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

Ben Dantzer[1,2] 🄳 | Andrew G. McAdam[3] 🄳 | Murray M. Humphries[4] | Jeffrey E. Lane[5] 🄳 | Stan Boutin[6] 🄳

[1]Department of Psychology, University of Michigan, Ann Arbor, MI, USA; [2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA; [3]Department for Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA; [4]Natural Resource Sciences Department, McGill University, Ste-Anne-de-Bellevue, QC, Canada; [5]Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada and [6]Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

Correspondence
Ben Dantzer
Email: dantzer@umich.edu

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Abstract

1. Long-term studies of wild animals provide the opportunity to investigate how phenotypic plasticity is used to cope with environmental fluctuations and how the relationships between phenotypes and fitness can be dependent upon the ecological context.

2. Many previous studies have only investigated life-history plasticity in response to changes in temperature, yet wild animals often experience multiple environmental fluctuations simultaneously. This requires field experiments to decouple which ecological factor induces plasticity in fitness-relevant traits to better understand their population-level responses to those environmental fluctuations.

3. For the past 32 years, we have conducted a long-term integrative study of individually marked North American red squirrels *Tamiasciurus hudsonicus* Erxleben in the Yukon, Canada. We have used multi-year field experiments to examine the physiological and life-history responses of individual red squirrels to fluctuations in food abundance and conspecific density.

4. Our long-term observational study and field experiments show that squirrels can anticipate increases in food availability and density, thereby decoupling the usual pattern where animals respond to, rather than anticipate, an ecological change.

5. As in many other study systems, ecological factors that can induce plasticity (such as food and density) covary. However, our field experiments that manipulate food availability and social cues of density (frequency of territorial vocalizations) indicate that increases in social (acoustic) cues of density in the absence of additional food can induce similar life-history plasticity, as does experimental food supplementation.

6. Changes in the levels of metabolic hormones (glucocorticoids) in response to variation in food and density are one mechanism that seems to induce this adaptive life-history plasticity.

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7. Although we have not yet investigated the energetic response of squirrels to elevated density or its association with life-history plasticity, energetics research in red squirrels has overturned several standard pillars of knowledge in physiological ecology.

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

1 | INTRODUCTION

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

Studies of life-history plasticity in a diversity of wild animal species have provided valuable tests of theory of adaptive phenotypic plasticity as well as empirical examples illustrating how plasticity can enable resilience through environmental change. Such studies are challenging because they usually involve following free-living but marked individuals across some environmental gradient (e.g. temperature, predation risk, food availability, conspecific density: Nussey et al., 2007). It is also quite difficult to identify and experimentally manipulate the putative ecological cue that induces plasticity in natural populations. A notable pattern is that many of these studies investigate life-history plasticity in response to temperature by regressing the life-history traits of an individual across a range of temperatures (or in some cases, different years of study). For example, the timing of breeding of individual birds varies across years and is related to ambient temperature around the time of breeding (Brommer et al., 2008; Charmantier et al., 2008; Nussey, Postma, Gienapp, & Visser, 2005; Porlier et al., 2012). In some of these studies, the plasticity in laying date that was apparently induced by temperature was adaptive and greater levels of plasticity were under positive selection (Nussey, Postma, et al., 2005; Porlier et al., 2012). Other studies in free-living mammals illustrate the effects of temperature or longitudinal trends in plasticity in the timing of other life-history traits such as emergence from hibernation (Lane et al., 2012), the timing of breeding (Bonnet et al., 2019; Nussey, Clutton-Brock, Elston, Albon, & Kruuk, 2005) or litter size (Ozgul et al., 2010; Tafani et al., 2013), which may only be adaptive in some cases (Nussey, Clutton-Brock, et al., 2005; Ozgul et al., 2010).

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

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

annually, there is typically a numerical response in the consumers where density of the species of interest also increases when food is elevated. For example, population densities of small mammal species that consume seeds from plant species that produce occasional pulses of these seeds, are elevated in the years following resource pulses (Wolff, 1996). Food supplementation studies support this same pattern where plasticity in the life-history traits of individuals in response to supplemental food can, in turn, elevate population densities (Prevedello et al., 2013). For example, supplementary food provided to rodents can cause a 50%–300% increase in population density within a few months by increasing litter sizes and elevating juvenile survival (Cole & Batzli, 1979; Gilbert & Krebs, 1981). This 'ecological coupling' where two environmental fluctuations co-occur or occur together after a brief lag time makes it challenging to disentangle which environmental cue (which are often the ecological agents of selection themselves: Wade & Kalisz, 1990) is inducing the plasticity. Others have described similar problematic issues

when aiming to disentangle the ecological agents of selection, such as population density and predation risk covarying and influencing the patterns of phenotypic evolution in fish (Reznick et al., 2002).

When it comes to this ecological coupling of food and density, one widely used solution to identify the ecological mechanism inducing plasticity is to carry out short-term food supplementation studies (Boutin, 1990; Ruffino et al., 2014). In these studies, supplemental food is provided to animals for short periods of time and the plasticity that is induced in a wide variety of traits is quantified and usually attributed to the increase in food rather than the change in resource competition behaviour. This is useful, but also only provides part of the story as very rarely is there an increase in food that is not coupled with an increase in density (due to altered patterns of birth, death or immigration) that in turn results in increased competition for that resource (Prevedello et al., 2013).
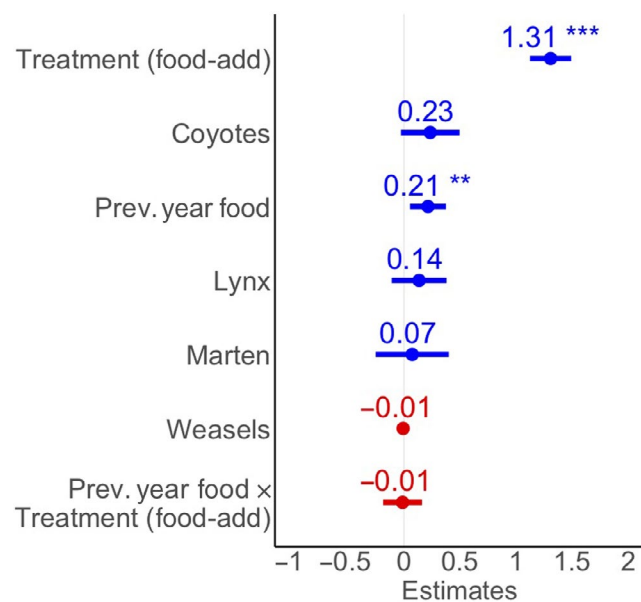
In our long-term study of North American red squirrels in the Yukon, Canada, we have taken an integrative and experimental

