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*Decoupling the effects of food and density on life history plasticity of wild animals using field experiments: insights from the steward who sits in the shadow of its tail, the North American red squirrel*

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**Summary:**

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- 30 1) Long-term studies of wild animals provide the opportunity to investigate how  
31 phenotypic plasticity is used to cope with environmental fluctuations, and how the  
32 relationships between phenotypes and fitness can be dependent upon the  
33 ecological context.
- 34 2) Most previous studies have only investigated life history plasticity in response to  
35 changes in temperature, yet wild animals often experience multiple  
36 environmental fluctuations simultaneously. This requires field experiments to  
37 decouple which ecological factor induces plasticity in fitness-relevant traits to  
38 better understand their population-level responses to those environmental  
39 fluctuations.
- 40 3) For the past 32 years, we have conducted a long-term integrative study of  
41 individually marked North American red squirrels (*Tamiasciurus hudsonicus*  
42 Erxleben) in the Yukon, Canada. We have used multi-year field experiments to  
43 examine the physiological and life history responses of individual red squirrels to  
44 fluctuations in food abundance and conspecific density.
- 45 4) Our long-term observational study and field experiments show that squirrels can  
46 anticipate increases in food availability and density, thereby decoupling the usual  
47 pattern where animals respond to, rather than anticipate, an ecological change.
- 48 5) As in many other study systems, ecological factors that can induce plasticity  
49 (such as food and density) co-vary. However, our field experiments that  
50 manipulate food availability and social cues of density (frequency of territorial  
51 vocalizations) indicate that increases in social (acoustic) cues of density in the  
52 absence of additional food can induce similar life history plasticity, as does  
53 experimental food supplementation.
- 54 6) Changes in the levels of metabolic hormones (glucocorticoids) in response to  
55 variation in food and density are one mechanism that seems to induce this  
56 adaptive life history plasticity.
- 57 7) Although we have not yet investigated the energetic response of squirrels to  
58 elevated density or its association with life history plasticity, energetics research  
59 in red squirrels has overturned several standard pillars of knowledge in  
60 physiological ecology.

61 8) We show how a tractable model species combined with integrative studies can  
62 reveal how animals cope with resource fluctuations through life history plasticity.  
63

64 **Introduction:**

65 For every species, population, or individual, there is an environmental factor that  
66 can induce changes in the characteristics of individuals (phenotypic plasticity). In some  
67 cases, environmental cues or the shift in the environment itself may induce adaptive  
68 plasticity in the physiology, behavior, or life history traits of an animal (Stearns, 1989;  
69 Via et al., 1995; Ghalambor et al., 2007). Models predict that this can, in turn, cause  
70 demographic changes in the population that facilitates resilience through that  
71 environmental fluctuation or adaptation to another type of novel selective environment  
72 (Caswell, 1983; Yeh and Price, 2004; Chevin and Lande, 2010; Chevin et al., 2010).  
73 Adaptive phenotypic plasticity may be especially likely to evolve if organisms are  
74 sensitive to cues that predict future environmental fluctuations (Levins, 1968; Moran,  
75 1992; Reed et al., 2010), which are probably more likely to occur in animals that have  
76 experienced recurrent temporal environmental fluctuations over their evolutionary  
77 history (Berrigan and Scheiner 2004).

78 Studies of life history plasticity in a diversity of wild animal species have provided  
79 valuable tests of theory of adaptive phenotypic plasticity as well as empirical examples  
80 illustrating how plasticity can enable resilience through environmental change. Such  
81 studies are challenging because they usually involve following free-living but marked  
82 individuals across some environmental gradient (e.g., temperature, predation risk, food  
83 availability, conspecific density: Nussey et al., 2007). It is also quite difficult to identify  
84 and experimentally manipulate the putative ecological cue that induces plasticity in  
85 natural populations. A notable pattern is that many of these studies investigate life  
86 history plasticity in response to temperature by regressing the life history traits of an  
87 individual across a range of temperatures (or in some cases, different years of study).  
88 For example, the timing of breeding of individual birds varies across years and is related  
89 to ambient temperature around the time of breeding (Nussey et al., 2005a; Brommer et  
90 al., 2008; Charmantier et al., 2008; Porlier et al., 2012). In some of these studies, the  
91 plasticity in laying date that was apparently induced by temperature was adaptive and

92 greater levels of plasticity were under positive selection (Nussey et al., 2005a; Porlier et  
93 al., 2012). Other studies in free-living mammals illustrate the effects of temperature or  
94 longitudinal trends in plasticity in the timing of other life history traits such as emergence  
95 from hibernation (Lane et al., 2012), the timing of breeding (Nussey et al., 2005b;  
96 Bonnet et al., 2019), or litter size (Ozgul et al., 2010; Tafani et al., 2013), which may  
97 only be adaptive in some cases (Nussey et al., 2005b; Ozgul et al., 2010).

98       Although most of the previous longitudinal studies regarding individual life history  
99 plasticity in wild animals has focused on the effects of temperature, one of the most  
100 common types of environmental fluctuation that induces plasticity is food availability.  
101 Nearly all individuals, populations, and species experience either seasonal changes in  
102 food availability or among-year variation in food abundance. Recurrent fluctuations in  
103 food are common in animals that rely upon seasonal pulses of food, such as bird  
104 species that time their reproduction to peak availability of insect prey (Lack, 1954; Daan  
105 et al., 1989; Visser et al., 2006; Charmantier et al., 2008). Inter-annual changes in food  
106 availability are also common, such as the number of prey available for predators  
107 changing from year to year in polar ecosystems or where food availability exhibits  
108 profound fluctuations across years in resource pulse ecosystems (Krebs et al., 1995;  
109 Yang et al., 2008; Krebs et al., 2018). Ecologists have long been interested in  
110 understanding how organisms respond to these fluctuations in food abundance (Elton,  
111 1924; Lack, 1954). Studies in a wide variety of taxa find plasticity in physiological,  
112 behavioral, or life history traits that is induced by these changes in food abundance and,  
113 in some cases, these seem to be adaptive. For example, food supplementation in free-  
114 living vertebrate species generally results in higher body weight, faster growth, and an  
115 earlier start to the breeding season (Boutin, 1990; Ruffino et al., 2014), responses that  
116 should increase individual survival or reproduction.

117       A central problem for those interested in understanding whether these  
118 fluctuations in food abundance induce adaptive phenotypic plasticity has been that  
119 changes in food availability tend to be coupled with increases in conspecific density  
120 (e.g., Prevedello et al., 2013), especially in populations that do not experience  
121 substantial top-down regulation. Given that food-supplementation induces life history  
122 plasticity that should modify both birth and death rates, it is not surprising that food and

123 density tend to be coupled in nature. Although food abundance may change seasonally  
124 or annually, there is typically a numerical response in the consumers where density of  
125 the species of interest also increases when food is elevated. For example, population  
126 densities of small mammal species that consume seeds from plant species that produce  
127 occasional pulses of these seeds, are elevated in the years following resource pulses  
128 (Wolff, 1996). Food-supplementation studies support this same pattern where plasticity  
129 in the life history traits of individuals in response to supplemental food can, in turn,  
130 elevate population densities (Prevedello et al., 2013). For example, supplementary food  
131 provided to rodents can cause a 50-300% increase in population density within a few  
132 months by increasing litter sizes and elevating juvenile survival (Cole and Batzli, 1979;  
133 Gilbert and Krebs, 1981). This “ecological coupling” where two environmental  
134 fluctuations co-occur or occur together after a brief lag time makes it challenging to  
135 disentangle which environmental cue (which are often ecological agents of selection  
136 themselves: Wade and Kalisz, 1990) is inducing the plasticity. Others have described  
137 similar problematic issues when aiming to disentangle the ecological agents of  
138 selection, such as population density and predation risk co-varying and influencing the  
139 patterns of phenotypic evolution in fish (Reznick et al., 2002).

140       When it comes to this ecological coupling of food and density, one widely used  
141 solution to identify the ecological mechanism inducing plasticity is to carry out short-  
142 term food supplementation studies (Boutin 1990; Ruffino et al., 2014). In these studies,  
143 supplemental food is provided to animals for short periods of time and the plasticity that  
144 is induced in a wide variety of traits is quantified and usually attributed to the increase in  
145 food rather than the change in resource competition behavior. This is useful, but also  
146 only provides part of the story as very rarely is there an increase in food that is not  
147 coupled with an increase in density (due to altered patterns of birth, death, or  
148 immigration) that in turn results in increased competition for that resource (Prevedello et  
149 al., 2013).

