Potential for using visual, auditory and olfactory cues to manage foraging behaviour and spatial distribution of rangeland livestock

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Abstract

This paper reviews the literature and reports on the current state of knowledge regarding the potential for managers to use visual (VC), auditory (AC) and olfactory (OC) cues to manage foraging behaviour and spatial distribution of rangeland livestock. We present evidence that free-ranging livestock use these sensory cues to make decisions about foraging, drinking, habitat selection and spatial distribution, and to detect and avoid predators. This knowledge provides managers with opportunities to favourably alter behavioural patterns of rangeland ungulates. Opportunities to use sensory cues to shape livestock spatial distribution patterns arise primarily from the abilities of animals to: (a) learn to respond to cue–consequence associations that enhance their ability to adapt to changing foraging environments on rangelands, (b) generalize learned cue–consequence associations across spatial and temporal foraging scales and (c) influence one another's behaviour through social learning. Key literature on cue–consequence principles is initially reviewed from fine-scale studies (e.g., controlled studies conducted in mazes, arenas). Applications of cue–consequence principles are then highlighted from literature dealing with field-scale studies (e.g., controlled and observational studies conducted in large pastures or paddocks). We then discuss potential management implications derived from these studies. Finally, we summarize conclusions and recommendations for potential future research directions. The studies reviewed here suggest that VC, AC and OC associated with positive or negative reinforcers can be used to effectively direct livestock towards or away from selected areas. The feasibility of favourably altering grazing pressure on rangelands without having to build expensive, static fences has the potential to provide substantial economic and ecologic advantages.

Introduction

Domestic ungulates use all of their senses to make decisions on rangelands, however, the primary environmental cues that animals rely on likely depends upon the spatial scale at which decisions are made [1, 2]. At fine scales, sheep can visually discriminate between objects of different hue or brightness [3], which may be indicative of protein and energy content of natural forages. It is also well-documented that domestic animals can associate the odour and taste (flavour) of specific foods with positive and negative post-ingestive consequences and adjust their

intake accordingly [4]. At the landscape scale, herbivores may associate visual (VC) cues (e.g., windmills, vegetation patches, mountains, wildlife trails) with the locations of water, forage and shade [1]. Social models also provide VC, auditory (AC) and olfactory (OC) cues to herd members that may direct them towards the locations of food, water and cover, or away from predators [5–8]. At finer scales, VC, AC and OC are important modes of communication to quickly establish mother–young bonds in precocial animals that exhibit a 'follower' strategy [9]. Within days after birth, vocalizations are used by both dams and their young to identify and locate one another [10].

Researchers have conducted numerous pen and field studies designed to explore the importance of VC, AC and OC in ethological investigations of livestock [11–17]. Recently, studies have begun to focus on how managers might use these cues to achieve rangeland management objectives. The purpose of this paper is to review the literature and report the current state of our knowledge regarding the potential for managers to use VC, AC and OC to manage foraging behaviour and spatial distribution of rangeland livestock. We first review key literature dealing with cue-consequence principles derived from fine-scale studies (e.g., controlled studies conducted in mazes, arenas). We then highlight applications of cue–consequence principles by reviewing field-scale studies (e.g., controlled and observational studies conducted in large pastures or paddocks) and discuss potential management implications. Finally, we summarize conclusions and recommendations for potential future research directions. Our goal is not to provide a comprehensive review of all studies that involve VC, AC and OC, but rather, to provide an overview of key studies and fundamental concepts that are critical to the stated purpose and scope of this paper. Our review is written with the mindset that animals do not use VC, AC and OC independently, and that interactions among cues are common on vast rangeland landscapes where animals must distinguish and respond to a myriad of sensory stimuli.

Cue–consequence Principles Derived from Fine-Scale Controlled Experiments

Cues, consequences and learning

It is important that managers understand how animals receive and process cue stimuli so that they can develop effective training regimes that will produce appropriate animal responses [18]. Garcia *et al.* [19] reported that animals have evolved two distinct neurophysiological systems that help them cope with internal or external threats to their environment, collectively known as the *skin–gut defence system* [18, 20]. Animals learn through the skin-defence system to avoid painful stimuli inflicted by a predator or other external stimuli (e.g., electric

stimulation). Stimulation of the skin-defence system via electric stimulation results in location avoidance behaviour that is apparently triggered by fear. Accordingly, when an animal experiences electric stimulation that is administered from 'real' or 'virtual' fences, the skin-defence system is stimulated and the animal typically responds by withdrawing and avoiding the general location in which it received the stimulation. On the other hand, when an animal overingests nutrients or toxins, the gut defence system is stimulated resulting in conditioned food or flavour aversions (CFA). The primary sensory cues that animals use to detect external or internal threats are mediated via the skin- or gut-defence system. Although neural sensory receptors do not function independently, animals appear to rely mostly on VC, AC and less on OC to signal threats to the skin-defence system, and more on OC and taste cues (i.e., food flavours), and less on VC and AC to signal threats to the gut-defence system [19–21]. This phenomenon is referred to as *cue–consequence specificity* [18, 20].