FIGURE 1 Red squirrels in the Yukon, Canada experience inter-annual fluctuations in (a) the availability of their major food source (seeds from white spruce trees) and, consequently, (b) conspecific density, and (c) the abundance of terrestrial predators. Food-supplementation ('Food-add') on some of our study areas compared to nearby control study areas where no food was added. Data shown are the number of cones on spruce trees (mean of 110 trees per study area, range = 77–200) distributed systematically across six different study areas ('Grid'). Mast years occurred in 1993, 1998, 2005, 2010, 2014, and 2019. Squirrel population density on the six different study areas estimated using live-trapping and behavioural observations in May of each year (spring density). Predator abundance data (provided by Kluane Ecological Monitoring Project) were estimated through counts of the number of snowtracks of each species on a 25 km linear transect near the study area. In each year, counts started after the first snowfall of each year and were carried out after each snowfall until late spring (O'Donoghue et al., 2001). Note that points overlap in (a) due to very similar estimates of spruce cone availability
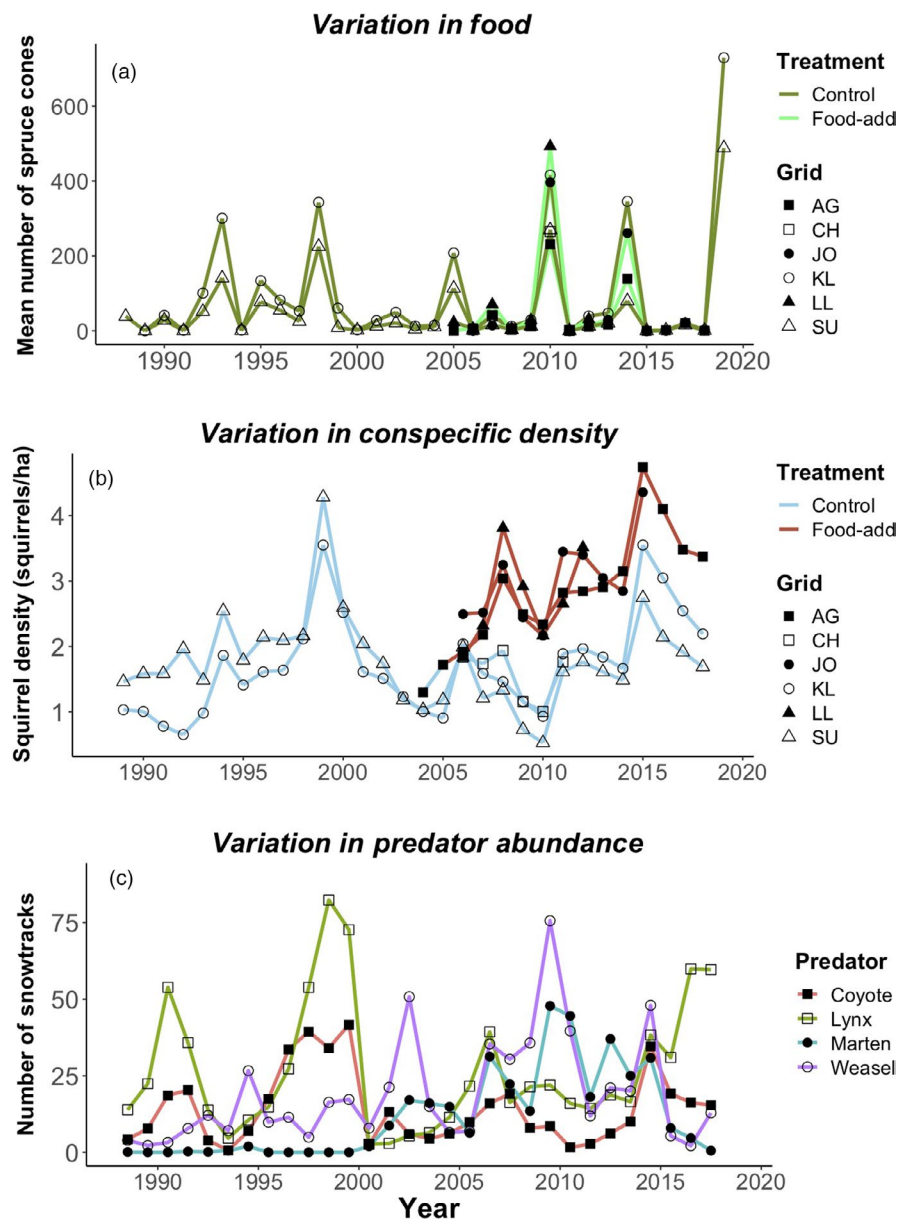
approach to understand the ecological mechanisms that induce phenotypic plasticity to better understand how red squirrels cope with their variable environment. Yukon red squirrels experience tremendous fluctuations in ecological factors that can induce plasticity and act as ecological agents of selection, such as food, conspecific density and predation risk (Figure 1). However, we have mostly focused our attention on food and conspecific density as previous experimental studies that excluded terrestrial predators and our long-term data analyses show that terrestrial predators seem to have minimal effects on overall squirrel densities (Boonstra et al., 2001; Figure 2), though it is likely that predators do influence the survival of individual juveniles (Hendrix et al., 2020; Studd et al., 2015). Using targeted experimental manipulations of food, density or the acoustic cues reflecting density, we have been able to unravel how changes in density and food induce plasticity in life-history traits in natural populations. We have also incorporated physiological and energetic approaches into the ecological context and natural history of our study species to aid and complement our research.

In this synthesis, we will discuss the key insights from our long-term observational study that tracked reproductive output in anticipation and response to naturally elevated food abundance and our field experiments that elevated both food and density or only the social (acoustic) cues of density without additional food. We will also describe some of the results from our physiological and energetic research that challenges existing paradigms in those fields. We note

that our past work has described life-history plasticity in response to spring temperatures (Lane et al., 2018; Réale et al., 2003) but here we focus on food and density. Overall, our long-term observational study on the life-history responses of free-living red squirrels to changes in food and density, in addition to our field experiments, provide some general lessons for animal ecologists. Specifically, the observation that increased food may not be necessary to enable animals to do the things they do (e.g. increase reproductive output) but instead do so only when the fitness benefits are sufficiently high to warrant the increased reproductive output. For example, red squirrels can have ample available food that allows them to breed early or produce fast-growing offspring, but they do this only when there is selection for early parturition dates and fast postnatal growth.

