An agent-based model of cattle grazing toxic Geyer's larkspur

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Abstract

By killing cattle and otherwise complicating management, the many species of larkspur (*Delphinium* spp.) present a serious, intractable, and complex challenge to livestock grazing management in the western United States. 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, as the risk of dead animals is too great. Agent-based models (ABMs) provide an effective method of realistically 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. Here, we introduce a spatially-explicit, behavior-based ABM of cattle grazing in a pasture with a dangerous amount of Geyer's larkspur (*D. geyeri*). This model indicates that herd cohesion and stocking density are key drivers of larkspur-induced toxicosis, and 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 a key driver of lethal acute toxicosis. As the first ABM to simulate grazing cattle at realistic scales, this model also demonstrates the tremendous potential of ABMs to address grazing management questions, including fundamental aspects of livestock behavior amidst heterogeneity.

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 [1–3]. 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 [3,4]. 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 grazing management goals [1,4].

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, as the risk of dead animals is too great. Additionally, 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 [5,6]. 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 [7]. They differ from other 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 [8]. ABMs are thus particularly useful in modeling complex systems, where the results of the interactions among system elements are not easily predicted or understood [9,10]. 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 [9,11,12].

As noted by Dumont and Hill [11], 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., 13–18]

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 [3,4,19–22]. Some papers have suggested that cattle behavior, influenced by management, can play a role in mitigating larkspur deaths [23,24], 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 at higher stocking density [25].

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* Green), in which MSAL-type alkaloids are the dominant toxin [26,27]. This model provides significant management-relevant insight for producers dealing with larkspur and demonstrates the great potential of ABMs to address questions in livestock grazing management, including not only other discrete challenges but also fundamental aspects of livestock behavior amidst heterogeneity.

Methods

The model description follows the updated Overview, Design Concepts, and Details (ODD) protocol, an accepted method for standardizing published descriptions of ABMs [28].

Purpose

We designed this model to test the effect of covarying instantaneous stocking density [29] and herd cohesion [also known as troop length, 28] on the likelihood of bovine alkaloid toxicosis

caused by *D. geyeri*. We developed and executed the model in NetLogo 6.01, using the BehaviorSpace tool to implement simulations [31].

Basic principles

Behavior-based encoding of cattle activities was the guiding principle of model design. As noted by Mclane et al. [7], "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 best estimates of cattle behavior from our years as livestock researchers and managers. The behavior-based approach also found expression in model validation, when one mode of validation was whether the cows in the model "act like cows". This was achieved through a lengthy process of visual debugging [32].

A second core principle was parsimony. Because this is the first ABM that we know of to incorporate cattle at the individual scale of interaction with the landscape (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 are 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.

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 (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 [33,34]. 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 [35].

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 [36] 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 [37]. 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%) [16,38,39]. Functionally relevant state variables for patches and cows, as well as global variables and inputs, are described in Table 1.

Table 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
	herdmates	Agent-set consisting of nearest 20 cows
	mean-herd-distance	Mean distance to herdmates
	consumption-level	Total amount of forage consumed during model run (g)
	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
	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})

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) [13]. 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 [40]. Total model run time is measured in animal-unit-months (AUMs) [41].

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 (1-10 ha) to a new site.

Thus, there are four programmed spatial scales (additional scales may emerge) 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, 165 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 [13].

Process overview and scheduling

Fig 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.

