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2 **Running head:** Forage quality shapes herbivore home range

3 **Forage stoichiometry predicts the home range size of a small**
4 **terrestrial herbivore**

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13 **Abstract**

14 Consumers make space use decisions based on resource quality. Most studies that investigate
15 the influence of resource quality on the spatial ecology of consumers use diverse proxies for
16 quality including measures based on habitat classification, forage species diversity and abun-
17 dance, and nutritional indicators, e.g., protein. Ecological stoichiometry measures resource
18 quality in terms of elemental ratios, e.g., carbon (C):nitrogen (N) ratio, but rarely have these
19 currencies been used to study consumer space use decisions. Yet, elemental ratios provide
20 a uniquely quantitative way to assess resource quality. Consequently, ecological stoichiom-
21 etry allows for investigation of how consumers respond to spatial heterogeneity in resource
22 quality by changing their space use, e.g. their home range size, and how this may influence
23 ecosystem dynamics and trophic interactions. Here, we test whether the home range size of a
24 keystone boreal herbivore, the snowshoe hare (*Lepus americanus*), varies with differences in

25 the C:N, C:phosphorus (P), and N:P ratios of two preferred forage species, lowland blueberry
26 (*Vaccinium angustifolium*) and red maple (*Acer rubrum*). We consider forage resources with
27 higher C content relative to N and P to be lower quality than resources with lower relative C
28 content. We use a novel approach, combining elemental distribution models with herbivore
29 home range size estimates to test our hypothesis that hare home range size will be smaller
30 in areas with access to high, homogeneous resource quality compared to areas with access
31 to low, heterogeneous resource quality during summer months. Our results support our pre-
32 diction for lowland blueberry, but not for red maple. Herbivore home range size decreased
33 with increasing blueberry foliage quality, but also with decreasing spatial heterogeneity in
34 blueberry foliage quality, i.e. N or P content. Herbivores in the boreal forest face strong
35 nutritional constraints due to the paucity of N and P. Access to areas of high, homogeneous
36 resource quality is paramount to meeting their dietary requirements with low effort. In
37 turn, this may influence community (e.g., trophic interactions) and ecosystem (e.g., nutrient
38 cycling) processes. Paradoxically, our study shows that taking a reductionist approach of
39 viewing resources through a biochemical lens can lead to holistic insights of consumer spatial
40 ecology.

41 **Keywords:** home range, ecological stoichiometry, snowshoe hare, boreal forest, resource
42 quality, space use

43 Introduction

44 Environmental and organismal variability within ecosystems are tightly interconnected. Geo-
45 chemical, atmospheric, and biological factors drive differences in the elemental composition
46 of primary producers across landscapes (Ågren and Weih, 2012; Borer et al., 2015; He et
47 al., 2015). For example, elemental ratios in marine phytoplankton can vary widely across
48 latitudinal gradients of environmental variables (e.g., ocean temperature; Martiny et al.,
49 2013). Indeed, environmental variability in the supply of key elements like phosphorus (P)

50 and nitrogen (N) is the single best predictor of differences in cellular concentrations of these
51 elements among phytoplankton (Galbraith and Martiny, 2015). As well, species composition
52 of local producer and consumer communities can influence carbon (C) and N concentrations
53 in foliar tissues of plant species (Borer et al., 2015). This variability in elemental compo-
54 sition of autotrophs produces areas of high and low quality resources for herbivores across
55 landscapes (Jean et al., 2015; Leroux et al., 2017). In turn, spatial heterogeneity in resource
56 elemental composition – i.e., their stoichiometry (Sterner and Elser, 2002) – can influence
57 consumers’ foraging strategies (Ball, Danell, and Sunesson, 2000; Youngentob et al., 2011).
58 However, few studies to date have investigated how consumers’ space use varies in response
59 to variability in resource stoichiometry (but see McNaughton et al., 1989). Here, we inves-
60 tigate how this mosaic of elemental hot and cold-spots in resource elemental composition
61 (*sensu* Bernhardt et al., 2017; McClain et al., 2003) may influence the home range size of a
62 small terrestrial mammal, the snowshoe hare (*Lepus americanus*).

63 The home range, the area an animal routinely uses to meet its daily needs (Burt, 1943;
64 Powell and Mitchell, 2012), varies in size within and across species under the effect of multiple
65 variables (Table 1; Tamburello, Côté, and Dulvy, 2015). For instance, the higher energetic
66 needs arising from bigger body size lead to larger home range size (Peters, 1983). Likewise,
67 diet composition and ecosystem function can also influence the size of an individual’s home
68 range (Tamburello, Côté, and Dulvy, 2015). Carnivores tend to have larger home ranges than
69 omnivores and herbivores due to the patchier nature of the resources they seek (Tamburello,
70 Côté, and Dulvy, 2015; Tucker, Ord, and Rogers, 2014). As well, species living in low
71 productivity habitats tend to have larger home ranges than species living in high productivity
72 ones, because they need to move more to find enough food to avoid starvation (Tucker,
73 Ord, and Rogers, 2014). For example, experimental evidence points to terrestrial herbivores
74 responding to variability in both quantity and quality of their preferred resources at multiple
75 spatio-temporal scales (e.g., Ball, Danell, and Sunesson, 2000; Nie et al., 2015). Yet, studies
76 often rely on proxies to measure variability in resource quality and these proxies can vary

77 among study systems, from forage species identity (van Beest et al., 2011), to nutritional
78 value (e.g., carbohydrate content; Saïd et al., 2009), to forage availability (Duparc et al.,
79 2020). Within the framework of ecological stoichiometry, resource quality is often defined
80 based on the elemental composition of the resource — that is, its content of key nutrients
81 such as C, N, and P (Leal, Seehausen, and Matthews, 2017). Here, we argue that spatial
82 variability in a resource’s elemental composition may inform consumer space use.

