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RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*) FEEDING ON SPRUCE BARK BEETLES (*DENDROCTONUS RUFIPENNIS*): ENERGETIC AND ECOLOGICAL IMPLICATIONS

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We report the novel occurrence of North American red squirrels (*Tamiasciurus hudsonicus*) feeding on spruce bark beetle (*Dendroctonus rufipennis*) larvae, and consider the energetic and ecological implications. Although a bark beetle outbreak was 1st noted at our study site in 1994, significant feeding on them by red squirrels was not observed until 2002, after which there was significant increase in the prevalence of autumn beetle foraging by squirrels into 2003. This increase corresponded with a decrease in spruce seed availability, the squirrels' preferred food source. Spruce bark beetles currently represent an important food source, with 73% of monitored squirrels engaged in beetle feeding in autumn 2003, providing 20% of daily energy requirements. In autumn 2002 and 2003, the density of beetle-infested trees on a squirrel's territory was a significant predictor of whether it fed on beetle larvae but not the proportion of its foraging bouts involving bark beetles. Feeding on larval spruce bark beetles by red squirrels represents a short-term solution to a climate-mediated beetle outbreak that will ultimately reduce local spruce seed production and habitat suitability for red squirrels.

Key words: cone failure, *Dendroctonus rufipennis*, omnivory, optimal foraging theory, prey image, prey switching, red squirrel, spruce beetle, *Tamiasciurus hudsonicus*

North American red squirrels (*Tamiasciurus hudsonicus*) are primarily granivorous. In the boreal forest they rely extensively on conifer seeds as a year-round food source (Brink and Dean 1966; Steele 1998). However, their diet is known to include a diversity of alternative food items, especially during seasons and years when conifer seed is scarce (Steele 1998). Primary alternative food sources include mushrooms, hypogeous fungi (truffles), berries, spruce buds, and cambium (Brink and Dean 1966; Currah et al. 2000; Layne 1954; Obbard 1987; Smith 1968; Steele 1998; Sullivan 1991; Sullivan et al. 1994), but multi–trophic-level omnivory also is common. In fact, red squirrels feeding on passerine young and snowshoe hare leverets is well-documented (Krebs et al. 2001; Willson et al. 2003).

The ecology, evolution, and life history of North American red squirrels has been studied by one of us (SB) and collaborators in the Kluane region, Yukon Territory, Canada (61°N, 138°W) for the past 15 years (Berteaux and Boutin 2000; Humphries and Boutin 2000; McAdam and Boutin 2003a, 2003b). In recent years, white spruce (*Picea glauca*) trees in this region (on our study sites) have been attacked by the spruce bark beetle (*Dendroctonus rufipennis*). This bark beetle outbreak was 1st detected in 1994, declined in vigor in the late 1990s, and increased in intensity in 2002 to become the largest outbreak affecting white spruce trees in Canada (Garbutt 2002). Spruce bark beetles typically have a 2-year life cycle but in recent years have begun to complete their life cycle in 1 year, presumably because of climate warming (Garbutt 2002; Logan et al. 2003; Stark 1982). Bark beetle larvae eat the cambium (living tissue under the bark) of spruce trees in coordinated mass attacks that overwhelm the trees' defenses, and thereby kill the host tree (Malmstrom and Raffa 2000). Bark beetles typically feed on cambium as larvae, metamorphose into adults, move to the bottom of the tree and burrow into the subcambium (presumably to avoid predation by woodpeckers), and finally emerge to disperse the next year (Malmstrom and Raffa 2000; Stark 1982).

In this paper we provide the 1st-ever documentation of red squirrel feeding on spruce bark beetle larvae. We quantify the frequency and spatiotemporal variation of squirrel feeding on bark beetles and calculate the energetic value of spruce bark beetle larvae relative to alternative food sources. Given red squirrels' preference for conifer seeds and opportunistic foraging (Brink and Dean 1966; Steele 1998), we expected consumption of beetle larvae to be positively correlated with

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density of attacked trees and negatively correlated with cone availability. Furthermore, given the recent (1999–2003) long-term scarcity in spruce cones (low production) at our study site and anecdotal observations of increased foraging by red squirrels on beetle larvae, we expected spruce bark beetles to represent a substantial portion of red squirrels' caloric intake.

