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4 **Effects of willow nutrition and morphology on calving success of moose**

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23 **ABSTRACT** Across much of North America, populations of moose (*Alces alces*) are declining
24 because of disease, predation, climate change, and anthropogenic-driven habitat loss. Contrary to
25 this trend, populations of moose in Colorado, USA have continued to grow. Studying successful
26 (i.e., persistent or growing) populations of moose can facilitate continued conservation by
27 identifying habitat features critical to persistence of moose. We hypothesized that moose using
28 habitat with higher quality willow (*Salix* spp.) would have a higher probability of having a calf-
29 at-heel (i.e., calving success). We evaluated moose calving success using repeated ground
30 observations of collared individuals with calves in an occupancy model framework to account
31 for detection probability. We then evaluated the impact of willow habitat quality and nutrition on
32 moose calving success by studying 2 spatially segregated populations of moose in Colorado.
33 Last, we evaluated correlations between willow characteristics (browse intensity, height, cover,
34 leaf length, and species) and willow nutrition (dry matter digestibility [DMD]) to assess the
35 utility of using those characteristics to assess willow nutrition. We found willow height and
36 cover had a high probability of being positively associated with higher individual-level calving
37 success. Willow DMD, browse intensity, and leaf length were not predictive of individual moose
38 calving success; however, the site with higher mean DMD consistently had higher mean
39 estimates of calving success for the same year. Our results suggest surveying DMD is likely not
40 a useful metric for assessing differences in calving success of individual moose but may be of
41 use at population levels. Further, the assessment of willow morphology and density may be used
42 to identify areas that support higher levels of moose calving success.

43 **KEY WORDS** *Alces alces*, calving success, Colorado, moose, nutrition, reproduction, *Salix*,
44 willow.

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45 Understanding the relationships between habitat and reproductive success is a key aspect of
46 successfully managing wildlife populations. Moreover, interpreting this relationship is especially
47 valuable for species in which direct annual evaluation of reproductive success is not feasible.
48 Reproductive success of ungulates is closely linked to nutrition intake (Belovsky 1978, Heard et
49 al. 1997, Testa and Adams 1998, Parker et al. 2009, Cook et al. 2013). In their broad-scale
50 assessment, Cook et al. (2013) noted the importance of adequate summer nutrition in driving
51 reproductive performance of female elk (*Cervus elaphus*) and their offspring in the Northwest
52 and Rocky Mountains. Similarly, Proffitt et al. (2016) noted differences in pregnancy rates of elk
53 related to differences in nutritional conditions. Further, given the impact of maternal condition,
54 which is directly attributed to nutritional condition, offspring survival can be affected (Bishop et
55 al. 2009, Shallow et al. 2015). In conjunction, these relationships suggest that monitoring the
56 condition of nutritional resources may be a suitable surrogate for measuring reproductive
57 success.

58 For moose (*Alces alces*), willow (*Salix* spp.) is often a key forage resource that likely
59 affects maternal condition and, subsequently, calving success. As a low-density and difficult to
60 monitor species, moose have proven challenging and costly to survey with low bias (Månsson et
61 al. 2011). When willow forage is available, moose will preferentially select willow over other
62 forage (Renecker and Schwartz 2007). In areas with high concentration of willow, willow can
63 comprise 90% of the diet of moose (Dungan and Wright 2005). The dietary importance of
64 willow in these areas in conjunction with the well-established links between nutrition intake,
65 body condition, and reproduction of moose (Edwards and Ritcey 1958, Testa and Adams 1998,
66 Ruprecht et al. 2016) suggest that the quality and quantity of willow forage are likely key factors
67 affecting calving success. Summer nutrition intake is especially important to moose as they build

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68 fat reserves for times of year, such as winter, when energy consumption is insufficient to meet
69 maintenance requirements (Schwartz et al. 1987, Renecker and Hudson 1989). Populations of
70 moose with low nutrition availability have been previously associated with delayed maturation,
71 pauses in reproduction, and low twinning rates (Boertje et al. 2019).

72 Colorado, USA, lies at the southern extent of the range of moose (Timmermann and
73 Rodgers 2017). Unlike many moose populations in the lower 48 states, populations of moose in
74 Colorado have been relatively robust over the past 2 decades (Timmermann and Rodgers 2017).
75 In Colorado, predation pressure on moose is minimal and the prevalence of parasites and disease
76 is relatively low (Colorado Parks and Wildlife, unpublished data). As such, the primary factors
77 limiting moose populations in Colorado are the ability to consume adequate nutrition and survive
78 at southern latitudes (Van Ballenberghe and Ballard 2007).

79 Researchers at Colorado Parks and Wildlife (CPW) reported moose pregnancy rates to
80 differ between 2 spatially segregated, geographically proximate populations of moose in
81 Colorado (E. J. Bergman, CPW, unpublished data). Similarities between populations in
82 landscape composition, habitat availability, and geography may reduce the set of alternative
83 explanatory factors. Forage quality and quantity remain poorly understood for these 2
84 populations and are logical variables to investigate that may explain differences between
85 populations.

86 Our objectives of this research were 2-fold. First, we sought to understand the correlation
87 between forage quality, quantity, and browse intensity on the probability of individual moose
88 having a calf-at-heel, which we term calving success, by evaluating 2 spatially separated
89 populations of moose in Colorado. We hypothesized that use of higher quality willow habitat
90 during summer months would be positively associated with higher calving success. Our second

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91 objective was to evaluate correlations between willow characteristics and willow nutrition. The
92 strong relationship between nutrition intake and calving success (Belovsky 1978, Heard et al.
93 1997, Testa and Adams 1998) makes nutrition desirable to monitor. That said, we recognize that
94 extensive monitoring of willow nutrition may not be possible for future studies given the time
95 and expense associated with these surveys. Thus, we evaluated relationships between willow
96 characteristics and willow nutrition that may be useful to future conservation- and management-
97 related studies in which analyzing nutrition directly is not feasible.

98 **STUDY AREA**

99 We conducted research in 2 study areas located in northern Colorado from 2015–2019. The first
100 study site, North Park, was located south of the Colorado-Wyoming border 100 km west of the
101 Rocky Mountain Front and near the town of Walden. Moose were first translocated to the area
102 during the 1970s and have been there since then. The North Park study area was a wide (14–46
103 km), high-elevation valley (2,400–2,750 m) composed of a mixture of rolling sagebrush
104 (*Artemisia* spp.) hills, irrigated agricultural fields, and riparian corridors dominated by willow.
105 Riparian willow communities were largely composed of Geyer’s willow (*S. geyeriana*),
106 mountain willow (*S. monticola*), planeleaf willow (*S. planifolia*), and Booth’s willow (*S.*
107 *boothii*). The hills surrounding North Park primarily comprised lodgepole pine (*Pinus contorta*)
108 with Englemann spruce (*Picea engelmannii*) intermixed.