83 Animals make space use decision at multiple spatio-temporal scales, from which food
84 items to forage on in a patch to where to establish their geographic range(Johnson, 1980).
85 Within a patch, available food items vary in their quality and quantity and animals, in
86 turn, forage only on some of these food items (4^{th} order selection; Johnson, 1980). Koalas
87 (*Phascolarctos cinereus*) and greater gliders (*Petauroides volans*) prioritize use of high-quality
88 *Eucalyptus* spp. patches, albeit in different ways: while koalas search for and forage longer
89 on trees whose leaves have high N concentrations (Marsh et al., 2014; Moore et al., 2010),
90 greater gliders actively avoid those trees with high levels of N-based secondary metabolites in
91 their leaves (Youngentob et al., 2011). Thus, animals tend to use some areas of the landscape
92 more than others (3^{rd} order selection; Johnson, 1980). For instance, in Scandinavia, moose
93 (*Alces alces*) and mountain hare (*Lepus timidus*) visited white birch (*Betula pubescens*) and
94 Scots pine (*Pinus sylvestris*) more frequently in N-fertilized areas compared to unfertilized
95 controls (Ball, Danell, and Sunesson, 2000). Home ranges arise from these patch use patterns.
96 For example, bamboo-exclusive giant pandas (*Ailuropodia melanoleuca*) seasonally shift their
97 range and vary their home range size in response to variation in N, P, and calcium content
98 in their food — consistently foraging on the highest-quality food available as a result (Nie
99 et al., 2015).

100 As these examples show, resource elemental composition can play an important role in
101 determining how animals use their space: where they forage, what they forage on, for how
102 long, and when. With the recent development of new statistical methods to predict resource
103 stoichiometry at landscape extents (e.g., Galbraith and Martiny, 2015; Leroux et al., 2017;

104 Soranno et al., 2019), we can investigate how resource elemental composition influences
105 consumers' distribution beyond the local patch. For example, stoichiometric distribution
106 models (henceforth, StDMs) can predict element distributions over landscapes and allow
107 identification of hot and cold spots of resource elemental composition across spatial extents
108 (Leroux et al., 2017). StDMs allow for studying patterns of consumers' space use and
109 distribution in a stoichiometrically informed way. For instance, Leroux et al. (2017) used
110 StDMs predictions to investigate the spatial distribution of moose (*A. alces*) at the landscape
111 extent, in the boreal forests of northern Newfoundland. Spatial distribution models of moose
112 performed consistently better when including a measure of forage elemental composition
113 (e.g., elemental dry weight, % content, or ratios), providing evidence that spatial gradients
114 in plant stoichiometry may influence herbivores' space use decisions (Leroux et al., 2017).
115 Consequently, as in the case of the giant panda mentioned above (Nie et al., 2015), spatial
116 variability in forage elemental composition may also drive an animal's home range size.

117 Here, we use elemental distribution models, i.e., StDMs, to investigate the relationship
118 between summer home range size and resource elemental composition in snowshoe hares
119 (*L. americanus*). Snowshoe hares are a keystone herbivore in the boreal forests of North
120 America (Feldhamer, Thompson, and Chapman, 2003). Snowshoe hare habitat is strongly
121 N and P-limited (Price et al., 2013), and these constraints influence their ecology, behavior,
122 and physiology (Murray, 2002; Thornton et al., 2013). These characteristics make snowshoe
123 hares uniquely suited to address these questions. We use stoichiometric ratios — e.g., C:N,
124 C:P, N:P ratios — as proxies for resource quality for snowshoe hares. High C:N or C:P
125 forage tends to be woody, hence less digestible, whereas high N:P forage may not offset the
126 boreal forest's strong P-limitation (Leroux et al., 2017; Townsend et al., 2007). Hence, we
127 consider food items with low C:N, C:P, and N:P ratios as higher quality resources than those
128 with high C:N, C:P, or N:P ratios. As well, snowshoe hares may respond to the overall
129 quality of an area — i.e., the area's average quality — or to the variation in quality within an
130 area — i.e., how heterogeneous the quality of an area is (Zweifel-Schielly et al., 2009). Thus,

131 we test the hypothesis that spatial differences in average resource quality, the variability of
132 resource quality, or both influence snowshoe hare home range size (Figure 1). We predict
133 that (i) snowshoe hares in areas of homogeneous resource quality (low variability) will have
134 smaller home ranges than individuals in areas with more spatially heterogeneous resources.
135 We further predict that (ii) snowshoe hares in areas of lower average forage C:N or C:P
136 ratio will have smaller home ranges than individuals in areas in which these forage ratios are
137 higher. For N:P ratio, we predict (iii) that snowshoe hares will have larger home ranges in
138 areas of high N:P ratio, i.e. P-limited, than in areas of low N:P ratio, i.e. N-limited. Finally,
139 we expect (iv) that in areas with low and spatially homogeneously stoichiometric ratios (low
140 mean and low variation), snowshoe hares will have smaller home ranges compared to areas
141 where these metrics are both high or where one is high and the other is low.