150       In our long-term study of North American red squirrels in the Yukon, Canada, we  
151 have taken an integrative and experimental approach to understand the ecological  
152 mechanisms that induce phenotypic plasticity to better understand how red squirrels  
153 cope with their variable environment. Yukon red squirrels experience tremendous

154 fluctuations in ecological factors that can induce plasticity and act as ecological agents  
155 of selection, such as food, conspecific density, and predation risk (Fig. 1). However, we  
156 have mostly focused our attention on food and conspecific density as previous  
157 experimental studies that excluded terrestrial predators and our long-term data analyses  
158 show that terrestrial predators seem to have minimal effects on overall squirrel densities  
159 (Fig. 2), though it is likely that predators do influence the survival of individual juveniles  
160 (Studd et al., 2015; Hendrix et al., 2020). Using targeted experimental manipulations of  
161 food, density, or the acoustic cues reflecting density, we have been able to unravel how  
162 changes in density and food induce plasticity in life history traits in natural populations.  
163 We have also incorporated physiological and energetic approaches into the ecological  
164 context and natural history of our study species to aid and complement our research.

165 In this synthesis, we will discuss the key insights from our long-term  
166 observational study that tracked reproductive output in anticipation and response to  
167 naturally elevated food abundance and our field experiments that elevated both food  
168 and density or only the social (acoustic) cues of density without additional food. We will  
169 also describe some of the results from our physiological and energetic research that  
170 challenges existing paradigms in those fields. We note that our past work has described  
171 life history plasticity in response to spring temperatures (Réale et al., 2003; Lane et al.,  
172 2018) but here we focus on food and density. Overall, our long-term observational study  
173 on the life history responses of free-living red squirrels to changes in food and density,  
174 in addition to our field experiments, provide some general lessons for animal ecologists.  
175 Specifically, the observation that increased food may not be necessary to enable  
176 animals to do the things they do (e.g., increase reproductive output) but instead do so  
177 only when the fitness benefits are sufficiently high to warrant the increased reproductive  
178 output. For example, red squirrels can have ample available food that allows them to  
179 breed early or produce fast-growing offspring, but they do this only when there is  
180 selection for early parturition dates and fast postnatal growth.

181

## 182 **Historical context:**

183 The Kluane Red Squirrel Project was formally initiated by Stan Boutin in 1988.  
184 Murray Humphries joined the project in 1994, Andrew McAdam joined in 1998, Jeff

185 Lane joined in 2003, and Ben Dantzer in 2006. All principal investigators (Boutin,  
186 Dantzer, Humphries, Lane, McAdam) have contributed to the conception,  
187 implementation, training of personnel, and funding of research associated with this  
188 project. A strength of this project is the confluence of research interests and expertise  
189 from the different principal investigators, which has allowed project personnel (including  
190 undergraduate and graduate students and postdoctoral researchers) to conduct  
191 interdisciplinary research. All principal investigators strongly believe in collaboration,  
192 data sharing, and democratic decision making.

193

#### 194 **Study system:**

195 Our research takes place in a forested glacial valley (Shakwak Trench, ~850 m  
196 elevation) in the southwest Yukon, between Haines Junction and Kluane Lake (Łù'àn  
197 Män in Southern Tutchone or “big fish lake”). The area in which we work is collectively  
198 known as Kluane (pronounced ‘Kloo-wah-nee’) or Dän Keyi (“Our people’s land”) and is  
199 part of the traditional territory of the Southern Tutchone people. Our study areas are  
200 located within territory of the Champagne and Aishihik First Nations, and near the  
201 traditional territories of the Kluane First Nation and White River First Nation. Members of  
202 these First Nations (dän) have lived off these lands for more than 8000 years.

203 The flora and fauna in our study area have been described through the long-term  
204 Kluane Boreal Forest Ecosystem Study (Krebs and Boonstra, 2001; see also  
205 supplementary materials). White spruce (*Picea glauca*) is the dominant vegetation and  
206 is the only conifer in this area. The climate in this area is cold, with January being the  
207 coldest month (-26.7 °C to -14.3 °C) and July being the warmest month (6.4 °C to 19.6  
208 °C: weather data from Burwash Landing Climate Station, available from Environment  
209 Canada). Typically, the ground is covered in snow from October until early May.

210 Red squirrels in the Yukon are small (adults weigh ~250 g) and relatively short-  
211 lived species (median lifespan of squirrels that acquire a territory as a juvenile = 3.5  
212 years, maximum lifespan = 8 years: McAdam et al., 2007). Red squirrels are highly  
213 territorial, with individuals of both sexes defending separate food-based territories year-

214 round (Smith, 1968). Their non-overlapping territories are centred on a cache of white  
215 spruce cones, which are stored in tunnels in a “midden” (a large accumulation of cone  
216 bracts created by consuming spruce cones in the same spot over many years). In each  
217 autumn (September), squirrels clip and collect cones from white spruce trees on their  
218 territory and store most of them in their midden (Fletcher et al., 2010). Middens help to  
219 keep the cones closed so that the seeds remain viable for at least 4 years after  
220 collection (Donald and Boutin, 2011). Although squirrels in the Yukon consume many  
221 different types of foods, from fungi to snowshoe hare (*Lepus americanus*) leverets,  
222 spruce seed is the major component of their diet (Fletcher et al., 2013; Ren et al.,  
223 2017). Middens contain an estimated mean  $\pm$  SD of  $19,790 \pm 1,429$  cones (range = 0 to  
224 146,500, Haines, 2017). Cones cached in the autumn of one year can have carry-over  
225 effects on squirrel life history traits in the following year (e.g., high spruce cones in the  
226 previous autumn is associated with earlier breeding in the following spring: Réale et al.,  
227 2003; Williams et al., 2014). Middens are also long-lasting and are often reused by  
228 other squirrels once a previous owner has died (e.g., one midden has been used  
229 continuously for up to at least 31 years: Fisher et al., 2019) such that cones cached by  
230 one squirrel can carry-over and influence the survival or reproduction of subsequent  
231 owners (Fisher et al., 2019). Squirrels primarily defend their territories using territorial  
232 vocalizations called “rattles” (Smith, 1978; Siracusa et al., 2017), which they emit  
233 frequently throughout the day and across the entire year (Dantzer et al., 2012; Siracusa  
234 et al., 2019). Juvenile squirrels usually must acquire a midden soon after weaning (from  
235 late spring to autumn depending upon the year) if they are to survive their first winter  
236 (Larsen and Boutin, 1994), and squirrels with more cones cached in their midden exhibit  
237 higher survival (Larivée et al., 2010; LaMontagne et al., 2013). Once a squirrel acquires  
238 a territory, they very rarely leave voluntarily even if there are vacancies available  
239 (Larsen and Boutin, 1995). However, this can happen in cases where adult females  
240 bequeath their territory to their offspring (Price and Boutin, 1993; Berteaux and Boutin,  
241 2000; Boutin et al., 2000; Lane et al., 2015).

242 Female and male squirrels are polygamous and have a scramble-competition  
243 mating system (Lane et al., 2009). Mating can occur from January to August but most  
244 mating happens from March to May. The timing of mating is heavily influenced by the



245 availability of spruce cones in the previous autumn (Boutin et al., 2006; McAdam et al.,  
246 2019). Females and males are usually sexually mature in the year following birth but  
247 some females do not breed successfully until their second year or later (Descamps et  
248 al., 2006; McAdam et al., 2007), although yearling females are much more likely to  
249 attempt to breed in mast years (Boutin et al., 2006). Female red squirrels are  
250 spontaneous ovulators that are typically in oestrus for 1 day per year, aside from mast  
251 years when females may enter oestrus multiple times (Boutin et al., 2006). Gestation is  
252 around 35 days and pups first emerge from their nest around 42 days before they are  
253 weaned around 70 days after birth (Stuart-Smith and Boutin, 1995; Boonstra et al.,  
254 2001; McAdam et al., 2007). Females usually only wean one litter of ~2-3 pups per year  
255 (see below). If their first litter fails before weaning, they will occasionally attempt to  
256 breed again (Williams et al., 2014), but squirrels only successfully wean two litters in  
257 mast years (see below: Boutin et al., 2006; McAdam et al., 2019).