109 The second study site was along the Laramie River roughly 40 km northeast of the North
110 Park study area and was separated from North Park by the Rawah Mountains (3,200–3,840 m).
111 Moose were translocated to Laramie River during the early 1980s and have been there since
112 then. The Laramie River Study area was composed of a narrow valley floor (3.0–8.5 km wide)
113 and characterized by riparian willow communities along the river with similar species

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114 composition to the North Park study site. Uplands around Laramie River were characterized by
115 rangeland co-dominated by sagebrush and a grass-forb mix but occurred with less frequency in
116 comparison to North Park. Larger hills located within the valley were dominated by quaking
117 aspen (*Populus tremuloides*), while slopes to the east and west were dominated by lodgepole
118 pine and Engelmann spruce.

119 Geographic features and climate of both study areas were similar. Elevation of riparian
120 areas ranged from 2,400 m to 2,800 m. Temperatures ranged from highs in July of 26.5° C to
121 lows of -15° C in January (U.S. Department of Agriculture National Resources Conservation
122 Service 2020). North Park tended to have slightly higher maximum temperatures than Laramie
123 River throughout the year by about 2.2° C. Mean low temperatures were more similar, although
124 North Park tended to be slightly colder during the winter months. Average annual precipitation
125 was around 40.4 cm for both sites.

126 Moose in both study areas were managed by CPW. Management actions included limited
127 male and female moose hunting. Predator assemblages were also similar between study sites.
128 American black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and coyotes (*Canis*
129 *latrans*) were present in both sites, whereas wolves (*Canis lupus*) and grizzly bears (*Ursus*
130 *arctos*) were absent. Black bears and mountain lions infrequently preyed upon moose, resulting
131 in minimal predation pressure (Bergman et al. 2020b).

132 **METHODS**

133 **Capture and observation of moose**

134 We captured moose in the North Park and Laramie River study areas as a part of a broader
135 research initiative from 2015 to 2019. Between 20 December and 27 January of each winter
136 (2015–2019), we captured adult (≥ 2 years old, as determined by body size) female moose via

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137 helicopter darting. We sedated moose using 1 of 3 different drug combinations: BAM (54.6 mg
138 of butorphanol, 18.2 mg of azaperone, and 21.8 mg of medetomidine) in combination with
139 ketamine (200 mg), carfentanil (3 mg) in combination with xylazine (100 mg), or thiafentanil (10
140 mg) in combination with xylazine (25 mg). After handling, we antagonized capture drugs with
141 naltrexone (100 mg, antagonist for carfentil and thiafentenil), tolazoline (500 mg, antagonist for
142 azaperone and xylazine), or atipamezole (100–150 mg, antagonist for medetomidine and
143 xylazine). Once sedated, we blindfolded moose to minimize stress. Moose received oxygen, via
144 nasal cannula, to minimize risks of adult and fetal hypoxia. We subsequently fitted moose with
145 satellite and global positioning system (GPS)-equipped very high frequency radio-collars (Vertex
146 Plus, Vectronics Aerospace GmbH, Berlin, Germany; G5-2D, Advanced Telemetry Systems,
147 Isanti, MN, USA), and uniquely numbered ear tags.

148 Following the first year of capture, we recaptured some previously captured moose, but
149 only on an opportunistic basis. Moose captured in previous years retained satellite collars and
150 remained available for observation in subsequent years. We captured 214 moose between 2015
151 and 2019. In total, there were 145 unique individuals, 80 from North Park and 65 from Laramie
152 River.

153 We initiated ground observations of collared moose beginning in mid-May of each year
154 when the probability of parturition was <0.50 (Bergman et al. 2020a). We attempted to observe
155 each collared individual ≥ 1 time/week. Typically, 1 observer completed ground observations by
156 radio-tracking the collared moose to document the presence or absence of a calf. Recent GPS
157 locations of moose expedited ground observations. When a single observer failed to gain an
158 observation after 4 repeated efforts, we used a 2-observer approach. During these scenarios, the
159 second observer was positioned along the exit route that the moose was expected to take, and the

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160 first observer radio-tracked the moose in the same manner as a single-observer approach. We
161 recorded an observation when we sighted an identifiable female moose and 1 of 2 conditions was
162 met: we observed a calf in the immediate vicinity of the identifiable female or the surrounding 1–
163 2-m area was visible with no calf present. Repeated observations continued through the end of
164 August. We initially prioritized moose for observation based on whether or not they had been
165 captured the previous winter (i.e., moose with known pregnancy status were a higher priority for
166 observation). Once individual moose had been observed ≥ 1 time, we prioritized animals based
167 on timing of the most recent observation (i.e., individual moose observed most recently were
168 lowest priority for upcoming observations and animals who had not been recently observed were
169 a higher priority). In addition to observations that occurred as a part of the formal study process,
170 we recorded a small number of opportunistic observations by the public ($n = 9$) during autumn.
171 We only recoded opportunistic observations when individual identification of moose (possible
172 because of unique ear tags) was available.

173 **Willow Surveys**

174 We collected willow samples from the North Park and Laramie River study sites from 2017 to
175 2019 during the month of July to assess spatial variation in willow quality, quantity, and
176 utilization (i.e., spatial samples). We used GPS locations from collared moose during June of the
177 same year to represent areas used by moose during summer (Jun to Aug). We then randomly
178 selected sample points from those classified as willow (Simpson et al. 2013). For the pilot year,
179 2017, we randomly selected 40 points from each study area from all points in June after filtering
180 for land cover type. For 2018 and 2019, we selected 60 points from each study area and
181 additionally stratified the random points by individual moose (i.e., we selected either 2 or 3
182 points from the used locations of each moose). By stratifying random locations by moose, we

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183 avoided biasing observation effort towards moose with more recorded used locations because of
184 collar type or geographic location. We restricted random locations to those ≥ 20 m apart. If a
185 point was too close to another location, did not have any willow present within 10 m, or was
186 inaccessible (i.e., inaccessible private property), we selected alternative random locations
187 (representing $\sim 15\%$ of sampled locations) from the same individual sequentially from a list of
188 replacement points.

189 At each spatial point, we flagged the location and identified the closest willow. We
190 identified each willow to species and collected leaves and twigs from the closest branches to the
191 marked point. We collected samples from the apical 15–20 cm of branches, which generally
192 represent the current year's growth and, depending on the growth stage, previous year's growth.
193 We restricted samples to branches between 0.5 m and 2.5 m above ground level, which is
194 consistent with observed use by moose in our area. The effective browse range of moose
195 reported in literature varies among studies (Stickney 1966, Bergström and Guillet 2002,
196 Burkholder et al. 2017) but typically falls within a similar range. We collected leaf samples by
197 stripping leaves from branches by hand to simulate moose foraging behavior and clipped twigs
198 from areas where we had stripped leaves. For leaf and twig samples, we collected ≥ 10 g (wet
199 weight) from each plant. We randomly selected 5 leaves from the sample and recorded the length
200 of each. We placed leaf and twig samples in open paper bags and allowed them to air-dry in a
201 low humidity environment for ≥ 2 months. Each year, once dry, we transferred samples into
202 sealed plastic bags to prevent further moisture exchange.