142 **Methods**

143 **Study Area**

144 We conducted our study in four boreal forest stands in eastern Newfoundland, Canada,
145 in and around Terra Nova National Park (48°31'50" N, 53°55'41" W; Figure S1). We se-
146 lected forest stands based on snowshoe hare habitat preferences and along a forest stand age
147 chronosequence with four categories; 20–40 years old, 41–60 y. o., 61–80 y. o., and 81–100
148 y. o. (see SI Section S3 for more details). In all four forest stands, black spruce (*Picea mar-*
149 *iana*) dominates the canopy, which also comprises balsam fir (*Abies balsamea*), red maple
150 (*Acer rubrum*), white birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Lowland
151 blueberry (*Vaccinium angustifolium*), Sheep laurel (*Kalmia angustifolia*), and Labrador tea
152 (*Rhododendrum groenlandicum*) dominate the understory. In May 2016, we established a
153 500 m×500 m snowshoe hare live trapping grid housing 50 Tomahawk live traps (Tomahawk
154 Live Trap Company, Hazelhurst, WI) along a meandering transect in each of the four forest
155 stands (see SI section S3 and fig. S2).

156 Spatial Variability in Food Stoichiometry

157 We collected plant samples, ~20 g wet weight, in and around each trap location on the
158 four live-trapping grids during the summer months of 2016 and 2017. We focused on three
159 important summer forage species for snowshoe hares (Dodds, 1960): lowland blueberry (*V.*
160 *angustifolium*), red maple (*A. rubrum*), and white birch (*B. papyrifera*). Our sampling
161 attempted to replicate hare browsing by collecting only new growth material — that is, new
162 leaves and terminal ends of branches. We shipped 10 g dry weight from each sample to the
163 Agriculture and Food Laboratory at the University of Guelph to measure content of C, N,
164 and P for each of our three plant species of interest (listed above; henceforth, SOI).

165 In our analyses, we used quantitative predictions of foliar C:N, C:P, and N:P ratios
166 obtained from fitting StDMs to the stoichiometry data obtained from plant samples from all
167 four grids. We built five StDMs. Here we briefly describe the procedure behind building and
168 fitting StDMs (see Heckford et al., n.d., *in revision* for detailed methods and Leroux et al.,
169 2017, for general background on StDMs). To build each StDM, we used three types of plant
170 SOI data: (i) sampling plot density data from a shrub belt sampled along the South-North
171 diameter (22.6m) of the plot, divided into 4 height classes; (ii) elemental percentages, i.e., %
172 C, N, P, extracted from foliar samples; and (iii) biomass data collected in areas adjacent to
173 our sampling grid. We first fit allometric models for each study species using the formula:
174 $\log(\text{biomass}) \sim \log(\text{basal diameter} + \text{height})$. At the sampling plot level, this allowed us
175 to estimate density of plant SOI by height class based on shrub belt data, and to use these
176 estimates to predict plant SOI biomass by height class in each sampling plot. We then
177 calculated C, N, P foliar content per SOI per plot by dividing a SOI's total plot biomass
178 by the product of plot area and foliar elemental content (% dry weight). We obtained C,
179 N, P quantity estimates by dividing elements' foliar content by their molar weight, and
180 stoichiometric ratios from these estimates (C:N, C:P, N:P; Heckford et al., n.d., *in revision*).

181 Each StDM included spatially explicit covariates, grouped into four categories: land
182 cover, productivity, biotic, and abiotic factors. Preliminary analyses of yearly variation in

183 plant SOI stoichiometry showed negligible variability between 2016 and 2017 (Richmond et
184 al., n.d., *in review*). Hence, we did not include year of sampling as a covariate in our StDMs.
185 We fit a set of 15 Generalized Linear Models based on *a priori* hypotheses (see Heckford
186 et al., n.d., *in revision*), including a null model, to nine response variables: percent element
187 content (% C, N, P), quantity element content (C, N, P, g/m^2), and stoichiometric ratios (C:N,
188 C:P, N:P). We used the Akaike Information Criterion corrected for small sample size (AICc;
189 Burnham and Anderson, 2002) to assess the weight of evidence supporting each model. After
190 removing uninformative parameters (*sensu* Leroux, 2019), we used the top-ranked model for
191 each SOI-stoichiometric ratio pair to produce predictive plant SOI stoichiometry surfaces as
192 proxies for resource quality available within hare home ranges.

193 **Home range size and stoichiometry**

194 In May–November of 2016 through 2019, we live-trapped and radio-collared snowshoe hares
195 in the youngest forest stands, 20–40 years old (henceforth, hare study area). We baited each
196 trap at dusk with apple slices, alfalfa, and rabbit chow, and checked them the following dawn.
197 We collected body weight (g) and other demographic data of each hare, before fitting it with
198 a 25 g radio collar (M1555, Advanced Telemetry Systems, Isanti, MN) and releasing it. We
199 did not fit individuals with radio-collars when the weight of the collar was $\geq 5\%$ of the hare’s
200 own body weight. The Animal Care Committee of Memorial University of Newfoundland
201 approved our live-trapping and handling protocol with permit 18-02-EV. Further details on
202 our live-trapping protocol can be found in SI section S3.

