

## Note

### Red Squirrel (*Tamiasciurus hudsonicus*) feeding on Balsam Poplar (*Populus balsamifera*) galls induced by aphids

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#### Abstract

Red Squirrel (*Tamiasciurus hudsonicus*) specializes in feeding on conifer cone seeds but will feed opportunistically on a wide variety of other food items, including fungi, eggs, small vertebrates, and invertebrates. In much of their range, Red Squirrels experience fluctuations in the availability of their primary diet (conifer seeds) seasonally and annually because of variation in seed production. We document a seemingly uncommon or unreported feeding behaviour by a Red Squirrel in a year of an exceedingly low conifer cone production in Yukon, Canada: a squirrel foraging for and feeding on aphids hidden within galls formed on Balsam Poplar (*Populus balsamifera*). We searched for community-reported observations of Red Squirrels through iNaturalist and found additional evidence of apparently similar gall feeding behaviour elsewhere in Canada. We estimate that aphids can be a substantial source of caloric energy for Red Squirrels. Our observation represents another example of the diet breadth of Red Squirrels during periods of low conifer seed availability.

Key words: Diet; foraging; insectivory; Poplar Leaf-base Gall Aphid; *Pemphigus populiglobuli*; Red Squirrel; *Tamiasciurus hudsonicus*

Red Squirrel (*Tamiasciurus hudsonicus*) is a common forest-dwelling rodent that is broadly distributed across much of North America (Steele 1998). Red Squirrels are conifer specialists, deriving much of their caloric intake from seeds in mature female cones, which they cache in centralized larders called middens. In regions where conifers produce non-serotinous cones (e.g., White Spruce [*Picea glauca* (Moench) Voss]), squirrels cache cones in late summer into autumn before the cones open naturally and release seeds (Archibald *et al.* 2012). Red Squirrels are opportunistic omnivores (Layne 1954) and will feed on fungi (Smith 1968a; Fletcher *et al.* 2010), non-seed plant material such as conifer pollen cones (Smith 1968a), and rust-induced pine galls (Salt and Roth 1980), as well as vertebrates, including leporids, birds, and salamanders (Sullivan 1991). Their diets can shift with the seasons and fluctuations in the availability of the food source (e.g., Salt and Roth 1980; Fletcher *et al.* 2010).

Even with stored resources available, Red Squirrels

will change their diets considerably during cone crop failures (Smith 1968b) and will feed on insects, even peeling the bark from standing White Spruce to feed on Spruce Beetle (*Dendroctonus rufipenni* (Kirby)) larvae in the cambium (Pretzlaw *et al.* 2006). During three years of low cone abundance and a simultaneous outbreak of Spruce Beetle in Yukon, 20% of Red Squirrels' energetic intake was from Spruce Beetle larvae (Pretzlaw *et al.* 2006). Here, we document another example of Red Squirrel feeding behaviour during an exceedingly low conifer cone crop.

