

1 **Running head:** Predatory plants and patchy cows

2 **Title:** Predatory plants and patchy cows: modeling cattle interactions with toxic larkspur amid

3 variable heterogeneity

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8 **Abstract**

9 The most common explanations for the evolution and persistence of herd behavior in large
10 herbivores relate to decreased risk of predation. However, poisonous plants such as larkspur
11 (*Delphinium* spp.) can present a threat comparable to predation. In the western United States,
12 larkspur diminishes the economic and ecological sustainability of cattle production by killing
13 valuable animals and restricting management options. Recommendations for mitigating losses
14 have long focused on seasonal avoidance of pastures with larkspur, despite little evidence that
15 this is practical or effective. Our ongoing research points to the cattle herd itself as the potential
16 solution to this seemingly intractable challenge and suggests that larkspur and forage patchiness
17 may drive deaths. In this paper, we present an agent-based model that incorporates neutral
18 landscape models to assess the interaction between plant patchiness and herd behavior within the
19 context of poisonous plants as predator and cattle as prey. The simulation results indicate that
20 larkspur patchiness is indeed a driver of toxicosis and that highly cohesive herds can greatly
21 reduce the risk of death in even the most dangerous circumstances. By placing the results in
22 context with existing theories about the utility of herds, we demonstrate that grouping in large
23 herbivores can be an adaptive response to patchily distributed poisonous plants. Lastly, our
24 results hold significant management-relevant insight, both for cattle producers managing grazing
25 in larkspur habitat and in general as a call to reconsider the manifold benefits of herd behavior
26 among domestic herbivores.

27 **Keywords:** Grazing; agent-based modeling; behavioral ecology; landscape ecology; poisonous
28 plants; larkspur; cattle; herd behavior

29 **Introduction**

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

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

49 While our findings in Jablonski et al. (2018) were relevant to grazing management within the
50 habitat of a particular larkspur species (*Delphinium geyeri* Green), the results also pointed
51 towards interesting relationships between plant patchiness, herd behavior, and toxicosis that we

52 explore further here. Specifically, we used modeling to test two general hypotheses, that: (1)
53 larkspur patchiness drives alkaloid toxicosis deaths, and (2) overlap between larkspur and
54 desirable forage drives alkaloid toxicosis deaths. We explore both hypotheses within the context
55 of variations in herd cohesion, using data from *D. geyeri*, wherein *N*-(methylsuccinimido)-
56 anthranoyllycoctonine (MSAL) type alkaloids are the dominant toxin (Panter et al. 2002).

57 *Neutral landscape models*

58 A test of the influence of larkspur patchiness and larkspur-forage overlap on toxicosis required a
59 model with variable landscapes, rather than the realistic but static landscape of Jablonski et al.
60 (2018). Specifically, this meant separating larkspur and forage distribution from one another and
61 varying patchiness while maintaining a realistic landscape with respect to cattle grazing. For this,
62 we used neutral landscape models, which are the most common landscape modelling approach
63 used in ecological studies, with frequent application to habitat fragmentation, animal movement
64 models, and metapopulation analysis (Gardner and Urban 2007, Synes et al. 2016). With a
65 primary aim of improving understanding of how ecological processes are affected by spatial
66 structure, neutral landscape models are ideal for testing the consequences of varying spatial
67 heterogeneity on foraging outcomes (With and King 1997). However, we are unaware of
68 previous application of neutral landscape models to cattle grazing dynamics.

69 *Behavioral ecology of herds*

70 Important context for this study comes from the literature on grouping in large herbivores, where
71 behavioral ecologists continue to debate the evolution and utility of herd behavior (e.g. Makin et
72 al. 2017, Ireland and Ruxton 2017, Stutz et al. 2018). The most widely studied explanations for
73 herd behavior relate to decreased risk of predation (Davies et al. 2012, Ebensperger and Hayes
74 2016). Of particular relevance to the cattle-larkspur interaction is what Krause and Ruxton

75 (2002) call dilution. Dilution refers to a $1/N$ effect whereby an attacking predator can only
76 capture a limited number of prey at a time and individual risk therefore declines with increasing
77 group size. Important considerations for the dilution effect are variation in the likelihood of
78 being attacked among individuals and the relative conspicuousness of larger versus smaller
79 groups (Krause and Ruxton 2002).

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

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

90 *Agent-based modeling*

91 Agent-based models are computational simulation tools that focus on bottom-up encoding of
92 individual "agent" behaviors as they interact with one another and the environment (Grimm
93 1999, McLane et al. 2011). Agent-based models are particularly useful in modeling complex
94 systems where the results of interactions between system elements are not easily predicted, and
95 thus useful for simulating the behavior of social herbivores foraging in a heterogeneous
96 environment (Dumont and Hill 2004, Grimm et al. 2005). Nevertheless, they have thus far been
97 little used in improving our understanding of livestock behavior and management.

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

104 **Methods**

105 *Overview*

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

115 Cows are classified as leaders (5% of herd), followers (85%), or independents (10%), with
116 leaders making decisions about broad-scale movements away from relatively over-grazed areas
117 (known as site changes) and independents being less tied to the herd than the other cows (Sato
118 1982, Harris et al. 2007). Other than seeking drinking water and making site changes, all cow
119 movements in the model are aimed at moving closer to herdmates and/or maximizing the amount

120 of forage in the next grazing location, depending on desired herd proximity. Consumption of
121 forage occurs in line with standard rates from the literature (Laca et al. 1994, WallisDeVries et
122 al. 1998). Forage and larkspur amounts decrease when eaten and do not regrow within the model
123 run, which is equivalent to 18 days.

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

128 *Purpose*

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

134 *Entities and state variables*

135 The model has two kinds of entities: pixels representing 1 m² of land and agents representing 500
136 kg adult cows (1.1 animal-units). Because computational demands would be higher with
137 additional covariates, and spatial extent was expected to be minimally influential, we shrank the
138 model landscape to ¼ the size of that of pasture 16 of the Colorado State University Research
139 Foundation Maxwell Ranch on which the model in Jablonski et al. (2018) was based. This
140 created a model landscape of 832 x 790 pixels (0.83 km x 0.79 km, equal to 65.73 ha), all of
141 which are accessible to the cows. Note that, for clarity, we will refer to each 1 m² land area as a
142 pixel, rather than as a patch, the typical nomenclature for agent-based models. We use “patch” in

143 the landscape ecology sense to refer to an area of habitat that is relatively discrete from its
144 surroundings in relation to some phenomenon of interest (Turner and Gardner 2015).

145 Stocking density was set at 1.0 animal-units \cdot ha⁻¹ throughout the simulation, totaling 59 cows.

146 Herd cohesion was determined using herd-distance-factor (HDF), in which increasing values

147 indicate greater inter-animal distance. All other state variables, including role, MSAL-tolerance,

148 and larkspur-attraction were assigned in the same way as Jablonski et al. (2018). All functionally

149 relevant state variables for pixels and cows, as well as global variables and inputs, are described

150 in Table 1.

151 Note that death occurs when an individual cow exceeds its assigned value for MSAL-tolerance at

152 the end of a grazing-day. However, the animal is not removed from the herd, but instead is

153 recorded as having died, has its MSAL-level set to zero, and continues in the model. This

154 preserves herd dynamics for the entire model run and makes it possible for total model-run

155 deaths to exceed 59.

156 *Process overview and scheduling*

157 Fig 1 illustrates the model execution process for each tick. Each cow moves through each step of

158 the process, but only performs those steps linked to its role. Only elements that have changed

159 from Jablonski et al. (2018) are described below, with explanation for the change.