203 We established 4 10-m transects at each spatial sample location, 1 in each cardinal
204 direction. We laid a tape reel along each transect and recorded each willow intercepting the tape,

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205 noting the intercepts, species, and plant height. We did not record willow intercepts outside of
 206 the typical browse range of moose (i.e., willow plants <0.5 m or with no leaves below 2.5 m).

207 We measured browse use of the willow closest to the spatial point and of the willows
 208 closest to 5 m and 10 m along each transect. For the 5-m and 10-m samples, we selected the
 209 closest willow within 2.5 m (to avoid overlapping samples) of the transect for each distance and
 210 direction. We followed the sampling protocol developed by Stickney (1966) and modified by
 211 Burkholder et al. (2017) for evaluating browse use. In brief, we sampled the closest branch to the
 212 sample location within the browse range of moose and evaluated ≥ 20 twigs. We define twigs as
 213 an unbranched portion of a branch with apical or lateral growth consisting of current and
 214 previous year's growth (Burkholder et al. 2017). We classified each twig as belonging to 1 of 5
 215 categories: unbrowsed (N_{ub}), twigs that do not show any evidence of foraging; browsed (N_b),
 216 twigs that have had the apical portion within 15–20 cm removed from foraging; leaf stripping (N_s),
 217 twigs that have not been browsed but that have leaves stripped off; browsed and leaf
 218 stripping (N_{bs}), twigs that have been browsed and have leaf stripping farther along the branch;
 219 and heavily browsed (N_{hb}), twigs that were browsed at a diameter of ≥ 0.5 cm. We expanded
 220 upon the adjusted estimator of browse use presented in Burkholder et al. (2017) to incorporate
 221 additional weighted classifications of browse intensity to reflect increased browse pressure (e.g.,
 222 N_b receives a weight of 1 and N_{hb} receives a weight of 3). We calculated adjusted browse
 223 intensity (B_{adj}) for each plant as:

$$224 \quad B_{adj} = \frac{N_b + N_s + (N_{bs} \times 2) + (N_{hb} \times 3)}{N_{ub} + N_b + N_s + (N_{bs} \times 2) + (N_{hb} \times 3)}$$

225

226 In 2017, we selected 5 willow plants spatially representative of each study site and
 227 proximate to vehicle access to enable monitoring of leaf quality as a function of phenology
 228 through weekly sampling (i.e., phenology samples). For each plant, we collected leaf and twig
 229 samples following the willow spatial sample methodology every week from May to August of
 230 each year (2017–2019). We dried phenology samples under the same conditions as the spatial
 231 samples.

232 For spatial and phenology samples, we standardized sample composition to include a 2:1
 233 ratio of forage and browse by dry weight. We sent samples to Dairy One Forage Laboratory
 234 (Dairy One, Ithaca, NY, USA) for analysis. We had all samples analyzed for neutral detergent
 235 fiber (NDF), acid detergent fiber (ADF), ash, and acid detergent lignin. We did not evaluate
 236 crude protein because pilot data (Colorado Parks and Wildlife, unpublished data) indicated low
 237 variability between the 2 study sites. For the pilot study year (2017), we analyzed all spatial
 238 samples in addition to bi-weekly phenology samples. For 2018 and 2019, we combined
 239 phenology samples from each study site in equal proportions prior to analysis to represent
 240 average study site nutritional conditions. For spatial samples, we analyzed each sample
 241 individually. We calculate percent dry matter digestibility (DMD) using ash and NDF values for
 242 each sample as follows (Robbins et al. 1987*a, b*):

$$243 \quad \text{DMD} = \left(0.9231 \times e^{\left(-0.0451 \times \frac{\text{lignin}}{\text{NDF}} \times 100 \right)} - 0.03 \times (\text{ash} \times 100) \right) \times \text{NDF} +$$

$$244 \quad \left((-16.03 + 1.02 \times (100 - \text{NDF})) - 0 \right)$$

245
 246 We did not analyze concentrations of secondary compounds (i.e., tannins) because previous
 247 researchers suggested estimations of digestibility in woody forage may not need to be adjusted
 248 for tannins for moose because they may benefit from ingesting tannins (Spaeth et al. 2002).

249 Further, although tannin concentrations may influence forage selection, they are not a driving
250 factor in selection by moose (Stolter et al. 2005). Last, the saliva of moose binds to some types
251 of tannins, reducing negative effects (Hagerman and Robbins 1993, Juntheikki 1996).

252

253 **Analytical methods**

254 For each willow sample at each spatial point, we modeled the effect of willow species, browse
255 intensity, leaf length, and willow intercept on DMD. We did not consider the effect of year on
256 nutrition as the intent of this analysis is to explain DMD through the lens of willow
257 characteristics. We used a Bayesian framework for the analysis and evaluated the effect of each
258 covariate based on 95% credible intervals using the following equation:

$$259 \quad \text{DMD} = \text{species} + \text{browse intensity} + \text{leaf} + \text{willow intercept}$$

260

261 Because we collected nutrition samples from a single willow at each spatial point (i.e.,
262 we did not use 5-m and 10-m samples for nutrition analysis), we used the species, browse
263 intensity, and leaf lengths from 1 plant per point. We limited analysis of species effect on DMD
264 to species with ≥ 10 samples. For leaf length, we averaged the 5 leaf lengths recorded during
265 collection of the vegetation sample. We averaged the amount of willow intercept (i.e., willow
266 overlapping transects) for each point. We chose to evaluate only a global model, containing all
267 covariates, and interpreted effects based on the strength of the effect and the 95% credible
268 intervals. We selected this approach based on the objective of evaluating the utility of each
269 covariate as opposed to building the most parsimonious model to describe willow nutrition.

270 We estimated the proportion of female moose with a calf for each year using multiple

271 repeated observations of calf presence using an occupancy model as described by Bergman et al.

272 (2020b). An occupancy model framework uses a flexible model structure and enables estimation
273 of occupancy (ψ) while accounting for imperfect detection (p). In this case, ψ represents calving
274 success (i.e., the probability of a female moose having a calf-at-heel). We chose to model ψ
275 varying for each year and site and p varying each month. This structure allowed us to evaluate
276 differences in calving success between study sites and the effect of additional covariates on ψ for
277 each study site.

