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Spruce Beetle outbreaks guide American Three-toed Woodpecker *Picoides dorsalis* occupancy patterns in subalpine forests

JULIA J. KELLY,[1]* QURESH S. LATIF,[2] VICTORIA A. SAAB[2] & THOMAS T. VEBLEN[1]
[1] *Department of Geography, University of Colorado, Boulder, CO 80309, USA*
[2] *Rocky Mountain Research Station, USDA Forest Service, Bozeman, MT 59717, USA*

American Three-toed Woodpeckers *Picoides dorsalis* are considered a sensitive species by the United States Bureau of Land Management and are on the United States Fish and Wildlife Service's Watch List. In Idaho, Oregon and Washington, they are of conservation concern due to low abundance and an apparent reliance on disturbed, old-growth forests. This species is strongly associated with Spruce Beetle *Dendroctonous rufipennis* epidemics, yet their occupancy relation with epidemic conditions have not been described. We studied Three-toed Woodpecker occupancy patterns in spruce–fir forests experiencing varying degrees of beetle infestation between 2013 and 2016. Accounting for detection probability, we found a strong positive relationship between occupancy and the density of currently infested trees. Estimated occupancy was 0.57 (Bayesian credible interval 0.49, 0.64) for 75-m-radius survey points with zero infested spruce trees vs. 0.99 (Bayesian credible interval 0.99, 1) for points with 235 recently infested stems per ha. In contrast, we found no relationships with density of trees infested at least 3 years prior to sampling, density of older snags (i.e. > 10 years dead) or quadratic mean diameter of healthy or recently infested trees. These results provide evidence of the importance of active Spruce Beetle infestation for Three-toed Woodpecker habitat. Conserving Spruce Beetle-infested trees for at least 3 years following the onset of a beetle epidemic would benefit Three-toed Woodpecker populations and other species that depend on woodpecker-excavated cavities. We suggest managers consider these results when planning logging activities aimed at Spruce Beetle mitigation.

Keywords: birds, disturbance, Engelmann Spruce, habitat conservation, Rocky Mountains.

American Three-toed Woodpeckers *Picoides dorsalis* are associated with recently disturbed forests of the Rocky Mountains from Utah, USA, to British Columbia, Canada. Outbreaks of Spruce Beetle *Dendroctonous rufipennis* represent resource pulses for Three-toed Woodpeckers, which colonize recently infested forests and feed on Spruce Beetles (Koplin 1969, 1972, Koplin & Baldwin 1970, Schmid & Frye 1977, Murphy & Lehnhausen 1998). Resource pulses directly influence consumer populations (Ostfeld & Keesing 2000), so the duration and severity of Spruce Beetle outbreaks may play a key role in Three-toed Woodpecker abundance. What remains unknown is the time period over which Three-toed Woodpeckers occupy Spruce Beetle-infested forests and what forest structure characteristics this species prefers.

Several lines of evidence indicate the likely importance of Spruce Beetle outbreaks as a resource pulse for Three-toed Woodpecker. Three-toed Woodpeckers exhibit foraging behaviour focused on beetles and they respond numerically to Spruce Beetle infestations and other disturbances associated with pulses in beetle populations (e.g. Yeager 1955, Koplin 1969, Murphy & Lehnhausen 1998). Three-toed Woodpecker diet can consist almost entirely (> 95%) of Spruce Beetles (Hutchinson 1951) where they are available. Given the apparent importance of bark beetles to

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*Corresponding author.
Email: juliajeankelly@gmail.com
Twitter: @avi_geo

Three-toed Woodpeckers (Koplin 1969), the commonly observed association with bark beetle outbreaks is thought to be driven by the pulse in this resource. The extent to which Spruce Beetles represent the primary factor drawing Three-toed Woodpeckers to infested forest, however, has not been explicitly examined. Such understanding is vital for the successful management and conservation of the Three-toed Woodpecker.

In North America, Three-toed Woodpeckers are thought to be the most important natural predators of Spruce Beetles (Hutchinson 1951, Koplin & Baldwin 1970, Schmid & Frye 1977). They are adapted for digging out bark beetle insect larvae, pupae and adults (Koplin 1969, 1972, Koplin & Baldwin 1970, Bock & Bock 1974, Schmid & Frye 1977, Saab *et al.* 2014) and focus their feeding on tree trunks where beetle colonies are concentrated (Koplin 1969, Fig. 1). Three-toed Woodpeckers are more common than other *Picoides* spp. in Engelmann Spruce *Picea engelmannii*–Subalpine Fir *Abies lasiocarpa* forests at higher elevations (Bock & Bock 1974) and may play an important role in regulating Spruce Beetle populations at endemic levels (Hutchinson 1951). Other native forest-dwelling woodpeckers such as the Hairy *Leuconotopicus villosus* and Downy Woodpecker *Dryobates pubescens* are not as effective bark beetle predators due to differences in their preferred foraging substrate (Koplin 1969). The Downy Woodpecker feeds more often on insects within small branches and bark, and the Hairy Woodpecker is a generalist of Subalpine Fir, Engelmann Spruce and Lodgepole Pine *Pinus contorta* tree trunks in various stages of decay (Koplin 1969). Three-toed Woodpeckers are more commonly observed feeding under the bark of freshly killed Engelmann Spruce (Koplin 1969). The Black-backed Woodpecker *Picoides arcticus* diet consists predominantly of wood-boring beetles (Cerambycidae) that are commonly found after forest fires (Tremblay *et al.* 2016). Three-toed Woodpeckers also occur in post-fire forests, where they forage on bark beetles that attack moderately burned trees (Murphy & Lehnhausen 1998).

