DISSERTATION

THE SKILL OF MANAGERS AND THE WISDOM OF HERDS: EXAMINING AN ALTERNATIVE APPROACH TO GRAZING MANAGEMENT IN LARKSPUR HABITAT

Submitted by

Kevin E. Jablonski

Department of Forest and Rangeland Stewardship

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2019

Doctoral Committee:

Advisor: Paul J. Meiman

Randall B. Boone
María E. Fernández-Giménez
Troy W. Ocheltree

ABSTRACT

THE SKILL OF MANAGERS AND THE WISDOM OF HERDS: EXAMINING AN ALTERNATIVE APPROACH TO GRAZING MANAGEMENT IN LARKSPUR HABITAT

The many species of larkspur (*Delphinium* spp. L.) are among the most dangerous poisonous plants on rangelands in the western United States, causing death losses estimated at 2-5% (up to 15%) per year for cattle grazing in larkspur habitat. Research has estimated the value of these losses at $234 million per year. Other effects, such as altered grazing management practices and consequent lost forage quantity and quality, are significant but poorly understood. Current best management practice recommendations stress seasonal avoidance of pastures with larkspur present, with little evidence that this is practical or ultimately effective. Alternative approaches to addressing this complex challenge are difficult to design, test, and apply due to the threat of dead livestock.

In this dissertation I explore an alternative approach based on the idea that it may be possible to manage cattle grazing such that no individual consumes a lethal dose, regardless of timing of grazing or larkspur density. This idea was inspired by producers past and present who have reported such success. I examine this hypothesis using agent-based models and a field experiment with Geyer's larkspur (*D. geyeri* Greene), the focal species throughout this research.

Chapter 2 presents a conceptual model that situates this work within the broader context of livestock grazing management and rangeland science. This synthesis also highlights the potential for conceptual models to aid in the design, application, communication, and consilience of research in rangelands. Drawing on a wide range of work, this model challenges the discipline of rangeland science to integrate a broader array of methods and epistemologies to create knowledge sufficient to the complexity of the systems under study.

Agent-based models (ABMs) provide an effective method of testing alternate management strategies without risk to livestock. ABMs are especially useful for modeling complex systems such as livestock grazing management and allow for realistic bottom-up encoding of cattle behavior. In Chapter 3, I introduce a spatially-explicit, behavior-based ABM of cattle grazing in a pasture with a dangerous amount of *D. geyeri*. This model tests the role of herd cohesion and stocking density in larkspur intake, finds that both are key drivers of larkspur-induced toxicosis, and indicates that alteration of these factors within realistic bounds can mitigate risk. Crucially, the model points to herd cohesion, which has received little attention in the discipline, as playing an important role in reducing lethal acute toxicosis. As the first agent-based model to simulate grazing behavior at realistic scales, this study also demonstrates the tremendous potential of ABMs to illuminate grazing management dynamics, including fundamental aspects of livestock behavior amidst ecological heterogeneity.

Chapter 3 raises the question of the potential response of larkspur to being grazed. In Chapter 4, I examine the response of *D. geyeri* to two seasons of 25% or 75% aboveground plant mass removal. The 75% treatment led to significantly lower alkaloid concentrations (mg•g^{-1}) and pools (mg per plant), while the 25% treatment had a lesser effect. Combined with lessons from previous studies, this indicates that Geyer's larkspur plants subject to aboveground mass removal such as may occur via grazing can be expected to become significantly less dangerous to cattle. We suggest that the mechanisms for this reduction are both alkaloid removal and reduced belowground root mass, as significant evidence indicates that alkaloids are synthesized and stored in the roots.

The most common explanations for the evolution and persistence of herd behavior in large herbivores relate to decreased risk of predation. However, poisonous plants such as larkspur can present a threat comparable to predation. Chapters 3 and 4 point to the cattle herd itself as the potential solution to this seemingly intractable challenge and suggest that larkspur and forage patchiness may drive deaths. In Chapter 5, I present an agent-based model that incorporates neutral landscape models to assess the interaction between plant patchiness and herd behavior within the context of poisonous plants as predator and cattle as prey. The simulation results indicate that larkspur patchiness is indeed a driver of toxicosis and that highly cohesive herds can greatly reduce the risk of death in even the most dangerous circumstances. By placing the results in context with existing theories about the utility of herds, I demonstrate that grouping in large herbivores can be an adaptive response to patchily distributed poisonous plants. Lastly, the results hold significant management-relevant insight, both for cattle producers managing grazing in larkspur habitat and in general as a call to reconsider the manifold benefits of herd behavior among domestic herbivores.

The findings in this dissertation build a strong case for an alternative approach to grazing management in larkspur habitat but fall short of actionable recommendations. For one, this is because a one-size-fits-all solution that would work across the great diversity of habitats and management systems in which larkspur is found is unlikely. Instead, these findings must be placed in context with existing knowledge and the complex multiscale decision-making processes of producers. Future work will thus focus on improving our understanding of the diverse set of management circumstances under which the many species of problematic larkspur are found.

ACKNOWLEDGEMENTS

I have been blessed to be part of a wonderful university community that is supportive and stimulating. Due in large part to my membership in this community, these past four years have been a time of significant intellectual and personal growth for me. This begins with my advisor, Paul Meiman, who has treated me as a colleague from day one. I have done my best to act the part. Paul's humility, kindness, and thoughtfulness have inspired me throughout, and I owe him an unpayable debt of gratitude for taking a chance on me.

María Fernández-Giménez generously invited me to participate in her Rangeland Social-Ecological Systems lab group and has consistently made the time to mentor me. In doing so, she has helped to open my eyes to a different way of looking at the questions that interest me, which is now so integral to who I am that it is easy to forget that it started with María's invitation. Randy Boone pointed me toward agent-based modeling in our first meeting and has patiently guided me through the modeling process from idea to publication. I appreciate his careful consideration of modeling minutiae, thorough editing, and always-open door. Troy Ocheltree has kept me honest on plant physiology and his humor, wit, and enthusiasm brightened every meeting.

Among the faculty, Michael Falkowski, Suellen Melzer, Dhruba Naug, and Mark Paschke taught engaging classes, brought new elements to my work, and modeled effective teaching and scholarship. Linda Nagle, who arrived as department chair the same year that I started, has been an unwavering advocate for an inclusive and communal learning environment for graduate students. I am also indebted to her for providing critical early support for my growing work in East Africa. CSU administrative staff too numerous to mention provided timely, effective assistance.

My fellow graduate students have been a source of inspiration and levity. Hailey Wilmer set the bar high and showed me I could reach for it without losing myself. Jasmine Bruno, Sarah Carroll, Jake Courkamp, Dominique Davíd-Chavez, Chris Dickey, Kristin Hoelting, Megan Jones, Tomas Pickering, Jordan Spaak, Alex Stoneburner, and Thomas Timberlake have argued with me, enlightened me, made me laugh, and made me think. Tanner Marshall worked with me for two field seasons and, through his thoughtful questions and hard work, advanced the work substantially.

At the Center for Collaborative Conservation, I am grateful to Robin Reid, Kim Skyelander, and Ch'aska Huayhuaca for their devotion to an all-important cause, and for choosing me as a CCC Fellow. Robin in particular has encouraged me in a few key moments which, coming from her, meant the world. A Sustainability Leadership Fellowship with the School of Global Environmental Sustainability has changed the way I talk about the work I do and given me the confidence to make an elevator pitch. Aleta Weller deserves tremendous credit for her work to make that program the success that it is.

My friends and colleagues at Lion Guardians have helped me to connect my interest in livestock grazing management to broader conservation questions, greatly expanding my horizons. For welcoming me into that conversation and respecting what I had to say, I am grateful to Stephanie Dolrenry, Leela Hazzah, Philip Briggs, John Merishi, and Luke Maamai. Closer to home, David Augustine, Sam Fuhlendorf, Fred Provenza, Randy Reichert, and Doug Tolleson have at various points expressed support for my work, encouraging me that I could make a difference in rangeland science.

Joel Vaad, manager of the CSU Research Foundation Maxwell Ranch, has always welcomed us onto the ranch to do our work and unreservedly shared his experience and insights. Dale Gardner of the USDA Poisonous Plants Laboratory generously tested larkspur samples and provided important information and feedback. Michael Smith and the Sims family of McFadden, WY provided a real-world verification that proper management could resolve the challenges presented by larkspur, an invaluable contribution to this research. Retta Bruegger and John Rizza are living evidence of the role extension can and should play in translating science into action, and simply fun people to work with. My wife Becca exemplifies my hope that hard work, meaningful work, and success need not be mutually exclusive, and my daughter Lila provides snuggles when I needed them most.

Lastly, I am ever-grateful to the people who taught me to love livestock. Bee Tolman, shepherdess and old-order New England contrarian, opened the door to a naïve suburbanite and spent years patiently teaching me to see everything that I was missing. Eve Ann Shwartz and Harmon Hoff shared all they know about beef cattle, though I am afraid I only absorbed what I was ready to learn. Their immense love for their land and their community is a model for the agrarian renewal desperately needed across rural America, and a continual inspiration to me for the difference that individual lives, well-lived in one place, can make. Troy Bishopp introduced me to the broader conversation about the role of human managers in the lives of grazing livestock, a conversation to which I hope this dissertation contributes.

This work was supported by funds from the Colorado State University Agricultural Experiment Station (grants AES-0650 and COL00770) and the Colorado State University Research Foundation. DigitalGlobe provided a generous imagery grant that greatly improved our ability to remotely assess forage distribution, and Hexagon Geospatial provided the software to analyze the imagery.

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

Plant poisoning of grazing livestock has been estimated to cause more than $500 million in annual losses in the US livestock industry (Holechek, 2002) and been the subject of thousands of research articles dating back more than a century (Knight and Walter, 2001). In nearly all of this literature, there appears to be an underlying assumption that "poisonous plants" are a discrete category of plants, distinctly different from other plants. "Poisonous plants are not considered as forages for livestock", say James et al. (1992).

However, the few definitions of poisonous plants that exist tend to define them not by their characteristics but by their effects, even in a paper that simultaneously reifies the group. "A plant can be defined as poisonous only in terms of its toxic effect on the animal that consumes it", write James et al. (1992). While the distinction between a focus on plant poisoning as a phenomenon and poisonous plants as the cause of that phenomenon might seem a subtle one, it has important ramifications for research and for producer outcomes.

A research paradigm is a "loose collection of logically related assumptions, concepts, or propositions that orient research and thinking" (Bogdan and Biklen, 2003, p. 22). Research paradigms define for a scientific community what subjects are worthy of study, the methods used to study them, and the interpretation of results (Kuhn, 2012). If the research paradigm states that there is a category of plants with uniquely dangerous characteristics that cause significant problems for livestock managers, it follows that the appropriate subjects are the plants themselves, and that applied research should focus on understanding how livestock can avoid eating them. On the other hand, if the research paradigm states that poisonous plants are not unique and that the challenge instead is the process of poisoning itself, it follows that the appropriate subject is the interaction between plants that might cause poisoning and the livestock that they may poison.

Starting with research by Fred Provenza and others in the 1990's, significant evidence has now accumulated indicating that the old binary of poisonous/non-poisonous is false. As Provenza wrote:

> "Thus, where we once thought only poisonous plants– those species that for one reason or another are a problem for herbivores– contain compounds that are potentially toxic, there is increasing awareness that all plants, including garden vegetables, contain toxins that limit intake." (2003a, p. 5)

We also know that these toxins generate post-ingestive feedbacks that causes the herbivore to seek homeostasis by consuming different plants, perhaps as a form of self-medication (Villalba and Provenza, 2007). This is part of a complex adaptive foraging process whereby herbivores are also seeking adequate nutrition while meeting other non-foraging needs (Provenza et al., 2003b).

Because plant toxins are ubiquitous and livestock are continually seeking to mitigate their effects as part of a complex process, the question of most importance is how the interaction between livestock and the plants that frequently kill them differs from the interaction with plants that do not. Such an approach should aim to understand how humans can assist the evolved capacity of livestock to mitigate the effects of even the most dangerous toxins. Unfortunately, much of the research on plant poisoning continues to reside within the outdated paradigm of poisonous plants as uniquely dangerous and ideally avoided, with little existing research on the ecological process of poisoning.

The chapters of this dissertation represent part of an ongoing effort to look at livestock poisoning by larkspur, a process responsible for tens of thousands of cattle deaths and hundreds of millions of dollars of losses every year in the western US (Knight and Walter, 2001), through this different lens. Instead of either seeking to eliminate these beautiful native plants or avoid having cattle eat them (what we term "fight or flight"), might it be possible to use agile grazing management and the innate intelligence of the herd to enable cattle to graze in larkspur habitat at any time of year, with the herd interacting with larkspur such that all eat some but none consume a lethal dose?

Chapter 2 situates this question within the broader discipline of livestock grazing management research. Though I managed grazing livestock for several years under a variety of rotational schemes, I began my studies with little formal training in the subject. I thus sought a firm conceptual and philosophical foundation on which to build my research. Finding that none was apparent in the literature, and that certain persistent disagreements seemed to exist primarily because of this, I sought to build one for myself. The synthesis paper presented is the result of that effort.

In Chapter 3, I describe an effort to understand the relationships among grazing management, herd behavior, and poisoning by Geyer's larkspur (*D. geyeri* Greene) as manifested on a single pasture on a single ranch. Because of the practical and ethical difficulty of testing this with living cattle, I instead sought a simulation-based method for doing so. This led to the creation of the first agent-based model incorporating individual grazing cattle, which simulated interactions between larkspur and cattle managed for different levels of stocking density and herd cohesion. The results offer significant insight into the drivers of larkspur poisoning and point toward the potential for a computational revolution in livestock grazing management research.

This would not be a true range management dissertation without a plant experiment, so I offer Chapter 4 as evidence of my worthiness for admission to the pantheon. Having learned that there is potential for cattle to be managed to graze larkspur without dying, we sought to understand how the plants might respond. Specifically, we tested the influence of two years of differing levels of aboveground mass removal, as might be expected to occur via grazing, on the toxicity and vigor of *D. geyeri*. The results of this experiment add to our understanding of larkspur-cattle dynamics and suggest that some of our problems with larkspur may be self-created.

The results from Chapters 3 and 4 led to questions about the interaction of livestock distributional heterogeneity with forage and larkspur patchiness. To test these questions, in Chapter 5 I again describe an agent-based model, in this case one that incorporated neutral landscape models to generate pastures with differing larkspur patchiness and levels of overlap between larkspur and forage. By placing the results in a behavioral ecology context, we can not only learn about the importance of larkspur patchiness to poisoning of cattle, but also contribute to existing theory on the evolution and utility of group behavior in large herbivores. In Chapter 6, I summarize the findings and discuss future directions for integrating these findings into producer-relevant recommendations.

Notably lacking from these chapters are the voices of the producers affected by larkspur poisoning of cattle. This should not be taken to suggest that they are unworthy of consideration, but only that we have not yet begun that essential element of the work. Indeed, in this dissertation I do not present management strategies or otherwise draw firm management conclusions for precisely that reason. Also note that each chapter has either been published, is under review, or is in preparation for publication in an academic journal, making this a "dissertation by publication". While this greatly eases the translation of dissertation chapter to journal article, it does lead to some repetitiveness for which I beg the reader's pardon.

1.1. POSITIONALITY

"A researcher's background and position will affect what they choose to investigate, the angle of investigation, the methods judged most adequate for this purpose, the findings considered most appropriate, and the framing and communication of conclusions." (Malterud, 2001, pp. 483–484)

"Of course there are several different ways to be." (Carson, 1998, p. 4)

That the "who" matters, along with the "what", "why", "how", and "when", in creating scientific knowledge is beyond debate. From physics to ecology to economics to sociology, we know that the observer can have a profound effect on not only the choice of question and method, but also on the measured response (Monahan and Fisher, 2010). As with many epistemological matters, the social sciences lead the way on this, with the reflexive identification of one's position as a researcher a fundamental element of many social science methodologies (Bourke, 2014; Rose, 1997). This dissertation is not a work of social science. Nevertheless, who I am and have been during the research described here is important, not only for me to consider but also for the reader to understand. That such communication is mostly lacking in the literature of my chosen discipline, rangeland ecology, represents a methodological failure. The successful conduct and communication of a usable science (Meiman et al., 2016) increasingly depends on our recognition of the simple fact that who we are matters.

However, this is no minor endeavor. We are each made up of many overlapping, sometimes conflicting, identities (Stets and Burke, 2000); we each "contain multitudes" (Whitman, 1897, p. 78). Considering these in relation to the questions we ask and how we go about answering them is difficult and made more so by our interactions with other equally multitudinous individuals. Include our interactions with the vibrant variety of the more-than-human (Abram, 2012) world and the simple act of asking a question becomes daunting. Nevertheless.

I am the bone-deep cold of a cloudy February morning, entering the barn to feed the steers, warming with my work. I am the contentment of a mama cow in a June meadow, chewing cud, eyes half closed. I am the pain of euthanizing an old cow, her work and joy and life ended upon a pull of my finger. I am the satisfaction of a well-fed herd and well-stewarded land. I am the pleasure of a nourishing meal.

I am not a cowboy, no jeans, no hat, no buckle. I am the wrong accent, the wrong diction, the wrong words. I am the suburbs and the ocean, the clacking train to the city. I am the wonder of the library stacks, the curiosity in a question, the hope in an answer. I am the challenge of a blank page awaiting words, a blank program awaiting code. I am the frustration of obstacles, institutional or self-created. I am the realization that an answer may never come because the world is more interesting than an answer.

I am the miracle of knowing every bird, every plant, every drainage, and that there are bears out there living bear lives. I am the rainforest chorusing at dawn, the coral reef gleaming at midday, the savannah roaring at night. I am an Adirondack winter, a North Cascade spring, a Sierra Nevada summer, a Rocky Mountain autumn. I am the strength of relishing the company kept in solitude.

Throughout, I am also we. The we of kinship, unspoken acceptance, shared loss. The we of collective work and entrusting oneself to another. The we of intellectual practice, of ideas exchanged and disputed. I am the chosen we of marriage, of fatherhood. I am the broken we of dispersed community and no place. I am the we of trying to stitch us back together, not really knowing how.

I am not a neutral observer. That I care deeply about rural livelihoods and ecological sustainability, about livestock and wilderness, cannot be separated from the things I seek to know. At the same time, the things I learn cannot help but be shaped by these different identities. The challenges presented by this are dwarfed by the opportunities.

In the first semester of my PhD program, my advisor, Paul Meiman, asked me to talk to a group of livestock extension agents about the challenges presented by larkspur (*Delphinium* spp. L.). I had been considering the topic for about a year and so was comfortable with the material. However, I had not yet been forced to consider who I was in relation to the work or to the people that might use the end results.

As I remember it now, it was a group made up entirely of men, all wearing boots and blue jeans, most older than me. I delivered a passionate talk to a silent room, answered a couple of tepid questions, and returned to my seat. Checking in later with Paul, he gently suggested that I might want to tone it down. “For example,” he said, “I wouldn’t say that you would be ‘pissed’ to lose so many cattle to larkspur.” “But we would have been,” I protested, “we didn’t lose that many to all the causes of death combined!" "I know," he answered, "but they aren't seeing you as a beef producer, they're seeing you as a researcher."

As understood in identity theory, the "core of an identity is the categorization of the self as an occupant of a role, and the incorporation, into the self, of the meanings and expectations associated with that role" (Stets and Burke, 2000, p. 225). Our role identification tells us how we relate to one another and what behaviors are appropriate. Until that conversation with Paul, it had not occurred to me that in shifting roles from producer to researcher, not only had the work changed but also, unavoidably, the person doing it.

However, I resolved that, despite the certain existence of these roles, in my work I did not have to be *either* observer *or* empathizer. Rather, I could be *both* observer *and* empathizer. Those extension agents, caricatured above, are certainly more than blue jeans and boots. I realized that I had a choice to make not only in how I saw them but also myself, and I chose to try to be both/and (Mullings, 1999).

As a former and future livestock producer, I am predisposed to view the challenge of larkspur in context with the many other challenges that livestock producers face. This means that, in choosing my research questions and methods, I have been biased toward a broad view of the phenomenon of plant poisoning, sometimes at the expense of analytic certainty. This manifests in a reluctance to make clear management recommendations from our findings, an inclination which I believe acknowledges the intelligence and skill of place-based managers to formulate their own strategies.

At the same time, as a highly educated white male with a lengthy background in ecological science, I have also been socialized to seek quantitative explanations for observed phenomena rather than rely on qualitative evidence. For larkspur, this means that my inclination has been toward modeling and field experiments despite my recognition of the importance of producer knowledge. My position as an outsider to the western ranching culture has further enhanced this inclination, as I have at times felt that people apparently within that culture have viewed me skeptically due to my apparent outsider status, though I must say that ranchers themselves have been uniformly welcoming.

On the other hand, as an outsider to rangeland science (and a general contrarian), my tendency has been to doubt the received scientific wisdom regarding the nature of larkspur poisoning of cattle. This is furthered by my epistemological position as a constructivist. Though I do believe that there is a reality independent of the human mind, I also believe that knowledge of that reality is inevitably a social construct. I have therefore examined our understanding of larkspur poisoning not only through the existing evidence, but also by examining the research paradigm under which that evidence was constructed.

My positionality has thus in many ways shaped the research presented in this dissertation. My life experience and natural proclivities push me toward a broad transdisciplinary approach that is nonetheless limited by my tendency to seek quantitative evidence. I am often of two minds in being biased toward knowledge generated by producer experience but also in doubting that knowledge unless it is backed up by scientifically-generated data. In hindsight, that I could look at this research from these different perspectives has worked to my great advantage, despite many frustrations. Complex challenges such as larkspur poisoning of cattle are perhaps best addressed by integrating divergent perspectives (Ostrom and Cox, 2010), and I unwittingly arrived with one.

CHAPTER 2

TOWARD A SCIENCE OF CONSILIENCE: A CONCEPTUAL MODEL OF LIVESTOCK GRAZING MANAGEMENT

2.1. INTRODUCTION

To address the challenge of the "range problem" in the 21st century, Sayre et al. (2012) present a "vision of our science" that will enable us to "understand big changes and answer big questions". This science, they note, must start from a "postnormal" (Funtowicz and Ravetz, 1993) mindset and incorporate a multiscale understanding of the landscape, more rigorously designed experiments, different ways of knowing, and open debate about objectives into a "science of consilience of facts and anecdotes across a landscape, thoroughly interdisciplinary in nature" (Sayre et al., 2012, p. 549). This is a bold vision, and a call to action that rangeland science must be willing to answer if it is to remain relevant in the coming decades.

Etymologically, "consilience" means "jumping together", sharing a root with "resilience". In the sciences it refers to the idea that evidence from distinct knowledge sources should converge on similar conclusions, strengthening confidence. Popularly, the phrase has been used to refer to hopes for a grand re-synthesis among the sciences, most prominently by the biologist E.O. Wilson (1999).

However, as observed by the ecological economist Robert Costanza (2003), the consilience proposed by Wilson does not represent a true synthesis but rather an extension of reductionism into the social sciences and humanities. Instead, Costanza (2003, p. 653) proposed "a more balanced and pluralistic" consilience, leading to a "science that is truly transdisciplinary and multiscale, rather than either reductionistic or wholistic" and "will be much more sophisticated and multifaceted in its view of the complex world in which we live, the nature of 'truth' and the potential for human 'progress'…".

Such a science requires honest and diligent grappling with the complexity of the challenges faced. This effort is underway in rangeland science, with increasing attention given to the complexity of rangeland systems (e.g., Boyd and Svejcar, 2009; Fuhlendorf et al., 2012; Provenza et al., 2013; Walker and Janssen, 2002) and the importance of transdisciplinarity and local knowledge (e.g., Briske et al., 2011; Brunson, 2012; Reid et al., 2014; Teague et al., 2013; Wilmer and Fernandez-Gimenez, 2015) to understanding them. A consistent element in these conversations has been the call for the development of conceptual models. For example, Briske et al. (2017, p. 217), in describing the "four broad, interrelated steps" for analyzing and managing resilience in social-ecological systems, start with "Step 1: Develop a Conceptual System Model".

Conceptual models are "external representations that are shared by a given community, and have their coherence with the scientific knowledge of that community" (Greca and Moreira, 2000, p. 5). They help to clarify the relationship between our research and the underlying reality that science seeks to understand, as Chafee and McNeill (2007, p. 238) point out, by providing "a lens through which ideas and relationships come into focus".

However, conceptual models in rangeland science appear to be primarily thought of as management tools rather than a means of organizing research (e.g. Briske et al., 2011). This is unfortunate, as shared conceptual models are essential to effective scientific consilience. Costanza (2003, p. 655) points this out in noting that analytic effort must necessarily be preceded by a "pre-analytic cognitive act" that creates a "shared vision of both how the world works and how we would like the world to be". Further, he notes that good science "can do no better than to be clear about its underlying pre-analytic vision, and to do analysis that is consistent with that vision" (Costanza, 2003, p. 656).

Conceptual models establish a "shared vision of… how the world works", serving as a bridge that joins disparate ways of knowing to generate reciprocal learning. Shared conceptual models prevent the academic literature from becoming "catalogs of spare parts for a machine they never build" (quoted in Miller, 1978, p. 5) by allowing numerous individual studies, unavoidably spatiotemporally bound, to cohere into consilience. Absent a shared conceptual model, scientists working in complex systems are too often the allegorical blind men grasping at different parts of an elephant.

In this synthesis, we demonstrate the importance of explicit conceptual models to creating the science of consilience that Sayre et al. (2012) envision by introducing a conceptual model of livestock grazing management, a sub-discipline of rangeland science. We begin by examining each of its elements and their connections to one another, reviewing relevant examples from the literature. We follow with discussion of the utility of this conceptual model in resolving persistent disagreements in the discipline and provide examples of how it can be used to organize and improve research. We close with a discussion of the implications of the conceptual model for the relevance and effectiveness of rangeland science.

2.2. A CONCEPTUAL MODEL OF LIVESTOCK GRAZING MANAGEMENT

Allen et al. (2011, p. 12) define "grazing management" as "the manipulation of grazing in pursuit of a specific objective or set of objectives". For livestock grazing management, we would be more specific regarding objectives and state that it almost always involves the manipulation of the grazing of domestic herbivores in pursuit of animal products. It also usually involves management of the resources necessary to produce those products such that sustained yield is possible, though many examples exist of resource mismanagement in pursuit of short-term yields.

The goal for our conceptual model is that it be instantly understandable yet increase in meaning with continued consideration. It should also be general enough to be applicable to any livestock grazing management scenario anywhere yet specific enough to be useful in addressing individual questions.

2.2.1. THE FUNDAMENTAL INTERACTION. The core of our conceptual model of livestock grazing management is what we term the fundamental interaction (Figure 2.1). The interaction of these two factors generates all grazing management outcomes, from vegetation condition to livestock weight gain to hydrologic improvement or degradation. Livestock distribution, the location of the animals under management, varies through time and over space, and so must be understood at different spatiotemporal scales. Similarly, the heterogeneity of environmental conditions, which includes everything with which the livestock might interact on the landscape (e.g. vegetation, water, wildlife, and weather), also varies according to the spatiotemporal scale at which it is examined.

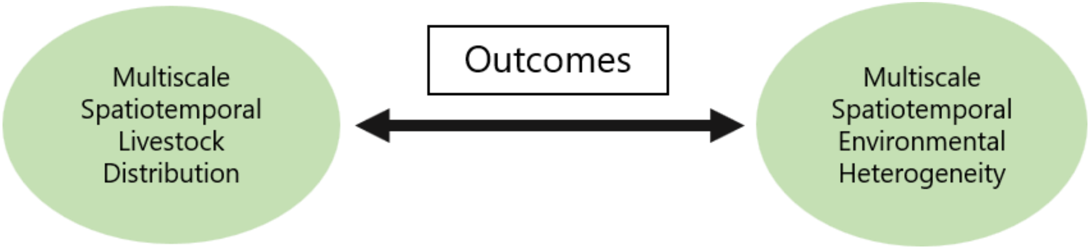

FIGURE 2.1. The fundamental interaction

The best existing characterization of the multiple spatiotemporal scales of livestock distribution and interaction with the landscape is provided by Bailey et al. (1996, p. 388; table 2.1). They present a multiscale scheme that includes, from narrow to broad scale: bite, feeding station, food patch, feeding site, daily range, seasonal range, and lifetime range. These nested scales of interaction are characterized by both spatial and temporal resolution, with associated behaviors, measurable variables, and vegetation interactions at each scale.

However, moving from this outline to a more precise understanding of how, why, and when livestock, as individuals and groups, distribute themselves on the landscape is incredibly complicated. This is because behavior at each of the aforementioned scales is influenced by a complex web of biotic

TABLE 2.1. Attributes of spatial and temporal scales useful for describing and evaluating foraging behavior of large herbivores. Spatial levels reflect units that large herbivores may select among. Reproduced and adapted from Bailey et al. (1996, p. 388).

Spatial level	**Spatial resolution of selected unit**	**Temporal interval between decisions**	**Defining behaviors or characteristics**	**Response variable**	**Vegetation entity**
Bite	0.0001 - 0.01 m2	1 - 2 s	Jaw, tongue, and neck movements	Bite size	Plant part
Feeding station	0.1 - 1 m2	2 s - 2 min	Front-feet placement	Bite rate	Plant (grass tuft, shrub)
Food patch	1 m2 - 1 ha	1 - 30 min	Animal reorientation to a new location. A break in the foraging sequence	Feeding duration	Clump of plants
Feeding site	1 - 10 ha	1 - 4 h	Grazing bout	Foraging movements	Plant species association
Daily range	10 - 100 ha	12 - 24 h	Area where animals drink and rest between grazing bouts	Daily time allocation	Landscape unit
Seasonal range	100 ha - 1000 ha	3 - 12 months	Migration	Metabolic allocation	Landscape type
Lifetime range	> 1000 ha	Several years	Dispersal or migration	Life history schedule	Geographical region

and abiotic, internal and external factors (Bailey and Provenza, 2008; Distel et al., 1995; Heitschmidt and Stuth, 1991; Laca, 2009; Prins and Langevelde, 2008; Provenza et al., 2003a, 1998; Villalba et al., 2015). Internal factors include cattle biology, physiology, behavioral ecology, and memory, among others. The external factors, both biotic and abiotic, fall under environmental heterogeneity.

As noted by Fuhlendorf et al. (2017), there is now a robust theoretical foundation establishing environmental heterogeneity as essential to the maintenance of ecological resilience, and managers are beginning to understand that historical attempts to minimize heterogeneity were misguided. For one, we now know that heterogeneous forage better enables livestock to meet their nutritional needs and regulate toxin intake (Provenza et al., 2003b). This is a multiscale phenomenon, working at the scale of the individual animal selecting bites at a feeding station as well as at the scale of herds grazing their daily, seasonal, or lifetime range. At these broader scales, there is evidence that human herders can improve livestock productivity by sequencing different grazing locations to include diverse forage types, thereby increasing forage intake (Meuret et al., 1994; Meuret and Provenza, 2015a).

However, the influence of heterogeneity on livestock distribution and productivity is much more complex than forage distribution alone, complex as that is. Across space and over time, inherent heterogeneity in the form of topography, geology, and hydrology interacts with the heterogeneity generated by disturbances such as herbivory, fire, and erosion to create a diverse landscape of attraction and repulsion for livestock (Fuhlendorf et al., 2017). The attraction and repulsion are generated by the at-times-conflicting needs of livestock for forage, water, and shelter, with these needs also varying across space and over time and from individual to group. In turn, the livestock themselves then generate heterogeneity, not only through herbivory but also through nutrient deposition, trampling, and facilitation of other abiotic and biotic disturbances.

