

1 **Plasticity and repeatability in spring migration and parturition**
2 **dates with implications for annual reproductive success**

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14 **Abstract**

15 Animals are faced with unprecedented challenges as environmental conditions change. Animals
16 must display behavioral plasticity to acclimate to changing conditions, or phenotypic variation
17 must exist within the population to allow for natural selection to change the distribution of trait
18 values. The timing of migration and parturition relative to important annual environmental
19 changes such as snowmelt and vegetation green-up and how they co-vary may influence
20 reproductive success. We tested for plasticity and individual differences in migration and
21 parturition timing as a function of the timing of snowmelt and green-up in a migratory herbivore
22 (caribou; *Rangifer tarandus*, $n = 92$) using behavioral reaction norms. We tested whether timing
23 of parturition, plasticity in parturition timing, or timing of green-up were correlated with calf
24 survival. Migration and parturition timing were plastic to the timing of spring conditions, and we
25 found moderate repeatability for migration timing, but no repeatability in timing of parturition.
26 We detected a novel behavioral syndrome where timing of migration and timing of parturition
27 were correlated. Our results suggest that observed shifts in caribou parturition timing in other
28 populations are due to plasticity as opposed to an evolutionary response to changing conditions.
29 We did not detect a correlation between annual reproductive success and either the timing of
30 spring or plasticity to the timing of spring events. While this provides evidence that many
31 populations may be buffered from the consequences of climate change via plasticity, we caution
32 that a lack of repeatability in parturition timing could impede adaptation as climate warming
33 increases.

34 **Significance Statement**

35 Animals have evolved to reproduce when resources are abundant. Climate change has altered the
36 timing of annual events, resulting in earlier peaks in resource abundance. Animals can cope with
37 this change in two ways. Individuals can display plasticity and alter the timing of reproductive
38 activities to match the change in the environment, or consistent differences among individuals
39 can result in sufficient variation to drive an evolutionary response. We tested these two
40 alternative hypotheses in caribou (*Rangifer tarandus*) using an individual-based modelling
41 framework. Caribou displayed plasticity in both when they migrated and gave birth, suggesting
42 they can acclimate to changing conditions, but we did not find evidence of differences among
43 individuals that would be likely to result in an evolutionary response.

44 Exhibiting life-history strategies to deal with fluctuations in habitat quality through time is
45 fundamental for species living in seasonal environments (1). In many species, migration is
46 viewed as a strategy to optimize use of seasonally available resources (2–4). In this context,
47 migration will be most effective when individuals adjust their movement to match the phenology
48 of their environment, which may serve as a cue to forecast spring conditions on summer range
49 (5, 6). Optimizing opportunities to reproduce in seasonal environments also depends on
50 individuals rearing young when resource availability is highest to properly finance reproduction
51 (7, 8). Climate change, however, decouples migrants from optimally timing migration, and
52 therefore reproduction. For example, warmer springs disproportionately affects the phenology, or
53 timing of annual events, in lower trophic levels compared to higher trophic levels. The result is
54 phenological asynchrony where consumers do not advance their phenologies to match that of
55 their resource (9, 10). This asynchrony can lead to reduced survival and fitness, a phenological
56 mismatch which can have significant population-level effects (10, 11). Plasticity in migratory
57 and reproductive behavior in response to phenological shifts at lower trophic levels is relevant to
58 species persistence as this plasticity likely buffers populations against adverse environmental
59 change (12). Likewise, consistent among-individual differences can provide capacity for
60 evolution within populations to adapt to changing conditions (13). Assessing potential outcomes
61 of climate change on populations will necessitate elucidating how individuals are able to
62 acclimate or adapt behaviors linked to annual reproductive success to inter-annual variation in
63 resource phenology.