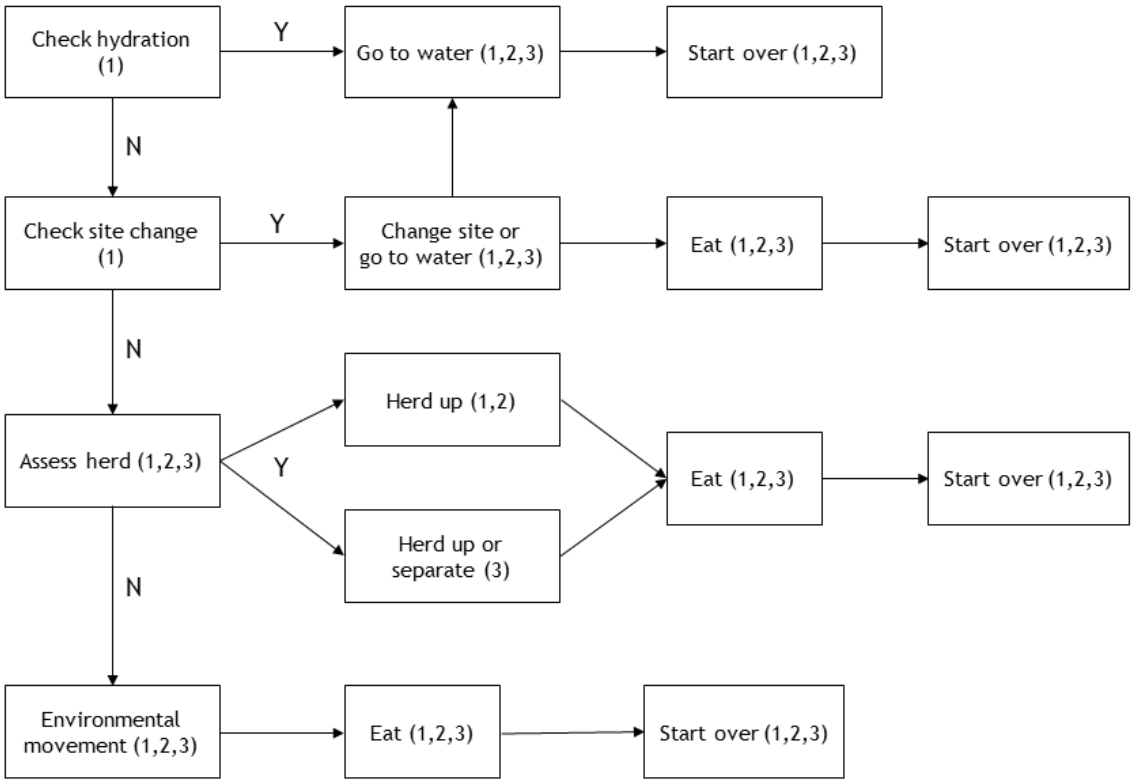


Figure 1. Pseudo-coded flow chart of model processes, with role of cows executing each process in parentheses. 1= leader, 2=follower, 3= independent.

Check hydration

Each leader cow checks it hydration level, which is tied to forage consumption such that it depletes to zero twice per day. 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.

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 tolerance – 1. This ensures that the herd is intolerant of remaining near a waterer if the area has been grazed already, and encourages a site change after drinking water. A global variable ensures that no other processes occur during a tick when watering occurs.

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 than the pasture as a whole (defined as >0.5 • mean times-grazed of all patches + 1.2), 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 they instead initiate the go-to-water procedure. We arrived at the threshold formula for increasing the value of ready-to-go by using visual debugging and validation related to site change frequency, as well as theory on the optimization of grazing effort [13,42].

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 (HCF) 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.

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.

Assess herd

This procedure begins the "normal" behavior portion of the model. In combination with the environmental-movement procedure, it represents >99% of cow actions in the model. Each cow

first sets its herdmates as the nearest 20 other cows [43]. 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 [14]. 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.

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. 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.

Eat

The eat procedure is the core interaction between the cows and the forage 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 [15,18]. 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 at the same level as the rest of the forage, and MSAL-intake values are increased. The corresponding patch values are decreased to account for consumption. Lastly, times-grazed in the patch is increased by one.

Design concepts

Emergence

Because the actions of the cows are encoded via simple behavior-based processes, nearly all model results can be considered emergent properties. These include the stochastic distribution of the herd and subherds, forage consumption, larkspur consumption, grazing pressure and patterns, and site changes [44].

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 [14]. 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.

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.

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 are highly stochastic, as most model processes involve a degree of randomization.

Observation

Of primary importance are data related to forage intake and different levels of daily and two-day MSAL alkaloid consumption, corresponding to dose-response studies in the literature [45]. 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 risk of death [45]. To measure the number of such cases, the model tracked the number of cows that received a dose of ≥ 8 mg • kg^{-1} of body weight over the course of one to two days [45].