Given the incredible complexity of these interactions and the nearly infinite variety of spatiotemporal scales at which they can be studied, a given scientific study will only shed light on a small portion of this fundamental interaction. This is fine so long as this fact is acknowledged, but we suggest that this occurs far too rarely. For example, Meiman et al. (2016) highlighted some problems that result from studies where this fundamental interaction is grossly over-simplified and insufficiently acknowledged. Addressing this limitation would support their recommendations for more usable science to support animal management and rangeland sustainability.

Failing to acknowledge this basic limitation is especially problematic when a study seeks to understand the outcomes of the interaction of livestock with their environment. A given outcome, such as a decrease in bare ground, may occur in one set of circumstances only to reverse in seemingly similar circumstances. To truly comprehend why an outcome is generated, a much fuller understanding of the interaction between multiscale spatiotemporal livestock distribution and multiscale spatiotemporal environmental heterogeneity is needed, one that can only come through the consilience of diverse knowledge. Because livestock grazing management is a social-ecological system, this knowledge must therefore also include an awareness of how human intervention affects this system.

2.2.2. THE GRAZING MANAGEMENT TOOLBOX. The management of grazing livestock aims to influence one or both factors in the fundamental interaction to achieve desired outcomes. To do so, tools from a grazing management toolbox are used (Figure 2.2). The contents of this toolbox will vary from place to place and manager to manager, but common tools include fencing, timing of grazing, watering location, vegetation management, herding, fire, and wildlife management.

In North America, fencing is by far the most commonly used grazing management tool as it effectively controls livestock distribution. However, because fence lines are most often determined by human convenience rather than environmental considerations, they often have unintended effects on the interaction between livestock distribution and environmental heterogeneity (Boone and Hobbs, 2004). When located according to environmentally arbitrary property boundaries or, especially in the western USA, section boundaries, fencing creates arbitrary fragments that negate many of the benefits of landscape heterogeneity and can even lower the overall carrying capacity of the land, not to mention negative effects on wildlife (Boone and Hobbs, 2004). On the other hand, fences that are carefully

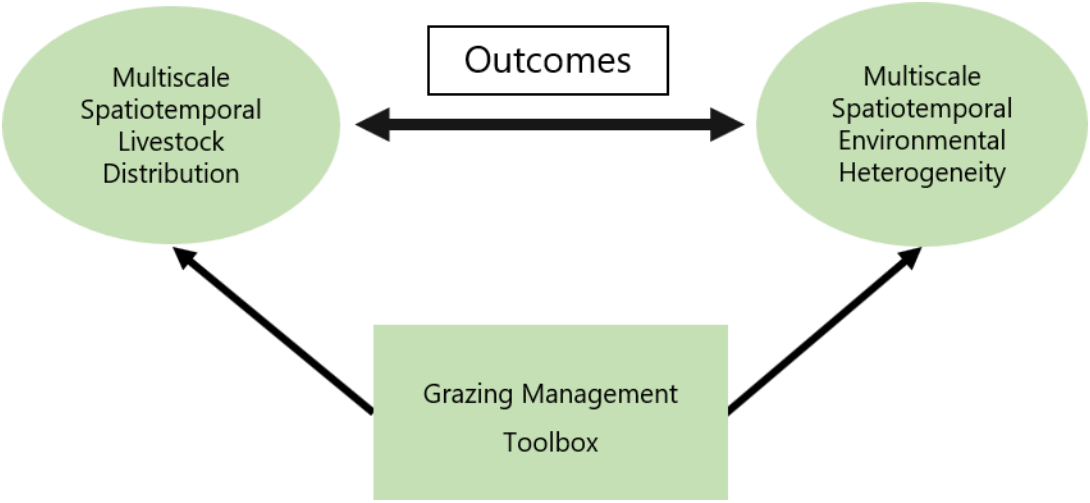

FIGURE 2.2. The grazing management toolbox.

located according to landscape features can have benign or even positive effects, particularly when they control access to sensitive resources (Goodwin et al., 1997).

Rangeland science is increasingly studying the effect and utility of other grazing management tools. Studies have shown that altering water and mineral locations can mitigate overgrazing around natural water sources and other sensitive areas (Bailey, 2004; Bailey and Welling, 2007; Miner et al., 1992; Porath et al., 2002). An expanding body of literature examines the complex relationships among livestock grazing, fire, wildlife, and heterogeneity (Augustine and Derner, 2015a, 2015b, 2014; Davies et al., 2017; Fuhlendorf et al., 2009; Holcomb et al., 2014). Herding, perhaps the second oldest grazing management tool after fire, has received significant attention in pastoralist systems (e.g., Fernandez-Gimenez, 2000; Krätli and Schareika, 2010; Oba and Kaitira, 2006; Wario et al., 2015) but relatively little attention in North America, though this may be changing as producers and researchers increasingly recognize the manifold benefits of herding (Bailey et al., 2008; Barnes, 2015; Butler, 2000; Cote, 2004; Meuret and Provenza, 2015b).

Though grazing management tools are often intended to influence just one of the elements of the fundamental interaction, the conceptual model tells us that they will inevitably affect the other item, either through direct impacts or feedback effects. Similarly, research that aims to identify the connection between grazing management tools and outcomes will be inevitably limited in its transferability, as the measured effects are filtered through the complexity of the fundamental interaction.

2.2.3. THE EFFECT OF CULTURE. The elements in Figure 2.2 can stand alone as a technical conceptual model of livestock grazing management as we observe it on the ground. However, the model is incomplete and will be less useful if it fails to incorporate two additional elements, which add the factor of culture (Figure 2.3). By including livestock culture, we indicate that the social factors unique to a given herd of livestock are influential enough to warrant a separate model element, with significant evidence that they play a fundamental role in in determining distribution. They can also dictate which grazing management tools are usable. Of course, herd characteristics have long been understood as important in influencing outcomes such as weight gain, but researchers are beginning to more fully understand how factors like memory, preference, learning, and knowledge transmission influence livestock behavior and thus outcomes (Bailey et al., 1989; Dumont and Hill, 2001; Hessle, 2009; Launchbaugh and Howery, 2005; Villalba et al., 2015).

A heuristic is a practical approach to decision-making in the face of complexity that results in "good-enough" rather than universal solutions, which are unlikely or even impossible in complex systems (Gigerenzer and Gaissmaier, 2011). Heuristics are shortcuts that enable effective decision making despite incomplete knowledge and are an essential component of, for example, systems engineering, where it is recognized that complexity necessitates adaptability (Kossiakoff, 2011, p. 179).

In livestock grazing management, heuristics help managers decide which tools in the grazing management toolbox to use, and when. Heuristics guide the use of the tools but are not themselves

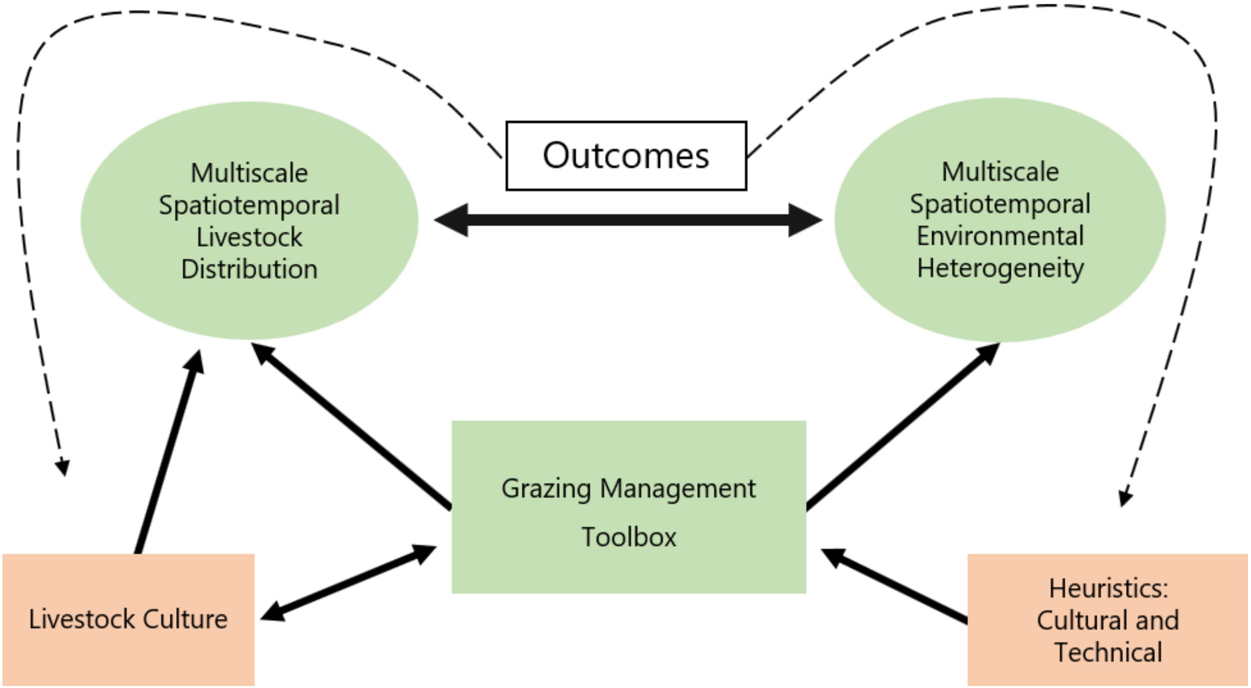

FIGURE 2.3. The complete conceptual model of livestock grazing management.

tools—an important distinction. Simple metrics like "take half, leave half" are heuristics. Most so-called grazing systems, such as multi-paddock grazing management (aka rotational grazing) are heuristics, in that they do not themselves influence livestock distribution or the environment, but instead provide a practical framework for decision making about the use of tools that will. As we will show, the term "grazing system" is more appropriately applied to a broader set of system elements.

Heuristics can be cultural, technical, or both. Cultural heuristics tend to be internal to an individual operation or region and are derived from place-based learning. Technical heuristics, on the other hand, are derived from scientific research and the application of technology. It is not always possible to separate these categories, and the most successful heuristics may be combinations of both, or interpretations of one within the context of the other. Additionally, heuristics are not applied in isolation but rather in context with one another in what may be best described as a pattern language (Salingaros, 2017).

A pattern is a proven solution to a recurring problem (Alexander et al., 1977; Borchers, 2000). A pattern language is a "a combinatorial framework akin to a spoken/written language for using design patterns" (Salingaros, 2017, p. 2), wherein the patterns relate non-hierarchically as do the words in a sentence. Though most prominently applied to architecture and software design (e.g., Alexander et al., 1977; Beedle et al., 1999), we suggest that the pattern language concept holds tremendous promise for increasing our understanding of producer thought processes and decision-making in agriculture.

While the explicit study of heuristics in livestock grazing management has been quite rare (e.g., Eastwood and Kenny, 2009), there is increasing recognition in rangeland science of the complexity of decision making by managers, highlighting their role as integrators of diverse sources of knowledge (e.g., Krätli and Schareika, 2010; Molnár, 2014; Wilmer and Fernandez-Gimenez, 2015). While science, even that which is intended to assist producers, usually reduces the number of included factors in pursuit of certainty, managers must act efficiently and effectively without reduction to properly address complexity (Holling, 2001; Holling and Meffe, 1996; Sayre, 2004; Walker and Janssen, 2002). This is what heuristics, applied in a pattern language, enable. It is essential that rangeland science begin to conduct research that integrates and is integrable into heuristic pattern languages.

The final conceptual model elements to note are the curved dashed lines. These lines represent feedback from system outcomes to each of the cultural elements of the model. Livestock respond to feedback from the result of their interaction with the environment by learning and adapting, both individually and in groups. Likewise, good human managers and researchers will recognize the correlation between observed conditions, their actions, and system outcomes (both desirable and undesirable) and seek to learn and adapt.

2.2.4. A NESTED SYSTEM. We have carefully delineated the livestock grazing management system boundaries using the criterion of "unity of purpose", which stipulates that included system elements be specifically dedicated to the outcomes of the system (Kossiakoff, 2011, p. 51). It is a common but critical error to set the boundaries of a system of interest too wide by including unnecessary elements (O'Connor and McDermott, 1997, p. 164). Elements such as economic factors, regulations, and policy may be influenced by the outcomes of livestock grazing management, and may exert an external influence on some elements, but are not inherently part of the system. However, the fact that these boundaries can be somewhat arbitrary reminds us of one of the fundamental characteristics of complex systems, which is nested-ness (Jackson, 2003).

Just as the six elements of our conceptual model are nested within a system known as livestock grazing management, this system is itself one element within other broader systems, in what is termed a "system of systems". For example, a conceptual model of beef production will have livestock grazing management as one element that interacts with others, perhaps including feed production, finishing, and meat processing, among others. At the same time, each of the elements within the conceptual model of livestock grazing management may be viewed as systems of their own, made up of smaller elements. For example, we could create a conceptual model of the interactions between different grazing management tools to better understand how the different tools available to a producer may affect one another, which in turn will improve our understanding of how grazing management tools influence livestock distribution and environmental heterogeneity. However, it is important to note that, as we break down systems into their constituent elements, at a certain point the system may no longer have the properties attributed to complex systems.

2.3. APPLICATION OF THE MODEL

2.3.1. A CLARIFYING ROLE. Once this conceptual model is in place, we can see that Allen et al.'s (2011, p. 13) definition of a "grazing system" fits quite well:

> "**Grazing system (n.)**. A defined, integrated combination of soil, plant, animal, social and economic features [note discussion above], stocking (grazing) method(s) and management objectives designed to achieve specific results or goals. **Note** ... A grazing system is site-specific because it integrates specific biotic and abiotic components and their environments, management objectives and social factors. System behaviour is a consequence of the interrelationships among the parts of the system. When a system component is managed in isolation away from the influence of the rest of the system, it is no longer under the same influences and may behave differently…"

A grazing system is a single manifestation of the conceptual model of livestock grazing management, with complexity ensuring that system structure and outcomes are unique to a specific time and place. Recognizing this, our model can then provide insight related to ongoing debates in the discipline.

For example, how might we view the "rotational grazing debate" through the lens of this conceptual model? Once we identify rotational grazing as a heuristic (or a set of heuristics), we can see that every application thereof will be necessarily distinct. Because we know that heuristics do not determine outcomes, we can also see that research and observation that seeks to connect any heuristic to outcomes is ignoring the complex determinants of outcomes, and therefore may sometimes find a link, other times not. Thus the "perceptual dichotomy" of Teague et al. (2013). Careful distinction of heuristics from grazing systems would effectively resolve the core disagreements in the rotational grazing debate.

A second illustrative example concerns the connections between stocking rate, stocking density, and outcomes. We propose that stocking rate is best understood as a heuristic, and stocking density as a tool. As noted by Allen et al. (2011, p. 15), stocking rate almost always is calculated using the total area of land that supports the total number of animals. On the other hand, stocking density, usually defined as an instantaneous value, refers to the actual number of animals grazing an actual unit of land at a given time. Stocking rate is therefore one guide that a manager integrates when making decisions about stocking density, which is what directly influences livestock distribution and environmental heterogeneity.

From the origins of rangeland science, many observers have identified stocking rate as the key factor in determining livestock grazing management outcomes, and much research supports this (Holechek et al., 2011; Sayre, 2017). However, exactly how stocking rate influences outcomes like ecological function has not always been clear, and the discipline has struggled to clearly quantify these relationships. When we recognize stocking rate as a heuristic, the reason for this becomes clear. Not only are there many other heuristics working within a single grazing system, but there are several other elements that are ignored if we focus only on stocking rate and outcomes. Clearly, a substantial body of literature indicates that the stocking rate heuristic can exert a strong influence on outcomes, but there are too many other system elements at play between heuristics and outcomes for this relationship to be consistently measurable. Because stocking rate is easily measured (particularly *post facto*), it will always be an important component of grazing studies. However, our conceptual model indicates that stocking density, which we find to be, tellingly, often conflated with stocking rate, warrants more attention.

2.3.2. APPLICATION TO GRAZING MANAGEMENT RESEARCH. To illustrate the usefulness of conceptual models in research design and implementation, here we present two examples of how our livestock grazing management research has been improved by examining it through the lens of this conceptual model. The first research project is aimed at finding novel solutions to the challenge of larkspur poisoning of cattle in the Western US, and the second is aimed at understanding and mitigating conflict between lions (*Panthera leo* L.) and Maasai pastoralists in Kenya. The many ecological and social differences between these two projects lend credence to the adaptability of the conceptual model.

At least eleven species of larkspur (*Delphinium* spp. L.) have been identified as causing significant cattle losses in the western United States, with yearly deaths estimated at 2-5% of cattle grazing in larkspur habitat, resulting in an annual cost of $234 million (B. Green et al., 2009; Knight and Walter, 2001; Pfister et al., 1997a; Welch et al., 2015a). Grazing management recommendations have long focused on seasonal avoidance, aimed at reducing exposure at larkspur growth stages when toxic alkaloid concentration is highest (Pfister et al., 1997a; Welch et al., 2015a). Because this strategy creates problems of its own by greatly limiting management flexibility, it appears that many producers simply accept the risk of deaths as a cost of doing business.

Examining the challenges presented by larkspur through the lens of the conceptual model of livestock grazing management (Figure 2.3) identifies flaws in the seasonal avoidance approach and suggests a different path forward. For example, we can see that the seasonal avoidance approach only considers the outcome of dead cattle, the environmental factor of varying alkaloid concentration, and the grazing management tool of timing of grazing. It largely fails to consider the role of livestock distribution, livestock culture, and heuristics, not to mention other outcomes, different aspects of environmental heterogeneity, and other relevant tools. This is not to say that research on these items is completely lacking (cf. Green et al., 2014; Pfister et al., 1997c; Ralphs et al., 1988; Smith et al., 2010), but rather that existing knowledge has not been effectively integrated into grazing management recommendations or progressive research.

This conceptual model has inspired us to consider larkspur poisoning from several new angles in pursuit of a different approach. Recognizing that the relationship between livestock distribution and poisoning is poorly understood, we created an agent-based model that demonstrated that reduced herd cohesion increases deaths (Jablonski et al., 2018; Chapter 3). This study also indicated that increases in stocking density, by increasing cohesion and otherwise altering how cattle interact with forage heterogeneity, can also reduce the risk of death. A second study examined the interaction between larkspur patchiness and herd cohesion to improve our understanding of how the fundamental interaction (Figure 2.1) drives the outcome of larkspur poisoning (Chapter 5). While we continue to conduct research aimed at other elements of the conceptual model, the conceptual model also tells us that a one-size-fits-all solution is unlikely (Darnhofer et al., 2012; Ostrom and Cox, 2010). Therefore, we have instead focused on providing information to affected producers in a way that will enable them to integrate our findings into their unique grazing systems.

Lion killing resulting from livestock depredation is one of the chief causes of the drastic and ongoing decline in lion populations (Hazzah et al., 2009; Ogada et al., 2003; Woodroffe and Frank, 2005). At the same time, many pastoralists, such as the Maasai people of East Africa, lose large numbers of livestock to carnivores, a significant threat to already tenuous livelihoods which in turn further reduces their tolerance of carnivores (BurnSilver, 2009; Hazzah et al., 2009; Patterson et al., 2004). Though some livestock depredation does occur while the animals are in night pens, Lion Guardians, a conservation organization working to reduce carnivore conflict in the Amboseli Ecosystem of southern Kenya, estimates that >80% of livestock predation deaths occur away from the night pen and are thus attributable to grazing management practices (Lion Guardians unpublished internal data). We can therefore use the conceptual model of livestock grazing management (Figure 2.3) to contextualize the situation and identify opportunities for novel solutions to the challenge of lion-livestock conflict in this region.

Risk of livestock predation by lions is an environmental factor that is heterogeneously distributed on the landscape (Dolrenry et al., 2014). When livestock distribution overlaps with predation risk under unfavorable circumstances, predation is likely to occur. These unfavorable circumstances can be environmental (e.g., at night, when lionesses have young cubs, or when wild game are sparse), livestock cultural (e.g., livestock stray from herdmates or are otherwise inexperienced) or related to the application of grazing management tools (e.g., herders are not present, have lost some livestock, or are intentionally taking risks in pursuit of forage), or a combination thereof. Because herding is the most significant (though not the only) grazing management tool used in Maasai culture, the suite of heuristics related to herding are highly developed, reflecting a deep "cosmoecological" mutuality among people, livestock, and environment, as well as significant cognitive proficiencies (BurnSilver, 2009; Despret and Meuret, 2016; Galaty, 1989; Hazzah et al., 2009; Krätli and Schareika, 2010). In short, we can understand lion-livestock conflict as an outcome driven by each of the elements in the conceptual model and, more to the point, by all of them simultaneously.

Existing efforts at preventing lion-livestock conflict can also be characterized according to the conceptual model. Creation and fencing of protected areas seeks to prevent overlap between livestock and lions but largely ignores pastoralist imperatives related to forage heterogeneity, grazing management tools, and heuristics, not to mention the environmental factor of wildlife migration needs (Creel et al., 2013; Packer et al., 2013). Compensation programs, whereby owners receive money for predated livestock, seek to prevent retaliation but, perhaps more importantly, also seek to encourage desired grazing management tool use by offering higher compensation when there is evidence that such practices were followed (Maclennan et al., 2009). Programs aimed at improving night pens, which are relatively simple to enact and effective at preventing the <20% of deaths that occur therein, ignore the many deaths that occur as a result of livestock grazing management (Lichtenfeld et al., 2015).

Though these efforts have each achieved success in reducing lion-livestock conflict, the steady decline of lion populations continues. This is in part due to limited capacity to implement partial solutions such as protected areas, compensation programs, and night pen improvement. However, we suggest that a more fundamental problem with such solutions is that they fail to acknowledge, understand, and integrate the full complexity of pastoralist grazing systems. Because such systems are deeply culturally-mediated, any research seeking to identify solutions therein must be fundamentally inclusive of pastoralists, including indigenous knowledge systems (David-Chavez and Gavin, 2018).

By integrating Maasai pastoralists into every aspect of their work, Lion Guardians has achieved significant reductions in lion killing as compared to other methods (Hazzah et al., 2014). This collaboration has also enabled them to see that changing livestock grazing management practices may be increasing the likelihood of lion-livestock predation despite the decrease in retaliation. Our research is thus aimed at assisting Lion Guardians in identifying ways to prevent the grazing-management-based causes of livestock predation. We can use the conceptual model of livestock grazing management to help us do so.

First, we have observed that the connection between Maasai cultural heuristics and grazing management tool use has received little attention. We are thus seeking to understand, via interviews and participant observation, how Maasai make decisions about herding practices and timing and location of grazing, and how such heuristic knowledge is transmitted. We can use this research to draw connections between management practices and livestock distribution to clarify how such decisions affect the likelihood of conflict with lions. We are also using our findings to inform an effort to ensure that knowledge transfer of heuristics continues amid cultural and environmental change. A second research interest inspired by the conceptual model is to identify how livestock culture among Maasai cattle influences the likelihood of conflict, and how this might be changing with increased trade and pressure to adopt "improved" breeds such as Boran cattle.

Though a conceptual model can aid in identifying new avenues for research and practice, it is ultimately more important that a given scientific community use such models to integrate disparate knowledge toward solutions that work. For both larkspur and lion-livestock conflict, this means that any potential recommendations or interventions must makes sense in light of research and practice related to each element of the model, as manifested within a particular system. In rangeland science, far too many recommendations have been made without considering the full complexity of livestock grazing management or the immense diversity in grazing systems (Boyd and Svejcar, 2009). In North America and East Africa alike, the blame for lack of adoption of such reductive solutions has usually fallen on producers, when in fact it usually belongs with scientists (Pretty, 1995; Turner, 2011; Vanclay, 2004; Wilson, 2001).

2.4. IMPLICATIONS FOR RANGELAND SCIENCE

We have demonstrated the usefulness of a conceptual model for inspiring, designing, clarifying, and organizing research in the complex system of livestock grazing management. The conceptual model we have offered is not intended to be definitive, but rather to provoke a conversation. Indeed, the principles that underlie it tell us that the authors of this paper hold limited knowledge and that dialogue with other types of experience and knowledge will improve the model. Most important is that we begin a discussion wherein the discipline is transparent about its "pre-analytic vision" (Costanza, 2003, p. 656).

However, the conceptual model also points toward a more significant challenge, one that addresses the statement of Sayre et al. (2012, p. 547) that "[i]f good rangeland management is an art as well as a science, the science has often been difficult to apply, and the art may be more important". We suggest that this common distinction of "science" and "art" is better understood as a distinction between positivist and constructivist approaches to knowledge generation.

The fundamental premise of positivism is that the world is real and fully knowable by means of observation. One implication of this premise is that only statements that can be verified by prescribed methods of direct observation are meaningful or true. Constructivist epistemology, on the other hand, states that the world is not fully knowable in any meaningful way. Though acknowledging that there is a world independent of the human mind, constructivists believe that knowledge about it is always a social construct. This means that the best we can do is develop useful explanations, rather than arrive at any "Truth".

It has been observed that the best science seeks to construct elegant and compelling narratives using any method that works (Allen and Hoekstra, 2015; Feyerabend, 1993). Such science recognizes that "the most abstract thing a scientist can do is make a measurement because one has to remove everything else in the universe to do so" (Allen and Hoekstra, 2015, p. 310). On the other hand, at its worst, science as ideology justifies, by tautology, domination of people and the environment (Feyerabend, 1993). This includes wanton destruction of knowledge systems that have helped people persevere in difficult environments for thousands of years. More subtly, science that treats people or places as interchangeable effectively erases them.

Rangeland science, in having validated policies and practices that caused significant ecological and social damage, is guilty in microcosm of the broader sins of science (LaRocque, 2014; Sayre, 2017). However, with its strong connection to the land and its people, and with its emphasis on applicability (Meiman et al., 2016), the discipline has the potential to exemplify the benefits of a more inclusive approach to knowledge generation, one that formalizes the validity of both "science" and "art". Such an approach need not reject the principles of experimentation and verification that have allowed science to make tremendous advances for much of humankind. Instead, it would open those knowledge-generating processes to spatial and temporal scales beyond those wherein traditional science thrives. By forcing us to acknowledge the complexity and diversity within livestock grazing management, this conceptual model presents to us a grand challenge—to open our minds and our science to a diversity of knowledge sufficient to the complexity of the systems we love.

CHAPTER 3[1]

AN AGENT-BASED MODEL OF CATTLE GRAZING TOXIC GEYER'S LARKSPUR

3.1. INTRODUCTION

The many species of larkspur (*Delphinium* spp. L.) present a serious, intractable, and complex challenge to livestock grazing management in the western United States (B. Green et al., 2009; Pfister et al., 1999; Welch et al., 2015a). Larkspur plants contain numerous norditerpinoid alkaloids, which are potent neuromuscular paralytics that, for reasons that are not entirely understood, are particularly effective at killing cattle, with yearly herd losses estimated at 2-5% for those grazing in larkspur habitat (Pfister et al., 1997a; Welch et al., 2015a). To avoid such losses, producers will often abandon or delay grazing in pastures with larkspur, which creates a substantial opportunity cost and an impediment to achieving management objectives (B. Green et al., 2009; Pfister et al., 1997a).

Among the many challenges to improving our understanding of cattle-larkspur dynamics has been the difficulty of testing different grazing management strategies in the field. Not only is risking dead cattle impractical and unethical, but the complexity of livestock grazing management, especially when considered across the wide range of habitats and management regimes in which larkspur is found, suggests that results from individual field experiments would be unlikely to be broadly useful anyway (Darnhofer et al., 2012; Provenza et al., 2013). What is needed instead is a method of realistically testing grazing management strategies without risk to livestock and with the flexibility to test multiple scenarios. Agent-based models (ABMs) provide such a method.

ABMs are computational simulation tools that focus on the behavior of individual "agents" as they interact with one another and the environment (McLane et al., 2011). They differ from other

---

[1] Published as: Jablonski, K.E., Boone, R.B., Meiman, P.J., 2018. An agent-based model of cattle grazing toxic Geyer's larkspur. PLOS ONE 13, e0194450. https://doi.org/10.1371/journal.pone.0194450.

types of simulation models in being bottom-up (versus top-down) with group-level behaviors emerging from (usually) realistic individual behaviors rather than deterministic formulae (Grimm, 1999). ABMs are thus particularly useful in modeling complex systems, where the results of the interactions among system elements are not easily predicted or understood (Grimm et al., 2005; Northrop, 2010). Indeed, it has been suggested that bottom-up-simulation may be the best way to increase our understanding of complex systems, which is one of the most important challenges confronting modern science (Dumont and Hill, 2004; Funtowicz and Ravetz, 1993; Grimm et al., 2005).

As noted by Dumont and Hill (2004, p. 426), ABMs are "particularly suited to simulate the behavior of groups of herbivores foraging within a heterogeneous environment". The authors encourage the use of ABMs in situations where experimentation is impractical, and those where comparison of different management strategies is needed. Despite this encouragement, and despite the growing enthusiasm for ABMs in other disciplines, they have been little used in livestock grazing management research, despite the existence of relevant studies to parameterize such a model (e.g., Bailey and Provenza, 2008; Distel et al., 1995; Laca et al., 1994; Sato, 1982; Shiyomi, 2004; WallisDeVries et al., 1998). This is at least partly due to confusion about the purpose and role of models in improving our understanding of complex systems.

Models can never be complete simulacra, and do not need to be in order to be useful. Instead, "models are neither true nor false but lie on a continuum of usefulness for which credibility can be built up only gradually" (Augusiak et al., 2014, p. 119). This credibility is built not just by model output but also, more importantly, through thoughtful model development. This ensures that the necessary simplification that occurs in modeling focuses in on rather than obscures the system processes of interest (Grimm and Martin, 2013). As noted by Augusiak et al. (2014), in well-designed models the important question is the extent to which the model achieves its purpose in the light of existing evidence, rather than a binary yes or no regarding its validity.

Previous research into the relationship between grazing management and larkspur toxicosis has largely focused on timing of grazing, with some attention paid to mineral supplementation, pre-grazing with sheep, and, increasingly, genetic susceptibility (Green et al., 2014; Pfister et al., 1988, 1997a, 2010; Ralphs et al., 1988; Welch et al., 2015a). Some papers have suggested that cattle behavior, influenced by management, can play a role in mitigating larkspur deaths (Pfister et al., 1997c, 2002), but these ideas have received little empirical study. Only anecdotally has it been observed that, regardless of timing of grazing, it may be possible to eliminate losses to larkspur by increasing stocking density, due to a dilution effect (same amount of alkaloids, more cattle) or perhaps changes in herd behavior (Smith et al., 2010).

In this paper, we introduce a spatially-explicit, behavior-based ABM of cattle grazing in a pasture with a dangerous amount of Geyer's larkspur (*Delphinium geyeri* Greene), in which MSAL-type alkaloids are the dominant toxin (Grina et al., 1986; Panter et al., 2002). This model provides significant management-relevant insight for producers dealing with larkspur and demonstrates the great potential of ABMs to credibly model livestock grazing management dynamics, including fundamental aspects of livestock behavior amidst ecological heterogeneity.

3.2. METHODS

The model description follows the updated Overview, Design Concepts, and Details (ODD) protocol, an accepted method for standardizing published descriptions of ABMs (Grimm et al., 2010).