Interactions among cues are likely to be a concern on vast rangeland landscapes where animals are subjected to a myriad of sensory stimuli, particularly given the fact that livestock can exhibit heightened attention to details that humans may not recognize as important [22]. Cue interactions have been scrutinized in CFA studies [23–26], as well as in electric stimulation-avoidance studies with rats [19, 27]. *Cue-blocking* is a phenomenon in electric stimulation-avoidance studies whereby prior conditioning to one cue effectively blocks an animal's ability to respond to a new cue [19, 27]. For example, an animal that is trained to associate a VC with electric stimulation, and is subsequently exposed to the same VC *plus a novel AC*, will form only a very weak association between the AC and electric stimulation. In other words, preconditioning to a VC stimulus with electric stimulation diminishes an animal's response to a novel AC [27]. Understanding how cue interactions can influence animal behaviour is particularly pertinent when developing training protocols using virtual fencing or other electric stimulation aversion systems.

Use of spatial memory and sensory cues in maze and arena studies

Maze and arena studies have been conducted to demonstrate how rangeland livestock and other animals can use spatial memory to locate food and habitat resources. For example, cattle used spatial memory to relocate food in mazes and arenas without the benefit of overt VC [28–30]. Other controlled studies with domestic livestock have demonstrated that spatial memory provides a mechanism for animals to remember where they have foraged and subsequently use that information to seek high reward areas and avoid low reward areas [31]. Researchers infer that animals have used spatial memory when their foraging or spatial

distribution behaviour can be predicted and measured as a result of prior experiences [32]. However, relying on spatial memory alone on vast landscapes would require rangeland herbivores to remember enormous amounts of information. Furthermore, the accuracy of spatial memory of free-ranging livestock would ostensibly become less reliable as heterogeneity and novelty among grazing paddocks change across space and time [31].

Sheep and cattle that learn to associate VC with preferred forages and habitat locations are much more adept at finding and consuming foods than animals relying on spatial memory alone, especially when food locations change across space and time [1, 3, 30, 33–35]. Auditory cues, VC and OC can serve either as positive or as negative stimuli and respectively assist animals to seek or avoid pleasant or unpleasant environmental consequences [35–37]. For example, dairy cows can learn to enter a milking parlour by associating AC with food rewards [38]. Rangeland cows can learn to associate wind chimes and other AC with the location of salt or mineral supplements [37], or can be gathered autonomously by playing recorded AC associated with previous manual gathering efforts [39]. On the other hand, livestock readily learn to avoid VC associated with negative consequences (e.g., electric fences) often after one trial [40]. Goats equipped with electric stimulation collars learned within 30 min to remain inside a designated safe area [41]. Steers rapidly learned (often in one trial) to avoid aversion areas demarked by VC (traffic cones) after receiving electric stimulation from collars [18]. Steers were also trained to avoid a designated aversion area in less than 2 days by pairing an AC with electric stimulation [42, 43]. By day 4, electric stimulation was not necessary because the AC alone was sufficient to keep the steers out of the aversion area [42]. Comparable results have been reported by researchers using electric stimulation equipment that was fitted around the muzzle [40, 41] or ear [44].

Sensory cues received from conspecifics and predators

Numerous studies have demonstrated that mothers, peers, and even live 'decoys' can serve as VC and influence the behaviour of other herd members. The role of a mother's influence on offspring diet and feeding site choices is well-documented, and these influences can sometimes last for years [4, 45]. Maternal influence on feeding site selection can be powerful and even override previous experiences that a young animal has had with 'safe' and 'unsafe' feeding sites. For example, ewes induced their lambs to enter 'unsafe' feeding sites that the lambs had been previously trained to avoid using electric stimulation collars [46]. On the other hand, electric stimulation-trained ewes induced their lambs to avoid a 'safe' high-quality (HQ) feeding site [46]. In the aforementioned study with goats [41], non-collared herd members remained close to collared cohorts and outside an aversion area negating the need to collar all animals in the herd to achieve the desired effect. In an 8-arm maze study with cattle, designated 'leaders' initially helped 'followers' to locate barley [47]. When leaders were removed from the maze, 81% of the followers were able to quickly find barley locations by themselves suggesting that cattle can learn the locations of HQ foods by observing one another's actions. Live sheep decoys have been successfully used to facilitate movements of other herd members through animal-handling facilities [48]. Decoys that were different in appearance from the majority of the herd or that were positioned to directionally face the herd hindered sheep movements [48].