278 To evaluate the effect of spatial willow covariates on ψ , we used average values from
279 each point and evaluated which points overlapped with individual moose core home ranges. For
280 each spatial point, we calculated the mean value of adjusted browse intensity (B_{adj}), leaf length,
281 and the proportion of amount of transect intersected by willow. We then calculated the 75%
282 home range for each moose and year using a kernel density estimate (KDE) with the
283 `adehabitatHR` R package (Calenge 2006). We chose the 75% KDE to represent the expanded
284 core home range of each animal in which the majority of habitat use occurs. We then intersected
285 spatial samples with each home range estimate. Last, we assigned covariate values from
286 intersecting points to the respective year and moose. We used a linear model to estimate the
287 effect of individual moose on the covariate of interest as follows:

$$288 \quad cov = \mu + moose\ effect_i,$$

289
290 where cov is the covariate of interest (e.g., DMD), μ is the mean value for all individuals, and
291 $moose\ effect$ varies by individual.

292 We used the estimate ($moose\ effect$) for each individual moose to evaluate the effect of
293 each covariate on ψ . This approach has 2 benefits. First, because the core home ranges of moose
294 overlap with differing numbers of spatial samples, the precision of observed covariates varies

295 between individual moose. The linear model accounts for this through varied precision of the
296 estimated effect. Second, this approach allows uncertainty from observed covariates to be
297 correctly propagated in the calf occupancy model.

298 We used a Bayesian framework for analysis of calving success as it offers the benefit of
299 accurate error propagation across estimated variables and simplifies interpretation of estimated
300 probabilities. We tested the effect of each covariate (DMD, leaf length, willow intercept, browse
301 intensity) on calf occupancy in a univariate model using a sin link function as follows:

$$302 \quad \psi = (\sin(b_0 + moose\ effect_i \times covariate\ value) + 1)/2,$$

303
304 where *moose effect* represents the modeled value from the previous equation and *covariate value*
305 represents the measured value for each covariate (e.g., DMD). The sin link function is used to
306 link the beta parameter (*moose effect*) to the real parameter (ψ) and constrain the real parameters
307 to the [0, 1] interval, the possible range of values of occupancy. The sin link function is poorly
308 documented but commonly used (White and Burnham 1999) instead of the logit link function
309 when estimating parameters close to 0 or 1. We ran all Bayesian models for 100,000 iterations
310 with 50,000 iterations of burn-in on 6 chains at which point all parameters had reached
311 convergence ($\hat{r} < 1.01$) as assessed by the Gellman-Rubin diagnostic (Gellman and Rubin
312 1992). We conducted all analyses using the Program R software system (R Version 3.6.0,
313 www.r-project.org, accessed 1 Feb 2020).

314 RESULTS

315 Analysis of spatial samples resulted in 319 measurements of DMD (Table 1). We censored 3
316 samples from North Park in 2017 because of poor drying. A linear model comparing sample
317 week of phenology samples and DMD percent for each study site and year combination showed

318 no trend in quality over time ($|r| \leq 0.01$). Spatial willow covariates (DMD, browse intensity,
319 leaf length, average willow height, willow cover) sampled during July of each year at each
320 spatial point displayed variance across both site and year (Fig. 1). Mean DMD was 3.7
321 percentage points higher in Laramie River than North Park in 2017 and 2.1 percentage points
322 lower in 2018. In 2019, mean DMD was functionally identical between study areas, separated by
323 0.5 percentage points. Browse intensity at both sites was highly variable with mean values
324 increasing slightly from 2017 to 2019. Leaf length was similar in both study sites and for all
325 years. Average willow height had high sample variance, was similar across years, and had a
326 higher mean in North Park for all years. Willow cover was also highly variable with a wide
327 distribution of values and similar means for both sites with slightly lower cover on transects
328 conducted in 2019. A Pearson's pairwise correlation test showed low correlation between all
329 combinations of covariates ($|r| < 0.25$) except for willow height and willow, cover which had a
330 positive correlation ($r = 0.47$).

331 Analysis of DMD relative to willow browse intensity, height, cover, leaf length, and
332 species revealed few of these factors had a strong influence on DMD with high certainty (Fig. 2).
333 Willow species was largely not a good predictor of DMD with wide credible intervals for each
334 species. Strapleaf willow (*Salix ligulifolia*) had the strongest effect of any species evaluated and
335 was the only species with credible intervals not overlapping zero. Estimates for Geyer's willow,
336 mountain willow, and planeleaf willow were similar with a slight positive effect on DMD.
337 Booth's willow had a slight negative effect on DMD, but the credible interval substantially
338 overlapped zero. Browse intensity and willow height both had mean effect estimates that were
339 close to zero and substantially overlapping credible intervals and thus were uninformative.
340 Willow cover had a very slight negative effect on DMD with credible intervals substantially

341 overlapping zero. The effect of leaf length also had a negative effect on DMD and was the only
342 non-species covariate with credible intervals not overlapping zero.

343 Ground observation efforts resulted in 352 observations of moose (North Park = 148,
344 Laramie River = 204) recorded during the study (Table 2). Mean time between observations was
345 32.8 ± 29.7 (SD) days. Of the observations, 201 (North Park = 88, Laramie River = 113) had no
346 calf observed, 144 (North Park = 58, Laramie River = 86) had one calf observed, and 7 had twin
347 calves observed (North Park = 2, Laramie River = 5). The observations consisted of 108 unique
348 individuals, 60 in North Park and 48 in Laramie River.

349 Mean calf occupancy estimates (ψ) for both study areas were highest in 2015 and 2016 (\bar{x}
350 range = 0.78–0.93, SD range = 0.07–0.11; Fig. 3). Estimates were most disparate between
351 populations in 2017 with means of $\psi = 0.40 \pm 0.13$ for North Park and $\psi = 0.72 \pm 0.14$ for
352 Laramie River. In 2018, the ψ estimate was higher for North Park ($\psi = 0.70 \pm 0.12$) than for
353 Laramie River ($\psi = 0.59 \pm 0.10$). In 2019, ψ was estimated at 0.50 for both populations (SD
354 range = 0.11–0.12). For each year with nutrition data, when mean values of DMD differed, the
355 site with higher DMD had higher estimates of ψ .

356 Detection probability was lowest for May, during parturition, with an estimate of $0.48 \pm$
357 0.09 (Fig. 4). Detection probability was highest during summer (Jun, Jul, Aug), increasing across
358 that period from 0.77 to 0.90 (SD range = 0.06–0.09). Estimated detection probability of a calf in
359 the fall was lower ($\bar{x} = 0.70 \pm 0.11$) relative to summer but remained higher than the detection
360 probability in May.

361 The univariate models testing covariate effects on occupancy showed mixed effects
362 characterized by large credible intervals. The effect of DMD ($\bar{x} = 41.16 \pm 5.80\%$) was
363 functionally zero ($\beta = 0.02$) with a wide credible interval (-0.92 – 0.97). The credible interval

364 for the effect of browse intensity ($\bar{x} = 0.40 \pm 0.15$) substantially overlapped zero ($\beta = -0.59$,
365 credible interval = $-1.88-0.79$) and was therefore uninformative.

