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The functional response of a hoarding seed predator to mast seeding

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Abstract. Mast seeding involves the episodic and synchronous production of large seed crops by perennial plants. The predator satiation hypothesis proposes that mast seeding maximizes seed escape because seed predators consume a decreasing proportion of available seeds with increasing seed production. However, the seed escape benefits of masting depend not only on whether predators are satiated at high levels of seed production, but also on the shape of their functional response (type II vs. type III), and the actual proportion of available seeds that they consume at different levels of seed production. North American red squirrels (*Tamiasciurus hudsonicus*) are the primary vertebrate predator of white spruce (*Picea glauca*) mast seed crops in many boreal regions because they hoard unopened cones in underground locations, preempting the normal sequence of cone opening, seed dispersal, and seed germination. We document the functional response of cone-hoarding by red squirrels across three non-mast years and one mast year by estimating the number of cones present in the territories of individual red squirrels and the proportion of these cones that they hoarded each autumn. Even though red squirrels are not constrained by the ingestive and on-body (fat reserves) energy reserve limitations experienced by animals that consume seeds directly, most squirrels hoarded $<10\%$ of the cones present on their territories under mast conditions. Cone availability during non-mast years also reached levels that satiated the hoarding activity of red squirrels; however, this occurred only on the highest-quality territories. Squirrels switched to mushroom-hoarding when cone production was low and mushrooms were abundant. This resulted in type III functional response whereby the proportional harvest of cones was highest at levels of cone availability that were intermediate within non-mast years. Overall, more cones escaped squirrel cone-hoarding during a mast event than when cone production was low in non-mast years, which supports the predator satiation hypothesis. However, the highly variable seed escape in non-mast years may help to explain why all spruce cone production is not concentrated into fewer, larger, mast years.

Key words: hoarding; mast seeding; North American red squirrel; Picea glauca; *predator–prey; predator satiation hypothesis; prey-switching; seed predation;* Tamiasciurus hudsonicus; *white spruce; Yukon, Canada.*

INTRODUCTION

Mast seeding is a common reproductive strategy of some perennial plants, whereby individuals produce episodic, large seed crops that are synchronous with those of the other individuals in the population (Silvertown 1980, Kelly 1994). This strategy generates a pattern of mast years with very high levels of population-wide seed production, interspersed with non-mast years when little or no seed is produced by the population. One of the most prominent explanations for the evolution of masting is the predator satiation hypothesis (reviewed in Kelly and Sork 2002). This hypothesis suggests that seed escape is enhanced during mast years when more seed is produced than can be consumed by seed predators, whose numbers are reduced during non-mast years as a result of food shortage (Janzen 1971, Silvertown 1980, Kelly and Sork 2002).

Determining the form of the functional response (Solomon 1949) of mast seed predators is critical for examining the predator satiation hypothesis (Koenig et al. 2003). Functional responses describe the per capita proportion of prey consumed by predators in response to variation in prey availability (Fig. 1; Solomon 1949, Holling 1959*a*, *b*). The central prediction of the predator satiation hypothesis with respect to seed predators is that proportional seed consumption declines with increasing seed production, which enhances seed escape

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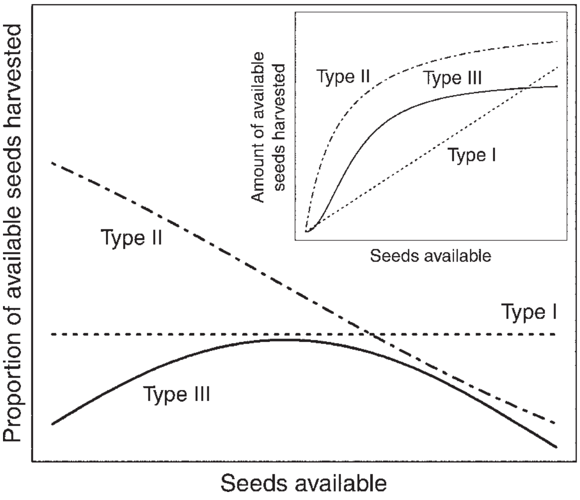

FIG. 1. The anticipated relationships between seed availability and the proportion (large graph) or total amount (inset) of available seeds harvested for type I, II, and III functional responses. As considered here, type I functional responses do not satiate and thus do not support the predator satiation hypothesis because the proportion of available seed harvested remains constant (main) and the amount of seeds harvested increases linearly (inset) across all levels of seed availability. Type II and III responses are satiating functional responses because the proportion of available seed harvested decreases at high levels of seed availability (main), which translates into a leveling off in the amount of seeds harvested (inset). Type III responses differ from type II responses in that the proportion of available seed harvested increases at low levels of seed availability generally because predators switch gradually to the seed of interest when it becomes more available in the environment (Jeschke et al. 2002). The peak proportion of available seeds harvested (main) of the hump-shaped type III response signifies the level of seed availability when predators start becoming satiated. Plants facing type II functional responses lose the highest proportion of their seed crop when population seed availability is low; thus, the synchronization of large seed crops by individuals into mast events is favored (Ims 1990). Type III functional responses may favor a masting strategy for the same reason; however, if proportional harvest at low levels of seed availability is less than at high levels, a masting strategy may not be favored (Ims 1990; see *Discussion* for further details).

in mast years (Kelly and Sork 2002). However, Ims (1990) also identified that the shape of the functional response at low levels of seed production is also important because prey-switching has the potential to reduce proportional consumption under conditions of low seed production. Although this has been generally acknowledged (Kelly 1994, Koenig et al. 1994, Curran and Leighton 2000, Kelly et al. 2001), it has been rarely examined (Klinger and Rejmánek 2009). The model of Ims (1990) suggests that if seed escape is facilitated by substantial prey-switching at low levels of seed production, the proportion of lifetime seed production that escapes predation might be maximized at low levels of seed production (as a result of prey-switching) as opposed to mast seeding (Ims 1990). Thus, evaluating the predator satiation hypothesis requires examining the form of the functional response of seed predators across low and high levels of seed production.

