Arboreal Squirrel Abundance in Response to a Gradient of Mountain Pine Beetle Attack in Sub-boreal Forests

J. Douglas **Steventon**

Abstract

To assist in evaluating habitat retention options, the abundance of northern flying squirrels (*Glaucomys sabrinus*) and North American red squirrels (*Tamiasciurus hudsonicus*) were examined in 2005 and again in 2010 across a gradient of mountain pine beetle (*Dendroctonus ponderosae*) attack intensity in sub-boreal forests of west-central British Columbia. Among 30, 16-ha live-trapping grids, estimated mean abundance of both species increased non-linearly with remaining basal area of live overstorey (live trees $\geq$ 7.5 cm diameter at 1.3 m height). A weak (most likely positive but possibly negative) additional response of flying squirrels to dead overstorey (on average 1 m²/ha dead $\approx$ +0.11 m²/ha live basal area) was evident. The basal area of live spruce-fir (*Picea* spp., *Abies* spp.) overstorey, understorey tree density, and tree diameter covariates did not have substantive additional effects on estimated squirrel abundance. Whereas survey year affected overall abundance, it did not change the relationship with habitat attributes. The results suggest that dead lodgepole pine (*Pinus contorta*) has low habitat value for arboreal squirrels and thus is of lower impact on squirrels if salvage-harvested; however, retention or re-growth of sufficient live overstorey is necessary to maintain or recover squirrel abundance. The basal area of live overstorey appears a simple yet useful management metric for prioritizing habitat value, at least as indicated by relative abundance for squirrels in beetle-affected forests.

KEYWORDS: habitat; mountain pine beetle; northern flying squirrel; red squirrel; sub-boreal

Introduction

The mountain pine beetle (*Dendroctonus ponderosae*) infestation has greatly changed the forests of the central interior of British Columbia. A better understanding of the impact of the outbreak and associated salvage harvesting on the ecology of these forests is needed for informed management decisions (Burton 2006; Chan-McLeod 2006). Habitat and future timber supply conservation options include not harvesting lightly attacked stands, protecting understorey trees during harvesting, and (or) partial cutting of overstorey to maintain mature forest habitat value in moderately attacked stands or non-lodgepole pine (*Pinus contorta*) dominated stands, and prompt reforestation when harvesting is applied. The basic management principle is to prioritize within-stand retention based on the amount of surviving overstorey and (or) understorey (Coates 2006).

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

To assess the management premise above, I examined the abundance of arboreal squirrels, namely the northern flying squirrel (*Glaucomys sabrinus*) and the North American red squirrel (*Tamiasciurus hudsonicus*), along a gradient of beetle mortality in sub-boreal forests. I selected these species based on their substantive ecological influence, their life-history dependence on live mature trees, and feasibility for study.

Arboreal squirrels play many roles in forest ecosystems (Sullivan & Klenner 1996; Koprowski 2005; Siepielski 2006; Smith 2007; Weigl 2007). The red squirrel consumes conifer seed, is a predator of tree seedlings, and uses trees for nesting and escape. The flying squirrel depends on trees for locomotion and nesting, and tree lichens as a food source. Both species consume fungi and disperse the spores, including (particularly for the flying squirrel) ectomycorrhizal species important for tree growth. Both are important prey for various larger predators, such as northern goshawk, fisher, marten, and forest owls. Both squirrels are in turn predators on insects, and red-squirrels are major predators of bird nests.

In a preliminary study (Marcot et al. 2006; Steventon 2006), I found little difference in apparent squirrel abundance for an area of high beetle impact versus an area of lower impact, as a function of forest age; however, a very high variability was apparent in estimated abundance within mature forest in both areas. In the only other mountain pine beetle squirrel response study available in 2005, Stone (2005) suggested little impact except in extreme cases (> 90% tree mortality). In the study reported here, I further examined the hypothesis that squirrel abundance in mature forest with beetle-killed trees would depend on site-specific (16-ha scale) surviving overstorey measured as live-tree basal area, with a possible additional benefit of dead-tree basal area.

As secondary habitat covariates, I also considered squirrel abundance in relation to the proportion of live-tree basal area composed of interior spruce (*Picea glauca* x *engelmannii*) and subalpine fir (*Abies lasiocarpa*), density of understorey trees, and tree sizes (indexed by quadratic mean diameter). Red squirrel population dynamics in boreal and sub-boreal forests are reportedly influenced by spruce cone crops (Sullivan 1987; Fisher & Bradbury 2006) more than lodgepole pine (but see Wheatley et al. 2002). Flying squirrels in sub-boreal forests show some preference for nesting in spruce and fir (Cotton & Parker 2000). Red squirrel re-use of logged areas may be enhanced by protecting the understorey (Fisher & Bradbury 2006), and larger tree sizes may provide better seed production, lichen production, gliding advantages (flying squirrel), and greater cavity-nesting opportunities.