160 Check hydration: This process is not found in Fig 1, as it was eliminated in favor of a single end-

161 of-grazing-day water visit by all cows. Because hydration was previously linked to forage

162 consumption, artificially high levels of forage heterogeneity necessitated a simplified water visit

163 routine. One visit per day achieves this without otherwise sacrificing realistic model function.

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

172 *Design concepts*

173 Stochasticity

174 Distinct from Jablonski et al. (2018), the environment was highly stochastic between different
175 levels of larkspur-patch-factor and larkspur-overlap factor and even within different iterations of
176 identical values for those factors.

177 *Initialization*

178 Input values for number of larkspur plants and forage mass within the modeled landscape were
179 derived from the measured values from pasture 16 (Jablonski et al. 2018). This provides an input
180 value of 107,500 total larkspur plants on the landscape. The model distributes these plants among
181 pixels according to a Poisson distribution with a mean of 2.5 larkspur plants per square-meter
182 pixel, resulting in 43,000 pixels with larkspur. This means that individual pixels with larkspur
183 are equally likely to be dangerous regardless of their spatial arrangement, an essential condition
184 for testing the effect of patchiness.

185 Landscape initialization within the model begins by using an input value for larkspur-patch-
186 factor (LPF) to randomly locate p larkspur patch origins, with $p = 43,000/10^{LPF}$, rounded up

187 to the nearest integer (i.e., $1 \leq p \leq 43,000$) At each larkspur patch origin, a modified random
188 walk is used to create realistic larkspur patch patterns. In this random walk, a temporary agent is
189 created that visits each patch origin location. After placing a random Poisson-distribution-
190 determined number of larkspur plants in the origin pixel, the agent then executes random turns
191 and one-pixel steps, placing larkspur plants whenever landing on a pixel with zero currently
192 present. This random walk proceeds in a given patch origin area until $43,000/p$ pixels have had
193 larkspur plants placed in them. The agent then proceeds to the next patch origin location,
194 following the same steps until all patch origin locations have been visited. Lastly, pixels are
195 assigned an MSAL-content value based on larkspur plant count and input values for mean-
196 larkspur-mass and MSAL-concentration.

197 Forage initialization begins with random placement of 80% of the total forage mass (100% being
198 equal to $\frac{1}{4}$ of the forage mass in pasture 16) across the landscape, according to a normal
199 distribution with a mean based on the input value for kgs-per-hectare. The remaining 20% is
200 assigned according to the input value for larkspur-forage-overlap-factor (LFOF). For LFOF=0,
201 all remaining forage is placed into forage patches (created using a similar random walk) that
202 occupy 5% of the total land area. These forage patches do not overlap with larkspur patches. For
203 LFOF=4, all remaining forage is placed within the larkspur patches and there are no forage
204 patches. Values from 1-3 place increasing amounts of forage within the larkspur patches and
205 decreasing amounts in the forage patches. We chose the values of 20% of forage in patches and
206 5% of land area in forage patches to approximate the forage heterogeneity found in pasture 16.
207 Instead of the seasonal stream watering locations found in pasture 16, the model places watering
208 points in each corner and in the center of the landscape to ensure limited effect of distance from
209 water (Bailey and Provenza 2008). Waterers are created as circular locations with a radius of 5

210 m. Finally, the model creates 59 cows ($1.0 \text{ AU} \cdot \text{ha}^{-1}$) and places them at the central watering
211 location. All other pixel values (Table 1) are derived from the various input values above.

212 *Simulation*

213 We used the BehaviorSpace tool in Netlogo to run a full factorial simulation using eight levels of
214 larkspur patchiness (LPF: 0, 1, 2, 3, 3.5, 4, 4.5, and 5), five levels of larkspur-forage overlap
215 (LFOF: 0, 1, 2, 3, and 4), and six levels of herd cohesion (HDF: 0.5, 1, 2, 4, 8, and 16). With 30
216 replications of these 240 combinations, we executed 7,200 total model runs. The computational
217 demands for this required creation and use of a virtual machine with 64 processors and 360 GB
218 of RAM in Google Compute Engine (Google, Inc. 2018).

219 Input mean-larkspur-mass was 3.5 g and MSAL-concentration was $3.0 \text{ mg} \cdot \text{g}^{-1}$, representative of
220 an excellent growing year with alkaloids at high levels. The input value for kgs-per-hectare was
221 $500 \text{ kg} \cdot \text{ha}^{-1}$. Individual model run duration was 18 grazing-days, resulting in consumption of
222 approximately 40% of available forage. All of these input values are based on our measurements
223 from the Maxwell Ranch.

224 *Observation*

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

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

235 *Statistical analysis*

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

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

245 **Results**

246 *Model output verification*

247 Because we have made only minor changes to grazing behavior in the model, we refer the reader
248 to Jablonski et al. (2018) for results and discussion of output verification as it relates to cows.
249 However, because landscape generation is greatly altered, we report landscape metrics in Table
250 2. Of the measured metrics, largest patch index and edge density were most strongly correlated
251 with LPF. Fig 2 shows example landscapes at different combinations of LPF and LFOF.

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

261 *Toxicosis mechanism*

262 In Jablonski et al. (2018) we identified the key mechanism for reducing larkspur deaths as
263 narrowing the variation in larkspur consumption among individuals in the herd, with associated
264 reduction in the count and extremity of outliers. As would be expected, deaths were once again
265 strongly linked to this mechanism, with model-run standard deviation of daily alkaloid intake
266 presenting a particularly striking pattern, wherein the likelihood and count of deaths increased
267 once the standard deviation exceeded a threshold of 500 mg (Fig 3). Overall, at least one death
268 occurred in 33.7% of model runs and on 6.2% of grazing-days.

269 *Larkspur patchiness and forage overlap*

270 Larkspur patchiness exerted a strong influence on intra-herd variation in alkaloid consumption
271 and thus deaths (Fig 4). Total deaths for different levels of LPF ranged from 0 (LPF=0, n=900
272 model runs) to 13,057 (LPF=5, n=900), with a threshold evident at LPF=3. An examination of
273 the relationships between landscape metrics and deaths using a global linear model and
274 comparison of AICc scores indicated that the model containing only largest patch index was best

275 (AICc=141.7). All other model combinations had Δ AICc values of at least 7.93, indicating all
276 were much less plausible models, given the data (Anderson 2008). The next best univariate
277 model contained only the intercept.

278 Deaths were distributed more evenly among the different levels of larkspur-forage overlap than
279 among the levels of larkspur patchiness, though there was a peak when there was desirable
280 forage both inside and outside of larkspur patches (LFOF=1-2). Total deaths (Table 3) ranged
281 from a minimum of 1,853 (LFOF=0, n=900) to a maximum of 7,230 (LFOF=1, n=900). Model-
282 run standard deviation of daily alkaloid intake largely mirrored deaths, while mean daily alkaloid
283 intake increased with increasing larkspur-forage overlap.

284 Additionally, there were distinctly different relationships among mean alkaloid intake and the
285 standard deviation of alkaloid intake at low, medium, and high LFOF. With zero larkspur-forage
286 overlap, an increase in alkaloid intake within a model run usually led to increased variation in
287 intake among the herd, leading to increased deaths (Fig 5). When there was high overlap
288 between forage and larkspur, increases in alkaloid consumption within the herd usually led to
289 decreased standard deviation, reducing deaths. At moderate levels (LFOF=1-2), this relationship
290 was more muddled. Each of these effects was modified by larkspur patchiness in a complex
291 interplay illustrated by Fig 5.