2 | HISTORICAL CONTEXT

The Kluane Red Squirrel Project was formally initiated by Stan Boutin in 1988. Murray Humphries joined the project in 1994, Andrew McAdam joined in 1998, Jeff Lane joined in 2003 and Ben Dantzer in 2006. All principal investigators (Boutin, Dantzer, Humphries, Lane and McAdam) have contributed to the conception, implementation, training of personnel and funding of research associated with this project. A strength of this project is the confluence of research interests and expertise from the different principal investigators, which has allowed project personnel (including undergraduate and graduate students and postdoctoral researchers) to conduct interdisciplinary research. All principal investigators strongly believe in collaboration, data sharing and democratic decision-making.

3 | STUDY SYSTEM

Our research takes place in a forested glacial valley (Shakwak Trench, ~850 m elevation) in the southwest Yukon, between Haines Junction and Kluane Lake (Łù'àn Män in Southern Tutchone or 'big fish lake'). The area in which we work is collectively known as Kluane (pronounced 'Kloo-wah-nee') or Dän Keyi ('Our people's land') and is part of the traditional territory of the Southern Tutchone people. Our study areas are located within the territory of the Champagne and Aishihik First Nations, and near the traditional territories of the Kluane First Nation and White River First Nation. Members of these First Nations (dän) have lived off these lands for more than 8,000 years.

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

FIGURE 2 Red squirrels in the Yukon experience variation in the abundance of terrestrial predators (Figure 1c) but squirrel density is unaffected by the abundance of terrestrial predators measured using snowtracking (see Figure 1). Only the presence of supplemental food and increased spruce cone production in the previous autumn significantly increased adult squirrel density (see also Figure 4). Densities were estimated in the spring (May) of each year using live-trapping and behavioural observations. These results are from a linear mixed-effects model shown in Figure 4. All continuous variables in this model were standardized (mean = 0, SD = 1) and standardized effect sizes are shown

Red squirrels in the Yukon are small (adults weigh ~250 g) and relatively short-lived species (median life span of squirrels that acquire a territory as a juvenile = 3.5 years, maximum life span = 8 years: McAdam et al., 2007). Red squirrels are highly territorial, with individuals of both sexes defending separate food-based territories year-round (Smith, 1968). Their non-overlapping territories are centred on a cache of white spruce cones, which are stored in tunnels in a 'midden' (a large accumulation of cone bracts created by consuming spruce cones in the same spot over many years). In each autumn (September), squirrels clip and collect cones from white spruce trees on their territory and store most of them in their midden (Fletcher et al., 2010). Middens help to keep the cones closed so that the seeds remain viable for at least 4 years after collection

(Donald & Boutin, 2011). Although squirrels in the Yukon consume many different types of foods, from fungi to snowshoe hare *Lepus americanus* leverets, spruce seed is the major component of their diet (Fletcher et al., 2013; Ren et al., 2017). Middens contain an estimated mean ± *SD* of 19,790 ± 1,429 cones (range = 0 to 146,500, Haines, 2017). Cones cached in the autumn of 1 year can have carry-over effects on squirrel life-history traits in the following year (e.g. high spruce cones in the previous autumn is associated with earlier breeding in the following spring: Réale et al., 2003; Williams, Lane, et al., 2014). Middens are also long-lasting and are often re-used by other squirrels once a previous owner has died (e.g. one midden has been used continuously for up to at least 31 years: Fisher et al., 2019) such that cones cached by one squirrel can carry over and
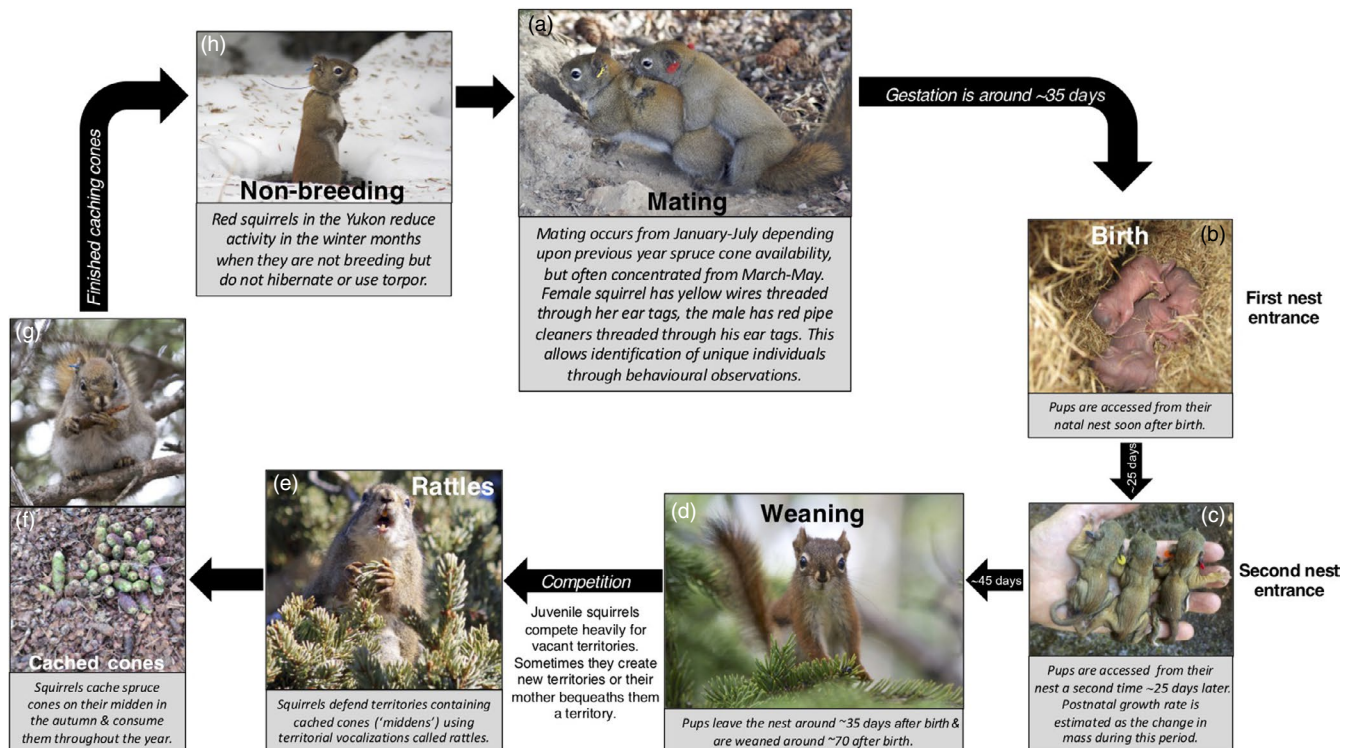
FIGURE 3 A typical year in the life of a North American red squirrel in Kluane, Yukon, Canada. Red squirrels are diurnal and we mark each individual squirrel uniquely with metal ear tags in addition to unique combinations of coloured electrical wire (females), pipe cleaners (males), or plastic washers (juveniles of both sexes) that are threaded through these ear tags (a, c, g). (a) Squirrels are polygamous and have a scramble-competition mating system (Lane et al., 2008). Mating can occur from January to July (and occasionally even later) but most mating happens from March to May. The timing of mating is heavily influenced by the availability of spruce cones in the previous autumn (Boutin et al., 2006; McAdam et al., 2019). Around 35 d after conception, females give birth. We access pups at two time periods: (b) immediately following birth and then again (c) around 25 d later when the pups are large enough to be permanently ear tagged. We use the change in body mass during this period to estimate postnatal growth rates, which is linear during this time period (McAdam et al., 2002). Until pups are around 30–35 days of age, they remain in their natal nest and only consume milk provided by their mother. (d) Pups typically remain on their natal territory with their mother until they are weaned around 70 days of age. Pups typically need to acquire a territory where they can cache spruce cones (in 'middens') if they are to survive their first winter (Larsen & Boutin, 1994). Pups compete for sole access to empty/vacant territories before the autumn in each year but they may also create new middens (in years where there is high spruce cone production) or their mother may bequeath them a territory (Berteaux & Boutin, 2000; Lane et al., 2015). (e) Regardless of how they acquire a midden, both females and males defend exclusive food-based territories year-round using territorial vocalizations called rattles (Siracusa et al., 2017), which they emit frequently across the year. (f) In the autumn of each year, squirrels collect and cache spruce cones and hoard most of them in a larder located on their midden (Fletcher et al., 2010). (g) Squirrels consume these hoarded cones throughout the following autumn and winter months and beyond (Fletcher et al., 2013). (h) When squirrels are finished caching cones in the autumn, they are typically in a quiescent stage where they reduce activity and do not breed but do not undergo hibernation or daily torpor (Brigham & Geiser, 2012; Pauls, 1978). Photos by Ben Dantzer (c), Ryan W. Taylor (a, b, d, g, h), and Andrea Wishart (e, f)