MATERIALS AND METHODS

Study area and species.—Data were collected on a 72-ha site near Kluane Lake, Yukon Territory, Canada (61°N, 138°W). This ecoregion consists of boreal forest dominated by white spruce, with some trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub community is dominated by willow (mostly *Salix glauca*) and dwarf birch (*Betula pumila*—see Krebs et al. [2001] for a more detailed description).

Red squirrels maintain year-round territories, containing 1 or more middens of hoarded spruce cones (Obbard 1987). All individuals on our 2 study grids have been censused since 1989. Squirrels are ear-tagged before emergence, and marked with colored wires for distant identification. Specific methods used to study these squirrels are described in detail by Boutin and Larsen (1993) and Humphries and Boutin (1996).

Prevalence of squirrel foraging on beetles and cones.—From May to August 1989–2003, direct focal observations were conducted each year on 10 radiocollared breeding female red squirrels between 0600 and 1200 h, once per week. Focal squirrels were followed for 10 min and their breeding, maintenance, and foraging behavior was recorded every 30 s. Approximately 90% of the squirrels observed in a given year had not been observed in previous years.

From 2001 to 2003, we also conducted autumn focal observations on radiocollared juvenile and adult squirrels, from early September to mid-October, between 0800 and 2000 h. Each autumn focal observation lasted 7 min and squirrels were observed 3 times per day, every 2nd day (2001: $n = 26$ squirrels [20 adult and 6 juvenile females], 2002: $n = 38$ squirrels [16 adult and 10 juvenile females], 2003: $n = 48$ squirrels [16 adult and 9 juvenile females, and 17 adult and 7 juvenile males]). From the autumn data, we calculated the proportion of feeding observations involving beetle larvae and cones. Three squirrels were observed in both 2001 and 2002, 9 squirrels were observed in both 2002 and 2003, and 3 squirrels were observed in all 3 years (2001–2003). In October 2003, behavior was recorded at 30-s intervals on a subset of the autumn focal squirrels that participated in beetle foraging ($n = 15$ squirrels [10 adult and 3 juvenile females and 1 adult and 1 juvenile male]). From this subset of individuals, we constructed a time budget to assess the amount of time red squirrels spent feeding on beetle larvae and cones and their potential energetic intake from each of these food sources. Focal squirrels were selected haphazardly and were distributed across the study grids.

Energy intake while feeding on larval beetles.—In the first 2 weeks of October 2003, we estimated red squirrel intake rate of bark beetle larvae according to the following equation:

$$\begin{aligned}&\text{spruce bark beetle larval intake rate } (\text{min}^{-1})\\&\quad = \text{flake removal rate } (\text{g/min})\\&\qquad \times \text{ surface area cambium exposed } (\text{cm}^2/\text{g})\\&\qquad \times \text{ larval density } (\text{cm}^{-2}).\end{aligned}$$

Flake removal rate was estimated by observing the number of pieces of bark (flakes) removed by squirrels ($n = 22$) during 5-min feeding bouts, then collecting and weighing all the flakes within a 15-cm-diameter circle randomly placed under trees where squirrels had been observed foraging on beetles (~100 flakes). The surface area of cambium exposed per gram of flake removed was estimated for the population by manually peeling bark from infested trees to expose 16 cm^2 of cambium, then weighing the removed pieces of bark to determine area per gram ($n = 45$ infested spruce trees). Finally, bark beetle larval density was estimated after each squirrel beetle foraging bout by manually removing bark from the area of the tree where the squirrel was just observed feeding to expose 12 cm^2 of cambium and counting the number of beetle larvae exposed (Powell et al. 2002). We converted intake rate to its energetic equivalence based on 0.02 kcal/larva (Koplin 1972), and converted this to metabolizable energy (expressed as kJ) assuming 4.184 kJ/kcal and an estimated apparent metabolizable energy coefficient of 80% (based on the energy assimilation of white-tailed antelope squirrels [*Ammospermophilus leucurus*], feeding on crickets—Karasov 1982). Energetic intake calculations were done using bark beetle larval density and flake removal rate (flakes/min) specific to individual squirrels, and average mass per bark flake and mass per bark area.