203 In May–September of 2017 through 2019, we located snowshoe hares using handheld
204 receivers (Biotracker, Lotek, Ontario, CA) and VHF antennas (RA–23K, Telonics, AZ).
205 We collected three or more azimuths per hare per day, storing them in an electronic data
206 collection form on an iPad (FileMaker Pro Advanced, v. 14; Claris International Inc., 2015)
207 and using digital maps (Avenza Maps, v. 3.7; Avenza Systems Inc., 2020) to check the
208 triangulation polygon’s size. We estimated home range size and ran all subsequent analyses

209 in R (v. 4.0.1; R Core Team, 2020). For each hare in our sample ($n = 30$), we used package
210 `razimuth` to estimate collar location based on the Azimuthal Telemetry Model (Gerber
211 et al., 2018). From these locations, we estimated the Utilization Distribution (UD) of our
212 snowshoe hares using the autocorrelated Kernel Density Estimator corrected for small sample
213 size (AKDEc) using the `ctmm` R package (Fleming and Calabrese, 2017; Fleming, Noonan,
214 et al., 2019). From the UDs, we estimated home range area in hectares (ha) at the 50%,
215 75%, and 90% isopleths. For more details on our home range estimation workflow, please
216 see SI section S5 and the Supporting Code document.

217 We used function `extract` from the `raster` R package (Hijmans, 2020) to overlay the
218 boundary of each snowshoe hare's home range area estimate, i.e, the 50%, 75%, 90% UD
219 isopleths, on the stoichiometric surfaces and get C:N, C:P, and N:P values for every pixel
220 covered by the home range (see Supporting Code for more details). From these data, for each
221 home range, we estimated (i) each stoichiometric ratio's mean value and (ii) its coefficient
222 of variation. The coefficient of variation (henceforth, CV), the ratio of a sample's standard
223 deviation to its mean value, provides an easy-to-interpret assessment of how variable the
224 predicted SOI stoichiometry of a given home range is, compared to its mean value. See
225 Supporting Code for more details.

226 **Statistical Analyses**

227 We used linear models to investigate the effects of resource stoichiometry, i.e., mean, CV,
228 and their interactive effects, and body weight on the size of the home range of snowshoe hares
229 estimated at the 50% (i.e., the core area; Börger et al., 2006), 75%, and 90% isopleths. We
230 included body weight to capture potential intraspecific variability in home range size due to
231 an individual's ecology and physiology (Peters, 1983). Conversely, we did not include year of
232 sampling, as preliminary analyses provided no evidence it influenced home range size of our
233 snowshoe hares (see Supplementary Code; Börger et al., 2006). As well, we did not include
234 sex in our models as evidence for snowshoe hares points to this variable being correlated with

235 body weight (Feldhamer, Thompson, and Chapman, 2003) and does not appear to influence
236 the elemental composition of snowshoe hares (Rizzuto et al., 2019). For each combination of
237 plant SOI and C:N, C:P, and N:P ($n = 5$), to test prediction (i) we fit a model including each
238 stoichiometric ratio's CV. Likewise, to test predictions (ii) and (iii) we fit a model including
239 the ratios' mean values. To test prediction (iv) we fit a model including the additive effects
240 and a model including the additive and interactive effects of the ratios' mean and coefficient
241 of variation. For each model, we also fit a version that included the hares' body weight.
242 We fit this set of 8 models, plus a null model, to our dataset and used function `AICc` in the
243 `AICcmodavg` R package to select top models based on parsimony (Burnham and Anderson,
244 2002; Mazerolle, 2017). Following Leroux (2019), we removed uninformative parameters
245 from the model set of each stoichiometric ratio. Below, we report summary AICc tables and
246 refer the interested reader to the Supporting Code document for full AICc tables.

247 Results

248 StDMs of red maple C:N, N:P ratios, and lowland blueberry C:N, C:P, N:P ratios all ranked
249 above the null model whereas all other StDMs (i.e., red maple C:P ratio, white birch C:N,
250 C:P, N:P ratios) were not supported by the data (Heckford et al., n.d., *in revision*). We used
251 this suite of five StDMs to produce geo-referenced predictions of resources' spatial variability
252 in and around our hare study area.

253 Our sample of radiocollared snowshoe hares included 30 individuals: 4 followed during
254 summer 2017, 6 in summer 2018, and 20 during summer 2019. We followed four snowshoe
255 hares for two consecutive sampling years: three in the 2018 and 2019 sampling seasons and
256 one in the 2017 and 2018 sampling seasons. For the individuals sampled in more than one
257 year, we included in the analyses only the home range size estimate from the year with the
258 most telemetry points. Our results are not sensitive to this decision (see Supplementary
259 Code). Our sample included 14 females, 12 males, and 4 individuals of unknown sex. Adult

260 hares comprised the majority of our sample ($n=27$), with two young-of-the-year and one
261 unknown. Mean core area size was 4.292 ha (range: 0.835–11.465) for 2017, 3.104 ha (range:
262 0.215–6.163) for 2018, and 2.68 ha (range: 0.486–7.403) for 2019 (3-year mean \pm SD: 2.996 ha
263 \pm 2.300). For lowland blueberry, within the core area, predicted C:N ratio ranged from 45.32
264 to 49.17 (median: 47.15), predicted C:P ratio ranged from 1201 to 2277 (median: 1279), and
265 predicted N:P ratio from 25.15 to 45.42 (median: 28.09). For red maple, predicted C:N ratio
266 ranged from 23.26 to 39.79 (median: 30.89) and predicted N:P ratio ranged from 28.39 to
267 39.09 (median: 34.13).