Study area and methods

The study area was the moist-cold Sub-boreal Spruce (SBSmc) biogeoclimatic subzone (Meidenger & Pojar 1991) within the Nadina Resource District of west-central British Columbia. The eastern half of the area is about 80% lodgepole pine and has seen extensive and severe mortality caused by the mountain pine beetle over the past 20 years. The western half is more diverse in tree species, with about half the forest comprised of lodgepole pine.

I selected 30, 16-ha sample sites clustered in three areas of the district (Figure 1). A habitat suitability index model was used to stratify each cluster area based on expected habitat quality (Steventon 2006). Sample sites were then randomly selected by strata to achieve a range of predicted habitat quality. For logistical practicality, if access was not available within 200 m another site from the same strata was selected. The southern-most cluster is an area of generally high beetle-caused pine mortality, mostly grey attack where the affected pine had been dead several years prior to 2005. The other two clusters had

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

highly variable beetle impact at the time, mostly green or red attack—affected trees were still alive or dead within the previous year (or 5 years for 2010 re-sample).

We live-trapped squirrels for three to five consecutive nights at each sample site between late August and early November of 2005, and for 24 of the grids, again in 2010. In 2010 we did not sample the two young clearcuts, and four other sites were no longer accessible or had been logged. Although we could not fully randomize grids by trapping date owing to travel logistics, we strove for a variety of beetle impact severity by date (Figure 2) to minimize any potential confounding effect on squirrel abundance caused by dispersal or other seasonal effects.

Centred on each sample site was a 3 by 3 trapping grid with 100-m spacing (nine traps per site). Our trap density per grid was low compared to many squirrel studies, a trade-off made to sample a wider geographic area. The goal was to conduct a preliminary assessment of squirrel abundance to guide future detailed demographic studies.

Traps (Tomahawk Live Trap, LLC, Hazelhurst, Wis., model 201) were mounted on trees at approximately 1.3 m height, wrapped in plastic for weather protection, equipped with a nest chamber and nesting material, and baited with lumps of a peanut butter/oatmeal mix the size of a golf ball and a slice of apple. We checked traps once daily with captured animals weighed, marked with a temporary mark (non-toxic felt marker),
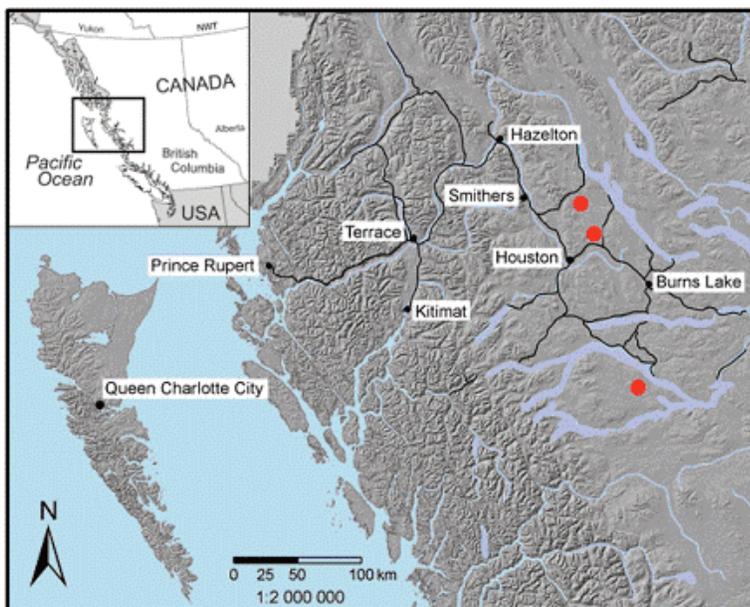
Figure 1. Locations of sample-site clusters (red dots) in study area.
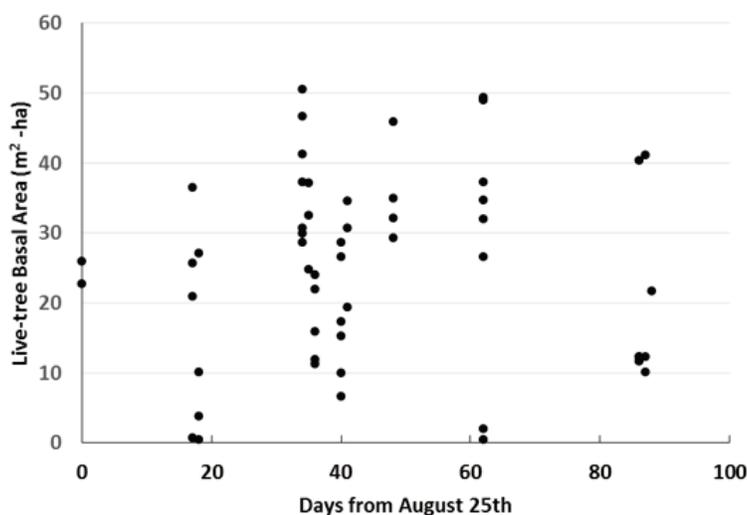
Figure 2. Live-tree basal area of trapping grids by trapping session start date

and released. Trapping procedures were conducted under a permit and animal care protocol approved by the B.C. Ministry of Environment (now administered by the B.C. Ministry of Forests, Lands and Natural Resource Operations).