Figure 1. Example of Spruce Beetle excavation by American Three-toed Woodpeckers at the Slumgullion site in 2015. Foraging is concentrated on bark beetle larvae residing in the bole of the spruce tree. Photo taken by Julia Kelly.

Observed increases in Three-toed Woodpecker populations following Spruce Beetle outbreaks are consistent with their specialization on bark beetle prey (Koplin 1972). Because of this specialization, Three-toed Woodpecker populations may be constrained by Spruce Beetle availability, making them potentially vulnerable to removal of beetle-infested trees during post-fire and post-beetle salvage logging (Fayt *et al.* 2005). The particular strength of Three-toed Woodpecker associations with beetle-infested trees in relation to onset of attack, however, has not been quantified, which limits information capable of guiding habitat management following outbreaks (Wiggins 2004).

The onset of a massive Spruce Beetle outbreak in the southern Rocky Mountains of Colorado provided the opportunity to quantify Three-toed Woodpecker relationships with beetle-infested forests at a fine spatial scale (i.e. tree-level). Periodic irruptions are a major component of forest succession in the southern Rocky Mountains (Baker & Veblen 1990, Veblen *et al.* 1991). The recent Spruce Beetle epidemic in Colorado affected 695 000 ha statewide from 1996 to 2016 (USDA Forest Service 2015, 2016). The progression of the infestation allowed us to quantify relationships between Three-toed Woodpecker occupancy and stages of infestation and forest structure. Infestation severity is influenced by disturbance history, proportion of canopy occupied by spruce, and age and diameter of spruce (Massey & Wygant 1954, Schmid & Hinds 1974, Schmid & Frye 1976). Spruce trees larger than 24 cm diameter at breast height (dbh) are more susceptible to Spruce Beetle attack (Hart *et al.* 2014b), so tree size may also influence Three-toed Woodpecker occupancy, as large trees support more beetles. Spruce Beetle spread across the landscape and brood development within a stand may influence the duration of Three-toed Woodpecker use. Woodpeckers feed predominantly on beetle larvae, the life-stage that is most abundant during year one of the 2-year life cycle of Spruce Beetles (Hutchinson 1951, Massey & Wygant 1954, Knight 1961, Holsten *et al.* 1999). The majority of larvae pupate after their first winter. Before their second winter, 95% of beetles emerge as adults and re-enter their parent tree at the base where woodpecker predation is lower and temperatures are higher beneath snowpack (Holsten *et al.* 1999). Approximately 2 years after infestation, adult beetles exit the overwintering site in search of new host material (Holsten *et al.* 1999). Synchronized with the life cycle of Spruce Beetles, we expect Three-toed Woodpeckers to increase 1–2 years post-outbreak and decline thereafter.

The goal of our study was to estimate occupancy of Three-toed Woodpeckers in relation to a Spruce Beetle infestation. Specifically, we sought to identify tree-level attributes that best predicted Three-toed Woodpecker occupancy across a range of infestation stages representing time since attack. Our objectives were: (1) to quantify Three-toed Woodpecker occupancy in relation to stage of infestation (early, mid, late), and (2) to evaluate the Three-toed Woodpecker relationship to infestation stage in the context of tree diameter. We expected occupancy to relate positively with early-stage beetle-infested spruce trees and less so with late-stage infested trees or older snags. Species that obtain their insect prey from wood, such as the Three-toed Woodpecker, rapidly colonize insect outbreaks and then decline in number with increasing time since initial beetle attack. This numerical pattern likely reflects declines in bark and wood-boring beetle larvae (Murphy & Lehnhausen 1998, Hoyt & Hannon 2002, Saab *et al.* 2014). Early-infested trees contain the greatest abundance of beetle larvae, whereas beetle colonies diminish during the later stages (Schmid & Frye 1977, Holsten *et al.* 1999). We considered occupancy relationships with large-diameter spruce because large trees provide more breeding substrate for Spruce Beetles (Schmid & Frye 1976, Hart *et al.* 2014b) and large-diameter trees and snags increase the quality of both foraging and nesting substrate for many woodpeckers (e.g. Bütler *et al.* 2004, Saab *et al.* 2009).