3.2.1. PURPOSE. We developed this model to test the effect of co-varying instantaneous stocking density (Allen et al., 2011) and herd cohesion (also known as troop length) (Shiyomi and Tsuiki, 1999) on cases of lethal acute alkaloid toxicosis caused by *D. geyeri*. Cases of lethal acute toxicosis are a product of intensity of exposure to alkaloids (via consumption) with passing time as a mitigating factor (via metabolism). Conceptually, this model functions as a mechanistic effect model (MEM) aimed at understanding the processes whereby toxic alkaloids kill grazing cattle. MEMs have been recognized for their potential to "close the gap between laboratory tests on individuals and ecological systems in real landscapes" (Grimm and Martin, 2013). We developed and executed the model in NetLogo 6.01, using the BehaviorSpace tool to implement simulations (Wilensky, 1999).

3.2.2. BASIC PRINCIPLES. Behavior-based encoding of cattle activities was the guiding principle of model design. As noted by Mclane et al. (2011), "the behavior-based approach leads to a more complex web of decisions, and the responses of the animal to stimuli are often more multifaceted". We add that the behavior-based approach is also more likely to allow for instructive emergent properties. In practice, the behavior-based approach means that at every step of the coding process we sought literature on actual cattle behavior and then encoded that behavior as realistically as possible. When literature was lacking we used our knowledge of cattle behavior from our years as livestock managers and researchers. The behavior-based approach also found expression in model evaluation, when one mode of evaluation was whether the cows in the model "act like cows". This was achieved through a lengthy process of visual debugging and other implementation verification (Augusiak et al., 2014; Grimm, 2002).

A second core design principle was parsimony. Because this is the first ABM that we know of to incorporate cattle at the individual scale of interaction with the environment (1 m^2) and extended to a realistic pasture size, we were initially tempted to include every cattle behavior we could. However, our focus on parsimony to the question at hand meant that we instead included only those behaviors relevant to the consumption of larkspur. A final guiding principle was that when a judgement call was needed, we erred on the side of making the effects of alkaloid toxicosis more prominent. If the model was to show an effect of grazing management on reducing larkspur-induced toxicosis, we wanted to be sure that we had taken every precaution against preconditioning it to do so.

Overall, we followed as closely as possible the process of "evaludation" laid out by Augusiak et al. (2014), which is aimed at moving beyond insufficient and often counterproductive ideas about model validation to a more thorough process of generating credible models. Specifically, we incorporated data evaluation, conceptual model evaluation, implementation verification, output verification, and other analysis of model output.

3.2.3. ENTITIES AND STATE VARIABLES. The model has two kinds of entities: pixels representing 1 m^2 patches of land and agents representing 500 kg adult cows (1.1 animal-units). The patches create a model landscape that is 1663 x 1580 patches (1.66 km x 1.58 km, equal to 262.75 ha, of which 258.82 ha are within the pasture under study and 3.93 ha are outside the fence line and thus inaccessible). This landscape aims to replicate pasture 16 at the Colorado State University Research Foundation Maxwell Ranch, a working cattle ranch in the Laramie Foothills ecoregion of north-central Colorado that is a transition zone between the Rocky Mountains and the Great Plains. Several pastures on the ranch, including pasture 16, have significant populations of *D. geyeri*, which generate ongoing management challenges and have fatally poisoned cattle.

To make the model appropriately spatially explicit we included three sets of geographic data. First, using data from the Worldview-2 satellite (8-band multispectral, resolution 2 m) from July 10, 2016, we created an index of non-tree/shrub vegetation distribution within the pasture using a soil-adjusted vegetation index (SAVI) within ERDAS Imagine 2016 software at a resolution of 1 m (Hexagon Geospatial, 2016; Huete, 1988). Second, as there are no developed watering locations in pasture 16, with ArcGIS Desktop 10.4 we digitized and rasterized (at 1 m) all locations of naturally occurring water as of July 2017 (ESRI, 2015).

Lastly, in June and July of 2017 we mapped larkspur distribution and density in pasture 16 using a hybrid approach. We began by digitally dividing the pasture into 272 1-ha sampling plots. Because we knew larkspur to be of patchy distribution, in each plot we first mapped all larkspur patches (defined as areas with >1 larkspur plant • m^{-2}) using an iPad equipped with Collector for ArcGIS 17.01 (ESRI, 2017) and a Bad Elf Pro+ Bluetooth GPS receiver accurate to 2.5 m. To sample areas outside of larkspur patches for larkspur density, we counted all living larkspur plants in a 6-m-wide belt transect running horizontally across the plot, with the origin randomly assigned and any patches excluded (Bonham, 1989). Using ArcGIS Desktop we then extended the belt-transect-derived larkspur density to the rest of the plot (excluding patches), and both sets of data were integrated into a 1 m raster of larkspur distribution.

The number of cows (individual agents) in the model varies according to the chosen stocking density (SD, in AU • ha^{-1}). Cows are assigned the role of "leader" (5%), "follower" (85%), or "independent" (10%) (Bailey, 1995; Harris et al., 2007; Sato, 1982). Each cow is also assigned a value for MSAL-tolerance and larkspur-attraction. MSAL-tolerance determines the MSAL-level at which a cow will "die" and is randomly assigned to create a normal distribution with 99.9% of values falling within 25% of a mean toxicosis threshold ($\bar{x}$=4,000 mg, σ=333.33 mg) (Welch et al., 2015b). In this model, death does not result in the removal of a cow from the herd; instead, in order to preserve herd and other model functions it is recorded as having died, its MSAL-level is set to zero, and it continues to graze. Note that MSAL-tolerance can be understood as modeling genetic, physiological, and situational susceptibility.

Larkspur-attraction determines how much larkspur the individual cow will consume when in a patch with MSAL-content and is also randomly assigned to create a normal distribution with 99.9% of values falling within 25% of the mean ($\bar{x}$=1.0, σ=0.083). A value of 1.0 means that the cow will consume larkspur at the same rate as other forage, while values greater or less than 1.0 cause the animal to, respectively, prefer or avoid larkspur. All functionally relevant state variables for patches and cows, as well as global variables and inputs, are described in Table 3.1.

TABLE 3.1. Relevant model variables.

Entity	Variable	Description
Patches	forage-mass	Amount of currently available forage (g)
	n-forage-mass	Mean initial available forage in patches within a radius of 3 m (g)
	MSAL-content	Amount of toxic alkaloids currently in patch (mg)
	times-grazed	Number of times patch has been grazed
Cows	role	Role in the herd: leader, follower, or independent
	MSAL-level	Current amount of MSAL alkaloids in cow's body (mg); metabolized with a half-life of one grazing-day
	MSAL-tolerance	Level at which cow will be recorded as having died (MSAL-level>MSAL-tolerance); assigned randomly from a normal distribution ($\overline{x}$=4,000 mg, σ=333.33 mg)
	larkspur-attraction	Factor determining the relative amount of larkspur a cow will eat when in a patch with MSAL-content; assigned randomly from a normal distribution ($\overline{x}$=1, σ=0.083)
	herdmates	Agent-set consisting of nearest 20 cows
	mean-herd-distance	Mean distance to herdmates
	total-MSAL-intake	Total amount of MSAL alkaloids consumed during model run (mg)
	daily-MSAL-intake	Amount of MSAL alkaloids consumed during current day (mg)
	hydration	Hydration level, decreases to zero between visits to water
	ready-to-go	Used by leader cows only, a measure of their inclination to move on from an overgrazed site
Globals	waterers	Patch-set of all watering locations
	site-tolerance	Herd-size-dependent variable determining leader cows' tolerance for relatively overgrazed sites
	site-radius	Radius of site when choosing a new site; product of herd-cohesion-factor and herd size resulting in space per cow ranging from 10 m^2 to 1000 m^2
	herd-distance	Desired mean-herd-distance; product of herd-cohesion-factor resulting in range from 10 m to 100 m
Inputs	kgs-per-hectare	Mean amount of usable forage (kg • ha^{-1})
	mean-larkspur-mass	Mean mass of larkspur plants (g)
	MSAL-concentration	MSAL alkaloid concentration in larkspur plants (mg • g^{-1})
	herd-cohesion-factor (HCF)	Determines herd-distance and site-radius; range 1-10, increase leads to more cohesive herd
	stocking-density (SD)	Instantaneous stocking density (AU • ha^{-1})

3.2.3. SCALES. The model simulates cow activities at multiple temporal and spatial scales. In each tick (one cycle through the model code), each cow interacts with a single 1 m^2 patch (a feeding station) by grazing (>99% of the time) or drinking water (twice per day) (Bailey and Provenza, 2008). A tick does not represent time, but rather the occurrence of this interaction. This is because the duration of this interaction will vary depending on the amount of forage available, among other factors. Instead, time is represented by consumption of forage. When the average consumption of the grazing herd is equal to the average daily consumption of a 500 kg cow (12.5 kg), the model counts a grazing-day as having passed (National Research Council, 2000). Total model run time is measured in animal-unit-months (AUMs) (Holechek et al., 2011).

The narrowest scale of spatial interaction is the eating interaction occurring within a single patch (1 m^2). When determining the next patch to graze, the cow's decision is based on a desire either to move closer to its herdmates or to choose a nearby patch with maximum available forage. This decision happens on the scale of 2-25 m. Finally, leader cows make decisions on the scale of the entire pasture by deciding when it is time to visit water or time to move from the current feeding site to a new site.

Thus, there are four programmed spatial scales (additional scales may be emergent) at which the cows interact with the landscape: 1) the individual patch; 2) the scale of herd cohesion, set by the user; 3) the current feeding site; and 4) other feeding sites, identifiable by leader cows. The number of ticks that will pass before reaching a stopping point (say, 150 AUMs) depends on the number of animals grazing, their herd cohesion, the amount and distribution of available forage, and stochastic emergent properties of the model. For an expanded discussion of temporal and spatial scales of foraging behavior of large herbivores, see Bailey and Provenza (2008).

3.2.4. PROCESS OVERVIEW AND SCHEDULING. Figure 3.1 illustrates the model execution process for each tick. Each cow moves through each step of the process, but only performs those steps linked to its role.

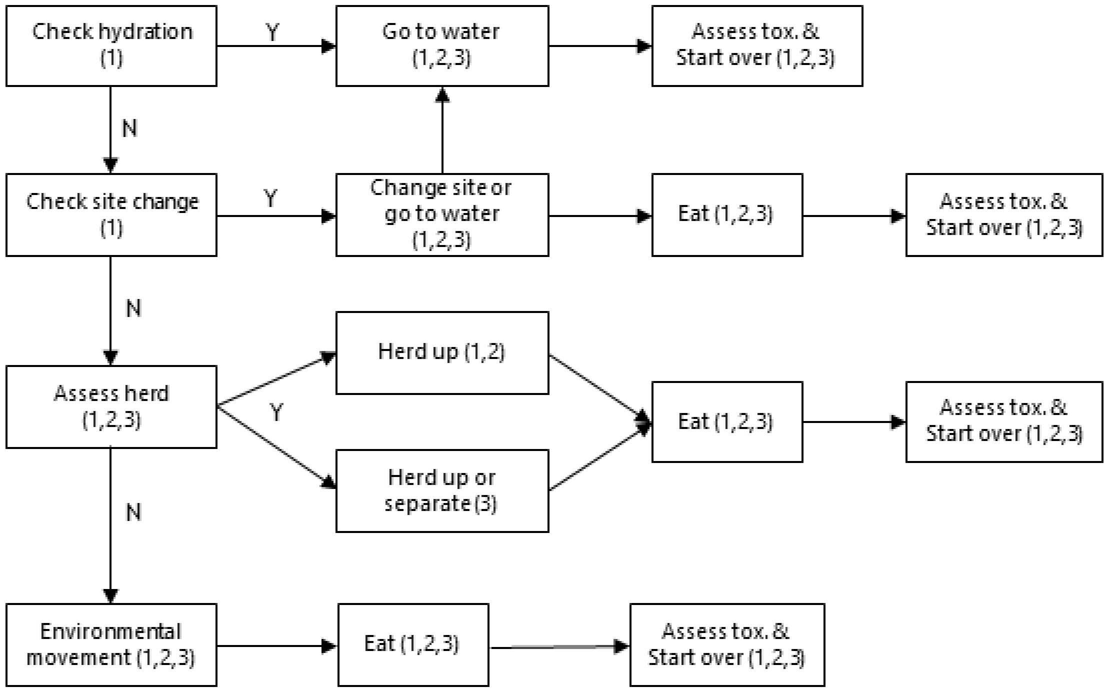

FIGURE 3.1. Pseudo-coded flow chart of model processes, with role of cows executing each process in parentheses. 1= leader, 2=follower, 3= independent.

3.2.4.1. *Check hydration*. Each leader cow checks it hydration level, which is tied to forage consumption such that it depletes to zero twice per day. We chose two water visits per day based on personal communication about GPS collar data for the region (D. Augustine, USDA ARS, pers. communication; see Augustine and Derner, 2014). If an individual leader detects its hydration level as less than or equal to zero, it initiates a movement to water for the whole herd.

3.2.4.2. *Go to water*. The water source in pasture 16 is a stream that is intermittently below ground. The go-to-water procedure directs each cow to go to the nearest waterer patch with two or fewer cows already present. The hydration value for each cow is then set to maximum, and the value for ready-to-go for leader cows is set to site-tolerance – 1. This reflects the understanding that cattle will quickly graze and trample areas around water, rendering them unsuitable for grazing. Instead, they will pick desirable foraging areas in proximity to but not directly surrounding a watering site, expanding outward as these areas are grazed (Bailey and Provenza, 2008). The model thus encourages a site change upon drinking water, but only if the area surrounding the watering site meets the criteria for increasing ready-to-go (explained below). A global variable ensures that no other processes occur during a tick when watering occurs.

3.2.4.3. *Check site change*. This process is only executed by leader cows, each of which assesses the mean number of times patches within a radius of 10 m have been grazed. If these patches have been grazed relatively more (defined as >0.5 • mean times-grazed of all patches + 1.2) than the pasture as a whole, the value of ready-to-go increases by one. If this value reaches a pre-defined threshold (which increases with herd size), the individual then initiates a site change, but only if the individual's hydration value is not approaching zero, in which case it instead initiates the go-to-water procedure. We arrived at the threshold formula for increasing the value of ready-to-go by using visual debugging and evaluation related to site change frequency, as well as theory on the optimization of grazing effort (Bailey and Provenza, 2008; Senft et al., 1987).

If conditions for a site change are satisfied, the deciding leader cow first identifies the best five available sites, using criteria of number of times-grazed, forage-mass, and n-forage-mass to determine a centroid patch. The nearest of these patches is then used to create a new site at a radius that is linked to the user selected herd-cohesion-factor and the size of the herd, resulting in 10-1,000 $m^2 \bullet cow^{-1}$ in the new site. The leader cow then initiates the change-site procedure for itself and all other cows.

3.2.4.4. *Change site*. This procedure is initiated according to role, so that leader cows have first choice of their location in the new site, followers second, and independents third. Within the allocated new site, each cow chooses the patch with the most forage that has no cows on it or any of its four direct neighbors.

3.2.4.5. *Assess herd*. In combination with the environmental-movement procedure, this process represents >99% of cow actions in the model. Each cow first sets its herdmates as the nearest

20 other cows (Lazo, 1994). For leader and follower cows, if the individual's mean distance to these herdmates is greater than herd-distance, it "herds up". This is achieved by facing the centroid of the herdmates and moving to the patch with maximum available forage that is 10-25 m in the direction of this centroid, within a cone of vision of ±45 degrees (Distel et al., 1995). For independent cows, the same process occurs but is only initiated if the distance from herdmates is greater than 2.5 times the herd-distance of the other cows. Independent cows are also repelled from the center of their herdmates by moving away by the same procedure when they are within one-half of the herd-distance.

3.2.4.6. *Environmental movement.* If none of the above procedures are implemented, each cow will make a movement decision based on local grazing conditions. If the patches within a radius of 10 m are relatively ungrazed (mean times-grazed < 0.5) the cow will move to the patch with the most available forage within 2 m, within a ±45 degree cone of vision (Bailey and Provenza, 2008). If the same area is relatively well grazed (mean times-grazed ≥ 0.5), the cow then looks further afield, choosing the patch with the most available forage within 10 m, within a cone of vision of ±45 degrees.

3.2.4.7. *Eat.* The eat procedure is the core interaction between the cows and the forage, both non-larkspur and larkspur. Behavior varies slightly depending on how many times the patch has previously been grazed. If the current visit is the first time it has been grazed, the cow eats 40% of the available forage (Laca et al., 1994; WallisDeVries et al., 1998). If it is the second visit, it eats 50% of what remains. In the third and any subsequent visits, it eats 60%. Each cow then increases its consumption-level by the same amount and decreases its hydration value. If there is larkspur present (in the form of MSAL-content), that is consumed according to the individual cow's larkspur-attraction value, increasing the MSAL-level of the cow. The corresponding patch values are decreased to account for consumption. Lastly, times-grazed in the patch is increased by one.

3.2.4.8. *Assess toxicosis.* This process is triggered at the end of each grazing-day for all cows in order to assess their toxicosis status, which is measured as their MSAL-level relative to their MSAL-tolerance. Note that MSAL-level is measured continuously throughout the model run, and has an elimination half-life of one grazing-day (B. T. Green et al., 2009). If MSAL-level exceeds MSAL-tolerance, the count of deaths for the model run is increased by one, MSAL-level is set to zero, and the cow continues. Numerous other data on toxicosis status are recorded for all cows at this point. Lastly, the MSAL-level for each cow is multiplied by 0.5.

3.2.5. DESIGN CONCEPTS. 3.2.5.1. *Emergence*. Because the actions of the cows are encoded via simple behavior-based processes, nearly all model patterns can be considered emergent. These include the stochastic distribution of the herd and subherds, forage consumption, larkspur consumption, grazing pressure and patterns, and site changes. Assessment of these un-coded emergent properties and patterns was critical to establishing the credibility of the model (Grimm and Martin, 2013).

3.2.5.2. *Adaptation, objectives, learning, and predictions*. The cows adapt to the grazing environment as they and their fellow cows graze, continually seeking their main model objective of maximizing forage consumption within behavioral limits (Distel et al., 1995). There is no encoded learning or prediction, as the cows are programmed to be familiar with the location of forage and water in the pasture. However, it may be that learning and prediction are emergent, in that activities that we might consider to be evidence of those behaviors are visible in the model as a result of the simple encoded behaviors.

3.2.5.3. *Sensing and interaction*. The cows sense each other and their environment at multiple spatial scales. Interaction occurs with other cows whenever moving to a new patch, both via sensing if a patch is already occupied and by seeking to herd up when too far from their herdmates.

3.2.5.4. *Stochasticity*. There is no environmental stochasticity in this model iteration, as we sought to make the landscape as realistic as possible by incorporating relevant data from the real pasture 16. However, cattle interactions with the forage and larkspur demonstrate moderate stochasticity.

3.2.6. INITIALIZATION. Landscape initialization begins by loading the SAVI layer and a user-input value for available forage per ha (kgs-per-hectare). The model uses a nonlinear exponential formula to distribute forage such that the patches with the least forage contain one-third of the mean forage, while the patches with the most contain three times the mean forage. Next, the model incorporates the larkspur distribution layer, using inputs of median larkspur mass (g) and mean MSAL concentration (mg • g^{-1}) to generate an MSAL alkaloid (hereafter simply "alkaloid") content for each patch. These values are based on our unpublished data on *D. geyeri* mass and toxicity at the Maxwell Ranch such that larkspur plants in areas of high SAVI were 50% larger than the median, and larkspur plants in areas of low SAVI were 50% smaller than the median. Finally, the model incorporates the water location layer. All other patch variables are derived from these inputs. Figure 3.2 shows the initialized landscape.

The final step in model initialization is to create the cows by using the input of stocking-density multiplied by the area of the pasture. All cows are initially in the same random location in the pasture. This location is largely irrelevant as the cows immediately go to water, but we did not want it to be the same location each time because this would be unrealistic (pasture 16 has multiple entrances for cattle) and would limit stochasticity. At this point, the model is fully initialized and is executed following the processes laid out above.

3.2.7. SIMULATION. We used the BehaviorSpace tool in NetLogo to run a full factorial simulation of four different levels of both herd-cohesion-factor (1, 4, 7, and 10) and stocking-density (0.25, 0.5, 1.0, and 2.0 AU • ha^{-1}). We replicated each combination 30 times, for a total of 480 simulations. Input median larkspur mass was 3.5 g and input MSAL alkaloid concentration was 3.0 mg • g^{-1}. We chose these values to be representative of an excellent growing year with larkspur plants at bud stage, when the alkaloid pool (total available mg) is highest—arguably the most dangerous possible conditions. This is also a time of year that cattle grazing in larkspur habitat is frequently avoided, despite being a

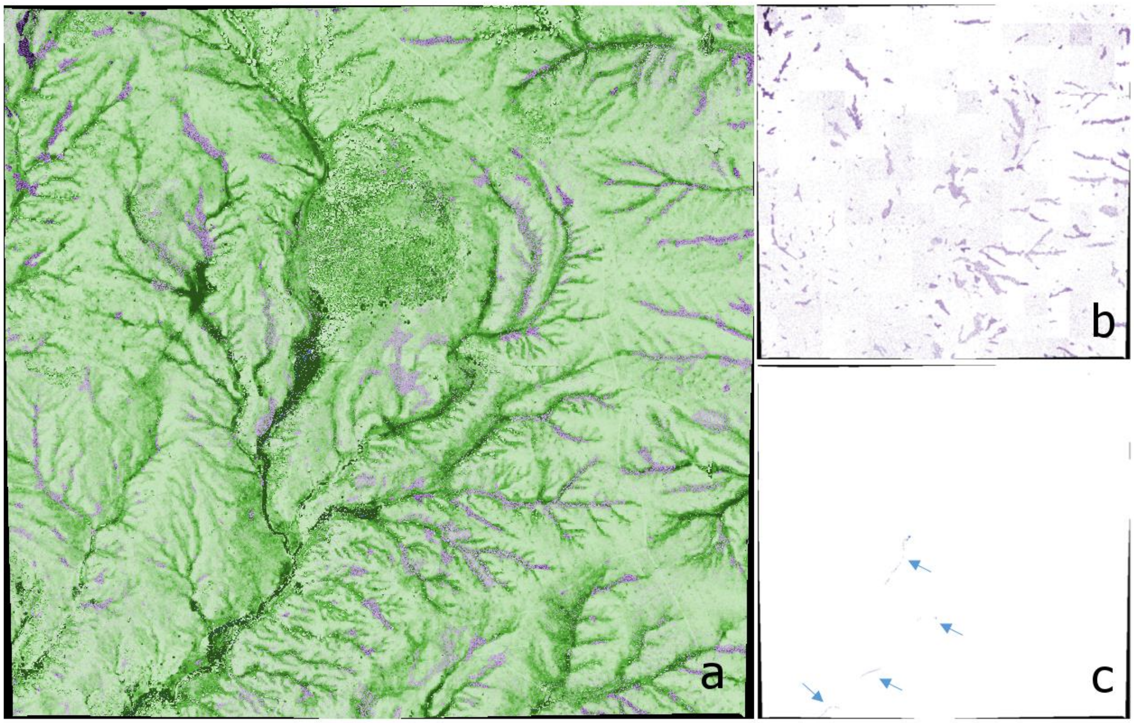

FIGURE 3.2. Model landscape, 1.66 km x 1.58 km. (a) Initialized full model landscape, with darker green indicating areas with greater aboveground forage biomass. (b) Landscape with larkspur locations only, with darker purple representing higher MSAL-content and with results of hybrid sampling method evident. (c) Landscape with watering locations only, pointed out by arrows.

highly desirable time for grazing (Gardner and Pfister, 2007; B. Green et al., 2009; Pfister et al., 1997a). Input value for kgs-per-hectare was 500 kg, based on current ranch usage and typical values for the area.

3.2.7.1. *Observation*. Of primary importance were data related to alkaloid consumption, assessed according to dose-response data from previous research (Welch et al., 2015b). Most interesting was the number of times in a model run that any individual cow crossed the threshold into potentially lethal acute toxicosis, during which they would be expected to be recumbent and unable to stand, with a high likelihood of death (Welch et al., 2015b). To measure the number of such cases, the model counted cows whose MSAL-level exceeded their MSAL-tolerance at the end of a grazing-day.

The model also recorded data underlying the trends found for lethal acute toxicosis, most importantly data on daily, total, and maximum alkaloid intake. These data assisted in identifying potential mechanisms for the role of herd cohesion and stocking density in influencing deaths. Additional data, such as forage consumption, number of site changes, travel distance per day, and evenness of grazing impact, provide additional insight and model output verification.

3.2.8. STATISTICAL ANALYSIS. We used both JMP Pro 13.0.0 and R statistical software, version 3.3.3 for data analysis and presentation (R Core Team, 2018; SAS Institute, 2016). Data for daily alkaloid intake, which amounted to 1.88 million data points, were organized and cleaned using OpenRefine 2.8 (Google/Open source, 2018). We began by assessing the role and relative influence of HCF and SD in generating lethal acute toxicosis, within two contexts: first, using their 16 combinations as "management levels" to explore overall trends in a management-relevant manner; and, second, using HCF and SD as continuous variables within a regression framework to provide more information on the relative influence of each. To regress the lethal acute toxicosis count data we used a generalized linear model (GLM) with a negative binomial distribution and a log-link function using the MASS package in R (Faraway, 2016; Hilbe, 2011). To confirm that the negative binomial distribution was the correct choice, we compared it to a GLM with a Poisson distribution and a log-link function. The GLM with the negative binomial distribution was superior, using residual deviance and Aikaike's information criterion (AIC) as judgment criteria (Anderson, 2008).

To identify mechanisms for how HCF and SD were influencing deaths, we used the same negative binomial GLM approach to analyze the relationship between various intake data and lethal acute toxicosis. We did so by first hypothesizing which factors were driving deaths, and then looked at single-factor models for each, assessed using AIC values and model coefficients (Anderson, 2008). Because the goal was to identify key mechanisms rather than determine the best predictive model, this provided more insight than examining a global model or various permutations of factors.

Finally, we analyzed the relationship of HCF and SD to the identified mechanisms using multiple linear regression (R base package). While there were some indications of heteroscedasticity and outliers, we determined that linear regression was robust to those errors in these cases. We confirmed this by also fitting alternate models within other regression frameworks (robust and non-parametric), which returned very similar results. Interaction effects are shown when significant; otherwise, they were excluded from the models.

3.3. RESULTS

3.3.1. MODEL OUTPUT VERIFICATION. A core element in the evaluation of behavior-based mechanistic effect models is a comparison between multiple emergent model patterns and observed patterns in the real system (Grimm and Martin, 2013). In this case, this helped to establish that the modeled cows, coded for individual behaviors, acted like real cows when interacting with one another and the landscape, at least in regard to behaviors relevant to larkspur consumption. Toward this end, first we offer Figure 3.3 to illustrate how varying HCF influences herding patterns, and to show how grazing was distributed across the pasture in one model run.

Decreasing HCF increases overall herd separation and leads to more wandering among the independent cows and others. Note that in Figure 3.3a the cows have formed distinct subherds. This appears to be an emergent property of cows grazing with high herd cohesion (herd-distance ≤ 20 m).

The cows initially graze the areas with high forage amounts (dark green) in relative proximity to the water, and gradually extend their impact outward, targeting high productivity areas. By the end of the grazing cycle (Figure 3.3d), they have visited the entire pasture, though areas furthest from water have been grazed less (Hart et al., 1993). Areas of initial high forage mass have been grazed two or more times, while many areas of low forage mass have not been grazed at all. These results are in line with well-established qualitative understanding of grazing patterns in large pastures (Bailey and Provenza, 2008; Holechek et al., 2011).

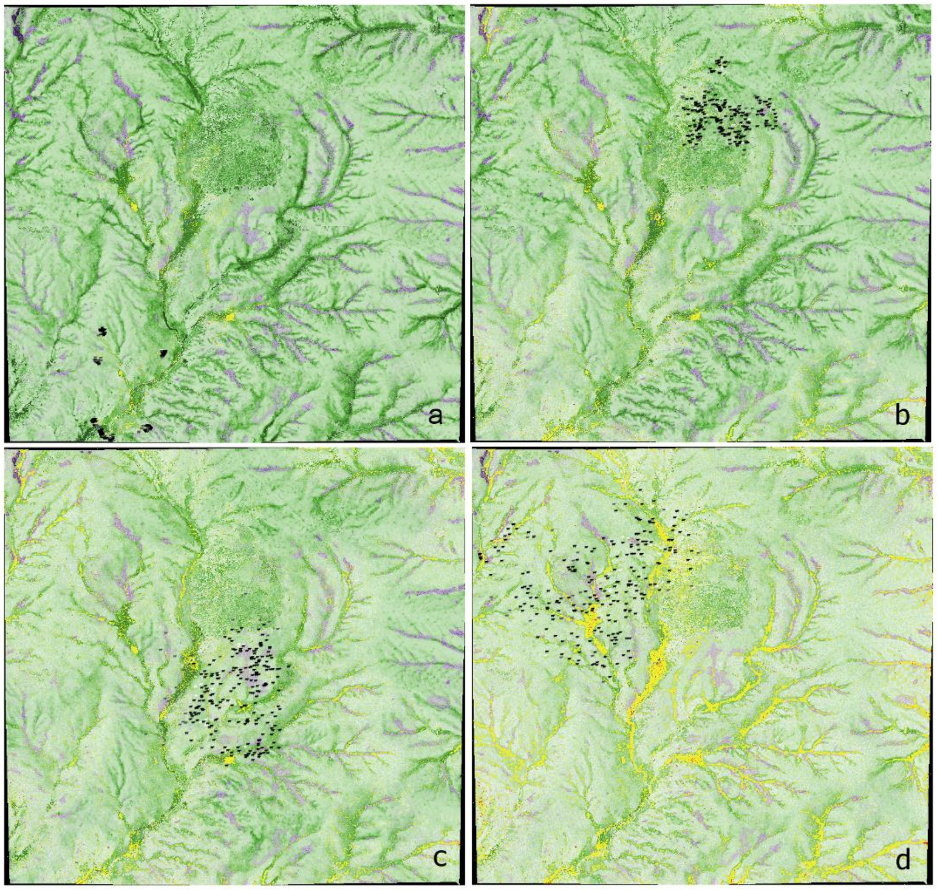

FIGURE 3.3. The effect of varying herd-cohesion-factor (HCF) on herd patterns, displayed at different levels of pasture usage (AUMs). Note that the cows depicted in these images are drawn 200 times larger than they really are to aid visualization, which makes them appear closer to one another than they are. Pasture size is 1.66 km x 1.58 km, and stocking density for all images is 1.0 AU • ha^{-1}. White cows are leaders, black followers, and gray independents. Yellow indicates patches that have been grazed twice, red three times. (a) HCF=10, AUMs=14; (b) HCF=7, AUMs=68; (c) HCF=4, AUMs=119; (d) HCF=1, AUMs=163. Typical usage for this pasture (258.82 ha) is 150 AUMs.

The variation in forage consumption among individuals also aligned well with the variation seen in real cows foraging native pasture. While a grazing-day for the whole herd was defined as mean consumption of 2.5% of body weight (12.5 kg), the mean 99.9% daily range of consumption for all model runs was 2.34-2.66% of body weight. This range of consumption aligns well with common "rules of thumb" and predictive formulae (Cordova et al., 1978; Galyean and Gunter†, 2016; National Research Council, 2000).

