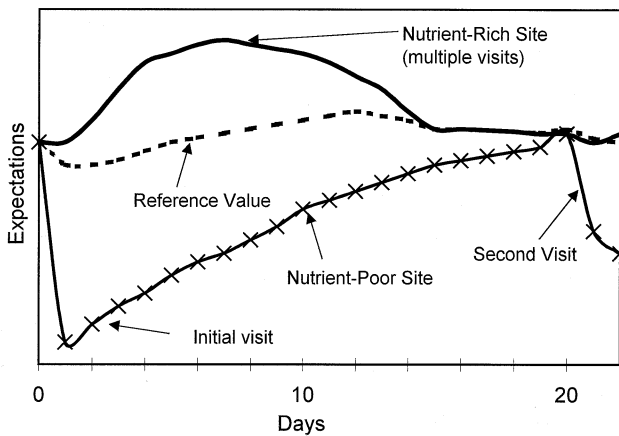
Although many foraging models ignore the cognitive abilities of animals, we submit that paradigms that disregard spatial memory (e.g., random search) may fail to accurately predict grazing distribution patterns of large herbivores because they do not recognize that animals can learn, retain, and react to previous foraging experiences. Livestock can remember areas that produce high quality forage and seek them out (Howery et al. 1996), and conversely, remember and avoid areas with low quality forage (Bailey 1995). Bailey et al. (1996) developed a conceptual model that incorporates spatial memory (Fig. 1). Their model predicts that selection of foraging areas is based on previous experience and that feeding sites are selected based on both abiotic and forage characteristics.

## Evidence of Spatial Memory in Livestock

Researchers have only recently begun to investigate spatial memory in livestock. Spatial memory has been studied in cattle (Bailey et al. 1989a,b, Laca 1998) and sheep (Edwards et al. 1996, Dumont and Petit 1998), as well as in a number of non-livestock species (Dyer et al. 1993, Healy and Krebs 1992, Langley 1994, MacDonald and Wilkie 1990, Noda et al. 1994, Olton and Samuelson 1976). When evaluating each piece of evidence, it is important to understand that other mechanisms can produce behaviors that appear to come from spatial memory. Laca (1998) discusses several mechanisms that can influence animal distribution and suggests experimental procedures to partition them from spatial memory. The anecdotal observations and experimental studies that follow are examples of how spatial memory can help explain many foraging behaviors.

## Observational and anecdotal evidence

Rangeland and livestock managers have observed that when animals are moved from a "home" pasture to a new pasture they congregate in and explore areas that are in the direction of the pasture they were moved from. This has been observed in cases where many miles of rough terrain separate the pastures. Spatial memory may also assist livestock that are familiar with a pasture to relocate preferred watering and feeding points (Howery et al. 1996).



**Figure 1.** Hypothetical simulation of expectations from nutrient-rich and nutrient-poor sites. Initially, an animal has no expectations and selects the poor site. However, because the perceived value is greater than the poor site, the nutrient-rich site is selected for 20 days. Repeated encounters with the nutrient-rich site causes its expectation to exceed the perceived site value for the first few days. The standard of comparison (reference value) increases and approaches the nutrient-rich site's expectation level in a few days because it is a moving average of perceived site values from encounters during the last 4 days. Repeated encounters with undesirable foraging sites occur rarely and are not reinforced. Within 20 days, however, memory of the encounter with the poor site decays to a level where the expectation for the poor site is approximately equal to the reference value, and the poor site is selected again (Modified from Bailey et al. 1996).

Some species of domestic and wild ungulates exhibit predictable distribution patterns that repeat year after year (Gruell and Papez 1963, Geist 1971, Festa-Bianchet 1986a,b, 1988, Cederlund and Okarma 1988, Cederlund et al. 1987). Sheep (Lynch 1974, Gluesing and Balph 1980, El Aich and Rittenhouse 1988), cattle (Hodder and Low 1978), goats (Biquand and Biquand-Guyot 1992), deer (Gillingham and Bunnell 1989), and moose (Andersen 1991) may walk long distances searching for preferred plants or habitats, often passing areas with abundant forage along the way. One explanation for this seemingly enigmatic behavior is that "long-term spatial memory" of an apparent safe home range area is passed from older to younger animals (Andersen 1991, Provenza and Cincotta 1993). For example, Geist (1977) suggested that bighorn sheep were unable to expand their established home ranges because young animals rigidly conformed to the range use patterns of their predecessors. Archaeological evidence along migration routes revealed that moose in Norway continued the same migration patterns for 5000 years despite deterioration of their range (Andersen 1991).