METHODS

Study area

We surveyed Three-toed Woodpeckers in subalpine spruce–fir forests of the San Juan National Forest, Colorado, between 3000 and 3650 m elevation (Fig. 2). The climate here is characterized by a bi-seasonal precipitation regime with snow from December to March and rain from July to September (Toney & Anderson 2006). Average maximum summer temperature (June–August) is *c.* 22 °C and average minimum winter temperature (December to February) is *c.* −14 °C (recorded at Rico, CO, weather station and retrieved on 19 February 2018 from: http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?corico).

We used mapped defoliation and mortality data generated by Aerial Detection Surveys (ADS) by the U.S. Forest Service to locate sites of recent Spruce Beetle activity (USDA Forest Service 2010; Table 1). To establish control sites, ADS data were used to avoid forest stands that had experienced a bark beetle infestation in the 5 years previous to our study. We confirmed that the sites had not been affected by Spruce Beetles by visually inspecting trees in the field before sampling commenced. To capture a range of spruce–fir stand conditions, we initially sampled in three sites unaffected by Spruce Beetles. None of the study sites had been harvested < 25 years prior to sampling, based on both Forest Service records and field observations. Each study site varied in terms of stand density, tree size and age, but all sites were relatively mature stands with maximum tree diameters exceeding 50 cm and the ages of small samples of the dominant trees ranging from *c.* 100 to 300 years. We did not sample in clear cuts, nor did we sample in young, dense stands.

After 2 years of sampling, one study site (Tuckerville) was attacked by Spruce Beetles. We added a fourth site (Slumgullion) in 2014, to better represent late-infested trees and a broader range of post-outbreak conditions on occupancy of Three-toed Woodpeckers. The onset of Spruce Beetle infestation occurred at Slumgullion during 2012–2014. By 2015, most Spruce Beetles had dispersed from the study area due to host depletion. Altogether there were four study sites representing a range of infestation stages (Table 1). Two control sites remained free of Spruce Beetles for the entire sampling period (2013–2016), a third site was

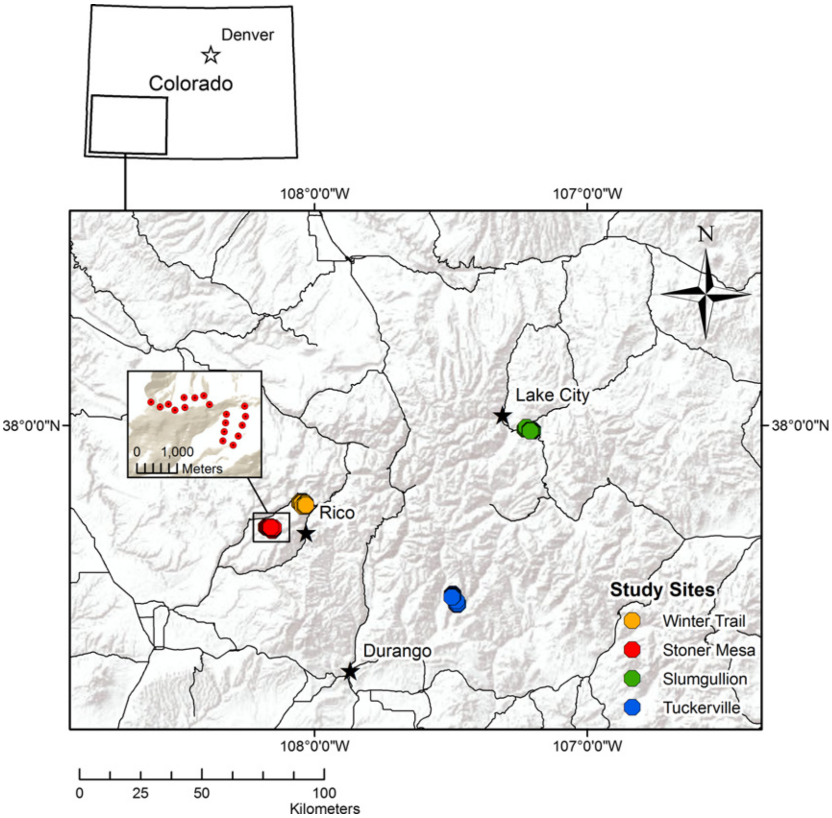

Figure 2. Southern Rocky Mountain study area depicting study site locations. Each study site (green, blue, yellow and red) consists of 18 point count locations where Three-toed Woodpeckers were sampled. The Stoner Mesa study site is enlarged to exemplify how points were arranged within the site.

Table 1. Description of sites where Three-toed Woodpeckers were sampled in forests with varying degrees of Spruce Beetle infestation.