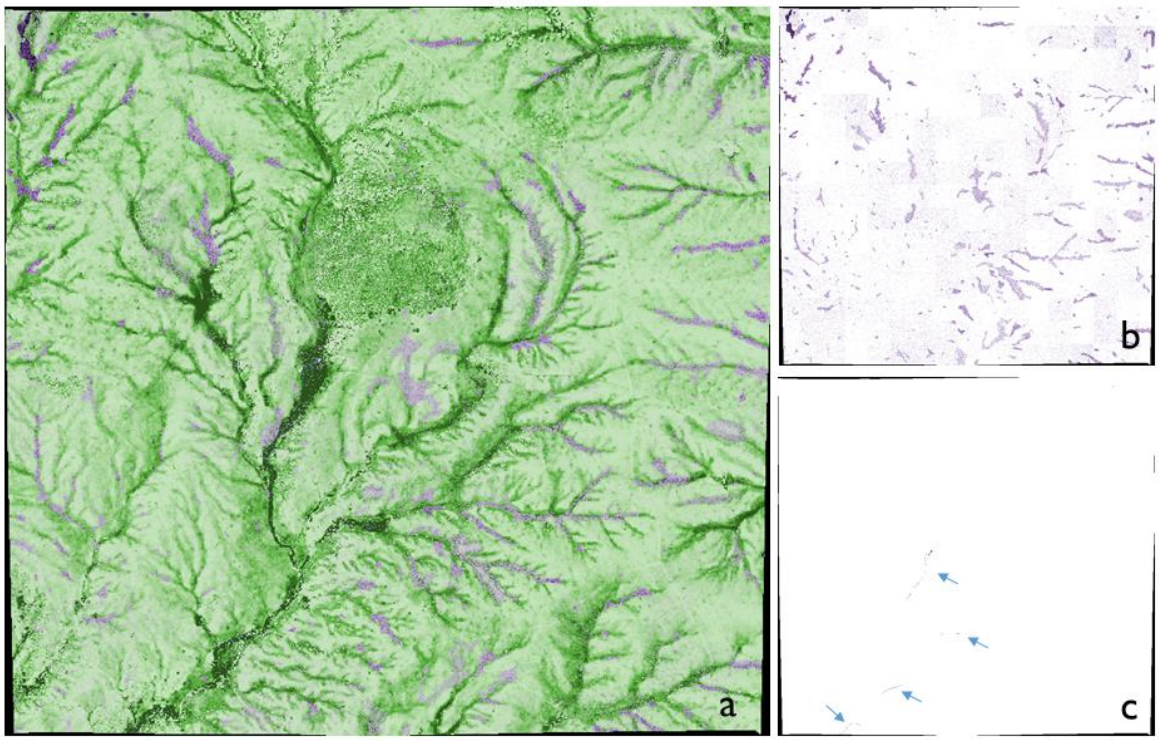
We were also interested whether the reduction in cases of acute toxicosis generated by increasing stocking density and, especially, herd cohesion, was mirrored by corresponding changes in the number of animals experiencing sub-lethal acute toxicosis. Specifically, we looked at two levels: instances where a cow consumed $\geq$4 mg • kg^{-1} and <8 mg • kg^{-1} or $\geq$2 mg • kg^{-1} and <4 mg • kg^{-1} of toxic alkaloids in one to two days. In the first case, while this level of consumption is unlikely to cause death, we can still consider this a "danger zone". We can consider the latter case to be a relatively safe outcome with a strong likelihood of "no observable adverse effect" and thus the "safe zone" [3,45].

A final statistical observation of interest was the distribution of individual overall total and maximum daily alkaloid intake. If cattle are going to consume larkspur with the aim of keeping consumption at sub-lethal levels, it is important to determine if it is possible to decrease the variance of alkaloid consumption through management. Lastly, the model also reported various validation data such as the count of site changes and travel distance per day.

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 waterer location layer. All other patch variables are derived from these inputs. Figs 2a-c shows the initialized landscape.



Figures 2a-c. Initialized full model landscape, with darker green indicating areas with greater aboveground forage biomass (a). Landscape with larkspur locations only, with darker purple representing higher MSAL-content and with results of hybrid sampling method evident (b). Landscape with watering locations only, pointed out by arrows (c).

The final step in model initialization is to create the cows by using the input of SD 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.

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 middle 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 highly desirable time for grazing [1,4,46]. Input value for kgs-per-hectare was 500 kg, based on current ranch usage and typical values for the area.

Statistical analysis

We used both JMP Pro 13.0.0 and R statistical software, version 3.3.3 for analysis [47,48]. To analyze count data from the model, we used a Generalized Linear Model (GLM) with a negative binomial distribution and a log-link function using the MASS package in R [49,50]. To confirm that the negative binomial distribution was the correct choice, we compared each to a GLM with a Poisson distribution and a log-link function. In all cases, the GLM with the negative binomial distribution was far superior, using residual deviance and Aikaike's information criterion (AIC) as judgment criteria [51].