258 All squirrels in our study population are individually marked using unique metal  
259 ear tags, which most squirrels receive while they are still in their natal nest soon after  
260 birth (~25 d of age: see overview of data collection in Fig. 3). Squirrels also receive  
261 unique combinations of small pieces of coloured telephone wire (adult females), pipe  
262 cleaners (adult males), or plastic washers (juveniles) threaded through these ear tags  
263 so that we can identify them without capture and handling (Fig. 3). In each year, roughly  
264 from March to October, we monitor the reproduction, survival, territorial ownership, and  
265 food availability of individual squirrels using capture and handling and behavioural  
266 observations. In May and August of each year, we completely enumerate all the  
267 squirrels on the study areas to quantify territory ownership and population density  
268 (Descamps et al., 2009). To monitor reproduction, we temporarily capture squirrels and  
269 palpate their abdomen (females) or testes (males) to assess reproductive condition.  
270 When females are lactating, we often apply VHF collars and then track them to their  
271 nests, though we also locate nests using behavioural observations. Pups are  
272 temporarily removed from their nest (for an average of ~12-15 min: Westrick et al.,  
273 2020) soon after birth and again when they are ~25 d of age (Fig. 3). We remove them  
274 from the nest so that we can determine their sex, weigh them, and, when they are ~25  
275 d, tag them with metal ear tags. These procedures then allow us to estimate the

276 parturition date, litter size, litter sex ratio, litter survival, and postnatal growth rates of  
277 each offspring for each female in our study population. Small pieces of ear tissue  
278 obtained from pups soon after birth allow us to identify sires of pups (Gunn et al., 2007)  
279 and construct multigenerational pedigrees (McFarlane et al., 2014).

280

281 **Key advances:**

282 Below we discuss four key insights generated by the observational and  
283 experimental data collected by the Kluane Red Squirrel Project. Each section aims to  
284 emphasize the value of interdisciplinary research where we combine our joint interests  
285 in ecology, evolution, behaviour, and physiology.

286

287 **1) Life history plasticity in anticipation of increased food availability:**

288 From basic population ecology, we typically expect that resource pulses induce life  
289 history plasticity, such as increased reproductive output that, in turn, elevates  
290 conspecific density (Yang et al., 2008). Traditional models in population ecology  
291 assume this creates a lagged response to the increase in food by the consumers  
292 (Ostfeld and Keesing, 2000). By contrast, theoretical models about the evolution of  
293 adaptive phenotypic plasticity predict that selection should favour individuals that  
294 respond to cues that accurately predict the future selective environment (Levins, 1968;  
295 Moran, 1992; Reed et al., 2010), that is individuals should do quite well if they predict  
296 the future increase in food. We have overturned these assumptions in population  
297 ecology by showing that red squirrels anticipate this increased food availability and  
298 respond through adaptive life history plasticity prior to the food being available for  
299 consumption (Boutin et al., 2006).

300 Red squirrels in the Yukon primarily consume seeds from white spruce trees that  
301 they cache underground in unopened cones in a central midden in the autumn (Fletcher  
302 et al., 2010, 2013). Squirrels need to rely upon cached spruce seed to mostly or  
303 completely fuel their survival and reproduction for the next 11-12 months or beyond as  
304 seeds produced in that year are not available to squirrels as a food source until around  
305 the first week of August (Boutin et al., 2013; Fletcher et al., 2013; Ren et al., 2017).

306 Cone production in white spruce is highly episodic, with a superabundance of cones  
307 (mast years) produced in some years followed by several years of little to no cone  
308 production (non-mast years: Boutin et al., 2006; LaMontagne and Boutin, 2007;  
309 McAdam et al., 2019, Figure 1A). Mast years lead to greater seed escape because the  
310 trees produce many more cones than can be harvested by the squirrels (Fletcher et al.,  
311 2010).

312 Over the past 32 years, we have recorded the life history responses of red  
313 squirrels to six mast events where there was a superabundance of spruce cones (1993,  
314 1998, 2005, 2010, 2014, 2019: Fig. 1A). Much to our surprise, in each mast year,  
315 squirrels exhibited striking increases in reproductive traits including increases in litter  
316 size (mean  $\pm$  SD litter size in mast years =  $3.3 \pm 0.95$  pups, 95% CI = 3.2 - 3.4 pups; in  
317 non-mast years =  $3.0 \pm 0.85$  pups, 95% CI = 2.9 - 3.0 pups: McAdam et al., 2019), an  
318 increase in the proportion of yearlings that bred, more breeding attempts, and in some  
319 cases, females were able to wean two litters (Boutin et al., 2006; Williams et al., 2014).  
320 The net result is that female annual reproductive success (i.e. the number of recruited  
321 offspring per year) is much higher in mast years than in non-mast years (McAdam et al.  
322 2019) and all of these changes take place prior to the current seed crop becoming  
323 available (July at the earliest) for consumption. Thus, red squirrels anticipate these  
324 pulses of food where some cue in their environment in spring reliably predicts food  
325 availability in autumn and induces this anticipatory life history plasticity. Squirrels  
326 increase their reproductive rates without additional food.

327 This anticipatory response leads to no time lag in density as density reaches its  
328 maximum in the autumn of the mast year due to the successful recruitment of juveniles  
329 (Descamps et al., 2008; Dantzer et al., 2013). In addition, juvenile red squirrels (but not  
330 adults: Descamps et al., 2009) have higher overwinter survival rates following autumns  
331 of high spruce cone production (Humphries and Boutin, 2000; McAdam and Boutin,  
332 2003; Williams et al., 2014) or when the amount of cones they cache underground is  
333 higher (Larivée et al., 2010; LaMontagne et al., 2013) so spring densities following an  
334 autumn mast in the previous year are at or near their maximum. By way of contrast,  
335 consumers in typical resource pulse systems would not show plastic reproductive  
336 responses until the year following the mast when seed is still available in spring to fuel

337 the increase. This leads to a temporary increase in density but the survival of these  
338 individuals is usually reduced because the pulse of seed has been consumed or  
339 germinated.

340 This life history plasticity in anticipation of food is adaptive in red squirrels as  
341 there are considerable fitness benefits for those that ramp up reproduction in  
342 anticipation of the increased food. Overwinter survival of juveniles produced in mast  
343 years is considerably higher than in non-mast years (Humphries and Boutin, 2000;  
344 McAdam and Boutin, 2003; Williams et al., 2013) such that squirrels that experience  
345 mast years have higher lifetime reproductive success than those that do not  
346 (Hamalainen et al., 2017; McAdam et al., 2019). In mast years, there is strong positive  
347 directional selection on litter size (McAdam et al., 2019) and likely strong positive  
348 selection on the number of litters produced in mast years (Boutin et al., 2006).

349 This pattern where animals anticipate future food abundance has now been  
350 documented in other species that experienced pulses of crucial food resources (e.g.,  
351 Eurasian red squirrels [*Sciurus vulgaris*]: Boutin et al. 2006; Eastern chipmunk [*Tamias*  
352 *striatus*]: Bergeron et al., 2011). We predict that if animals have cues to predict the  
353 future and experience high fitness benefits from exhibiting adaptive life history plasticity  
354 in response to these cues (as red squirrels do), individuals should follow a conservative  
355 life history strategy until they encounter these cues whereupon they should increase  
356 their reproductive output (Boutin et al., 2013). Whether or not this pattern is more  
357 widespread remains to be seen.

358

359

360

361 **2) Experimental decoupling of food and density reveals that social cues of**  
362 **density induce life history plasticity that is often attributed to increased**  
363 **food**

364 Density-dependent selection is a phenomenon that has been widely studied in  
365 observational data collected from longitudinal studies where individuals are marked  
366 uniquely (Sinervo et al., 2000; Calsbeek and Smith, 2007; Reznick et al., 2012;  
367 Schrader and Travis, 2012; Bassar et al., 2013). However, because food and density

368 typically co-vary, it is difficult to tease apart the influence of food and density on any life  
369 history plasticity observed when population density increases. Thus, experimental  
370 manipulation of food and density is typically required to identify the ecological agent of  
371 selection (Wade and Kalisz, 1990) that favors this life history plasticity that may be an  
372 adaptive response to the increase in density. In Yukon red squirrels, we have been able  
373 to quantify the life history plasticity in response to experimental manipulations of food,  
374 density, and also the social cues that reflect increased density. By doing so, we have  
375 shown that social cues in spring induce adaptive life history plasticity without access to  
376 additional food and foreshadow upcoming density-dependent selection.

