

## Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles

Amanda B. Edworthy<sup>a</sup>, Mark C. Drever<sup>a,\*</sup>, Kathy Martin<sup>a,b</sup>

<sup>a</sup> Centre for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, Canada, V6T 1Z4

<sup>b</sup> Environment Canada, Pacific Wildlife Research Centre, 5421 Robertson Rd, RR1, Delta, British Columbia, Canada, V4K 3N2

### ARTICLE INFO

#### Article history:

Received 2 May 2010

Received in revised form 5 October 2010

Accepted 7 October 2010

#### Keywords:

Population regulation

Woodpeckers

Resource pulse

Insect outbreak

*Dendroctonus ponderosae*

Fecundity

Mountain pine beetle

Lodgepole pine

### ABSTRACT

Many temperate woodpecker species are thought to be highly conservative in their fecundity with little response to fluctuations in availability of resources. In a 15-year field study in interior British Columbia, we evaluated responses in abundance and fecundity of six species of resident and migrant woodpeckers (downy woodpecker [*Picoides pubescens*], hairy woodpecker [*Picoides villosus*], American three-toed woodpecker [*Picoides dorsalis*], pileated woodpecker [*Drycopus pileatus*], northern flicker [*Colaptes auratus*], and red-naped sapsucker [*Sphyrapicus nuchalis*]) to a large-scale outbreak of mountain pine bark beetles that resulted in a strong positive pulse in food supply. Population densities of woodpecker species increased during outbreak years. Despite the year-round multi-annual increase in food resources, and in contrast to the strong increases in fecundity shown by nuthatches and chickadees, annual fecundity (as indicated by clutch size and number of nestlings that fledged) did not change for any woodpecker species over the study. Similarly, we found no changes in fecundity in response to selective forest harvesting despite numerical increases for woodpeckers at these sites. Our study confirms that these woodpecker species are conservative in their reproductive investment patterns even during strong multi-annual increases in food. Our findings indicate woodpecker populations are regulated numerically through variable survival and/or greater immigration rates, which can result in higher breeding densities temporarily during resource pulses.

© 2010 Elsevier B.V. All rights reserved.

### 1. Introduction

Resource pulses in natural systems provide excellent opportunities to examine processes and mechanisms involved in individual- and population-level responses to resource fluctuations (Yang et al., 2008). During a resource pulse, consumers capitalize on unusually abundant and ephemeral resources, such as food or nest sites, leading to increased population abundance, followed by a sharp decline when the resource is depleted (Ostfeld and Keesing, 2000). Numerical population responses may be caused by immigration of adults and juveniles, increased reproductive effort to increase offspring production and survival, or a combination of immigration and reproductive effort (Yang et al., 2008). Ostfeld and Keesing (2000) suggested two patterns that might emerge in response to a resource pulse: some species will respond by increasing reproductive output, while other species will respond by tracking the food source and immigrating to resource rich areas. Experimentally increasing food supply in bird populations produces variable fecundity responses (Arcese and Smith, 1988). Some species significantly

increase their fecundity in response to increasing food supply (Both, 1998; Norris and Martin, 2008). Other species do not exhibit a functional (reproductive) response, but instead their populations are regulated numerically through emigration or survival (Greenwood and Baillie, 1991). Further, differences in functional response may be explained by seasonal variability in food resources. Birds that use highly seasonal resources tend to invest heavily in reproductive effort during the breeding season when food is abundant (Wiebe et al., 2006). In contrast, species that have access to a consistent year-round food source should have high juvenile and adult winter survival. High winter survival results in strong competition during the breeding season, and subsequently lower allocation to reproduction (Ashmole, 1963).

In this study, we take advantage of a large-scale outbreak of bark beetles, mountain pine beetle (*Dendroctonus ponderosae*), in British Columbia to test fundamental questions about population regulation in birds. We examine functional and numerical responses of six woodpecker species—downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), pileated woodpecker (*Drycopus pileatus*), northern flicker (*Colaptes auratus*), and red-naped sapsucker (*Sphyrapicus nuchalis*). The study period, 1995–2009, encompassed the period of endemic levels before the beginning of outbreak con-

\* Corresponding author. Tel.: +1 604 827 5843.