In both 2005 and 2010, we sampled forest characteristics at nine plots within each trapping grid, with plots centred 3 m from each trap-tree in a randomly chosen direction.

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

We estimated overstorey basal area (live and dead), species composition, and diameter distribution of mature trees ($\geq$ 7.5 cm diameter at 1.3 m height) using the plot-less prism method. We tallied immature trees (< 7.5 cm diameter at 1.3 m in height) by species in a 3.99 m fixed-radius circular plot. Green-attack pines (i.e., those under beetle attack but with mostly green needles) were tallied as live trees. This grid sampling approach is essentially the same as that used in operational forest management timber assessments, allowing the potential for extrapolation of our results to operational timber inventory results.

I modelled squirrel abundance as a function of habitat attributes, adjusted for detection probability, using the analysis approach of Royle et al. (2005). The basal areas (m²/ha) of live and dead overstorey trees were the variables of primary interest. The first model applied was with live-tree basal area only. The second model added weighted (–0.5 to 0.5 x basal area) dead basal area to the live basal area. The proportion of live basal area consisting of spruce or fir, density (stems per hectare) of understorey trees, and tree quadratic mean diameter (Curtis & Marshall 2000) at a 1.3 m height (diameter at breast height, dbh) were then applied as linearly additive covariates to tree basal area effect.

As per Royle et al. (2005), observed captures at site i on night j were considered the product of a random variable having a Poisson distribution with mean of *Lambda* (λ), in turn predicted as a Weibull function of tree basal area and other covariates, multiplied by detection probability modelled as a logistic regression function. The predictions for *Lambda* and detection probability took the forms:

$$\lambda \text{ (mean abundance) in grid}_i =$$
$$(64 * d) * (1\text{-exp}(-1 * (\text{basal\_area}_i / b_0)^c)) + (b_1 * \text{covariate}_i)$$

where: 64 was a ceiling on the abundance estimate; and

$$\textit{Detection probability} \text{ in grid}_i \text{ per night}_j =$$
$$\exp(a_0 + a_1 * \text{covariate}_j)/(1 + \exp(a_0 + a_1 * \text{covariate}_j)).$$

The detection rate logistic models considered survey date, live and dead tree basal areas, and number of traps sprung or occupied by other species (and thus possibly unavailable) as potential predictor variables.

I implemented the analyses in a Bayes net framework, using Netica® software (version 5.18, Norsys Software Corp., Vancouver B.C.). Bayes nets describe a system by specifying relationships of conditional dependence among the variables in a directed graph. Each node represents a variable and the arcs (arrows) represent the relationships among the variables (Figure 3). This graph, together with a joint probability distribution for the variables, creates a model that can be used for inference (Marcot et al. 2006). Candidate models were first structured with flat (uninformative) prior-probability distributions for all nodes, then parameterized with the field data using the Expectation Maximization learning algorithm (Netica documentation, Do & Batzoglou 2008). The procedure optimizes the model fit to the observed nightly capture rates. All candidate models were assessed for strength of evidence using Akaike's Information Criterion for small sample sizes (Burnham & Anderson 2002). Sensitivity analyses used percent variance reduction (Marcot 2010) to compare the influence of individual variables (nodes).

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

Weighting of Dead-Tree BA

-0.5 to -0.4	.004
-0.4 to -0.3	1.38
-0.3 to -0.2	46.5
-0.2 to -0.01	.002
-0.01 to 0	0+
0 to 0.1	0+
0.1 to 0.2	0+
0.2 to 0.3	.001
0.3 to 0.4	4.22
0.4 to 0.5	47.9
0.109 ± 0.35	

Logistic Regression Parameter

1 to 1.2	0+
1.2 to 1.4	0+
1.4 to 1.6	0+
1.6 to 1.8	0+
1.8 to 2	0+
2 to 2.2	0+
2.2 to 2.4	0+
2.4 to 2.6	31.2
2.6 to 2.8	6.06
2.8 to 3	2.33
3 to 3.2	12.7
3.2 to 3.4	21.9
3.4 to 3.6	22.8
3.6 to 3.8	2.63
3.8 to 4	0.32
3.04 ± 0.42	

Detection Probability

0 to 0.025	1.50
0.025 to 0.05	55.6
0.05 to 0.075	9.58
0.075 to 0.1	33.3
0.1 to 0.125	0+
0.125 to 0.15	0+
0.15 to 0.175	0+
0.175 to 0.2	0+
0.0562 ± 0.025	