292 *Herd cohesion*

293 Inter-animal distance was an important factor in alkaloid toxicosis deaths. Regardless of larkspur
294 patchiness and larkspur-forage overlap, just 14.4% of model runs at the minimum herd distance
295 level (HDF=0.5) had at least one death, while 56.3% of model runs resulted in at least one death
296 at the maximum herd distance level (HDF=16). Overall, mean deaths per model run ranged from
297 0.72 at HDF=0.5 to 8.67 at HDF=16.

298 The relationship between patchiness, overlap, and herd behavior becomes clearer when larkspur
299 patchiness, larkspur-forage-overlap, and herd distance are used to plot standard deviation of
300 alkaloid consumption and total deaths (Fig 6). Increases in herd distance consistently generated
301 increases in variation in alkaloid consumption, with the magnitude modified by larkspur
302 patchiness and larkspur-forage overlap. However, deaths did not begin to occur until standard
303 deviation approached the threshold of 500 mg, with this being reached at different levels
304 depending on herd cohesiveness and plant patchiness. This means that the degree of herd
305 cohesiveness necessary to prevent deaths was determined by the patchiness of the threat.

306 *1/N and encounter dilution*

307 The relationship of “plant predators” to the 1/N concept of predation risk reduction in herds is
308 best understood at LPF=5 and LFOF=4, where there was one large and dangerous patch that
309 overlapped with highly desirable forage, meaning that encounter was inevitable. If we restrict the
310 analysis to only those days when at least one cow consumed larkspur, we can see the distribution
311 of risk when encounter occurred (Fig 7).

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

318 Encounter dilution, where cohesive herds avoid detection by predators with limited capacity to
319 find them, is best understood at LPF=5 and LFOF=0. In this circumstance, a single larkspur
320 patch is undesirable for foraging but a serious threat to cows that nevertheless encounter it. Table

321 4 shows rates of larkspur encounter and death among different levels of HDF under these
322 conditions. For herds grazing at HDF=0.5, 38.2% of grazing-days passed without a single animal
323 encountering larkspur. On the other hand, herds grazing at HDF=16 managed to entirely avoid
324 larkspur on just 9.4% of grazing-days. This contributed to substantially different rates of death
325 occurrence.

326 **Discussion**

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

337 Rarest of all has been research seeking to understand how plant patchiness influences group
338 behaviors and outcomes in livestock (though note the significant body of research on “grazing
339 lawns” that at times includes reciprocal relationships between plants and wild herbivores, e.g.,
340 McNaughton 1984). Because this type of research requires integration of environmental and
341 animal data at a wide array of scales, it is difficult to design, conduct, and analyze. Nevertheless,
342 if we are to improve our understanding and management of heterogeneity we must expand our

343 capacity to connect pattern and process to illuminate these multiscale relationships (Fuhlendorf
344 et al. 2012).

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

351 *Evaluating hypotheses*

352 Every simulated pasture contained 1.13 million mg of MSAL-type alkaloids, enough to provide
353 282 lethal doses to 500 kg cows, and each pixel was equally likely to be dangerous, regardless of
354 spatial arrangement. We were thus surprised that disaggregated larkspur, distributed randomly or
355 in small patches, caused zero deaths, even when overlapping completely with desirable forage.
356 Regardless of herd cohesion, deaths did not occur regularly until the largest patch exceeded
357 3,800 m², with 4.3 ha of larkspur divided among 31 patches or fewer. Clearly, patchy larkspur
358 kills, and non-patchy larkspur does not. Despite occasional observations in the literature of the
359 patchy growth of most dangerous larkspur species (Kotliar 1996, Pfister et al. 2010), this is a
360 novel conclusion.

361 Results for larkspur-forage overlap ran counter to our hypothesis. We had expected that
362 increased forage draw within larkspur patches would always lead to increased deaths. This was
363 not the case. Instead, deaths were maximized when there was some desirable forage within large
364 larkspur patches but most remained outside of larkspur patches. Fig 5 indicates that even though
365 mean larkspur intake is lower in these situations, intake variation among individuals in the herd

366 is higher. Thus, it appears that moderate levels of larkspur-forage overlap effectively split herds,
367 with some individuals entering larkspur patches and others remaining outside to graze other
368 desirable forage.

369 *Behavioral ecology of herds*

370 The 1/N effect typically describes a situation where a predator can capture one (or whatever the
371 numerator value is) prey, thus the chance of any individual being selected declines with an
372 increasing denominator (N). However, we propose that a more flexible way to understand
373 dilution is as $risk/N$. Here, a predator presents potential prey with a certain amount of risk and
374 individual risk is diluted as N increases. In this case, not only is the amount of risk presented by
375 the predator important, but also the distribution of that risk. Assuming equal vulnerability, if the
376 distribution of risk is such that a given herd member will not equal or exceed the level of risk it
377 would acquire on its own, then herd membership is beneficial to the individual. As opposed to
378 1/N, which usually assumes that at least one death will occur on encounter, $risk/N$ allows for
379 cases where risk is so broadly and evenly distributed that all herd members evade death by virtue
380 of simply being in a group.

381 If we conceptualize larkspur intake as consumption of risk, it is clear that “plant predators”
382 provide an interesting application of $risk/N$. In Fig 7, where at least one herd member has met the
383 predator, members of tightly cohesive herds accumulate greater median risk but with more even
384 distribution. The herd is thus beneficial to the individual not because it lowers absolute risk, but
385 because it lowers the likelihood of accumulating excessive risk when encountering a predator. If
386 the absolute risk presented by a predator is high enough it can still cause death regardless of herd
387 behavior (as in highly patchy larkspur), but it is less likely to regularly do so when risk is evenly
388 distributed amid a cohesive herd.

389 As noted by Turner and Pitcher (1986), risk of death upon encounter must be considered along
390 with the chance of first encountering predators that have limited perception. In our study,
391 larkspur-forage overlap, which increases the likelihood of the herd encountering larkspur, was
392 akin to perception, so this phenomenon is best illustrated by limiting overlap, as in Table 4. In
393 these circumstances, it is clear that more cohesive herds are less likely to encounter the threat.
394 This largely holds true at different levels of larkspur-forage overlap, though at high levels of
395 overlap moderate levels of herd cohesion lead to the fewest encounters. Nevertheless, overall
396 death counts (Fig 6), which incorporate the benefits of both *risk/N* and encounter dilution,
397 indicate that tightly cohesive herds provide the best overall strategy for avoiding predation by
398 plant predators.

399 *Limitations*

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

408 Ultimately, it is most important to recognize that our model was designed to address the
409 questions analyzed here and was not intended to fully replicate cattle behavior. Notably lacking
410 are the more complex (and poorly understood) elements of inter-animal interactions, such as

411 those mediated by familial relationships. Nevertheless, we are confident that our conclusions are
412 sound within the context of the questions we asked.

413 *Conclusions and implications*

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

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

429 While the benefits of social grouping are well documented in wild herbivores, they have been
430 largely ignored in domestic herbivores, especially within production agriculture in the US and
431 Europe. The result is livestock that are ill-prepared to deal with the pressures that herd cohesion
432 mitigates (e.g., Laporte et al. 2010). Having demonstrated that increased herd cohesion alone can
433 reduce larkspur-induced deaths by greater than 90% in a variety of scenarios, we suggest that the

434 time has arrived for managers to reconsider the importance of herd behavior in their cattle.
435 Because the adaptive functions of herds are manifold, it is likely that the benefits of a renewed
436 focus on herd behavior in our domestic livestock will be manifold as well.