366 Of the 5 univariate models, willow cover ($\bar{x} = 0.44 \pm 0.23$) was the only covariate with a
367 credible interval not overlapping zero (Fig. 5). Willow cover showed a moderately strong
368 positive effect on ψ with a mean estimate of 1.32 (credible interval = $0.15-1.88$). In biological
369 terms, willow cover of 45% was correlated with a calving success of 0.53 whereas willow cover
370 of 65% was correlated with a calving success of 0.75. Willow height ($\bar{x} = 2.47 \pm 0.90$ m) had a
371 positive effect on ψ with an estimate of 0.79 (credible interval = $-0.20-1.90$) but included a
372 small probability of a negative effect (1.5%). Leaf length ($\bar{x} = 49.69 \pm 12.70$ mm) substantially
373 overlapped zero with the widest credible interval ($\beta = -0.42$, credible interval = $-1.93-1.75$).

374 **DISCUSSION**

375 The lack of trend in willow phenology (i.e., DMD through time) for both study sites supports 2
376 of our key assumptions when designing this project. First, nutrition at both study sites is
377 consistent across the survey period. Second, sampling willow nutrition during July provides a
378 representative sample of nutrition throughout summer. Evidence that these 2 assumptions have
379 been met supports the subsequent analyses of DMD and willow covariates gathered during July
380 of each year.

381 Site-level DMD varied substantively across site and year without a consistent pattern
382 during the study period (Fig. 1). Of particular interest, mean DMD was higher in Laramie River
383 than North Park in 2017, lower in 2018, and practically equal in 2019. These site differences in
384 measurements of DMD closely track site differences in estimates of ψ in which Laramie River
385 had higher (2017) then lower (2018) then equal (2019) estimates of ψ in comparison to North
386 Park. While credible intervals substantially overlap between study areas, the observed pattern is

387 consistent with the established relationship between nutrition and reproduction in ungulates
388 (Parker et al. 2009) and is supported by studies showing suppressed reproduction in populations
389 with low nutritional availability (Severud et al. 2019).

390 For moose, pregnancy rates have been positively correlated with body condition (Testa
391 and Adams 1998), suggesting prior-year nutrition intake may influence calving success. To meet
392 the energetic demands of reproduction, most ungulates depend on prior accumulation of energy
393 reserves, although females rely, at least in part, on energy gained during the breeding season
394 (Mysterud et al. 2005). Further, moose display relatively strong site fidelity, especially during
395 summer (Ofstad 2013, Morrison et al. 2021). Moreover, site fidelity is strongest in predictable
396 landscapes, such as our study sites, where vegetative greening occurs at regular intervals
397 (Morrison et al. 2021). This suggests that observed individual-level nutrition availability may be
398 similar to prior-year nutrition availability. While prior-year nutrition intake is a critical
399 component of an animal's current-year condition, numerous other climatic variables can also
400 have dramatic carryover impacts on condition. For example, delayed impacts of temperature,
401 which may extend for multiple years, and spring-summer precipitation have been observed to
402 influence recruitment of moose (Monteith et al. 2015). Additionally, snow depth, a measure of
403 winter severity, influences population growth rates over a multiple-year period (Mech et al.
404 1987, Post and Stenseth 1998). As a result, such factors confound the effect of prior-year
405 nutrition and reduce its utility for evaluating calving success.

406 Credible intervals overlapped zero for most covariates in the analysis of DMD relative to
407 willow characteristics (Fig. 2), which suggests that the covariates considered in this study are not
408 sufficient to accurately predict DMD. Prior researchers identified differences in nutrition based
409 on willow species (Stolter et al. 2005, Stumph and Wright 2007); however, these differences

410 may be overshadowed by temporal, geographic, or morphological characteristics (Stumph and
411 Wright 2007). If the objectives of future survey efforts are to assess the relative nutrition quality
412 of willow, simply monitoring the covariates used here is not sufficient. That said, these data can
413 still provide valuable information when used to evaluate calving success (i.e., the probability of
414 female moose having a calf-at-heel). The general trends in ψ (Fig. 3) align closely with Bergman
415 et al. (2020b) who evaluated 4 years of data and did not differentiate between populations. Of
416 note, when compared to previously reported estimates of ψ , the decrease in 2017 can largely be
417 ascribed to a single population (North Park) rather than a decrease in ψ across both populations.
418 Additionally, ψ appears to be more variable between sites through time than previously thought.
419 Estimates for 2015 to 2017 support observations by CPW biologists that a higher proportion of
420 female moose in Laramie River had calves each year than in North Park. This pattern, however,
421 does not hold for 2018 and 2019 in which Laramie River had lower ψ estimates (2018) and then
422 functionally identical estimates to North Park (2019). Notably, 2017 was the only year in which
423 the mean estimate of ψ for each population fell outside of the 95% credible interval of the other.
424 Thus, the results presented suggest that ψ did not differ significantly between these populations
425 with the exception of the year 2017.

426 The greatest advantage of employing a Bayesian framework in these analyses was the
427 ability to use an integrated model evaluating the effect of each covariate on ψ with appropriate
428 error propagation. In this model, the uncertainty in calf occupancy for each individual moose was
429 carried into the estimate of covariate effects on ψ . Although this results in broader credible
430 intervals for estimates, it provides a more truthful assessment of covariate uncertainty. This
431 uncertainty is readily apparent in the estimate of covariate effects on calf occupancy (Fig. 5).
432 While credible intervals of all but 1 estimate ended up overlapping zero, these estimates can still

433 provide biologically relevant trends when there is a high probability of either a positive or
434 negative correlation.

435 The high probability of a positive effect of willow height and the positive effect of
436 willow cover suggest that these covariates result in an increase in ψ . Overall, female moose were
437 more likely to have a calf when they had access to large (i.e., tall), high density (i.e., high ratio of
438 willow cover) willow. Although a substantial body of work has documented moose preference
439 for willow communities and forage (Dorn 1970, Stevens 1970, Dungan and Wright 2005,
440 Renecker and Schwartz 2007), our findings provide evidence that high density, mature
441 willow is even more important for female moose with calves. These findings are consistent with
442 previous research showing selection by female moose for dense habitats providing both food and
443 protection from predation (Dussault et al. 2005). Thermoregulatory demands may also drive
444 habitat selection and contribute to increased use of areas with taller willows (Street et al. 2015).
445 Our results provide the foundation for further investigation of this relationship and draw to light
446 the possibility of incorporating remote-sensed vegetation surveys (e.g., vegetation height from
447 light detection and ranging [lidar]) to evaluate habitat quality for reproducing female moose.