268 We found mixed support for prediction (i), resource quality heterogeneity influencing
269 home range size. The CV of lowland blueberry C:N ratio and red maple N:P ratio appeared
270 in the top models for home range core area size (slope = 3.429 ± 0.664 , $R^2 = 0.548$, and
271 slope = 0.866 ± 0.378 , $R^2 = 0.15$, respectively; Table 2 and fig. 2). This trend holds at all
272 kUD isopleths for lowland blueberry, but not for red maple (Tables S1 and S2). Indeed, the
273 CV of lowland blueberry C:N ratio explained a higher portion of the variation in snowshoe
274 hare home range size, compared to the mean value of this ratio (CV-only model $R^2 = 0.376$,
275 mean-only model $R^2 = 0.102$; Table 2). We found no evidence of this relationship for the
276 CV of lowland blueberry C:P, N:P ratios, and only weak evidence supporting this trend for
277 the CV of red maple C:N ratio for home range size estimates at 50% (slope = 0.127 ± 0.089 ,
278 $R^2 = 0.166$; Table 2) and 75% kUD (Table S1).

279 We found mixed support for our prediction (ii) on the effects of average C:N ratio and C:P
280 ratio on home range size. The mean values for lowland blueberry foliage C:N ratio and C:P
281 ratio appeared in top models (slope = 4.224 ± 1.316 , $R^2 = 0.548$, and slope = 0.008 ± 0.004 ,
282 $R^2 = 0.116$, respectively; Table 2 and fig. 2), with the trend holding at all three isopleths for
283 average C:N ratio, but only at the 75% isopleth for average C:P ratio (Tables S1 and S2).
284 While the top model included both mean and CV of lowland blueberry C:N ratio, the mean-
285 only model was ranked 3rd overall and explained 10% of the variation in hare home range
286 size (Table 2). No support for this prediction came from models using average red maple

287 C:N ratio (Tables S1, 2 and S2). As well, we found weak evidence supporting prediction
288 (iii), home range size increasing as resources' N:P ratio increases, from lowland blueberry
289 foliage (slope = 0.327 ± 0.245 , $R^2 = 0.159$; Table 2) but the trend does not hold at either
290 the 75% or 90% isopleth (Tables S1 and S2). We found no support for prediction (iv) at
291 any kUD isopleth for C:N and C:P any of the three ratios considered, as the top models for
292 lowland blueberry C:N ratio and C:P included the additive effects of mean and CV and only
293 the mean, respectively (Table 2, and Tables S1 and S2).

294 Discussion

295 Animals forage on a variety of resources whose elemental composition may influence space use
296 and foraging patterns at multiple spatial scales (Duparc et al., 2020; Lima and Zollner, 1996;
297 van Beest et al., 2011). We found evidence that spatial differences in a preferred resource's
298 predicted average elemental composition or its variability correlated with herbivore home
299 range size. Additionally, forage species identity may also play a role, further influencing
300 these relationships. Together, our results provide evidence supporting the role that resources'
301 elemental content plays in influencing consumers' spatial ecology. Our results suggest that
302 exploring the fundamental question of animal space use through an elemental lens may
303 allow researchers to better trace the feedbacks between animals and ecosystem functions,
304 e.g., elemental cycling (Schmitz et al., 2018).

305 The boreal forest is a strongly N and P-limited ecosystem (Price et al., 2013). Snowshoe
306 hares need to carefully balance their intake of C-heavy plant food against their N and P
307 growth requirements (Sterner and Elser, 2002). Our results provide explicit evidence of
308 this elemental trade-off at the home range scale and highlight how differences in resource
309 elemental phenotype within and across areas used by snowshoe hares underlie variation
310 in home range size in a heterogeneous landscape. In particular, results for both lowland
311 blueberry foliage C:N ratio and red maple foliage N:P ratio support prediction (i), that

312 variability in N and P content within a home range core area can influence its size (Table 2).
313 Snowshoe hares in our study appear to readily respond to stoichiometric changes in lowland
314 blueberry, one of their preferred summer forage (Dodds, 1960). Variability in the elemental
315 phenotype of the main components of a consumer's diet appears to influence both their
316 spatial and temporal distribution over the environment (McNaughton et al., 1989; Nie et al.,
317 2015). In our study area, lowland blueberry is more abundant than red maple as well as,
318 overall, more browsed (SI Figure S7). A higher sensitivity to the variability in quality of this
319 resource, then, may point to the elemental composition of these two plant species playing
320 a fundamental role in a snowshoe hare's efforts to meet its high nutritional requirements
321 (Murray, 2002).