As prey species, wild and domestic ungulates use VC, AC and OC to discern between 'friends and foes', and accordingly, decrease or increase their level of vigilance according to the cues received from heterospecifics or predators [49, 50]. In an arena study, individual cows decreased vigilance, increased foraging rates and increased use of HQ forage areas when OC and VC from deer (a heterospecific species) were placed near a HQ food. The opposite results occurred when OC and VC from wolves (a predator species) were placed near the HQ food [50]. In another arena study [51], sheep exhibited the following levels of increasing vigilance towards live animal stimuli: goats < humans < dogs, providing corroborating evidence for prey species being able to discriminate among potential friends and foes via sensory cues.

Applications of Cue–consequence Principles to Paddock or Landscape-Scale Grazing Environments

The evidence reviewed thus far clearly shows that domestic ungulates have the ability to associate sensory cues with either positive or aversive environmental consequences in fine-scale (often artificial) foraging experiments. Environmental cues in natural foraging environments likely enhance the spatial capabilities of free-ranging ungulates, allowing them to forage more efficiently across rangeland landscapes where the only constant is change [52, 53]. Therefore, the next logical step researchers have taken has been to determine whether learning that has occurred in fine-scale, controlled environments can be transferred and applied to natural rangeland landscapes.

Applying the concept of generalization to field-scale grazing environments

Generalization is the tendency of animals to respond similarly to like stimuli across different environmental contexts [54]. Renken et al. [55] tested the ability of

heifers to generalize VC associations that animals had initially learned in pens to a rangeland setting. Heifers were first trained in pens to associate VC with a protein (15% CP) supplement. Heifers were then placed in a semi-desert field site dominated by HQ and low-quality (LQ) Lehmann lovegrass (*Eragrostis lehmanniana*, Nees) patches. The researchers subsequently utilized the same VC that were employed during pen training (traffic cones) to test animal responses to cued and non-cued Lehmann love-grass patches growing naturally at the field site. Heifers spent more time grazing in both HQ and LQ patches when the VC was placed within those patches. However, heifers preferred HQ over LQ patches regardless of VC presence or absence, suggesting that positive, post-ingestive feedback that animals experienced while grazing in non-cued HQ patches overrode VC presence in LQ patches [4].

Targeted grazing (TG) is defined as ' . . .the application of a specific kind of livestock at a determined season, duration, and intensity' [56]. The objectives of TG vary but can involve reducing the risk of unwanted wildfires, improving wildlife habitat, managing invasive plants, and providing other ecosystem services [57]. Targeted grazing projects that use cattle typically combine low-stress herding to attractive supplements that have been placed in 'target' areas for the purpose of concentrating livestock utilization to accomplish specific vegetation management objectives [58]. Frost *et al.* [59] recently described how managers in Nebraska trained 150 heifers to associate surveyor's tape (VC) with a low-moisture block (LMB) supplement. After a training period, the surveyor's tape was tied to trees above a 114 kg barrel containing the LMB supplement that was placed in areas dominated by cheatgrass (*Bromus tectorum* L.), an exotic annual cool season grass from southwestern Asia. When cattle were herded to locations where the surveyor's tape was visible, their previously trained response in pens was to seek the LMB. Because cheatgrass was still green and palatable, cattle heavily grazed this invasive annual grass, preventing it from going to seed while consuming the LMB. Cattle were rotated through several pastures where the VC and LMB supplement were relocated. In addition to controlling cheatgrass, cattle were herded to ungrazed upland locations where VC and LMB had been placed in ungrazed areas that contained decadent native forage. Thus, this TG project effectively used the animals' ability to generalize a trained VC association to manage cheatgrass while expanding forage utilization into native rangeland areas not normally utilized by cattle.