64 For terrestrial herbivores, spring migration is often driven by seasonal changes in the
65 availability of high-quality forage resources (14) or snow cover that may presage future
66 conditions on summer range (6). The forage maturation hypothesis suggests that herbivores

67 should get the highest nutritional benefit by foraging on plants at an intermediate stage of growth
68 when biomass is sufficient and digestibility is high (15, 16). Animals that forage on high-quality
69 vegetation gain a nutritional benefit (17) and experience increased fat gain (18). While many
70 populations or individuals track the emergence of high-quality forage as it matures along
71 elevational and latitudinal gradients (14, 19), others use a strategy of “jumping” the green wave,
72 arriving on summer range prior to when it peaks in forage quality (“green-up”; 19). Jumping the
73 green wave may be related to snowmelt, with individuals tracking the progression of melting
74 snow along migratory routes (6). The progression of snowmelt appears to be an important factor
75 in migration timing for many northern ungulates. For example, in caribou (*Rangifer tarandus*) in
76 Alaska and northern Canada, timing of arrival on summer range was correlated with the timing
77 of snowmelt (20). Similarly for elk (*Cervus canadensis*) in Yellowstone National Park, departure
78 from winter range was correlated with snowmelt date on winter range, and timing of arrival on
79 summer range was associated with the timing of snowmelt on summer range and on migration
80 routes (21). Using melting snow to time migrations may allow individuals to arrive on calving
81 grounds to optimally take advantage of green-up during the calving season.

82 Animals that live in seasonal environments should be adapted to time their reproductive
83 phenology such that the most energetically expensive times correspond with when resources are
84 most highly abundant (7, 8). For ungulates, energetic requirements can more than double during
85 the peak of lactation (22–24). In *Rangifer*, parturition date varies among populations as a
86 function of the mean annual timing of green-up (25). Climate change disproportionately alters
87 the phenology of lower trophic levels, resulting in phenological asynchrony where consumer
88 breeding phenologies occur after the peak in resources at lower trophic levels, resulting in
89 depressed reproductive success—a phenological mismatch (9, 26, 27). For example, changing

90 sea ice phenology has altered vegetation phenology in Greenland, resulting in a phenological
91 mismatch and reduced calf survival in caribou (28, 29). Long-term data suggests advancing
92 migration and parturition dates in caribou over the last three decades, likely in response to
93 changing resource phenologies (30) or spring temperatures (31). In the case of parturition, this is
94 especially true for northern populations where climate warming has been more acute (32).

95 Populations can adjust their phenologies to cope with changes in the phenology of their
96 resources in two ways. Individuals may acclimate their phenologies directly via behavioral
97 plasticity. Alternatively, sufficient variation in phenotypes in the population might result in some
98 individuals being better adapted to novel conditions (12, 33). If that variation is consistent among
99 individuals, it may provide the pre-requisites for evolution. Plasticity is estimated over shorter,
100 i.e., within generation, timescales by making repeated observations of individual phenologies
101 and correlating them with environmental changes. Meanwhile, directly quantifying evolutionary
102 responses requires data spanning multiple generations (34). The potential for evolution, however,
103 can be inferred from shorter-term behavioral data. For example, natural selection requires traits
104 that vary among individuals, and repeatability provides a measure of the proportion of variance
105 in a trait that is attributable to differences among individuals (35). Highly repeatable behaviors
106 are consistent within individuals but vary among individuals (36). Estimates of repeatability can
107 therefore be used as tentative estimates for the potential for evolutionary responses when genetic
108 data are unavailable (37)—see for example (38–40). Behavioral reaction norms (41) provide a
109 framework to test whether contemporary changes in phenology are due to plasticity or a potential
110 evolutionary response by modelling individual-level plasticity to changing environmental
111 conditions while also estimating repeatability. Behavioral reaction norms can also quantify
112 behavioral syndromes, the degree to which behaviors and behavioral plasticity are correlated

113 (42). Exploring potential for syndromes in phenological traits, including migration and
114 parturition timing, could demonstrate the importance of individuals properly timing migration to
115 optimize the timing of parturition, with consequences to adaptation under changing
116 environmental conditions.