Site name	Location	UTM Coordinates (Zone 13S)	Sampling occasions	Year of Spruce Beetle onset
Stoner Mesa	San Juan National Forest	0750697.1E, 4176534.1N	2013[a], 2014–2016[b]	None
Winter Trail	San Juan National Forest	0760398.3E, 4185489.1N	2013[a], 2014–2016[b]	None
Tuckerville	San Juan National Forest	0280716.1E, 4150973.2N	2013[a], 2014–2016[b]	2015
Slumgullion	Gunnison National Forest	0305853.9E, 4206622.6N	2014–2016[b]	2013–2014

[a] Sampling at the site occurred once during the 2013 breeding season.
[b] Sampling occurred three times during each breeding season.

un-infested for two of four sampling years (2013–2016) and a fourth site was Spruce Beetle-infested for the entire sampling period (2014–2016). All four study sites were approximately 180 ha, with 18 total point count stations (hereafter 'points'), and the study sites were located at least 10 km from each other.

Bird surveys and vegetation measurements

We surveyed Three-toed Woodpeckers within 75 m of 72 points spaced ≥ 250 m apart and ≥ 75 m from any forest edge (Hanni *et al.* 2013). We used GPS units to locate co-ordinates for points in the field, and then marked centred points on the nearest tree to those co-ordinates (hereafter ‘point tree’). Points had to be located in the field due to the irregular shape of each stand. To facilitate re-location, the first point was always located within 500 m of a trail or forest road. Each consecutive point (2–18) was located by walking 250 m from the previous point at a random compass bearing. We located as many points as possible along the 1st compass bearing (usually 3–6 points) before choosing a new bearing (Fig. 2). We recorded and stored point co-ordinates in handheld GPS units (Magellan MobileMapper 6). Point locations were adjusted to avoid obstacles (cliffs, running water, bogs) that would have limited accessibility or aural detection of birds (Hanni *et al.* 2013).

We conducted 6-min point-count surveys from 05:00 to 10:00 h during the breeding season (10 June to 15 July) on days without inclement weather. Surveyors avoided counting the same individual at multiple neighbouring points by establishing 250-m spacing between survey points, an area approximating movements within breeding home-ranges of several *Picoides* spp. (Hogstad 1977, Tingley *et al.* 2014, Lorenz *et al.* 2015). We surveyed 54 points (18 at each of three sites) once each during the 2013 breeding season. We then added a fourth site, resulting in 72 points, which we surveyed three times annually during the 2014–2016 breeding seasons (Table 1). Surveys were conducted by different field biologists in any given year. During surveys, we recorded every individual Three-toed Woodpecker detected visually or aurally (Table S1).

We measured stand- and tree-level attributes within 400-m^2 plots (18 plots per site) centred on the point tree. For each individual tree, we recorded tree species, dbh, status (live or dead), mortality agent and decay class (Table 2). To estimate time since beetle attack, we recorded decay classes of each infested tree based on the amount and colour of needles remaining (e.g. Temperli *et al.* 2014, Table 2). From these data, we compiled the quadratic mean diameter (QMD) of all trees, number of early-infested trees and number of trees in middle and late stages of infestation within each plot (Table 3). See Table S2 for compiled plot-level data and Table S3 for tree-level data collected within 400-m^2 plots in the field.

Table 2. Status classes for each tree measured within the plot.

Time since beetle infestation	Status	Classification criteria based on visual assessment
None	Live	No evidence of Spruce Beetles
0–1 year	Green	Beetle entrance holes, pitch tubes, live bark beetles or larvae on tree, green needles indicating first year of attack; early infestation
1–2 years	Yellow	Yellow needles, Spruce Beetle frass and galleries, pitch tubes; early infestation
< 5 years	Needle Drop	> 50% of needles remain on tree, evidence of Spruce Beetle galleries; mid infestation
6–10 years	Twig	< 50% of needles remain on tree, > 90% bark retention, > 50% of < 1 cm twigs on tree, evidence of Spruce Beetle galleries; mid infestation
11–15 years	Branch	< 10% of needles remain on tree, bark retention variable, < 50% of < 1 cm twigs on tree, evidence of Spruce Beetle galleries; late infestation
> 15 years	Snag	No branches, > 1.37 m; late infestation
None	Stump	< 1.37 m, cut by chainsaw

Visual assessments of each tree were used to classify trees into decay-class status categories (adapted from Temperli *et al.* 2014).

Data analysis

We used an occupancy model to analyse species distribution relations with habitat features of interest. Given adequate data, occupancy models estimate species detectability (p) conditional upon occupancy (presence of at least one individual), to allow unbiased estimation of occupancy probabilities (ψ) utilizing repeated survey data (MacKenzie *et al.* 2002, 2006). Because our sampling occurred over a relatively short period of time (*c.* 1 month), we assumed that the occupancy state for a species at a given survey point did not change between within-year visits. Individual movement was possible between visits, so the occupancy state of a point described whether the point intersected at least one Three-toed Woodpecker home-range (Efford & Dawson 2012, i.e. detection probability included availability, *sensu* Latif *et al.* 2016). We excluded detections ≥ 75 m from the surveyor, making the effective area surveyed a 75-m-radius circle centred on each point. Given the spacing between points, an individual home-range (Hogstad 1977, Tingley *et al.* 2014, Lorenz *et al.* 2015)

Table 3. Covariates used to model American Three-toed Woodpecker occupancy in spruce–fir forests of the San Juan Mountains, Colorado. Covariates by plot were compiled for each year 2014–2016.