influence the survival or reproduction of subsequent owners (Fisher et al., 2019). Squirrels primarily defend their territories using territorial vocalizations called 'rattles' (Siracusa et al., 2017; Smith, 1978), which they emit frequently throughout the day and across the entire year (Dantzer et al., 2012; Siracusa et al., 2019). Juvenile squirrels usually must acquire a midden soon after weaning (from late spring to autumn depending upon the year) if they are to survive their first winter (Larsen & Boutin, 1994), and squirrels with more cones cached in their midden exhibit higher survival (LaMontagne et al., 2013; Larivée et al., 2010). Once a squirrel acquires a territory, they very rarely leave voluntarily even if there are vacancies available (Larsen & Boutin, 1995). However, this can happen in cases where adult females bequeath their territory to their offspring (Berteaux & Boutin, 2000; Boutin et al., 2000; Lane et al., 2015; Price & Boutin, 1993).

Female and male squirrels are polygamous and have a scramble-competition mating system (Lane et al., 2008). Mating can occur from January to July (and occasionally even later) but most mating happens from March to May. The timing of mating is heavily influenced by the availability of spruce cones in the previous autumn (Boutin et al., 2006; McAdam et al., 2019). Females and males are usually sexually mature in the year following birth but some females do not breed successfully until their second year or later (Descamps et al., 2006; McAdam et al., 2007), although yearling females are much more likely to attempt to breed in mast years (Boutin et al., 2006). Female red squirrels are spontaneous ovulators that are typically in oestrus for 1 day per year, apart from mast years when females may enter oestrus multiple times (Boutin et al., 2006). Gestation is around 35 days and pups first emerge from their nest around 42 days before they are weaned around 70 days after birth (Boonstra et al., 2001; McAdam et al., 2007; Stuart-Smith & Boutin, 1995). Females usually only wean one litter of ~two or three pups per year (see below). If their first litter fails before weaning, they will occasionally attempt to breed again (Williams, Lane, et al., 2014), but squirrels only successfully wean two litters in mast years (see below: Boutin et al., 2006; McAdam et al., 2019).

All squirrels in our study population are individually marked using unique metal ear tags, which most squirrels receive while they are still in their natal nest soon after birth (~25 days of age: see overview of data collection in Figure 3). Squirrels also receive unique combinations of small pieces of coloured telephone wire (adult females), pipe cleaners (adult males) or plastic washers (juveniles) threaded through these ear tags so that we can identify them without capture and handling (Figure 3). In each year, roughly from March to October, we monitor the reproduction, survival, territorial ownership and food availability of individual squirrels using capture and handling and behavioural observations. In May and August of each year, we completely enumerate all the squirrels on the study areas to quantify territory ownership and population density (Descamps et al., 2009). To monitor reproduction, we temporarily capture squirrels and palpate their abdomen (females) or testes (males) to assess reproductive condition. When females are lactating, we often apply very high frequency collars and then track

them to their nests, though we also locate nests using behavioural observations. Pups are temporarily removed from their nest (for an average of ~12–15 min: Westrick et al., 2020) soon after birth and again when they are ~25 days of age (Figure 3). We remove them from the nest so that we can determine their sex, weigh them, and, when they are ~25 days, tag them with metal ear tags. These procedures then allow us to estimate the parturition date, litter size, litter sex ratio, litter survival and postnatal growth rates of each offspring for each female in our study population. Small pieces of ear tissue obtained from pups soon after birth allow us to identify sires of pups (Gunn et al., 2007) and construct multigenerational pedigrees (McFarlane et al., 2014).

4 | KEY ADVANCES

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

4.1 | Life-history plasticity in anticipation of increased food availability

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

Red squirrels in the Yukon primarily consume seeds from white spruce trees that they cache underground in unopened cones in a central midden in the autumn (Fletcher et al., 2010, 2013). Squirrels need to rely upon cached spruce seed to mostly or completely fuel their survival and reproduction for the next 11–12 months or beyond as seeds produced in that year are not available to squirrels as a food source until around the first week of August (Boutin et al., 2013; Fletcher et al., 2013; Ren et al., 2017). Cone production in white spruce is highly episodic, with a superabundance of cones (mast years) produced in some years followed by several years of little to no cone production (non-mast years: Boutin et al., 2006; LaMontagne & Boutin, 2007; McAdam et al., 2019; Figure 1a). Mast

years lead to greater seed escape because the trees produce more cones than can be harvested by the squirrels (Fletcher et al., 2010).