Cone availability and energetic return.—We estimated the availability of white spruce cones for 2001–2003. The cone crop index was calculated by counting all the cones in the top 3 m of the tree that were visible from 1 side of trees with a minimum diameter at breast height of 5 cm (2001: $n = 170$ trees, 2002: $n = 170$ trees, 2003: $n = 172$ trees). The cone index was converted to cones per tree based on the formula provided in LaMontagne et al. (2005). For the subset of bark beetle–feeding red squirrels we calculated energetic return from cone foraging based upon the time budget of these squirrels (proportion of time spent feeding on cones) and energy returns of 0.15 kcal/min foraging on cones (Humphries 1996), and an apparent metabolizable energy coefficient of 87% (white-tailed antelope squirrels feeding on grains—Karasov 1982).

Bark beetle activity and availability to squirrels.—We determined the spatial distribution of trees attacked by spruce bark beetles in 2002 and 2003 by counting the number of attacked trees in transects in July 2002 and 2004. Attacked trees were identified based on the presence of many boring holes and boring dust (frass) at the base of trees that had mostly green needles (referred to as green attack), and the subsequent changing of needle color to red (red attack—Koot 1997; Safranyik and Humphreys 1993). We assumed that green attack trees were 1st attacked in the year they were detected and that red attack trees had been attacked the previous year (Garbutt 2002; Koot 1997). As a result, trees that were considered red attack in 2004 were assumed to have been 1st attacked in 2003. We quantified newly attacked trees in 2002 and extrapolated newly attacked trees in 2003 from red attacked trees in 2004. We sampled 3 transects radiating from central origins at 0°, 120°, and 240°, located evenly across the study area (4 × 25-m transects; $n = 189$ origins; 60 m between origins). The number of attacked trees in each transect was reported as trees per 10 m^2, and this value was spatially assigned to the midpoint of the transect (Jenness 2003). Ordinary kriging, a method of interpolation that uses data observed at known locations to predict unknown values (Isaaks and Srivastava 1989), was then performed on the 567 points (189 central points × 3 transects) through a fit to a spherical semivariogram in ArcGIS (Environmental Systems Research Institute, Inc. [ESRI] 2002) to create a distribution of spruce trees that were newly attacked by beetle larvae for 2002 and 2003, using a cell size of 10 m^2.

To determine the availability of larval beetles to each individual squirrel, the number of newly attacked trees within a circular area

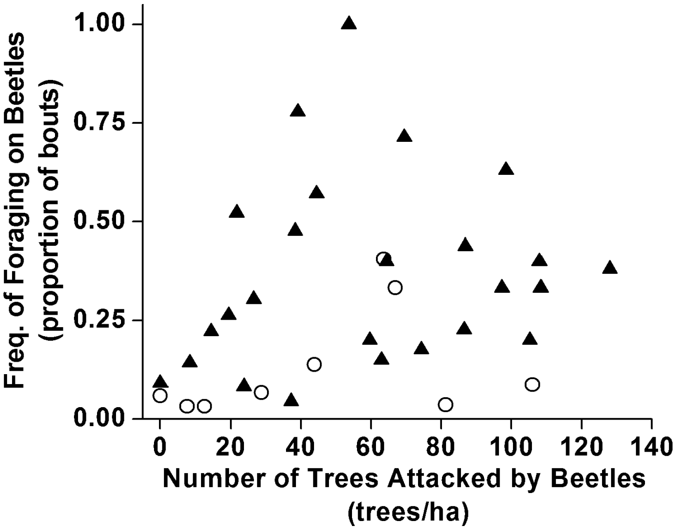

FIG. 1.—Prevalence of red squirrel (*Tamiasciurus hudsonicus*) foraging on larvae of spruce bark beetles (*Dendroctonus rufipennis*) as a function of the density of trees attacked by bark beetles in their territory. Foraging on spruce bark beetles is expressed as proportion of foraging bouts involving beetles during autumn 2002 (open circles) and 2003 (closed triangles).