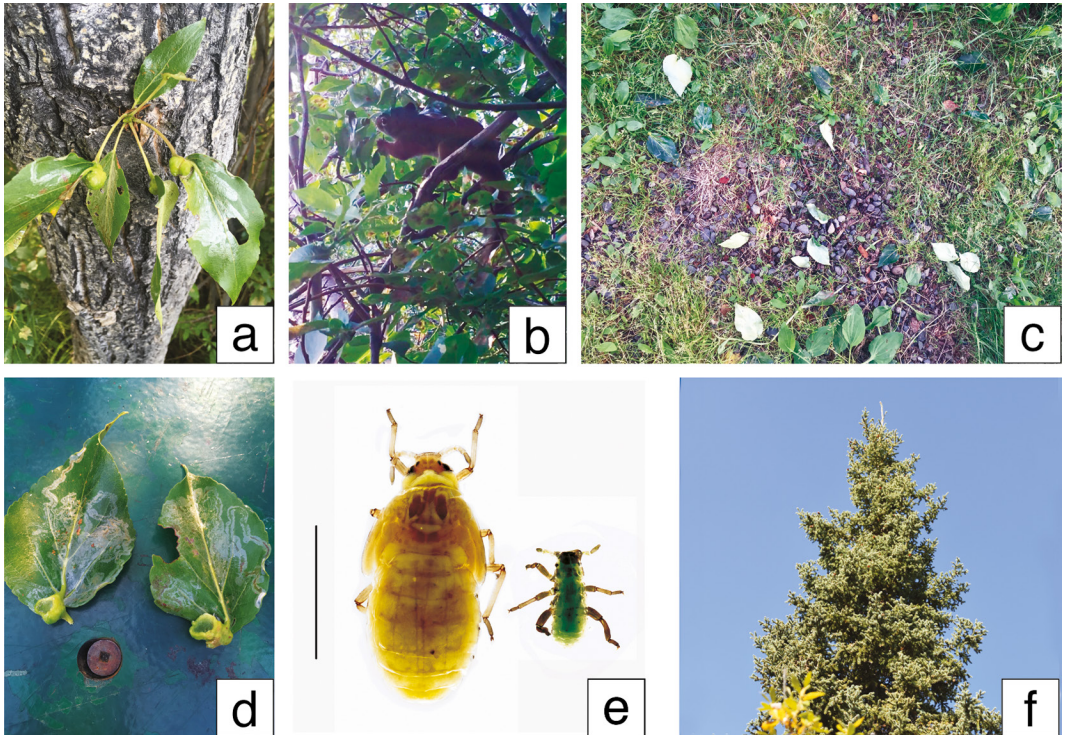
In the early evening of 7 July 2019, at Twin Lakes Campground in central Yukon (130 km north of Whitehorse; 61.702424°N, 135.935528°W), M.D.J. observed a Red Squirrel that appeared to be feeding on the leaves of Balsam Poplar (*Populus balsamifera* L.) and recorded a 1.33-min video of its behaviour (Jackson 2019) using a smart phone (Apple iPhone SE 2016 model, Apple Inc., Cupertino, California, USA). Closer observation revealed that the squirrel was not eating the leaves but rather chewing open

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surface galls located near the leaf petiole (Figures 1a,d), feeding on the contents, and then dropping the leaf with the emptied gall to the ground before moving on to another leaf (Figure 1b; Jackson 2019). The squirrel fed in this fashion for ~1 h, leaving the discarded leaves below its perch (Figure 1c). Uneaten galls, collected from the tree in which the squirrel was observed, were later found to have been induced by aphids (Hemiptera: Aphididae; Figure 1e); galls and the aphids within, preserved in 95% ethanol, were deposited in the Lyman Entomological Museum at McGill University (LEMQ; accession numbers not yet assigned). Although the density of aphid galls in the area was not quantified, the occupied tree and surrounding poplars appeared heavily infested with galls; most leaves visible from the ground showed evidence of galls. The Red Squirrel was not observed feeding on larvae of Aspen Serpentine Leaf Miner (*Phyllocnistis populiella* Chambers, Lepidoptera: Gracillariidae), which could be found in most of the leaves on the tree, including leaves with predated aphid galls (Figure 1d).

We calculated the maximum caloric intake of the squirrel during the 1-h observation period by estimating mean ( $\pm$  SD) time spent searching for and feeding on aphid galls by evaluating the video recording (Jackson 2019). We used the energy intake equation in Pretzlaw *et al.* (2006), established for bark beetle larvae predation by Red Squirrels, to estimate energy consumption assuming 56 reproductive adult aphids per gall as established by previous studies (Harper 1959a) and an energy content of three calories per adult aphid based on previous studies involving microbomb calorimetry (Dixon 1971; Randolph *et al.* 1975).