Virtual fencing: a tool to manage livestock spatial distribution using sensory cues

Virtual fencing is a relatively new and innovative method to control and move free-ranging animals on a landscape by applying basic principles of *cue–consequence specificity*

to stimulate the animal's *skin defence system* [18, 20]. According to *cue–consequence specificity theory* (explained earlier), VC and AC are more likely to be used by animals to predict potential insults (e.g., electric shock) to the skin-defence system than are OC. Accordingly, virtual fencing systems have typically used either VC or AC and electrical stimulation cues to alter an animal's forward movement. Fay *et al.* [41] suggested that the presence of the wire necessary to produce the electronic signal when laid on the soil surface provided a VC to goats. Quigley *et al.* [42] described a training protocol that involved humans and electric fence serving as VC, which helped cattle to initially delineate the boundary of an exclusion area. Training involved humans standing along the boundary of the exclusion area and raising their hands as cattle approached and attempted to penetrate the electronic boundary. Preliminary research investigating the use of a VC in the form of an electronic flashing light located near the corner of an animal's eye and tactile (vibration) cues have also been evaluated [60] and appear promising.

Goats were the first domestic livestock species controlled using virtual fencing [41]. Since then, virtual fencing has mostly been tested on cattle [42, 61–63], however, sheep [64] and even ponies [65] have also been successfully controlled. Most virtual fencing requires the animal to carry an electronics package that is capable of receiving an externally generated electronic signal that defines a non-visible boundary most frequently in the radio frequency (RF) range with current virtual fencing RF coming from satellites [66]. The RF signals are used to activate AC and electrical stimulation cues necessary for making the animal aware of invisible boundaries. Power is supplied to the electronics from batteries, some housed within the electronics package itself [42, 62, 64] or mounted separately on the collar [60]. In other designs, the battery hangs below the cow's neck and solar panels on top of the electronics package provide power to trickle charge the batteries [67]. A more compact electronic equipment package has been proposed but has not yet been field-tested [68].

Providing reliable and consistent power remains a major challenge to commercializing virtual fencing. Research suggests that powering down the system at certain non-critical times such as when animals are not active [69], as well as duty cycling (i.e., periodically turning off the device) to provide discontinuous aversive stimuli [44], appears promising for extending the battery life of virtual fencing systems. Recently, Umstatter *et al.* [70] reported that animals can learn to associate AC that are broadcast from loudspeakers with virtual boundaries eliminating the need for animals to carry batteries. However, this type of static control may only be practical in smaller paddocks. If the management goal is to reduce but not completely eliminate the use of certain areas of the landscape the use of discontinuous aversive cues show considerable promise [44].

Regardless of when and how sensory cues are applied, adopters must be able to tolerate occasional inappropriate responses and 'leaky boundaries' because modifying the temporal and spatial movements of animals via virtual fencing is not yet an exact science. Research into the variety of behavioural responses that free-ranging livestock can exhibit when given various sensory cues associated with virtual fencing have only begun to be documented. For the cues to produce the correct behavioural response, i.e., for animals to turn away from the virtual boundary perimeter, a period of training is required [40–44]. However, there is no established protocol that has been consistently followed for the purpose of training animals in virtual fencing experiments. Because animal behaviour has a potentially wide range of responses to the same stimuli the sample size used to achieve statistical validity may need to be considerably larger than those deemed acceptable for animal nutrition studies [60].

With virtual fencing, the paddock geometry can take any shape and result in a polygon for either including or excluding livestock from environmental VC (e.g., soils, plant communities, topographic features and other animals [71]). Most field studies to date have attempted to contain animals within a polygon that is either held stationary on the landscape [62, 72] or that can be moved spatially and temporally across the landscape at various rates based on management goals [62, 73]. In addition, virtual fencing has been successfully used to exclude selected bulls from a polygon that contained a cow in induced oestrus in Australia [71, 74].

Directional virtual fencing (DVF™) [67, 75] is a unique kind of virtual fencing that applies increasing levels of an AC followed by ramped electrical stimulation selectively applied to one side of an animal's head to induce a prescribed change in its direction of movement [75]. The intensity of the stimuli administered is dictated by the distance the animal penetrates into a virtual boundary (VB™) and the level of stimulation required to change the animal's direction of forward travel [67, 75]. Because laterality is a ubiquitous animal trait [76], the DVF™ is programmed to detect the angle at which an animal approaches the virtual centre line (VCL™) and stimulate the side of the cow's head that will be most likely to elicit a desired change in travel direction with the least stress. No universally accepted animal-based scale exists for ranking level of cue stimulation. However, scales of relative energy comparisons among different electronic devices have been published [77]. Although 'proof-of-concept' has revealed that DVF™ is a viable method of changing the movement direction of free-ranging cows, its use to date has been limited to 3–12 devices deployed on numerous head of cattle in different seasons and among different years.