## Maze studies

Maze studies (i.e., radial- and parallel-arm) have clearly demonstrated spatial memory in birds and small mammals (Lanke et al. 1993, Olton and Samuelson 1976, Olton et al. 1977, 1978, 1981, Kovalcik and Kovalcik 1986), and have been recently used to study the same phenomenon in livestock (Bailey et al. 1989a). Cattle were as capable as other species (rats and pigeons) tested in 8-arm radial mazes. Cattle performed much better than expected by chance, evincing an accurate working memory (Bailey et al. 1989a). For example, cattle revisited a maze arm  $< 0.4$  times in the first 8 arm choices. Pigeons and rats reentered arms at a similar frequency (Beatty and Shavalia 1980, Roberts and Van Veldhuizen 1985). Working memory in cattle persists for at least 8 hours. Bailey et al. (1989a) removed cattle from a radial maze after they had consumed food in 4 or 8 arms and then returned the animals after a delay interval. Cattle were able to remember where they had foraged after delays of up to 8 hours but performed poorly, equivalent to chance levels, after delays of 12 hours. This decline in performance may have been an artifact of the experimental design. Trials were completed on successive days, 24 hours apart. After a 12-hour delay, cattle may not have distinguished between the delay interval within a trial (e.g., 0700 to 1900) and the 12-hour interval between trials (1900 to 0700). Rather than a failure of working memory, cattle in this study may have "reset" their working memory in anticipation of a new trial.

If food quantity or quality at a foraging location is consistent, this information also becomes an important component of reference memory. Cattle in a parallel arm maze were able to associate a location with the *quantity* of food found there and avoided locations with less food until areas with more food were exploited (Bailey et al. 1989b). Cattle are also capable of associating a location with the *quality* of food found there. Animals avoided radial arm locations with low quality food and selected locations with higher quality food first (Bailey and Sims 1998). The strength of association between food quality and spatial locations appeared to decline after 30 days because animals more frequently visited low-quality sites. Although this observation could have reflected a decay in reference memory, cattle may have been revisiting the low-quality sites to update their assessment of those locations. This behavior would be adaptive in natural environments where forage quality periodically changes across space and time (see Fig. 1).

## Arena studies

Arena studies can be characterized as a "bridge" between maze and field studies because they attempt to

quantify spatial memory in a controlled environment that approximates an open field (i.e., landscape level studies). Ksiksi and Laca (1995) found that steers were able to remember 4 food locations (from 64 potential locations) in an 0.62-acre arena for up to 45 days. In a much more difficult test involving 20 food sites (64 potential locations), steers maintained an accurate spatial memory for at least 15 days after being exposed to the arena 28 times (Laca 1998).

Arena experiments have also been instrumental in elucidating the role of vision as a critical component for the development of spatial memory. Arnold (1966a,b) was probably the first researcher to experimentally evaluate the relative importance of the senses (i.e., sight, smell, taste, and touch) in grazing behavior. Arnold's tests were primarily restricted to the bite and patch levels. He concluded that "preventing sheep from seeing what they ate had remarkably little effect on their total food intake and productivity", and that the sense of sight is important mainly in orientation of the animal in space. More recent studies (Bazely and Ensor 1989, Edwards et al. 1997, Howery et al. 1999a,b, Kidunda and Rittenhouse 1992, Ortega and Laca 1997, Renken et al. 1998) indicate that animals that learn to associate forages with visual cues forage more efficiently than without cues. For example, Howery et al. (1999a) found that steers searching for fixed or variable forage locations in a 1.58-acre arena with artificial visual cues spent more time feeding and less time in non-foraging activities than without cues (i.e., animals relying on spatial memory or random search). Animals exposed to fixed and variable forage arrangements with cues also located feed more efficiently and had higher intakes than without cues.