We also estimated cone abundance in the area to understand better the resource context of this behaviour. Twin Lakes campground lies among small lakes in the boreal forest of the Central Yukon Plateau region. The dominant conifer is Black Spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg), which produces small semi-serotinous cones. Also present was White Spruce, which produces



**FIGURE 1.** a. Galls of the Poplar Leaf-base Gall Aphid (*Pemphigus populiglobuli*) on Balsam Poplar (*Populus balsamifera*) leaves *in situ*. b. Still from video (Jackson 2019) showing a Red Squirrel (*Tamiasciurus hudsonicus*) feeding on Poplar Leaf-base Gall Aphid galls. c. Example of undergrowth below the Red Squirrel's perch; 22 discarded Balsam Poplar leaves can be seen, at least nine of which show evidence of damaged petiole galls. d. Recovered Balsam Poplar leaves displaying results of Red Squirrel aphid gall feeding and serpentine leaf mines of Aspen Serpentine Leaf Miner (*Phyllocnistis populiella*). e. Poplar Leaf-base Gall Aphid specimens recovered from a collected uneaten gall. Scale bar = 1 mm. f. Spruce cone survey photo from Twin Lakes Campground, Yukon. Photos a–c: Morgan Jackson. Photo f: Ashley Mills.

non-serotinous cones that release wind-dispersed seeds in late autumn. Cone production by both species varies in abundance from year to year and the year we made our observations was one of the lowest cone-crop years on record (A.E.W. and M.D.J. pers. obs.). In early fall (1 September), we returned to the same cluster of trees where the Red Squirrel was observed and photographed the crowns of 20 spruce trees in the vicinity with diameter at breast height >5 cm. From these photos of Black Spruce and White Spruce (e.g., Figure 1f), we counted all cones in the top 3 m of the crown of each tree and applied the transformation by LaMontagne *et al.* (2005) to estimate the total number of cones per tree (Wishart and Jackson 2020).

Finally, we searched for additional observations of potential aphid gall feeding by Red Squirrels by downloading all iNaturalist (inaturalist.org) research-grade observations (those with a date, a geolocation, a photo, and a confirmed species-level identification by at least one other user) of Red Squirrels in Canada, with observation dates from May to September. We archived this iNaturalist dataset using the Global Biodiversity Information Facility (GBIF 2021) and looked at all the photos for gall-aphid feeding behaviour.

Using Harper (1959b), we identified the aphids as Poplar Leaf-base Gall Aphid (*Pemphigus populiglobuli* Fitch) based on the position and morphology of the galls. Of the four instances of aphid gall-feeding captured in the 1.33-min video (Jackson 2019), the Red Squirrel spent an average of  $3.0 \pm 0.8$  s searching for galls and an average of  $14.5 \pm 6.9$  s/gall feeding. If the squirrel fed at this rate continuously during the hour-long observation period, we estimate it could consume up to 206 galls representing a maximum of 117 kJ of metabolizable energy derived from aphids.

The 20 photographed spruce trees had an average of  $1.6 \pm 0.8$  SE cones per tree. When we photographed the tree tops, one squirrel was observed caching cones but not in a visibly discernable larder (the conspicuous area of discarded cone refuse in which squirrels cache newly harvested cones and which squirrels defend from conspecifics; Smith 1968a).

Only two of the 4447 iNaturalist records showed squirrels apparently feeding in a similar fashion on poplar leaf galls, both from Gwillim Lake Provincial Park, northeastern British Columbia (Headley 2019; Kushneryk 2019). These two records were submitted by different users but were ~100 m from each other on concurrent days (30 July and 31 July 2019) and may be of the same squirrel foraging for galls.