Although functional responses are foundational in ecological theory (Hassell and Comins 1978, Murdoch et al. 2003, Sarnelle and Wilson 2008) and estimates of functional responses in field studies are starting to accumulate (reviewed in Jeschke et al. 2004), the functional responses of mast-seed predators are poorly resolved. Observational studies that have primarily focused on insect seed predators have generally shown that the proportion of seed consumed by the entire community of seed predators is reduced during mast years (Nilsson 1979, Curran and Leighton 2000, Kelly and Sork 2002, Kon et al. 2005, Poncet et al. 2009; but see Kelly et al. 2000). Studies also have shown that vertebrates consume less experimentally placed seed under mast than non-mast conditions, which is consistent with the predator satiation hypothesis (Crawley and Long 1995, Hart 1995). House mice (*Mus musculus*) in laboratory cages and 1-m^3 field enclosures show a type II functional response when feeding on mountain beech (*Nothofagus solandri*) nuts provided at mast and non-mast levels, whether or not alternative food is present (Ruscoe et al. 2005). The next step in testing the predator satiation hypothesis is to quantify the seed available to vertebrate seed hoarders that are free-ranging in their natural environment, and to determine the form of the functional response across the entire range of seed production.

Vertebrate seed-hoarders might represent a particularly challenging seed predator to satiate because they face neither the immediate ingestion and assimilation constraints, nor the on-body reserve size constraints, experienced by species that directly consume seed (Humphries et al. 2001, Vander Wall 2001, 2002). Most research on vertebrate mast-hoarders has focused on hoarders that can act as seed dispersers as well as seed predators. These studies suggest that massive amounts of seed can be hoarded under mast conditions, but only a small fraction of hoarded seeds are actually recovered, which facilitates seed dispersal and escape (animal-mediated seed dispersal hypothesis; Vander Wall 2001, 2002, Jansen et al. 2004). Because seed-hoarding species may contradict the predator satiation hypothesis at the initial hoarding stage, but support it at the hoard recovery stage (reviewed in Jansen et al. 2004), an important distinction among mast-seed hoarders is whether they prevent seed germination as soon as seed is hoarded or only after they retrieve and consume seed.

The North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel) is a territorial sciurid rodent that specializes on conifer seed throughout much of its range (Steele 1998). At our study site in southwestern Yukon, Canada, red squirrels are the dominant vertebrate predator of white spruce (*Picea glauca*) seed, which is the only conifer tree present (Krebs and Boonstra 2001). White spruce is a wind-pollinated and wind-dispersed tree species that produces mast cone crops intermittently (LaMontagne and Boutin 2007, 2009). Because red squirrels hoard white spruce cones underground in autumn (Streubel 1968), where conditions prevent cone opening, they effectively prevent seed germination at the point of hoarding, whether or not the hoarded cones are eventually recovered and consumed (Brink and Dean 1966). Here, we evaluate whether the functional response of red squirrel hoarding of white spruce cones matches the form expected if mast seeding has evolved according to the predator satiation hypothesis as a strategy to enhance seed escape from seed predators. To determine the form of the functional response, we quantified the proportion of the cones available on individual red squirrel territories that were hoarded during three non-mast years and one mast year. The form of the functional response was used to test the prediction that the proportional harvest of white spruce cones decreases with increasing levels of cone production, and to determine whether seed escape was also enhanced at low levels of seed production as a result of prey-switching.

METHODS

Study area and natural history

We determined the functional response of cone-hoarding by red squirrels in a natural population that we have examined since 1988 near Kluane National Park in southwestern Yukon, Canada (61° N, 138° W). White spruce (*Picea glauca*) is the dominant tree species in this part of the boreal forest (Krebs and Boonstra 2001, McAdam et al. 2007). Past research suggests that the evolution of the mast-seeding strategy of white spruce trees is likely to have been influenced by red squirrel hoarding activity. Red squirrels are the dominant vertebrate pre-dispersal seed predators of many conifers (Benkman et al. 2003, Benkman and Siepielski 2004), and the presence of red squirrels has been shown to have important effects on the morphological evolution of conifer cones (Benkman et al. 1984, 2003). Pre-dispersal seed predation by White-winged Crossbills (*Loxia leucoptera*) is rare and irruptive at this study site (Smith and Folkard 2001).