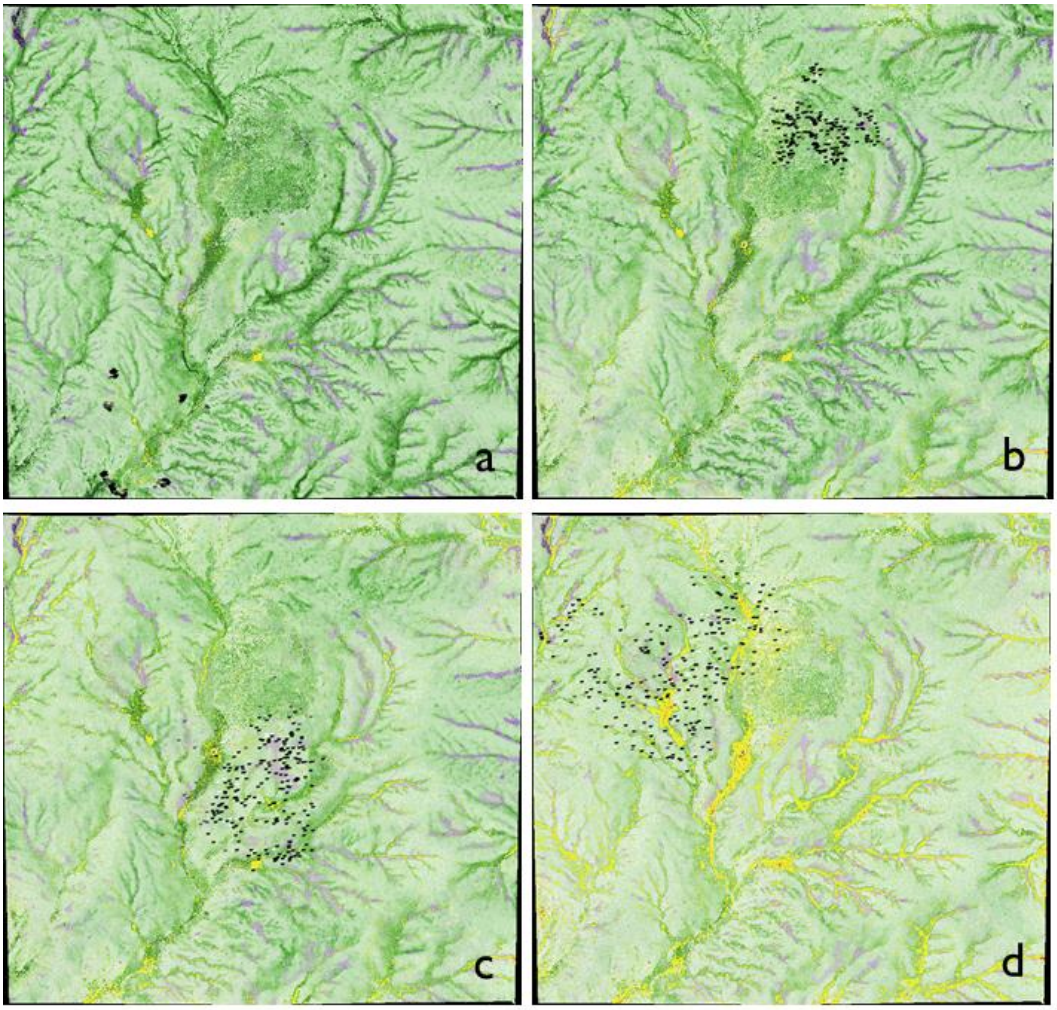
We further analyzed the count data using combinations of HCF and SD as "treatments" with a non-parametric Games-Howell test for multiple comparison of means (R package

307 userfriendlyscience), which is robust to unequal variances [52]. For data on total and maximum daily
308 alkaloid intake, we used multiple linear regression (R base package) and a Tukey HSD test (JMP) for
309 comparison of "treatments" [52].

310 Results

311 Model function and validation

312 While a complete detailing of ABM function and validation for overall grazing behavior is
313 beyond the scope of this paper, it is nonetheless important to demonstrate that the modeled cows
314 "act like cows" insofar as larkspur consumption is concerned, and that their effect on the landscape
315 was plausibly that of real cows. Toward this end, we offer Figs 3a-d to illustrate how varying HCF
316 influences herding patterns, and to show how grazing was distributed across the pasture in one
317 model run.
318



Figures 3a-d. The effect of varying herd-cohesion-factor (HCF) on herd patterns, and an example of grazing impact distribution. 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. 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) as currently managed is 165 AUMs.

Decreasing HCF increases overall herd separation and leads to more wandering among the independent cows and others. Note that in Fig 3a the cows have formed distinct independent 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 proximity to the water, and gradually extend their impact outward. By the end of the grazing cycle (Fig 3d), they have visited the entire pasture, though areas further from water have been grazed less. Areas of initial

333 high forage mass have been grazed two or more times, while many areas of low forage mass have
334 not been grazed at all. These results are in line with well-established understanding of grazing
335 patterns in large pastures [41].

336 The mean value for site changes per day for the 16 different combinations of HCF and SD
337 varies from 2.5 for few cows grazing very loosely (HCF=1, SD=0.25) to 6.9 for many cows grazing
338 very cohesively (HCF=10, SD=2.0). These values are in line with the estimate of 1-4 hours per
339 "feeding site" by Bailey and Provenza [13]. For runs with few cows grazing with little cohesion
340 (HCF=1, SD=0.25), mean daily travel was 4.44 km, while many cows grazing very cohesively
341 (HCF=10, SD=2.0) traveled an average of 8.06 km per day. These numbers and the positive trend
342 also track well with data from previous studies [e.g., 53].

343 As a last point of model validation, we were interested to see if the number of modeled cases
344 of larkspur-induced lethal acute toxicosis would parallel numbers from the literature when we
345 modeled grazing to be similar to the current management scheme. When modeled to reflect current
346 management practices, with HCF=4, SD=0.5, and for 165 AUMs (removing approximately 45% of
347 available forage), we recorded a mean of 5.2 cases of lethal acute toxicosis across 30 model
348 iterations. This amounts to 4.0% of cows, which falls within the estimate in the literature of losses of
349 2-5% in pastures with dangerous amounts of larkspur [4,54].

350 Lethal acute toxicosis

351 The coefficient for HCF (Table 2), as a log odds ratio, indicates that an increase of 1 in HCF
352 resulted in an 19.0% decrease in occurrences of lethal acute toxicosis. The coefficient for SD
353 indicates that an increase of 1 in SD resulted in a 52.3% decrease. Lastly, the coefficient for the
354 interaction of HCF with SD indicates that an increase in either HCF or SD increases the effect of
355 the other.