Red Squirrel feeding ecology has been studied intensively in Yukon for decades (Dantzer *et al.* 2020), yet their handling and feeding from galls formed by aphids has yet to be reported in the

literature. Published records of Red Squirrels feeding on aphids directly was first noted by Smith (1968a), who observed squirrels eating aphids (likely *Tamalia* spp.) exposed by chewing leaves of Common Bearberry (*Arctostaphylos uva-ursi* (L.) Sprengel) in southern British Columbia. He hypothesized that the relatively greater use of “animal materials” (including aphids) by juvenile or reproductive females (pregnant or lactating) compared with adult males may indicate that these materials could provide dietary salts. A Pallas’s Squirrel (*Callosciurus erythraeus*) was observed feeding on four galls of *Astegopteryx bambucifoliae* (Takahashi) in Taiwan (Chou *et al.* 1985). Pallas’s Squirrels have also been observed feeding on gall-forming *Pseudoregma carolinensis* (Takahashi) in Thailand (Aoki *et al.* 2007). In North America (Arizona), a Mount Graham Red Squirrel (*Tamiasciurus hudsonicus grahamensis*) was seen eating spruce aphids (*Elatobium abietinum* (Walker); Lynch 2009). More distantly related chipmunks also feed on aphids, but it is not known whether they are retrieved from galls (Baysinger 1940; Tevis 1953).

Globally, accounts of aphid gall predation by vertebrates are limited (Sunose 1980; Burstein and Wool 1992), with some Old World aphid species actively deterring vertebrate grazing via galls that produce volatile organic compounds and are aposematically coloured (Rostás *et al.* 2013). The galls of Poplar Leaf-base Gall Aphid reported here were similar in colour to the remaining leaf, and the squirrel appeared to have little hesitation in opening the galls, suggesting that any sequestered noxious chemicals were insufficient to deter squirrel predation.

Previous estimates of Red Squirrel daily energy expenditure in autumn (when not actively hoarding food) in southwestern Yukon were ~300–400 kJ/day (Fletcher *et al.* 2010). Our estimated maximum hourly caloric intake of 117 kJ from consuming gall aphids implies that aphid gall feeding may provide a substantial source of energy when the abundance of a primary food source is low. Even in a highly infested tree, such as we observed, a Red Squirrel is unlikely to sustain that estimated maximum hourly caloric intake for long periods, but the ready availability of gall aphids as a high-calorie food source for squirrels warrants consideration in future research. In addition, aphid galls contain much higher concentrations of amino acids than the surrounding leaf tissue (Suzuki *et al.* 2009), possibly providing a valuable nitrogen source.

We observed a three-way mammal–insect–plant interaction that could be important to consider from a behavioural ecology and community ecology framework. Feeding innovation rate is associated with invasion success in birds (Sol *et al.* 2002); whether this holds true for mammals may be important to monitor

as ranges are likely to shift with a changing climate. Insect galls are likely to be reliably accessible as a food source in southern Yukon, with at least three other species of gall-inducing aphids known from the territory (Footitt and Maw 1997), as well as an unknown number of species of gall-inducing sawflies (Hymenoptera: Tenthredinoidea) on willow (*Salix* spp.) and leaf-rolling sawflies on aspen (*Populus* spp.; S. Monckton pers. comm. 2020). However, given that the squirrel we observed dismissed leaf-mining insects in favour of more densely populated gall aphids on the same leaf, discrimination among species by Red Squirrels presents opportunities for further study.

Our observation of a Red Squirrel feeding on poplar-gall aphids, accompanied by community science documentation of apparently similar behaviour elsewhere, expands our collective knowledge of Red Squirrel diet breadth and behaviour. This observation is also significant for entomology and forestry applications in that this is the first documentation of Poplar Leaf-base Gall Aphid in Yukon (Footitt and Maw 1997). Finally, our observation serves as a timely reminder that much remains to be discovered about the biology and associations of even the most common species. Moreover, this observation further points to the increasing role that new technologies and platforms (i.e., iNaturalist) may have in new scientific findings.

### Author Contributions

Writing – Original Draft: A.E.W. and M.D.J.; Writing – Review & Editing: A.E.W. and M.D.J.; Conceptualization: M.D.J.; Investigation: A.E.W. and M.D.J.; Methodology: A.E.W. and M.D.J.

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