Spruce cones are wind-pollinated and their seeds mature in late summer (Nienstaedt and Zasada 1990). Shortly after seed maturation, red squirrels bite off and drop cones from trees on their territories (hereafter referred to as clipping). These cones are then scatter-hoarded underground throughout their territory or larder-hoarded within the core of their territory in a midden consisting of cone bracts and additional hoarded cones (C. C. Smith 1968, Hurly and Robertson 1987, Hurly and Lourie 1997, Steele 1998). White spruce cones remaining on the trees (and many of the cones that are clipped and fall to the ground but are not hoarded) open and release their seeds due to a drop in moisture content about two months after maturation (Nienstaedt and Zasada 1990). Neither wind-dispersed seeds nor empty cones are hoarded by red squirrels (Q. E. Fletcher, *personal observation*). Red squirrels also hoard mushrooms and hypogeous fungi on their territories by wedging them into the branches of spruce trees (Smith and Reichman 1984, Hurly and Robertson 1990, Currah et al. 2000). We focused our analyses on hoarded cones and mushrooms because hoarded cones represent predated seeds and mushrooms are the primary alternative hoarded food source of squirrels in this area and might influence the functional response of white spruce cone-hoarding activity due to prey-switching.

Cone-hoarding by individual squirrels

This study was performed on two study grids (~40 ha each), Kloo and Sulphur, where the red squirrel populations have been completely enumerated since 1988 (Boutin et al. 2006, McAdam et al. 2007). These study areas are staked at 30-m intervals to provide spatial coordinates for field observations. Squirrels were marked with ear tags (Monel #1) and colored wires threaded through their tags for visual identification at a distance.

We determined the total amount of cones hoarded by individual squirrels by repeatedly observing them between late August/early September and late September/early October in four years (2001–2003, 2005; see Appendix A for the yearly range of study dates). Hurly and Lourie (1997) found a strong correspondence between behavioral and direct-sampling estimates of the proportion of cones that were scatter- vs. larder-hoarded by red squirrels, suggesting that behavioral estimates provide a reliable index of hoarding activity. In our study, squirrels were located using radiotelemetry and were kept in sight for 7-minute observation periods, three times per day (morning, 06:45–12:00; afternoon, 12:01–16:00; evening, 16:01–21:45), three days per week. Squirrels are diurnal and their activity ranges between sunrise and sunset at our site (S. Boutin, *personal observation*). During each observation period we recorded: (1) the number, type (cone or mushroom), and location of all hoarded items; (2) the location of cones that squirrels clipped; and (3) the location of all territorial rattle calls (C. C. Smith 1968, Altmann 1974). Hoarding rates for each observation period (cones/min) were calculated by dividing the amount of cones hoarded during the period by the duration of the period (7 minutes). Daily cone hoarding rates (cones/min) for each squirrel were calculated by averaging the three observation periods per day. To obtain a more complete estimate of the total number of cones hoarded that spanned the same range of dates in all years, we modeled daily cone-hoarding rates (cones/min) on all unsampled days between 15 August and 15 October using a shape-preserving piecewise cubic modeling technique (Fritsch and Carlson 1980; see Appendix A for further details). To calculate the total number of cones hoarded for each squirrel, we multiplied the observed and modeled daily cone-hoarding rates by the

TABLE 1. Summary table with study years sorted in ascending order by median levels of available *Picea glauca* cones, year-specific mushroom indices, and yearly median percentages items hoarded by red squirrels that were cones and mushrooms.

Year	Available cones	Mushroom index	Hoarded items that were cones (%)	Hoarded items that were mushrooms (%)
2003	2238 (919–5429)	0.58	39 (19–64)	61 (36–81)
2001	8570 (7074–13 895)	0.98	40 (31–58)	60 (42–69)
2002	12 192 (7796–20 664)	0.33	99 (95–100)	1 (0–5)
2005	73 052 (40 280–123 039)	1.94	99 (98–100)	1 (0–2.5)

Notes: Mushroom indices are the $\ln(x+1)$-transformed average number of mushrooms within a 3-m radius of $\geq$80 grid stakes. Levels of available cones and hoarded item percentages are presented with 25th and 75th percentiles in parentheses.

amount of daylight minutes per day (sunrise to sunset; southwestern Yukon; Herzberg Institute of Astrophysics; National Research Council of Canada) and summed all the values between 15 August and 15 October. Appendix C (Table C1, Fig. C1) examines the robustness of estimating the total number of cones hoarded from daily cone-hoarding rates on both observed and modeled days.

Cone and mushroom availability

To determine the number of cones available on the territory of each squirrel, henceforth referred to as the available cones, we first determined the boundaries of territory polygons using hoarding activity behaviors (cone-clipping, cone-hoarding, and mushroom-hoarding events) and territorial rattle calls (C. C. Smith 1968). The territory boundaries of neighboring squirrels that we examined did not overlap (LaMontagne 2007). We then overlaid these territory polygons onto yearly spatial cone production estimates in ArcGis 9.0 (ESRI, Redlands, California, USA) to determine the available cones of each squirrel (Beyer 2004, LaMontagne et al. 2005, LaMontagne 2007; see Appendix B for more details).

We also quantified the yearly availability of mushrooms on the Sulphur study grid prior to squirrel hoarding activity in late July. This index was the $\ln(x+1)$-transformed average of all the mushrooms within a 3 m radius of $\geq$80 grid stakes in the core of the grid (Table 1). Mushrooms were not quantified on the Kloo study grid, but we used the Sulphur index for both study grids because there is a high degree of spatial synchrony among the mushroom crops at this study location (Krebs et al. 2008).