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

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

This life-history plasticity in anticipation of food is adaptive in red squirrels as there are considerable fitness benefits for those that ramp up reproduction in anticipation of the increased food. Overwinter survival of juveniles produced in mast years is considerably higher than in non-mast years (Humphries & Boutin, 2000; McAdam & Boutin, 2003; Williams, Lane et al., 2014) such that squirrels that experience mast years have higher lifetime reproductive success than those that do not (Hämäläinen et al., 2017; McAdam et al., 2019). In mast years, there is strong positive directional selection on litter size (McAdam et al., 2019) and likely strong positive selection on the number of litters produced in mast years (Boutin et al., 2006).

This pattern where animals anticipate future food abundance has now been documented in other species that experienced pulses of crucial food resources (e.g. Eurasian red squirrels *Sciurus vulgaris*: Boutin et al., 2006; Eastern chipmunk *Tamias striatus*: Bergeron

et al., 2011). We predict that if animals have cues to predict the future and experience high fitness benefits from exhibiting adaptive life-history plasticity in response to these cues (as red squirrels do), individuals should follow a conservative life-history strategy until they encounter these cues whereupon they should increase their reproductive output (Boutin et al., 2013). Whether this pattern is more widespread remains to be seen.

4.2 | Experimental decoupling of food and density reveals that social cues of density induce life-history plasticity that is often attributed to increased food

Density-dependent selection is a phenomenon that has been widely studied in observational data collected from longitudinal studies where individuals are marked uniquely (Bassar et al., 2013; Calsbeek & Smith, 2007; Reznick et al., 2012; Schrader & Travis, 2012; Sinervo et al., 2000). However, because food and density typically covary, it is difficult to tease apart the influence of food and density on any life-history plasticity observed when population density increases. Thus, experimental manipulation of food and density is typically required to identify the ecological agent of selection (Wade & Kalisz, 1990) that favours this life-history plasticity that may be an adaptive response to the increase in density. In Yukon red squirrels, we have been able to quantify the life-history plasticity in response to experimental manipulations of food, density and also the social cues that reflect increased density. By doing so, we have shown that social cues in spring induce adaptive life-history plasticity without access to additional food and foreshadow upcoming density-dependent selection.

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

Red squirrels are amenable to experimental manipulations at the individual level because both sexes exhibit year-round territoriality,
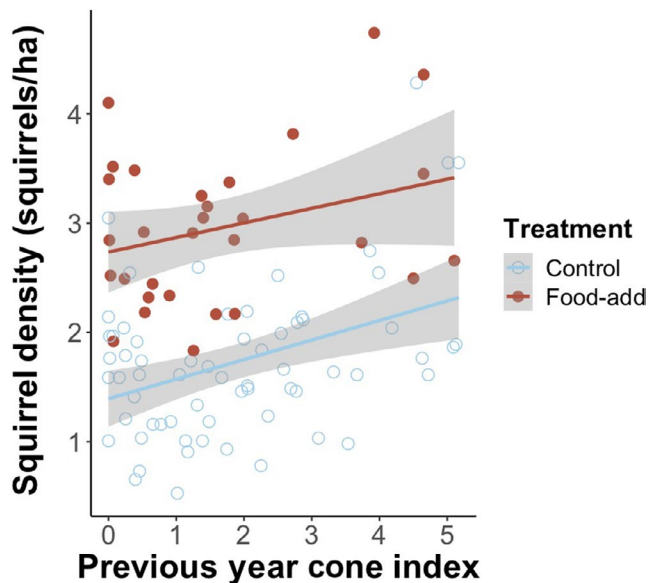
FIGURE 4 The spring breeding density of red squirrels is positively correlated with the production of white spruce cones in the previous autumn where density is elevated following years of high food availability ($b = 0.21 \pm 0.08$, $t_{66.5} = 2.61$, $p = 0.011$). Although spring density on the food-supplemented areas was an average of 68.5% higher than density on the control areas (effect of treatment: $b = 1.31 \pm 0.09$, $t_{66.4} = 13.97$, $p < 0.0001$), spring density on the food-supplemented areas still increased at a similar rate when spruce cone production was elevated in the previous autumn (interaction between treatment and previous year spruce cone production: $b = -0.01 \pm 0.09$, $t_{68.5} = -0.14$, $p = 0.89$). Data shown are from up to six different study areas (2–3 control study areas, 1–3 food-addition study areas) from 1988 to 2019. These results are from a linear mixed-effects model (containing random effect for study year) that included snowtrack abundance of the four predatory species, an index of previous year cone production (on a ln scale: LaMontagne et al., 2005), treatment (control, food-addition), and the interaction between treatment and previous year cone production (marginal R^2 of full model = 0.59). All continuous variables in this model were standardized (mean = 0, $SD = 1$) and full results shown in Figure 2

strong site fidelity and low adult dispersal (Berteaux & Boutin, 2000). From 2004 to 2017, we provided supplemental food to individual squirrels on three study areas (Dantzer et al., 2013; Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012). We provided squirrels with ad libitum food to simulate high food conditions that they experience following a mast year. Squirrels were provided with 1 kg of all-natural peanut butter (no salt or sugar added) in a bucket that was hung between two trees on the centre of their territory. Squirrels cannot cache peanut butter underground and pilferage by other bird or mammal species or conspecifics was extremely low (van Kesteren et al., 2019). Peanut butter was replenished every 6 weeks from October to May of each year. One kilogram of peanut butter approximates that of the resting metabolic need of an individual red squirrel for ~70 days (Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012).

Squirrel density on the food-supplemented areas was an average of 65% higher than on control study areas (Figures 1b and 4; Dantzer et al., 2013). However, squirrel densities on the food-supplemented

areas still increased after a mast year and the magnitude of increase was not different from control study areas (Figure 4). This is probably because squirrels on the food-supplemented study areas still exhibit natural food caching behaviour (Donald & Boutin, 2011).

To separate the effects of this additional food and consequent increases in density on life-history plasticity in female red squirrels, we manipulated the social cues of density by elevating the frequency with which squirrels heard territorial vocalizations to simulate a high-density environment. This took advantage of the fact that squirrels exhibit extreme site fidelity and advertise territorial ownership using specific vocalizations (rattles). On average, squirrels emit a territorial vocalization once every 7–10 min (Dantzer et al., 2012; Siracusa et al., 2019) and they respond behaviourally to acoustic playbacks of territorial calls (Dantzer et al., 2012; Goble, 2008; Shonfield et al., 2012; Wilson et al., 2015). We created a unique set of acoustic stimuli for nearly every squirrel where each squirrel would experience an additional four squirrels (two females and two males) that were unrelated and unknown to them (Dantzer et al., 2013). Playbacks were broadcast ~15 m away from the centre of their territories to simulate an ambient increase in density rather than a direct territorial intrusion. Playbacks were broadcast from dawn to dusk in an alternating fashion where a squirrel would experience one rattle per 7 min, thereby simulating naturally high-density conditions (Dantzer et al., 2012). Vocalizations from boreal chickadees *Poecile hudsonicus* were used as a control stimulus, as they are common in the Yukon year-round and are not known to harm red squirrels. Females experienced the control or rattle playbacks when they were in the middle stages of pregnancy (around the second trimester) until immediately after parturition (Figure 5).