Variable	Description
QMD	Quadratic mean diameter (squared diameter at breast height) of non-infested and early-infested spruce trees in the plot. Ecological significance: tree size is related to the presence of old-growth trees and approximates forest structure (Antos & Parish 2002)
Early infestation	Total number of trees with a status classified as Green[a] and Yellow[a] within a plot. Ecological significance: This variable represents the extent of active Spruce Beetle infestation
Mid infestation	Total number of trees with a status classified as Needle Drop[a] and Twig[a] within a plot. This variable represents trees killed by Spruce Beetles for > 2–3 years, where galleries are visible but Spruce Beetles are no longer present on the tree. Ecological significance*:* These trees represent potential sites for nest cavity excavation, but represent harder wood than late infestation snags
Late infestation or snag	Total number of standing dead trees classified as Branch[a], Snag[a] and ≥ 23 cm diameter at breast height. Includes late-infestation trees and trees killed by any mortality agent > 10 years ago. Ecological significance: These trees represent potential sites with the softest wood for nest cavity excavation

[a]See Table 1 for list of status classification names and criteria.

could have included more than one neighbouring point, but the extent of sampling spanned multiple home-ranges. Thus, occupancy estimates here reflected both space use and local abundance (Efford & Dawson 2012, Latif *et al.* 2016).

We compiled and analysed a two-dimensional data matrix y, where element y_{jt} was the sum of binary indicators for Three-toed Woodpecker detections (Sanderlin *et al.* 2014). Given a binary indicator $x_{jkt} = 1$, we detected one Three-toed Woodpecker at point j ($j = 1,\ldots,J$) during visit k ($k = 1,\ldots,K$; $K = 1$ in 2013 and 3 in 2014, 2015 and 2016) in year t ($t = 1,\ldots,T$; $T = 4$). Because we did not have covariates that differed for detection between visits, we analysed the sum of all binary detections for Three-toed woodpeckers over all visits at each point j in year t, where $y_{jt} = \sum_{s=1}^{3} x_{jts}$ and $y_{jt}\ \varepsilon\ \{0, 1, 2, 3\}$. We modelled detection frequencies given the probability of detection p and occupancy latent state z_{jt} as a binomial distribution with K trials (K = number of visits; $K = 1$ in 2013 and 3 in 2014–2016):

$$\left[y_{jt} \middle| p, z_{jt}\right] \sim \mathrm{Bin}(K, p \times z_{jt}) \tag{1}$$

We modelled the occupancy state for site j in year t given a probability of occupancy ψ_{jt} as a Bernoulli latent variable z_{jt} (Royle & Kéry 2007):

$$\left[z_{jt} \middle| \psi_{jt}\right] \sim \mathrm{Bern}(\psi_{jt}) \tag{2}$$

We analysed occupancy relationships with four covariates of interest (Table 2). We modelled occupancy probability ψ_{jt} for point j in year t as a logit-linear function of early infestation (β_{Einf}), mid infestation (β_{Minf}), snags (β_{sng}) and quadratic mean diameter (β_{QMD}):

$$\mathrm{logit}(\psi_{jt}) = \begin{cases} \beta_0 + \beta_1 \times z_{j0} + \beta_{\mathrm{Einf}} \\ \times \mathrm{Einf}_{jt} + \beta_{\mathrm{Minf}} \times \mathrm{Minf}_{jt} \\ + \beta_{\mathrm{QMD}} \times \mathrm{QMD}_{jt} + \beta_{\mathrm{sng}} & t = 1 \\ \times \mathrm{sng}_{jt} \\ \beta_0 + \beta_1 \times z_{j(t-1)} + \beta_{\mathrm{Einf}} \\ \times \mathrm{Einf}_{jt} + \beta_{\mathrm{Minf}} \times \mathrm{Minf}_{jt} \\ + \beta_{\mathrm{QMD}} \times \mathrm{QMD}_{jt} + \beta_{\mathrm{sng}} & t > 1 \\ \times \mathrm{sng}_{jt} \end{cases} \tag{3}$$

where β_1 quantified the partial dependency of ψ_{jt} on the previous year's occupancy state ($z_{j(t-1)}$, z_{j0}) and thereby accounted for resampling of points across years (Royle & Kéry 2007). Thus, the quantity $\beta_0 + \beta_1$ is the logit probability of Three-toed Woodpecker persistence at a given point. We examined the overlap of Bayesian credible intervals (BCIs) with zero to assess statistical support, where non-overlap of 95% and 90% BCIs indicated strong and limited support, respectively, for the estimated parameter. All covariates were scaled to mean = 0, sd = 1 to facilitate computation and comparison of covariate effect estimates.