Statistical analyses

We determined the total number of hoarded cones and available cones for 23–39 squirrels per year for an overall total of 119 individual paired estimates of hoarded and available cones. Adult and juvenile squirrels were represented in the samples each year, with juveniles making up 22–29% of the annual hoarding estimates. The total sample included 103 different individuals, and the remaining samples were from individuals that were sampled in multiple years. Because the vast majority of the data resulted from a single estimate per individual, we included one random sample per individual in each analysis and included these data in the figures. However, all qualitative descriptions of the data presenting measures of central tendency or differences between groups are based on all 119 estimates.

For all analyses, the dependent variable was the total number of cones hoarded divided by the available cones, which represents the proportion of available cones hoarded. First, we examined the effect of the available cones on the proportion of available cones hoarded over the entire range of variation in cone production. We performed this analysis twice. We first used the untransformed number of available cones as the independent variable, and second used the $\log_{10}(x+1)$-transformed number of available cones as the independent variable. The analysis that used the untransformed number of available cones presented the data on a more biologically meaningful scale. However, it was difficult to determine the form of the functional response with respect to untransformed available cones, because levels of available cones were extremely right-skewed (LaMontagne 2007), and discriminating among functional responses depends primarily on hoarding rates at low levels of cone availability. The $\log_{10}$-transformation of available cones reduced the right skew in the number of available cones, and thus allowed the functional response to be discriminated more easily.

Second, we determined the form of the functional response only within the non-mast years (2001, 2002, and 2003) by examining the relationship between the proportion of available cones hoarded and untransformed available cones. Available cones were not $\log_{10}$-transformed in this analysis because they were not strongly right-skewed. In a separate analysis, we also determined the effect of mushroom availability on the form of the functional response within these non-mast years.

More specifically, we determined the form of the functional response (type I, II, or III; Fig. 1) following the suggestions of Trexler et al. (1988), who compared the efficacy of various statistical techniques. In all analyses, we used logistic regression to examine the linear and quadratic effects of available cones on the proportion of available cones hoarded (glm; R Development Core Team 2008). Despite large annual differences in cone availability, none of our analyses included a categorical effect to specify the year in which the data were collected. The inclusion of a year effect would have restricted the assessment of the functional response to variation in available cones within each year, whereas variation across the entire range of cone production (i.e., both within and among years) is most relevant to interactions between perennial seed producers and seed predators. One analysis also included the effect of mushroom availability and its interactions with the linear and quadratic effects of available cones on the proportion of available cones hoarded. All analyses required that squirrels did not hoard more cones than were available on their territory (i.e., total cones hoarded/available cones ≤ 1). Individuals that were estimated to hoard more cones than were available on their territories were adjusted such that the proportion of available cones hoarded equaled 1.0 ($n = 13$ out of 119 hoarding estimates; for similar adjustments, see Hille Ris Lambers et al. [2002] and Wright et al. [2005]). Appendix C (Table C2, Fig. C2) examines the implications of analyzing individuals that appeared to hoard more cones than were available on their territory by removing these individuals from a subset of analyses. Our analyses showed strong signs of overdispersion; therefore, P values were adjusted using a quasi-binomial distribution (Crawley 2005); however the high levels of overdispersion did not affect the major qualitative conclusions of our analyses (Appendix C: Table C3). We used backwards stepwise model simplification to eliminate nonsignificant terms from our analyses (Juliano 2001). One effect was removed at each step ($P > 0.10$), with the highest-order interactions considered first and main effects considered next, ensuring that main effects were retained if their interactions were retained. P values were calculated by comparing models that included and excluded the effect of interest using F tests (Faraway 2006). Alpha was set to 0.05 in all analyses.

We used the term "satiation" to refer to the inability of squirrels to proportionally increase the amount of cones they hoard in response to the same proportional increase in available cones. Therefore, satiation was inferred by a negative relationship between the proportion of available cones hoarded (y = hoarded cones/available cones) and available cones (x = available cones). This resulted in the analysis of a ratio variable response against its own denominator, which could result in a negative relationship if hoarded cones and available cones are independent. However, Trexler et al. (1988) pointed out that the independence of these values is a meaningful result, and that there would only be a problem if a negative relationship between the proportion of available cones hoarded and available cones was interpreted to result due to a causal mechanism, other than the independence of hoarded cones and available cones. Differentiating among the functional responses was done by examining the coefficients of the linear and quadratic effect terms of available cones that were retained following model simplification (Trexler et al. 1988, Juliano 2001). Type I functional responses were identified by nonsignificant linear and quadratic coefficients; type II responses were inferred from a negative linear coefficient of available cones, and type III responses were inferred from positive linear and negative quadratic coefficients of available cones (Trexler et al. 1988, Juliano 2001). Finally, to illustrate predator satiation in the classic predation rate vs. prey availability form, we fit a Holling's (1959*a*, *b*) type II functional response to the relationship between cones hoarded and available cones using the disc equation (cones hoarded = $aNT/1 + aNT_{\mathrm{h}}$, where a is the attack constant, N is available cones, T is total time available [62 days between 15 August and 15 October], and T_{h} = handling time per cone; Holling 1959*a*, *b*) over the entire range of variation in cone production using the statistical software R (nls; R Development Core Team 2008).