377 In most animal populations, conspecific density increases with food availability  
378 due to life history plasticity (increased litter sizes or higher quality offspring) of  
379 individuals and higher survival of adults or offspring. In Yukon red squirrels, conspecific  
380 density increases when white spruce cone abundance is increased in the autumn of the  
381 previous year (Fig. 4). For example, the spring breeding density on our two long-term  
382 control study areas (KL and SU: Figure 1) increases in the spring following a mast year  
383 (where there is a superabundance of cones) going from 1.32 squirrels/ha to 2.61  
384 squirrels/ha, an average increase in density of 97.7% (range percentage increase in  
385 density following a mast year = 78.5-139.6%, Figure 4). Squirrels also exhibit life history  
386 plasticity in response to this change in conspecific density. In years of high conspecific  
387 density that often follow mast years, squirrels breed earlier and produce small litters of  
388 faster-growing offspring (Réale et al., 2003; Dantzer et al., 2013; Williams et al., 2014;  
389 Fisher et al., 2017). This may be adaptive life history plasticity due to density-dependent  
390 selection where in high-density years, squirrels have higher reproductive success if they  
391 breed earlier and produce faster growing offspring (Dantzer et al., 2013; Williams et al.,  
392 2014; Fisher et al., 2017).

393 Red squirrels are amenable to experimental manipulations at the individual level  
394 because both sexes exhibit year-round territoriality, strong site fidelity, and low adult  
395 dispersal (Berteaux and Boutin, 2000). From 2004 to 2017, we provided supplemental  
396 food to individual squirrels on three study areas (Fletcher et al., 2012; Dantzer et al.,  
397 2013). We provided squirrels with *ad libitum* food to simulate high food conditions that  
398 they experience following a mast year. Squirrels were provided with 1 kg of all-natural

399 peanut butter (no salt or sugar added) in a bucket that was hung between two trees on  
400 the center of their territory. Squirrels cannot cache peanut butter underground and  
401 pilferage by other bird or mammal species or conspecifics was extremely low (van  
402 Kesteren et al., 2019). Peanut butter was replenished every six weeks from October to  
403 May of each year. One kg of peanut butter approximates that of the resting metabolic  
404 need of an individual red squirrel for ~70 d (Fletcher et al., 2012).

405 Squirrel density on the food-supplemented areas was an average of 65% higher  
406 than on control study areas (Fig. 1B, Fig. 4, Dantzer et al., 2013). However, squirrel  
407 densities on the food-supplemented areas still increased after a mast year and the  
408 magnitude of increase was not different from control study areas (Fig. 4). This is  
409 probably because squirrels on the food supplemented study areas still exhibit natural  
410 food caching behavior (Donald and Boutin, 2011).

411 To separate the effects of this additional food and consequent increases in  
412 density on life history plasticity in female red squirrels, we manipulated the social cues  
413 of density by elevating the frequency with which squirrels heard territorial vocalizations  
414 to simulate a high-density environment. This took advantage of the fact that squirrels  
415 exhibit extreme site fidelity and advertise territorial ownership using specific  
416 vocalizations (rattles). On average, squirrels emit a territorial vocalization once every 7-  
417 10 min (Dantzer et al., 2012; Siracusa et al., 2019) and they respond behaviourally to  
418 acoustic playbacks of territorial calls (Goble, 2008; Shonfield et al., 2012; Dantzer et al.,  
419 2012; Wilson et al., 2015). We created a unique set of acoustic stimuli for nearly every  
420 squirrel where each squirrel would experience an additional four squirrels (two females,  
421 two males) that were unrelated and unknown to them (Dantzer et al., 2013). Playbacks  
422 were broadcast ~15 m away from the center of their territories to simulate an ambient  
423 increase in density rather than a direct territorial intrusion. Playbacks were broadcast  
424 from dawn to dusk in an alternating fashion where a squirrel would experience one rattle  
425 per 7 min, thereby simulating naturally high density conditions (Dantzer et al., 2012).  
426 Vocalizations from boreal chickadees (*Poecile hudsonicus*) were used as a control  
427 stimulus, as they are common in the Yukon year-round and are not known to harm red  
428 squirrels. Females experienced the control or rattle playbacks when they were in the

429 middle stages of pregnancy (around the second trimester) until immediately after  
430 parturition.

431 We were able to assess whether this experimental increase in social cues of  
432 density induced life history plasticity in females and how it compared to control playback  
433 females, control females on separate study areas that did not experience any  
434 playbacks, and the females on our above mentioned food-supplemented study areas  
435 that also experienced high densities. Because there were no differences between  
436 control playback and control females in terms of life history traits or faecal glucocorticoid  
437 metabolite levels (discussed below), we combined the data for these two control  
438 treatment groups (Dantzer et al., 2013). The results from this playback experiment were  
439 surprising when it came to the classical life history trade-off between the quantity and  
440 quality of offspring (Smith and Fretwell, 1974; Stearns, 1992). In red squirrels, this is  
441 reflected in the trade-off between the number of offspring (litter size) and the rate at  
442 which offspring grow after birth (offspring postnatal growth). Our previous work has  
443 identified that offspring growth is influenced by natal food availability or other aspects of  
444 the maternal phenotype and there is a negative phenotypic correlation between litter  
445 size and offspring growth rate (Humphries and Boutin, 2000; McAdam et al., 2002;  
446 McAdam and Boutin, 2003). We observed that the pups of control females producing  
447 large litters grew, on average, slower, confirming this expectation of a negative  
448 phenotypic correlation between quantity and quality of offspring. However, females  
449 experiencing supplemental food and an increase in actual density, as well as those  
450 females experiencing elevated social cues of density without additional food  
451 ameliorated this trade-off compared to control females (Dantzer et al., 2013).  
452 Specifically, females in the experimental treatment groups that produced larger litters  
453 did not experience as strong of a reduction in the growth rate of each pup as did the  
454 control females. This suggests that experimental females are increasing their resource  
455 allocation in pups, however, how females experiencing elevated social cues of density  
456 do this without additional food was not clear to us. We are now conducting new  
457 experiments using a similar protocol to examine if there is some cost to these females in  
458 terms of their future survival or reproduction.

459

460 **3) Hormonal responses to food and density are one mechanism that induces**  
461 **adaptive life history plasticity**

462 Among- or trans-generational phenotypic plasticity occurs when characteristics of  
463 the parental environment or the parental phenotype itself triggers plasticity in the  
464 offspring phenotype, thereby causing the transference of information across generations  
465 (Uller, 2008). Hormone-mediated maternal effects can induce trans-generational  
466 plasticity by providing a bridge between a developing offspring and the outside world  
467 experienced by a mother. Breeding females may experience a shift in food availability,  
468 predation risk, or conspecific density and this can alter their circulating hormones.  
469 Similar to other types of maternal effects (Wolf and Wade, 2009), changes in hormone  
470 levels can provide offspring with a cue predictive of the environment that they will  
471 encounter upon birth or hatching. If these cues reliably predict the selective environment  
472 that the offspring will encounter, offspring should pay attention to those cues and modify  
473 their phenotype appropriately. The pathways by which changes in maternal hormone  
474 levels can impact offspring are diverse in mammals. They could impact offspring  
475 characteristics directly by being transmitted across the placenta (Barbazanges et al.,  
476 1996) or through milk (Zarrow et al., 1970; Casolini et al., 1997). They could also modify  
477 offspring phenotypes indirectly by modifying maternal behavior towards offspring  
478 (Herrenkohl et al., 1976; Brummelte and Galea 2010; Patin et al., 2002; Nephew and  
479 Bridges, 2011) or modifying the behavior of offspring towards their mother (Moore and  
480 Power, 1986).

481 We examined if a glucocorticoid-mediated maternal effect was the mechanism by  
482 which mothers experiencing elevated densities mitigated the typical trade-off between  
483 litter size and offspring growth rate. In other words, we examined if high-density  
484 conditions increased maternal GCs and this elevated offspring growth, which should  
485 increase offspring survival under high-density conditions. We focused on GCs because  
486 they are well-known to respond to changes in density (Christian, 1950; Creel et al.,  
487 2013) and studies of laboratory rodents had indicated that elevated maternal GCs may  
488 decrease offspring birth weight but promote postnatal compensatory growth (e.g., Patin  
489 et al., 2002; now reviewed in Berghanel et al., 2017).