Obs. Captures Night 1

0	54.8
1	26.1
2	12.1
3	4.73
4	1.60
5	0.48
6	0.13
0.742 ± 1	

Dead-Tree Basal Area

0 to 5	37.5
5 to 10	37.5
10 to 15	0+
15 to 20	12.5
20 to 25	0+
25 to 30	12.5
30 to 35	0+
35 to 40	0+
40 to 45	0+
45 to 50	0+
50 to 55	0+
55 to 60	0+
60 to 65	0+
65 to 70	0+
9.38 ± 8.4	

Live-Tree Basal Area

0 to 5	0
5 to 10	0
10 to 15	0
15 to 20	0
20 to 25	0
25 to 30	0
30 to 35	100
35 to 40	0
40 to 45	0
45 to 50	0
50 to 55	0
55 to 60	0
60 to 65	0
65 to 70	0
32.5 ± 1.4	

Mean Abundance (Poisson)

0 to 2	23.9
2 to 4	0.70
4 to 6	.004
6 to 8	.055
8 to 10	0.62
10 to 12	2.53
12 to 14	7.10
14 to 16	15.4
16 to 18	21.9
18 to 20	15.1
20 to 22	6.98
22 to 24	3.81
24 to 26	1.67
26 to 28	0.22
28 to 30	.004
30 to 32	0+
13.2 ± 7.5	

Obs. Captures Night 2

0	54.9
1	26.1
2	12.1
3	4.72
4	1.61
5	0.48
6	0.13
0.741 ± 1	

Obs. Captures Night 3

0	55.2
1	25.8
2	12.1
3	4.71
4	1.59
5	0.47
6	0.13
0.736 ± 1	

Proportion of max density (intercept)

0 to 0.05	24.6
0.05 to 0.1	.002
0.1 to 0.15	.002
0.15 to 0.2	.001
0.2 to 0.25	.001
0.25 to 0.3	.001
0.3 to 0.35	.009
0.35 to 0.4	0.63
0.4 to 0.45	8.69
0.45 to 0.5	66.1
0.359 ± 0.19	

Weibull Shape Parameter

0 to 0.5	0+
0.5 to 1	0+
1 to 1.5	0+
1.5 to 2	68.1
2 to 2.5	30.9
2.5 to 3	0.96
3 to 3.5	0.01
3.5 to 4	.001
4 to 4.5	0+
4.5 to 5	0+
1.91 ± 0.28	

Weibull Scale Parameter

20 to 22	0+
22 to 24	0+
24 to 26	0+
26 to 28	0+
28 to 30	0+
30 to 32	.006
32 to 34	3.22
34 to 36	48.0
36 to 38	35.9
38 to 40	12.8
36.2 ± 1.6	

Obs. Captures Night 4

0	54.8
1	26.1
2	12.2
3	4.74
4	1.60
5	0.48
6	0.13
0.742 ± 1	

Obs. Captures Night 5

0	54.8
1	26.1
2	12.1
3	4.71
4	1.59
5	0.48
6	0.13
0.741 ± 1	

Survey Year

2005	55.6
2010	44.4
2007.2 ± 2.5	

Figure. 3. Example parameterized Bayes net for the influence on flying squirrel abundance of live-trees, showing predictions for 30–35 m²/ha live-tree basal area.

Results

The sampled sites represented a gradient of forest conditions (Figures 4 and 5). In 2005, we had a total of 85 flying squirrel captures on 22 of the grids, and 22 red squirrel captures on 12 of the grids, with a total of 1242 trap-nights. In 2010, we had 44 flying squirrel captures on 12 of the grids, and 19 red squirrel captures on 9 of the grids, with a total of 1080 trap-nights. For both species of squirrels, a detection probability response to the habitat variables or other correlates was not evident. Despite the low trapping intensity and resulting low detection probabilities (mean of 0.07 for flying squirrels, 0.04 for red squirrels), I detected functional responses to the amount of live overstorey for both species. A clear effect of year was evident on overall base abundance, so it was included in all models; however, there was little support for a year effect on the habitat attribute weightings for abundance or detection probability.
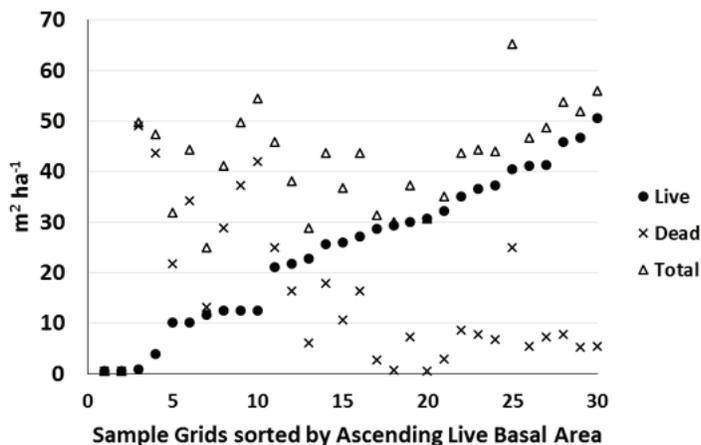
Figure 4. Mean overstorey (all species) live and dead tree (≥ 7.5 cm diameter at 1.3 m height) basal area (m²/ha) for the squirrel live-trapping grids in 2005.