surrounding each squirrel's primary midden (determined by midden census), equal to the average territory size in each year (2002: 0.29 ha, 2003: 0.37 ha—J. M. LaMontagne, in litt.), was clipped from each of 2002 and 2003 kriged layers in ArcView Version 3.2 (DeLaune 2003; ESRI 1999). We then converted this to density of attacked trees available to each squirrel.

Statistical analyses.—All data are presented as mean ± *SE*. We pooled data for females and males, as well as adults and juveniles, after it was determined there was no significant difference in the participation in or prevalence of beetle foraging between these demographic classes. All data analyses were conducted using Systat Version 10.2 (SYSTAT Software, Inc. 2002). Proportion of squirrels feeding on bark beetles between summer and autumn in 2001, 2002, and 2003 was compared using 2 × 2 contingency tables. Mann–Whitney *U*-tests were used to compare the proportion of feeding bouts on beetle larvae compared to spruce cones because of large difference in sample sizes of beetle-foraging squirrels between 2002 and 2003. Logistic regression was used to determine if the density of beetle-attacked trees could be used to predict whether or not a squirrel participated in larval foraging. Linear regression was used to determine if there was a correlation between density of beetle-attacked trees and the amount of larval foraging for participating squirrels. Regressions were performed using data on density of trees attacked by the bark beetle from the spatial analyses and the proportion of feeding bouts that involved spruce bark beetles in 2002 and 2003 autumn focals. All research was performed following guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998), and was approved by University of Alberta's Animal Care and Use Committee.

RESULTS

Foraging for larval spruce bark beetles by red squirrels is an obvious and stereotyped behavior; squirrels situate themselves on the trunk of the tree near ground level and peel off the bark to reveal and ingest larvae. Larval beetles are easily differentiated from adults (Stark 1982). We observed no incidence of squirrels caching larvae and no incidence of squirrels eating adult beetles.

Although spruce bark beetles 1st invaded the study site in 1994 (Krebs et al. 2001) and anecdotal observations of bark beetle feeding by red squirrels were noted shortly after, this behavior did not become prevalent enough to be recorded in weekly summer focal observations until 2002. There was a nonsignificant increase in larval beetle foraging from summer 2001 to 2003 (2 × 2 contingency table: $\chi^2 = 3.36$, $d.f. = 1$, $P = 0.186$). In 2002, 2 (20%) of 10 squirrels were observed feeding on beetle larvae and in 2003, 3 (30%) of 10 squirrels fed on beetle larvae.

There was a significant increase in beetle foraging from autumn 2001 to 2003 (2 × 2 contingency table: $\chi^2 = 42.676$, $d.f. = 1$, $P < 0.0005$). In autumn 2001, no squirrels were observed feeding on larval bark beetles (0 of 26 squirrels), whereas in autumn 2002, 9 (24%) of 38 squirrels were observed feeding on larvae, and in autumn 2003, 35 (73%) of 48 were observed feeding on larvae. Among the squirrels that fed on larvae in autumn, the mean frequency of this behavior also increased significantly from 13.2% ± 4.7% of feeding bouts in 2002 to 35.8% ± 3.7% in 2003 (Mann–Whitney *U*-test: $U = 49.5$, $P = 0.002$; Fig. 1).