E-mail address: [mdrever@interchange.ubc.ca](mailto:mdrever@interchange.ubc.ca) (M.C. Drever).

ditions in 2003 to the peak in fresh beetle attack in 2004 (Drever and Martin, 2010). This outbreak was the largest mountain pine bark beetle outbreak ever recorded for North America, infecting 9.2 million ha of forest (Aukema et al., 2006; BCMFR, 2007). Bark beetles provide an excellent food source for many woodpeckers: adult beetles are eaten in the summer, and beetle larvae are largest in late winter and early spring, thus providing a year-round food source for excavators (Martin et al., 2006). At our sites, woodpeckers and other bark insectivores showed significant numerical increases that tracked the beetle outbreak (Drever et al., 2009; Norris and Martin, 2008), as has been reported for other woodpecker populations during insect outbreaks (Hutto, 1995; Kreisel and Stein, 1999; Yeager, 1955). For example, Koplín (1969) observed a fifty-fold increase in woodpecker (downy, hairy, and American three-toed) populations in response to an increase in bark beetle populations in a 4-ha patch of forest killed by fire in Colorado. In addition to the initial food pulse created by the presence of live mountain pine beetle, secondary infestations of other bark insects (Paine et al., 1997) and wood-boring beetles (Buprestidae and Cerambycidae) often occur in forest recently killed by beetles (Amman and Ryan, 1991; Murphy and Lehnhausen, 1998), which can also serve as prey for woodpeckers for 2–5 years following the outbreak.

Limited nest-site availability and seasonality of food supply are both thought to contribute to conservative clutch sizes in woodpeckers (Martin and Li, 1992; Wiebe et al., 2006). In mature forests, woodpeckers do not appear to be limited by nest sites (Aitken and Martin, 2004). Ricklefs (1980) and Koenig (1984) tested the role of seasonality of food supply in woodpecker fecundity by comparing geographic variation in the seasonality of resources with variation in clutch size, and found that low disparity between summer and winter resource availability was associated with smaller clutch sizes. Low disparity between summer and winter food supply resulted in high winter survival of birds and hence less food per breeding pair in the summer, whereas relatively low winter food supply resulted in higher winter mortality and more food per breeding pair during the summer (Ricklefs, 1980; Koenig, 1984). Because other factors besides stability of resources may vary with geographical location, an examination of the temporal variability of conditions within sites rather than spatial responses of woodpecker fecundity to seasonal changes in food availability makes a useful complement to tests of limitation in woodpecker fecundity based on spatial differences.

We hypothesize that woodpeckers, due to their aseasonal food supply, are regulated numerically and therefore will track the outbreak with changes in density, and not changes in annual fecundity. Because strong excavators can access wood-boring insects during the winter, their food supply levels may be relatively consistent, despite changing food sources from summer to winter (Wiebe et al., 2006). Of the six woodpecker species detected in significant numbers at our sites, four were residents (downy, hairy, American three-toed, and pileated woodpeckers) and two were migrants (northern flicker and red-naped sapsucker). This contrast in resident status can help illuminate the importance of winter food supply, or seasonality of resources, in woodpecker population regulation. Adult mortality is tied to winter food supply in many bird species and may determine summer population density; thus winter food supply affects food per breeding pair available for investment into larger clutches (Ricklefs, 2000). An increase in the fecundity of migrant woodpecker species but not residents following high bark beetle populations would suggest that fecundity is related to seasonality of food resources and is not entirely dependent on summer food supply. Because residents live in the beetle outbreak region for the whole year, residents may show a stronger response to the outbreak than migrants. In our case, migrants may show a further dampened response because they are opportunistic species that do not eat the quantity of bark beetles that resident

species eat, whereas resident woodpeckers are bark insect specialists that can benefit strongly from the mountain pine bark beetle outbreak. Northern flickers are primarily ground foragers (Wiebe and Moore, 2008) and red-naped sapsuckers are omnivores, feeding on tree sap, aspen buds, and bark insects (Walters et al., 2002). Nonetheless, the comparison of resident to migrant species remains informative because if both types of woodpeckers have the same response to the resource pulse, a focus on winter food supply may be misplaced. Here, we examine variation in densities and two fecundity variables (clutch size, fledglings/nest) for six woodpecker species over a 15-year period at 20 study sites to evaluate functional and numerical responses to the food pulse provided by the beetle outbreak.