Table 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=519.7 on 476 degrees of freedom; AIC=2086.3.

Coefficient	Estimate	Std. error	p-value	β
Intercept	3.161	0.142	<0.001	
HCF	-0.211	0.025	<0.001	-0.162
SD	-0.74	0.137	<0.001	-0.127
HCF:SD	0.086	0.029	0.003	

Because our goal is to provide management-relevant insight, we compared the 16 combinations of HCF and SD as treatments, which present a clearer parallel to grazing management practices. Fig 4 shows box plots of the distributions for the 16 combinations of HCF and SD, and Table 3 shows the results of a post-hoc multiple comparisons of means using a Games-Howell test.

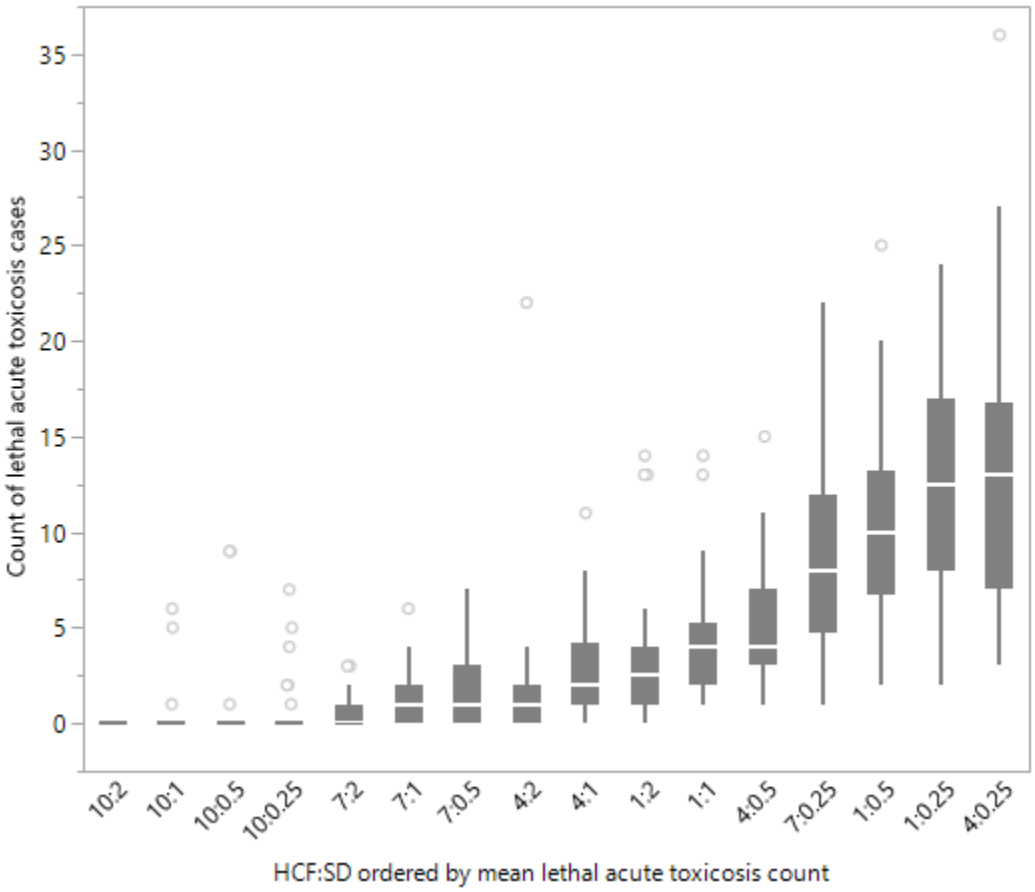


Figure 4. Box plots of distribution of counts of lethal acute toxicosis (≥ 8 mg • kg^{-1} in 1-2 days) cases from 30 model runs for each combination of herd-cohesion factor (HCF) and stocking-density (SD), ordered by mean count of lethal acute toxicosis cases, with outliers as jittered circles.

Table 3. Connected letters table for the results of multiple comparisons of means using a Games-Howell test for mean count of lethal acute toxicosis (LAT) by herd-cohesion-factor (HCF) and stocking-density (SD). Levels not connected by the same letter are significantly different at α=0.05.

HCF:SD								Mean ct. of LAT
4:0.25	A							13.20
1:0.25	A							12.77
1:0.5	A							10.23
7:0.25	A	B						9.00
4:0.5		B	C					5.20
1:1			C					4.37
4:1			C	D				3.07
1:2			C	D	E			3.70
4:2*			C	D	E	F	G	1.90
7:0.5				D	E	F		1.73
7:1					E	F		1.13
7:2						F		0.70
10:0.25						F	G	0.70
10:0.5						F	G	0.63
10:1						F	G	0.40
10:2							G	0.00

*Single large outlier with otherwise tight distribution makes 4:2 difficult to interpret. See Fig 4.