Posterior estimates were sampled using JAGS v. 3.3.0 (Plummer 2003) operated with the R2jags package (Su & Yajima 2015) in the R statistical computing environment (R Core Team 2016). We used independent non-informative priors for all parameters, i.e. a *Normal* (0,100)T(−30,30) prior for all parameters in Equation 3 and *Uniform*(0,1) for detection probability (for R script, including BUGS code, see Appendix S1). We verified that $n_{\text{effective}} \geq 100$ and $\hat{R} \leq 1.1$ for all parameters (Gelman & Hill 2007). Model goodness-of-fit was examined for the fully parameterized model (i.e. with all covariates) using a posterior predictive test based on deviance. We simulated data from the model's posterior predictive distribution and calculated a *P*-value quantifying the probability of deviance for observed data ≥ simulated deviance, where $P < 0.05$ or $P > 0.95$ provided evidence for poor fit.

RESULTS

We modelled Three-toed Woodpecker occupancy using data from 702 point surveys conducted during 270 point-by-year sampling occasions. The total sampling effort of 702 surveys was derived from 54 points sampled once in year 2013, and 72 points sampled three times per year in 2014, 2015 and 2016 ($702 = 54 + (3(3 \times 72))$). We detected Three-toed Woodpeckers during 259 surveys on 154 point-by-year occasions. We recorded the greatest number of detections ($n = 107$ at 59 points) in 2016 and the fewest detections ($n = 10$ at 10 points) in 2013, when Spruce Beetles were not present in the plots sampled.

Covariates of occupancy were not strongly correlated with each other ($|r|$ 0.42; Table 4) so multicollinearity was not a concern. Goodness-of-fit tests provided no evidence for lack of model fit ($P = 0.68$). Estimated detectability of Three-toed Woodpeckers was moderate for a single survey (posterior median (95% BCI) $P = 0.51$ (0.45, 0.56)) and high for three repeat surveys ($P^* = 0.88$ (0.83, 0.91)) implemented during most of the study.

We found strong statistical support for a Three-toed Woodpecker occupancy relationship with the number of early-infested spruce trees within plots (Fig. 3, Table 5). We commonly observed Three-toed Woodpeckers debarking spruce trees to obtain Spruce Beetles, particularly in 2014–2016 at infested plots (Fig. 1). Estimated Three-toed Woodpecker occupancy increased from 0.57 (0.41, 0.93), when there were zero early-infested trees, to 0.99 (0.89, 1) when point occupancy reached an asymptote at 235 early-infested stems per ha (Fig. 3). We found limited support for higher Woodpecker occupancy rates at points with larger diameter trees (Fig. 4, Table 5). The magnitude of this effect was small, i.e. for minimum QMD = 16 vs. maximum QMD = 3717, occupancy was 0.92 (0.71, 1) and 0.99 (0.89, 1), respectively. We note, however, that early-infested spruce trees were larger (mean diameter ± sd = 26.1 ± 14.5 cm ($n = 778$)) than spruce

Table 4. Covariate correlation (Pearson's *r*, $n = 270$ point-by-year occasions) matrix for variables used to model occupancy of American Three-toed Woodpeckers in spruce–fir forests of the San Juan Mountains, Colorado.

	Early infestation	Mid infestation	Late infestation	QMD
Early infestation	1.00			
Mid infestation	0.42	1.00		
Late infestation or snag	0.05	0.21	1.00	
QMD	−0.32	−0.26	−0.22	1.00

See Table 2 for variable descriptions.

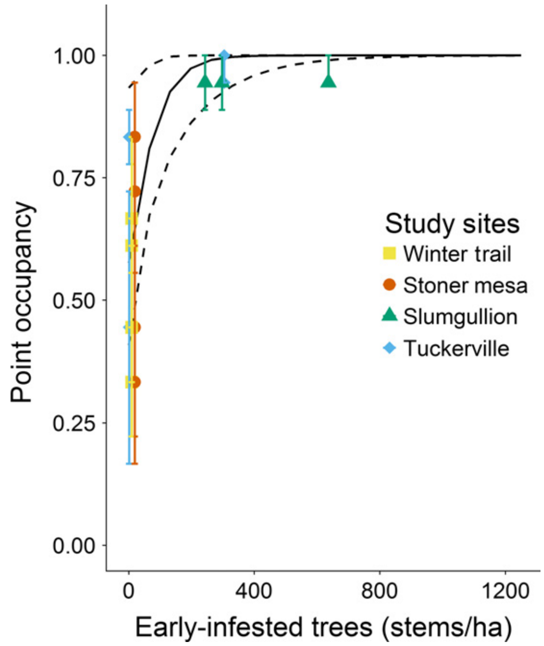

Figure 3. American Three-toed Woodpecker occupancy in relation to the density (stems/ha) of early-infested spruce trees (Green or Yellow status). The solid and dashed lines are median and 95% BCIs respectively for predicted occupancy probabilities. Points and error bars are finite sample estimates (median and 95% confidence limits) for individual sites ($n = 18$ points) in each year surveyed plotted at their mean early-infested tree density values.