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

Spruce-fir Basal Area

Understory Density

Quadratic Mean Diameter
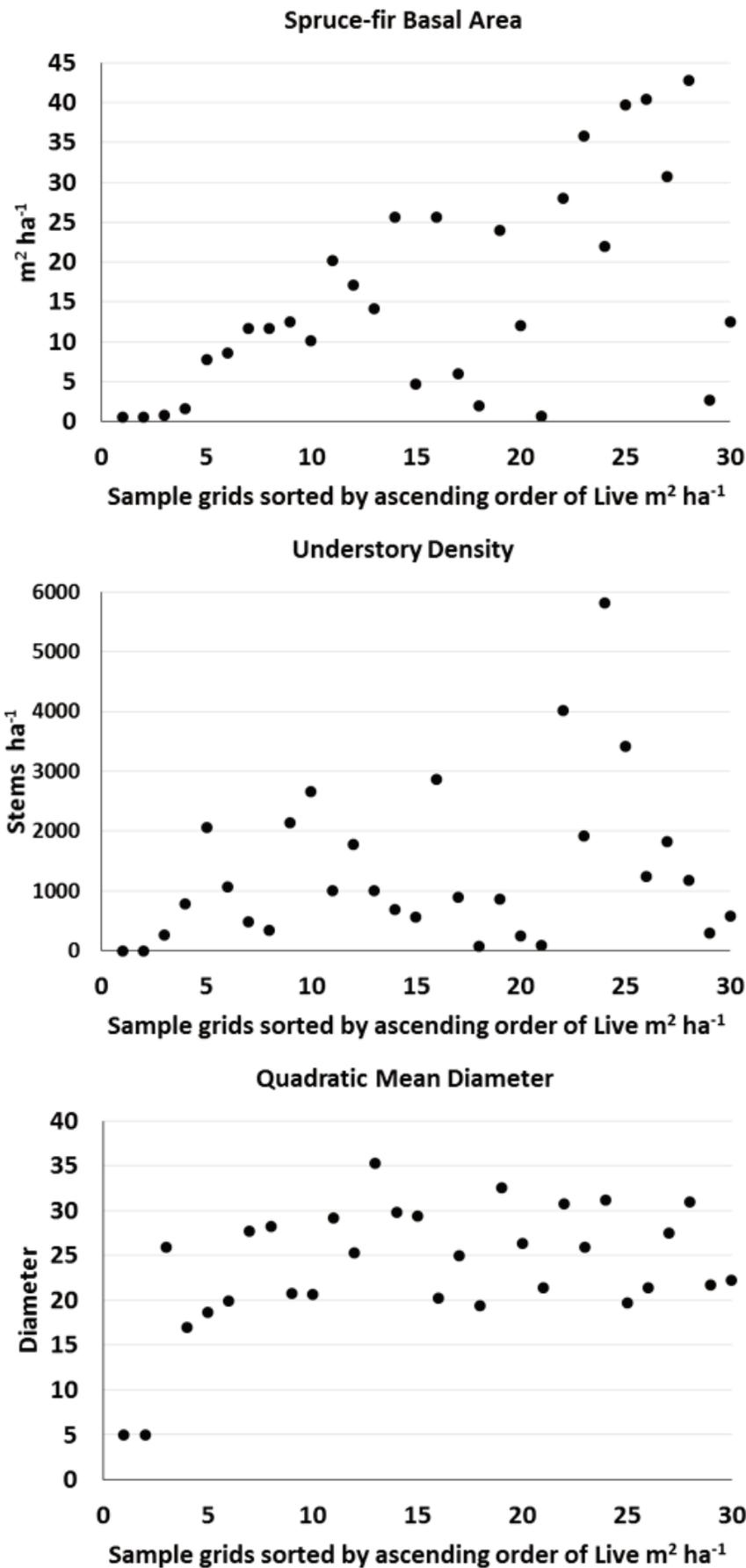
Figure 5. Mean values for grid covariates, in same grid order as Figure 4.

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

For flying squirrels, a strongly non-linear response to live-tree basal area was evident (Figure 6). The model including dead-tree basal area was only weakly supported based on Akaike's Information Criterion weights (Table 1), and gave ambiguous results with about equal weight to the possibilities of a negative or positive effect (Figure 3, node "dead-tree weight"). The mean weighting of dead to live basal area was +0.11. If the positive dead-tree effect was in fact true, the response in Figure 6 rose more steeply in the range of 10–20 m²/ha. None of the other covariates were supported by Akaike's Information Criterion weights as improving the model, although all had a possible positive effect on abundance additional to live-tree basal area.