We were able to assess whether this experimental increase in social cues of density induced life-history plasticity in females and how it compared to control playback females, control females on separate study areas that did not experience any playbacks and the females on our above-mentioned food-supplemented study areas that also experienced high densities. Because there were no differences between control playback and control females in terms of life-history traits or faecal glucocorticoid metabolite levels (discussed below), we combined the data for these two control treatment groups (Dantzer et al., 2013). The results from this playback experiment were surprising when it came to the classical life-history trade-off between the quantity and quality of offspring (Smith & Fretwell, 1974; Stearns, 1992). In red squirrels, this is reflected in the trade-off between the number of offspring (litter size) and the rate at which offspring grow after birth (offspring postnatal growth). Our previous work has identified that offspring growth is influenced by natal food availability or other aspects of the maternal phenotype and there is a negative phenotypic correlation between litter size and offspring growth rate (Humphries & Boutin, 2000; McAdam & Boutin, 2003; McAdam et al., 2002). We observed that the pups of control females producing large litters grew, on average, slower, confirming this expectation of a negative phenotypic correlation between quantity and quality of offspring. However, females experiencing supplemental food
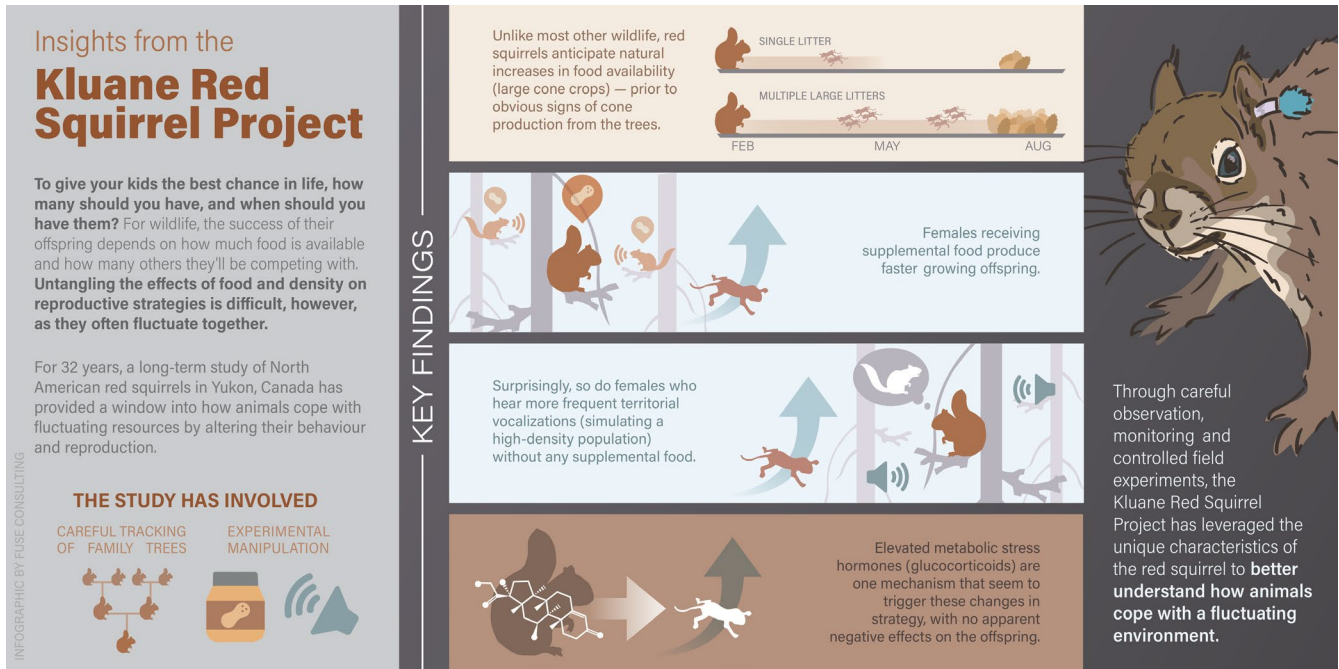
FIGURE 5 Infographic summarizing key insights about life history responses of North American red squirrels in the Yukon, Canada to variation in food availability and population density as well as experimental manipulations of food and density

and an increase in actual density, as well as those females experiencing elevated social cues of density without additional food ameliorated this trade-off compared to control females (Dantzer et al., 2013). Specifically, females in the experimental treatment groups that produced larger litters did not experience as strong of a reduction in the growth rate of each pup as did the control females. This suggests that experimental females are increasing their resource allocation in pups; however, how females experiencing elevated social cues of density do this without additional food was not clear to us. We are now conducting new experiments using a similar protocol to examine if there is some cost to these females in terms of their future survival or reproduction.

4.3 | Hormonal responses to food and density are one mechanism that induces adaptive life-history plasticity

Among- or trans-generational phenotypic plasticity occurs when characteristics of the parental environment or the parental phenotype itself triggers plasticity in the offspring phenotype, thereby causing the transference of information across generations (Uller, 2008). Hormone-mediated maternal effects can induce transgenerational plasticity by providing a bridge between a developing offspring and the outside world experienced by a mother. Breeding females may experience a shift in food availability, predation risk or conspecific density and this can alter their circulating hormones. Similar to other types of maternal effects (Wolf & Wade, 2009), changes in hormone levels can provide offspring with a cue predictive of the environment that they will encounter upon birth or hatching.

If these cues reliably predict the selective environment that the offspring will encounter, offspring should pay attention to those cues and modify their phenotype appropriately. The pathways by which changes in maternal hormone levels can impact offspring are diverse in mammals. They could impact offspring characteristics directly by being transmitted across the placenta (Barbazanges et al., 1996) or through milk (Casolini et al., 1997; Zarrow et al., 1970). They could also modify offspring phenotypes indirectly by modifying maternal behaviour towards offspring (Brummelte & Galea, 2010; Nephew & Bridges, 2011; Patin et al., 2002) or modifying the behaviour of offspring towards their mother (Moore & Power, 1986).