Sub-lethal acute toxicosis

The coefficient for HCF (Table 4) indicates that an increase of 1 in HCF resulted in a 4.8% decrease in occurrences of sub-lethal acute toxicosis in the danger zone. The coefficient for SD indicates that an increase of 1 in SD resulted in a 12.2% decrease. The coefficient for the interaction of HCF with SD indicates an interaction such that an increase in either HCF or SD slightly increases the effect of the other. Table 5 shows the result of the post-hoc means comparison of occurrences of sub-lethal acute toxicosis in the danger zone for the 16 combinations of HCF and SD.

Table 4. Results of GLM with negative binomial distribution and log-link function for count of sub-lethal acute toxicosis in the danger zone (≥4 mg • kg^{-1} and <8 mg • kg^{-1} in 1-2 days) 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=499.7 on 476 degrees of freedom; AIC=5127.9.

Coefficient	Estimate	Std. error	p-value	β
Intercept	6.036	0.029	<0.001	
HCF	-0.05	0.004	<0.001	$-2.88 \cdot 10^{-3}$

SD	-0.13	0.025	<0.001	$-1.95 \cdot 10^{-3}$
HCF:SD	-0.017	0.004	<0.001	

Table 5. Connected letters table of the results of post-hoc multiple comparisons of means using a Games-Howell test for mean counts of sub-lethal acute toxicosis (SLAT) in the danger zone (≥4 mg • kg^{-1} and <8 mg • kg^{-1} in 1-2 days) by herd-cohesion-factor (HCF) and stocking-density (SD). Levels not connected by the same letter are significantly different at α=0.05.

HCF:SD													**Mean ct. of SLAT**
1:0.25	A												361.3
4:0.25	A	B											352.2
1:0.5		B	C										336.2
7:0.25		B	C	D									327.4
4:0.5			C	D	E								319.3
1:1				D	E	F							309.5
4:1					E	F	G						293.9
7:0.5						F	G	H					289.5
1:2							G	H					275.3
7:1								H	I				258.4
4:2									I	J			241.7
10:0.25									I	J	K		220.9
7:2										J	K		215.3
10:0.5											K	L	184.1
10:1												L	165.1
10:2												M	122.0

The coefficient for HCF (Table 6) indicates that an increase of 1 in HCF resulted in an 3.3% increase in occurrences of sub-lethal acute toxicosis in the safe zone. The coefficient for SD indicates that an increase of 1 in SD resulted in a 1.5% decrease. Table 7 shows the result of the post-hoc means comparison of occurrences of sub-lethal acute toxicosis in the safe zone for the 16 combinations of HCF and SD.

Table 6. Results of GLM with negative binomial distribution and log-link function for count of sub-lethal acute toxicosis in the safe zone (≥2 mg • kg^{-1} and <4 mg • kg^{-1} in 1-2 days) as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). As there was very little interaction between the terms, the results shown are for the GLM without the interaction. GLM fit: Fisher scoring iterations=1; residual deviance=478.2 on 476 degrees of freedom; AIC=5947.4.

Coefficient	**Estimate**	**Std. error**	**p-value**	**β**
Intercept	7.28	0.007	<0.001	

HCF	0.033	0.005	<0.001	-4.29•10-5
SD	-0.015	0.001	<0.001	-4.64•10-4

Table 7. Connected letters table of the results of post-hoc multiple comparisons of means using a Games-Howell test for mean counts of sub-lethal acute toxicosis (SLAT) in the safe zone (≥2 mg • kg^{-1} and <4 mg • kg^{-1} in 1-2 days) by herd-cohesion-factor (HCF) and stocking-density (SD). Levels not connected by the same letter are significantly different at α=0.05.

HCF:SD									**Mean ct. of SLAT**
10:1	A								2164.5
10:0.5	A								2145.7
10:0.25	A								2133.0
10:2		B							1988.8
7:0.5			C						1828.6
7:1			C	D					1804.4
7:0.25				D	E				1725.0
7:2					E	F			1690.8
4:1					E	F	G		1661.5
4:2					E	F	G		1654.2
4:0.5						F	G		1643.4
4:0.25						F	G	H	1618.4
1:1							G	H	I	1590.3
1:0.5								H	I	1560.2
1:0.25									I	1545.6
1:2									I	1542.5

Distribution of total and maximum alkaloid consumption

While there were some indications of heteroscedasticity and outliers for both models, we determined that linear regression was robust to those errors in this case. We confirmed this by also fitting alternate models within other regression frameworks (robust and non-parametric), which returned very similar results. Because interaction between HCF and SD was weak in both cases, we left this term out of both models. Tables 8-11 show the results of multiple linear regression and the post-hoc means comparison of the standard deviation of total MSAL alkaloid consumption and maximum MSAL alkaloid consumption for the 16 combinations of HCF and SD.

Table 8. Results of multiple linear regression for the standard deviation of mean total MSAL alkaloid consumption as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). Adj. R^2=0.79.