The mean value for site changes per day for the 16 management levels varies from 2.3 for few cows grazing very loosely (HCF=1, SD=0.25) to 6.0 for many cows grazing very cohesively (HCF=10, SD=2.0). These values are in line with the estimate of 1-4 hours per feeding site by Bailey and Provenza (2008). For runs with few cows grazing with little cohesion (HCF=1, SD=0.25), mean daily travel was 4.16 km, while many cows grazing very cohesively (HCF=10, SD=2.0) traveled an average of 7.40 km per day. These numbers and the positive trend also track well with data from previous studies (Walker et al., 1985).

As a last point of output verification, we were interested to see if the number of modeled cases of larkspur-induced lethal acute toxicosis would parallel numbers from the literature when we modeled grazing to be similar to the current management scheme. When modeled to reflect current management practices, with HCF=4, SD=0.5, and for 150 AUMs (removing approximately 45% of available forage), we recorded a mean of 2.8 cases of lethal acute toxicosis across 30 model iterations. This amounts to 2.4% of cows, which falls within the estimate of 2-5% in pastures with dangerous amounts of larkspur (Pfister et al., 1997a). Additionally, individual model runs of zero deaths occurred in all but four of the management levels, which aligns with our anecdotal understanding of producer experience.

3.3.2. LETHAL ACUTE TOXICOSIS. On its own, increased herd cohesion demonstrated the potential to significantly reduce deaths. For example, at a stocking density of 0.5 AU • ha^{-1}, mean deaths declined from 4.33 at HCF=1 to 1.37 at HCF=10. Similarly, increased stocking density in the absence of changes in herd cohesion also greatly reduced deaths, for example from a mean of 7.5 at SD=0.25 to 0.70 at SD=2 at a constant HCF of 4. Working together, increases in both herd cohesion and stocking density from the minimum to the maximum achieved a 99.6% reduction in deaths (Figure 3.4). The mean value for MSAL-tolerance among dead cows was 3,725.8 mg, while the mean value for larkspur-attraction was a factor of 1.06. Of 1,132 total deaths in the simulation, 3.9% were among cows with the role of leader, 78.7% were among followers, and 17.4% were among independents.

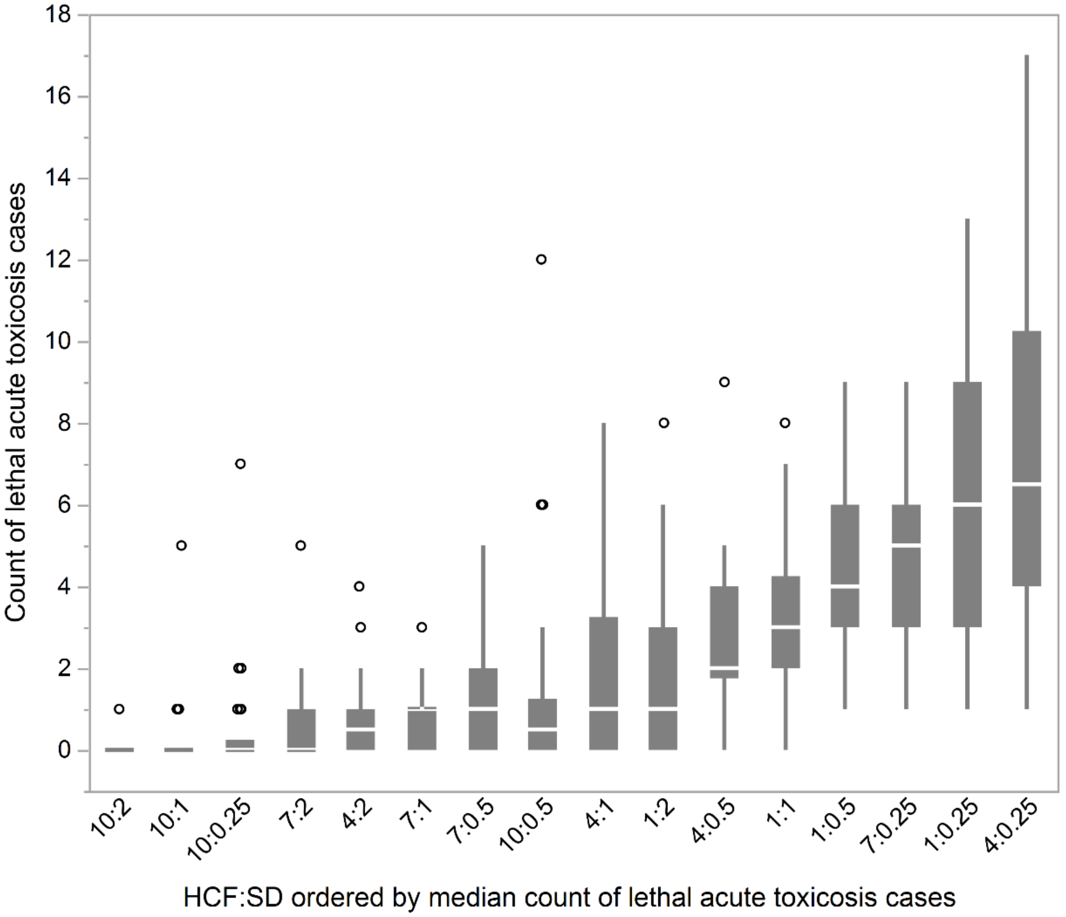

FIGURE 3.4. Box plots of distribution of counts of lethal acute toxicosis cases (MSAL-level ≥ MSAL-tolerance at end of grazing-day). From 30 model runs for each combination of herd-cohesion factor (HCF) and stocking-density (SD), ordered by median count of lethal acute toxicosis cases, with outliers as jittered circles.

The coefficient for HCF (Table 3.2), as a log odds ratio, indicates that an increase of one in HCF resulted in a 13.5% decrease in occurrences of lethal acute toxicosis. The coefficient for SD indicates that an increase of one in SD resulted in a 54.8% decrease. Lastly, the coefficient for the interaction of HCF with SD indicates that an increase in either HCF or SD slightly increases the effect of the other. The GLM β coefficients indicate that HCF had 91.8% of the influence of SD in reducing deaths.

TABLE 3.2. Results of GLM with negative binomial distribution and log-link function for count of lethal acute toxicosis as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). β coefficients are from the same GLM without the interaction present. GLM fit: Fisher scoring iterations=1; residual deviance=516.94 on 476 degrees of freedom; AIC=1686.3.

Coefficient	Estimate	Std. error	p-value	β
Intercept	2.341	0.128	<0.001	
HCF	-0.145	0.024	<0.001	-0.225
SD	-0.793	0.136	<0.001	-0.245
HCF:SD	-0.079	0.029	0.007	

3.3.3. IDENTIFYING MECHANISMS. We hypothesized that five factors might explain how HCF and SD were reducing deaths: mean individual daily alkaloid intake (the average single-day alkaloid intake in a model run), standard deviation of individual daily alkaloid intake, mean maximum individual daily alkaloid intake (each cow's worst day), standard deviation of maximum individual daily alkaloid intake, and the coefficient of variation for individual total alkaloid intake. Results for the comparison of single-factor models reveal varying influence on lethal acute toxicosis among these factors (Table 3.3).

TABLE 3.3. Results for comparison of single-factor negative binomial generalized linear models with a log-link function using corrected Aikaike's information criterion. All values for quartiles are in mg, except for CV total, which is unitless. Percent Δ deaths from Q_1 to Q_3 is observed percent change in lethal acute toxicosis count between quartile one and three.

Mechanism	AICc	GLM coefficient	Quartile 1	Quartile 3	Pct. Δ deaths from Q1 to Q3
σ Maximum	1473.3	0.0072	410.3	591.2	130.70%
σ Daily	1510.1	0.0265	363.8	435.4	192.36%
Mean maximum	1671.2	0.0019	1275.0	1987.7	135.55%
Mean daily	1911.4	-0.0374	527.9	543.0	-55.58%
CV total	1930.2	-7.044	0.118	0.185	-6.69%

3.3.4. DAILY ALKALOID INTAKE. Mean individual daily alkaloid intake represents the mean of every single-day alkaloid intake for every cow and ranged from a low of 525.1 mg (HCF=4, SD=0.25) to a high of 550.9 mg (HCF=10, SD=0.25). Multiple linear regression results indicate that HCF and SD had limited influence on mean daily intake (adj. $R^2<0.19$), with both associated with slight increases. On the other hand, the standard deviation of daily alkaloid intake, which quantifies the spread of the distribution of daily alkaloid intake values, differed significantly between management levels, from a high mean of 460.5 mg (HCF=1, SD=0.25) to a low mean of 301.3 mg (HCF=10, SD=2). Multiple linear regression results indicate that HCF and SD were strongly influential, with HCF exerting 93.0% more influence than SD (Table 3.4). A box plot showing the distribution of all individual daily alkaloid intake values (*n*=1.88 • 10^5) at each management level further illustrates these patterns (Figure 3.5).

TABLE 3.4. Results of multiple linear regression for the standard deviation of individual daily alkaloid intake as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). Adj. R^2=0.76.

Coefficient	Estimate	Std. error	p-value	β
Intercept	487.79	2.61	<0.001	
HCF	-11.33	0.33	<0.001	-0.774
SD	-29.38	1.64	<0.001	-0.401

3.3.5. MAXIMUM DAILY ALKALOID INTAKE. Mean maximum individual daily alkaloid intake quantifies the mean worst day for all cows during a model run, and ranged from 1,045.6 mg (HCF=10, SD=2) to 2,450.2 mg (HCF=1, SD=0.25). The standard deviation of maximum individual daily alkaloid intake quantifies how widely dispersed this value was among the herd members, and ranged from 303.0 mg (HCF=10, SD=2) to 704.0 mg (HCF=4, SD=0.25). Regression results for both factors provide further insight into the relationship of HCF and SD to lethal acute toxicosis (Tables 3.5 and 3.6).

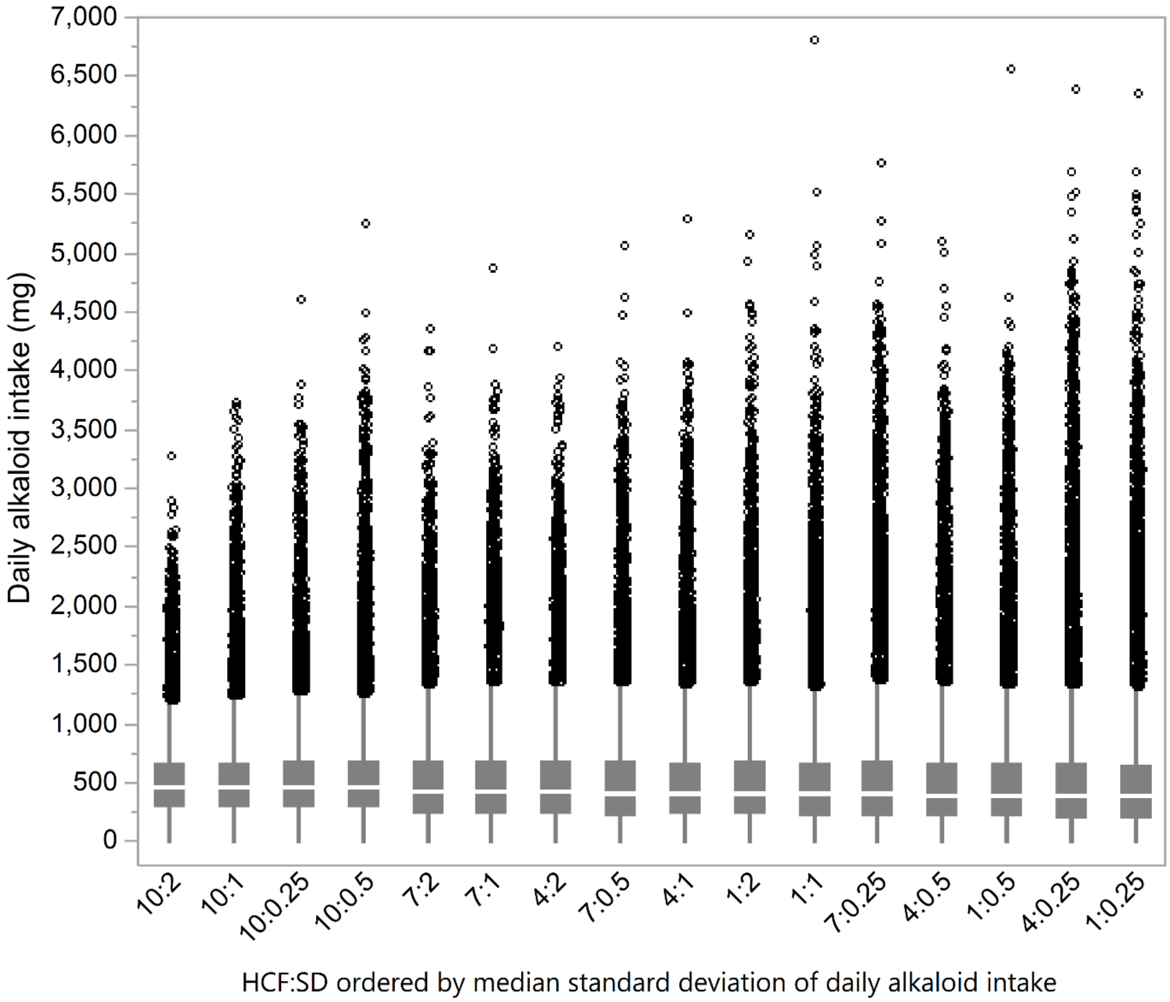

FIGURE 3.5. Box plots of distribution of individual daily alkaloid intake (mg; *n*=1.88 • 10^5). From 30 model runs for each combination of herd-cohesion factor (HCF) and stocking-density (SD), ordered by median standard deviation of daily alkaloid intake, with outliers as jittered circles.

TABLE 3.5. Results of multiple linear regression for the mean of maximum individual daily alkaloid intake as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). Adj. R^2=0.82. β coefficients are from the same model without the interaction present.

Coefficient	Estimate	Std. error	p-value	β
Intercept	2547.56	28.58	<0.001	
HCF	-61.86	4.44	<0.001	-0.31
SD	-686.15	24.80	<0.001	-0.84
HCF:SD	22.75	3.85	<0.001	

TABLE 3.6. Results of multiple linear regression for the standard deviation of maximum individual daily alkaloid intake as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). Adj. $R^2=0.47$. No significant interaction was present.

Coefficient	**Estimate**	**Std. error**	**p-value**	**β**
Intercept	718.57	11.33	<0.001	
HCF	-22.34	1.42	<0.001	-0.52
SD	-96.06	7.12	<0.001	-0.45

3.3.6. DISTINCT PERSISTENT SUBHERDS. Model outputs (Figure 3.6) suggested an apparent scalar behavioral discontinuity between HCF=7 and HCF=10, which we believe results from the emergent property of distinct persistent subherds.

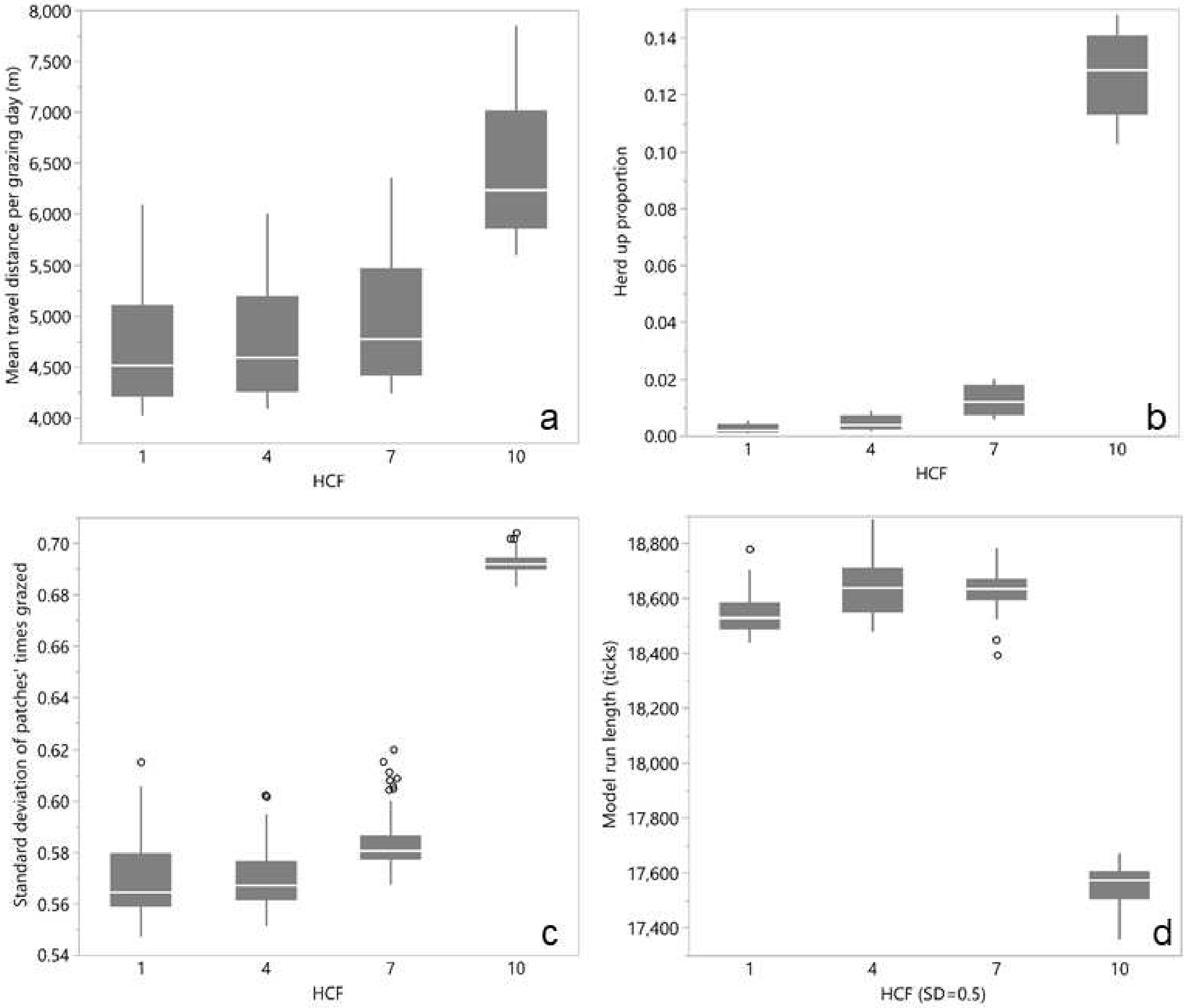

FIGURE 3.6. Box plots of various model evaluation data by herd cohesion factor (HCF), demonstrating effect of distinct persistent subherds. (a) Mean individual travel distance per grazing day (m); (b) Proportion of use of assess herd procedure (versus environmental movement) to choose a new grazing patch, a measure of herd-based versus individual optimization; (c) Standard deviation of times-grazed count for all patches at end of model run, a measure of grazing heterogeneity; (d) Total model run length, an inverse indicator of grazing efficiency, at stocking density=0.5.

3.4. DISCUSSION

Research into best practices for grazing management in larkspur habitat has long focused on either attempts to eliminate larkspur or on phenological avoidance (what we term "fight or flight"). Because elimination through herbicides or mowing is costly and often impractical (Nielsen et al., 1994), most research and current recommendations focus on avoiding grazing in larkspur habitat at times of year when it is considered most dangerous to cattle, exemplified by the toxic window concept (Pfister et al., 1997a, 1988; Welch et al., 2015a). While this approach has certainly helped many producers better understand larkspur toxicity dynamics, there is no evidence that it has reduced the overall number of deaths. There are many reasons for this, and interactions are complex and place-based, but we suggest that a reliance on a static view of palatability is largely to blame.

An alternative to fight or flight is to manage grazing such that larkspur intake remains below the threshold where there is an observable negative effect on the cattle. This study provides an indication that this may be possible even in pastures with dangerous amounts of Geyer's larkspur. For the first time, this model suggests that herd cohesion and stocking density are key drivers of larkspur-induced toxicosis, and that management decisions that influence these factors hold potential to limit deaths. Of crucial importance is the observation that herd cohesion, which has received almost no consideration in the broader grazing management literature, is an important determinant of risk of death from larkspur.

An essential point for understanding how increased herd cohesion and stocking density reduced deaths is that Geyer's larkspur grows most densely in relatively productive areas, which are thus desirable areas for foraging. Functionally, increased herd cohesion and stocking density lead to increased competition for forage, making it more difficult for any individual to monopolize a resource- and larkspur-rich area. Additionally, increased herd cohesion leads to less wandering among individuals, making it less likely an individual cow will wander into a dense larkspur patch alone. Evidence for the danger of wandering behavior is found in the disproportionate death rate of cows with the role of independent. Lastly, increased stocking density does appear to lead to dilution, but in the form of lowered maximum individual daily intake rather than lowered mean individual daily intake.

Mechanistically, decreased risk of lethal acute toxicosis occurred through: 1) a narrowed distribution of individual daily alkaloid intake, 2) lowered mean and narrowed distribution of outlier alkaloid intake days. Herd cohesion played a stronger role in narrowing the distribution of daily intake, stocking density was more influential in lowering the mean of outlier intake, and both played a relatively equal role in narrowing the distribution of outlier intake events. Strong evidence for the role of these as mechanisms is provided by the much lower AICc score for the model with the mechanisms than for the model with HCF and SD (1386.3 vs. 1686.3). This suggests that other management interventions that succeed in influencing these mechanisms would have similar success in reducing deaths.

When we recognize that even in the worst-case scenario lethal acute toxicosis is a rare event among thousands of grazing-days, it becomes clear why narrowing the distribution of individual intake and reducing outliers is so important. With a mean MSAL-tolerance of 4,000 mg, an average bad day in a herd with low herd cohesion and low stocking density would put an individual (especially one with lower tolerance or higher attraction to larkspur) in danger. Meanwhile, individuals grazing in a herd with high herd cohesion and at a high stocking density in the same pasture, even those with low tolerance, would need at least a few upper-end intake days in a row to risk death—an unlikely occurrence.

Note that we selected the bounds of herd cohesion and stocking density to align with what we believe to be realistically achievable by managers in the western US. While stocking density is easily understood, it may be worthwhile to describe how we think the various levels of herd-cohesion-factor (HCF) could be achieved (reference Figure 3.3). We think of HCF values of 1 and 4 as representative of most current extensive management, such that there is a small to moderate amount of herding behavior but in which animals are often spread out across a large area. The difference between these two might be accounted for by differences in breeding history, carnivore pressure, or genetic drift. To achieve an HCF of 7, we think cattle would need to be selected for strong herding instinct or be regularly, but not necessarily continually, herded. An HCF of 10 is comparable to many herds of wild ungulates and is achievable through the continual presence of a herder or a sustained effort at selecting for herding behavior.

There are two additional ways that a rapid increase in herd cohesion may be achieved. First, a drastic increase in stocking density (via increased animal-units or subdivided pastures) to a level that approaches "mob" grazing can forcibly increase cohesion. Second, the emerging technology of virtual fencing holds tremendous promise for achieving rapid changes in grazing behavior, including herd cohesion (Anderson et al., 2014).

An unexpected emergent phenomenon occurred at HCF=1, in the form of distinct persistent subherds (see Figure 3.3a). These subherds are small groups of >20 but usually <35 cows that stick closely together for an entire inter-watering period, with some exchange of individuals or combining when two groups meet. This does not occur at higher levels of HCF. Cows in distinct persistent subherds traveled significantly greater distances, spent more time seeking to be closer to herdmates rather than maximizing forage intake, and grazed more heterogeneously (Figs 3.6a-c). Nevertheless, these cows reached 150 AUMs of forage consumption in 94.3% of the model run time of cows at lower herd cohesion levels, suggesting higher grazing efficiency (Figure 3.6d). We believe that these data are evidence of a scale-dependent behavioral discontinuity that may hold relevance to other grazing management challenges (Allen and Holling, 2008).

3.4.1. MODEL PARSIMONY AND STUDY LIMITATIONS. Perhaps the most obvious omissions from the model are those behaviors that we determined to hold little to no relevance to larkspur consumption, at least in this pasture. These include response to slope, resting, and some inconsistently understood aspects of dominance behaviors. While there is nothing preventing them from being included, we decided that in this case these behaviors would introduce uncertainty while adding little realism to cattle-larkspur dynamics. The model also excludes plant regrowth. For Geyer's larkspur, this is not an issue, as plants that are clipped or grazed during the bud stage exhibit very little regrowth [K. Jablonski, pers. obs.]. For other forage, we determined that regrowth in July in this semi-arid climate would not be substantial enough within a single grazing period to warrant inclusion.

The occurrence and measurement of death in the model might strike some as unrealistic. However, given that deaths in a herd would change herd behavior in unknown ways, and that the owner of the cattle would likely intervene once one death-event had occurred, we believe that counting the death and resetting the cow's MSAL-level is the most accurate way to assess risk at different management levels.

Another potential limitation concerns the model used for alkaloid metabolism. While there has been some effort at the generation of such a model (e.g., B. T. Green et al., 2009), these efforts have been limited to highly controlled settings using hay and other stored feeds and periodic dosing with alkaloids. Additionally, little to nothing is known about the role of other forage in exacerbating or mitigating the effects of larkspur consumption. As such, we had no confidence that a continuous metabolic model would be more useful than the simple daily half-life model that we used. Similarly, we felt that the complexity of susceptibility to toxicosis, which is likely driven by not only innate genetic tolerance (Green et al., 2014) but also specific situational tolerance (e.g., body condition, heart rate, life stage, or even weather) meant that a normal distribution around the estimated toxicosis threshold (Welch et al., 2015b, 2015a) from the literature was the best choice.

Despite these limitations, we are confident that we have realistically modeled cattle-larkspur dynamics, that increased herd cohesion and stocking density lower the risk of lethal acute toxicosis, and that variations in mean and maximum daily alkaloid intake are the predominant mechanism for this reduction. However, the exact values for when risk approaches zero may be dependent on the circumstances of this model iteration—that of *D. geyeri*, at the input values for mass and toxicity, on a ranch in northern Colorado.

It is worth noting that dangerous levels of *D. geyeri* are typically found on a limited number of a single operation's grazing units. This means that the inclusion of herding to increase herd cohesion, for example, would usually only be necessary for a relatively brief period. In addition, it means that any potential secondary effects of sub-lethal larkspur consumption, such as appetite suppression or lethargy (whether and how these would occur is unclear), would be of similarly limited duration. Nevertheless, in pastures with a dangerous amount of larkspur, negative sub-lethal effects may be unavoidable even (or especially) when death is avoided.

As with any research where cattle lives and producer livelihoods are at stake, it is most important to emphasize that producers should exercise caution when incorporating our findings into their own management, including careful assessment of other potential effects of increased herd cohesion or stocking density. Those with low amounts of Geyer's larkspur or with no history of losses might find comfort in altering their grazing management to incorporate this study's findings. Those with a great deal of larkspur (Geyer's or other species) or a history of losses should be more careful.

3.4.2. OTHER MODEL IMPLICATIONS AND FUTURE DIRECTIONS. There is a broad literature on the effect of stocking rate/stocking density on many outcomes (though not larkspur-induced toxicosis) but very little on the effects of herd cohesion, nor on the interaction of these factors (Holechek et al., 2011). This is likely due to the relative ease of varying cattle numbers versus manipulating cattle behavior. Because this study provides evidence that it is not only the number of animals but also how they behave that affect the likelihood of death by larkspur, we are excited to explore the role of herd cohesion, particularly the emergent property of distinct persistent subherds, in other aspects of grazing ecology. If herd cohesion is genetically encoded, matrilineally-oriented, or management-determined (or a combination thereof), what role might it play in other negative outcomes, such as overgrazing of riparian areas or exposure to predation by carnivores (Barnes, 2015), and how might we influence it in different scenarios? The evolving promise of affordable GPS tags means that we may also start to be able to test this through direct observation of entire herds (Bailey et al., 2017).

For cattle-larkspur dynamics, our next step is to place these modeling results in context with ongoing plant experiments and producer surveys to better formulate management recommendations that work. Additionally, we would like to improve our understanding of alkaloid metabolism and tolerance, as well as the role of preference in larkspur intake. For alkaloid metabolism and tolerance, this means building upon previous studies (e.g., Green et al., 2014), which have been undertaken in highly controlled settings using periodic high dosing, to model the stochastic dosing in a dynamic environment that occurs in reality. For larkspur preference, this means moving beyond the entirely anecdotal evidence of bouts of larkspur consumption (e.g., Ralphs et al., 1994) to a more sophisticated understanding of the role of preference, diet mixing, and satiation in larkspur-induced toxicosis (Provenza, 2003b; Provenza et al., 2003b).

A final next step for the model presented here is what Augusiak et al. (2014) term model output corroboration, wherein model outputs are compared to new, independent data and patterns. As noted above, this is very difficult when cattle lives are at risk. However, the results presented here have encourage us to start to think about how such corroborative data could be collected. This will likely entail a combination of full-herd GPS with careful on-the-ground monitoring by a herder.

Though ABMs have some limitations, we believe they offer an exciting new tool for understanding the grazing behavior of livestock. Indeed, the synergistic emergence of financially viable GPS technology (Bailey et al., 2017) and “virtual fencing” (Anderson et al., 2014), along with the increasing power of desktop computers, suggests that the time is right for a computational revolution in livestock grazing management. We are excited that this study provides a first example of the potential of agent-based models to contribute to this revolution.

CHAPTER 4

EFFECT OF ABOVEGROUND MASS REMOVAL ON TOXICITY OF GEYER'S LARKSPUR, WITH IMPORTANT IMPLICATIONS FOR GRAZING MANAGEMENT

4.1. INTRODUCTION

Larkspur (*Delphinium* spp. L.) are perennial herbaceous plants in the family Ranunculaceae, with approximately 300 total species distributed across the Northern Hemisphere and the mountains of tropical Africa, and 61 species in North America (Warnock, 1995). Larkspur plants constitutively contain numerous norditerpinoid alkaloids, which are potent neuromuscular paralytics capable of damaging or killing many organisms, including humans, mice, insects, and livestock (Welch et al., 2015a). In the western United States, researchers have identified eleven species that cause significant cattle death losses, with a recent estimate indicating an average cattle herd loss of 2-5% (15% in some cases) per year, amounting to an estimated $234 million in losses per year in 1988 (B. Green et al., 2009; Nielsen, 1988; Pfister et al., 1997b; Welch et al., 2015a). Such losses have been remarkably intractable for more than a century despite significant research and extension efforts (Cronin and Nielsen, 1972; Glover, 1906; B. Green et al., 2009; Marsh et al., 1916).

Recommended best management practices in larkspur habitat focus on seasonal avoidance, aimed at reducing exposure to the plants when alkaloid concentration is highest (Pfister et al., 1997a; Welch et al., 2015a). Though it is based on sound science, this strategy may create problems of its own as producers lose flexibility to meet their management objectives, both economic and ecological, with little evidence of reduced losses. Regardless of recommendations, many producers abandon grazing on pastures where larkspur is present, either as a precaution or because of past losses (B. Green et al., 2009). There is a large opportunity cost to this practice, as larkspur tends to grow in resource-rich micro-habitats, where stocker cattle have the potential to gain 2.5 pounds per day (B. Green et al., 2009; Pfister et al., 1997b). Other producers appear to accept the risk of deaths, experiencing gains when lucky and losses when not. All told, larkspur presents one of the most significant challenges to grazing management in the western US.