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

In support of our hypothesis that density increased maternal GCs that, in turn, adaptively altered offspring traits, we first found that squirrels have higher faecal glucocorticoid metabolites (FGMs) under high densities (Dantzer et al., 2013). Squirrels on our food-supplemented high-density study area had higher FGMs than those on the control study area experiencing lower densities (Dantzer et al., 2013). This difference was not due to

dietary differences (Dantzer et al., 2011), which are known to impact gut passage time and therefore faecal hormone metabolite levels (Goymann, 2012). This is surprising as observational and experimental studies typically find that there is a negative association between food availability and GCs (Dantzer et al., 2017; Kitaysky et al., 2007; Lynn et al., 2003; reviewed by Romero & Wingfield, 2015) and that short-term food supplementation can decrease GCs (Schoech et al., 2004). We showed that food-supplemented squirrels also experiencing high densities had the highest GCs. This suggests that the method of acquiring food may change the direction of the impact of food availability on GCs. Territorial species like red squirrels that defend a central food cache may exhibit an increase in GCs when they experience increased food due to the concomitant increase in the number of competitors for that food cache. However, we note that future studies must address the additive and interactive impacts of food and density on GCs.

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

Given that changes in GCs are well-known to induce phenotypic plasticity (Crespi & Denver, 2005; Denver, 2009), we next investigated whether it was the change in GCs in breeding females that induced an adaptive shift in offspring growth rates that effectively prepared them for the selective environment they would encounter at independence from their mother. Using an observational dataset, we found that maternal FGMs were positively correlated with offspring growth (Dantzer et al., 2013). We then confirmed this experimentally by conducting a GC manipulation experiment over four different years where we treated pregnant females with a small amount of peanut butter containing exogenous GCs (experimental females) or the same amount of peanut butter lacking the GCs (controls). These GC treatments elevated their circulating (blood) levels of GCs and caused elevation of FGMs (van Kesteren et al., 2019). Crucially, the elevation in GCs was within their natural physiological range such that this was not a supraphysiological or unnatural increase in circulating GCs (van Kesteren et al., 2019). Females that were treated with exogenous GCs also produced faster growing offspring, but only if they were treated with GCs during pregnancy and not during lactation (Dantzer, van Kesteren, et al., 2020). Females with experimentally elevated GCs during lactation tended to produce slower growing offspring, which is consistent with some studies of laboratory rodents (Nephew & Bridges, 2011). How pregnant females with elevated GCs produced faster growing offspring is not yet clear, but a reduction in litter size or a change in litter sex ratio do not appear to be the cause as experimental (fed GCs) and control females had similar litter sizes and similar litter sex ratios (Dantzer, van Kesteren, et al., 2020; Dantzer et al., 2013).

4.4 | The energetics of opportunity in a seasonal, pulsed-resource system

We have not yet directly assessed the effects of social density on energetic traits. Accordingly, the remaining section examines how three non-social drivers of energetic traits—resources, seasonality/climate and opportunity—interact and coalesce to co-define each other, energetic status and life-history outcomes in this population. We focus in particular on the third driver—opportunity—because it is the least conventionally labelled or discussed predictor of energy expenditure and yet, we believe, the primary determinant of energetic status in red squirrels and perhaps many other organisms. Here, when we refer to 'opportunity', we are focusing on fitness opportunities that allow a squirrel to enhance its survival or reproduction by adjusting its energetic status. We first briefly describe the major methodologies we have used to quantity red squirrel energetic status.

We have primarily measured red squirrel energetic status using the doubly labelled water (DLW) technique to estimate daily energy expenditure (DEE: Speakman, 1997). The DLW technique estimates the DEE (also referred to as field metabolic rate: FMR) of free-ranging individuals by quantifying CO_2 production during a multi-day interval (Speakman, 1997). The use of this technique is challenging because of the difficulty of capturing and recapturing free-ranging individuals at specific intervals. The highly trappable nature and territoriality of red squirrels means that we can almost always find and trap an individual red squirrel when needed. Another advantage of red squirrels is that the behaviour of free-ranging individuals can be quantified through direct focal observations (Dantzer et al., 2012), meaning that we can also relate DEE to behaviour expressed during the sampling interval (Humphries & Boutin, 2000). We have complemented free-ranging DEE measures with estimates of resting metabolic rate (RMR: Lighton, 2018), measured on the same individuals, using controlled-environment, flow-through respirometry measures of O_2 consumption in a mobile energetics laboratory (Larivée et al., 2010). Most recently we have also classified squirrel behaviour using light loggers (Williams, Wilsterman, et al., 2014), temperature loggers (Studd et al., 2016) and accelerometers (Studd et al., 2019).

Variation in red squirrel DEE and RMR reflects the energetics of fitness opportunities, with rates of energy expenditure being exceedingly low when energy conservation is prioritized, possible and increases fitness, and exceedingly high when energy expenditure enables either resource acquisition or reproductive gain (thereby increasing fitness). The responsiveness of red squirrels to the energetics of fitness opportunities causes them to contradict many standard pillars of physiological ecology. Whole animal rates of energy expenditure are described to increase with body size and body temperature (Brown et al., 2004; Burton et al., 2011; Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012; Humphries et al., 2005; McNab, 2003; Scholander et al., 1950; Speakman, 1999), but in red squirrels, energetic expenditure is weakly correlated with body size under almost all circumstances (Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012). Lactation is known to incur

some of the highest energetic costs in mammals (Gittleman & Thompson, 1988), but red squirrels expend as much or more energy during the autumn cone hoarding period and (for males) during peak mating (Lane et al., 2010), as females expend during peak lactation (Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012). Energetic ceilings experienced during lactation are described to constrain maximum litter size in mammals (Hammond & Diamond, 1997; Speakman and Król, 2010), but lactating red squirrels can sustain experimental increases in litter size with elevated energy expenditure (Humphries & Boutin, 2000). Energy expenditure is often considered to be a cost or a subtraction term in defining individual or population production (Humphries & McCann, 2014), but red squirrel energy expenditure generally increases in response to abundant resources (Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012) and is a positive predictor of reproductive success (Fletcher et al., 2015). Although contradictory to many standard expectations, red squirrel energetic responses are readily understandable as long as it is realized that expenditure is not only a cost to energy conservation but at other times a beneficial allocation towards acquiring resources and reproductive opportunities (Humphries & McCann, 2014; Studd et al., 2020). Understanding these energetic opportunities and constraints within a species requires identifying how resources, seasons and climate combine to define when individuals should reduce or increase activity and energetic expenditure (Humphries et al., 2017; Studd et al., 2020).