Pilot studies conducted in extensive desert grazing paddocks of New Mexico, which monitored livestock heart rates suggest that animals are not adversely stressed by wearing the DVF™ equipment or by encountering the VB™ [72, 78]. In an Australian study, steers were given electrical stimulation while restrained in a crush and evaluated for blood cortisol and β-endorphin levels; results showed no difference between control and treated animals [79]. Quigley et al. [42] reported that cattle controlled with a pet containment system returned to foraging shortly after being cued. Similar patterns were observed by Anderson [61].

The number of animals that need to be instrumented in order to control the entire herd is an important issue in the implementation of virtual fence systems. Quigley et al. [42] found that cattle instrumented with virtual fencing devices that fail to respond correctly to program cues may be willing to follow non-controlled cattle regardless of the sensory consequences. Anderson [77] observed that non-instrumented steers remained in the proximity of conditioned cows fitted with the DVF™ equipment. Thus, cues derived from social interactions (see next section) could allow managers to equip a few key individuals in a herd which may be critical to the success of virtual fencing systems in free-ranging commercial livestock operations.

Social models provide sensory cues that influence animal distribution patterns

Gregarious ungulates may provide VC, AC and OC to other herd members when leading naïve conspecifics to critical habitats, such as the location of food, water, and cover in foraging environments [52, 80]. Naïve herd mates that follow and learn about foraging environments from experienced animals generally spend less time exploring their environment, ingest more forage, suffer less from predation and malnutrition, and ingest a fewer toxic plants than animals foraging alone [81]. Wild ungulates are well-known for exhibiting predictable landscape distribution patterns due to transgenerational learning of traditional migration patterns from experienced herd members [82–85]. Domestic livestock have shown similar tendencies as a young animal's diet and habitat selection patterns are influenced by mothers and peers [7, 8]. Furthermore, research has demonstrated that behaviour modification (bonding) of small ruminants to cattle through sensory modification, preferably soon after weaning, can facilitate mixed-species stocking [86]. As a result of bonding, flerds [87, 88] have been shown to receive less predation from canines, require less labour in carrying out husbandry practices, and provide sheep and goat control without conventional small ruminant-proof fencing. Bonded small ruminants with cattle also exhibit better distribution over a landscape during foraging compared with a group of non-bonded small ruminants (flock) and cattle (herd) foraging simultaneously in the same paddock [88, 89].

Management Implications

Manipulating animal distribution with sensory cues

This review has presented evidence from both fine- and field-scale studies, which clearly indicates that rangeland livestock use sensory cues (i.e., VC, AC and OC) to make decisions about foraging, drinking, habitat selection and detecting or avoiding predators. This knowledge provides managers with opportunities to favourably alter behavioural patterns of rangeland ungulates [37]. Opportunities to use sensory cues to shape livestock distribution patterns arise primarily from the abilities of animals to: (a) learn to respond to cue–consequence associations, which enhances their ability to adapt to changing foraging environments on rangelands [1, 18, 81]; (b) generalize learned cue–consequence associations across spatial and temporal foraging scales [55]; and (c) influence one another's behaviour through social learning [8, 90, 91]. Hence, training livestock in confinement to associate sensory cues with avoidance- or preference-eliciting stimuli would allow managers to use these concepts to strategically and tactically manipulate livestock behaviour in large paddocks. Creative rangeland managers could shift their efforts towards manipulating associations between cues and habitat attributes in order to tailor training regimes for livestock to use rangeland resources more effectively. Reasons for doing this would vary according to management objectives but could include implementing concepts associated with virtual fencing, using social models as environmental cues, and addressing TG or other rangeland management objectives (e.g., reducing the risk of unwanted wildfires, improving wildlife habitat, managing invasive plants and expanding use of underutilized forage).