117 We used behavioral reaction norm analyses of individual caribou ($n = 92$) in
118 Newfoundland, Canada to test the non-mutually exclusive hypotheses that caribou exhibit
119 plasticity in the timing of migration and parturition as a function of the timing of spring, and that
120 these behaviors are repeatable traits providing variation that could result in an evolutionary
121 response. We also tested for behavioral syndromes linking both timing of migration and
122 parturition and their plasticity, and the phenological mismatch hypothesis by testing whether
123 early springs reduced annual reproductive success. We tested several predictions, including:

- 124 1) Both timing of migration (P_{1a}) and timing of parturition (P_{1b}) would display plasticity as
125 a function of changes in the annual timing of spring snowmelt. Individuals would both
126 migrate early and give birth early in years where snowmelt occurred earlier. We also
127 predicted that timing of parturition would display plasticity as a function of the timing of
128 green-up (P_{1c}), with individuals giving birth earlier when green-up was earlier.
- 129 2) Both timing of migration (P_{2a}) and timing of parturition (P_{2b}) would be repeatable
130 behaviors. Individuals that migrate or give birth early do so consistently.
- 131 3) There is a correlation between timing of migration and timing of parturition (P_3).
132 Individuals that migrate early give birth early.
- 133 4) There is a correlation in degree of plasticity in migration timing and parturition timing
134 (P_4). Individuals that are more plastic in the timing of their migration are also more
135 plastic in the timing of parturition.

136 5) Finally, we predicted that timing of green-up would influence calf survival, with lower
137 survival in early springs which represent a phenological mismatch (P₅).

138 **Results**

139 We quantified the timing of spring migration and parturition of caribou as well as the timing of
140 spring snowmelt and green-up (Figure 1). We fit two sets of behavioral reaction norm models:
141 one with timing of migration and timing of parturition as response variables with timing of
142 snowmelt as a fixed effect, and one with timing of parturition and calf survival to four weeks of
143 age as response variables, with timing of green-up as a fixed effect. Both of the top behavioral
144 reaction norm models included random slopes by individual ID for our response variables
145 (timing of arrival on summer range, timing of parturition, and calf survival) as a function of our
146 explanatory variables (timing of snowmelt and timing of green-up). This provided evidence for
147 the importance of an individual \times environment interaction (Δ DIC of both models to the next
148 most supported model > 16). At the population-level, later snowmelt was significantly associated
149 with later timing of arrival on summer range ($\beta + 95\%$ credible interval: 0.332 [0.192, 0.455], p
150 < 0.001 , supporting P_{1a}) and nearly-significantly correlated with later parturition (0.138 [-0.006,
151 0.286], $p = 0.067$, partially supporting P_{1b}), see Table 1 and Figure 2. We did not detect an effect
152 of the timing of green-up on the timing of parturition (0.094 [-0.066, 0.270], $p = 0.270$, partial
153 support for P_{1c}), see Table 1 and Figure 2.

154 We found some evidence of among individual differences in the timing of migration
155 across individuals, with repeatability for arrival on summer range being moderate (r [SD] =
156 0.377 [0.045], moderate support for P_{2a}, Figure 3, red symbols). Overall repeatability for timing
157 of parturition was quite low, suggesting that timing of parturition was not a trait that exhibited
158 consistent individual differences in these populations (snowmelt model: 0.112 [0.004], green-up

159 model: 0.051 [0.002] no support for P_{2b}, Figure 3, blue-green symbols). We found evidence of a
160 correlation between the intercept of migration timing and the intercept of parturition timing
161 (0.679 [0.162, 0.986]), where early migrators also give birth earlier (P₃; Figure 4a). We did not,
162 however, find any evidence of a link between the plasticity in arrival on summer range and
163 plasticity in timing of parturition (P₄), individuals that were more plastic in the timing of their
164 migration were not more plastic in the timing of parturition (-0.039 [-0.841, 0.757], Figure 4b).
165 There was no support for our prediction that later green-up was correlated with higher calf
166 survival (0.316 [-0.377, 1.101], $p = 0.381$, no support for P₅, Table 1). We also did not find a
167 significant correlation between timing of parturition and calf survival in an average environment
168 (the mean date of green-up; -0.254 [-0.940, 0.568], Figure 4c). There was also no evidence that
169 higher plasticity in parturition date resulted in higher overall calf survival (0.274 [-0.530, 0.951],
170 Figure 4d).