Table 1. Model comparisons and performance as indicated by Akaike's Information Criterion (AICc).

Parameters	AICc	AICwt	% Variance reduction[f]
Flying Squirrel			
Live_BA[a]	14.89	0.47	36.0
Live_BA, Understorey[b]	17.00	0.17	35.2, 1.9
Live_BA, Non-Pine_BA[c]	17.62	0.12	37.1, 16.2
Live_BA, Dead_BA[d]	17.63	0.12	37.1, 16.2
Live_BA, DBH[e]	17.66	0.12	10.3, 4.7
Red Squirrel			
Live_BA	11.1	0.46	2.21
Live_BA, Understorey	13.36	0.17	8.2, 5.0

a Live-tree basal area, all species; *b* Understorey trees, stems per hectare; *c* Live-tree basal area, non-pine; *d* Dead-tree basal area. *e* Quadratic mean diameter of live trees, all species; *f* Percentage of variance of mean abundance explained by the prediction parameters. Provides a relative indication of parameter importance, weighted by observed frequency of input variable values (Marcot et al. 2006). The % variance reduction for dbh, for instance, is limited by the narrow range of input values.
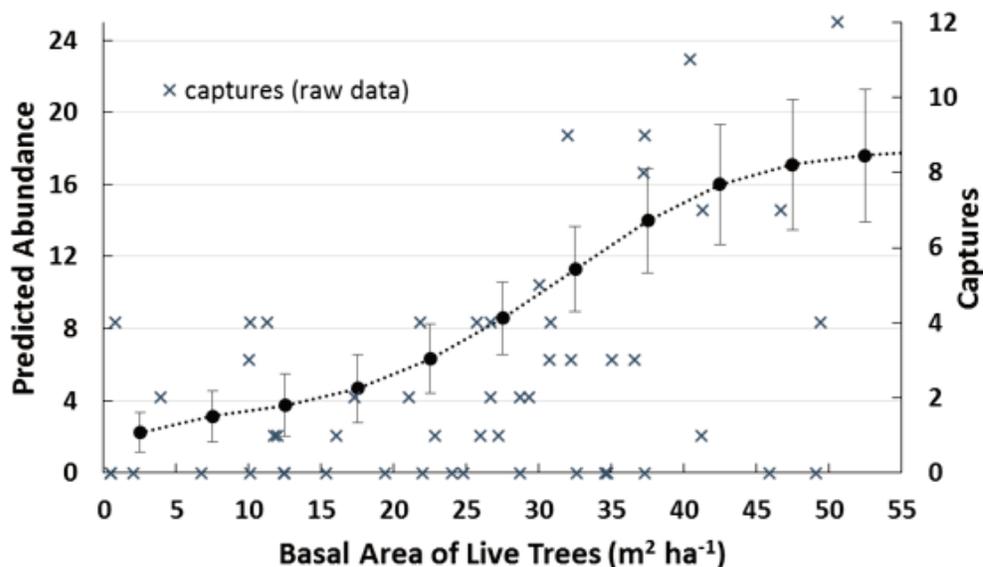
Figure 6. Total live-trapping captures (raw data) and predicted mean ±95% confidence intervals for predicted abundance of flying squirrels as a function of live-tree basal area.

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

For red squirrels, the non-linear response was less dramatic (Figure 7), and none of the covariates substantially improved the model (Table 1).
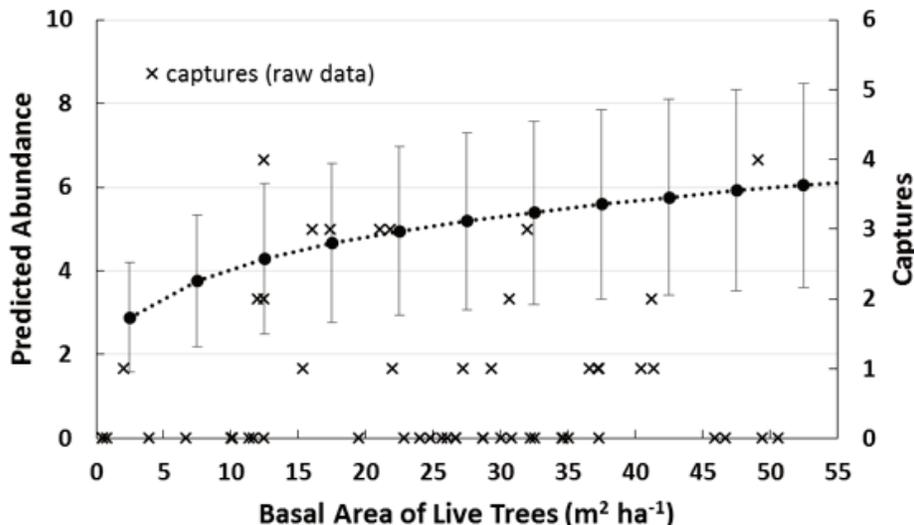
Figure 7. Total live-trapping (raw data) and predicted mean ±95% confidence intervals for predicted abundance of red squirrels as a function of live-tree basal area.