Table 5. Parameter estimates (median with 90% and 95% BCIs) for occupancy of Three-toed Woodpeckers.

	Estimates by percentile				
Parameter	2.5th	5th	50th	95th	97.5th
β_0	0.44	0.69	2.47	5.32	6.06
β_1	−0.9	−0.68	0.65	2.71	4.52
β_{Einf}	1.5	1.81	4.28	8.96	10.12
β_{Minf}	−0.77	−0.65	−0.1	0.46	0.58
β_{sng}	−0.36	−0.3	0.01	0.37	0.47
β_{QMD}	−0.03	0.03	0.37	0.82	0.93

Covariates were early infestation (Einf), mid infestation (Minf), late infestation or snag (sng), and quadratic mean diameter (QMD; for descriptions, see Table 3).

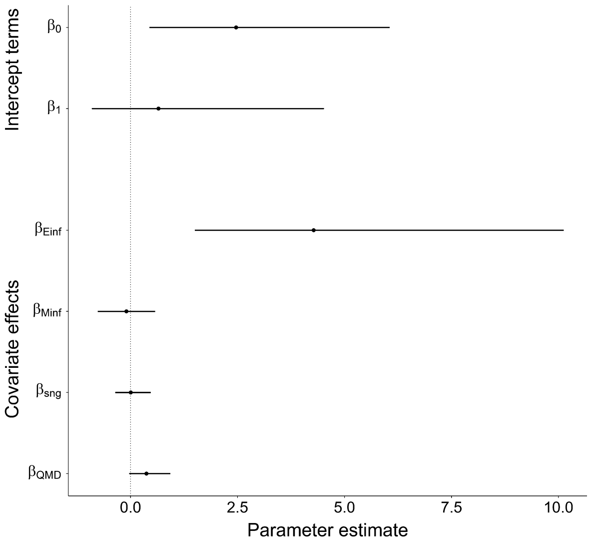

Figure 4. Parameter estimates (median) and 95% BCIs for occupancy of American Three-toed Woodpecker. The quantities β_0 and $\beta_0 + \beta_1$ are the logit-linear probabilities of occupancy at average covariate values for previously unoccupied and occupied points, respectively. Covariate effects quantify the estimated logit-linear effect of covariates scaled to mean = 0 and sd = 1. Covariates are β_{Einf} (total number of trees with active Spruce Beetle infestation and classified as Green and Yellow within plot), β_{Minf} (total number of trees killed by Spruce Beetles for > 2–3 years with a status classified as Needle Drop and Twig within plot), β_{sng} (total number of standing dead trees classified as Branch or Snag and ≥ 23 cm diameter at breast height and includes trees killed by any mortality agent > 10 years ago), and β_{QMD} (quadratic mean diameter (squared diameter at breast height) of all spruce in plot regardless of status).

(10.3 ± 7.9 cm ($n = 189$)) unaffected by insects in our study area. We found no support for relationships with the number of trees in the middle or late stages of infestation (Fig. 4, Table 5).

DISCUSSION

Early-stage infestation was the best predictor of Three-toed Woodpecker occupancy compared with later stages or tree diameter. This relationship plausibly reflects Three-toed Woodpecker dependence on larval stages of Spruce Beetles for foraging because the pulse in this resource coincides with early infestation. Similar to the reliance of Black-backed Woodpeckers on post-fire habitat and wood-boring beetles (Hutto 1995, Dixon & Saab 2000), Three-toed Woodpeckers are strongly related to bark beetle outbreaks (Bock & Bock 1974, Murphy & Lehnhausen 1998). As infestations progress to later stages, beetles become less abundant and Three-toed Woodpeckers presumably disperse to more recently infested forest stands (Siegel *et al.* 2015).

Snag density and diameter enhance nesting and foraging substrate for most woodpeckers (e.g. Bütler *et al.* 2004, Saab *et al.* 2009), but in our study we did not find a positive relation between Three-toed Woodpecker occupancy and snag density. Trees at later stages of infestation or killed by other causes appear to influence Three-toed Woodpecker distributions much less compared with recently infested trees, when densities of beetle larvae are highest (Weslien & Schroeder 1999). Our results further suggest the importance of early-infested trees as a critical foraging resource that attracts colonization by Three-toed Woodpeckers.