437 **Acknowledgements**

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439 with Michael A. Smith and the Sims family of McFadden, WY provided crucial insight into the
440 relationship between grazing management and larkspur. Jasmine Bruno and David Augustine made
441 small suggestions that led to important changes to the model.

442 **Literature cited**

443 Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer,

444 New York ; London.

445 Augusiak, J., P. J. Van den Brink, and V. Grimm. 2014. Merging validation and evaluation of

446 ecological models to ‘evaluation’: A review of terminology and a practical approach.

447 Ecological Modelling 280:117–128.

448 Bailey, D. W., and F. D. Provenza. 2008. Mechanisms Determining Large-Herbivore Distribution.

449 Pages 7–28 *in* H. H. T. Prins and F. V. Langevelde, editors. Resource Ecology. Springer

450 Netherlands.

451 Cromsigt, J. P. G. M., and H. Olff. 2008. Dynamics of grazing lawn formation: an experimental test

452 of the role of scale-dependent processes. *Oikos* 117:1444–1452.

453 Davies, N. B., J. R. Krebs, and S. A. West. 2012. An Introduction to Behavioural Ecology. John

454 Wiley & Sons.

455 Diaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Milchunas, C. Skarpe, G. Rusch,

456 M. Sternberg, I. Noy-Meir, J. Landsberg, W. Zhang, H. Clark, and B. D. Campbell. 2007.

457 Plant trait responses to grazing - A global synthesis. *Global Change Biology* 13:313–341.

458 Dumont, B., and D. R. C. Hill. 2004. Spatially explicit models of group foraging by herbivores: what

459 can Agent-Based Models offer? *Animal Research* 53:419–428.

460 Ebensperger, L. A., and L. D. Hayes. 2016. Causes and evolution of group-living. Pages 173–200 *in*

461 L. A. Ebensperger and L. D. Hayes, editors. Sociobiology of Caviomorph Rodents. John

462 Wiley & Sons, Ltd, Chichester, UK.

463 Fuhlendorf, S. D., D. M. Engle, R. D. Elmore, R. F. Limb, and T. G. Bidwell. 2012. Conservation of

464 Pattern and Process: Developing an Alternative Paradigm of Rangeland Management.

465 Rangeland Ecology & Management 65:579–589.

- 466 Gardner, R. H., and D. L. Urban. 2007. Neutral models for testing landscape hypotheses. *Landscape*
467 *Ecology* 22:15–29.
- 468 Google, Inc. 2018. Google Compute Engine. Virtual Machine Server.
469 <https://cloud.google.com/compute/>.
- 470 Google/Open source. 2018. OpenRefine 3.0.
- 471 Green, B., D. Gardner, J. Pfister, and D. Cook. 2009. Larkspur poison weed: 100 years of
472 delphinium research. *Rangelands* 31:22–27.
- 473 Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and
474 what could we learn in the future? *Ecological Modelling* 115:129–148.
- 475 Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD
476 protocol: A review and first update. *Ecological Modelling* 221:2760–2768.
- 477 Grimm, V., and B. T. Martin. 2013. Mechanistic effect modeling for ecological risk assessment:
478 Where to go from here? *Integrated Environmental Assessment and Management* 9:e58–e63.
- 479 Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H.-H. Thulke, J. Weiner,
480 T. Wiegand, and D. L. DeAngelis. 2005. Pattern-Oriented Modeling of Agent-Based
481 Complex Systems: Lessons from Ecology. *Science* 310:987–991.
- 482 Harris, N. R., D. E. Johnson, N. K. McDougald, and M. R. George. 2007. Social Associations and
483 Dominance of Individuals in Small Herds of Cattle. *Rangeland Ecology & Management*
484 60:339–349.
- 485 Ireland, H. M., and G. D. Ruxton. 2017. Zebra stripes: an interspecies signal to facilitate mixed-
486 species herding? *Biological Journal of the Linnean Society* 121:947–952.
- 487 Jablonski, K. E., R. B. Boone, and P. J. Meiman. 2018. An agent-based model of cattle grazing toxic
488 Geyer’s larkspur. *PLOS ONE* 13:e0194450.

- 489 Knight, A., and R. Walter. 2001. *A Guide to Plant Poisoning of Animals in North America*. Teton
490 NewMedia, Incorporated.
- 491 Kotliar, N. B. 1996. Scale dependency and the expression of hierarchical structure in *Delphinium*
492 patches. *Vegetatio* 127:117–128.
- 493 Krause, J., and G. D. Ruxton. 2002. *Living in Groups*. OUP Oxford.
- 494 Laca, E. A., R. A. Distel, T. C. Criggs, and M. W. Demment. 1994. Effects of Canopy Structure on
495 Patch Depression by Grazers. *Ecology* 75:706–716.
- 496 Laporte, I., T. B. Muhly, J. A. Pitt, M. Alexander, and M. Musiani. 2010. Effects of Wolves on Elk
497 and Cattle Behaviors: Implications for Livestock Production and Wolf Conservation. *PLOS*
498 *ONE* 5:e11954.
- 499 Larson-Praplan, S., M. R. George, J. C. Buckhouse, and E. A. Laca. 2015. Spatial and temporal
500 domains of scale of grazing cattle. *Animal Production Science* 55:284–297.
- 501 Launchbaugh, K. L., and L. D. Howery. 2005. Understanding Landscape Use Patterns of Livestock
502 as a Consequence of Foraging Behavior. *Rangeland Ecology & Management* 58:99–108.
- 503 Makin, D. F., S. Chamaille-Jammes, and A. M. Shrader. 2017. Herbivores employ a suite of
504 antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal*
505 *Behaviour* 127:225–231.
- 506 Manners, G. D., K. E. Panter, and S. W. Pelletier. 1995. Structure-Activity Relationships of
507 Norditerpenoid Alkaloids Occurring in Toxic Larkspur (*Delphinium*) Species. *Journal of*
508 *Natural Products* 58:863–869.
- 509 Maschinski, J., and T. G. Whitham. 1989. The Continuum of Plant Responses to Herbivory: The
510 Influence of Plant Association, Nutrient Availability, and Timing. *The American Naturalist*
511 134:1–19.

- 512 McGarigal, K., S. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program
513 for Categorical and Continuous Maps. University of Massachusetts, Amherst.
- 514 McGarigal, K., S. Cushman, M. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis
515 Program for Categorical Maps.
- 516 McLane, A. J., C. Semeniuk, G. J. McDermid, and D. J. Marceau. 2011. The role of agent-based
517 models in wildlife ecology and management. *Ecological Modelling* 222:1544–1556.
- 518 McNaughton, S. J. 1984. Grazing Lawns: Animals in Herds, Plant Form, and Coevolution. *The*
519 *American Naturalist* 124:863–886.
- 520 Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A Generalized Model of the Effects of
521 Grazing by Large Herbivores on Grassland Community Structure. *The American Naturalist*
522 132:87–106.
- 523 Panter, K. E., G. D. Manners, B. L. Stegelmeier, S. Lee, D. R. Gardner, M. H. Ralphs, J. A. Pfister,
524 and L. F. James. 2002. Larkspur poisoning: toxicology and alkaloid structure–activity
525 relationships. *Biochemical Systematics and Ecology* 30:113–128.
- 526 Pfister, J. A., D. R. Gardner, and K. E. Panter. 2010. Consumption of Low Larkspur (*Delphinium*
527 *nuttallianum*) by Grazing Sheep. *Rangeland Ecology & Management* 63:263–266.
- 528 Pfister, J. A., D. R. Gardner, and K. W. Price. 1997. Grazing risk on tall larkspur-infested ranges.
529 *Rangelands* 19:12–15.
- 530 Provenza, F. D., J. J. Villalba, L. E. Dziba, S. B. Atwood, and R. E. Banner. 2003. Linking herbivore
531 experience, varied diets, and plant biochemical diversity. *Small Ruminant Research* 49:257–
532 274.
- 533 R Core Team. 2018. R: a language for statistical computing. R Foundation for Statistical Computing,
534 Vienna, Austria.