5 | CURRENT THINKING/CONSENSUS

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

6 | UNANSWERED QUESTIONS AND SOME PREDICTIONS

1. How do squirrels predict future food availability? We suspect that red squirrels use a cue in the spruce trees (such as levels of phytoestrogens) to predict mast years. It is possible that increased consumption of phytoestrogens in mast years can induce life-history plasticity including elevating litter sizes.
2. What happens to those squirrels that wrongly predict a mast or high-density conditions? Error management theory (EMT) predicts that individuals should commit a less costly error when it comes to life-history plasticity (Sheriff et al., 2018) when the costs of false-positives (producing Phenotype A that is adaptive for Environment A but Environment A is not actually experienced in the future) are less than false-negatives (not producing Phenotype

A that is adaptive for Environment A when Environment A is actually experienced in the future). According to EMT, when there is uncertainty about which environment will be encountered in the future, individuals should play it safe and, in this example, produce Phenotype A. Red squirrels achieve higher reproductive success by increasing reproductive output in anticipation of mast years and by producing faster growing offspring in high-density years. Are the costs for those females that wrongly predict an upcoming mast or high-density (false-positive) lower than the costs of not responding adaptively when there is an actual mast or high-density year (false-negative)?

3. What are the short- and long-term costs to females of increasing reproductive output in anticipation of food or high-density conditions? Female red squirrels do experience increased energetic expenditure when they ramp up reproduction (Fletcher, Selman, et al., 2012; Fletcher, Speakman, et al., 2012; Humphries & Boutin, 2000) but do these short-term costs carry over to the future and alter their future fitness? In addition, are there costs to phenotypic plasticity (i.e. do those females that exhibit greater plasticity in response to food and/or density experience some cost, particularly if they do not encounter a mast or high-density year in their lifetime)?
4. Food and density are important ecological agents of selection and alter GCs in red squirrels but what is the interplay between other factors (weather, predators) on life-history plasticity and GCs? Are the effects additive or interactive? We know that the abundance of terrestrial predators in Kluane is highly variable (Figure 1c) but previous experimental work shows that individual survival rates or population dynamics of red squirrels are not heavily influenced by the number of terrestrial predators (Boonstra et al., 2001; but see Studd et al., 2015; Hendrix et al., 2020). Nonetheless, GCs are likely affected by both predation risk and warmer than average ambient temperatures. If these other factors alter maternal GCs, how do they affect their life-history traits and are these effects in the same direction as we see when females encounter high-density years or when we experimentally elevate their GCs?
5. How widespread is the anticipation of food or density in animals, and what are the relative impacts of the anticipated versus actual reproductive response to food availability on population growth? Red squirrels inhabit a fairly simple ecological food web where the amount of one food type (spruce seed) has pervasive effects on their population dynamics by inducing life-history plasticity associated with changes in food or density. Is this a realistic representation of the world or only found in these simple systems representing one seed consumer and one plant species? Red squirrels also provide an opportunity to examine if the effects of increased reproductive output in anticipation of elevated food outweigh the effects of the lagged (actual) response to increased food on population growth.
6. How is global climate change going to alter predictability of the future in red squirrels? Our study area in the Yukon has already seen substantial changes in temperature and precipitation such that it is now hotter and wetter in the Yukon than in recorded

history and is expected to continue into the future according to general predictions of the Intergovernmental Panel on Climate Change (IPCC, 2018). Temperature and precipitation patterns have been shown to affect masting dynamics in white spruce, such as warmer summer (July–August: Krebs et al., 2012, 2017) temperatures in the 2 years previous or wetter conditions in the preceding May (Krebs et al., 2012) are positively associated with white spruce cone crop production. Regional change in the climate of the Yukon may therefore also affect squirrel population dynamics and perhaps alter the predictability of the future from the perspective of red squirrels. If the cues red squirrels use to anticipate mast years or high-density years become less reliable, we would expect that squirrels should eventually no longer exhibit the life-history plasticity we have documented in response to food and density or that the responses we have observed in the past may become maladaptive.

7 | DISCUSSION

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

- Red squirrels anticipate food pulses where they increase reproductive output before the food is available; they uncouple the typical life-history plasticity that is observed after an increase in food availability by correctly predicting its presence in the future. This overturns some of the assumptions in basic population ecology about consumers exhibiting a lagged response to increases in food;
- As in most organisms, food and conspecific density covary in red squirrels and induce plasticity in life-history traits. However, in red squirrels, social cues of density in the absence of additional food can also induce life-history plasticity and females do this in anticipation of patterns of natural selection resulting from high densities. This indicates that social cues can foreshadow density-dependent selection;
- Glucocorticoid levels in red squirrels respond to changes in both food and density and changes in GCs can induce adaptive life-history plasticity. Few studies have disentangled the effects of food versus density on GCs. We show that social interactions, rather than food, seem to be the overriding ecological mechanism that causes fluctuations in their glucocorticoids.
- Red squirrels overturn standard expectations in physiological ecology: their energetic expenditure is typically only weakly related to body size, lactation is not the most energetically

demanding life-history stage, even during peak lactation (it can be higher in females and males during food hoarding or during mating in males), squirrels can cope with increased litter sizes and increase expenditure, and they expend more energy (not less) when food resources are abundant.

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

Third, unlike most long-term studies of birds, natal dispersal is generally quite low, there does not appear to be a substantial sex-bias in long-distance natal dispersal, and adult dispersal is very low (Berteaux & Boutin, 2000; Boutin et al., 1993; Cooper et al., 2017). This means that nearly all of the offspring that are born in our population can be tracked from birth until death. The disappearance of juveniles or adults is common in most long-term studies of wild animals, which makes it challenging to distinguish between death and successful dispersal outside the study area. In our study system, our current understanding is that juvenile red squirrels that disappear are extremely likely to be dead rather than successfully dispersed. Although we note that our recent study showed that juvenile males that do successfully disperse may do quite well (Martinig et al., 2020) and our current work focuses on better estimating the exact proportion of juveniles that do disperse and successfully settle outside our study grids. Our lifetime fitness estimates are not perfect but given the low natal dispersal distances, our current understanding is that we can characterize the number of offspring each female or male red squirrel produces in a year and the number of those offspring that they produce that actually recruit into the population (i.e. acquire a territory and survive to

the spring following their year of birth) and, therefore, contribute to the genetic composition of the population and to population growth itself.

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

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

AUTHORS' CONTRIBUTIONS

B.D. led the writing of the manuscript with contributions from S.B., M.M.H., J.E.L. and A.G.M. All the authors collected the data and B.D. analysed the data.

DATA AVAILABILITY STATEMENT

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

ORCID

Ben Dantzer https://orcid.org/0000-0002-3058-265X
Andrew G. McAdam https://orcid.org/0000-0001-7323-2572
Jeffrey E. Lane https://orcid.org/0000-0003-0849-7181
Stan Boutin https://orcid.org/0000-0001-6317-038X

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SUPPORTING INFORMATION

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