490 In support of our hypothesis that density increased maternal GCs that, in turn,  
491 adaptively altered offspring traits, we first found that squirrels have higher fecal  
492 glucocorticoid metabolites (FGMs) under high densities (Dantzer et al., 2013). Squirrels  
493 on our food-supplemented high-density study area had higher FGMs than those on the  
494 control study area experiencing lower densities (Dantzer et al., 2013). This difference  
495 was not due to dietary differences (Dantzer et al., 2011), which are known to impact gut  
496 passage time and therefore faecal hormone metabolite levels (Goymann, 2012). This is  
497 surprising as observational and experimental studies typically find that there is a  
498 negative association between food availability and GCs (Lynn et al., 2003; Kitaysky et  
499 al., 2007; Dantzer et al., 2017; reviewed by Romero and Wingfield, 2015) and that  
500 short-term food supplementation can decrease GCs (Schoech et al., 2004). We showed  
501 that food-supplemented squirrels also experiencing high densities had the highest GCs.  
502 This suggests that the method of acquiring food may change the direction of the impact  
503 of food availability on GCs. Territorial species like red squirrels that defend a central  
504 food cache may exhibit an increase in GCs when they experience increased food due to  
505 the concomitant increase in the number of competitors for that food cache. However, we  
506 note that future studies must address the additive and interactive impacts of food and  
507 density on GCs.

508 To identify whether food availability or conspecific density influenced GCs, we  
509 examined if females experiencing the acoustic playbacks of social cues of density had  
510 higher FGMs than those experiencing the control playbacks. Females experiencing the  
511 rattle playbacks (simulating high-density conditions) without additional food had higher  
512 FGMs than those experiencing the control playbacks (Dantzer et al., 2013). This  
513 indicated that the social environment affects GCs in red squirrels and that we can  
514 experimentally induce elevations in GCs by simply broadcasting acoustic cues of  
515 density.

516 Given that changes in GCs are well-known to induce phenotypic plasticity (Crespi  
517 and Denver, 2005; Denver 2009), we next investigated whether it was the change in  
518 GCs in breeding females that induced an adaptive shift in offspring growth rates that  
519 effectively prepared them for the selective environment they would encounter at  
520 independence from their mother. Using an observational dataset, we found that

521 maternal FGMs were positively correlated with offspring growth (Dantzer et al., 2013).  
522 We then confirmed this experimentally by conducting a GC manipulation experiment  
523 over four different years where we treated pregnant females with a small amount of  
524 peanut butter containing exogenous GCs (experimental females) or the same amount of  
525 peanut butter lacking the GCs (controls). These GC treatments elevated their circulating  
526 (blood) levels of GCs and caused elevation of FGMs (van Kesteren et al., 2019).  
527 Crucially, the elevation in GCs was within their natural physiological range such that this  
528 was not a supra-physiological or unnatural increase in circulating GCs (van Kesteren et  
529 al., 2019). Females that were treated with exogenous GCs also produced faster-  
530 growing offspring, but only if they were treated with GCs during pregnancy and not  
531 during lactation (Dantzer et al., 2020). Females with experimentally elevated GCs  
532 during lactation tended to produce slower-growing offspring, which is consistent with  
533 some studies of laboratory rodents (Nephew and Bridges, 2011). How pregnant females  
534 with elevated GCs produced faster-growing offspring is not yet clear, but a reduction in  
535 litter size or a change in litter sex ratio do not appear to be the cause as experimental  
536 (fed GCs) and control females had similar litter sizes and similar litter sex ratios  
537 (Dantzer et al., 2013; Dantzer et al., 2020).

538

#### 539 **4) The energetics of opportunity in a seasonal, pulsed-resource system.**

540 We have not yet directly assessed the effects of social density on energetic traits.  
541 Accordingly, the remaining section examines how three non-social drivers of energetic  
542 traits – i) resources, ii) seasonality/climate, and iii) opportunity – interact and coalesce to  
543 co-define each other, energetic status, and life history outcomes in this population. We  
544 focus in particular on the third driver - opportunity – because it is the least  
545 conventionally labeled or discussed predictor of energy expenditure and yet, we believe,  
546 the primary determinant of energetic status in red squirrels and perhaps many other  
547 organisms. Here, when we refer to “opportunity”, we are focusing on fitness  
548 opportunities that allow a squirrel to enhance its survival or reproduction by adjusting its  
549 energetic status. We first briefly describe the major methodologies we have used to  
550 quantify red squirrel energetic status.

551 We have primarily measured red squirrel energetic status using the doubly  
552 labeled water (DLW) technique to estimate daily energy expenditure (DEE: Speakman,  
553 1997). The DLW-technique estimates the DEE (also referred to as field metabolic rate:  
554 FMR) of free-ranging individuals by quantifying CO<sub>2</sub> production during a multi-day  
555 interval (Speakman, 1997). The use of this technique is challenging because of the  
556 difficulty of capturing and recapturing free-ranging individuals at specific intervals. The  
557 highly trappable nature and territoriality of red squirrels means that we can almost  
558 always find and trap an individual red squirrel when needed. Another advantage of red  
559 squirrels is that the behaviour of free-ranging individuals can be quantified through  
560 direct focal observations (Dantzer et al. 2012), meaning that we can also relate DEE to  
561 behaviour expressed during the sampling interval (Humphries and Boutin, 2000). We  
562 have complemented free-ranging DEE measures with estimates of resting metabolic  
563 rate (RMR: Lighton, 2008), measured on the same individuals, using controlled-  
564 environment, flow-through respirometry measures of O<sub>2</sub> consumption in a mobile  
565 energetics laboratory (Larivee et al., 2010). Most recently we have also classified  
566 squirrel behaviour using light loggers (Williams et al. 2014), temperature loggers (Studd  
567 et al. 2016) and accelerometers (Studd et al., 2019).

568 Variation in red squirrel DEE and RMR reflects the energetics of fitness  
569 opportunities, with rates of energy expenditure being exceedingly low when energy  
570 conservation is prioritized, possible, and increases fitness, and exceedingly high when  
571 energy expenditure enables either resource acquisition or reproductive gain (thereby  
572 increasing fitness). The responsiveness of red squirrels to the energetics of fitness  
573 opportunities causes them to contradict many standard pillars of physiological ecology.  
574 Whole animal rates of energy expenditure are described to increase with body size and  
575 body temperature (Speakman, 1999; Brown et al., 2004; Burton et al., 2011; Scholander  
576 et al., 1950; McNab, 2002; Humphries et al., 2005; Fletcher et al., 2012), but in red  
577 squirrels, energetic expenditure is weakly correlated with body size under almost all  
578 circumstances (Fletcher et al., 2012). Lactation is known to incur some of the highest  
579 energetic costs in mammals (Gittleman & Thompson, 1988), but red squirrels expend as  
580 much or more energy during the autumn cone hoarding period and (for males) during  
581 peak mating (Lane et al., 2010), as females expend during peak lactation (Fletcher et

582 al., 2012). Energetic ceilings experienced during lactation are described to constrain  
583 maximum litter size in mammals (Hammond & Diamond, 1997; Speakman & Krol, 2010),  
584 but lactating red squirrels can sustain experimental increases in litter size with elevated  
585 energy expenditure (Humphries & Boutin, 2000). Energy expenditure is often  
586 considered to be a cost or a subtraction term in defining individual or population  
587 production (Humphries & McCann, 2014), but red squirrel energy expenditure generally  
588 increases in response to abundant resources (Fletcher et al., 2012b; Fletcher et al.,  
589 2012a) and is a positive predictor of reproductive success (Fletcher et al., 2015).  
590 Although contradictory to many standard expectations, red squirrel energetic responses  
591 are readily understandable as long as it is realized that expenditure is not only a cost to  
592 energy conservation but at other times a beneficial allocation towards acquiring  
593 resources and reproductive opportunities (Humphries & McCann, 2014, Studd et al.  
594 2020). Understanding these energetic opportunities and constraints within a species  
595 requires identifying how resources, seasons, and climate combine to define when  
596 individuals should reduce or increase activity and energetic expenditure (Humphries et  
597 al., 2017, Studd et al. 2020).

598

599 **Current thinking/Consensus:**

600 Our collaborative research program leverages our research interests in ecology,  
601 evolution, behavior, and physiology, to use an integrative approach that asks simple but  
602 fundamental questions about how animals respond to shifts in key ecological  
603 parameters such as food, density, and the anticipated fitness payoffs of energetic and  
604 phenotypic plasticity (“opportunities” as described above).

605

606 **Unanswered questions and some predictions:**

- 607 1) How do squirrels predict future food availability? We suspect that red squirrels  
608 use a cue in the spruce trees (such as levels of phytoestrogens) to predict mast  
609 years. It is possible that increased consumption of phytoestrogens in mast years  
610 can induce life history plasticity including elevating litter sizes.