### Managing Animal Distribution

Experimental and anecdotal evidence strongly suggests that rangeland herbivores have well-developed spatial memories. This is not surprising because of the apparent adaptive value that a cognitive process like spatial memory affords free-ranging animals. Yet, more extensive tests in realistic grazing situations are necessary before grazing distribution can be reliably managed using our knowledge of spatial memory. With that caveat in mind, we offer some working hypotheses about ways to achieve desirable animal distribution patterns by applying the current understanding of spatial memory.

Management of animal distribution using spatial memory principles can be classified based on whether the manipulation is focused upon the animal or the environment. Manipulations of animals may be invasive (e.g., hormones, emetics, electric shock), moderately invasive (e.g., herding), or noninvasive (e.g., selection for

behavioral traits within or among breeds). On the other hand, environmental manipulations are those that are completely external to the animal; such manipulations (e.g., reward schedules, pasture configurations, visual cues) are intended to modify an animal's experience with the environment to alter their use of a particular location or habitat.

### Manipulating the animal

**Invasive techniques.** Hormones influence the spatial abilities of birds and mammals (Gaulin and Fitzgerald 1986, Hess and Birecree 1978). Males generally have better spatial memory than females, although there are notable exceptions depending on the adaptive value of spatial performance between the sexes (e.g., female brown-headed cow birds have better spatial memories than their male counterparts apparently because nest parasitism is a spatial task). Female rats given masculinizing hormones performed as well as males (Williams et al. 1990 op cit by Sherry 1998). Conversely, male rats gonadectomized shortly after birth perform about the same as females in radial mazes. Castration of livestock may produce a similar outcome, however, we know of no experiments that have compared the spatial capacities of cows, steers, and bulls. The potential for using these treatments in livestock management is remote but experimentation could be considered.

Animals have evolved 2 fundamentally different systems to protect them from hazards in their environment (Garcia and Holder 1985, Garcia et al. 1985). The gut-defense system protects animals from hazards to their internal environment (e.g., toxins in foods), whereas the skin-defense system protects animals from hazards in their external environment (e.g., predators). These 2 systems are stimulated by different events with different behavioral outcomes. For example, rats more easily associate taste stimuli with gastro-intestinal illness and audio-visual stimuli with shock (Garcia and Koelling 1966). Herbivores are no different from rats in this regard because they readily learn to avoid foods paired with emetics (see Provenza and Launchbaugh this volume) and places associated with electric shock. For example, steers were trained to avoid a designated "aversion area" in less than 2 days by using remotely controlled audio-electrical stimulation (Quigley et al. 1990). The audio signal alone was sufficient to keep steers out of the area after 4 days. Heifers that were shocked after entering an aversion area avoided it for 7 days, whereas heifers that were prevented from entering the aversion area with electric fence readily entered the area when the fence was removed (Markus et al. 1998). Goats wearing shock-collars learned within 30 minutes to remain within a designated area (Fay et al. 1989). Non-collared goats

remained close to collared goats and thus also remained in the designated area.

**Moderately invasive techniques.** Herding or drifting has been used for many years by rangeland managers to promote desirable distribution patterns in domestic livestock, typically sheep (Skovlin 1957). More recently, herding has been employed on public rangelands to decrease the amount of time that cattle spend in riparian habitats. In order for herding to be effective, the new area that animals are herded to must have adequate forage, cover, and water so they do not immediately return to their previous location. Moreover, initial efforts may need to be exercised daily to effectively modify a pleasurable spatial memory that ostensibly causes the distribution problem. For example, cattle on Idaho summer range were drifted from gentle to more rugged terrain in an attempt to achieve more uniform distribution across the grazing unit (Howery 1993). Although more forage, water, and shade were present in the rugged area, about half of the herded animals returned to the gentler terrain within 24 to 48 hours of being moved. A favorable memory of the gentle area apparently overrode any desire to remain in the rugged area. On the other hand, persistent herding over a series of years has proven effective in training cattle to use upland areas more and riparian areas less in mountainous terrain (Butler 1998). Animals eventually learn to associate a negative event (e.g., aggressive herding using horses and dogs) with the area they previously found attractive.