322 Furthermore, we find evidence that elements can influence home range core area size
323 even when considering an area's average quality — i.e., when smoothing the variation to
324 a single value — in accordance with predictions (ii) and (iii). In particular, low average
325 values of C:N, C:P, and N:P ratios for lowland blueberry consistently correspond to smaller
326 home range size (Table 2 and Figure 2). This held true for C:N ratio whether estimated
327 home range size from the core area or from larger UD slices — suggesting that resource
328 quality may influence space use decisions at a higher order of selection (i.e., landscape or 3rd
329 order of selection Johnson, 1980). Interestingly, we additionally find evidence that a ratio's
330 coefficient of variation may add an additional side to this relationship, as it appears in the
331 top model for lowland blueberry foliage C:N ratio at all three UD slices. Indeed, hares living
332 in areas of high mean and high coefficient of variation for the foliage C:N ratio of lowland
333 blueberry appear to have larger home ranges than those living in areas where mean values
334 are high but the coefficient of variation is small (Figure 1, panel d, Table 2, and Tables S1
335 and S2). Thus, consumers may use different information cues to make space use decisions
336 at different spatial scales — e.g., across vs. within patches on the landscape.

337 Similar effects of resource quality on herbivore space use patterns have been described
338 in other study systems. For instance, other species of leporids, as well as ungulates, tend

339 to increase use of areas where they have access to forage with higher content of limiting
340 nutrients (Ball, Danell, and Sunesson, 2000). In turn, this preferential use of areas where
341 forage is high in limiting nutrient content appears related to reproductive and physiological
342 benefits (Mcart et al., 2009) or to population dynamics (Merkle et al., 2015). Overall, the
343 elemental composition of forage items appears to be a fundamental driver of herbivore space
344 use across spatial scales; from which food items to eat within a patch, to which habitats
345 to establish a home range in, to which areas to visit over the landscape (Ball, Danell, and
346 Sunesson, 2000; Nie et al., 2015; Zweifel-Schielly et al., 2009).

347 Evidence of resource quality influence on space use decisions of consumers arising from
348 several study system corroborates this result (e.g., Nie et al., 2015; Saïd et al., 2009; van
349 Beest et al., 2011). Indeed, the majority of the hares in this study appear to live in areas
350 of relatively high N and P values in the foliage of both red maple and lowland blueberry
351 (Figure 1, panel d). The few cases of use of areas with high resource heterogeneity may
352 result from population dynamics, particularly the increase in hare numbers from 2017 to
353 2019. In 2017, our collared snowshoe hares all had home ranges in relatively high quality
354 areas for lowland blueberry. As more snowshoe hares appeared on the landscape in 2018
355 and 2019, new individuals increasingly established larger home ranges that extended beyond
356 the areas of lower heterogeneity or higher overall N or P availability. Furthermore, the high
357 degree of overlap we found between home range estimates calculated for hares with more
358 than one year of telemetry data may point to a limited ability of older snowshoe hares to
359 retain their range across years (Table S3 and Figures S3 to S6). Other herbivores appear to
360 have similar growth-dependent colonization of less-favorable areas of a landscape. Among
361 bison (*Bison bison*), individuals appeared to expand their population range to include areas
362 of lower resource quality and establish larger home ranges in them as population density
363 increased over time (Merkle et al., 2015). Similar patterns of population spatial distribution
364 driven by resource availability and foraging strategies are fairly well-known among passerine
365 birds (Piper, 2011). The elemental composition of foraging resources, then, may not only

366 influence the size of a consumer's home range, but also its location over the landscape.
367 However, to our knowledge, this study is the first to show that key chemical elements may
368 drive animal space use decisions.

369 We modeled our measure of forage quality, forage stoichiometry, based on a suite of en-
370 vironmental, biotic, and abiotic covariates (Heckford et al., n.d., *in revision*). This approach
371 may help investigate direct drivers of consumer space use and shed light on ecosystem char-
372 acteristics allowing high-quality resources to persist in an area. In turn, the environmental
373 drivers that correlate with forage stoichiometry may indirectly influence a consumer's spa-
374 tial ecology even in the absence of the resource itself. Further, StDMs allow accounting
375 for multiple ecological currencies shaping a consumer's ecology at varying spatio-temporal
376 scales (Levin, 1992; Lima and Zollner, 1996). Thus, applying stoichiometric measures of
377 forage to model consumer space use may be a fundamental tool in bridging metabolic, nu-
378 tritional, landscape, and behavioural ecology (Sturner, 2004). In turn, this may allow us
379 to disentangle the ubiquitous relationships and feedbacks among consumer, resources, and
380 the environmental and ecological processes they are part of (Levin, 1992; Lima and Zollner,
381 1996). Furthermore, our StDM-driven approach explains a large portion of the variance ob-
382 served in our sample, albeit with some variability among model sets (see Tables S1 and S2).
383 Indeed, the elemental composition of resources has been shown to accurately describe and
384 predict the spatial distribution patterns of consumers in a variety of biomes, from boreal
385 (this study), to tropical (McNaughton et al., 1989), to temperate (Merems et al., 2020; Nie
386 et al., 2015).

387 Overall, our results provide evidence that ecological stoichiometry may help researchers
388 understand fundamental components of consumers' space use. Based on the emergent field
389 of spatial stoichiometry (Galbraith and Martiny, 2015; Leroux et al., 2017; Soranno et al.,
390 2019) and our own results, we argue that using the elemental composition of resources to
391 investigate patterns of consumer space use may provide a comparable and potentially more
392 parsimonious approach than other, more widespread methods — e.g., habitat classification

393 (Zweifel-Schielly et al., 2009), forage species identity (van Beest et al., 2011), or availability
394 (Duparc et al., 2020). Focusing on stoichiometric currencies would allow for consistency in
395 defining and measuring fundamental metrics, e.g., resource quality, across studies and study
396 systems. It would also reduce the need to rely on elemental conversion factors, increasingly
397 recognized as problematic due to their lack of generality across different food items and
398 outdated estimation methods (Mariotti, Tomé, and Mirand, 2008). As well, stoichiometric
399 currencies may help investigate the different experiential layers that make up an animal's
400 home range (*sensu* Powell and Mitchell, 2012), further refining how researchers measure,
401 describe, and interpret animal space use at multiple spatio-temporal scales (Levin, 1992).
402 Finally, rooting theoretical models of ecological processes in stoichiometric units may make
403 them more widely applicable to real world scenarios (Schmitz et al., 2018).