Squirrel body weights at first capture within a trapping session (Figure 8) did not show any clear pattern by live-tree basal area (Figure 8) nor by trapping date (not shown). Thus, biomass of squirrels essentially paralleled abundance.
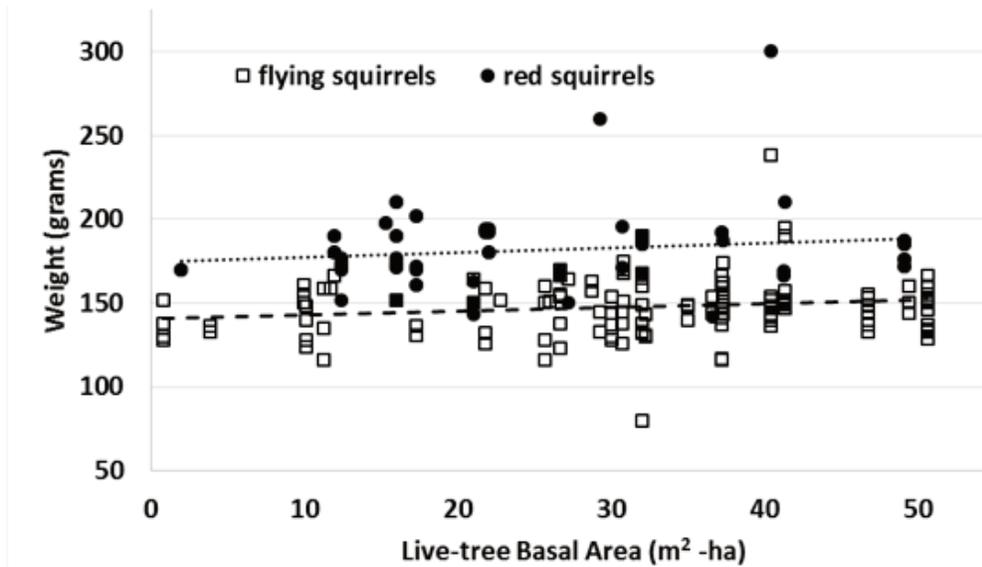
Figure 8. Squirrel body weight as a function of live-tree basal area. Recaptures within a trapping session were excluded to minimize influence of re-capture on weights.

Discussion

The abundance estimates reported here should be considered relative rather than absolute densities (i.e., the number of animals using a grid but not necessarily confined to it). Many home ranges or territories likely overlapped grid boundaries and animals could move in and out of the grids.

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

The predicted mean abundance of both squirrel species responded positively to live-tree basal area, although predicting abundance at any particular location was highly uncertain. Dead trees may have added a small amount of habitat benefit additional to live trees, or possibly a negative effect. Either way, forest stands composed mostly of beetle-killed trees were clearly of lower value; however, some grids with little live-tree basal area still had captures and a non-zero abundance estimate, thus heavily beetle-affected forest still received some use. The negative effect of beetle-kill on squirrel abundance is a change from earlier preliminary findings of limited beetle effect (Steventon 2006) that did not examine stand-specific attributes. Completely killed forest on the scale of our 16 ha sample grids, however, was a rarity even in the heavily beetle-affected area. Others have likewise reported that surviving trees in both the overstorey and understorey are more common in beetle-affected landscapes than often assumed (Burton 2006; Astrup et al. 2008). Body weights are influenced by many factors, including age and food availability. The lack of a relationship of live basal area to observed squirrel body weight, however, provides some support (at least in the fall) of abundance as a likely reflection of relative habitat value.

At least three studies have found a negative effect of mountain pine beetle mortality on red squirrel abundance (Saab et al. 2014). Severe insect-induced tree mortality has also resulted in dramatic red squirrel reductions, at least temporarily, in spruce-fir types in Alaska (Matsuoka et al. 2001) and Arizona (Zugmeyer & Koprowski 2009). In the context of the present beetle outbreak in British Columbia, it is likely the lodgepole pine cone resource is, or will be, severely limited for several decades and red squirrel populations may become vulnerable to fluctuations in cone crops of other conifer species.

In contrast, Stone (1995), who sampled 1-ha sites in mountain pine beetle-attacked lodgepole pine stands in northern Utah, reported both squirrel species generally increased in relative abundance with overstorey mortality (up to 8 years after attack), with red squirrels only declining with severe mortality (> 95%). This seems to imply a negative response to live-tree abundance, clearly rejected in my data and the literature generally. One possibility for the discrepancy is that Stone (1995) conducted trapping in the summer when dispersing juveniles may temporarily occupy sub-optimal habitat, whereas our trapping was conducted in fall to early winter when settlement of dispersers may have been more complete. The much smaller spatial scale (1 ha) of Stone's (1995) sample stands may also have affected results (i.e., effects of the surrounding stand).