171 **Discussion**

172 An animals ability to match the phenology of life history events with changing snowmelt and
173 green-up timing is vital for persistence, both across seasonal and inter-annual changes (8). We
174 found evidence of individual differences in migration timing (P_{2a}), such that some individuals
175 consistently migrated earlier, and other individuals migrated later. Despite this, we found little
176 evidence that timing of parturition was consistent among individuals (P_{2b}). Our results suggest a
177 primary role of plasticity in contributing to shifting life history phenology in caribou over the last
178 few decades in other caribou populations (30, 32). With limited repeatability in parturition
179 timing ($r = 0.05\text{--}0.11$), likely little of the variance is genetic (35), and therefore able to respond
180 to selection. Migratory caribou in Newfoundland acclimated the timing of migration to the
181 timing of snowmelt (P_{1a}), and to a lesser extent, they also acclimated birth date to timing of

182 snowmelt (P_{1b}) but not to timing of green-up (P_{1c}). This plasticity may have been sufficient to
183 mitigate the effects of phenological mismatch on calving success in caribou, as we found no
184 evidence for reduced annual reproductive success in early springs (P₅). We also highlight a
185 behavioral syndrome where individuals that migrate early also give birth early (P₃). However, we
186 did not find evidence that plasticity in timing of migration correlates with timing of parturition,
187 suggesting that plasticity in these traits is independent (P₄).

188 The results of our study indicate that migration timing is both a repeatable trait and
189 plastic to the timing of snowmelt, outlining the importance of snow in many systems to
190 synchronize animal phenology. In our populations, individuals migrated approximately one week
191 prior to snowmelt, supporting the hypothesis that caribou use melting snow as a cue for when to
192 migrate (6). Being plastic in migration timing to changes in snow phenology likely allows
193 individuals to migrate at an optimal time to increase movement efficiency on ground or lakes
194 that are still frozen (43) but without the impediment of deep snow. Moderate repeatability
195 suggests that there are some individual differences in migration timing that could allow for
196 evolutionary change as selective pressures on optimal migration dates change. Repeatability
197 could have a genetic basis or a social one, for example, if individuals learn to migrate from
198 conspecifics (44). The repeatability of arrival timing in our population ($r = 0.377$) was slightly
199 higher than the mean value of arrival repeatability for long distance migratory birds ($r = 0.31$;
200 45). Consistent individual variation may be more favoured in environments where conditions on
201 winter range are less reliable indicators of conditions on summer range, reducing the ability of
202 individuals to be plastic to environmental variation (45). Relatively short-distance migrants like
203 caribou in Newfoundland may be more adapted to migrate at the optimal time, reducing
204 between-individual variation and therefore repeatability.

205 Caribou in our study displayed some plasticity in the timing of parturition to changes in
206 the timing of snowmelt, suggesting individuals can acclimate their reproductive ecology to
207 interannual environmental change. While timing of parturition is primarily correlated with the
208 timing of the rut, environmental conditions have also been shown to impact the timing of
209 parturition, including female body condition and spring temperature (31). Plasticity in breeding
210 date is thought to buffer populations against the consequences of changes in optimal breeding
211 date (46, 47). Earlier spring green-up has been shown to result in earlier birth in mule deer
212 (*Odocoileus hemionus*; 48). Parturition date does vary across *Rangifer* population ranges to
213 match local plant phenology (25, 32), and prior studies have documented long-term shifts in
214 parturition date in caribou (30, 32). Repeatability of parturition date was low to moderate in red
215 deer (*Cervus elaphus*, $r = 0.19$, 49) and even lower in our study on caribou (see Figure 3).
216 Newfoundland has an unpredictable climate with large inter-annual variation driven primarily by
217 the North Atlantic Oscillation (50, 51), which could have resulted in selection for plasticity in
218 parturition date as opposed to selection for a specific optimal date (52, 53). Large variance in
219 climate also suggests that trends of advancing parturition dates may be driven more by plasticity
220 within generations as opposed to adaptive evolution across generations, especially given that
221 these are still relatively short evolutionary timeframes.