404 Life builds itself using a limited subset of elements (Kaspari and Powers, 2016). These
405 are continuously transformed and exchanged, globally, among organisms and their abiotic
406 environment, and within and across ecosystem borders. Ecological stoichiometry offers an
407 ultimately reductionist approach that, by providing common units of measurement with
408 which to describe both actors and currencies involved in these exchanges, may effectively
409 provide researchers with a holistic perspective to explore animal space use.

410 **Data Availability:** All the data and code used in the analyses are available in a figshare
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582 Tables

Table 1: Environmental and ecological drivers of home range size among mammals.

Variable	Effect	References
Body Size	larger body mass corresponds to larger home ranges	Jetz (2004), Kelt and Van Vuren (2001), Mace and Harvey (1983), Ofstad et al. (2016), Peters (1983), and Tucker, Ord, and Rogers (2014)
Habitat	richer habitats usually corresponds to smaller home ranges	Dussault et al. (2005), Fridell and Litvaitis (1991), Ofstad et al. (2016), Tucker, Ord, and Rogers (2014), Walton et al. (2017), and Willems and Hill (2009)
Information	previous knowledge of an area's distribution of resources, risk sources, mates, and refugia varies how individuals use available space	Merkle et al. (2015), Powell and Mitchell (2012), Spencer (2012), and Zweifel-Schielly et al. (2009)
Diet	carnivores have larger home ranges than herbivores and omnivores	Kelt and Van Vuren (2001), Mace and Harvey (1983), and Tucker, Ord, and Rogers (2014)
Energy	increasing energetic demands lead to larger home ranges	Kelt and Van Vuren (2001) and Mcart et al. (2009)
Behaviour	sociality can reduce home range size by allowing for more efficient foraging (e.g., pack hunting)	Carbone, Teacher, and Rowcliffe (2007)

Table 2: Top ranking GLMs describing the relationship between home range core area and resource stoichiometry, after removing uninformative parameters (see Supporting Code for full AICc tables). For each plant SOI and stoichiometric ratio pair, we report the top model, any model above the intercept, and the intercept. For coefficients, we report values as *estimate* ($\pm SE$). Column headers: K, number of parameters in the model; LL, log-likelihood; CV, Coefficient of Variation; BW, body weight.

K	$\Delta AICc$	LL	R^2	Coefficients			
				Intercept	Mean	CV	BW
Blueberry C:N top models							
4	0.000	-55.783	0.548	-199.097 (± 62.029)	4.224 (± 1.316)	3.419 (± 0.664)	
3	7.025	-60.634	0.376	0.058 (± 0.789)		3.110 (± 0.757)	
3	17.952	-66.098	0.102	-148.049 (± 84.809)	3.208 (± 1.802)		
2	18.792	-67.707	0.000	2.974 (± 0.430)			
Blueberry N:P top models							
3	0.000	-65.859	0.116	-3.230 (± 7.684)	0.327 (± 0.245)		-0.002 (± 0.001)
2	0.033	-67.707	0.000	2.974 (± 0.430)			
Blueberry C:P top models							
3	0.000	-65.859	0.116	-7.999 (± 5.741)	0.008 (± 0.004)		
2	1.218	-67.707	0.000	2.974 (± 0.430)			
Red Maple N:P top models							
3	0.000	-65.130	0.158	0.162 (± 1.291)		0.866 (± 0.378)	
2	2.676	-67.707	0.000	2.974 (± 0.430)			
Red Maple C:N top models							
4	0.000	-64.980	0.166	5.080 (± 2.338)		0.127 (± 0.089)	-0.002 (± 0.001)
3	0.000	-66.318	0.088	1.644 (± 0.908)		0.149 (± 0.090)	
2	0.299	-67.707	0.000	2.974 (± 0.430)			

583 Figure Legends

584 **Figure 1.** Predictions of the relationship between resource elemental composition and home
585 range size in snowshoe hares. **(a)**: as variability in resource elemental composition increases,
586 home range size will also increase, as per predictions (i) and (iii). **(b)**: with increasing av-
587 erage resource elemental composition, home range size will increase, as per predictions (ii)
588 and (iii). **(c)**: jointly, these two dimensions of variation produce a “resource quality space”,
589 where they interact to influence home range size — as per prediction (iv). In this space,
590 where average resource quality is high and its variability low, herbivore home range size will
591 be small (quadrant 1). Conversely, when variability is high and average quality is low, home
592 range size will be large (quadrant 3). When either average quality is high and its variability is
593 low or vice versa, home range size will be intermediate between the two extremes (quadrants
594 2 and 4). **(d)**: distribution of snowshoe hare home range size estimates (ha) from this study
595 ($n = 30$) in lowland blueberry resource quality space, defined by foliage C:N ratio. Most
596 hares in our sample live in areas of moderate lowland blueberry C:N content and variability.
597 Some individuals maintain small home ranges in areas of relatively homogeneous, medium-
598 to-high lowland blueberry foliage C:N ratio (e.g., A1673, A2702, A2081). Conversely, a few
599 snowshoe hares with large home ranges live in areas of heterogeneous, low-quality lowland
600 blueberry (e.g., A3705). The empty lower left corner may indicate that no areas of high and
601 homogenous resource quality are available in our study area, or that no hares are using it if it
602 is present. Data point size reflects 50% UD home range size; different colors identify different
603 individuals. Different shapes separate individuals with more than one year of telemetry sam-
604 pling (squares, A1425; diamonds, A1698; triangles, A3719; upside-down triangles, A3769)
605 from individuals with only one year of telemetry (circles). The Supplementary Information
606 contains additional details on the degree of overlap between home ranges from consecutive
607 years for these four individuals (Table S3 and Figures S3 to S6).