One potential alternative to current avoidance-based strategies is to manage grazing such that all individuals consume some larkspur, but no individual consumes a lethal dose. Our recent paper (Jablonski et al., 2018; Chapter 3) presented an agent-based model simulation that indicated this may be possible if cattle are managed for high stocking density, high herd cohesion, or both. The potential for this solution has also been noted anecdotally by producers (e.g. Smith et al., 2010). This raises questions about the potential response of larkspur to being grazed, as well as the effects of years of generally not being grazed by cattle.

Two previous studies have examined the response of larkspur species to manual clipping. Laycock (1975) tested the effect of clipping on groups (n=11-16) of duncecap larkspur (*D. occidentale* S. Watson) in Idaho and found a reduction in both alkaloid concentration and plant mass in subsequent years. Ralphs and Gardner (2001) tested the effect of clipping on twenty subalpine larkspur (*D. barbeyi* Huth) plants and found a reduction in plant mass but not in alkaloid concentration in subsequent years. Both studies consisted of a single-level treatment of clipping of the full plant at or near ground level, and both interpreted their findings through the lens of mechanical clipping. Neither mentioned the potential long-term ramifications of non-grazing of larkspur on plant vigor and toxicity nor the potential for grazing to play a role similar to mechanical clipping.

Nearly all previous studies of larkspur toxicity have focused on alkaloid concentration (typically $mg \bullet g^{-1}$) as the key measure of poisoning risk to cattle. However, we have come to focus on aboveground alkaloid pool as a more useful comprehensive measure of poisoning risk. Aboveground alkaloid pool is the product of aboveground plant biomass and alkaloid concentration, and can be measured on a per-plant, per-hectare, or per-pasture basis. An understanding of aboveground alkaloid pools is essential if we shift from thinking of larkspur consumption as something to be avoided to something that can be managed at sub-lethal levels.

We focused on larkspur measurements at the bud stage of growth. We chose bud stage because this is when aboveground alkaloid pools are maximized (Ralphs and Gardner, 2003). This growth stage of larkspur also corresponds to the one of the most favorable times for livestock grazing in the foothill rangelands of *D. geyeri* Greene. It is also a time of year when otherwise attractive pastures are often avoided when larkspur is abundant (B. Green et al., 2009).

In this paper we assess the potential response of larkspur to incomplete removal of aboveground plant material, as might occur via grazing. Specifically, we compare the effect of two seasons of 25% and 75% removal of aboveground plant mass to unclipped (control) plants. In combination with our agent-based model findings, the results continue to build support for an alternative approach to one of the most intractable challenges faced by western livestock producers.

4.2. METHODS

4.2.1. STUDY AREA. We collected field data for *D. geyeri* in June of 2016, 2017, and 2018 at the Colorado State University Research Foundation Maxwell Ranch, a working cattle ranch in the Laramie Foothills ecoregion of north-central Colorado that is a transition zone between the Rocky Mountains and the Great Plains. There are significant populations of Geyer's larkspur at several locations on the ranch which have historically created management challenges and resulted in poisoned cattle. We focused our sampling in an area of particularly dense Geyer's larkspur stands (N40° 54.85' W105° 13.64') where no larkspur treatments for either management or research purposes had occurred for at least ten years.

4.2.2. ABOVEGROUND DRY MASS ESTIMATION. Because repeated measurements of individual plants were required, we devised a non-destructive method of estimating aboveground Geyer's larkspur plant dry mass (Catchpole and Wheeler, 1992). While challenging for herbaceous plants, such a method can be reliable if it is applied to an individual species, is calibrated for the specific situation, and incorporates multiple plant traits (Catchpole and Wheeler, 1992; Ohsowski et al., 2016). In this case a linear model was sufficient.

To create the model, in 2016 we randomly selected 120 Geyer's larkspur plants of any size once all plants had reached early bud stage. We began with number of leaves, number of stems, and total stem length as predictor variables for plant mass, chosen for their ease of measurement and hypothesized correlation with mass. To measure number of leaves, we simply counted the total number of fully-formed leaves on each plant. We did not include leaves that were mostly brown and dead but did include leaves that were mostly green with some browning. To measure number of stems, we counted the total number of stems emerging from the ground for an individual plant. To measure total stem length (cm), we summed the total length of all the stems for a given plant. We cut each plant at ground level, and then dried and weighed it.

We analyzed the mass estimation data using R statistical software, version 3.5.1 (R Core Team, 2018). We used multiple linear regression within an information-theoretic framework (R package MuMIn) to generate and compare models (Anderson, 2008). Because the raw data violated assumptions of homoscedasticity and normal distribution of error, we performed a natural log transformation of the predictor variables and plant dry mass. A variance inflation factor test then indicated that there was a problem with multicollinearity among the predictor variables (Graham, 2003). This was largely driven by a strong correlation between number of stems and total stem length. Not wanting to drop one of the terms and lose the unique information it provided, we instead combined these two terms into one term, length per stem. During our field work, we had in fact suspected that length per stem would be a good predictor of plant mass, as it corrected for cases where there were many short stems. This change solved the issue of multicollinearity and greatly lowered the standard error on the coefficient estimates. We used corrected AIC to assess whether the full model was superior to models containing each of the single predictor variables.

4.2.3. MASS REMOVAL TREATMENTS. To apply the mass removal treatments, we began in June 2016 by randomly selecting 81 *D. geyeri* plants, within a total of nine 3.0 m by 9.1 m sampling areas that did not overlap with the area wherein the 120 plants for the dry mass estimation were sampled. These sampling areas were used merely for aiding in re-finding treated plants in subsequent years. Within each area, three plants were randomly assigned to each of three treatments— unclipped control, 25%, or 75%— and marked with a durable metal stake. Individual plants were thus independent experimental units, resulting in a total of 27 plants initially assigned to each treatment across the nine sampling areas. Plants remained in their assigned treatment category for the duration of the study.

In June of both 2016 and 2017, once all plants were in early bud stage, we recorded number of leaves and length per stem. We then applied the assigned treatment to the plant. For the 25% and 75% mass removal treatments, we used our measured values for leaf count, stem count, and stem length to determine the amount of plant material to remove. For the control group, we removed three leaves (including the petiole) for assessment of alkaloid concentration but otherwise left the plant untreated. In June of 2018 we measured the same variables and then cut each entire plant at ground level, regardless of treatment level, to compare our linear model mass predictions to the measured actual mass.

4.2.4. SAMPLE PREPARATION AND ALKALOID ANALYSIS. All plant samples were oven-dried, weighed, and ground until sufficiently fine to pass through a 2 mm mesh screen. They were then individually labeled and shipped to the USDA Poisonous Plant Laboratory in Logan, UT for assessment of alkaloid concentration. The dried ground samples were then extracted and analyzed using standardized methods for alkaloid assessment in larkspur (Gardner et al., 1999). For this study, we focus on the reported measures for total MSAL alkaloid concentration in the plants.

4.2.5. TREATMENT DATA ANALYSIS. Note that we used actual weights instead of predicted weights for 2018. Group means were similar, but we saw no reason to use predicted weights when we had access to actual weights. Due to concerns about non-normal distribution of error, heteroscedasticity, and difficulty of transforming percent change data, we used a Steel-Dwass non-parametric multiple comparisons test to examine differences in the distribution of data among the three treatments (Douglas and Michael, 1991). The Steel-Dwass test is conservative and thus helps avoid Type-I (false-positive) errors. We used JMP 13.0.0 (SAS Institute, 2016) for analysis and data visualization.

4.3. RESULTS

4.3.1. ABOVEGROUND MASS ESTIMATION. Data for the linear model using number of leaves (*leaves*) and length per stem (*lpstem*) are shown in Table 4.1. AIC_c scores indicated that the model containing both *leaves* and *lpstem* was best, with single-factor models highly implausible in comparison, given the data (Anderson, 2008). It is worth noting that in 2018, when we obtained estimated and actual dry mass for all plants, the estimated mean for all plants was 2.34 g while the actual weighed mean was 2.36 g. This demonstrates that even if standard error is relatively high a moderate number of samples will ensure accuracy to the group mean.

4.3.2. MASS REMOVAL TREATMENTS. Of the 81 larkspur plants initially selected, we could not relocate the markers for four during either the second or third season. We attribute losing these markers to rodent activity. Of the remaining 77 plants, three died after 2017 but prior to 2018. Of these, one was in the 25% mass removal treatment group and two were in the 75% mass removal treatment group. As each of these three plants had declined greatly when measured in the second year,

TABLE 4.1. Results for multiple linear regression of natural log transformed data for predicting *D. geyeri* plant mass from plant characteristics (n=120).

Variable (ln transf.)	**β[1]**	**SE**	**CI[2]**
Intercept	-4.90	0.19	-5.28, -4.53
leaves	1.09	0.04	1.01, 1.18
lpstem	0.79	0.07	0.65, 0.92
SE of residuals= 0.29			
Adj. R2= 0.92			

[1] All coefficients significant $p<0.001$ [2] 95% confidence interval

we attributed these deaths to the treatments and thus included them in the analysis. Ultimately, there were 26 plants included in the control group, 25 plants in the 25% group, and 26 plants in the 75% group.

It is first important to note that the all three treatment groups experienced overall declines in mass, MSAL alkaloid concentration, and MSAL alkaloid pools (Figure 4.1). We attribute this general decline (which we also observed, anecdotally, across the study ranch) to a return to relatively normal precipitation patterns from heavier than normal precipitation in 2013-2015. Despite this general decline, there were nevertheless clear differences among the treatments.

While there was some indication of a decline in mass due to treatments, these differences were not statistically significant. On the other hand, significant declines in MSAL alkaloid concentration and plant alkaloid pools occurred at the 75% treatment level versus the control and, for concentration, at both treatment levels. Additionally, the treatments had a clear effect on the variance of alkaloid concentration and alkaloid pools. Table 4.2 shows the mean values for the responses, as well as the measured morphological changes.

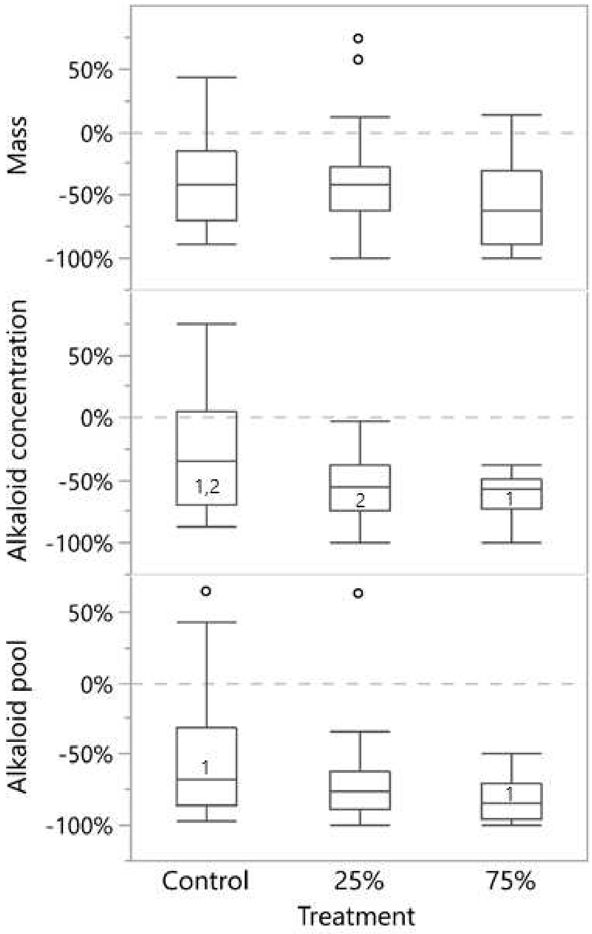

FIGURE 4.1. Box plots (with outliers) of the distribution of *D. geyeri* treatment responses (2016-2018), as measured by percent change from 2016 plant mass, MSAL alkaloid concentration, and MSAL alkaloid pools. Shared numbers indicate a significant difference in group medians (1- indicates that the group medians were significantly different at α=0.05. 2- indicates that the group medians were significantly different at α=0.1).

TABLE 4.2. Mean *D. geyeri* treatment responses (2016-2018) for plant mass, MSAL alkaloid concentration, MSAL alkaloid pool, number of leaves, total stem length, and number of stems.

	Percent change					
	Mass	**Conc.**	**Pool**	**Leaves**	**Stem length**	**Stems**
Control	-36.9	-25.6	-53.9	-16.9	-34.4	8.5
25%	-38.9	-54.3	-70.4	-29.3	-36.2	-9.7
75%	-55.3	-61.1	-81.7	-42.0	-47.6	-28.9

An examination of year-on-year results reveals that plant mass decreased greatly after the first year, while alkaloid concentration responded more strongly after the second year (Figure 4.2). Alkaloid pools, as the product of mass and concentration, responded more evenly. Note the increase in control group alkaloid concentration in 2017.

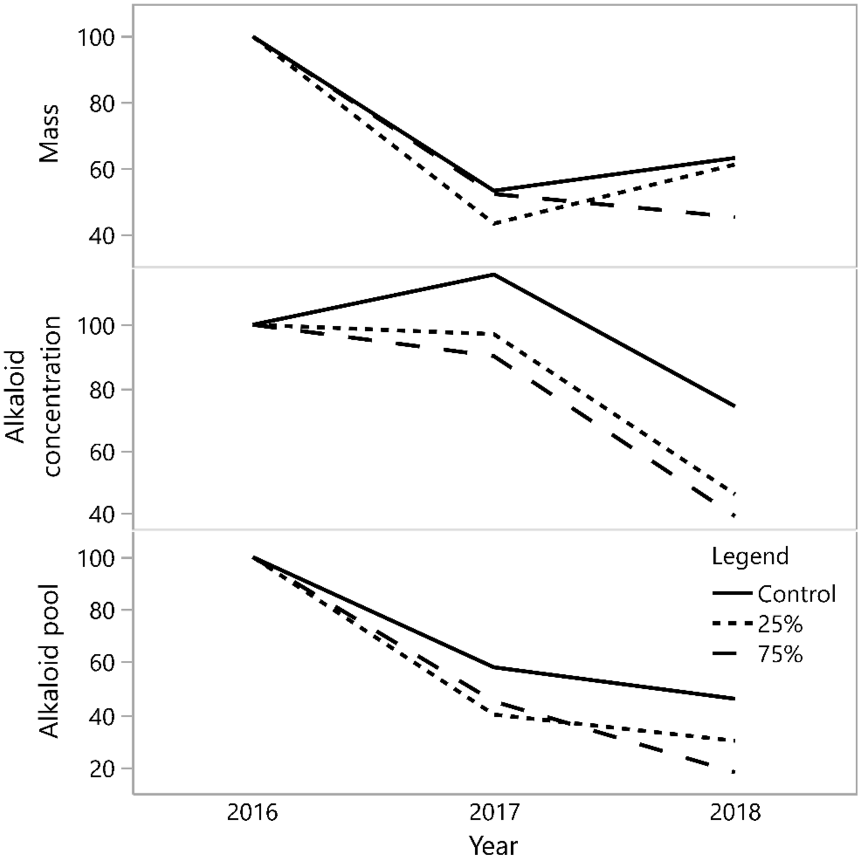

FIGURE 4.2. Indexed (2016=100) mean *D. geyeri* treatment responses for plant mass, MSAL alkaloid concentration, and MSAL alkaloid pools by year.

4.4. DISCUSSION

The mechanisms by which larkspur plants generate, transfer, and store toxic alkaloids are still somewhat unclear, and may differ among species. However, the most likely general scenario is as follows: Alkaloids are synthesized in the roots and translocated upward into stems and leaves early in the growing season (Ralphs and Gardner, 2003). This relatively fixed amount of alkaloids is then diluted as aboveground plant mass increases during the growing season (Gardner and Pfister, 2007; Ralphs et al., 2000). As the plant begins to senesce, most of the alkaloids are translocated back to the roots and stored for the following growing season (Ralphs et al., 2000; Ralphs and Gardner, 2003).

Norditerpenoid alkaloids are high in nitrogen and are thus expensive for larkspur plants to produce. Nevertheless, numerous studies have indicated that these alkaloids are generated constitutively and that levels are relatively unresponsive to stress or environmental factors, being frequently measured at a concentration that is higher than necessary for general plant defense. These are unusual dynamics and beg further exploration.

Because insect pressure on larkspur is quite low and the different species are generally quite nutritious for large herbivores (Pfister et al., 1997c), the place to start this exploration is with herbivore pressure. While science has been studying larkspur in the western US for just over 100 years, the genus *Delphinium* has co-evolved with herbivores for millions of years (Jabbour and Renner, 2012). We suggest that this most recent 100-year period is highly anomalous in that humans have, broadly-speaking, replaced a diverse set of millions of wild large herbivores with a similar number of domestic large herbivores (Burkhardt, 1996) and then generally managed cattle to avoid grazing larkspur during its growing season (B. Green et al., 2009). Released from grazing pressure, larkspur has continued to produce alkaloids at its historical rate, but these alkaloids are no longer being consistently removed from the plants via herbivory. Meanwhile, larkspur has also increased in abundance and mass, as is suggested by its plant characteristics (i.e., tall perennial forb), which place it into the category of a likely "decreaser" under heavy grazing (Diaz et al., 2007; Milchunas et al., 1988).

The combined findings of Laycock (1975), Ralphs and Gardner (2001), and this study indicate that larkspur plants that suffer moderate-to-heavy grazing will indeed contain lower amounts of toxic alkaloids, greatly reducing the risk to grazing herbivores. Conversely, ungrazed larkspur will hold onto precious alkaloids, increase its root mass, increase its alkaloid synthesis and storage capacity (Ralphs et al., 2000; Ralphs and Gardner, 2003), and increase the amount and toxicity of the plant material that it presents to herbivores. In short, our management of cattle to avoid grazing larkspur, especially when it is most vulnerable, may have worsened, if not created, the problem of consistent cattle poisoning.

There is of course complexity and nuance to this story. For example, while both previous studies found a significant difference in mass after full aboveground plant mass removal, we found a lesser (p=0.16) effect from 75% aboveground mass removal. Whether this was due to the lower level of mass removal, environmental conditions lowering overall plant mass regardless of treatment, or something else, was unclear. Because we saw a continued decline in mass in 2018 from the 75% removal treatment while the other two treatment groups increased in mass (Figure 4.2), we suspect that environmental conditions were the driver in 2017.

Interestingly, we saw a lag between a reduction in aboveground plant mass and a reduction in alkaloid concentration (Figure 4.2). If we consider root mass and vigor to be the driver of alkaloid concentration, this makes perfect sense. A significant removal of aboveground biomass in one year would likely lead to reduced root mass the following year, and thus reduced capacity to synthesize and store toxic alkaloids. However, we believe that alkaloid removal also explains the especially strong decline in concentration across the two mass removal treatment levels. By simply removing more alkaloids from the plant than it may be able to regenerate in a year, mass removal lowers concentration. This means that grazing may have a double effect on larkspur toxicity—it steals what was expensive to produce and makes it harder to re-produce it.

If we accept the control group as status quo under normal fluctuations, even when the status quo alkaloid pool declined by greater than 50%, removal of 25% of aboveground larkspur mass led to an additional mean yearly decline of 8.2% in alkaloid pools while removal of 75% of aboveground mass led to an additional mean yearly decline of 13.9% in alkaloid pools. Though it is impossible to accurately extrapolate further, with the cumulative declines among living plants and expected continued deaths of weaker plants (3 of 51 treated plants died from the treatments), we think it is reasonable to expect a 50% decline in pasture-level alkaloid pools within a few years of moderate-to-heavy grazing during bud stage. Because it is believed that the majority of larkspur deaths occur from brief periods of over-ingestion (Pfister et al., 1997c), cutting alkaloid pools in half would be likely to dilute risk below a threshold where the animal is likely to satiate on larkspur before they consume a lethal dose of alkaloids. Indeed, the data for our control group demonstrate that alkaloid pools fluctuate widely even without intervention, providing explanation for such a threshold as a driver of inconsistent losses among producers.

4.4.1. CONCLUSIONS AND IMPLICATIONS. Grazing management in the broad array of environments that constitute larkspur habitat is always a complex, multifaceted endeavor. This means that any solution to the seemingly intractable challenge of larkspur poisoning must account for the spatiotemporally unique multiple objectives that producers and managers seek to fulfill on grazing lands, rather than treating larkspur as an isolated, singular challenge. Thus, we offer no such solution here. Instead, this study continues to build support for our theory that the solution to the larkspur challenge lies not in avoidance but rather in the skill of managers and the wisdom of herds.

Building on the many years of research on larkspur toxicology patterns, we have demonstrated that Geyer's larkspur plants subject to aboveground mass removal similar to what might occur with grazing can be expected to become significantly less dangerous to cattle. When we consider what is known about alkaloid synthesis, translocation, and storage in larkspur, the reasons for this are clear. We can expect that *D. geyeri* and other larkspur species will be "decreasers" and, as such, grazing will lead to reduced above- and below-ground biomass, with consequent reductions in alkaloid concentration and pools.

For managers, we echo the advice from Jablonski et al. (2018; Chapter 3) of caution in the face of this threat, especially for those producers that have experienced serious losses. Nevertheless, these two papers indicate that amid high populations of *D. geyeri* it is possible to manage grazing such that all cattle consume larkspur but none die and that, having done so, the risk will decline over time. This may require alterations to management practices and increased attention to herding, but we expect that improved management flexibility and increased capacity to graze pastures when they are at full productivity will offset these increased efforts. Avoidance may always be simpler, but we put faith in the fact that ranchers prefer effectiveness to ease.

CHAPTER 5

PREDATORY PLANTS AND PATCHY COWS: MODELING CATTLE INTERACTIONS WITH TOXIC LARKSPUR AMID VARIABLE HETEROGENEITY

5.1. INTRODUCTION

Of the more than 60 species of larkspur (*Delphinium* spp. L.) found in North America, at least eleven are known to cause significant cattle losses, primarily those species found on rangelands in the western United States and Canada (B. Green et al., 2009; Welch et al., 2015a). High levels of norditerpinoid alkaloids, which cause neuromuscular paralysis when consumed in sufficient quantity, are the chief culprit in these toxicosis deaths (Manners et al., 1995; Ralphs et al., 1988). Total yearly deaths due to larkspur toxicosis have been estimated at 2-5% of grazing cattle in some regions, with an annual cost of $234 million to producers (Knight and Walter, 2001; Pfister et al., 1997a; Welch et al., 2015a). This makes larkspur one of the leading causes of death losses in the US cattle industry (Knight and Walter, 2001).

Grazing management recommendations in larkspur habitat have long focused on seasonal avoidance, aimed at reducing exposure during spring and early summer when alkaloid concentration is highest (Pfister et al., 1997a; Welch et al., 2015a). This strategy creates problems of its own as producers lose flexibility to meet their management objectives, both economic and ecological, with little evidence of reduced losses. Because of this, many producers appear to simply accept the risk of deaths, achieving gains when lucky and losses when not. One alternative to avoidance is to manage grazing such that no individual is able to consume a lethal dose of alkaloids, regardless of season. Our recent paper (Jablonski et al., 2018; Chapter 3) presented an agent-based model that indicated this may be possible if cattle are managed for high stocking density, high herd cohesion, or both.

While our findings in Jablonski et al. (2018) were relevant to grazing management within the habitat of a particular larkspur species (*Delphinium geyeri* Greene), the results also pointed towards interesting relationships between plant patchiness, herd behavior, and toxicosis that we explore further here. Specifically, we used modeling to test two general hypotheses, that: (1) larkspur patchiness drives alkaloid toxicosis deaths, and (2) overlap between larkspur and desirable forage drives alkaloid toxicosis deaths. We explore both hypotheses within the context of variations in herd cohesion, using data from *D. geyeri,* wherein *N*-(methylsuccinimido)-anthranoyllycoctonine (MSAL) type alkaloids are the dominant toxin (Panter et al., 2002).

5.1.1. NEUTRAL LANDSCAPE MODELS. A test of the influence of larkspur patchiness and larkspur-forage overlap on toxicosis required a model with variable landscapes, rather than the realistic but static landscape of Jablonski et al. (2018). Specifically, this meant separating larkspur and forage distribution from one another and varying patchiness while maintaining a realistic landscape with respect to cattle grazing. For this, we used neutral landscape models, which are the most common landscape modelling approach used in ecological studies, with frequent application to habitat fragmentation, animal movement models, and metapopulation analysis (Gardner and Urban, 2007; Synes et al., 2016). With a primary aim of improving understanding of how ecological processes are affected by spatial structure, neutral landscape models are ideal for testing the consequences of varying spatial heterogeneity on foraging outcomes (With and King, 1997). However, we are unaware of previous application of neutral landscape models to cattle grazing dynamics.

5.1.2. BEHAVIORAL ECOLOGY OF HERDS. Important context for this study comes from the literature on grouping in large herbivores, where behavioral ecologists continue to debate the evolution and utility of herd behavior (Ireland and Ruxton, 2017; e.g. Makin et al., 2017; Stutz et al., 2018). The most widely studied explanations for herd behavior relate to decreased risk of predation (Davies et al., 2012; Ebensperger and Hayes, 2016). Of particular relevance to the cattle-larkspur interaction is what

Krause and Ruxton (2002) call dilution. Dilution refers to a 1/N effect whereby an attacking predator can only capture a limited number of prey at a time and individual risk therefore declines with increasing group size. Important considerations for the dilution effect are variation in the likelihood of being attacked among individuals and the relative conspicuousness of larger versus smaller groups (Krause and Ruxton, 2002).

A second relevant mechanism for decreased predation risk in herds is predator avoidance, also known as encounter dilution. In this case, predators with limited perceptual range encounter clumped prey at a lower frequency than single prey (Krause and Ruxton, 2002). It is necessary to consider dilution and encounter dilution in context with one another, as increased detectability can offset the benefits of herd members' reduced likelihood of death when encountering a predator (Turner and Pitcher, 1986).

We examine larkspur as predator and cattle as prey. This is a novel approach, and poisonous plants certainly differ from typical predators in many ways. However, there is enough similarity to enable this "plants as predators" concept to be useful addressing both theoretical and practical questions.

5.1.3. AGENT-BASED MODELING. Agent-based models are computational simulation tools that focus on bottom-up encoding of individual "agent" behaviors as they interact with one another and the environment (Grimm, 1999; McLane et al., 2011). Agent-based models are particularly useful in modeling complex systems where the results of interactions between system elements are not easily predicted, and thus useful for simulating the behavior of social herbivores foraging in a heterogeneous environment (Dumont and Hill, 2004; Grimm et al., 2005). Nevertheless, they have thus far been little used in improving our understanding of livestock behavior and management.

In this paper, we present an agent-based model simulation of cattle grazing with varied herd cohesion in larkspur-rich pastures with varied plant patchiness. Our approach represents a novel application of neutral landscape models and agent-based models to the relationship between herbivore grazing behavior and environmental heterogeneity. The results offer insights to landscape ecology, behavioral ecology, and livestock grazing management, and point toward a fundamental reconsideration of the importance of herd behavior among domestic herbivores.

5.2. METHODS

5.2.1. OVERVIEW. The model functions as a mechanistic effects model (Grimm and Martin 2013) whereby cattle seek to maximize forage intake within behavioral and physiological bounds and are exposed to toxic alkaloids via consumption of larkspur distributed within the forage. Deaths are a product of temporal intensity of larkspur consumption with passing time as a mitigating factor via metabolism. The guiding principles of model design were behavior-based encoding (McLane et al. 2011) of cattle activities, based in the literature and our own livestock management experience, and parsimony aimed at including only those behaviors and landscape variables relevant to the question at hand. Model evaluation followed the process of "evaludation" laid out by Augusiak et al. (2014).

Cows are classified as leaders (5% of herd), followers (85%), or independents (10%), with leaders making decisions about broad-scale movements away from relatively over-grazed areas (known as site changes) and independents being less tied to the herd than the other cows (Sato 1982, Harris et al. 2007). Other than seeking drinking water and making site changes, all cow movements in the model are aimed at moving closer to herdmates and/or maximizing the amount of forage in the next grazing location, depending on desired herd proximity. Consumption of forage occurs in line with standard rates from the literature (Laca et al. 1994, WallisDeVries et al. 1998). Forage and larkspur amounts decrease when eaten and do not regrow within the model run, which is equivalent to 18 days.

Other details of model function can be found in the complete Overview, Design Concepts, and Details (ODD; Grimm et al. 2010) description in Jablonski et al. (2018). Here we focus on model elements that have changed, using the ODD format but omitting sections where methods were the same.

5.2.2. PURPOSE. The agent-based model tests the effect of co-varying herd cohesion (also known as troop length; Shiyomi and Tsuiki 1999), larkspur patchiness, and larkspur-forage overlap on cases of lethal alkaloid toxicosis caused by larkspur similar in size and toxicity to measured values for D. geyeri. We developed and executed the model in NetLogo 6.01, using the BehaviorSpace tool to implement simulations (Wilensky 1999).

5.2.3. ENTITIES AND STATE VARIABLES. The model has two kinds of entities: pixels representing 1 m^2 of land and agents representing 500 kg adult cows (1.1 animal-units). Because computational demands would be higher with additional covariates, and spatial extent was expected to be minimally influential, we shrank the model landscape to ¼ the size of that of pasture 16 of the Colorado State University Research Foundation Maxwell Ranch on which the model in Jablonski et al. (2018) was based. This created a model landscape of 832 x 790 pixels (0.83 km x 0.79 km, equal to 65.73 ha), all of which are accessible to the cows. Note that, for clarity, we will refer to each 1 m^2 land area as a pixel, rather than as a patch, the typical nomenclature for agent-based models. We use "patch" in the landscape ecology sense to refer to an area of habitat that is relatively discrete from its surroundings in relation to some phenomenon of interest (Turner and Gardner 2015).

Stocking density was set at 1.0 animal-units • ha^{-1} throughout the simulation, totaling 59 cows. Herd cohesion was determined using herd-distance-factor (HDF), in which increasing values indicate greater inter-animal distance. All other state variables, including role, MSAL-tolerance, and larkspur-attraction were assigned in the same way as Jablonski et al. (2018). All functionally relevant state variables for pixels and cows, as well as global variables and inputs, are described in Table 5.1.

Note that death occurs when an individual cow exceeds its assigned value for MSAL-tolerance at the end of a grazing-day. However, the animal is not removed from the herd, but instead is recorded

TABLE 5.1. Relevant model variables. Sources for variable parameters are cited in the body of the text.