611

- 612 2) What happens to those squirrels that wrongly predict a mast or high-density  
613 conditions? Error management theory (EMT) predicts that individuals should  
614 commit a less costly error when it comes to life history plasticity (Sheriff et al.,  
615 2018) when the costs of false-positives (producing Phenotype A that is adaptive  
616 for Environment A but Environment A is not actually experienced in the future)  
617 are less than false-negatives (not producing Phenotype A that is adaptive for  
618 Environment A when Environment A is actually experienced in the future).  
619 According to EMT, when there is uncertainty about which environment will be  
620 encountered in the future, individuals should play it safe and, in this example,  
621 produce Phenotype A. Red squirrels achieve higher reproductive success by  
622 increasing reproductive output in anticipation of mast years and by producing  
623 faster-growing offspring in high-density years. Are the costs for those females  
624 that wrongly predict an upcoming mast or high-density (false-positive) lower than  
625 the costs of not responding adaptively when there is an actual mast or high-  
626 density year (false-negative)?  
627
- 628 3) What are the short- and long-term costs to females of increasing reproductive  
629 output in anticipation of food or high-density conditions? Female red squirrels do  
630 experience increased energetic expenditure when they ramp up reproduction  
631 (Humphries and Boutin, 2000; Fletcher et al., 2012) but do these short-term costs  
632 carry-over to the future and alter their future fitness? In addition, are there costs  
633 to phenotypic plasticity (i.e., do those females that exhibit greater plasticity in  
634 response to food and/or density experience some cost, particularly if they do not  
635 encounter a mast or high-density year in their lifetime)?  
636
- 637 4) Food and density are important ecological agents of selection and alter GCs in  
638 red squirrels but what is the interplay between other factors (weather, predators)  
639 on life history plasticity and GCs? Are the effects additive or interactive? We  
640 know that the abundance of terrestrial predators in Kluane is highly variable (Fig.  
641 1C) but previous experimental work shows that individual survival rates or  
642 population dynamics of red squirrels are not heavily influenced by the number of

643 terrestrial predators (Boonstra et al. 2001; but see Studd et al., 2015; Hendrix et  
644 al., 2020). Nonetheless, GCs are likely affected by both predation risk and  
645 warmer than average ambient temperatures. If these other factors alter maternal  
646 GCs, how do they affect their life history traits and are these effects in the same  
647 direction as we see when females encounter high-density years or when we  
648 experimentally elevate their GCs?

649

650 5) How widespread is the anticipation of food or density in animals, and what are  
651 the relative impacts of the anticipated vs. actual reproductive response to food  
652 availability on population growth? Red squirrels inhabit a fairly simple ecological  
653 food web where the amount of one food type (spruce seed) has pervasive effects  
654 on their population dynamics by inducing life history plasticity associated with  
655 changes food or density. Is this a realistic representation of the world or only  
656 found in these simple systems representing one seed consumer and one plant  
657 species? Red squirrels also provide an opportunity to examine if the effects of  
658 increased reproductive output in anticipation of elevated food outweigh the  
659 effects of the lagged (actual) response to increased food on population growth.

660

661 6) How is global climate change going to alter predictability of the future in red  
662 squirrels? Our study area in the Yukon has already seen substantial changes in  
663 temperature and precipitation such that it is now hotter and wetter in the Yukon  
664 than in recorded history and is expected to continue into the future according to  
665 general predictions of the Intergovernmental Panel on Climate Change (Masson-  
666 Delmotte et al., 2018). Temperature and precipitation patterns have been shown  
667 to affect masting dynamics in white spruce, such as warmer summer (July-  
668 August: Krebs et al., 2012, 2017) temperatures in the two years previous or  
669 wetter conditions in the preceding May (Krebs et al., 2012) are positively  
670 associated with white spruce cone crop production. Regional change in the  
671 regional climate of the Yukon may therefore also affect squirrel population  
672 dynamics and perhaps alter the predictability of the future from the perspective of  
673 red squirrels. If the cues red squirrels use to anticipate mast years or high-

674 density years become less reliable, we would expect that squirrels should  
675 eventually no longer exhibit the life history plasticity we have documented in  
676 response to food and density or that the responses we have observed in the past  
677 may become maladaptive.

678

679 **Discussion:**

680 Our long-term observational study of red squirrels in the Yukon has involved the  
681 collection of life history data from individual red squirrels and ecological data (food  
682 availability, predators, climate) for the past 32 years. We have used patterns that  
683 emerged from correlative analyses of these life history data to then generate  
684 hypotheses that we test experimentally by manipulating the key ecological variables  
685 such as food availability, density, or cues of density without altering food availability. We  
686 believe that our work provides three general lessons for animal ecologists:

- 687 ● Red squirrels anticipate food pulses where they increase reproductive output  
688 before the food is available; they uncouple the typical life history plasticity that is  
689 observed after an increase in food availability by correctly predicting its presence  
690 in the future. This overturns some of the assumptions in basic population ecology  
691 about consumers exhibiting a lagged response to increases in food;
- 692 ● As in most organisms, food and conspecific density co-vary in red squirrels and  
693 induce plasticity in life history traits. However, in red squirrels, social cues of  
694 density in the absence of additional food can also induce life history plasticity and  
695 females do this in anticipation of patterns of natural selection resulting from high  
696 densities. This indicates that social cues can foreshadow density-dependent  
697 selection;
- 698 ● Glucocorticoid levels in red squirrels respond to changes in both food and density  
699 and changes in GCs can induce adaptive life history plasticity. Few studies have  
700 disentangled the effects of food vs. density on GCs. We show that social  
701 interactions, rather than food, seem to be the overriding ecological mechanism  
702 that causes fluctuations in their glucocorticoids.

- 703       • Red squirrels overturn standard expectations in physiological ecology: their  
704       energetic expenditure is typically only weakly related to body size, lactation is not  
705       the most energetically demanding life history stage, even during peak lactation (it  
706       can be higher in females and males during food hoarding or during mating in  
707       males), squirrels can cope with increased litter sizes and increase expenditure,  
708       and they expend more energy (not less) when food resources are abundant.

709       —

710       The Klwane Red Squirrel Project has been existence for more than 30 years. We  
711       believe that the longevity of this project and any success that we have had can be  
712       attributed to the following. First, we have been incredibly lucky with many hardworking,  
713       dedicated, and cheery field personnel from undergraduates to professional wildlife  
714       technicians. The focus on tracking the individual life histories of red squirrels has  
715       allowed many graduate students and postdoctoral researchers to diversify our research  
716       portfolio by capitalizing on the life history data and complementing it with their own  
717       creative set of research questions. Second, our study species has several attributes that  
718       make them well-suited for long-term studies of individual life histories and how  
719       ecological factors induce plasticity in their life history traits. Because of their extreme  
720       site fidelity, conspicuous territorial behaviour, and the fact that they are diurnal, red  
721       squirrels can be easily tracked using live-trapping and behavioral observations, thereby  
722       allowing us to completely enumerate all individuals in our study populations. Red  
723       squirrels are similar to birds as their nests can be easily located with radio-telemetry  
724       and the offspring can be accessed from their natal nests soon after birth. This is unlike  
725       many other rodent species where offspring are located underground in an inaccessible  
726       burrow. This provides us with detailed life history data of each individual squirrel even if  
727       those offspring do not survive beyond emergence. Moreover, it provides us with the  
728       opportunity to collect data on the rate of offspring postnatal (i.e. pre-emergent) growth,  
729       which is also rare in most mammal species.

730       Third, unlike most long-term studies of birds, natal dispersal is generally quite  
731       low, there does not appear to be a substantial sex-bias in long-distance natal dispersal,  
732       and adult dispersal is very low (Boutin et al., 1993; Berteaux and Boutin, 2000; Cooper  
733       et al., 2017). This means that nearly all of the offspring that are born in our population



734 can be tracked from birth until death. The disappearance of juveniles or adults is  
735 common in most long-term studies of wild animals, which makes it challenging to  
736 distinguish between death and successful dispersal outside the study area. In our study  
737 system, our current understanding is that juvenile red squirrels that disappear are  
738 extremely likely to be dead rather than successfully dispersed. Although we note that  
739 our recent study showed that juvenile males that do successfully disperse may do quite  
740 well (Martinig et al., 2020) and our current work focuses on better estimating the exact  
741 proportion of juveniles that do disperse and successfully settle outside of our study  
742 grids. Our lifetime fitness estimates are not perfect but given the low natal dispersal  
743 distances, our current understanding is that we can characterize the number of offspring  
744 each female or male red squirrel produces in a year and the number of those offspring  
745 that they produce that actually recruit into the population (i.e., acquire a territory and  
746 survive to the spring following their year of birth) and, therefore, contribute to the genetic  
747 composition of the population and to population growth itself.