222 It is unlikely that phenological mismatch is currently affecting caribou reproduction and
223 fitness in Newfoundland. Timing of green-up did not significantly affect calf survival, although
224 we note that this was due to large confidence intervals around a relatively large coefficient
225 estimate. We cautiously suggest that early springs do not result in depressed reproductive
226 success, likely because this scenario is mitigated by plasticity in the timing of parturition
227 allowing individuals to avoid significant mismatch. Despite indications of phenological

228 mismatch in caribou (29), other studies have failed to detect a significant effect of spring
229 asynchrony on caribou forage availability (54). Some of our results however raise the spectre
230 that caribou may not be able to continue to acclimate or adapt to future conditions. If individuals
231 are plastic to a cue that is increasingly unreliably correlated with fitness-maximizing resources,
232 this can result in phenological mismatch despite plasticity. For example, differences in the
233 amount of warming experienced in the Netherlands in early versus late spring resulted in
234 mismatch between great tits (*Parus major*) and their caterpillar prey, as the birds displayed
235 plasticity to the former and the caterpillars the latter (55, 56). Reproductive success in caribou
236 appears to be linked to timing parturition to coincide with peak green-up (29); however, we
237 found that individuals were more plastic in the timing of birth in response to the timing of
238 snowmelt than to green-up itself. The timing of green-up was only loosely correlated with the
239 timing of snowmelt ($R^2 = 0.21$), with green-up only advancing by 0.30 days for each day that
240 snowmelt advanced (Figure S3). It is likely that climate change will continue to disrupt the
241 predictability of the relationship between these two phenological events, which may result in
242 caribou using an increasingly unreliable cue to time reproduction.

243 Evidence from our study suggests that earlier parturition date in our populations and
244 potentially in other *Rangifer* populations (32) is primarily driven by plastic changes as
245 individuals acclimate to changing conditions as opposed to natural selection acting to select for
246 individuals that give birth earlier in the season. Repeatability is often considered to represent an
247 upper bound to heritability (35), and as such the low repeatability of parturition date we observed
248 suggests it is unlikely that parturition date is heritable in caribou. Plasticity alone, without any
249 evolutionary change, could simply delay population decline if populations are driven beyond the
250 limits of their ability to acclimate (57, 58). Experimental evidence from both frogs and

251 passerines suggest that current rates of evolution are insufficient to account for observed shifts in
252 reproductive phenologies (59, 60).

253 Our behavioral reaction norm framework allowed us to test for correlations in individual
254 responses in environmental change to timing of snowmelt and green-up. For both of our model
255 sets, the top model included random slopes for individuals, suggesting the existence of among-
256 individual variation in the degree of plasticity to environmental change. However, we only
257 detected significant among-individual correlations among two traits: timing of migration and
258 timing of parturition, providing evidence of a link between these two behavioral traits. Counter
259 to our fourth prediction however, we did not find a link between plasticity in timing of migration
260 and plasticity in timing of parturition, suggesting that the ability to acclimate migration timing is
261 not related to plasticity in parturition date. We also failed to detect a significant relationship
262 between plasticity in parturition date and reproductive success. For a telemetry study, we have a
263 large sample of individuals, repeated across several years, and replicated among herds. Despite
264 our relatively large sample size, bivariate mixed effects models, like those used in this study, are
265 data hungry (61). While some of our conclusions may be based on what could be considered
266 modest statistical inference, we suggest that finding strong inference in our data will be more
267 challenging than in contexts where behavioral tests can be performed across a range of
268 environments that can be replicated numerous times in a single year to obtain a robust sample
269 size (i.e, 62, 63).

270 Climate change represents an imminent threat to migratory animals such as caribou (4,
271 64). Despite indications that phenologies of some migratory species are shifting to compensate
272 for changes at lower trophic levels (30, 32), understanding the mechanism remains an important
273 question. By empirically demonstrating individual plasticity to changing environmental

274 conditions and low repeatability in parturition time, our results suggest that much of the observed
275 contemporary shifts in phenology are due to plastic responses to environmental change as
276 opposed to an evolutionary response. Plasticity also appeared to buffer populations against
277 depressed fitness, as we found no effect of the timing of spring on annual reproductive success.
278 We demonstrate an important link between migration timing and parturition timing, suggesting
279 that phenological synchrony is a two-part process in caribou—individuals must not only give
280 birth when conditions are optimal, but this synchrony is also dependent on migration timing.
281 Caribou are globally threatened (65), and as a northern ungulate exposed to high levels of
282 climate change-induced warming, provide an important litmus test for understanding the impact
283 of climate change on migratory herbivores globally.