Entity	Variable	Description
Pixels	forage-mass	Amount of currently available forage (g)
	n-forage-mass	Mean initial available forage in pixels within a radius of 3 m (g)
	MSAL-content	Amount of MSAL alkaloids currently in pixel (mg)
	times-grazed	Number of times pixel has been grazed
Cows	role	Role in the herd: leader, follower, or independent
	MSAL-level	Current amount of MSAL alkaloids in cow's body (mg); metabolized with a half-life of one grazing-day
	MSAL-tolerance	Level at which cow will be recorded as having died (MSAL-level>MSAL-tolerance); assigned at start from a random normal distribution ($\bar{x} = 4{,}000$ mg, σ=333.33 mg)
	larkspur-attraction	Factor determining the relative amount of larkspur a cow will eat when in a patch with MSAL-content; assigned at start from a random normal distribution ($\bar{x} = 1,\ \sigma = 0.083$)
	herdmates	Agent-set consisting of nearest 20 cows
	mean-herd-distance	Mean distance to herdmates (m)
	distance-traveled	Total distance traveled during model run (m)
	ready-to-go	Used by leader cows only, a measure of their inclination to move on from an overgrazed site
Globals	waterers	Pixel-set of all watering locations
	site-tolerance	Herd-size-dependent variable determining leader cows' tolerance for relatively overgrazed sites
	site-radius	Radius of site when choosing a new site; product of herd-distance-factor and herd size
	herd-distance	Desired mean-herd-distance; equal to herd-distance-factor x 10
Inputs	kgs-per-hectare	Mean amount of usable forage (kg • ha-1)
	mean-larkspur-mass	Mean mass of larkspur plants (g)
	MSAL-concentration	MSAL alkaloid concentration in larkspur plants (mg • g-1)
	larkspur-patch-factor (LPF)	Determines number of larkspur patches; range 0-5 with increase of one leading to roughly ten-fold decrease in patch count.
	larkspur-forage-overlap-factor (LFOF)	Determines degree of overlap between forage patches and larkspur patches; range 0-4
	herd-distance-factor (HDF)	Determines herd-distance and site-radius; increase leads to less cohesive herd

as having died, has its MSAL-level set to zero, and continues in the model. This preserves herd dynamics for the entire model run and makes it possible for total model-run deaths to exceed 59.

5.2.4. PROCESS OVERVIEW AND SCHEDULING. Figure 5.1 illustrates the model execution process for each tick. Each cow moves through each step of the process, but only performs those steps linked to its role. Only elements that have changed from Jablonski et al. (2018) are described below, with explanation for the change.

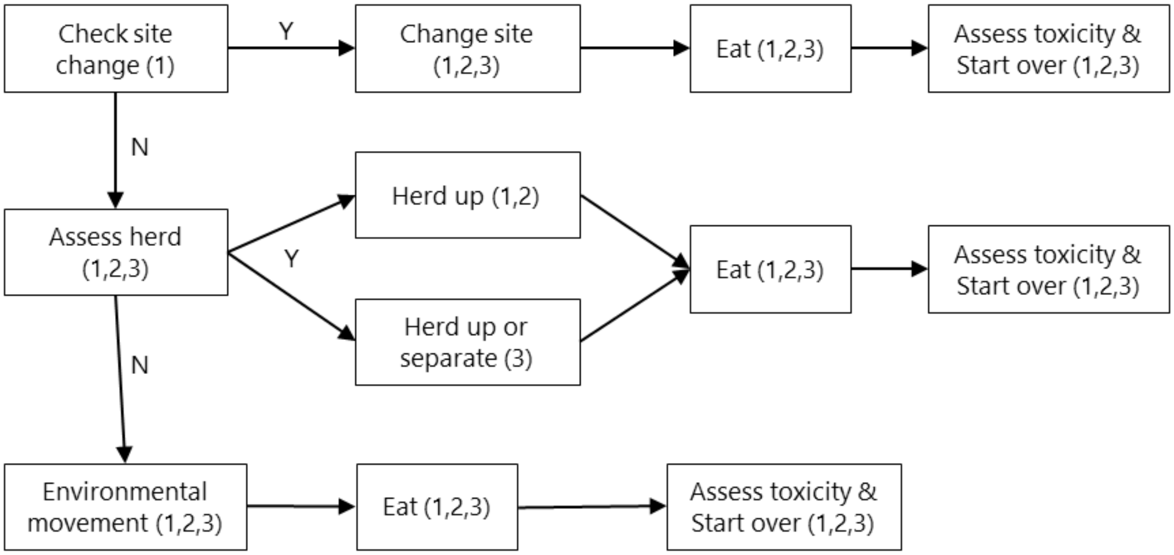

FIGURE 5.1. Pseudo-coded flow chart of model processes, with role of cows executing each process in parentheses. 1=leader, 2=follower, 3=independent.

5.2.4.1. *Check hydration.* This process is not found in Figure 5.1, as it was eliminated in favor of a single end-of-grazing-day water visit by all cows. Because hydration was previously linked to forage consumption, artificially high levels of forage heterogeneity necessitated a simplified water visit routine. One visit per day achieves this without otherwise sacrificing realistic model function.

5.2.4.2. *Assess herd.* Herd-based movements are fundamentally the same as in Jablonski et al. (2018), with individuals moving closer to the herd centroid when mean-herd-distance exceeds herd-distance. However, we altered the minimum movement distance when "herding up" such that it is now based on the cow's current distance from the herd centroid. This was to accommodate movement patterns in the tightly cohesive herds modeled at the low end of the herd-distance-factor range, where an arbitrary static minimum movement distance may cause them to frequently move through the herd and then beyond their desired mean-herd-distance, resulting in "ping-pong" type movements.

5.2.5. DESIGN CONCEPTS. 5.2.5.1. *Stochasticity*. Distinct from Jablonski et al. (2018), the environment was highly stochastic between different levels of larkspur-patch-factor and larkspur-overlap factor and even within different iterations of identical values for those factors.

5.2.5.2. *Initialization*. Input values for number of larkspur plants and forage mass within the modeled landscape were derived from the measured values from pasture 16. This provides an input value of 107,500 total larkspur plants on the landscape. The model distributes these plants among pixels according to a Poisson distribution with a mean of 2.5 larkspur plants per square-meter pixel, resulting in 43,000 pixels with larkspur. This means that individual pixels with larkspur are equally likely to be dangerous regardless of their spatial arrangement, an essential condition for testing the effect of patchiness.

Landscape initialization within the model begins by using an input value for larkspur-patch-factor (LPF) to randomly locate p larkspur patch origins, with p=43,000/10^LPF, rounded up to the nearest integer (i.e., $1 \leq p \leq 43{,}000$) At each larkspur patch origin, a modified random walk is used to create realistic larkspur patch patterns. In this random walk, a temporary agent is created that visits each patch origin location. After placing a random Poisson-distribution-determined number of larkspur plants in the origin pixel, the agent then executes random turns and one-pixel steps, placing larkspur plants whenever landing on a pixel with zero currently present. This random walk proceeds in a given patch origin area until 43,000/p pixels have had larkspur plants placed in them. The agent then proceeds to the next patch origin location, following the same steps until all patch origin locations have been visited. Lastly, pixels are assigned an MSAL-content value based on larkspur plant count and input values for mean-larkspur-mass and MSAL-concentration.

Forage initialization begins with random placement of 80% of the total forage mass (100% being equal to ¼ of the forage mass in pasture 16) across the landscape, according to a normal distribution with a mean based on the input value for kgs-per-hectare. The remaining 20% is assigned according to the input value for larkspur-forage-overlap-factor (LFOF). For LFOF=0, all remaining forage is placed into forage patches (created using a similar random walk) that occupy 5% of the total land area. These forage patches do not overlap with larkspur patches. For LFOF=4, all remaining forage is placed within the larkspur patches and there are no forage patches. Values from 1-3 place increasing amounts of forage within the larkspur patches and decreasing amounts in the forage patches. We chose the values of 20% of forage in patches and 5% of land area in forage patches to approximate the forage heterogeneity found in pasture 16.

Instead of the seasonal stream watering locations found in pasture 16, the model places watering points in each corner and in the center of the landscape to ensure limited effect of distance from water (Bailey and Provenza 2008). Waterers are created as circular locations with a radius of 5 m. Finally, the model creates 59 cows (1.0 AU • ha^{-1}) and places them at the central watering location. All other pixel values (Table 1) are derived from the various input values above.

5.2.6. SIMULATION. We used the BehaviorSpace tool in Netlogo to run a full factorial simulation using eight levels of larkspur patchiness (LPF: 0, 1, 2, 3, 3.5, 4, 4.5, and 5), five levels of larkspur-forage overlap (LFOF: 0, 1, 2, 3, and 4), and six levels of herd cohesion (HDF: 0.5, 1, 2, 4, 8, and 16). With 30 replications of these 240 combinations, we executed 7,200 total model runs. The computational demands for this required creation and use of a virtual machine with 64 processors and 360 GB of RAM in Google Compute Engine (Google, Inc. 2018). Input mean-larkspur-mass was 3.5 g and MSAL-concentration was 3.0 mg • g^{-1}, representative of an excellent growing year with alkaloids at high levels. The input value for kgs-per-hectare was 500 kg • ha^{-1}. Individual model run duration was 18 grazing-days, resulting in consumption of approximately 40% of available forage. All of these input values are based on our measurements from the Maxwell Ranch.

5.2.7. OBSERVATION. As in Jablonski et al. (2018), data related to alkaloid intake were of prime importance, with deaths quantified according to a tolerance threshold (MSAL-tolerance) based on dose-response studies with larkspur (Welch et al. 2015b). The model also recorded numerous other data related to herd interactions, cow behavior, and landscape structure for purposes of model verification. These include inter-animal distance, frequency of herd-based movements, site-change frequency, travel distance, grazing impact, and mean larkspur count in pixels, among others.

In addition to model-run level outputs, each model run also recorded daily alkaloid consumption data for each cow. For 7,200 runs this amounted to 7.65 million data points. We compiled and organized this dataset using OpenRefine 3.0 (Google/Open source 2018). We also used this daily dataset to generate statistics on consumption for each individual grazing-day (n=129,600).

5.2.7.1. *Statistical analysis.* To assess landscape structure, we analyzed a sample (n=10 for each level of larkspur-patch-factor) of the generated landscapes using class metrics in Fragstats 4.2.1 (McGarigal et al. 2012). We used the metrics number of patches (NP), percent land area in patches (PLAND; used to confirm uniformity), largest patch index (LPI), edge density (ED), clumpiness index (CLUMPY), and percent like adjacencies (PLADJ) (McGarigal et al. 2002).

We used both JMP 13.0.0 and R statistical software, version 3.5.1 for data exploration, analysis, and visualization (SAS Institute 2016, R Core Team 2018). We used the R base package to generate linear models, and the package MuMIn to compare models with AICc (Anderson 2008). We used the package ggplot2 in R to generate explanatory graphics.

5.3. RESULTS

5.3.1. MODEL OUTPUT VERIFICATION. Because we have made only minor changes to grazing behavior in the model, we refer the reader to Jablonski et al. (2018) for results and discussion of output verification as it relates to cows. However, because landscape generation is greatly altered, we report landscape metrics in Table 5.2. Of the measured metrics, largest patch index and edge density were most strongly correlated with LPF. Figure 5.2 shows example landscapes at different combinations of LPF and LFOF.

TABLE 5.2. Mean landscape metrics for sample landscapes (n=10 per level) generated at different levels of larkspur-patch-factor (LPF). Reference McGarigal et al. (2002) for descriptions of metrics.

LPF	Number of patches	Pct. land in patches	Largest patch index	Edge density	Clumpiness index	Pct. like adjacencies
0	32463.10	6.54	0.00	2442.92	0.00	6.52
1	3400.10	6.54	0.01	1235.56	0.50	52.69
2	331.50	6.54	0.10	720.41	0.71	72.38
3	31.00	6.54	0.58	498.00	0.80	80.91
3.5	10.20	6.54	1.50	439.49	0.82	83.15
4	3.80	6.54	3.01	389.41	0.84	85.05
4.5	1.80	6.54	3.93	347.22	0.86	86.67
5	1.00	6.54	6.54	343.99	0.86	86.76

Note that, although HDF sets the desired maximum distance from herdmates (herd-distance), herds do not necessarily strictly adhere to this parameter. This is particularly true in less cohesive herds, where actual mean distance from herd mates was much lower than the maximum allowed by the HDF setting. For example, at HDF=16, herd-distance is set at 160 m, but overall mean distance from herdmates for all model runs at this level was 104.0 m, with a range from 83.6 m to 118.8 m. This is likely due to the overall size of the pasture and the time between regrouping at watering locations. Only at the lowest level of HDF (0.5) was overall mean herdmate distance at the maximum, as herdmates were essentially forced to stay closer to one another than foraging behavior would otherwise require.

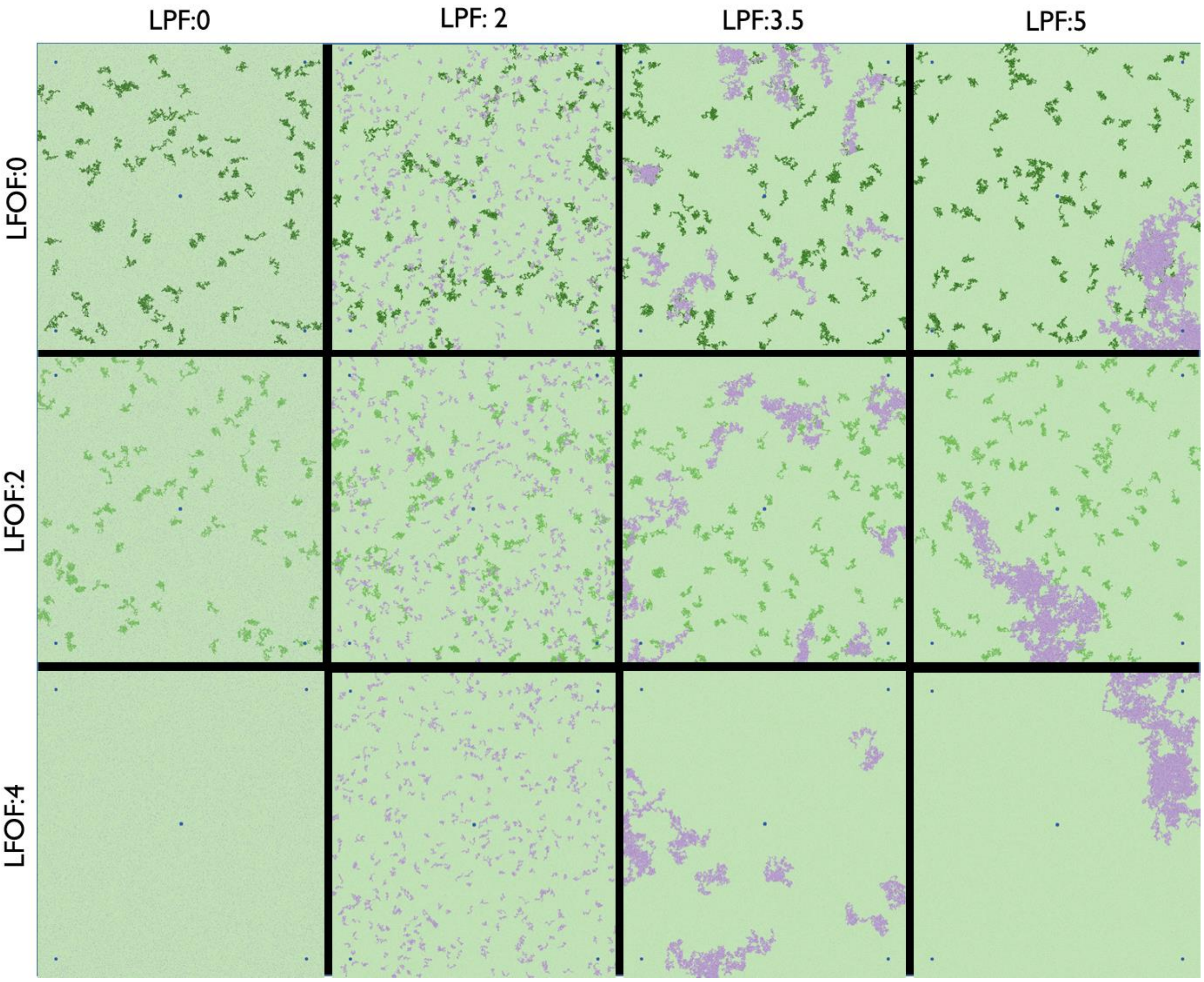

FIGURE 5.2. Sample landscapes for different levels of larkspur-patch-factor (LPF) and larkspur-forage-overlap (LFOF). Green indicates the distribution of forage, with darker green equal to more forage (forage patches), and purple indicates larkspur. No forage patches are visible at LFOF=4 because they are obscured by the larkspur. Watering locations are blue.

5.3.2. TOXICOSIS MECHANISM. In Jablonski et al. (2018) we identified the key mechanism for reducing larkspur deaths as narrowing the variation in larkspur consumption among individuals in the herd, with associated reduction in the count and extremity of outliers. As would be expected, deaths were once again strongly linked to this mechanism, with model-run standard deviation of daily alkaloid intake presenting a particularly striking pattern, wherein the likelihood and count of deaths increased once the standard deviation exceeded a threshold of 500 mg (Figure 5.3). Overall, at least one death occurred in 33.7% of model runs and on 6.2% of grazing-days.

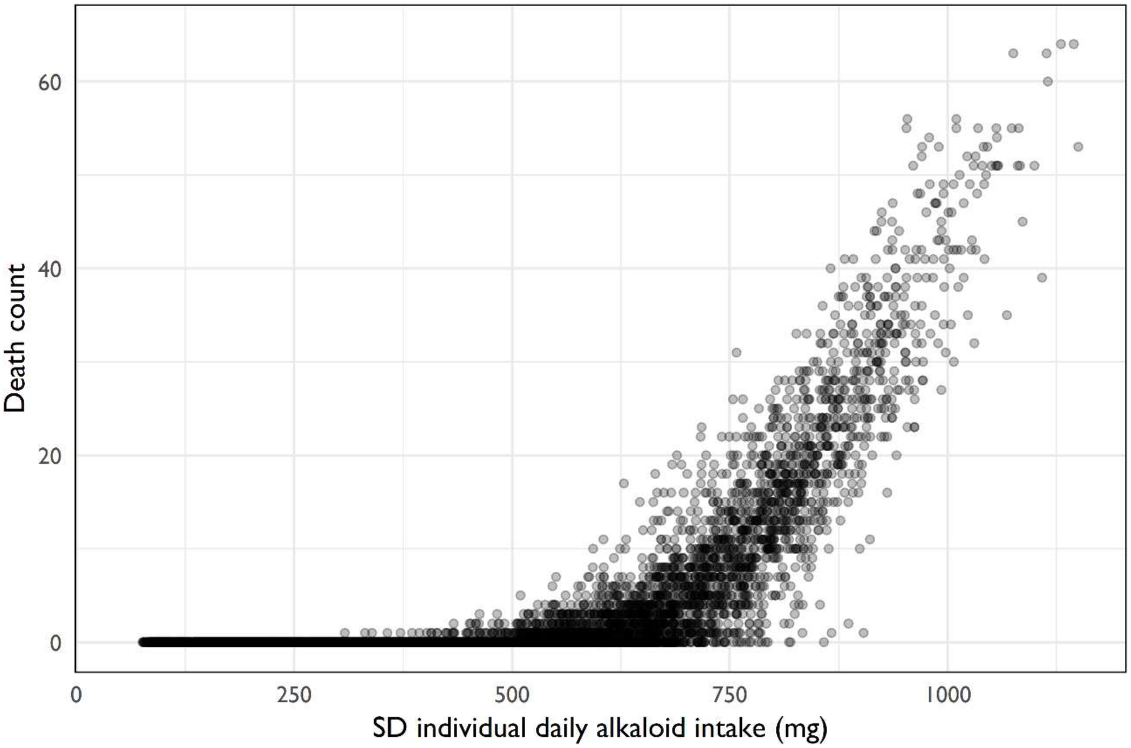

Figure 5.3. Distribution of model-run death count by model-run standard deviation of individual daily alkaloid intake (mg) (n=7200).

5.3.3. LARKSPUR PATCHINESS AND FORAGE OVERLAP. Larkspur patchiness exerted a strong influence on intra-herd variation in alkaloid consumption and thus deaths (Figure 5.4). Total deaths for different levels of LPF ranged from 0 (LPF=0, n=900 model runs) to 13,057 (LPF=5, n=900), with a threshold evident at LPF=3. An examination of the relationships between landscape metrics and deaths using a global linear model and comparison of AICc scores indicated that the model containing only largest patch index was best (AICc=141.7). All other model combinations had ΔAICc values of at least 7.93, indicating all were much less plausible models, given the data (Anderson 2008). The next best univariate model contained only the intercept.

Deaths were distributed more evenly among the different levels of larkspur-forage overlap than among the levels of larkspur patchiness, though there was a peak when there was desirable forage both inside and outside of larkspur patches (LFOF=1-2). Total deaths (Table 5.3) ranged from a

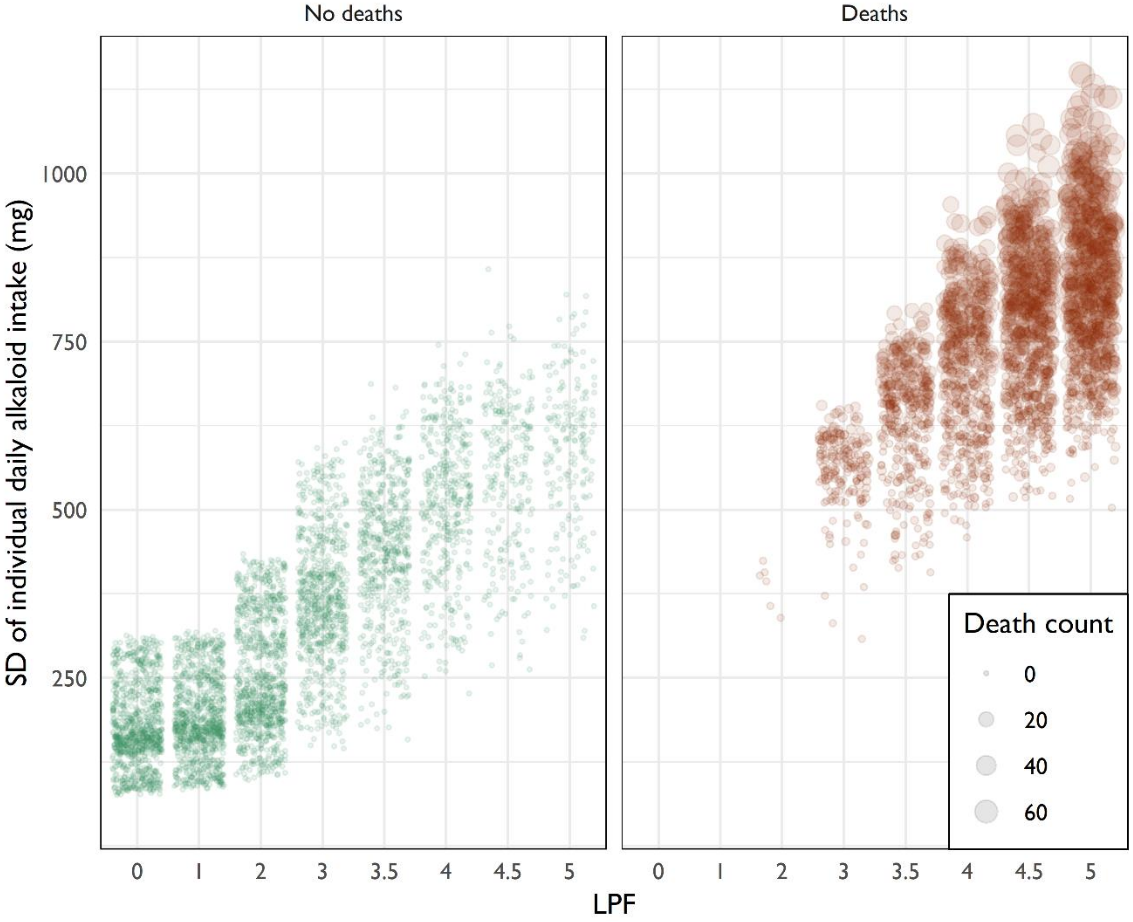

FIGURE 5.4. Distribution of model-run standard deviation of individual daily alkaloid intake (mg) by larkspur-patch-factor (LPF) across all levels of other variables. For visibility, data are split by whether or not any deaths occurred during the model run, with points sized to indicate the number of deaths. Points are semi-transparent so that darker areas indicate more points (n=7,200).

minimum of 1,853 (LFOF=0, n=900) to a maximum of 7,230 (LFOF=1, n=900). Model-run standard deviation of daily alkaloid intake largely mirrored deaths, while mean daily alkaloid intake increased with increasing larkspur-forage overlap.

Additionally, there were distinctly different relationships among mean alkaloid intake and the standard deviation of alkaloid intake at low, medium, and high LFOF. With zero larkspur-forage overlap, an increase in alkaloid intake within a model run usually led to increased variation in intake

TABLE 5.3. Data for total deaths, mean deaths, standard deviation of individual daily alkaloid intake (mg), and mean individual daily alkaloid intake (mg) for different levels of larkspur-forage-overlap (LFOF) across all levels of other variables (n=7,200).

LFOF	Total deaths	Mean deaths	SD intake	Mean intake
0	1853	1.29	392.31	337.76
1	7230	5.02	554.64	524.98
2	6890	4.79	563.80	575.85
3	6324	4.40	552.92	617.70
4	5440	3.78	535.08	624.47

among the herd, leading to increased deaths (Figure 5.5). When there was high overlap between forage and larkspur, increases in alkaloid consumption within the herd usually led to decreased standard deviation, reducing deaths. At moderate levels (LFOF=1-2), this relationship was more muddled. Each of these effects was modified by larkspur patchiness in a complex interplay illustrated by Figure 5.5.

5.3.4. HERD COHESION. Inter-animal distance was an important factor in alkaloid toxicosis deaths. Regardless of larkspur patchiness and larkspur-forage overlap, just 14.4% of model runs at the minimum herd distance level (HDF=0.5) had at least one death, while 56.3% of model runs resulted in at least one death at the maximum herd distance level (HDF=16). Overall, mean deaths per model run ranged from 0.72 at HDF=0.5 to 8.67 at HDF=16.

The relationship between patchiness, overlap, and herd behavior becomes clearer when larkspur patchiness, larkspur-forage-overlap, and herd distance are used to plot standard deviation of alkaloid consumption and total deaths (Figure 5.6). Increases in herd distance consistently generated increases in variation in alkaloid consumption, with the magnitude modified by larkspur patchiness and larkspur-forage overlap. However, deaths did not begin to occur until standard deviation approached the threshold of 500 mg, with this being reached at different levels depending on herd cohesiveness and plant patchiness. This means that the degree of herd cohesiveness necessary to prevent deaths was determined by the patchiness of the threat.

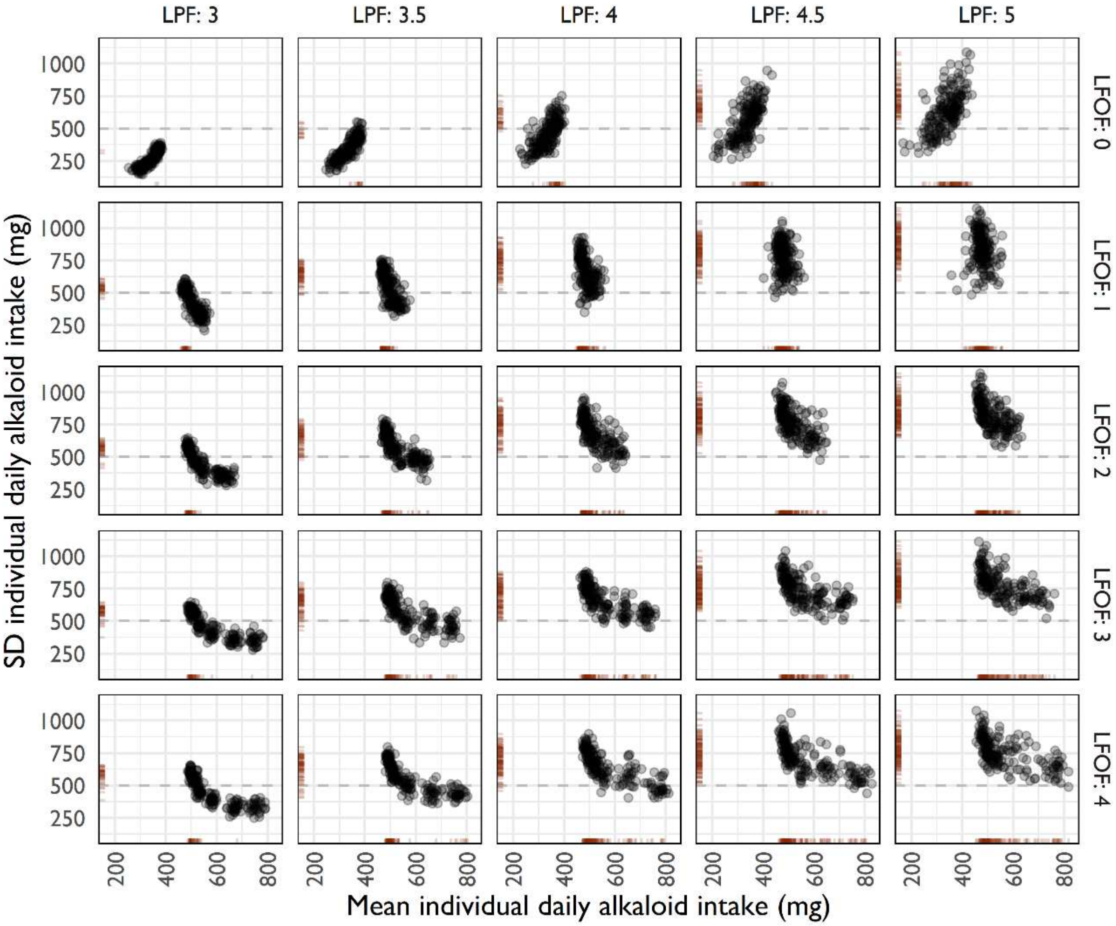

FIGURE 5.5. The relationship between mean individual daily alkaloid intake (mg) and standard deviation of individual daily alkaloid intake (mg) at different levels of larkspur-patch-factor (LPF) and larkspur-forage-overlap-factor (LFOF), across all levels of herd-distance-factor. Displayed results are limited to LPF≥3, where the vast majority of deaths occurred. Rug plots on the x and y axes show the distribution of deaths. A dashed line marks a standard deviation of 500 mg, an apparent threshold where deaths increase greatly. Points are semi-transparent so that darker areas indicate more points (n=7,200).