- 535 Ralphs, M. H., J. D. Olsen, J. A. Pfister, and G. D. Manners. 1988. Plant-animal interactions in
536 larkspur poisoning in cattle. *Journal of Animal Science* 66:2334–2342.
- 537 SAS Institute. 2016. JMP. SAS Institute, Inc., Cary, NC.
- 538 Sato, S. 1982. Leadership during actual grazing in a small herd of cattle. *Applied Animal Ethology*
539 8:53–65.
- 540 Shiyomi, M., and M. Tsuiki. 1999. Model for the spatial pattern formed by a small herd in grazing
541 cattle. *Ecological Modelling* 119:231–238.
- 542 Stutz, R. S., U. A. Bergvall, O. Leimar, J. Tuomi, and P. Rautio. 2018. Cohesiveness reduces foraging
543 efficiency in a social herbivore. *Animal Behaviour* 135:57–68.
- 544 Synes, N. W., C. Brown, K. Watts, S. M. White, M. A. Gilbert, and J. M. J. Travis. 2016. Emerging
545 Opportunities for Landscape Ecological Modelling. *Current Landscape Ecology Reports*
546 1:146–167.
- 547 Turner, G. F., and T. J. Pitcher. 1986. Attack Abatement: A Model for Group Protection by
548 Combined Avoidance and Dilution. *The American Naturalist* 128:228–240.
- 549 Turner, M. G., and R. H. Gardner. 2015. *Landscape Ecology in Theory and Practice: Pattern and*
550 *Process*. Springer.
- 551 Villalba, J. J., F. D. Provenza, F. Catanese, and R. A. Distel. 2015. Understanding and manipulating
552 diet choice in grazing animals. *Animal Production Science* 55:261–271.
- 553 WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1998. From feeding station to patch: scaling
554 up food intake measurements in grazing cattle. *Applied Animal Behaviour Science* 60:301–
555 315.
- 556 Welch, K. D., D. Cook, B. T. Green, D. R. Gardner, J. A. Pfister, T. G. McDanel, and K. E.
557 Panter. 2015a. Adverse effects of larkspur (*Delphinium* spp.) on cattle. *Agriculture* 5:456–
558 474.

- 559 Welch, K. D., B. T. Green, D. R. Gardner, D. Cook, and J. A. Pfister. 2015b. The effect of
560 administering multiple doses of tall larkspur (*Delphinium barbeyi*) to cattle. *Journal of*
561 *Animal Science* 93:4181.
- 562 Wiens, J. A. 1976. Population Responses to Patchy Environments. *Annual Review of Ecology and*
563 *Systematics* 7:81–120.
- 564 Wilensky, U. 1999. Netlogo 6.01. Center for Connected Learning and Computer-Based Modeling,
565 Northwestern University, Evanston, IL.
- 566 With, K. A., and A. W. King. 1997. The Use and Misuse of Neutral Landscape Models in Ecology.
567 *Oikos* 79:219–229.
- 568

569 **Tables**

570 Table 1. Relevant model variables. Sources for variable parameters are cited in the body of the
571 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, $\sigma = 333.33$ 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 ($\text{kg} \cdot \text{ha}^{-1}$)
	mean-larkspur-mass	Mean mass of larkspur plants (g)
	MSAL-concentration	MSAL alkaloid concentration in larkspur plants ($\text{mg} \cdot \text{g}^{-1}$)
	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
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572

573 Table 2. Mean landscape metrics for sample landscapes (n=10 per level) generated at different
574 levels of larkspur-patch-factor (LPF). Reference McGarigal et al. (2002) for descriptions of
575 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

576

577

578 Table 3. Data for total deaths, mean deaths, standard deviation of individual daily alkaloid intake
579 (mg), and mean individual daily alkaloid intake (mg) for different levels of larkspur-forage-
580 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

581

582

583 Table 4. Percent of grazing-days where larkspur was encountered or a death occurred, at
584 different levels of herd-distance-factor (HDF). Data are restricted to cases where highly patchy
585 larkspur did not overlap at all with highly desirable forage (LPF=5, LFOF=0) (n=3,240).

HDF	Larkspur encountered?		Death occurred?	
	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%

586

587

588 **Figure legends**

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

591 Fig 2. Sample landscapes for different levels of larkspur-patch-factor (LPF) and larkspur-forage-
592 overlap (LFOF). Green indicates the distribution of forage, with darker green equal to more
593 forage (forage patches), and purple indicates larkspur. No forage patches are visible at LFOF=4
594 because they are obscured by the larkspur. Watering locations are blue.

595 Fig 3. Distribution of model-run death count by model-run standard deviation of individual daily
596 alkaloid intake (mg) (n=7200).

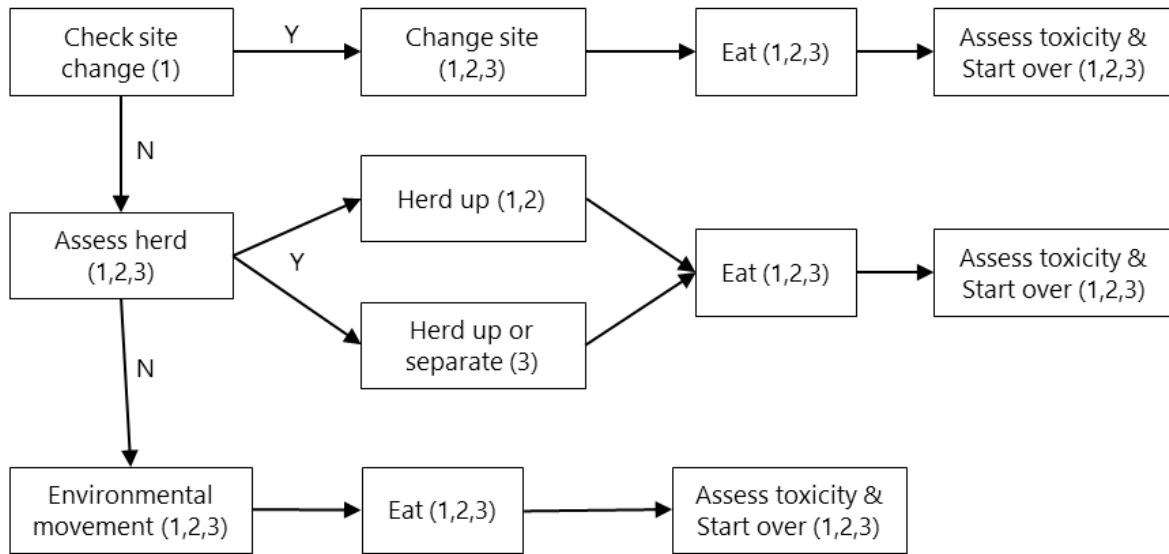
597 Fig 4. Distribution of model-run standard deviation of individual daily alkaloid intake (mg) by
598 larkspur-patch-factor (LPF) across all levels of other variables. For visibility, data are split by
599 whether or not any deaths occurred during the model run, with points sized to indicate the
600 number of deaths. Points are semi-transparent so that darker areas indicate more points
601 (n=7,200).