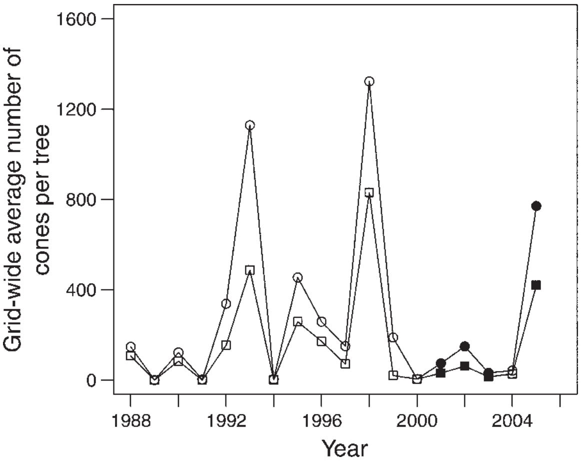

FIG. 2. Average levels of white spruce (*Picea glauca*) cones produced per tree over 18 years on the two grids (southwestern Yukon, Canada) examined in this study: Kloo (circles) and Sulphur (squares). Solid symbols represent years when hoarding by red squirrels (*Tamiasciurus hudsonicus*) was examined.

RESULTS

Yearly variation in cone production and hoarding activity

The yearly average number of cones per tree on the Kloo and Sulphur study grids between 1988 and 2005 ranged over more than two orders of magnitude, with some years characterized by almost no cones per tree (Fig. 2). Hoarding activity was monitored when cone production was relatively low in 2001 and 2003, intermediate in 2002, and was at mast levels in 2005 (Table 1, Fig. 2). Cone production in the 2005 mast year was the smallest of the three mast years that have occurred between 1988 and 2005 (Fig. 2; the three mast years were 1993, 1998, and 2005; LaMontagne and Boutin 2009).

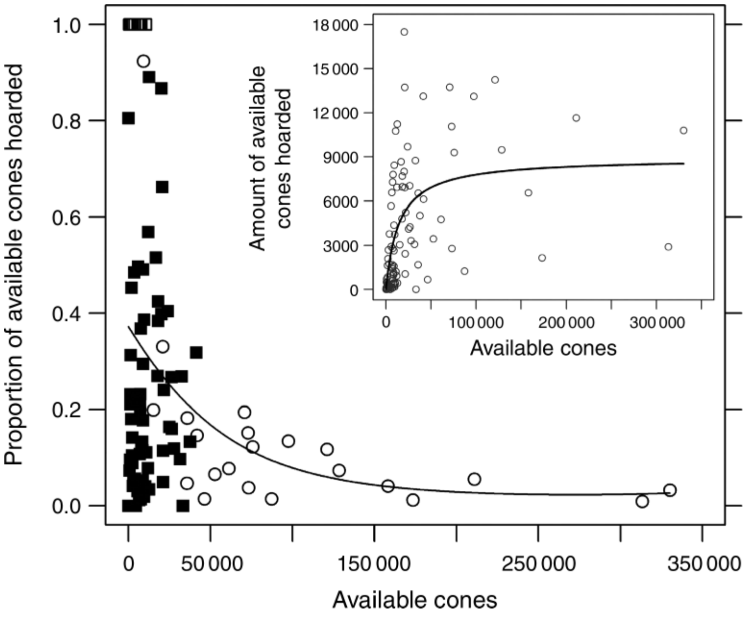

Fig. 3. The relationship between the availability of cones on a squirrel's territory and the proportion (main graph) and amount (inset) of available cones that were hoarded. Each point represents one point per individual red squirrel observed in one of the four years of this study. In the main figure, open circles signify individuals examined during the mast year, solid squares signify individuals examined in the three non-mast years, and open squares signify individuals examined during non-mast years that appeared to hoard more cones than were available on their territory, which were adjusted to have a proportional harvest of 1. The inset shows a Holling's (1959*a*, *b*) type II functional response (solid black line) fit to all data in the main figure to demonstrate the satiation of cone-hoarding at high levels of available cones. Presentation of the relationship in this form obscures a large proportion of individuals (49%) that had <50 000 available cones and <2000 cones hoarded. Furthermore, although the number of cones hoarded appears to vary widely when territory cones exceeds 50 000 cones, the severity and consistency of the hoarding satiation we observed is reflected in the number of cones hoarded remaining primarily between 1000 and 15 000 cones (and showing little evidence of an increasing trend) as the number of available cones increased from 50 000 to 350 000 cones.

The percentage of all observed hoarded items that were cones ranged from 39% to 99% over the four years of the study (Table 1). Cones comprised 99% of hoarded items in the mast year (2005), which is when mushrooms were also most available over the four study years (Table 1). In 2002, when cone production was intermediate and mushrooms were least available, 99% of hoarded items were cones. In the other two non-mast years, when cones were less available and mushrooms were more available than they were in 2002 (2001 and 2003), cones comprised ~40% of hoarded items.

The functional response across the entire range of cone production

Including all study years, the proportion of available cones hoarded strongly decreased as available cones increased (Fig. 3). This relationship was driven by a negative linear effect of available cones on the proportion of cones hoarded (Table 2a). The quadratic effect of available cones was also significantly positive in this model; however, this parameter was small, and it suggested only a very slight increase in levels of proportional harvest at high levels of available cones that is almost undetectable in Fig. 3. The number of cones hoarded by squirrels leveled off at ~8500 cones as the number of available cones increased to ~340 000 cones (Fig. 3 inset; type II response: $a = 9.98 \times 10^{-3} \pm 2.61 \times 10^{-3}$, $t_{101} = 3.82$, $P = 0.0002$; $T_\mathrm{h} = 6.96 \times 10^{-3} \pm 9.09 \times 10^{-4}$; $t_{101} = 7.66$, $P < 0.0001$).