284 **Methods**

285 **Study site**

286 We conducted our study on the island of Newfoundland, Canada (~47° 44' N, 52° 38' W to 51°
287 44' N, 59° 28' W). Caribou habitat in Newfoundland primarily consists of coniferous forest and
288 mixed wood forests dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*),
289 and white birch (*Betula papyrifera*), interspersed with bog and heath habitats. Barren rock and
290 lakes are also common features in Newfoundland (see study area map, Figure S1).

291 **Data collection and cleaning**

292 GPS collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g) were
293 deployed on 112 adult female caribou from five populations on Newfoundland between 2007–
294 2013. Caribou were captured by darting from a helicopter. GPS fixes were obtained every 1–5
295 hours depending on season and collar. All animal capture and handling followed guidelines from

296 the Canadian Council on Animal Care. We initially had data from 112 individuals over 326 ID-
297 years. Cleaning the data and removing ID-years with insufficient data, and non-parturient
298 individuals left us with data for 103 individuals across 294 ID-years. A further nine individuals
299 and 78 ID-years were dropped after removing individuals that did not migrate at least 30 km.
300 Our final dataset consisted of data for 92 caribou across 212 ID-years.

301 **Defining timing of snowmelt and green-up**

302 We used two measures of phenological change to quantify the timing of spring events for
303 caribou populations in Newfoundland, the timing of snowmelt and the timing of green-up. We
304 used the timing of snowmelt as the presumed driver of spring migration timing as snowmelt has
305 been shown to correspond to the timing of migration of caribou in Newfoundland (Laforge et al
306 2021). We used the normalized difference snow index (NDSI) derived from daily MODIS data at
307 a spatial resolution of 250×250 m to determine the date of snowmelt. We determined the day
308 that each pixel first had a recorded negative value of NDSI as the date upon which each pixel
309 was considered snow-free. We used the timing of snowmelt within each population's range (99%
310 MCP of all locations from the start of spring migration to three weeks after parturition) to define
311 the timing of snowmelt for each individual in each year as the median date of when pixels in the
312 population-range became snow-free.

313 To quantify the timing of plant green-up, we used the instantaneous rate of green-up
314 (IRG). IRG represents the first derivative of a series of normalised difference vegetation index
315 values at a given location. We used data from both MODIS satellites (Terra and Aqua), each of
316 which produced 16-day composite NDVI images at a resolution of 250×250 m. The sensors on
317 each of the two satellites produce composite images at opposite times (i.e., phased), so
318 combining the two data records provides an 8-day temporal resolution. We first set to NA any

319 NDVI values where the snow cover band of the MODIS data indicated snow cover and replaced
320 it with the 3rd percentile of all snow-free observations at that pixel. This procedure ensures that
321 the resulting curves are only plotting the change in plant growth and not confounded by melting
322 snow (14, 19). We also set any pixels contaminated by cloud (~10.0%) to NA. For each location
323 in our study area and for each year of our study, we used a 3-observation moving median filter to
324 smooth the time series then fit a logistic curve to the time series of NDVI values at that location.
325 We then calculated as IRG the first derivative of this curve and determined the date that IRG had
326 the highest value. This date represented the day in which plant growth was occurring fastest and
327 therefore represented the highest nutritional quality for caribou (17, 18). To calculate the date of
328 green-up in each herd's range each year, we generated a population-level MCP range (as defined
329 above for snowmelt) and calculated the median date each year that pixels in the home range
330 reached peak IRG. The median date of snowmelt across ranges and years was Apr 27, and the
331 median date of green-up was May 29 (see Figure 1).

332 **Defining caribou migration timing**

333 To define timing of migration, we used Migration Mapper V. 2.0 (66). Migration Mapper plots
334 GPS locations on a map along with a profile of net squared displacement to allow the user to
335 visually inspect these profiles to specify when individuals begin and complete migratory
336 movements. As we were only interested in spring migration, we only quantified the timing of
337 departure from winter range and arrival on summer range. We used the date of arrival on
338 summer range as our measure of timing of migration. We removed any individuals that did not
339 migrate at least 30 km. The median date for departure from winter range was Mar 25 (range: Feb
340 9–May 19). The median duration of migration was 43 days (range: 4–128) covering a median

341 distance of 62.2 km (range: 30.5–174.9). The median date for arrival on summer range was May
342 10 (range: Mar 20–Jul 13, see Table 1).