The lack of substantive added predictive value from the covariates (proportion spruce–fir, tree diameter, abundance of understorey) in our study is perhaps not too surprising given their correlation with live-tree basal area, and our limited number of survey grids. Forests in the SBSmc biogeoclimatic subzone with higher basal area tend to have more trees of larger diameter, a larger component non-pine, and more understorey (Clark et al. 2003). All these covariates, however, showed some potential added positive effect and should not be dismissed as unimportant. Examination of the Bayes nets showed that grids with the highest abundance estimates (for both species) had a high live-tree basal area but also a higher proportion of non-pine, larger mean quadratic tree diameters, and higher densities of understorey trees. These attributes have been widely reported as important to flying squirrels (Holloway et al. 2012).

Arboreal squirrel population dynamics and abundance in various habitats are clearly a complex combination of fluctuating food resources, social interactions, predation, and landscape context (Stuart-Smith & Boutin 1994; Wheatley et al. 2002; Fisher et al. 2005; Smith 2007). Further longer-term, process-based study of squirrel demography in varying contexts

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

is needed to further our understanding of the dynamics of these species in response to a changing environment.

Management implications

Coates (2006), focussing on future timber supply, suggested a management strategy of preserving beetle-attacked stands when surviving trees represent ≥ 30 m²/ha basal area; partial cutting that salvages the dead pine; or full protection if there is sufficient understorey, for stands with 10–30 m²/ha live basal area; and clearcut salvaging with prompt reforestation when live basal area is < 10 m²/ha. Similar strategies have also been proposed for minimizing wildlife impacts (Chan-McLeod 2006; Saab et al. 2014).

My results with arboreal squirrels support this prioritization approach: there was increasing squirrel abundance with greater overstorey survival and low added value (or possibly even negative effects) from dead pine. This suggests potential conservation benefit from partial-cutting techniques that retain live overstorey while salvaging dead pine. Partial cutting in a variety of western North American conifer forests has generally shown reduced squirrel abundance, yet still maintained substantive populations (reviewed in Herbers & Klenner 2007; Holloway and Smith 2011; Holloway et al. 2012). Herbers and Klenner (2004) suggested 10 m²/ha as a threshold for habitat retention for flying squirrels and red squirrels in Douglas-fir (*Pseudotsuga menziesii*) forests, and Holloway et al. (2012) found a positive (though noisy) relationship of tree basal area and flying squirrel abundance. The use of live-tree basal area as a squirrel habitat value metric allows ready assessment of habitat value, at least as indicated by relative abundance, from routine operational timber inventories. Surviving trees or patches (especially non-pine) would be suitable foci for wildlife tree patch management in otherwise clearcut beetle-attacked stands.

Substantive live understorey beneath dead pine overstorey apparently provided little immediate compensating value as squirrel habitat in these forests, but if protected it can be expected to accelerate development of a future overstorey (Coates 2006; Astrup et al. 2008). In areas with little live overstorey or understorey, harvesting followed by prompt reforestation will likely be the fastest route to habitat recovery. Sullivan et al. (2010) examined squirrel abundance 30 years after salvage harvesting with varying levels of live-tree retention of beetle-affected lodgepole pine/Douglas-fir stands, compared to unharvested old-growth in south-central British Columbia. They found both squirrel species had similar mean abundance among treatments, although somewhat lower in young pine with no live-tree retention (at time of harvest) for flying squirrel, and (surprisingly) lowest in old growth for red squirrels. All their treatments had recovered to mean live-tree basal area values greater than 30 m²/ha. Similarly, Ransome et al. (2004) showed managed second-growth sub-boreal lodgepole pine forests can be productive habitat for both squirrel species within 30–50 years following harvest, and I had three grids of such age that had substantial captures of both squirrel species.

This project was a first-look at squirrel abundance in response to the mountain pine beetle outbreak in sub-boreal forests of central British Columbia. Arboreal squirrels appear to be useful and practical model species for further monitoring and research aimed at developing a better understanding of the implications of environmental change from mountain pine beetle, logging, and climate change.

Acknowledgements

ARBOREAL
SQUIRREL
RESPONSE
TO MOUNTAIN
PINE BEETLE

Steventon

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ARBOREAL
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Author information

J. Douglas Steventon, RPBio is a consulting wildlife ecologist based in Smithers BC. His interest centres on wildlife habitat and population ecology in a forest landscape context. He recently retired after 32 years with the BC Government, most recently as a research wildlife ecologist with the Ministry of Forests, Lands and Natural Resource Operations. Email: doug.steventon@yahoo.com