Another approach that has potential to enhance animal dispersion involves introducing animals to underused areas within a grazing unit the first day of the grazing season. Roath and Krueger (1982a) suggested that heavy cattle use of riparian areas might be reduced by changing the turn-in point so that animals are not initially exposed to a high resource location (i.e., riparian area). In a later paper, Roath and Krueger (1982b) recommended introducing naive animals to underused areas within grazing units so they would become "behaviorally bonded" to those areas. Naive animals would theoretically not be predisposed to overuse high resource areas because they would have no spatial memory or expectations of concentrated food rewards in specific locations on the grazing unit (Bailey et al. 1996, Laca 1998). However, naive animals may also exhibit lower productivity because of lower intake levels (Provenza and Launchbaugh this volume). This problem needs to be resolved before this approach can be considered practical to livestock managers.

**Non-invasive techniques.** Changes in grazing patterns and behavior can be accomplished by changing

animal species, breed, and perhaps individual animals (Bailey this volume). Grazing patterns differ among animal species and cattle breeds with some being more willing to use slopes and travel further from water. Grazing patterns also differ greatly among individual animals. These differences in grazing behavior may be related to the animal's spatial memory capabilities and temperament. In the future, managers may be able to select both within and between breeds to improve livestock grazing distribution.

Just as there may be genetic differences concerning forage or habitat selection within species or within livestock breeds, there may also be differences that are perpetuated socially (Mosley this volume). Ungulate offspring glean critical information from their mothers about the specific environment in which they are reared, such as the location of food, water, and cover resources. Thus, a young animal's spatial memory of a grazing unit is likely shaped early in life through exposure to a home range area with its mother. For example, replacement heifers returning to a grazing unit their second and third years of life tended to repeat their mother's or foster-mother's general location and habitat use patterns (Howery et al. 1996, 1998). Other researchers have also reported that offspring of both wild and domestic ungulates use the same general location they were exposed to by their mothers early in life (Hunter and Milner 1963, Geist 1971, Key and MacIver 1980, Festa-Bianchet 1986a,b, Cederlund and Okarma 1988, Lawrence and Wood-Gush 1988, Nixon et al. 1988, 1991). These studies suggest that ungulate herbivores apparently remember and respond to certain biotic and abiotic factors within their camps or home range areas. Thus, it would seem that waiting for animals to forget such information by moving them to another pasture is not a promising method to modify animal distribution. However, these findings do suggest an additional opportunity for managers to manipulate animal foraging and distribution patterns through animal selection. A herd's "spatial memory" of a pasture might be molded over several years by selecting animals with desirable distribution patterns that would ostensibly be transmitted to young herd members.

## Manipulating the environment

### Associative learning and reward schedules.

Animals can learn to associate specific behaviors, such as searching or moving in certain directions, with the consequences of the action (Skinner 1981, McSweeney this volume). Thus, within the proper context, animals will perform actions in order to obtain rewards such as food, water, or cover. The intensity and rate of a behavior depend on the "schedule of reinforcement"

(McSweeney this volume). In the jargon of experimental psychology, a “fixed interval” schedule of reinforcement is one in which a reward (food pellet) results from an action (pressing lever) only after a fixed time has elapsed. Animals learn to respond (i.e., perform the action) intensively just prior to the expiration of the fixed time, and to completely cease responding immediately after the reward is delivered. A “variable-interval” schedule of reinforcement involves a random time interval between rewards which results in a more constant response by the animal over time.