748 Fourth, the reliance of red squirrels on primarily one food source (white spruce  
749 seed) and their food caching behaviour in a central location enables us to accurately  
750 quantify how much food is available in the environment (in the trees: Boutin et al., 2006;  
751 Fletcher et al., 2010), but also the amount of available food that is cached by each  
752 individual squirrel (Larivee et al., 2010; LaMontagne et al., 2013; Fisher et al., 2019). In  
753 the past, this has allowed us to better understand how food availability influences the  
754 life history traits of red squirrels to better understand resource allocation issues (e.g.,  
755 Boutin et al., 2006). In the future, we will be able to look at how individual variation in  
756 resource acquisition (how much food they actually cache) influences these life history  
757 traits to better understand how both resource acquisition and allocation influences  
758 lifetime reproductive success (*sensu* van Noordwijk and de Jong, 1986). Although other  
759 studies in free-living animals can track food availability through different indices of the  
760 amount of a food resource in a specific area (e.g., by measuring availability of seeds,  
761 fruits, caterpillars, other insects, etc.) or track resource acquisition through food  
762 consumption (e.g., changes in body mass during some specific time period), our ability  
763 to track both food availability and food acquisition is relatively unique and should prove

764 useful in the future for questions related to life history plasticity and population  
765 dynamics.

766 Finally, we adhere to the “Krebsian” view that observational studies of wild  
767 animals should be one part of a research program that seeks to test ecological  
768 hypotheses, but that large-scale experimental manipulation of key ecological variables  
769 is a necessary second step, and is better suited to test these hypotheses than ever  
770 more advanced statistical analyses (Krebs 1991; Krebs et al., 2001; Wolff and Krebs,  
771 2008; Krebs et al., 2018). Throughout our field research program, we have aimed to use  
772 our observational data to test specific hypotheses, but also to help generate hypotheses  
773 to test in future field experiments. This is largely the outcome of geography as our study  
774 area in the Yukon is also the site of one of the most ambitious large-scale field  
775 experiments ever undertaken in nature that was designed to examine the ecological  
776 factors that cause snowshoe hare (*L. americanus*) population cycles (Krebs et al., 1995,  
777 2001, 2018). Past mentors or collaborators on this project and others emphasized the  
778 importance of proposing credible alternative hypotheses and the need for developing  
779 field experiments that allow you to reject one of the alternative hypotheses (sensu  
780 Popper, 1963; Platt, 1964). We realize that experiments are not possible in all study  
781 species due to their threatened or endangered status. When possible, we believe that  
782 long-term research projects will thrive by employing basic hypothesis testing including  
783 field experiments that manipulate key variables that allow one to reject a hypothesis.

784

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801

### 802 **Authors Contributions**

803 BD led the writing of the manuscript with contributions from SB, MMH, JEL, and AGM.  
804 All authors collected the data and BD analysed the data.

805

### 806 **Data Availability Statement**

807 Data used to generate Figures 1, 2, and 4 are available from Dryad Digital Repository  
808 doi:10.5061/dryad.rfj6q5788 (Dantzer et al 2020).

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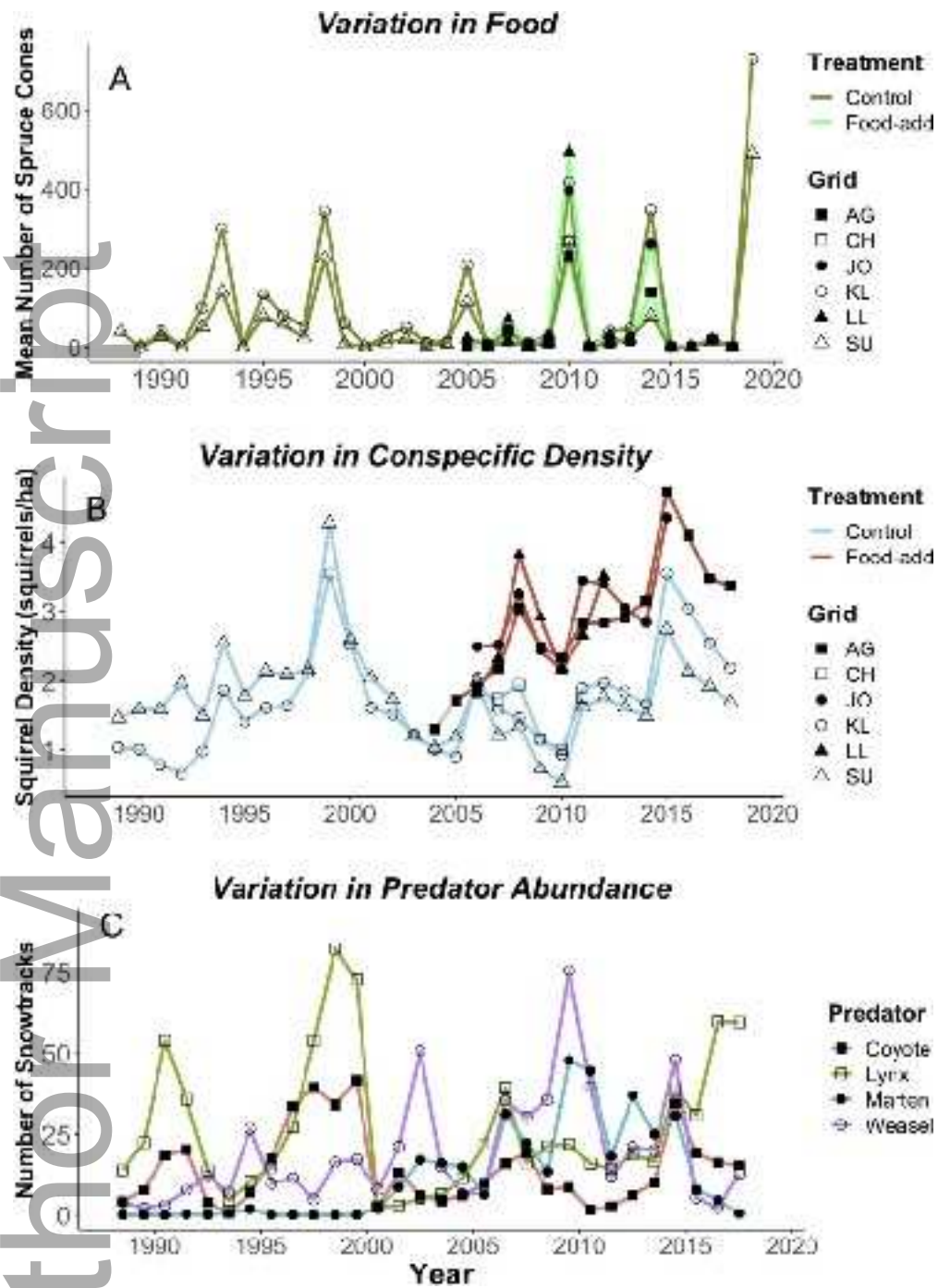
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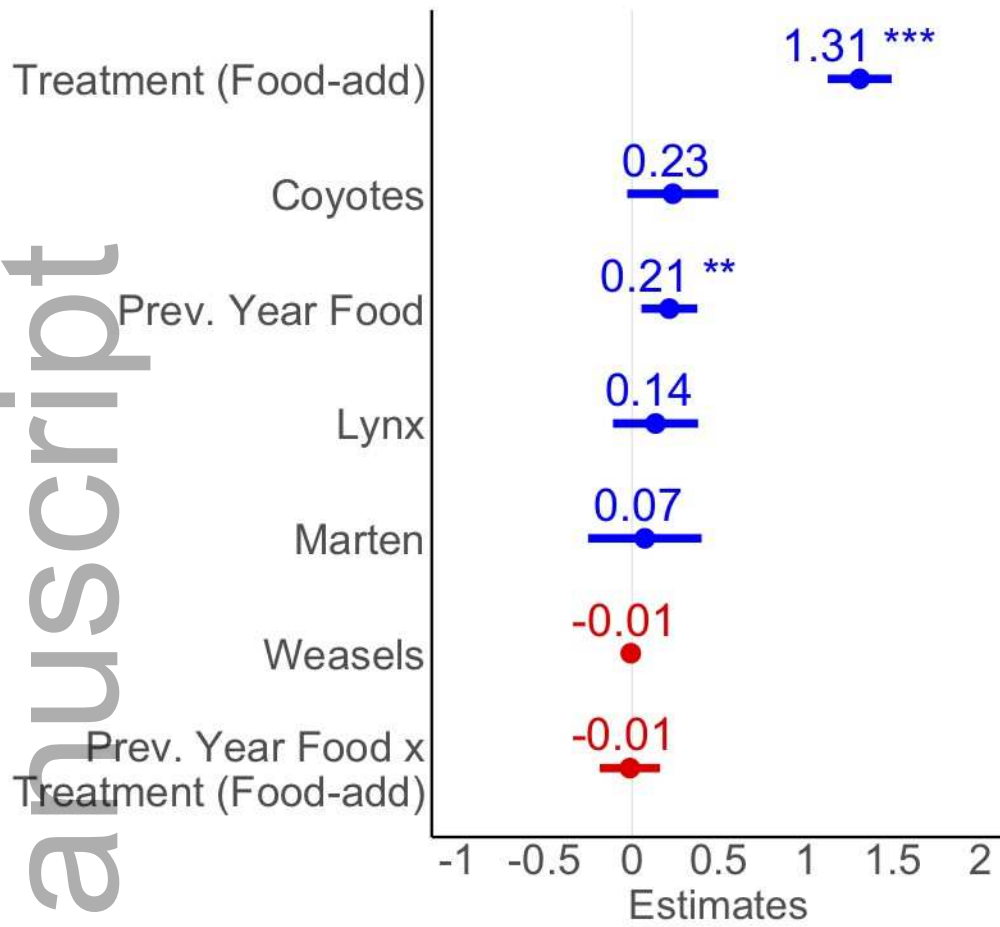
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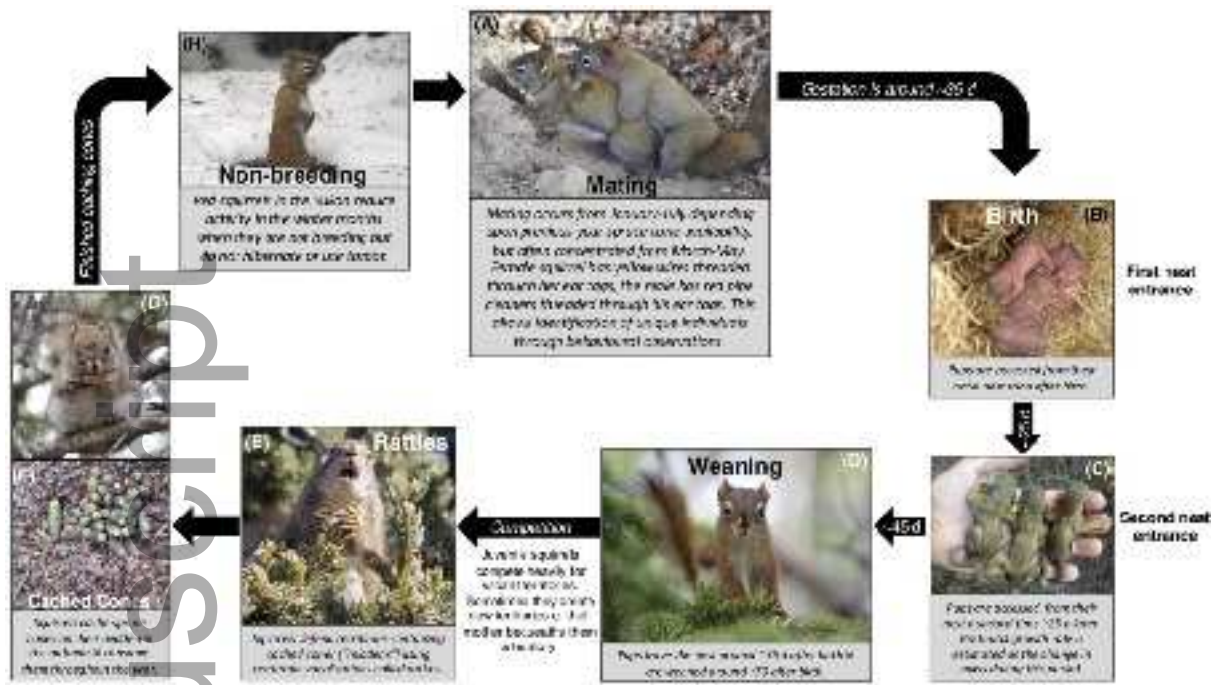