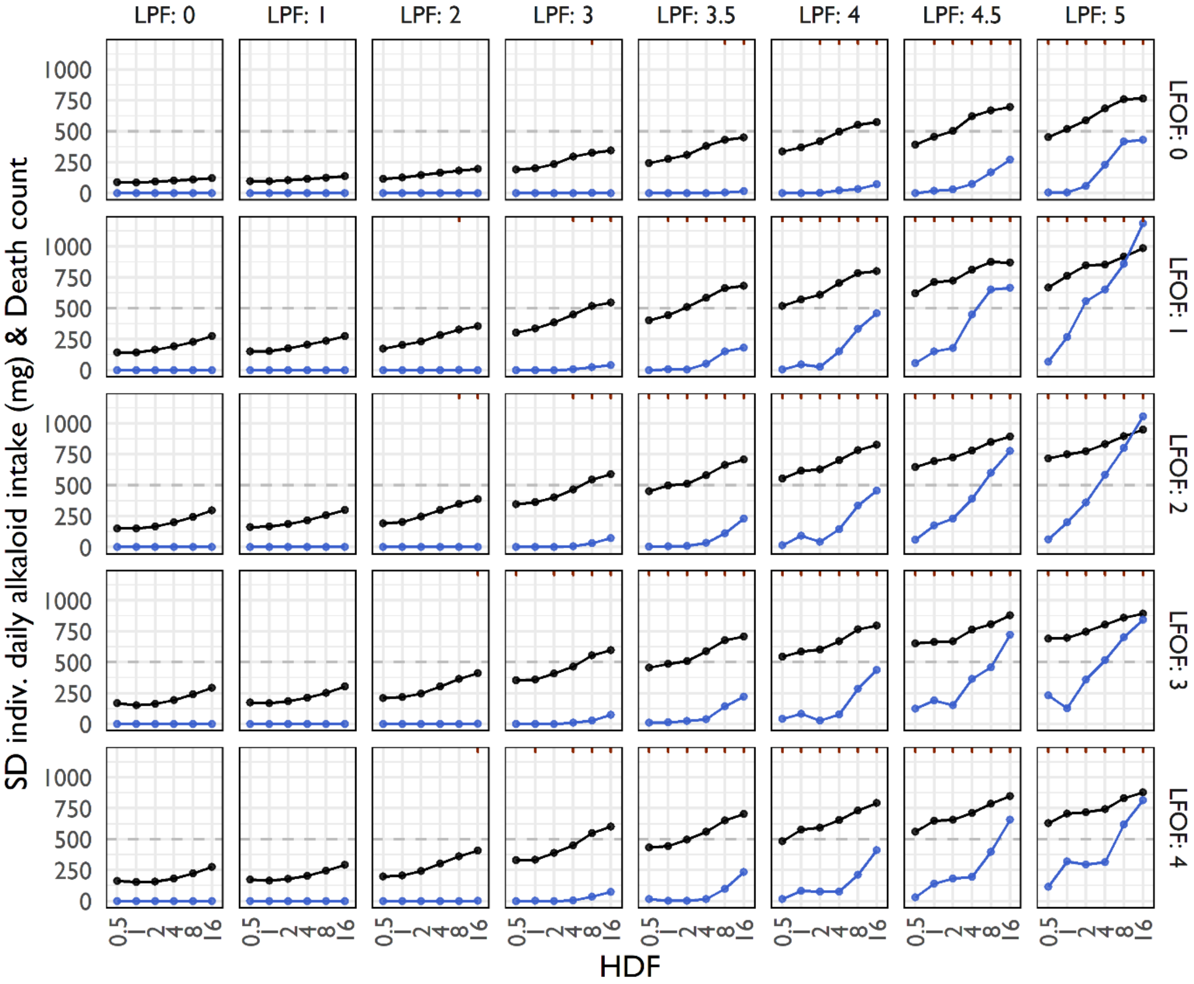

Figure 5.6. The relationship of herd-distance-factor (HDF), larkspur-patch-factor (LPF), and larkspur-forage-overlap (LFOF) to standard deviation of individual daily alkaloid intake (black) and total deaths (blue). Hash marks on the upper x axis indicate levels where at least one death occurred, and a dashed horizontal line marks a standard deviation of 500 mg, an apparent threshold where deaths begin to occur. Points represent mean model-run values (n=30 per point, 7,200 overall).

5.3.5. 1/N AND ENCOUNTER DILUTION. The relationship of "plant predators" to the 1/N concept of predation risk reduction in herds is best understood at LPF=5 and LFOF=4, where there was one large and dangerous patch that overlapped with highly desirable forage, meaning that encounter was inevitable. If we restrict the analysis to only those days when at least one cow consumed larkspur, we can see the distribution of risk when encounter occurred (Figure 5.7).

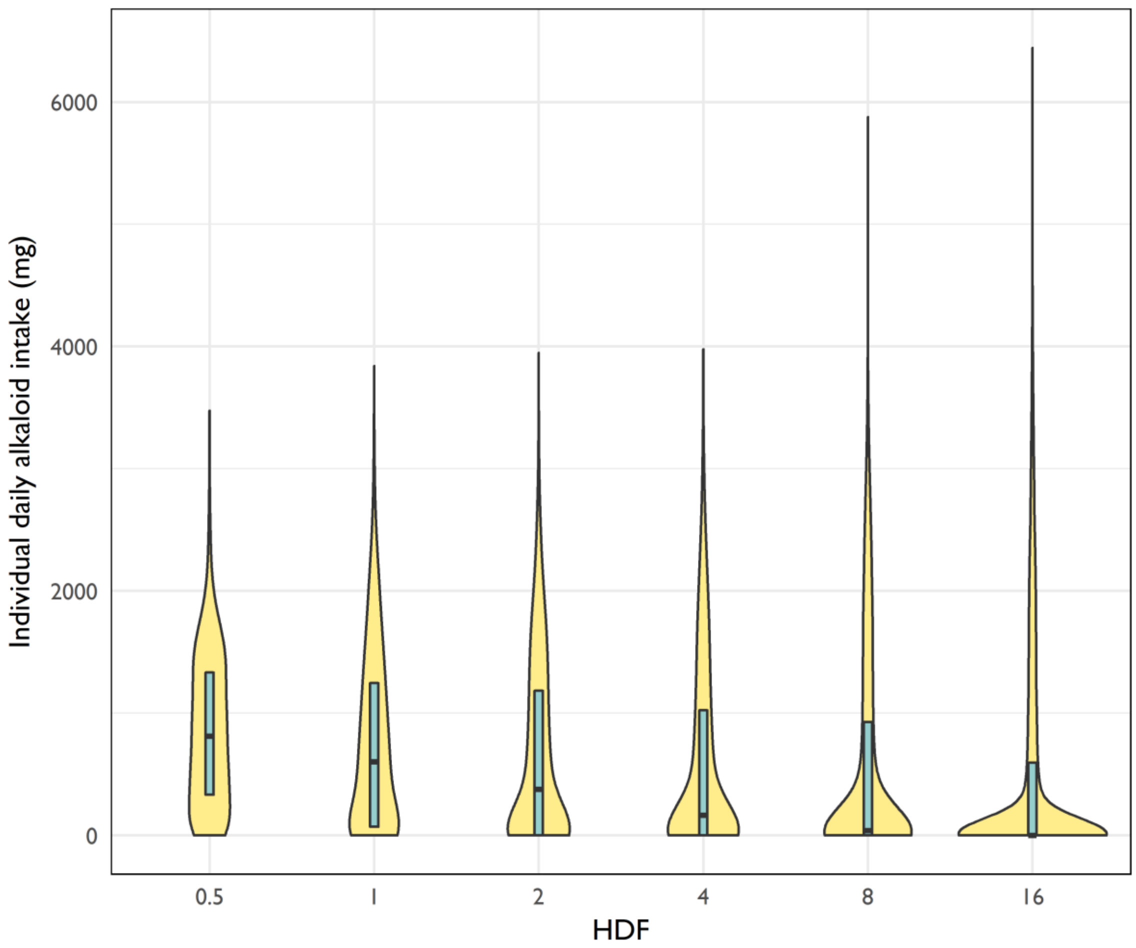

Figure 5.7. Violin plots of the distribution of individual daily alkaloid intake at different levels of herd-distance-factor (HDF), restricted to highly patchy larkspur overlapping completely with highly desirable forage (LPF=5, LFOF=4) and days where at least one cow consumed larkspur (n=167,383). Within the violins, box plots show the location of the median and first and third quantiles.

In herds with high inter-animal distance (e.g., HDF=16) many cows avoided larkspur encounter entirely, while others consumed a great deal of larkspur, thereby dying. On the other hand, in herds with low inter-animal distance (e.g., HDF=0.5) few cows avoided larkspur entirely, with consumption concentrated at sub-lethal levels. In other words, in highly cohesive herds encountering a serious threat, when one cow encountered larkspur it was likely that all cows in the herd would, reducing the distribution of individual risk and resulting in fewer deaths.

Encounter dilution, where cohesive herds avoid detection by predators with limited capacity to find them, is best understood at LPF=5 and LFOF=0. In this circumstance, a single larkspur patch is undesirable for foraging but a serious threat to cows that nevertheless encounter it. Table 5.4 shows rates of larkspur encounter and death among different levels of HDF under these conditions. For herds grazing at HDF=0.5, 38.2% of grazing-days passed without a single animal encountering larkspur. On the other hand, herds grazing at HDF=16 managed to entirely avoid larkspur on just 9.4% of grazing-days. This contributed to substantially different rates of death occurrence.

TABLE 5.4. Percent of grazing-days where larkspur was encountered or a death occurred, at different levels of herd-distance-factor (HDF). Data are restricted to cases where highly patchy larkspur did not overlap at all with highly desirable forage (LPF=5, LFOF=0) (n=3,240).

	Larkspur encountered?		**Death occurred?**	
HDF	**No**	**Yes**	**No**	**Yes**
0.5	38.2%	61.9%	99.8%	0.2%
1	33.7%	66.3%	98.9%	1.1%
2	31.5%	68.5%	97.4%	2.6%
4	24.4%	75.6%	93.3%	6.7%
8	22.8%	77.2%	85.9%	14.1%
16	9.4%	90.6%	79.1%	20.9%

5.4. DISCUSSION

Interactions between domestic herbivores and forage plants are complex, with many important spatiotemporal scales of interaction (Wiens 1976, Launchbaugh and Howery 2005, Larson-Praplan et al. 2015). Perhaps due to the relative simplicity, most research attention has been paid to the interaction of individual livestock with individual plants (including sequences of individuals), and the consequent effects on the grazer and the grazed (e.g., Provenza et al. 2003, Diaz et al. 2007, Villalba et al. 2015). This has been especially true of research on the effect of plant toxins on livestock (Knight and Walter 2001, Welch et al. 2015a). Less common has been research examining aggregations of plants, groups of herbivores, or both. What research there has been in this category has focused largely on how livestock affect plants (e.g., Milchunas et al. 1988, Maschinski and Whitham 1989, Cromsigt and Olff 2008).

Rarest of all has been research seeking to understand how plant patchiness influences group behaviors and outcomes in livestock (though note the significant body of research on "grazing lawns" that at times includes reciprocal relationships between plants and wild herbivores, e.g., McNaughton 1984). Because this type of research requires integration of environmental and animal data at a wide array of scales, it is difficult to design, conduct, and analyze. Nevertheless, if we are to improve our understanding and management of heterogeneity we must expand our capacity to connect pattern and process to illuminate these multiscale relationships (Fuhlendorf et al. 2012).

Here, we have addressed this challenge via the use of a bottom-up agent-based model, incorporating empirical data and neutral landscape models to provide novel insight into why large herbivores may have evolved to respond to plant patchiness with patchiness of their own. Our results show that herd behavior and plant patchiness interact in a complex but conclusive manner to generate or mitigate risk from dangerous plant toxins, with important implications for grazing management and for theory on group behavior in herbivores.

5.4.1. EVALUATING HYPOTHESES. Every simulated pasture contained 1.13 million mg of MSAL-type alkaloids, enough to provide 282 lethal doses to 500 kg cows, and each pixel was equally likely to be dangerous, regardless of spatial arrangement. We were thus surprised that disaggregated larkspur, distributed randomly or in small patches, caused zero deaths, even when overlapping completely with desirable forage. Regardless of herd cohesion, deaths did not occur regularly until the largest patch exceeded 3,800 m^2, with 4.3 ha of larkspur divided among 31 patches or fewer. Clearly, patchy larkspur kills, and non-patchy larkspur does not. Despite occasional observations in the literature of the patchy distribution of most dangerous larkspur species (Kotliar 1996, Pfister et al. 2010), this is a novel conclusion.

Results for larkspur-forage overlap ran counter to our hypothesis. We had expected that increased forage draw within larkspur patches would always lead to increased deaths. This was not the case. Instead, deaths were maximized when there was some desirable forage within large larkspur patches but most remained outside of larkspur patches. Figure 5.5 indicates that even though mean larkspur intake is lower in these situations, intake variation among individuals in the herd is higher. Thus, it appears that moderate levels of larkspur-forage overlap effectively split herds, with some individuals entering larkspur patches and others remaining outside to graze other desirable forage.

5.4.2. BEHAVIORAL ECOLOGY OF HERDS. The 1/N effect typically describes a situation where a predator can capture one (or whatever the numerator value is) prey, thus the chance of any individual being selected declines with an increasing denominator (N). However, we propose that a more flexible way to understand dilution is as risk/N. Here, a predator presents potential prey with a certain amount of risk and individual risk is diluted as N increases. In this case, not only is the amount of risk presented by the predator important, but also the distribution of that risk. Assuming equal vulnerability, if the distribution of risk is such that a given herd member will not equal or exceed the level of risk it would acquire on its own, then herd membership is beneficial to the individual. As opposed to 1/N, which usually assumes that at least one death will occur on encounter, risk/N allows for cases where risk is so broadly and evenly distributed that all herd members evade death by virtue of simply being in a group.

If we conceptualize larkspur intake as consumption of risk, it is clear that "plant predators" provide an interesting application of risk/N. In Figure 5.7, where at least one herd member has met the predator, members of tightly cohesive herds accumulate greater median risk but with more even distribution. The herd is thus beneficial to the individual not because it lowers absolute risk, but because it lowers the likelihood of accumulating excessive risk when encountering a predator. If the absolute risk presented by a predator is high enough it can still cause death regardless of herd behavior (as in highly patchy larkspur), but it is less likely to regularly do so when risk is evenly distributed amid a cohesive herd.

As noted by Turner and Pitcher (1986), risk of death upon encounter must be considered along with the chance of first encountering predators that have limited perception. In our study, larkspur-forage overlap, which increases the likelihood of the herd encountering larkspur, was akin to perception, so this phenomenon is best illustrated by limiting overlap, as in Table 5.4. In these circumstances, it is clear that more cohesive herds are less likely to encounter the threat. This largely holds true at different levels of larkspur-forage overlap, though at high levels of overlap moderate levels of herd cohesion lead to the fewest encounters. Nevertheless, overall death counts (Figure 5.6), which incorporate the benefits of both risk/N and encounter dilution, indicate that tightly cohesive herds provide the best overall strategy for avoiding predation by plant predators.

5.4.3. LIMITATIONS. These results must be considered within the context of other benefits and detriments of herd behavior. For example, within the model, individuals in the most cohesive herds traveled 56% greater distance than individuals in herds with the least cohesion. This may indicate that less cohesiveness is desirable when the threat from larkspur is low, as increased cohesion is likely to increase energy expenditure. However, even in this case this observation is offset by the fact that the most cohesive herds met their forage needs 9% faster than the least cohesive herds, likely due to reaching desirable forage more quickly when traveling to stay with the herd. These are complex phenomena, so simple answers are unlikely.

Ultimately, it is most important to recognize that our model was designed to address the questions analyzed here and was not intended to fully replicate cattle behavior. Notably lacking are the more complex (and poorly understood) elements of inter-animal interactions, such as those mediated by familial relationships. Nevertheless, we are confident that our conclusions are sound within the context of the questions we asked.

5.4.4. CONCLUSIONS AND IMPLICATIONS. In his influential review of "population responses to patchy environments", Wiens (1976 p. 97) observed that the "patch structure of resources in space and/or their transiency in time governs the form of social organization expressed within a population." Even 42 years later, this strikes us as a bold and insightful statement, as empirical evidence for the influence of resource patchiness on social organization remains rather weak (outside of social insects). This study provides clear evidence that social organization in large herbivores can be an adaptive response to patchily distributed poisonous plants.

However, Wiens (1976 p. 96) also wrote that "[s]ocial patterns have no unitary adaptive function, but are the creations of multiple selective pressures, and are thus likely to confer multiple adaptive advantages to individuals." Even if herd cohesion mitigates plant toxin risk and this functions similarly to demonstrated mechanisms for predation risk mitigation, we think it is unlikely that herd behavior would emerge from the sole pressure of plant toxins. Instead, as Wiens suggested, a strategy as durable as herd behavior in large herbivores is likely to be an adaptation to many pressures, including predation, mate-finding, and heterogeneous forage resources. Here, we have added poisonous plants to that list.

While the benefits of social grouping are well documented in wild herbivores, they have been largely ignored in domestic herbivores, especially within production agriculture in the US and Europe. The result is livestock that are ill-prepared to deal with the pressures that herd cohesion mitigates (e.g., Laporte et al. 2010). Having demonstrated that increased herd cohesion alone can reduce larkspur-induced deaths by greater than 90% in a variety of scenarios, we suggest that the time has arrived for managers to reconsider the importance of herd behavior in their cattle. Because the adaptive functions of herds are manifold, it is likely that the benefits of a renewed focus on herd behavior in our domestic livestock will be manifold as well.

CHAPTER 6

CONCLUSION

Instead of continued application of what has been called the "loading dock approach to linking science and action" (Beier et al., 2017, p. 288), effective applied science in complex social-ecological systems requires reflexive dialogue between scientists and practitioners (Ostrom and Cox, 2010; Ripamonti et al., 2016). An important element of this dialogue is the recognition by scientists that practitioners may not need us in the ways that we assume, and that some may have already solved the challenges that we seek to address. For the larkspur research presented in this dissertation, this initially manifested in two ways.

First, I noted anecdotal evidence that altered grazing management practices had eliminated larkspur-related deaths for some producers. This led me to conclude that it is likely that many producers have solved this problem (perhaps unknowingly) and that we do not hear from them because they don't have a problem—they have too many other things to work on to worry about problems that they don't have. Second, recognizing this, I realized that my role as a scientist in this case was not to discover some new solution but rather to build a foundation of evidence around the solutions some producers appeared to have already found.

This led to the overarching question of whether it may be possible to use agile grazing management and the innate intelligence of the herd to enable cattle to graze in larkspur habitat at any time of year, with the herd interacting with larkspur such no individual consumes a lethal dose. Though much remains to be learned, in this dissertation I have presented evidence that, at least in the case of *Delphinium geyeri*, the answer to this question appears to be yes.

In Chapter 2, I presented a conceptual model of livestock grazing management that helped to situate this larkspur research within the broader discipline. In addition, this model informed my understanding of the nature of the cattle-larkspur interaction and guided the development, design, implementation, and communication of the larger research project. On its own this model also offers a path forward for effective consilience in the field of livestock grazing management research, including the integration of diverse methods that assist in understanding the complex multiscale phenomena of which livestock grazing management is composed.

Chapter 3 described the creation and structure of the first agent-based model to simulate the grazing behavior of cattle at both a realistic grain and extent. By setting this model within a realistic landscape with a dangerous amount of Geyer's larkspur, I was able to realistically test the relationships among herd cohesion, stocking density, and larkspur-induced toxicosis. The results from this model establish that increases in herd cohesion and stocking density, within bounds achievable my many producers, have the potential to greatly reduce the number of deaths. A key finding was that this reduction in deaths did not occur via an overall reduction in larkspur intake by the herd, but rather reduced variability in consumption among individuals in the herd.

Chapter 4 reported that, if cattle are managed to consume more Geyer's larkspur, the plants can be expected to become smaller, less abundant, and less toxic, and thus less dangerous to cattle. I suggested that the mechanism for this reduced toxicity is two-fold. First, removal of plant mass via grazing simultaneously removes toxic alkaloids, which are expensive for the plant to produce. Second, this aboveground mass removal likely leads to reduced root mass which, given that alkaloids in larkspur are believed to be synthesized in the roots, may reduce the capacity of the plant to generate alkaloids to replace those that were removed. These results, especially when placed in context with the existing literature and Chapter 3, indicate that a synergistic cycle of increased grazing of larkspur leading to a reduction in the danger of larkspur may be possible.

In Chapter 5, I took a step back to ask a broader question about the relationships among plant patchiness and herd behavior in the context of poisonous plants. Using an agent-based model that incorporated neutral landscape models, I demonstrated that randomly distributed larkspur is unlikely to kill cattle, while highly patchy larkspur is quite dangerous. Regardless of plant patchiness, cattle in highly cohesive herds were much less likely to die than those in dispersed herds. When placed in context with our existing understanding of the utility of grouping behavior in large herbivores, these results indicate that herd interactions with poisonous plants function much like herd interactions with predatory carnivores. This suggests that herds may be adaptively beneficial when grazing amid poisonous plants, and that a reconsideration of the manifold benefits of herd behavior among domestic herbivores is warranted.

These chapters build a strong case for this alternative approach to grazing management to address the challenges presented by larkspur but fall short of arriving at usable recommendations for producers. This is in large part because I have not yet done the work necessary to understand how our findings will fit within the complex multiscale decision-making processes of grazing managers. As noted in Chapter 2, in many ways we have yet to fully comprehend these processes and how science can assist them. Nevertheless, for this larkspur work, the first step is to engage producers affected by larkspur to understand how our findings are received and how they might act upon them. This is likely to take the shape of focus groups with interested producers, followed by more in-depth conversations.

A second research need, especially if we want to effectively apply our findings to other larkspur species beyond *D. geyeri*, is to better understand the variation in toxicity, mass, and abundance among the different larkspur species within individual grazing management units. Despite important differences, toxicity patterns and effects are broadly similar among these species. As such, I have felt comfortable extending many of our conclusions to larkspur species as a whole. However, when it comes to applying our findings to management practices, it will be essential to better understand the spatiotemporal risk profile of the different species. While this is a difficult undertaking, we are hopeful that remote-sensing combined with on-the-ground assessment may prove effective.

Finally, because I do not expect to generate a one-size-fits-all larkspur panacea, the end goal is to synthesize the results of this work and the broader literature into information that larkspur-challenged producers can integrate into their unique circumstances. If the design and conduct of our science must evolve to better match the complex realities that producers face, so must the communication of what we have learned. Such communication must integrate the many lessons of research on the social dimensions of agriculture, including that "adoption is a socio-cultural process", producers "construct their own knowledge", and "the best method of extension is multiple methods" (Vanclay, 2004). This is compelled not only by good science but also, ultimately, by my deep affection for livestock and the people whose lives and livelihoods are entwined with them. After all, as Wendell Berry writes in "Life is a Miracle" (2003, p. 40), the "wholeness of creatures and places together is never going to be apparent to an intelligence coldly determined to be empirical or objective. It shows itself to affection and familiarity".

REFERENCES

Abram, D., 2012. The Spell of the Sensuous: Perception and Language in a More-Than-Human World. Knopf Doubleday Publishing Group.

Alexander, C., Ishikawa, S., Silverstein, M., 1977. A Pattern Language: Towns, Buildings, Construction. Oxford University Press, New York.

Allen, C.R., Holling, C.S., 2008. Discontinuities in Ecosystems and Other Complex Systems. Columbia University Press.

Allen, T.F.H., Hoekstra, T.W., 2015. Toward a Unified Ecology. Columbia University Press.

Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters, A., Sanderson, M., The Forage and Grazing Terminology Committee, 2011. An international terminology for grazing lands and grazing animals. Grass Forage Sci. 66, 2–28. https://doi.org/10.1111/j.1365-2494.2010.00780.x

Anderson, D.M., Estell, R.E., Holechek, J.L., Ivey, S., Smith, G.B., 2014. Virtual herding for flexible livestock management – a review. Rangel. J. 36, 205–221. https://doi.org/10.1071/RJ13092

Anderson, D.R., 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York ; London.

Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. Ecol. Model., Population Models for Ecological Risk Assessment of Chemicals 280, 117–128. https://doi.org/10.1016/j.ecolmodel.2013.11.009

Augustine, D.J., Derner, J.D., 2015a. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. J. Wildl. Manag. 79, 927–936. https://doi.org/10.1002/jwmg.909

Augustine, D.J., Derner, J.D., 2015b. Patch burn grazing management in a semiarid grassland: consequences for pronghorn, plains pricklypear, and wind erosion. Rangel. Ecol. Manag. 68, 40–47. https://doi.org/10.1016/j.rama.2014.12.010

Augustine, D.J., Derner, J.D., 2014. Controls over the strength and timing of fire-grazer interactions in a semi-arid rangeland. J. Appl. Ecol. 51, 242–250. https://doi.org/10.1111/1365-2664.12186

Bailey, D.W., 2004. Management strategies for optimal grazing distribution and use of arid rangelands. J. Anim. Sci. 82, E147–E153. https://doi.org/10.2527/2004.8213_supplE147x

Bailey, D.W., 1995. Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. Appl. Anim. Behav. Sci. 45, 183–200. https://doi.org/10.1016/0168-1591(95)00586-H

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., Sims, P.L., 1996. Mechanisms That Result in Large Herbivore Grazing Distribution Patterns. J. Range Manag. 49, 386–400. https://doi.org/10.2307/4002919

Bailey, D.W., Provenza, F.D., 2008. Mechanisms Determining Large-Herbivore Distribution, in: Prins, H.H.T., Langevelde, F.V. (Eds.), Resource Ecology, Wageningen UR Frontis Series. Springer Netherlands, pp. 7–28.

Bailey, D.W., Rittenhouse, L.R., Hart, R.H., Richards, R.W., 1989. Characteristics of spatial memory in cattle. Appl. Anim. Behav. Sci. 23, 331–340. https://doi.org/10.1016/0168-1591(89)90101-9

Bailey, D.W., Trotter, M.G., Knight, C.W., Thomas, M.G., 2017. Use of GPS tracking collars and accelerometers for rangeland livestock production research. J. Anim. Sci. 95, 360–360. https://doi.org/10.2527/asasann.2017.740

Bailey, D.W., Van Wagoner, H.C., Weinmeister, R., Jensen, D., 2008. Evaluation of Low-Stress Herding and Supplement Placement for Managing Cattle Grazing in Riparian and Upland Areas. Rangel. Ecol. Manag. 61, 26–37. https://doi.org/10.2111/06-130.1

Bailey, D.W., Welling, G.R., 2007. Evaluation of Low-Moisture Blocks and Conventional Dry Mixes for Supplementing Minerals and Modifying Cattle Grazing Patterns. Rangel. Ecol. Manag. 60, 54–64. https://doi.org/10.2111/05-138R1.1

Barnes, M., 2015. Livestock Management for Coexistence with Large Carnivores, Healthy Land and Productive Ranches (White paper). Keystone Conservation.

Beedle, M., Devos, M., Sharon, Y., Schwaber, K., Sutherland, J., 1999. SCRUM: An extension pattern language for hyperproductive software development. Pattern Lang. Program Des. 4, 637–651.

Beier, P., Hansen, L.J., Helbrecht, L., Behar, D., 2017. A How-to Guide for Coproduction of Actionable Science. Conserv. Lett. 10, 288–296. https://doi.org/10.1111/conl.12300

Berry, W., 2003. Life Is a Miracle: An Essay Against Modern Superstition. Catapult.

Bogdan, R.C., Biklen, S.K., 2003. Qualitative Research in Education. An Introduction to Theory and Methods. Third Edition. Allyn & Bacon, A Viacom Company, 160 Gould St.

Bonham, C.D., 1989. Measurements for Terrestrial Vegetation. Wiley.

Boone, R.B., Hobbs, N.T., 2004. Lines around fragments: effects of fencing on large herbivores. Afr. J. Range Forage Sci. 21, 147–158. https://doi.org/10.2989/10220110409485847

Borchers, J.O., 2000. A Pattern Approach to Interaction Design 10.

Bourke, B., 2014. Positionality: Reflecting on the Research Process. Qual. Rep. 19, 1–9.

Boyd, C.S., Svejcar, T.J., 2009. Managing complex problems in rangeland ecosystems. Rangel. Ecol. Manag. 62, 491–499. https://doi.org/10.2111/08-194.1

Briske, D.D. (Ed.), 2017. Rangeland Systems: Processes, Management and Challenges, Springer Series on Environmental Management. Springer International Publishing.

Briske, D.D., Sayre, N.F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B., Derner, J.D., 2011. Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research. Rangel. Ecol. Manag. 64, 325–334. https://doi.org/10.2111/REM-D-10-00084.1

Brunson, M.W., 2012. The elusive promise of social-ecological approaches to rangeland management. Rangel. Ecol. Manag. 65, 632–637. https://doi.org/10.2111/REM-D-11-00117.1

Burkhardt, J.W., 1996. Herbivory in the Intermountain West. Ida. For. Wildl. Range Exp. Stn. Bull. 58.

BurnSilver, S., 2009. Pathways of Continuity and Change: Maasai Livelihoods in Amboseli, Kajiado District, Kenya, in: Homewood, K., Kristjanson, P., Trench, P. (Eds.), Staying Maasai? Livelihoods, Conservation, and Development in East African Rangelands, Studies in Human Ecology and Adaptation. Springer.

Butler, P.J., 2000. Cattle Distribution under Intensive Herded Management. Rangelands 22, 21–23.

Carson, A., 1998. Autobiography of Red. Knopf Doubleday Publishing Group.

Catchpole, W.R., Wheeler, C.J., 1992. Estimating plant biomass: a review of techniques. Aust. J. Ecol.

Chaffee, M.W., McNeill, M.M., 2007. A model of nursing as a complex adaptive system. Nurs. Outlook 55, 232-241.e3. https://doi.org/10.1016/j.outlook.2007.04.003

Cordova, F.J., Wallace, J.D., Pieper, R.D., 1978. Forage Intake by Grazing Livestock: A Review. J. Range Manag. 31, 430–438. https://doi.org/10.2307/3897201

Costanza, R., 2003. A vision of the future of science: reintegrating the study of humans and the rest of nature. Futures 35, 651–671. https://doi.org/10.1016/S0016-3287(02)00105-2

Cote, S., 2004. Stockmanship: a powerful tool for grazing lands management. USDA Natural Resources Conservation Service.

Creel, S., Becker, M.S., Durant, S.M., M'Soka, J., Matandiko, W., Dickman, A.J., Christianson, D., Dröge, E., Mweetwa, T., Pettorelli, N., Rosenblatt, E., Schuette, P., Woodroffe, R., Bashir, S., Beudels-Jamar, R.C., Blake, S., Borner, M., Breitenmoser, C., Broekhuis, F., Cozzi, G., Davenport, T.R.B., Deutsch, J., Dollar, L., Dolrenry, S., Douglas-Hamilton, I., Fitzherbert, E., Foley, C., Hazzah, L., Henschel, P., Hilborn, R., Hopcraft, J.G.C., Ikanda, D., Jacobson, A., Joubert, B., Joubert, D., Kelly, M.S., Lichtenfeld, L., Mace, G.M., Milanzi, J., Mitchell, N., Msuha, M., Muir, R., Nyahongo, J., Pimm, S., Purchase, G., Schenck, C., Sillero-Zubiri, C., Sinclair, A.R.E., Songorwa, A.N., Stanley-Price, M., Tehou, C.A., Trout, C., Wall, J., Wittemyer, G., Zimmermann, A., 2013. Conserving large populations of lions – the argument for fences has holes. Ecol. Lett. 16, 1413-e3. https://doi.org/10.1111/ele.12145

Cronin, E.H., Nielsen, D.B., 1972. Controlling Tall Larkspur on Snowdrift Areas in the Subalpine Zone. J. Range Manag. 25, 213–216. https://doi.org/10.2307/3897058

Darnhofer, I., Gibbon, D., Dedieu, B., 2012. Farming Systems Research: an approach to inquiry, in: Darnhofer, I., Gibbon, D., Dedieu, Benoît (Eds.), Farming Systems Research into the 21st Century: The New Dynamic. Springer Netherlands, Dordrecht, pp. 3–31.

David-Chavez, D.M., Gavin, M.C., 2018. A global assessment of Indigenous community engagement in climate research. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/aaf300

Davies, K.W., Gearhart, A., Boyd, C.S., Bates, J.D., 2017. Fall and spring grazing influence fire ignitability and initial spread in shrub steppe communities. Int. J. Wildland Fire 26, 485. https://doi.org/10.1071/WF17065

Davies, N.B., Krebs, J.R., West, S.A., 2012. An Introduction to Behavioural Ecology. John Wiley & Sons.