448 The high degree of uncertainty in the effect of browse intensity on ψ (Fig. 5) is likely due
449 to high variance in the raw parameter estimates (Fig. 1). The estimated effect of browse intensity
450 trended negative but is inconclusive ($P > 0.87$). Two possible biological explanations of a
451 negative effect are that female moose are more likely to have a calf either in areas with lower
452 densities of moose or in areas with sufficiently dense willow that it results in lower browse
453 intensity. The first explanation is supported by literature that has documented female moose to
454 calve in areas that are less frequently used by solitary moose (Dussault et al. 2005). Further,
455 some evidence suggests that individual moose exhibit different habitat selection strategies (Poole

456 et al. 2007), which may explain the uncertainty in this estimate. Because of the lack of a clear
457 relationship between browse intensity and DMD (Fig. 2) it is unlikely that this effect is being
458 driven by selection for more nutritious plants.

459 Leaf length was the least informative of the covariates considered for calf occupancy,
460 having the widest credible interval (Fig. 5). This is likely due to relatively low variation in the
461 parameter between site, year, and individual sample (Fig. 1). These results indicate that leaf
462 length is not a useful parameter for explaining moose calving success.

463 The approach we employed, evaluating spatial samples based on the overlap with
464 individual home ranges, proved to be a useful technique to evaluate sparse measures of nutrition
465 and vegetation quality at landscape scales. In using this method, we were able to leverage
466 available spatial use data from individual moose to provide estimates for each individual rather
467 than distilling all analyses to the site level. This approach enables a much more robust analysis of
468 effects than solely looking at effects at the site level. Despite this benefit, limitations in the
469 amount of fine-resolution data available led to reduction in the precision of estimates.

470 Collecting and analyzing DMD at the scale required to estimate individual nutrition for
471 multiple populations of animals is likely not feasible without spatial averaging. High-resolution
472 data can be collected through the direct observation of feeding behavior and counting of
473 individual bites (Dungan and Wright 2005), but inference is limited by the number of individuals
474 that can be observed simultaneously. Other researchers focused on creating landscape-level
475 models of digestible energy (Rowland et al. 2018) but typically focused on forecasting habitat
476 use rather than nutrition consumption for individuals. The methodology we employed has the
477 benefit of optimizing nutrition sampling effort by targeting known areas of use. Future studies

478 addressing this question may wish to analyze composite samples consisting of multiple willow
479 plants to reduce sampling variability.

480 At a site level, when mean values of DMD differed, the site with higher DMD had higher
481 estimates of ψ , suggesting that variation in willow DMD may be biologically significant to
482 moose. That said, the predictive utility of this relationship is likely limited because of sampling
483 variability and model uncertainty in ψ . Our findings suggest a comparison of site-level
484 covariates would only be useful with large differences in ψ between populations or years.
485 Further, given the small observed differences in DMD between study sites, future studies
486 evaluating this relationship may benefit from including analysis of secondary compounds, like
487 tannins, in evaluation of forage nutrition. When comparing populations with similar estimates of
488 ψ (e.g., study populations in 2015, 2016, 2019), the variance in DMD measurements will likely
489 be greater than the difference in occupancy, thereby reducing the utility of the covariate.

490 Annually monitoring wildlife populations can be very expensive but is recognized to be
491 of greater importance for species near critical thresholds in population abundance (Hauser et al.
492 2006). As southern populations of moose may be demographically more vulnerable than
493 northern populations (Ruprecht et al. 2016), management would benefit from frequent
494 populations assessment. While our results suggest monitoring willow characteristics is not
495 sufficient to detect small-scale changes in calving success, they offer a coarse assessment that
496 may be more easily conducted than direct observation. If substantive changes are observed in
497 willow habitat availability or nutrition, our results suggest increased effort in population
498 monitoring should be conducted.

499 **MANAGEMENT IMPLICATIONS**

500 Our results provide evidence that an assessment of willow height and cover may serve as a good
501 indicator of spatial areas that support higher levels of calving success. In practice, this may be
502 applied as a coarse measure of habitat suitability when making conservation or land management
503 decisions. Additionally, if managers wish to determine fine-scale differences or changes in
504 calving success, assessment of willow quality is likely ineffective, and resources are better
505 allocated towards obtaining direct estimates of calving success.

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511 **ETHICAL APPROVAL**

512 All animal capture, handling, and monitoring was conducted in accordance with approved
513 Institutional Animal Care and Use Committee (IACUC) protocols (University of Montana
514 IACUC file 032-17CBWB-060517 and CPW ACUC 08-2013).

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- 640 *Associate Editor: Kelly Proffitt.*

642 Figure 1. Measurements of willow dry matter digestibility (A), browse intensity (B), leaf length
643 (C), willow height (D), and willow cover (E) from willow samples within 2 moose population
644 home ranges in Laramie River and North Park, Colorado, USA, 2017–2019.

645

646 Figure 2. Effect of willow browse intensity (proportion), height (m), cover (proportion), leaf
647 length (mm), and species on percent dry matter digestibility in Laramie River and North Park,
648 Colorado, USA, 2017–2019. Willow species are Booth’s willow (SABO2), Geyer’s willow
649 (SAGE2), strapleaf willow (SAERL), mountain willow (SAMO2), and planeleaf willow
650 (SAPL2). Bold lines and thin lines represent 50% and 95% credible intervals, respectively.

651

652 Figure 3. Predicted moose calving success (i.e., the probability of a moose having ≥ 1 calf-at-
653 heel; ψ), using an occupancy model in a Bayesian framework, for 2 populations of moose in
654 Laramie River and North Park, Colorado, USA, 2015–2019. The center point represents the
655 mean estimate for each combination of population and year. Bold and thin vertical lines
656 represent 50% and 95% credible intervals, respectively.

657

658 Figure 4. Estimates of moose calf detection probability (i.e., the probability of observing
659 uniquely identifiable female moose with a calf-at-heel; p) in Laramie River and North Park,
660 Colorado, USA, 2015–2019. We used an occupancy model framework to estimate a separate
661 probability for each survey period (May, Jun, Jul, Aug, fall). The center point represents the
662 mean estimate. Bold and thin vertical lines represent 50% and 95% credible intervals,
663 respectively.

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665 Figure 5. Effect size of willow dry matter digestibility (%; DMD), browse intensity (proportion),
666 willow height (m), willow cover (proportion), and leaf length (mm) on moose calf occupancy in
667 Laramie River and North Park, Colorado, USA, 2015–2019. Points represent the mean estimate
668 for each covariate. Bold lines and thin lines represent 50% and 95% credible intervals,
669 respectively.
670

672 Table 1. Numeric summary of spatial willow samples by species in Laramie River and North
 673 Park, Colorado, USA, 2017–2019. Willow species are Bebb’s willow (*S. bebbiana*; SABE2),
 674 Booth’s willow (SABO2), Drummond’s willow (*S. drummondiana*; SADR), strapleaf willow
 675 (SAERL), Geyer’s willow (SAGE2), Pacific willow (*S. lasiandra*; SALAC), mountain willow
 676 (SAMO2), and planeleaf willow (SAPL2).