608 **Figure 2.** Relationship between lowland blueberry foliage C:N ratio quality metrics
609 and home range size, at 50%, 75%, and 90% UD. **Upper panels:** the size of home range

610 core area for our snowshoe hares is smaller in areas of lower mean lowland blueberry foliage
611 C:N ratio and increases with the ratio's mean value (panel a). Home range sizes estimated
612 from larger isopleths shows similar trends (panels b, c). Higher values of C:N ratio point
613 towards lower availability of N in blueberries, so that individuals living in such areas (e.g.,
614 A2084) may have to forage over larger areas to meet their elemental requirements of N to
615 survive (Sturner and Elser, 2002). **Lower panels:** at increasing values of the variability in
616 lowland blueberry foliage C:N ratio corresponds a sharp increasing in home range core area
617 size of snowshoe hares (panel d), a trend repeated at larger isopleths (panels e, f). Snowshoe
618 hares in areas of high variability of lowland blueberry N content may resort to foraging over
619 much larger areas than individuals that have access to food items of less variable quality —
620 regardless of whether this is high or low quality. Grey lines are regression lines drawn from
621 the top-ranking model for lowland blueberry C:N ratio at the relevant UD isopleth (Table 2
622 and Tables S1 and S2) and light grey shaded areas around them represent 95% Confidence
623 Intervals. All other specifications as in Figure 1.

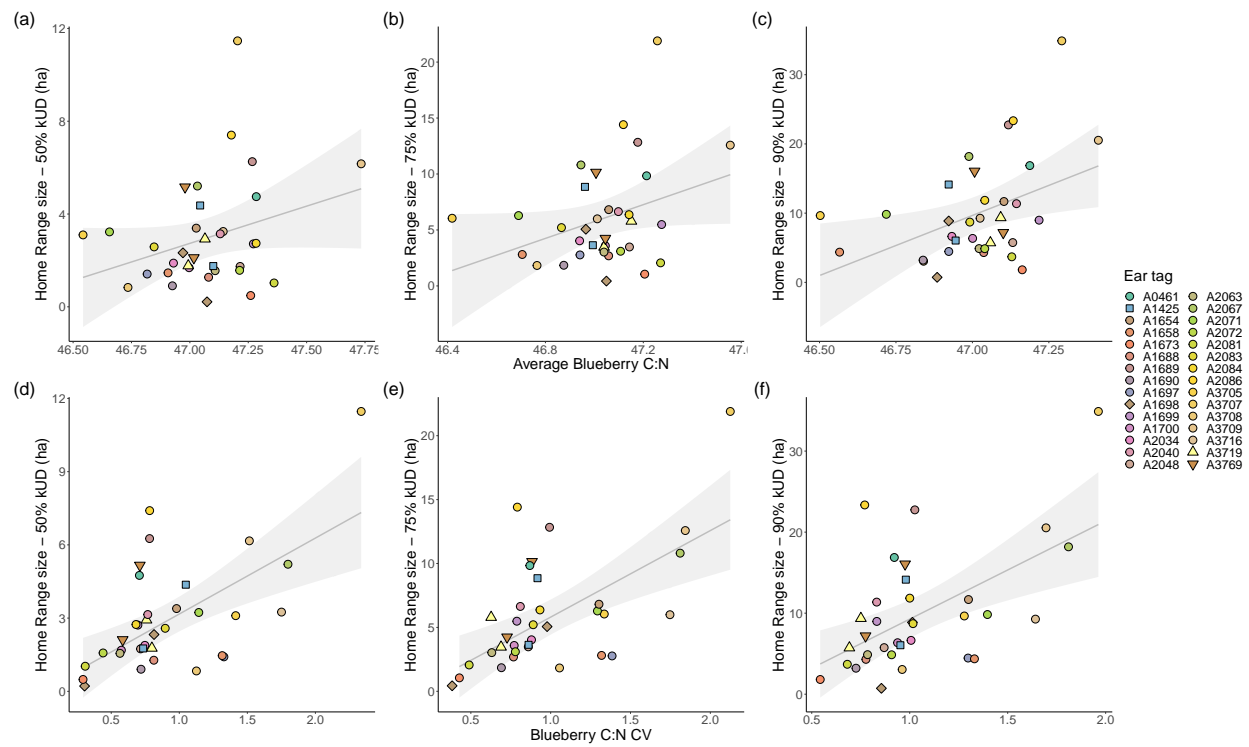


Figure 2