602 Fig 5. The relationship between mean individual daily alkaloid intake (mg) and standard
603 deviation of individual daily alkaloid intake (mg) at different levels of larkspur-patch-factor
604 (LPF) and larkspur-forage-overlap-factor (LFOF), across all levels of herd-distance-factor.
605 Displayed results are limited to $LPF \geq 3$, where the vast majority of deaths occurred. Rug plots on
606 the x and y axes show the distribution of deaths. A dashed line marks a standard deviation of 500
607 mg, an apparent threshold where deaths increase greatly. Points are semi-transparent so that
608 darker areas indicate more points (n=7,200).

609 Fig 6. The relationship of herd-distance-factor (HDF), larkspur-patch-factor (LPF), and larkspur-
610 forage-overlap (LFOF) to standard deviation of individual daily alkaloid intake (black) and total
611 deaths (blue). Hash marks on the upper x axis indicate levels where at least one death occurred,
612 and a dashed horizontal line marks a standard deviation of 500 mg, an apparent threshold where
613 deaths begin to occur. Points represent mean model-run values (n=30 per point, 7,200 overall).

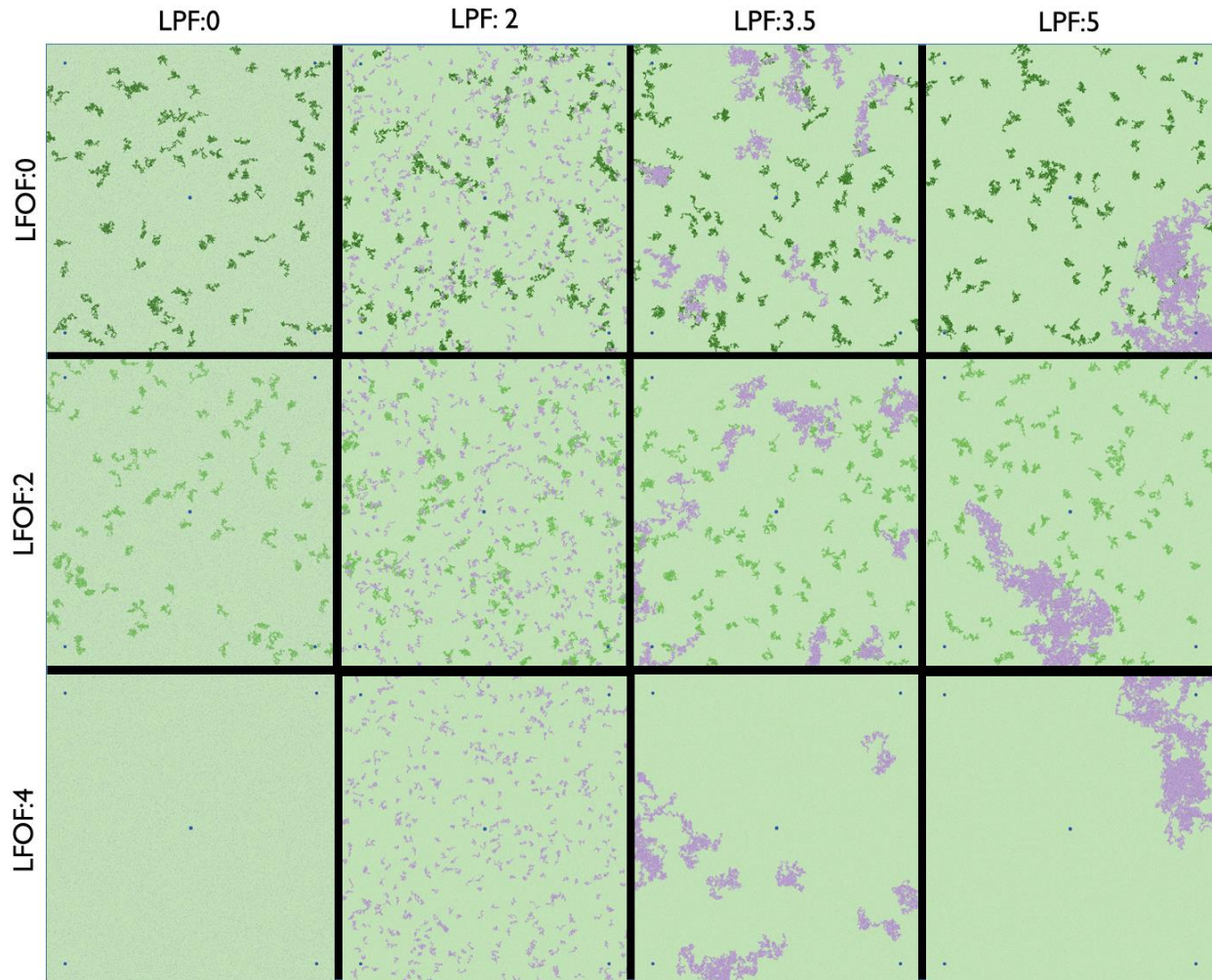
614 Fig 7. Violin plots of the distribution of individual daily alkaloid intake at different levels of
615 herd-distance-factor (HDF), restricted to highly patchy larkspur overlapping completely with
616 highly desirable forage (LPF=5, LFOF=4) and days where at least one cow consumed larkspur
617 (n=167,383). Within the violins, box plots show the location of the median and first and third
618 quantiles.