Examining the proportion of available cones hoarded with respect to $\log_{10}$-transformed available cones suggested a type III functional response. The quadratic effect of $\log_{10}$-transformed available cones was negative, whereas the linear effect was positive, suggesting a hump-shaped, type III relationship between $\log_{10}$-transformed available cones and the proportion of available cones hoarded (Table 2b).

The functional response during non-mast years

The functional response of cone-hoarding in non-mast years was a type III, based on the sign of the significant effects of available cones (Table 3a; Fig. 4 dash-dot line). Although the proportion of available cones hoarded varied widely for given levels of available cones, the fitted functional response curve suggested that individuals on the least productive territories hoarded ~20% of the available cones. Maximum proportions hoarded (~40%) occurred at intermediate levels of available cones. Individuals with the highest levels of available cones in the non-mast years hoarded only ~10% of these cones (Fig. 4 dash-dot line).

TABLE 2. Form of the functional response of squirrel cone-hoarding activity in all four study years (one mast, three non-mast): linear and quadratic effects of untransformed and transformed available cones on the proportion of available cones that individual squirrels hoarded.

Effects	Parameter ± SE	F	df	P
a) Untransformed				
Available cones	$-2.37 \times 10^{-5} \pm 0.45 \times 10^{-5}$	27.07	1, 100	<0.0001
Available cones^2	$4.34 \times 10^{-11} \pm 1.45 \times 10^{-11}$	7.65	1, 100	0.007
b) $\log_{10}(x + 1)$-transformed				
$\log_{10}$(available cones)	5.30 ± 2.66	3.72	1, 100	0.057
$\log_{10}$(available cones^2)	−0.78 ± 0.30	6.58	1, 100	0.01

Notes: P values were obtained by comparing the deviance of a model including the effect of interest to a model excluding only this effect using F tests, with residual and F df values.

Analysis of non-mast years that included the effect of mushroom availability and its interaction with available cones confirmed that squirrels with many available cones always hoarded a small proportion of these cones (Fig. 4). However, the proportion of cones hoarded by squirrels with few available cones varied with mushroom abundance (Table 3b: available cones × mushroom availability interaction; Fig. 4). The proportion of available cones hoarded decreased with the increasing availability of available cones in the two non-mast years when mushroom availability was low and intermediate (linear available cones; mushrooms low: $F_{1,26} = 8.75$, $P = 0.007$; mushrooms intermediate: $F_{1,32} = 20.78$, $P < 0.0001$). However, when mushroom availability was high, even squirrels with few available cones hoarded a small proportion of available cones (linear available cones: ($F_{1,18} = 0.13$, $P = 0.72$).

The overall type III functional response in the non-mast years was somewhat sensitive to our treatment of the data (see Appendix C1); however, in all examinations of the robustness of our findings, we detected an interaction between mushroom abundance and available cones (Appendix C1, C3) and/or a negative effect of mushroom availability on the proportion of available cones hoarded (Appendix C1, C2, C3) that suggested prey-switching, which is the underlying mechanism of type III functional responses.

DISCUSSION

Hoarding species have great potential to harvest seed because they are not constrained by the ingestive and on-body energy reserve limitations that are faced by species that directly consume seed (Humphries et al. 2001). The proportion of cones available to individual red squirrels that were hoarded, however, still decreased strongly with increasing cone availability to very low levels during the mast year. The findings of our four-year study support the central prediction of the predator satiation hypothesis of mast seeding because cone-hoarding by red squirrels can be equated with seed predation (Brink and Dean 1966).

The extent to which red squirrel hoarding was satiated by large cone crops was dramatic. The maximum amount of cones a squirrel was observed to hoard in one year (17 502 cones in 2002) could be provided during a mast year by the cone production of two out of the 248 trees on an average squirrel territory, given that masting spruce trees can produce >10 000 cones at this site (S. Boutin, *unpublished data*; the average territory size in this study was 0.24 ha and there are, on average, 1033 trees/ha in this forest; LaMontagne 2007). Moreover, although the median number of available cones on a territory during the mast year (2005, 73 052 available cones), was six times higher than in the second highest year (2002, 12 192 available cones; Table 1), the median number of total cones hoarded was virtually identical in

TABLE 3. Form of the functional response of squirrel cone-hoarding activity in the three non-mast years determined with respect to untransformed available cones.

Effects in non-mast years	Parameter ± SE	F	df	P
a) Overall form of hoarding functional response				
Available cones	$1.07 \times 10^{-4} \pm 0.68 \times 10^{-4}$	2.24	1, 79	0.14
Available cones^2	$-3.72 \times 10^{-9} \pm 1.81 \times 10^{-9}$	4.02	1, 79	0.048
b) Effect of mushroom availability on functional response				
Available cones	$-1.03 \times 10^{-4} \pm 0.35 \times 10^{-4}$	7.83	1, 78	0.006
Available cones^2		1.57	1, 77	0.21
Mushrooms	−4.54 ± 1.23	14.02	1, 78	0.0003
Mushrooms : available cones	$1.20 \times 10^{-4} \pm 0.60 \times 10^{-4}$	3.35	1, 78	0.07
Mushrooms : available cones^2		2.21	1, 76	0.14

Notes: Terms that are not bolded were removed from the models with the specified residual degrees of freedom using backwards stepwise model simplification if $P \geq 0.10$ or an interaction including these terms had $P \geq 0.10$; bolded terms were retained in the models.