Year	Willow species								Total
	SABE2	SABO2	SADR	SAERL	SAGE2	SALAC	SAMO2	SAPL2	
2017	0	7	0	1	52	0	22	1	83
2018	2	8	1	7	56	4	29	10	117
2019	1	8	0	16	53	3	16	22	119
Total	3	23	1	24	161	7	67	33	319

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679 Table 2. Numeric summary of observations of female moose in Laramie River and North Park,
 680 Colorado, USA, 2015–2019. Observations are categorized by month and year, and were used to
 681 model detection probability (p) and calf presence (ψ). Fall observations were opportunistic and
 682 include observations during September–December.

Year	Observation period					Total
	May	June	July	August	Fall	
2015	19	40	19	6	1	85
2016	20	20	8	11	13	72
2017	12	18	8	12	2	52
2018	18	19	13	17	7	74
2019	2	49	8	5	5	69
Total	71	146	56	51	28	352

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685 **Summary for online Table of Contents:** Willow height and cover had a high probability of
686 being positively associated with higher individual-level calving success. Our results suggest that
687 an assessment of willow morphology and density may be used to identify areas that support
688 higher levels of moose calving success.

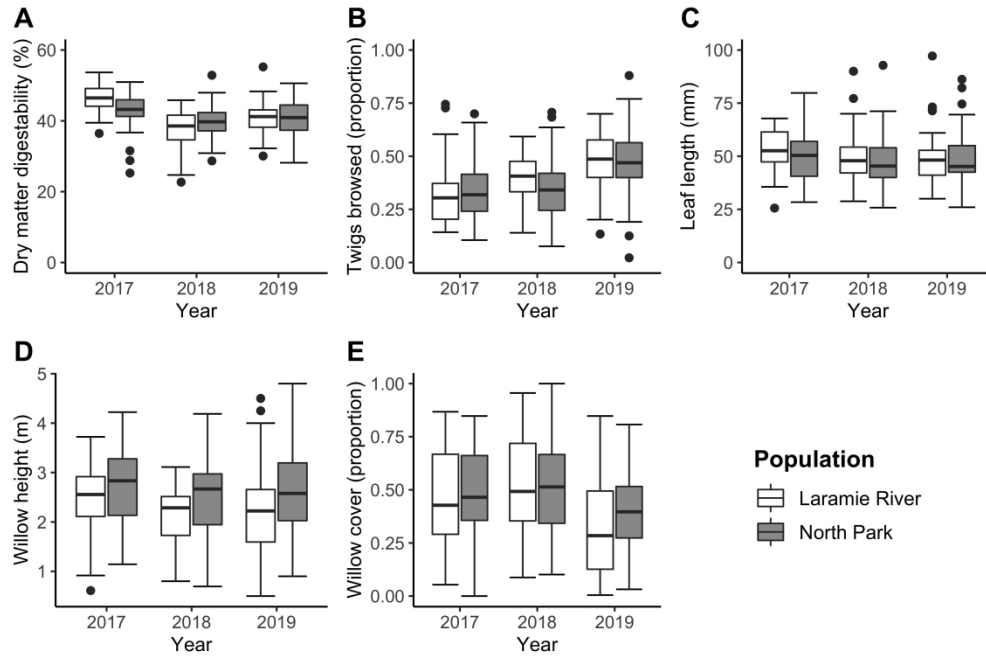


Figure 1. Measurements of willow dry matter digestibility (A), browse intensity (B), leaf length (C), willow height (D), and willow cover (E) from willow samples within 2 moose population home ranges in Laramie River and North Park, Colorado, USA, 2017–2019.

179x119mm (600 x 600 DPI)

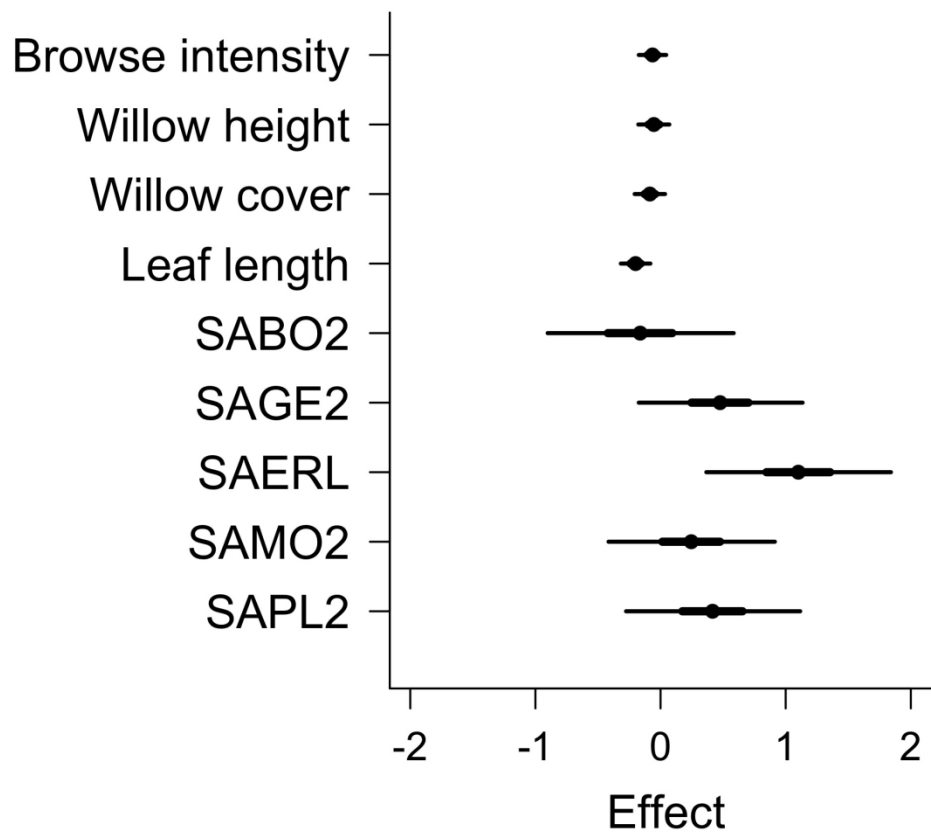


Figure 2. Effect of willow browse intensity (proportion), height (m), cover (proportion), leaf length (mm), and species on percent dry matter digestibility in Laramie River and North Park, Colorado, USA, 2017–2019. Willow species are Booth’s willow (SABO2), Geyer’s willow (SAGE2), strapleaf willow (SAERL), mountain willow (SAMO2), and planeleaf willow (SAPL2). Bold lines and thin lines represent 50% and 95% credible intervals, respectively.