Conversely, the prevalence of red squirrels feeding on spruce seeds decreased from 2002 to 2003. Mean annual cone crops in our study site were 52.0 ± 7.6 cones per tree in 2001, 105.2 ± 17.8 cones per tree in 2002, and 22.7 ± 4.8 cones per tree in 2003. For the squirrels that fed on beetle larvae, spruce-seed foraging became significantly less common, accounting for 73.1% ± 5.4% of the 2002 feeding observations, and only 11.9% ± 1.9 % of the 2003 autumn feeding observations (Mann–Whitney *U*-test: $U = 314$, $P < 0.0005$). According to the time budget developed in 2003, when cone abundance was low, squirrels spent 0.64% ± 0.21% of their active time foraging on cones. Assuming that squirrels are active for 12 h per day in autumn (based on the observation by SB that squirrels are restricted to diurnal activity in this population and an average daylight period of 12 h at the study site during September–October), this translates into 4.6 ± 2.1 min/day spent foraging on cones, and a total estimated consumption of 0.69 kcal/day (Humphries 1996), representing approximately 2.5 kJ of metabolizable energy per day.

We estimated that red squirrels uncovered 3.97 ± 0.33 beetle larvae per minute while foraging, which, assuming every larvae was eaten, represents 0.08 kcal/min. The time budget developed in 2003 showed that the subset of squirrels that fed on bark beetles dedicated an average of 21.16% ± 0.38% of their active time to foraging on beetle larvae. Assuming 12 h of activity per day, squirrels spent 152.3 ± 27.1 min/day to foraging on beetle larvae, for a total estimated consumption of 604 bark beetle larvae per day (12.2 kcal/day), representing approximately 41 kJ of metabolizable energy per day.

The density of bark beetle–attacked trees surrounding the primary midden was a significant predictor of the occurrence of larval foraging in both 2002 and 2003 (logistic regression: for 2002, coefficient of determination = 0.033, $P = 0.009$; for

2003, coefficient of determination = 0.054, $P = 0.001$). The logistic model predicted that the likelihood of a squirrel feeding on larvae increased 3.3% and 5.5% with each additional beetle-attacked tree in 2002 and 2003, respectively. However, of the squirrels that fed on bark beetles in 2002 or 2003, there was no significant correlation between density of attacked trees and the proportion of squirrel feeding bouts on beetle larvae (linear regression: for 2002, $r^2 = 0.128$, $F = 1.031$, $d.f. = 1, 7$, $P = 0.344$; for 2003, $r^2 = 0.007$, $F = 0.218$, $d.f. = 1, 31$, $P = 0.644$; Fig. 1.).

Discussion

No feeding on bark beetles was observed in summer focal observations from 1989 to 2002 and no feeding was observed in autumn 2001. Twenty percent and 30% of summer focal squirrels fed on bark beetle larvae in 2002 and 2003, respectively. Twenty-four percent and 73% of focal squirrels fed on bark beetle larvae in 2002 and 2003, respectively, and, as we hypothesized, this prey represented a substantial caloric intake for some individuals. Given that nonreproducing red squirrels expend between 165 and 240 kJ/day (Humphries et al. 2005), individuals feeding on beetle larvae in autumn 2003 received 20% (41 kJ) of their daily energy requirement from bark beetles. By comparison, squirrels observed feeding on beetle larvae in autumn 2003 received only 1% (3 kJ) of their daily energy requirement from spruce cones. Squirrels opportunistically eat berries, mushrooms, and animal matter (carrion and hare leverets), which likely accounts for the other 159 kJ of daily energy required (Brink and Dean 1966; Currah et al. 2000; Krebs et al. 2001; Layne 1954; Obbard 1987; Smith 1968; Sullivan 1991; Sullivan et al. 1994; Willson et al. 2003).

In our study area, the main food source for red squirrels has traditionally been the seeds of white spruce, the only conifer species present (Brink and Dean 1966; Krebs et al. 2001). Squirrels obtain 0.15 kcal/min foraging on cones (Humphries 1996), which represents a 2-fold higher energy return than foraging on beetle larvae. The energetic benefits of spruce seeds relative to bark beetles may be partially offset by the need for squirrels to satisfy particular protein or other nutrient requirements from larvae and other omnivorous feeding. Further, red squirrels may eat fewer spruce seeds in autumn when cones are not abundant to ensure the availability of cones over winter when most other food sources are not available. However, from a purely energetic perspective, spruce seeds offer substantially more reward per unit foraging effort than beetle larvae and are thus likely a preferred food source.