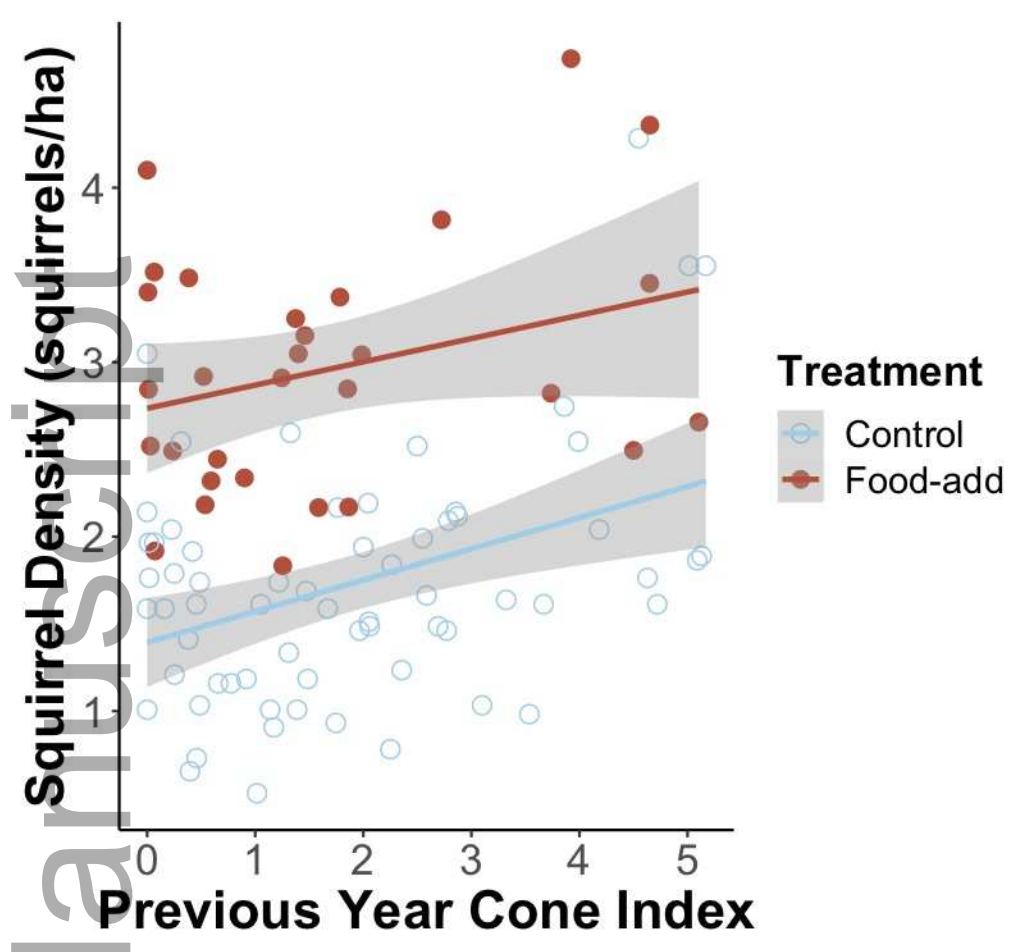
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# Insights from the Kluane Red Squirrel Project

To give you the best chance of the best results, read the following and when should you have them? For a full list of available data, visit the project website: <http://www.kluane.slu.se>

Learn more about the project and the study on the effects of food and climate on reproduction and survival of red squirrels in the Kluane region.

### THE STUDY HAS INVOLVED

- 2000-2001
- 2002-2003
- 2004-2005
- 2006-2007
- 2008-2009
- 2010-2011
- 2012-2013
- 2014-2015
- 2016-2017
- 2018-2019
- 2020-2021

### KEY FINDINGS

1. **Reproduction**  
 The number of offspring produced by a squirrel is affected by the amount of food available in the autumn. In years with high food availability, squirrels produce more offspring.


2. **Survival**  
 The survival of offspring is affected by the amount of food available in the autumn. In years with high food availability, more offspring survive.

3. **Climate**  
 The amount of food available in the autumn is affected by the amount of snow in the autumn. In years with high snow cover, there is less food available.

4. **Climate**  
 The amount of food available in the autumn is affected by the amount of snow in the autumn. In years with high snow cover, there is less food available.

5. **Climate**  
 The amount of food available in the autumn is affected by the amount of snow in the autumn. In years with high snow cover, there is less food available.

6. **Climate**  
 The amount of food available in the autumn is affected by the amount of snow in the autumn. In years with high snow cover, there is less food available.



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