708x624mm (72 x 72 DPI)

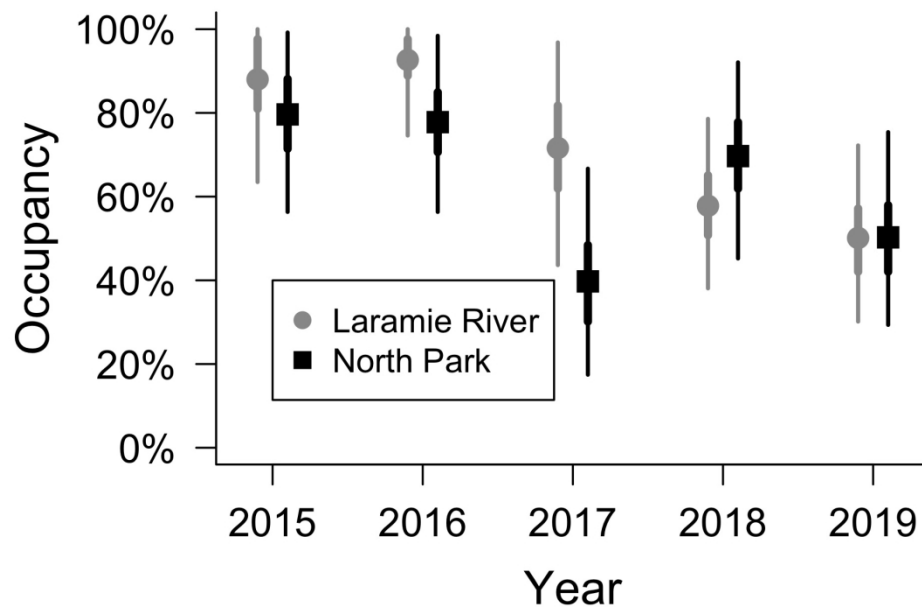


Figure 3. Predicted moose calving success (i.e., the probability of a moose having ≥ 1 calf-at-heel; Ψ), using an occupancy model in a Bayesian framework, for 2 populations of moose in Laramie River and North Park, Colorado, USA, 2015–2019. The center point represents the mean estimate for each combination of population and year. Bold and thin vertical lines represent 50% and 95% credible intervals, respectively.

708x466mm (72 x 72 DPI)

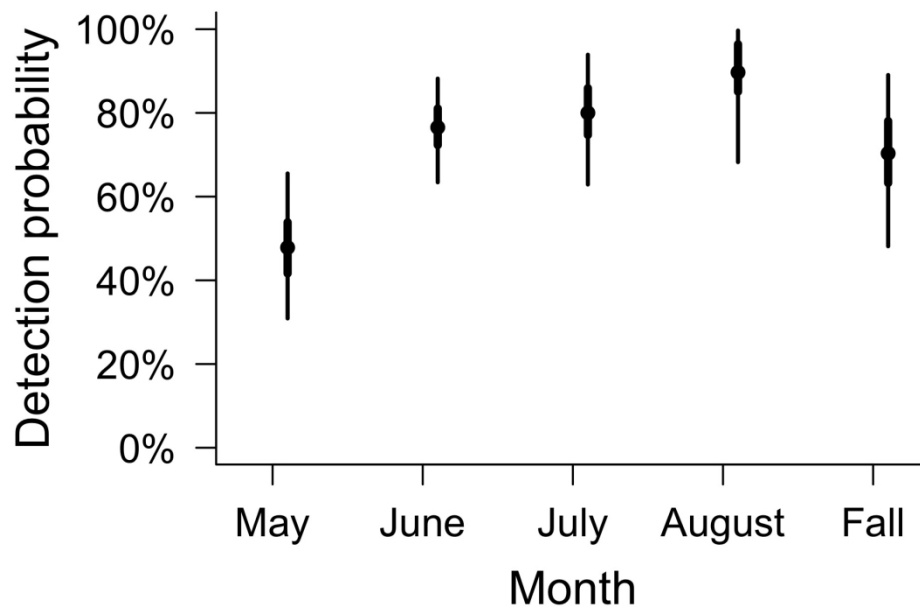


Figure 4. Estimates of moose calf detection probability (i.e., the probability of observing uniquely identifiable female moose with a calf-at-heel; p) in Laramie River and North Park, Colorado, USA, 2015–2019. We used an occupancy model framework to estimate a separate probability for each survey period (May, Jun, Jul, Aug, fall). The center point represents the mean estimate. Bold and thin vertical lines represent 50% and 95% credible intervals, respectively.

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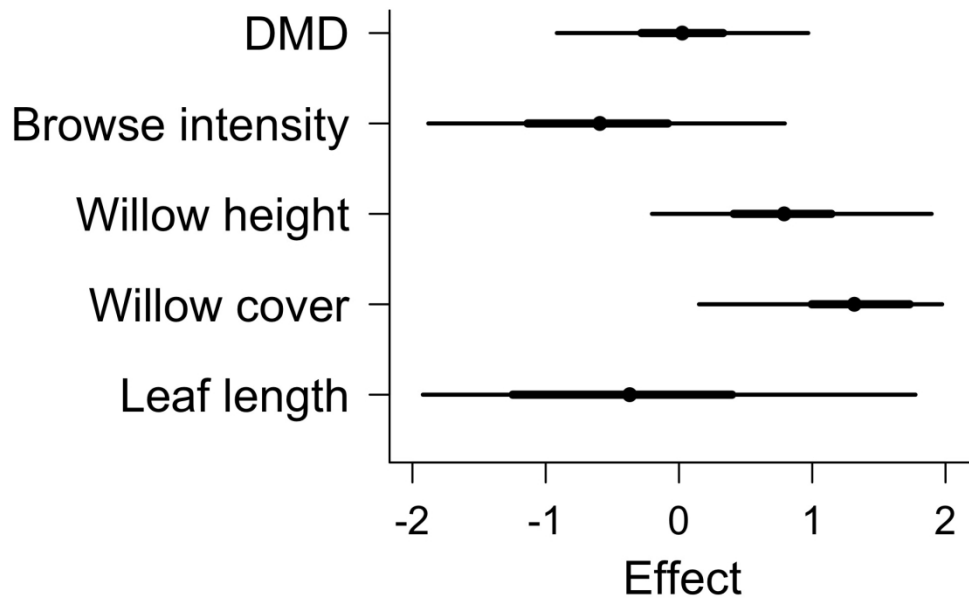


Figure 5. Effect size of willow dry matter digestibility (%; DMD), browse intensity (proportion), willow height (m), willow cover (proportion), and leaf length (mm) on moose calf occupancy in Laramie River and North Park, Colorado, USA, 2015–2019. Points represent the mean estimate for each covariate. Bold lines and thin lines represent 50% and 95% credible intervals, respectively.

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