619 **Figures**



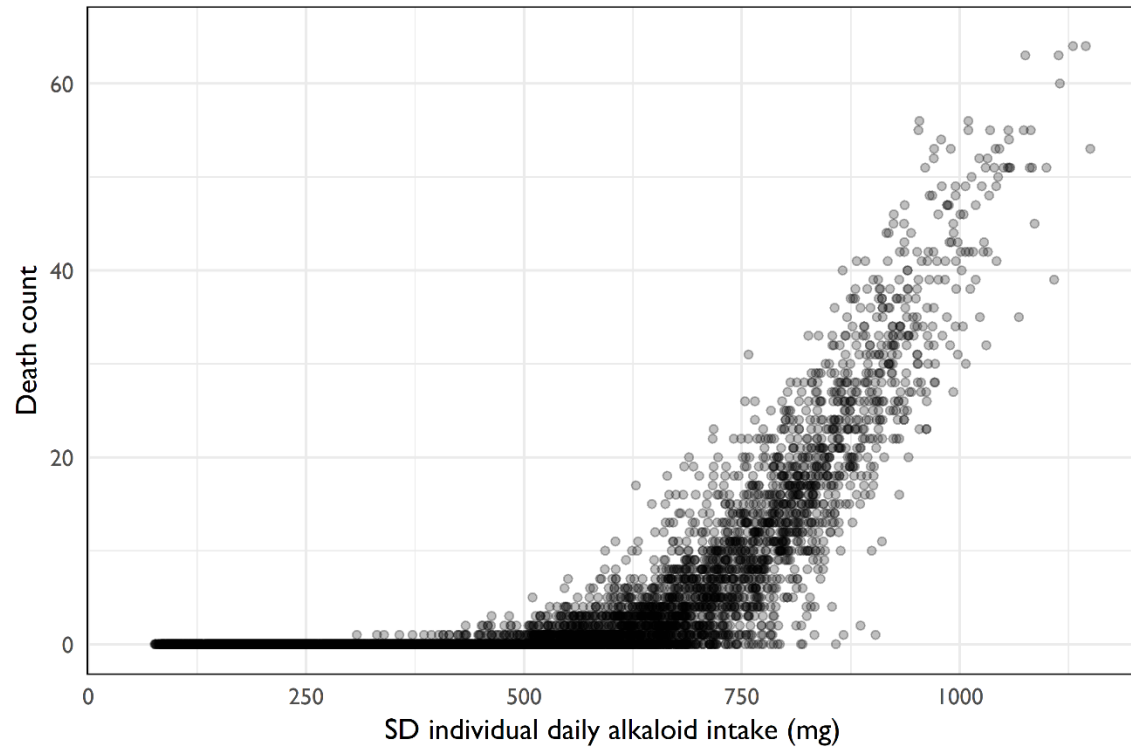
620

621 Figure 1



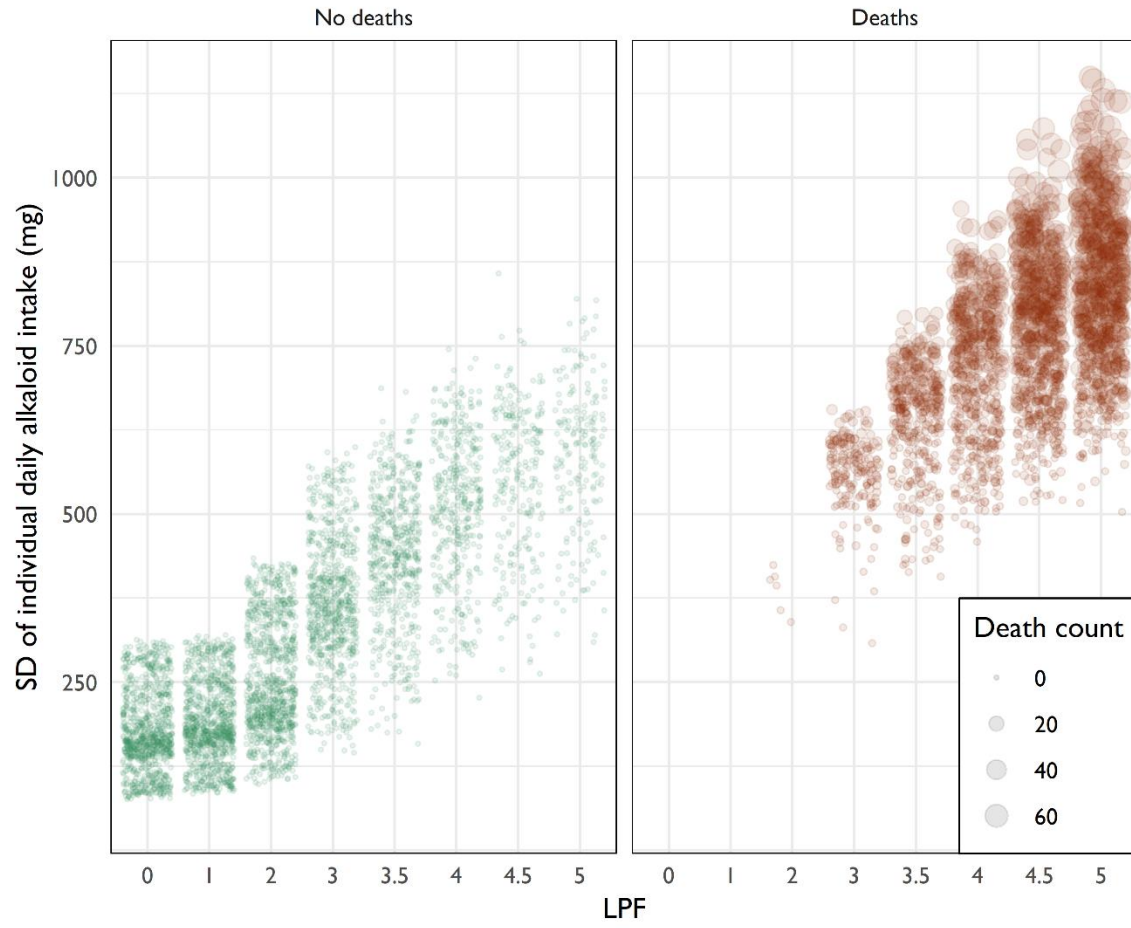
622

623 Figure 2



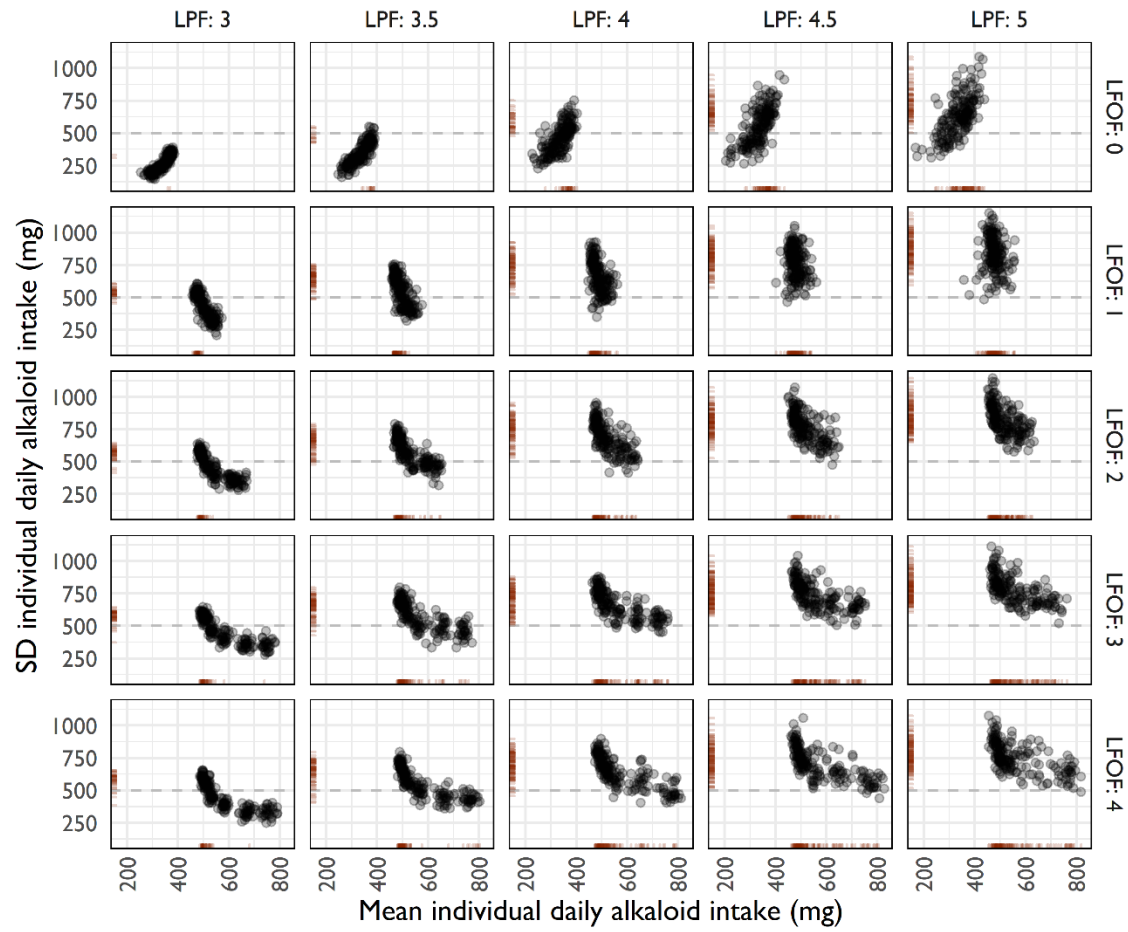
624

625 Figure 3



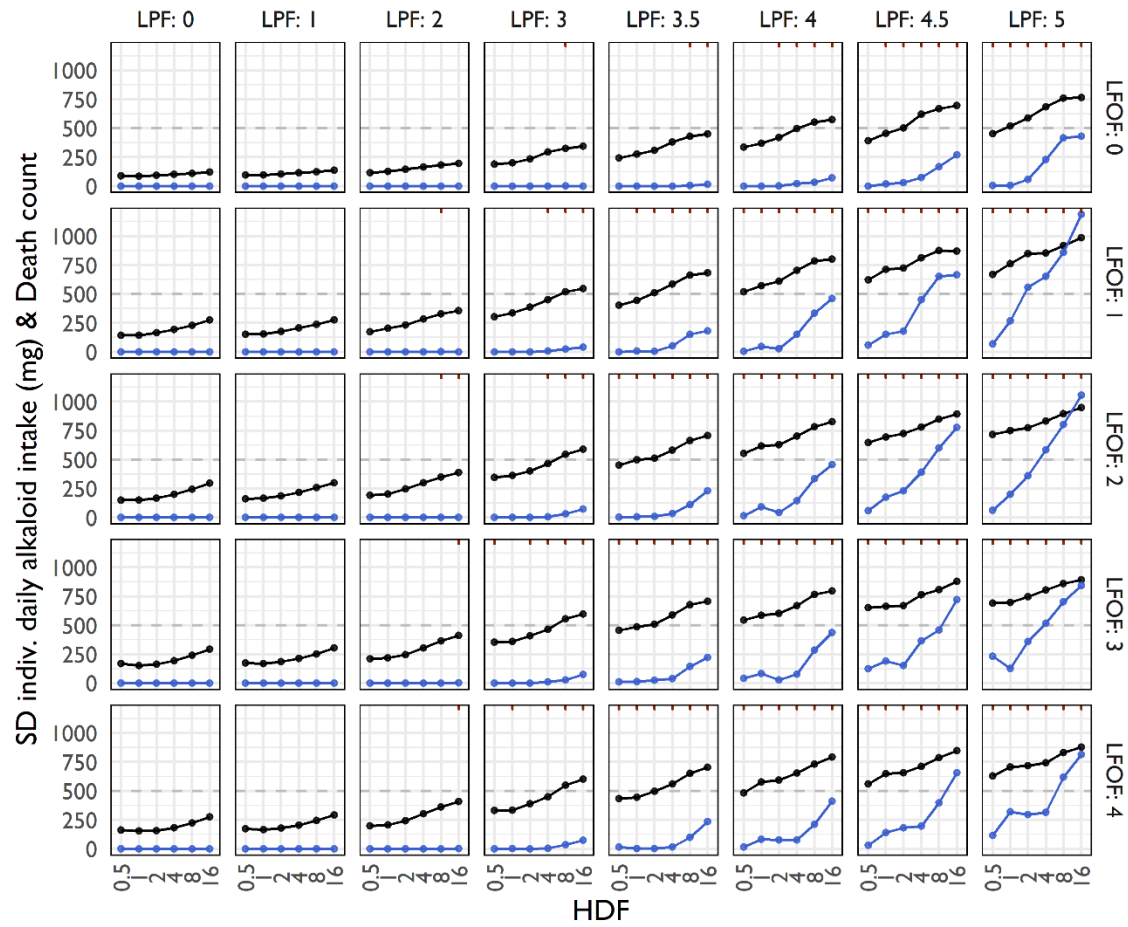