Coefficient	Estimate	Std. error	p-value	β
Intercept	1989.548	34.578	<0.001	
HCF	-76.907	4.339	<0.001	-0.372
SD	-834.55	21.713	<0.001	-0.807

Table 9. Connected letters table of the results of post-hoc multiple comparisons of means using a Tukey HSD test for the mean standard deviation (σ) of total MSAL alkaloid consumption (mg) by herd-cohesion-factor (HCF) and stocking-density (SD). Levels not connected by the same letter are significantly different at α=0.05.

HCF:SD											Mean σ tot. alk. cons.
1:0.25	A										3034.5
4:0.25		B									2834.0
7:0.25			C								2451.8
1:0.5				D							2119.3
4:0.5				D							2001.2
7:0.5					E						1761.2
10:0.25					E						1742.9
1:1						F					1467.4
4:1						F	G				1409.1
10:0.5						F	G				1397.2
7:1							G				1290.3
1:2								H			1015.3
10:1								H			1015.2
4:2								H	I		973.5
7:2									I		889.5
10:2										J	680.0

Table 10. Results of multiple linear regression for the standard deviation of maximum daily alkaloid consumption as predicted by herd-cohesion-factor (HCF) and stocking-density (SD). Adj. R^2=0.55.

Coefficient	Estimate	Std. error	p-value	β
Intercept	401.441	9.82	<0.001	
HCF	-25.042	1.232	<0.001	-0.621
SD	-82.856	6.167	<0.001	-0.411

Table 11. Connected letters table of the results of post-hoc multiple comparisons of means using a Tukey HSD test for the mean standard deviation (σ) of maximum daily MSAL alkaloid consumption (mg) by herd-cohesion-factor (HCF) and stocking-density (SD). Levels not connected by the same letter are significantly different at α=0.05.

HCF:SD					Mean σ max. daily alk. cons.
1:0.25	A				646.6
4:0.25	A	B			621.6
7:0.25	A	B			607.2
1:0.5		B	C		575.8
4:0.5			C	D	538.2

1:1	C	D	E						509.9
4:1		D	E	F					475.2
1:2			E	F					468.7
7:0.5			E	F					462.3
4:2				F	G				423.2
7:1				F	G	H			414.2
7:2					G	H	I		375.2
10:0.5						H	I		346.6
10:1							I	J	330.5
10:0.25							I	J	311.2
10:2								J	277.4

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, 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 [3,4,21]. 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.

The alternative to "fight or flight", of course, is to manage grazing such that intake remains below the threshold where there is an observable negative effect on the cattle. This study provides the first answers to the question of whether this may be possible, and under which circumstances. For the first time, this model suggests that herd cohesion and stocking density are key drivers of toxicosis, and that management decisions that influence these factors hold potential to limit the risk of death. Of crucial importance is the observation that herd cohesion, which has received almost no

consideration in the broader grazing management literature, may be the most important determinant of risk of death.

Lethal acute toxicosis

We observed significant differences in the count of cases of lethal acute toxicosis. The simplest interpretation is that management that results in few cows grazing very loosely is much more dangerous to cattle than management that results in many cows grazing very cohesively. However, the model results point to more nuance than that. The standardized coefficients (Table 2) indicate that herd cohesion is 28% more influential than stocking density, and we can see that influence in the ordering of Table 3. These results suggest that, regardless of stocking density, cattle that graze very cohesively (especially subherds with mean inter-animal distance ≤ 10 m) significantly lower the risk of death caused by *D. geyeri*. A combination of highly cohesive herd behavior with high stocking density (2.0 animal units per ha) eliminated lethal acute toxicosis.

Sub-lethal acute toxicosis

Because we seek to manage cattle to consume larkspur without dying, the results for sub-lethal acute toxicosis are also of interest. For sub-lethal acute toxicosis in the danger zone, similar ordering between Tables 4 and 3 suggests similar management lessons to those of the lethal acute toxicosis analysis. The GLM coefficients confirm this, with the standardized coefficients indicating that herd cohesion is 48% more influential than stocking density in this case. In short, if we aim to limit alkaloid consumption that approaches lethality, once again highly cohesive herds grazing at high stocking density is our best approach. Note, however, that elimination of sub-lethal acute toxicosis in the danger zone may not be possible when there are high levels of toxic Geyer's larkspur.

Herd cohesion and stocking density have opposite effects on the number of cases of sub-lethal acute toxicosis, unlike the previous two cases. This means that increased herd cohesion actually increases the number of safe zone cases, while increased stocking density still lowers them, with herd cohesion exerting an 8% stronger influence. This points to the dilution effect of increased stocking density interacting with the smoothing effect of herd cohesion on the distribution of consumption, which we explore further in the next section.

Distribution of total and maximum alkaloid consumption

Table 8 makes apparent that stocking density, which is strongly correlated with total alkaloid consumption, also exerts a strong influence on its distribution, with 217% of the influence of herd cohesion. This means that increased stocking density not only limits total alkaloid consumption through dilution, but also, in combination with herd cohesion, plays a strong role in limiting the likelihood of extreme total consumption for individual cows.