Despret, V., Meuret, M., 2016. Cosmoecological Sheep and the Arts of Living on a Damaged Planet. Environ. Humanit. 8, 24–36. https://doi.org/10.1215/22011919-3527704

Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing - A global synthesis. Glob. Change Biol. 13, 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Distel, R.A., Laca, E.A., Griggs, T.C., Demment, M.W., 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. Appl. Anim. Behav. Sci. 45, 11–21. https://doi.org/10.1016/0168-1591(95)00593-H

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R.S., Frank, L., 2014. A Metapopulation Approach to African Lion (Panthera leo) Conservation. PLOS ONE 9, e88081. https://doi.org/10.1371/journal.pone.0088081

Douglas, C.E., Michael, F.A., 1991. On distribution-free multiple comparisons in the one-way analysis of variance. Commun. Stat. - Theory Methods 20, 127–139. https://doi.org/10.1080/03610929108830487

Dumont, B., Hill, D.R., 2001. Multi-agent simulation of group foraging in sheep: effects of spatial memory, conspecific attraction and plot size. Ecol. Model. 141, 201–215.

Dumont, B., Hill, D.R.C., 2004. Spatially explicit models of group foraging by herbivores: what can Agent-Based Models offer? Anim. Res. 53, 419–428. https://doi.org/10.1051/animres:2004028

Eastwood, C., Kenny, S., 2009. Art or Science?: Heuristic versus Data Driven Grazing Management on Dairy Farms. Ext. Farming Syst. J. 5, 95.

Ebensperger, L.A., Hayes, L.D., 2016. Causes and evolution of group-living, in: Ebensperger, L.A., Hayes, L.D. (Eds.), Sociobiology of Caviomorph Rodents. John Wiley & Sons, Ltd, Chichester, UK, pp. 173–200. https://doi.org/10.1002/9781118846506.ch7

ESRI, 2017. Collector for ArcGIS 17.01. ESRI, Redlands, CA.

ESRI, 2015. ArcGIS Desktop 10.4. ESRI, Redlands, CA.

Faraway, J.J., 2016. Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models, Second Edition. CRC Press.

Fernandez-Gimenez, M.E., 2000. The Role of Mongolian Nomadic Pastoralists' Ecological Knowledge in Rangeland Management. Ecol. Appl. 10, 1318–1326. https://doi.org/10.2307/2641287

Feyerabend, P., 1993. Against Method. Verso.

Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of Pattern and Process: Developing an Alternative Paradigm of Rangeland Management. Rangel. Ecol. Manag. 65, 579–589. https://doi.org/10.2111/REM-D-11-00109.1

Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. Conserv. Biol. 23, 588–598. https://doi.org/10.1111/j.1523-1739.2008.01139.x

Fuhlendorf, S.D., Fynn, R.W.S., McGranahan, D.A., Twidwell, D., 2017. Heterogeneity as the Basis for Rangeland Management, in: Briske, D.D. (Ed.), Rangeland Systems. Springer International Publishing, Cham, pp. 169–196. https://doi.org/10.1007/978-3-319-46709-2_5

Funtowicz, S.O., Ravetz, J.R., 1993. Science for the post-normal age. Futures 25, 739–755. https://doi.org/10.1016/0016-3287(93)90022-L

Galaty, J.G., 1989. Cattle and cognition: aspects of Maasai practical reasoning, in: Clutton-Brock, J. (Ed.), The Walking Larder: Patterns of Domestication, Pastoralism, and Predation.

Galyean, M.L., Gunter†, S.A., 2016. Predicting forage intake in extensive grazing systems. J. Anim. Sci. 94, 26–43. https://doi.org/10.2527/jas.2016-0523

Gardner, D.R., Panter, K.E., Pfister, J.A., Knight, A.P., 1999. Analysis of Toxic Norditerpenoid Alkaloids in Delphinium Species by Electrospray, Atmospheric Pressure Chemical Ionization, and Sequential Tandem Mass Spectrometry. J. Agric. Food Chem. 47, 5049–5058. https://doi.org/10.1021/jf990615j

Gardner, D.R., Pfister, J.A., 2007. Toxic alkaloid concentrations in Delphinium nuttallianum, Delphinium andersonii, and Delphinium geyeri in the Intermountain Region. Rangel. Ecol. Manag. 60, 441–446. https://doi.org/10.2111/1551-5028(2007)60[441:TACIDN]2.0.CO;2

Gardner, R.H., Urban, D.L., 2007. Neutral models for testing landscape hypotheses. Landsc. Ecol. 22, 15–29. https://doi.org/10.1007/s10980-006-9011-4

Gigerenzer, G., Gaissmaier, W., 2011. Heuristic Decision Making. Annu. Rev. Psychol. 62, 451–482. https://doi.org/10.1146/annurev-psych-120709-145346

Glover, G.H., 1906. Larkspur and Other Poisonous Plants. Agricultural Experiment Station of the Agricultural College of Colorado.

Goodwin, C.N., Hawkins, C.P., Kershner, J.L., 1997. Riparian Restoration in the Western United States: Oveview and Perspecive. Restor. Ecol. 5, 4–14. https://doi.org/10.1111/j.1526-100X.1997.tb00200.x

Google/Open source, 2018. OpenRefine 3.0.

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815.

Greca, I.M., Moreira, M.A., 2000. Mental models, conceptual models, and modelling. Int. J. Sci. Educ. 22, 1–11.

Green, B., Gardner, D., Pfister, J., Cook, D., 2009. Larkspur poison weed: 100 years of delphinium research. Rangelands 31, 22–27. https://doi.org/10.2111/1551-501X-31.1.22

Green, B.T., Welch, K.D., Gardner, D.R., Stegelmeier, B.L., Davis, T.Z., Cook, D., Lee, S.T., Pfister, J.A., Panter, K.E., 2009. Serum elimination profiles of methyllycaconitine and deltaline in cattle following oral administration of larkspur (Delphinium barbeyi). Am. J. Vet. Res. 70, 926–931. https://doi.org/10.2460/ajvr.70.7.926

Green, B.T., Welch, K.D., Pfister, J.A., Chitko-McKown, C.G., Gardner, D.R., Panter, K.E., 2014. Mitigation of Larkspur Poisoning on Rangelands Through the Selection of Cattle. Rangelands 36, 10–15. https://doi.org/10.2111/RANGELANDS-D-13-00031.1

Grimm, V., 2002. Visual Debugging: A Way of Analyzing, Understanding and Communicating Bottom-up Simulation Models in Ecology. Nat. Resour. Model. 15, 23–38. https://doi.org/10.1111/j.1939-7445.2002.tb00078.x

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecol. Model. 115, 129–148. https://doi.org/10.1016/S0304-3800(98)00188-4

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: A review and first update. Ecol. Model. 221, 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019

Grimm, V., Martin, B.T., 2013. Mechanistic effect modeling for ecological risk assessment: Where to go from here? Integr. Environ. Assess. Manag. 9, e58–e63. https://doi.org/10.1002/ieam.1423

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-Oriented Modeling of Agent-Based Complex

Systems: Lessons from Ecology. Science 310, 987–991. https://doi.org/10.1126/science.1116681

Grina, J.A., Schroeder, D.R., Wydallis, E.T., Stermitz, F.R., 1986. Alkaloids from Delphinium geyeri. Three new C20-diterpenoid alkaloids. J. Org. Chem. 51, 390–394. https://doi.org/10.1021/jo00353a023

Harris, N.R., Johnson, D.E., McDougald, N.K., George, M.R., 2007. Social Associations and Dominance of Individuals in Small Herds of Cattle. Rangel. Ecol. Manag. 60, 339–349. https://doi.org/10.2111/1551-5028(2007)60[339:SAADOI]2.0.CO;2

Hart, R.H., Bissio, J., Samuel, M.J., J. W. Waggoner, J., 1993. Grazing Systems, Pasture Size, and Cattle Grazing Behavior, Distribution and Gains. J. Range Manag. 46, 81–87. https://doi.org/10.2307/4002452

Hazzah, L., Borgerhoff Mulder, M., Frank, L., 2009. Lions and Warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. Biol. Conserv. 142, 2428–2437. https://doi.org/10.1016/j.biocon.2009.06.006

Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C.T.T., Mwebi, O., Kearney, F., Frank, L., 2014. Efficacy of Two Lion Conservation Programs in Maasailand, Kenya. Conserv. Biol. 28, 851–860. https://doi.org/10.1111/cobi.12244

Heitschmidt, R., Stuth (Eds.), 1991. Grazing management: an ecological perspective. Timber Press.

Hessle, A.K., 2009. Effects of social learning on foraging behaviour and live weight gain in first-season grazing calves. Appl. Anim. Behav. Sci. 116, 150–155. https://doi.org/10.1016/j.applanim.2008.08.004

Hexagon Geospatial, 2016. ERDAS IMAGINE 2016. Madison, Alabama.

Hilbe, J.M., 2011. Negative Binomial Regression. Cambridge University Press.

Holcomb, E.D., Davis, C.A., Fuhlendorf, S.D., 2014. Patch-burn management: Implications for conservation of avian communities in fire-dependent sagebrush ecosystems. J. Wildl. Manag. 78, 848–856. https://doi.org/10.1002/jwmg.723

Holechek, J.L., 2002. Do Most Livestock Losses to Poisonous Plants Result from "Poor" Range Management? J. Range Manag. 270–276.

Holechek, J.L., Pieper, R.D., Herbel, C.H., 2011. Range management: principles and practices., 6th ed. Pearson Education, Inc.

Holling, C.S., 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4, 390–405. https://doi.org/10.1007/s10021-001-0101-5

Holling, C.S., Meffe, G.K., 1996. Command and Control and the Pathology of Natural Resource Management. Conserv. Biol. 10, 328–337. https://doi.org/10.1046/j.1523-1739.1996.10020328.x

Huete, A.R., 1988. A soil-adjusted vegetation index (SAVI). Remote Sens. Environ. 25, 295–309. https://doi.org/10.1016/0034-4257(88)90106-X

Ireland, H.M., Ruxton, G.D., 2017. Zebra stripes: an interspecies signal to facilitate mixed-species herding? Biol. J. Linn. Soc. 121, 947–952. https://doi.org/10.1093/biolinnean/blx037

Jabbour, F., Renner, S.S., 2012. A phylogeny of Delphinieae (Ranunculaceae) shows that Aconitum is nested within Delphinium and that Late Miocene transitions to long life cycles in the Himalayas and Southwest China coincide with bursts in diversification. Mol. Phylogenet. Evol. 62, 928–942. https://doi.org/10.1016/j.ympev.2011.12.005

Jablonski, K.E., Boone, R.B., Meiman, P.J., 2018. An agent-based model of cattle grazing toxic Geyer's larkspur. PLOS ONE 13, e0194450. https://doi.org/10.1371/journal.pone.0194450

Jackson, M.C., 2003. Systems Thinking: Creative Holism for Managers. Wiley, England.

James, L.F., Nielsen, D.B., Panter, K.E., 1992. Impact of Poisonous Plants on the Livestock Industry. J. Range Manag. 45, 3–8. https://doi.org/10.2307/4002517

Knight, A., Walter, R., 2001. A Guide to Plant Poisoning of Animals in North America. Teton NewMedia, Incorporated.

Kossiakoff, A. (Ed.), 2011. Systems engineering: principles and practice, 2nd ed. ed, Wiley series in systems engineering and management. Wiley-Interscience, Hoboken, N.J.

Krätli, S., Schareika, N., 2010. Living Off Uncertainty: The Intelligent Animal Production of Dryland Pastoralists. Eur. J. Dev. Res. 22, 605–622. https://doi.org/10.1057/ejdr.2010.41

Krause, J., Ruxton, G.D., 2002. Living in Groups. OUP Oxford.

Kuhn, T.S., 2012. The Structure of Scientific Revolutions: 50th Anniversary Edition. University of Chicago Press.

Laca, E.A., 2009. New approaches and tools for grazing management. Rangel. Ecol. Manag. 62, 407–417.

Laca, E.A., Distel, R.A., Criggs, T.C., Demment, M.W., 1994. Effects of Canopy Structure on Patch Depression by Grazers. Ecology 75, 706–716. https://doi.org/10.2307/1941728

LaRocque, O., 2014. Revisiting distinctions between ranching and pastoralism: A matter of interspecies relations between livestock, people, and predators. Crit. Anthropol. 34, 73–93. https://doi.org/10.1177/0308275X13510190

Launchbaugh, K.L., Howery, L.D., 2005. Understanding Landscape Use Patterns of Livestock as a Consequence of Foraging Behavior. Rangel. Ecol. Manag. 58, 99–108. https://doi.org/10.2111/03-146.1

Laycock, W.A., 1975. Alkaloid Content of Duncecap Larkspur after Two Years of Clipping. J. Range Manag. 28, 257–259. https://doi.org/10.2307/3897769

Lazo, A., 1994. Social segregation and the maintenance of social stability in a feral cattle population. Anim. Behav. 48, 1133–1141. https://doi.org/10.1006/anbe.1994.1346

Lichtenfeld, L.L., Trout, C., Kisimir, E.L., 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. Biodivers. Conserv. 24, 483–491. https://doi.org/10.1007/s10531-014-0828-x

Maclennan, S.D., Groom, R.J., Macdonald, D.W., Frank, L.G., 2009. Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biol. Conserv. 142, 2419–2427. https://doi.org/10.1016/j.biocon.2008.12.003

Makin, D.F., Chamaillé-Jammes, S., Shrader, A.M., 2017. Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. Anim. Behav. 127, 225–231. https://doi.org/10.1016/j.anbehav.2017.03.024

Malterud, K., 2001. Qualitative research: standards, challenges, and guidelines. The Lancet 358, 483–488. https://doi.org/10.1016/S0140-6736(01)05627-6

Manners, G.D., Panter, K.E., Pelletier, S.W., 1995. Structure-Activity Relationships of Norditerpenoid Alkaloids Occurring in Toxic Larkspur (Delphinium) Species. J. Nat. Prod. 58, 863–869. https://doi.org/10.1021/np50120a007

Marsh, C.D., Clawson, A.B., Marsh, H., 1916. Larkspur Poisoning on Live Stock. U.S. Department of Agriculture.

McGarigal, K., Cushman, S., Neel, M., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps.

McLane, A.J., Semeniuk, C., McDermid, G.J., Marceau, D.J., 2011. The role of agent-based models in wildlife ecology and management. Ecol. Model. 222, 1544–1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020

Meiman, P.J., Tolleson, D.R., Johnson, T., Echols, A., Price, F., Stackhouse-Lawson, K., 2016. Usable Science for Managing Animals and Rangeland Sustainability. Rangelands 38, 79–84. https://doi.org/10.1016/j.rala.2016.01.003

Meuret, M., Provenza, F.D., 2015a. How French shepherds create meal sequences to stimulate intake and optimise use of forage diversity on rangeland. Anim. Prod. Sci. 55, 309–318.

Meuret, M., Provenza, F.D., 2015b. When Art and Science Meet: Integrating Knowledge of French Herders with Science of Foraging Behavior. Rangel. Ecol. Manag. 68, 1–17. https://doi.org/10.1016/j.rama.2014.12.007

Meuret, M., Viaux, C., Chadœuf, J., 1994. Land heterogeneity stimulates intake rate during grazing trips. Ann. Zootech. 43, 296.

Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. Am. Nat. 132, 87–106.

Miller, J.G., 1978. Living Systems. Mcgraw-Hill.

Miner, J.R., Buckhouse, J.C., Moore, J.A., 1992. Will a Water Trough Reduce the Amount of Time Hay-Fed Livestock Spend in the Stream (And Therefore Improve Water Quality)? Rangelands 14, 35–38.

Molnár, Z., 2014. Perception and Management of Spatio-Temporal Pasture Heterogeneity by Hungarian Herders. Rangel. Ecol. Manag. 67, 107–118. https://doi.org/10.2111/REM-D-13-00082.1

Monahan, T., Fisher, J.A., 2010. Benefits of 'observer effects': lessons from the field. Qual. Res. 10, 357–376. https://doi.org/10.1177/1468794110362874

Mullings, B., 1999. Insider or outsider, both or neither: some dilemmas of interviewing in a cross-cultural setting. Geoforum 30, 337–350. https://doi.org/10.1016/S0016-7185(99)00025-1

National Research Council, 2000. Nutrient Requirements of Beef Cattle: Seventh Revised Edition: Update 2000. National Academies Press, Washington, D.C. https://doi.org/10.17226/9791

Nielsen, D.B., 1988. Economic Impact of Poisonous Plants on the Rangeland Livestock Industry. J. Anim. Sci. 66, 2330–2333. https://doi.org/10.2527/jas1988.6692330x

Nielsen, D.B., Ralphs, M.H., Evans, J.O., Call, C.A., 1994. Economic feasibility of controlling tall larkspur on rangelands. J. Range Manag. Arch. 47, 369–372.

Northrop, R.B., 2010. Introduction to Complexity and Complex Systems. CRC Press.

Oba, G., Kaitira, L.M., 2006. Herder knowledge of landscape assessments in arid rangelands in northern Tanzania. J. Arid Environ. 66, 168–186. https://doi.org/10.1016/j.jaridenv.2005.10.020

O'Connor, J., McDermott, I., 1997. The Art of Systems Thinking: Essential Skills for Creativity and Problem Solving. Thorsons.

Ogada, M.O., Woodroffe, R., Oguge, N.O., Frank, L.G., 2003. Limiting Depredation by African Carnivores: the Role of Livestock Husbandry. Conserv. Biol. 17, 1521–1530. https://doi.org/10.1111/j.1523-1739.2003.00061.x

Ohsowski, B.M., Dunfield, K.E., Klironomos, J.N., Hart, M.M., 2016. Improving plant biomass estimation in the field using partial least squares regression and ridge regression. Botany 94, 501–508. https://doi.org/10.1139/cjb-2016-0009

Ostrom, E., Cox, M., 2010. Moving beyond panaceas: a multi-tiered diagnostic approach for social-ecological analysis. Environ. Conserv. 37, 451–463. https://doi.org/10.1017/S0376892910000834

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. t., Pfeifer, M., Zander, K. k., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C. m., Begg, K. s., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A. c., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak,

S. m., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H. h., Joubert, C. j., Kasiki, S. m., Kissui, B., Knocker, W., Leathem, B., Lindsey, P. a., Maclennan, S. d., McNutt, J. w., Miller, S. m., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J. o., Okot-Omoya, E., Patterson, B. d., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E. a., Stratford, K. j., Winterbach, C., Winterbach, H., Polasky, S., 2013. Conserving large carnivores: dollars and fence. Ecol. Lett. 16, 635–641. https://doi.org/10.1111/ele.12091

Panter, K.E., Manners, G.D., Stegelmeier, B.L., Lee, S., Gardner, D.R., Ralphs, M.H., Pfister, J.A., James, L.F., 2002. Larkspur poisoning: toxicology and alkaloid structure–activity relationships. Biochem. Syst. Ecol. 30, 113–128. https://doi.org/10.1016/S0305-1978(01)00123-5

Patterson, B.D., Kasiki, S.M., Selempo, E., Kays, R.W., 2004. Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National ParkS, Kenya. Biol. Conserv. 119, 507–516. https://doi.org/10.1016/j.biocon.2004.01.013

Pfister, J.A., Gardner, D.R., Panter, K.E., 2010. Consumption of Low Larkspur (Delphinium nuttallianum) by Grazing Sheep. Rangel. Ecol. Manag. 63, 263–266. https://doi.org/10.2111/REM-D-09-00084.1

Pfister, J.A., Gardner, D.R., Panter, K.E., Manners, G.D., Ralphs, M.H., Stegelmeier, B.L., Schoch, T.K., 1999. Larkspur (Delphinium spp.) poisoning in livestock. J. Nat. Toxins 8, 81–94.

Pfister, J.A., Gardner, D.R., Price, K.W., 1997a. Grazing risk on tall larkspur-infested ranges. Rangelands 19, 12–15. https://doi.org/10.2307/4001275

Pfister, J.A., Gardner, D.R., Price, K.W., 1997b. Grazing Risk on Tall Larkspur-Infested Ranges. Rangelands 19, 12–15. https://doi.org/10.2307/4001275

Pfister, J.A., Manners, G.D., Ralphs, M.H., Hong, Z.X., Lane, M.A., 1988. Effects of Phenology, Site, and Rumen Fill on Tall Larkspur Consumption by Cattle. J. Range Manag. 41, 509–514. https://doi.org/10.2307/3899528

Pfister, J.A., Provenza, F.D., Manners, G.D., Gardner, D.R., Ralphs, M.H., 1997c. Tall Larkspur Ingestion: Can Cattle Regulate Intake Below Toxic Levels? J. Chem. Ecol. 23, 759–777. https://doi.org/10.1023/B:JOEC.0000006409.20279.59

Pfister, J.A., Provenza, F.D., Panter, K.E., Stegelmeier, B.L., Launchbaugh, K.L., 2002. Risk Management to Reduce Livestock Losses from Toxic Plants. J. Range Manag. 55, 291–300. https://doi.org/10.2307/4003137

Porath, M.L., Momont, P.A., DelCurto, T., Rimbey, N.R., Tanaka, J.A., McInnis, M., 2002. Offstream water and trace mineral salt as management strategies for improved cattle distribution. J. Anim. Sci. 80, 346–356. https://doi.org/10.2527/2002.802346x

Pretty, J.N., 1995. Participatory learning for sustainable agriculture. World Dev. 23, 1247–1263. https://doi.org/10.1016/0305-750X(95)00046-F

Prins, H.H.T., Langevelde, F. van, 2008. Resource Ecology: Spatial and Temporal Dynamics of Foraging. Springer.

Provenza, F.D., 2003a. Twenty-Five Years of Paradox in Plant-Herbivore Interactions and “Sustainable” Grazing Management. Rangelands 4–15.

Provenza, F.D., 2003b. Twenty-five years of paradox in plant-herbivore interactions and “sustainable” grazing management. Rangel. Arch. 25, 4–15.

Provenza, F.D., Pringle, H., Revell, D., Bray, N., Hines, C., Teague, R., Steffens, T., Barnes, M., 2013. Complex Creative Systems. Rangelands 35, 6–13. https://doi.org/10.2111/RANGELANDS-D-13-00013.1

Provenza, F.D., Villalba, J., Bryant, J., 2003a. Foraging by Herbivores: Linking the Biochemical Diversity of Plants to Herbivore Culture and Landscape Diversity. Landsc. Ecol. Resour. Manag. Link. Theory Pract. 387–421.

Provenza, F.D., Villalba, J.J., Cheney, C.D., Werner, S.J., 1998. Self-organization of foraging behaviour: From simplicity to complexity without goals. Nutr. Res. Rev. 11, 199–222. https://doi.org/10.1079/NRR19980015

Provenza, F.D., Villalba, J.J., Dziba, L.E., Atwood, S.B., Banner, R.E., 2003b. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Rumin. Res., Advanced research on nutrition of sheep and goats, with special reference to pasture and rangeland use 49, 257–274. https://doi.org/10.1016/S0921-4488(03)00143-3

R Core Team, 2018. R: a language for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ralphs, M.H., Gardner, D.R., 2003. Distribution of norditerpene alkaloids in tall larkspur plant parts through the growing season. J. Chem. Ecol. 29, 2013–2021. https://doi.org/10.1023/A:1025678217092

Ralphs, M.H., Gardner, D.R., 2001. Influence of Defoliation on Toxic Alkaloid Concentration and Alkaloid Pools in Tall Larkspur. J. Chem. Ecol. 27, 151–160. https://doi.org/10.1023/A:1005680319490

Ralphs, M.H., Gardner, D.R., Pfister, J.A., 2000. A Functional Explanation for Patterns of Norditerpenoid Alkaloid Levels in Tall Larkspur (Delphinium barbeyi). J. Chem. Ecol. 26, 1595–1607. https://doi.org/10.1023/A:1005530627792

Ralphs, M.H., Jensen, D.T., Pfister, J.A., Nielsen, D.B., James, L.F., 1994. Storms Influence Cattle to Graze Larkspur: An Observation. J. Range Manag. 47, 275–278. https://doi.org/10.2307/4002547

Ralphs, M.H., Olsen, J.D., Pfister, J.A., Manners, G.D., 1988. Plant-animal interactions in larkspur poisoning in cattle. J. Anim. Sci. 66, 2334–2342.

Reid, R.S., Fernández-Giménez, M.E., Galvin, K.A., 2014. Dynamics and Resilience of Rangelands and Pastoral Peoples Around the Globe. Annu. Rev. Environ. Resour. 39, 217–242. https://doi.org/10.1146/annurev-environ-020713-163329

Ripamonti, S., Galuppo, L., Gorli, M., Scaratti, G., Cunliffe, A.L., 2016. Pushing Action Research Toward Reflexive Practice. J. Manag. Inq. 25, 55–68. https://doi.org/10.1177/1056492615584972

Rose, G., 1997. Situating knowledges: positionality, reflexivities and other tactics. Prog. Hum. Geogr. 21, 305–320. https://doi.org/10.1191/030913297673302122

Salingaros, N.A., 2017. Pattern Language, in: The Wiley-Blackwell Encyclopedia of Social Theory. American Cancer Society, pp. 1–3. https://doi.org/10.1002/9781118430873.est0504

SAS Institute, 2016. JMP. SAS Institute, Inc., Cary, NC.

Sato, S., 1982. Leadership during actual grazing in a small herd of cattle. Appl. Anim. Ethol. 8, 53–65. https://doi.org/10.1016/0304-3762(82)90132-8

Sayre, N.F., 2017. The Politics of Scale: A History of Rangeland Science. University of Chicago Press.

Sayre, N.F., 2004. Viewpoint: The Need for Qualitative Research to Understand Ranch Management. J. Range Manag. 57, 668–674. https://doi.org/10.2111/1551-5028(2004)057[0668:VTNFQR]2.0.CO;2

Sayre, N.F., deBuys, W., Bestelmeyer, B.T., Havstad, K.M., 2012. "The range problem" after a century of rangeland science: new research themes for altered landscapes. Rangel. Ecol. Manag. 65, 545–552. https://doi.org/10.2111/REM-D-11-00113.1

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large Herbivore Foraging and Ecological Hierarchies. BioScience 37, 789–799. https://doi.org/10.2307/1310545

Shiyomi, M., 2004. How are distances between grazing cows determined: A case study. Appl. Entomol. Zool. 39, 575–581. https://doi.org/10.1303/aez.2004.575

Shiyomi, M., Tsuiki, M., 1999. Model for the spatial pattern formed by a small herd in grazing cattle. Ecol. Model. 119, 231–238. https://doi.org/10.1016/S0304-3800(99)00059-9

Smith, M.A., Waggoner, Jr., J.W., Sims, S., 2010. Larkspur: Managing grazing to avoid poisoning cattle (No. MP-111.13), Wyoming Range Facts. University of Wyoming Cooperative Extension.

Stets, J.E., Burke, P.J., 2000. Identity Theory and Social Identity Theory. Soc. Psychol. Q. 63, 224–237. https://doi.org/10.2307/2695870

Stutz, R.S., Bergvall, U.A., Leimar, O., Tuomi, J., Rautio, P., 2018. Cohesiveness reduces foraging efficiency in a social herbivore. Anim. Behav. 135, 57–68. https://doi.org/10.1016/j.anbehav.2017.11.004

Synes, N.W., Brown, C., Watts, K., White, S.M., Gilbert, M.A., Travis, J.M.J., 2016. Emerging Opportunities for Landscape Ecological Modelling. Curr. Landsc. Ecol. Rep. 1, 146–167. https://doi.org/10.1007/s40823-016-0016-7

Teague, R., Provenza, F.D., Kreuter, U., Steffens, T., Barnes, M., 2013. Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience? J. Environ. Manage. 128, 699–717. https://doi.org/10.1016/j.jenvman.2013.05.064

Turner, G.F., Pitcher, T.J., 1986. Attack Abatement: A Model for Group Protection by Combined Avoidance and Dilution. Am. Nat. 128, 228–240. https://doi.org/10.1086/284556

Turner, M.D., 2011. The New Pastoral Development Paradigm: Engaging the Realities of Property Institutions and Livestock Mobility in Dryland Africa. Soc. Nat. Resour. 24, 469–484. https://doi.org/10.1080/08941920903236291

Vanclay, F., 2004. Social principles for agricultural extension to assist in the promotion of natural resource management. Aust. J. Exp. Agric. 44, 213–222. https://doi.org/10.1071/ea02139

Villalba, J.J., Provenza, F.D., 2007. Self-medication and homeostatic behaviour in herbivores: learning about the benefits of nature's pharmacy. animal 1, 1360–1370. https://doi.org/10.1017/S1751731107000134

Villalba, J.J., Provenza, F.D., Catanese, F., Distel, R.A., 2015. Understanding and manipulating diet choice in grazing animals. Anim. Prod. Sci. 55, 261–271.

Walker, B.H., Janssen, M.A., 2002. Rangelands, pastoralists and governments: interlinked systems of people and nature. Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 357, 719–725. https://doi.org/10.1098/rstb.2001.0984

Walker, J.W., Heitschmidt, R.K., Dowhower, S.L., 1985. Evaluation of Pedometers for Measuring Distance Traveled by Cattle on Two Grazing Systems. J. Range Manag. 38, 90–93. https://doi.org/10.2307/3899343

WallisDeVries, M.F., Laca, E.A., Demment, M.W., 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. Appl. Anim. Behav. Sci. 60, 301–315. https://doi.org/10.1016/S0168-1591(98)00158-0

Wario, H.T., Roba, H.G., Kaufmann, B., 2015. Shaping the Herders' "Mental Maps": Participatory Mapping with Pastoralists' to Understand Their Grazing Area Differentiation and Characterization. Environ. Manage. 56, 721–737. https://doi.org/10.1007/s00267-015-0532-y

Warnock, M.J., 1995. A taxonomic conspectus of North American Delphinium. Phytologia 78, 73–101.

Welch, K.D., Cook, D., Green, B.T., Gardner, D.R., Pfister, J.A., McDaneld, T.G., Panter, K.E., 2015a. Adverse effects of larkspur (Delphinium spp.) on cattle. Agriculture 5, 456–474. https://doi.org/10.3390/agriculture5030456

Welch, K.D., Green, B.T., Gardner, D.R., Cook, D., Pfister, J.A., 2015b. The effect of administering multiple doses of tall larkspur (Delphinium barbeyi) to cattle. J. Anim. Sci. 93, 4181. https://doi.org/10.2527/jas.2015-9101

Whitman, W., 1897. Song of Myself, in: Leaves of Grass. G. P. Putnam's Sons, Boston, MA.

Wilensky, U., 1999. Netlogo 6.01. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Wilmer, H., Fernandez-Gimenez, M.E., 2015. Rethinking rancher decision-making: a grounded theory of ranching approaches to drought and succession management. Rangel. J. 37, 517. https://doi.org/10.1071/RJ15017

Wilson, E.O., 1999. Consilience: The Unity of Knowledge. Vintage Books.

Wilson, G.A., 2001. From productivism to post-productivism … and back again? Exploring the (un)changed natural and mental landscapes of European agriculture. Trans. Inst. Br. Geogr. 26, 77–102. https://doi.org/10.1111/1475-5661.00007

With, K.A., King, A.W., 1997. The Use and Misuse of Neutral Landscape Models in Ecology. Oikos 79, 219–229. https://doi.org/10.2307/3546007

Woodroffe, R., Frank, L.G., 2005. Lethal control of African lions (Panthera leo): local and regional population impacts. Anim. Conserv. 8, 91–98. https://doi.org/10.1017/S1367943004001829