343 **Quantifying timing of parturition and annual reproductive success**

344 We used the method developed by DeMars et al. (67) and validated by Bonar et al (68) to define
345 calving date and whether calves survived to four weeks of age. This method quantifies birthing
346 events by detecting constraints on movement in females who must stop to give birth and whose
347 movements are constrained by calves-at-heel that have a slower movement rate. Females whose
348 calves die in the first four weeks of life display a sudden return to baseline movement rates,
349 whereas females whose calves display a gradual return to baseline rates as calves are able keep
350 pace with their mothers. We used a population-based method to detect calving and calf mortality
351 events that examined three-day average movement rates of collared females to ascertain whether
352 females gave birth that year and quantify the date of parturition. In some instances, the model
353 output suggested that individuals gave birth in the first day of the time series provided to the
354 model. In these instances, we manually validated parturition dates by inspecting a plot of daily
355 movement rates. These data were validated using the Middle Ridge population, in which the
356 method correctly classified 100% of parturition events (68). The median date of calving was
357 May 30 (range: May 18–Jul 13), and 60% of calves survived to four weeks of age (see Table S1).

358 **Behavioral reaction norms**

359 Behavioral reaction norms quantify how individual behavior changes across an environmental
360 gradient. To evaluate how individual phenotypes for timing of migration, parturition, and annual
361 reproductive success are expressed across an environmental gradient (timing of snowmelt or
362 green-up), we quantified behavioral reaction norms (BRNs; 41) using two sets of bivariate
363 Bayesian mixed effects models (R package *MCMCglmm*, version 2.29; 61, 69). We predicted that

364 timing of migration and parturition would both be affected by timing of snowmelt, and that
365 timing of parturition would also be affected by the timing of green-up, as would calf survival.
366 Therefore, the response variables for our first set of models were the date of arrival on summer
367 range and the timing of parturition, with timing of snowmelt used as our main explanatory
368 variable. For our second model, response variables were timing of parturition and whether
369 caribou calves survived to four weeks of age, with timing of green-up used as the explanatory
370 variable. Variables were scaled independently for each population. Models were fit with
371 uninformative priors (34) and Gaussian error structures for timing of migration and parturition,
372 and with a categorical (binomial) error structure for calf survival. We ran models with a total of
373 420,000 iterations with a burn-in of 20,000 and a thinning rate of 100. We evaluated eight
374 models using different combinations of random and fixed effects structures (Table S2). We
375 tested for the effect of individual ID, and for the effect of an individual \times environment
376 interaction (i.e., an interaction between individual caribou and relative date of snowmelt or green
377 up; 70) in the random terms. In our BRN analyses, fixed effects were used to control for changes
378 in the random effects. In each of our two model sets, we chose the model with the lowest
379 deviance information criterion (DIC, see Table 1). We extracted best linear unbiased predictors
380 (e.g., random intercept and slope estimates for each ID-year) and calculated repeatability (r) of
381 BRN intercepts for migration date, parturition date, and calf survival as the amount of between-
382 individual variance (V_{ind}) attributable to the residual variance among groups (V_{res}) for each trait
383 (71):

384
$$r = \frac{V_{ind}}{(V_{ind} + V_{res})} \quad [1].$$

385 We examined the correlation between the slope and intercept of best linear unbiased estimators
386 (random effects) for both variables in each model to examine the relationships between
387 individual differences and plasticity within and between the traits (61; Table S3).

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562

563 **Table 1:** Estimates for fixed effects from the most parsimonious models from two bivariate
 564 Bayesian mixed effects models testing the effects of timing of snowmelt (model 1) and timing of
 565 green-up (model 2) on the timing of migration (model 1), timing of parturition (models 1 and 2)
 566 and probability of calf survival (model 2) for caribou (*Rangifer tarandus*, $n = 92$) in
 567 Newfoundland, Canada, 2007–2013. Estimates are presented with 95% credible intervals. The
 568 reference category for population is Buchans.