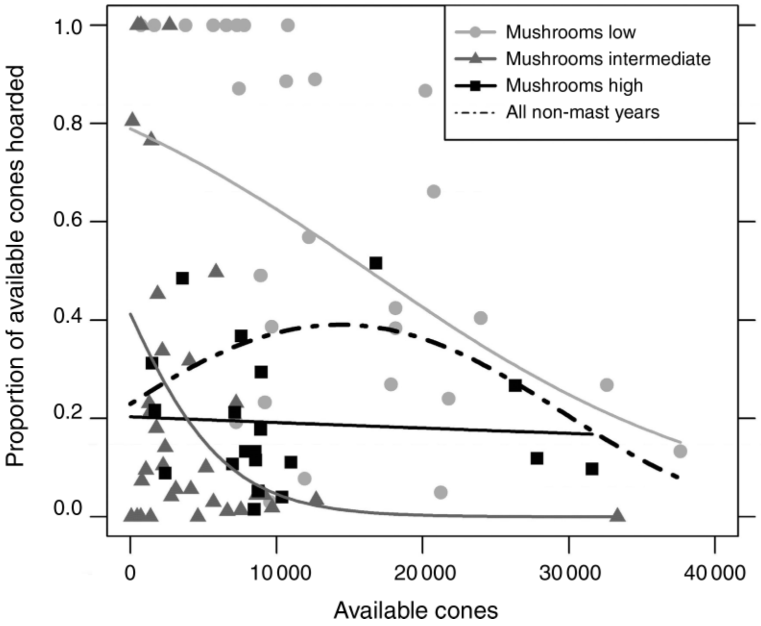

FIG. 4. The type III functional response of hoarding activity in non-mast years when mushroom availability was not considered in the analysis (dash-dot line), as well as an examination of the interaction between the effect of available cones and mushroom availability on the proportion of available cones hoarded. Examining the linear effect of available cones within each year, a type I functional response was suggested in the non-mast year with the highest mushroom availability (2001; mushroom index = 0.98) by a nonsignificant linear effect of available cones, which is plotted for illustrative purposes (coefficient = $-7.40 \times 10^{-6} \pm 0.21 \times 10^{-6}$). Type II functional responses were suggested by significant linear effects of available cones when mushroom availability was intermediate (2003; mushroom index = 0.58, coefficient = $-2.68 \times 10^{-4} \pm 0.89 \times 10^{-4}$) and low (2002; mushrooms index = 0.33, coefficient = $-8.08 \times 10^{-5} \pm 2.74 \times 10^{-5}$). Each point represents one random point per individual red squirrel observed in one of the three non-mast years. Individuals that appeared to hoard more cones than were available were adjusted to have a proportional harvest of 1.0 but are displayed with unchanged symbols.

these two years (6475 cones hoarded in 2002; 6330 cones hoarded in 2005). Based on these median values, the proportion of available cones hoarded was 6% in the mast year and 43% in the second highest year for cone production, which translates into more than an order of magnitude greater cone escape in the mast year (cone escape in 2005 = 66 722, and in 2002 = 5717). The proportion of available cones hoarded in the second highest year is similar to the proportion of available cones that were clipped from trees by red squirrels during a non-mast year at a more southerly site (55%; Peters et al. 2003). The mast year in which we observed hoarding activity was the smallest of the three cone masts that have occurred over 18 years at our study site (1993, 1998, and 2005; Fig. 2); thus, we expect that the proportion of cones hoarded would have been even less in the two larger masts.

We detected a satiating functional response of hoarding activity when analyses were restricted to the three non-mast years (Table 3a). The type III functional response curve generated by examining only the non-mast years (Fig. 4, dash-dot line) suggests that hoarding activity satiated in the non-mast years of our study, with the proportion of available cones hoarded beginning to decline noticeably when available cones exceeded ~15 000. This value approximates the maximum amount of cones hoarded by a squirrel in this study (17 502 cones). In the three non-mast years, 26% (2001), 45% (2002), and 3% (2003) of territories had more than 15 000 cones, suggesting that only high-quality territories in non-mast years satiated the hoarding activity of squirrels. This is in contrast to the mast year, when 96% of territories had more than 15 000 cones, which further demonstrates that the vast majority of squirrels were satiated in their hoarding activity in the mast year.