Laca (1998) studied a spatial analogue of temporal schedules of reinforcement. Cattle were exposed for a few weeks to either fixed or variable food locations that were not identifiable by any proximate cue other than spatial location. Steers developed contrasting search patterns that reflected their experimental treatment. When food was always in the same locations, animals used the long-term strategy (reference memory) of returning to places where food was previously found. Search efficiency was very high and animals traversed only a fraction of the experimental arena. Conversely, when food locations were randomly changed before each trial (i.e., long-term spatial memory rendered useless), animals used the short-term strategy (working memory) to avoid places visited within a trial. Search efficiency was low because animals explored most of the available area to find foods. Thus, animals apparently used reference or working memory depending on the spatial arrangement of foods: return to locations that previously contained food (fixed treatment, use reference memory), or, systematically search until food is located, avoiding previously visited sites that contained no food (variable treatment, use working memory).

More information is needed to determine if distribution patterns can be made more uniform by manipulating spatial reinforcement “schedules”. For example, managers might apply various spatial reinforcement schedules by manipulating fertilization or burning practices, or by strategic supplement placement. The configuration and timing of such treatments could be applied as fixed or variable reinforcement schedules depending on management objectives. However, the effect these practices might have on animal productivity must also be addressed (e.g., increased distance traveled and declining search efficiency).

**Spatial configuration of pastures.** Bailey and Rittenhouse (1989) asserted that the addition or removal of physical barriers are powerful tools to limit or vary forage and habitat choices of grazing animals. For example, choices can be limited by locating pasture fences to restrict cattle from critical habitats while providing

access to gentle inclines that afford passage to more rugged, well-watered, but underused country. Choices can be varied by subdividing large pastures to attain more homogeneity among forage patches. The more homogeneous the forage choices are within a pasture, the less likely animals will concentrate in certain areas (Bailey 1995). Conversely, the more heterogeneous a grazing area is, the more likely animals will overuse more desirable patches and avoid undesirable ones. Integrating spatial configuration of pastures with other range management techniques (e.g., judicious water and salt placement, prescribed burning) provides managers with additional tools to manipulate grazing patterns.

**Visual cues.** As stated earlier, visual cues have recently been shown to enhance the foraging efficiency of grazing animals (Bazely and Ensor 1989, Edwards et al. 1997, Howery et al. 1999a, Kidunda and Rittenhouse 1992, Ortega and Laca 1997, Renken et al. 1998). Animals using visual cues were more efficient in tracking variable and constant forage environments in small arenas (Ortega and Laca 1997, Howery et al. 1999a,b). Additional research is needed to determine whether strategic placement of visual cues can be used under field conditions to alter undesirable distribution patterns across landscapes.

### What Should Be Studied Next?

We have argued that until the underlying behavioral mechanisms responsible for aggregate distribution patterns are better understood, grazing behavior models usually will be site-specific. Although grazing behavior is always site-specific to some degree, understanding how ungulate herbivores use spatial memory will improve our ability to predict and desirably manipulate animal distribution patterns.

Numerous gaps remain in understanding the cognitive abilities of herbivores during foraging. For example, the persistence of reference memory has only begun to be examined. Effects of social interactions on spatial memory must be thoroughly evaluated because actions of herd members can override the actions of an individual (Lane et al. 1990). Current research has not thoroughly evaluated the cognitive abilities among or within livestock breeds. The ability of cattle and other species to solve complex spatial tasks needs further study. More complex tasks should be developed to further test the extent of spatial memory in large ungulates and to determine if some individuals are more adept than others. If there are individual differences in spatial abilities, are such differences inherited, learned, or both?

Many of the research ideas recently tested under controlled conditions need further evaluation in the field (surgical and hormonal treatments, visual cues, shock collars, etc.). Recent advances in navigational technology will provide new and improved ways to accurately track animal movements and behavior. For example, global positioning system (GPS) receivers have been incorporated into collars and placed on cattle and other animals. This new system can track animals within 15 feet and record their position at intervals of minutes to hours for periods of weeks to months. Data collected from GPS units might be used to test how manipulations of animals and their environment affect grazing distribution patterns across landscapes (e.g., Bailey et al. 1996).

In conclusion, recent research demonstrates that ungulate herbivores have excellent spatial memories. These abilities likely evolved as a survival mechanism to allow herbivores to forage more efficiently and safely. Increased understanding of spatial memory presents new opportunities to better predict where animals forage and to develop new management strategies to improve grazing distribution. Continued research at both basic and applied levels is needed to advance current understanding.

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