That the ordering of Tables 3, 5, and 11 are similar should not come as a surprise. Tables 10 and 11 tell us that herd cohesion and stocking density work together to narrow the distribution of maximum daily alkaloid consumption, which represents each cow's worst day in a given model run, with herd cohesion exerting 51% more influence than stocking density. This is the key to preventing risky levels of alkaloid consumption—keep the distribution of maximum daily consumption evenly distributed, avoiding outliers.

Parsimony and study limitations

Perhaps the most obvious omissions from our model are individual cattle preference and stochastic consumption of larkspur. A growing body of evidence indicates that individuals do develop preferences, and past anecdotes have suggested that cattle may engage in brief but intense bouts of larkspur consumption [55,56]. Why not, then, include these factors? First, because past

evidence of bouts of larkspur consumption is entirely anecdotal, there are no data to use to parameterize consumption. It is not even clear if this really occurs, or if the anecdotes are due to selective observation.

Second, we are comfortable with preference and stochastic consumption remaining below the minimum scale of the model. That this is the case is not a reason to discount the ability of the model to address the question of larkspur consumption. Indeed, it is reasonable to understand the model as though behaviors such as preference and diet mixing are happening. Because there is heterogeneity in the distribution of forage and larkspur, and heterogeneity and stochasticity in the cows' consumption, within the context of larkspur consumption we believe these behaviors are sufficiently realized.

Aside from behaviors and environmental factors occurring below 1 m^2, the model also excludes 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. Despite our decision to exclude these behaviors, it is important to note that they could be incorporated if they become relevant.

The model also excludes plant regrowth. For 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. Regrowth of non-larkspur forage would also serve to lessen the risk of larkspur-induced toxicosis.

Most important are the limitations to making direct management-relevant conclusions from the model results. While we are confident that the fundamental conclusion that increased herd cohesion and stocking density lower the risk of larkspur-induced death, the exact values for when that 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 of course also essential that every manager interpret these conclusions in context.

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 [41]. This is likely due to the relative ease of varying stocking rate versus manipulating cattle behavior. Because this study provides evidence that it is not only the number of animals but perhaps more importantly how they behave that affects the likelihood of death by larkspur, we are interested in what other challenges this finding might apply to. The emerging promise of affordable GPS tags means that we may also start to be able to test this through direct observation of entire herds, which can be used to validate and improve grazing ABMs [58].

We are also excited to explore the emergent property of distinct persistent subherds that appears to emerge when the desired mean inter-animal distance of the cows is < 20 m. If this desire is either genetically encoded or management-determined (or both), and this subherd behavior is important to reducing the risk of death by larkspur, how might it affect other negative outcomes, such as overgrazing of riparian areas or exposure to predation by carnivores [59]?

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 [58] and "virtual fencing" [60], along with the increasing power of desktop computers, suggests that the time is right for a modeling revolution in livestock grazing management. We are excited that this study provides a first example of the potential of ABMs to contribute to this revolution.

Management implications

535 The model results indicate that it may be possible to limit or eliminate the risk of fatal
536 poisoning of cattle by Geyer's larkspur by increasing herd cohesion and/or stocking density. This
537 provides context for the anecdotal report of Smith et al. [25] for the Sims Ranch in McFadden, WY,
538 where it was found that an increase in stocking density all but eliminated deaths due to *D. geyeri*.
539 However, an important caveat is that it is of utmost important that manager's understand their level
540 of risk, which we suggest is best represented by the total alkaloid pool of a pasture. Though we have
541 modeled a pasture that ranks among the densest (overall, 0.17 plants • m^{-2}) and most toxic
542 populations of *D. geyeri* that we have seen, it could be worse elsewhere.

543 We selected the bounds of herd cohesion and stocking density to align with what we believe
544 to be realistically achievable by managers in the western US. While stocking density is easily
545 understood, it may be worthwhile to describe how we think the various levels of herd cohesion
546 could be achieved (reference Fig 3). We think of HCF values of 1 and 4 as representative of most
547 current extensive management, such that there is a small to moderate amount of herding behavior
548 but in which animals are often spread out across a large area. The difference between these two
549 might be accounted for by differences in breeding history, carnivore pressure, or genetic drift. To
550 achieve an HCF of 7, we think cattle would need to be selected for strong herding instinct or be
551 actively, but not necessarily continually, herded. An HCF of 10 is comparable to many herds of wild
552 ungulates, and may be achievable through the continual presence of a herder or a sustained effort at
553 selecting for herding behavior.

554 It is worth noting that dangerous levels of *D. geyeri* are typically found on a limited number
555 of a single operation's grazing units. This means that the inclusion of active herding, for example,
556 would usually only be necessary for a relatively brief period. In addition, it means that any potential
557 secondary effects of sub-lethal larkspur consumption, such as appetite suppression (whether and
558 how this would occur is unclear) would be of similarly limited duration.

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 [60].

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. Those with low amounts of Geyer's larkspur and 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) and a history of losses should be more careful. As researchers, 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.

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