The type III functional response that we detected examining the entire range of cone production (including the mast year; Table 2b), and focusing on the non-mast years (Table 3a, Fig. 4), suggested that a lower proportion of available cones was hoarded at low levels of cone production than at intermediate levels of cone production. Type III functional responses commonly result from prey-switching at low levels of prey availability (reviewed in Jeschke et al. 2002), and our results are consistent with red squirrels switching from hoarding cones to mushrooms when cones are scarce. When cones were least available, mushrooms comprised >60% of observed hoard items (2001 and 2003), whereas mushrooms comprised 1% of hoarding events when cones were more readily available in the intermediate cone year (2002) and the mast year (2005; Table 1). In these years of relatively abundant cones (2002 and

2005), 99% of hoarding events were of spruce cones. The predominance of cone-hoarding in these years is consistent with a preference for hoarding cones, rather than a lack of mushrooms, because mushrooms were most abundant during the mast year (2005, Table 1). Prey-switching is also suggested by the interaction between mushroom availability and available cones affecting the proportion of available cones hoarded in non-mast years (Table 3b). When mushrooms were scarce (2002, 2003), squirrels with low available cones hoarded a high proportion of the available spruce cones (type II functional response; Fig. 4). This is in contrast to the non-mast year when mushrooms were most abundant (2001), when squirrels with few cones on their territories hoarded a small proportion of these cones (type I functional response; Fig. 4), which suggests that they had switched their attention away from hoarding cones when they were scarce. Overall, our results suggest that spruce cone-hoarding by squirrels depends on the availability of both spruce cones and mushrooms. Future research over more years will better resolve how the availability of these food items interacts to influence squirrel hoarding decisions and the shape of the functional response.

Based on the Fig. 3 inset, the amount of cones hoarded by squirrels leveled off at ~8500. This estimate is similar to the average number of hoarded lodgepole pine (*Pinus contorta*) cones per squirrel territory reported in Hurley and Lourie (1997; 9007 ± 478 cones), who estimated squirrel hoard size within one year by performing systematic searches of squirrel territories. Based on previous estimates of the number of sound spruce seeds per cone (48; Beaulieu et al. 1998), spruce seed mass (2.0 mg; Greene and Johnson 1994), the caloric value of spruce seeds (0.0293 kJ/mg; M. C. Smith 1968), an assumed digestibility of 90% (Robbins 1993), and the winter field metabolic rate of red squirrels (196 kJ/day; Humphries et al. 2005), squirrels could survive for 110 days feeding exclusively on a hoard of 8500 cones. However, our study clearly demonstrates that many squirrels hoard less than 8500 cones per year, which underscores the importance of alternative food sources such as hoarded mushrooms and spruce buds (M. C. Smith 1968).

The extreme variability in the proportion of available cones that were harvested when cones were scarce during non-mast years was striking. In the three non-mast years, there was considerable variation in levels of proportional harvest at low levels of available cones. For example, squirrels with <11 000 available cones ranged from hoarding all the available cones to few or none of the available cones. Part of this variation appeared to be related to prey-switching to mushrooms, which is presumably influenced by mushroom availability within individual territories (we estimated only the annual abundance of mushrooms and did not consider spatial variation in the abundance of mushrooms within each year), but most of this variation remains currently unexplained. Regardless of the responsible drivers, our results suggest that there is a large potential for cones to escape hoarding in non-mast years, which may explain why many trees produce at least some cones (and some trees produce many cones; LaMontagne and Boutin 2007) in years between masts.

The potential for high proportional cone escape at low levels of cone production is related to Ims' (1990) prediction that type III functional responses may favor asynchronous, rather than mast-seeding, strategies. For this to be the case, predators must have lower levels of proportional harvest at low levels of seed production than they have in response to mast crops; otherwise masting is still a strategy superior to asynchronous seed production. The shape of the type III functional response that we documented did not meet this criterion. Levels of proportional harvest during the mast year were generally much lower than at low levels of seed production. Fig. 4 demonstrates that the hoarding activity of squirrels was satiated by available cone levels that exceeded 15 000, which represents only a small fraction of the maximum amount of cones that were produced on territories in this study. Thus, at our site, the shape of the type III functional response of squirrel hoarding activity suggests that a masting strategy maximizes the proportion of lifetime cone production that escapes predation. We have started to quantify predation by invertebrate seed predators in our study site to determine if this remains the case when the entire suite of seed predators is considered. Moreover, future research at this site will examine the influence of the numerical response on the form and shape of the functional response of hoarding activity (Klinger and Rejmánek 2009).

Even though the type III cone-hoarding functional response suggests that a masting strategy minimizes the proportion of total lifetime seed production that is preyed upon (Ims 1990), our results also demonstrate that a considerable proportion of cones may escape hoarding during non-mast years. This may help to select for more asynchronous cone production, similar to a bet-hedging strategy (Simons 2009), whereby the production of small cone crops in inter-mast years might maximize fitness in the face of unpredictable rates of seed predation. This may help to explain why small cone crops are produced in the inter-mast years at our study site (Fig. 2).

In conclusion, seed predation by red squirrel is consistent with selection for both mast seeding and scattered seed production during inter-mast intervals by white spruce trees at our study site in the southwest Yukon Territory. Our determination of the functional response of cone-hoarding activity by squirrels suggests that white spruce cone production in mast years strongly satiates the cone-hoarding activity of red squirrels, thus supporting the predator satiation hypothesis of masting. Cone production also reached levels in non-mast years that satiated the hoarding activity of red squirrels. The most striking finding in non-mast years, however, was the tremendous variation in levels of cone-hoarding. This variation in hoarding rates was partially related to prey-switching and might facilitate seed escape at low levels of cone production, providing a possible explanation for the persistence of low levels of cone production during inter-mast years.

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APPENDIX A

Estimating total hoard accumulation (*Ecological Archives* E091-191-A1).

APPENDIX B

Estimating the availability of cones on the territories of individual squirrels (*Ecological Archives* E091-191-A2).

APPENDIX C

Robustness analyses (*Ecological Archives* E091-191-A3).