Although the spruce bark beetle 1st invaded the study site in 1994 and anecdotal observations of bark beetle feeding by red squirrels were noted shortly after, this behavior did not become prevalent enough to be recorded in weekly summer focal observations until 2002. This late detection of beetle foraging during summer focals, which have been conducted annually since 1993 using the same methods, is unlikely to be a result of an increase in observer attention paid to beetle larvae foraging because the primary purpose of this summer focal sampling was to quantify changes in the food sources of squirrels over time and because bark beetle feeding is an obvious and easily observed type of squirrel feeding behavior. Autumn observations of squirrel behavior confirm that bark beetle feeding 1st became widespread in the population in 2002 and rapidly increased in prevalence thereafter. This abrupt increase in the amount of larval foraging between years for participating squirrels likely results from the squirrels' increasing reliance on bark beetles as an alternative food source, as a result of 4 successive low cone crops at our study site since 1998. In addition, availability of beetle larvae as an alternative food source increased in 2002, after several years of declining intensity in the bark beetle outbreak (Garbutt 2002). Although red squirrels' foraging on beetle larvae represents a novel behavior, the feeding method is similar to the tactics employed for feeding on spruce cambium (Hosely 1928; Pike 1934; Sullivan et al. 1994). Red squirrels have been observed stripping the bark of conifer trees to feed on cambium at multiple locations during conecrop–failure years (Steele 1998), although this has not been observed in our study area.

There was substantial variation in participation and prevalence of bark beetle foraging between individuals. There seems to be a minimum density of beetle-attacked tress necessary for bark beetle foraging by red squirrels to occur, after which the amount of foraging by individuals is not contingent upon the degree of beetle attack. Even though the density of beetle-attacked trees predicted the presence or absence of larval beetle foraging, density of trees attacked by the beetle was not a good predictor of the prevalence of this behavior. This pattern could result from a required encounter rate necessary for squirrels to form a prey image (Getty 1993; Tinbergen 1960). Variability in the prevalence of beetle feeding also may have resulted from variable access to alternative food resources because of habitat heterogeneity (Steury and Murray 2003). Cone availability on each squirrel's territory may be a good predictor of squirrel foraging on bark beetles. However, over the long term, low cone availability may be correlated with high density of the beetle larvae because of detrimental effects of bark beetle attack on cone production. Alternatively, the availability of other foods spatially specific to each squirrel may explain the spatial variation in feeding, where recent cone production has culminated in an all time low in white spruce seed availability.

The observed spruce bark beetle outbreak is thought to have been caused by climate warming (Garbutt 2002; Logan et al. 2003). The seeming increase of beetle larvae in the squirrel diet and relative importance of this behavior is thus mediated by climate change. Despite the recent importance of larvae in the diet of these squirrels, this represents an exhaustible and a seemingly uncacheable food item. Bark beetles ultimately kill host trees and reduce the average age and density of spruce. The subsequent reduction in stand density will lead to lower seed availability and inevitably lower squirrel densities (Koprowski et al. 2005; Matsuoka et al. 2001).

In any event, given the high availability of beetle larvae where they occur (Malmstrom and Raffa 2000) and the territorial nature of red squirrels, individual squirrels that have initiated beetle feeding will have virtually ad libitum access to this food source for the immediate future. The prey switching by red squirrels from spruce cones to beetle larvae seems to have occurred much too late and to be too spatially restricted to have significant influence on the continued spread of the bark beetle invasion at our study site and its long-term impacts on spruce cone production. Ultimately this may lead to lower densities of red squirrels with increased reliance on larval spruce bark beetles and other alternative foods.

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