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627 Figure 4



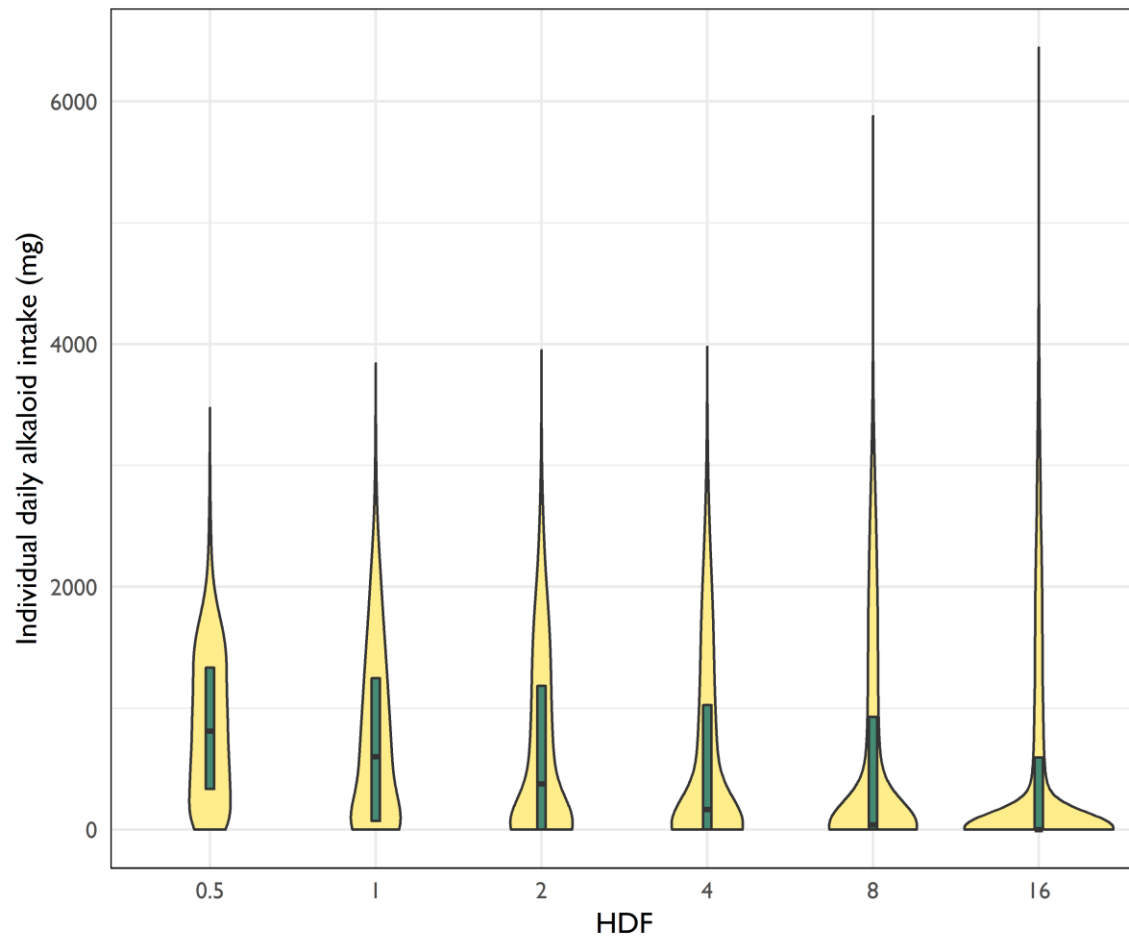
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629 Figure 5



630

631 Figure 6



632

633 Figure 7