	Model 1: Snowmelt, arrival timing	Model 1: Snowmelt, parturition timing
Arrival timing	-	0.04 (-0.387, 0.457)
Parturition timing	0.032 (-0.347, 0.367)	-
Snowmelt	0.332 (0.192, 0.455)	0.138 (-0.006, 0.286)
Grey River	-0.065 (-0.702, 0.559)	-0.021 (-0.532, 0.5)
Lapoile	-0.046 (-0.676, 0.471)	-0.002 (-0.469, 0.476)
Middle Ridge	-0.047 (-0.563, 0.472)	-0.024 (-0.473, 0.447)
Topsails	0.09 (-0.568, 0.697)	-0.02 (-0.581, 0.535)
	Model 2: Green-up, parturition timing	Model 2: Green-up, calf survival
Parturition timing	-	-0.037 (-0.375, 0.267)
Calf survival	1.222 (-0.206, 2.817)	-

Green-up	0.094 (-0.066, 0.27)	0.316 (-0.377, 1.101)
Grey River	0.063 (-0.401, 0.507)	-0.971 (-3.282, 1.091)
Lapoile	0.099 (-0.38, 0.526)	-1.284 (-3.258, 0.665)
Middle Ridge	0.027 (-0.395, 0.444)	0.652 (-1.326, 3.132)
Topsails	0.007 (-0.521, 0.554)	-0.968 (-3.34, 1.13)

569

570

571 **Figure captions:**

572 **Figure 1:** Phenology of snowmelt and green-up (a) and migration and parturition (b) for caribou
573 (*Rangifer tarandus*, $n = 32$) in the Middle Ridge population, 2010–2013. a) represents the
574 number of pixels within the population's spring/summer range in which snow has melted (NDSI
575 > 0 , solid line) or that have reached the peak of green-up (instantaneous rate of green-up; dotted
576 lines) in each spring. Colors represent different years, and the dashed line represents the median
577 (the measure used for determining date of snowmelt/green-up). b) the timing of migration as
578 horizontal lines for each individual in each year (each line's extent represents the time they were
579 migrating). Points represent the timing of parturition. Black vertical lines represent the median
580 dates of snowmelt (solid) and green-up (dashed) for each year. See Figure S2 for plots using the
581 other four populations used in this study.

582 **Figure 2:** Mean-centred behavioral reaction norms for five caribou populations assessing timing
583 of arrival on summer range and timing of parturition as a function of median date of spring
584 snowmelt and green-up (see Materials and methods) for migratory caribou (*Rangifer tarandus*; n
585 $= 92$) in Newfoundland, Canada. Each line represents a different individual. Panel a) represents
586 timing of arrival on summer range as a function of timing of snowmelt, panel b) represents
587 timing of parturition as a function of timing of snowmelt, and c) represents timing of parturition
588 as a function of timing of green-up. Best linear unbiased predictors represent point estimates of
589 the random effects from the mixed effects model.

590 **Figure 3:** Repeatability estimates and 95% credible intervals for timing of arrival on summer
591 range (red) and timing of birth (cyan) for caribou (*Rangifer tarandus*; $n = 92$) in Newfoundland,
592 Canada. Repeatability estimates were derived from the top Bayesian mixed effects model
593 describing timing of migration and parturition as a function of timing of snowmelt (the first
594 model set).

595 **Figure 4:** Correlations and 95% credible intervals between random slopes and intercepts from
596 bivariate mixed effects behavioral reaction norm models quantifying timing of caribou (*Rangifer*
597 *tarandus*; $n = 92$) migration, parturition, and calf survival as a function of the timing of spring
598 snowmelt and green-up. Colors represent different populations. Panel a) represents the
599 correlation between the intercept for timing of migration and the intercept for timing of
600 parturition. Panel b) represents the correlation between the slopes (e.g., plasticity) of migration
601 and parturition timing. Panel c) represents the correlation between the intercept for timing of
602 parturition and the probability of calf survival to four weeks of age in an average environment.
603 Panel d) represents the correlation between the plasticity in parturition time as a function of
604 green-up and the probability of calf survival. Note, correlations are considered significant when
605 credible intervals do not overlap zero and non-significant when credible intervals overlap zero.