Many other vertebrate species, including small mammals and secondary cavity-nesting birds, rely on cavities initially excavated by woodpeckers (Martin & Eadie 1999, Burdett & Niemi 2002). Three-toed Woodpeckers were the most commonly observed excavator in outbreak as well as live, non-infested forest conditions in our study area (J. Kelly unpubl. data). Additionally, Three-toed Woodpeckers are strong excavators and excavate new cavities virtually every year (Martin *et al.* 2004, Rodewald 2015). Consequently, they may be particularly important for producing cavities upon which other species rely. In our study area, wrens *Troglodytes* spp., swallows *Tachycineta* spp., bluebirds *Sialia* spp. and some owls (e.g. *Glaucidium* spp.) are secondary cavity nesters (Scott *et al.* 1980, Martin & Eadie 1999). These secondary cavity nesters are likely to respond positively to a pulse in cavity resources when Three-toed Woodpeckers are abundant, so protection of Three-toed

Woodpecker habitat (i.e. beetle-infested trees) will promote production of valuable resources (i.e. nesting substrate) for other avian species. Post-beetle salvage harvesting may put Three-toed Woodpecker habitat at risk, in addition to eliminating potential nesting resources for secondary cavity nesters.

Our study focused on occupancy relationships to identify key habitat relationships for Three-toed Woodpecker conservation. Occupancy relationships could reflect space use patterns within home-ranges, the distribution of home-ranges (i.e. local abundance) or both. Further study could reveal particular mechanisms and scales of population responses suggested here. In addition to early-infestation stages, the diameter of infested spruce trees could be an important habitat attribute for Three-toed Woodpecker foraging use. Spruce trees of dbh > 23 cm are more likely to be infested and can support a larger volume of Spruce Beetles compared with smaller diameter trees (Massey & Wygant 1954, Schmid & Frye 1977, Hart *et al.* 2014b). The average diameter of early-infested spruce trees was larger than the diameter of remaining spruce in our study area. This suggests that large spruce provide suitable habitat for Spruce Beetles and thereby fundamental foraging substrate for Three-toed Woodpeckers. We commonly detected more than one individual at occupied points, indicating variation in local abundance not necessarily reflected by occupancy. A focused analysis of abundance could therefore provide more information for identifying additionally important habitat features (e.g. tree size). With our data, however, such analysis would ostensibly require more complex modelling to account for spatial dependencies among neighbouring points and probably would not change our conclusions regarding the importance of early-infested trees to this species.

Broader implications and future directions

Dependence on Spruce Beetles may help explain the Three-toed Woodpecker distribution at broader scales and range limits. For example, Three-toed Woodpeckers may be absent from the Sierra Nevada Mountains because spruce is not a dominant species in these forests (Bock & Bock 1974). Numerical responses of Three-toed Woodpeckers to Mountain Pine Beetle *Dendroctonous ponderosae* epidemics are also reported in south-central British Columbia (Drever *et al.* 2009, Edworthy *et al.* 2011, Saab *et al.* 2014). Compared with Spruce Beetle outbreaks, however, the value of resource pulses generated by Mountain Pine Beetle might be less important in the southern Rockies (Leatherman 2012). Additional data from different forest types across the Rocky Mountain region could aid our understanding of the relative value of different bark beetle species to Three-toed Woodpeckers.

Future research is needed to identify habitat requirements for successful reproduction (Fayt *et al.* 2005). Other woodpecker species (*Leuconotopicus* and *Picoides* spp.) experience higher nesting success in recently disturbed forests than in relatively undisturbed forests, suggesting that disturbed forests function as a source habitat (e.g. Saab *et al.* 2005, Wightman *et al.* 2010, Rota *et al.* 2014). White-headed Woodpeckers *Leuconotopicus albolarvatus* select nesting sites with large, decayed snags (Wightman *et al.* 2010) and Hairy and Black-backed Woodpeckers have higher nesting densities in burned, unlogged forests (Saab *et al.* 2007). Nest-site selection and nest survival studies could similarly identify additional habitat features of interest for the conservation of Three-toed Woodpeckers.

With climate warming, the frequency and the size of beetle outbreaks are expected to increase (Bentz *et al.* 2010, Hart *et al.* 2014a, Temperli *et al.* 2015). We argue that the life cycle of Spruce Beetles influences the timing and duration of Three-toed Woodpecker use of beetle-infested forests. A 2-year life cycle is generally common during endemic and outbreak infestations (Knight 1961). Higher temperatures, however, can influence Spruce Beetle population size through a combination of halving the maturation rate from 2 to 1 year, increased overwinter survival, and regional drought-induced stress of mature host trees (Berg *et al.* 2006, Hart *et al.* 2014a). These climate drivers will promote more Spruce Beetle outbreaks and benefit Three-toed Woodpeckers. Widespread tree mortality, however, increases opportunities for post-beetle salvage logging. Forest management efforts aimed at reducing risks of beetle infestation are potentially in conflict with Three-toed Woodpecker habitat conservation. Moreover, post-beetle salvage logging could reduce availability of beetle resources for Three-toed Woodpecker populations and also reduce potential nest-sites for secondary cavity nesters. Retention of early-infested spruce trees and a 3-year delay in tree harvest following infestation could allow managers to meet the habitat needs of the Three-toed Woodpecker and other cavity-nesting species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. BUGS model code used to fit American Three-toed Woodpecker occupancy model using JAGS.

Table S1. Clean detection data.

Table S2. Clean plot data.

Table S3. Clean tree data.