Management implications of using virtual fencing

Virtual fencing for livestock control will not provide a panacea for managers when it becomes available commercially. However, understanding how sensory cues can be optimally applied to plant–herbivore interactions managed with virtual fencing will lead to proactive management of domestic herbivores across rangeland landscapes. It is important to note that using punishment via the skin defence system to manipulate livestock spatial patterns can in some instances generate undesirable side effects. For example, animals subjected to the presence of predators increase vigilance, spend less time foraging, avoid HQ habitats [50, 92–95], or respond in other counterproductive ways that may be detrimental to animal production objectives (e.g., weight gains, milk and wool yields, reproductive performance) [43]. Laca [96] suggested that it would be more desirable and effective to design behavioural systems that 'chained' cues associated with *positive* reinforcers in the natural environment rather

than using punishment. Using positive reinforcement would ostensibly accelerate shaping of desired behavioural responses and simultaneously reduce unwanted behaviours [96]. A study in Arizona [57] (described below), and the aforementioned TG study in Nebraska [59], both applied positive reinforcement training principles that were learned, generalized and transferred socially by cattle from fine to coarse spatial scales.

Management implications of using social models

While it is clear that managers can use sensory cues to manipulate animal distribution, whether animals choose to remain or return to desired locations will depend on the ability of the site to continue to meet animal needs [80], as well as the ongoing behavioural dynamics of the herd. Gregarious ungulates are naturally social animals and their foraging behaviour and distribution patterns are strongly influenced by one another, especially mother and peers [33, 45] as well as through peer and interspecies associations [8, 88, 93]. In a recent TG study in southern Arizona [57], cow–calf pairs were trained to eat a LMB supplement and quickly became accustomed to low-stress herding being associated with finding LMB 'rewards' that were placed in upland areas dominated by unused Lehmann lovegrass monocultures. After being herded to a targeted area, cow–calf pairs created and used new trails to navigate to and from the TG sites on their own volition, and remained in or near these sites until all the LMB supplements had been consumed. Herd dynamics and social cues provided by conspecifics, including VC, AC and OC, likely contributed to the significantly higher utilization rates of Lehmann lovegrass observed in the TG sites compared with control sites [57]. Social models have also been observed to influence animal spatial distribution patterns in other studies applying TG concepts [97].

Careful manipulation of social influences can help shape animal cultures [98], which can promote persistence of learned cue-stimulus associations across multiple generations [99]. Managing groups of animals in ways that promote social learning (mother–infant, leader–follower, experienced–naïve) has the potential to reduce the effort and cost involved in applying periodic reinforcement schedules. For example, location avoidance training, used together with maternal learning, might prove to be an important management tool to manipulate the spatial distribution of grazing, and over time, reduce the need for electric stimulation applied to all herd members by training 'social models' (cows, ewes) that could act as VC. On the other hand, our research [90, 91] suggests that induction of social-learning of food and feeding site *preference* has higher success rates than the converse (i.e. social-induction of food and site *avoidance*). These findings would agree with Laca's [96] aforementioned implication that the 'carrot' may be mightier than the 'stick' for

managers to use as a tool to work with, rather than against, the nature of rangeland animals [22, 58]. Increased understanding and use of animal behaviours that result from sensory cue responses will result in more humane and efficient management strategies.

Conclusions and Suggestions for Future Research

Rangeland managers have historically attempted to favourably alter animal spatial distribution in large paddocks by placing 'rewards', such as salt or other attractive supplements in locations where greater forage utilization is desired [100–102]. While these time-honoured approaches can be effective, they could be enhanced by introducing VC, AC and OC and social models as part of the training process [80, 103]. Again, the choice of cue and consequence will vary with the scale of desired response and associated management objectives. The studies reviewed here suggest that sensory cues associated with positive or negative rein-forcers can be used to direct livestock towards or away from selected rangeland areas. The feasibility of favourably altering grazing pressure on rangelands without having to build expensive, static fences has the potential to produce economic and ecologic advantages. Although this paper documents that much has been learned we suggest there is a need for additional studies in the following areas:

(a) How do various stocking densities, rotations, and other conventional rangeland management practices influence the ability of animals to learn and apply cue consequence associations [104]?

(b) How do aversive versus positive and/or fixed versus variable reinforcement schedules influence animal learning?

(c) Which social models are most effective in perpetu-ating the persistence of trained behaviours (e.g., mothers, peers, inter- versus intraspecific leaders, herders, flerds)?

(d) Can managers exploit individual variability in will-ingness and ability to learn and respond appropriately to environmental cues [105–107]? What role does breed play? Is ability to learn correlated with other desirable behavioural traits?

(e) Are there innovative ways to manage herd social structure (e.g. maintaining family or breed groups) to enhance learning and strengthen desired animal behaviours and cultures?

(f) What influence do training protocols have on live-stock production metrics (e.g., weight gains, milk and wool yields, reproductive performance)?

(g) How does the ratio of cues to consequences or duty cycling influence animal responses in virtual fencing studies?

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