## 2. Methods

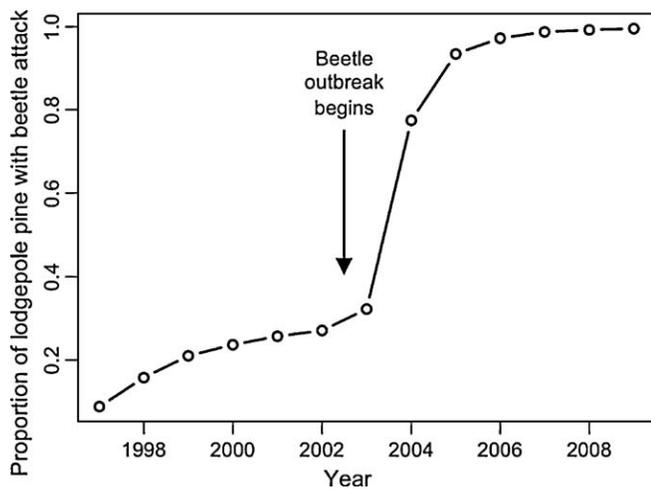
### 2.1. Study sites

Fieldwork was conducted between 1995 and 2009 at 20 study sites (range = 7–32 ha, mean = 17 ha, total area = 318.5 ha) in the Cariboo-Chilcotin region of British Columbia, within 50 km of the City of Williams Lake (Williams Lake location: 52° 08'30"N, 122° 08'30"W). Our sites were originally selected to represent a wide range of habitat types and forest harvest treatments. Because many of our sites were forestry blocks or small forest groves, their sizes and shapes varied. Sites were all mature forest stands (80–100 years old) at the beginning of the study. Forest stands varied from deciduous, predominantly quaking aspen (*Populus tremuloides*) stands, surrounded by grassland and shallow ponds, to coniferous stands typical of the Interior Douglas-fir zone (Meidinger and Pojar, 1991), dominated by a mix of lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii*). Across the 20 study sites, lodgepole pine was the most abundant tree species (41% of stem counts), followed by Douglas fir (28%) and quaking aspen (16%), and hybrid white spruce (*Picea engelmannii* × *glauca*; 15%), with remainder being birch (*Betula* spp.), alder (*Betulaceae* spp.), willow (*Salix* spp.), and juniper (*Juniperus* spp.). In addition to being the most abundant species, pine was present in all of our study plots and within sites occurred in 79% of the established vegetation sampling plots located around our 340 point count stations.

From 1995, we monitored tree health and signs of beetle attack in established vegetation sampling plots spaced evenly across all habitat types at our sites. Mountain pine beetle detections were first observed in 1999, increased over the study period until 2002, then increased strongly to a peak in densities of pines attacked by beetles in 2004 (Drever et al., 2009). By 2007, almost all mature lodgepole pine trees at our sites were dead (99%; Fig. 1). Most sites were uncut mature forest, and 8 were clear-cut with reserves, which involved removal of 50–90% of trees greater than 12.5 cm diameter at breast height, including all pine and/or hybrid white spruce, with retention of most quaking aspen and veteran Douglas-fir, between 1997 and 2002, coincidental with the beetle invasion. To obtain a large sample size of nests, we pooled cut and uncut sites, and thus we also examined the potential effects of harvest treatments on fecundity measures (see Section 3). Additional study area details are given in Martin and Eadie (1999), Aitken et al. (2002), and Martin et al. (2004).

### 2.2. Vegetation monitoring

To assess forest health we surveyed trees (diameter at breast height ≤ 12.5 cm) annually in 11.2 m radius plots laid out 100 m apart with 7–32 vegetation sampling plots at each site. At continuous forest and cut sites, plots were laid out in a 100 m grid pattern throughout the site such that all habitat sites were surveyed pro-



**Fig. 1.** Annual proportion of lodgepole pine trees (>12.5 cm dbh) surveyed that showed signs of attack by mountain pine beetle at 20 sites in interior British Columbia, 1997–2009. The beginning of the mountain pine beetle outbreak in 2003 is indicated with an arrow (Drever et al., 2009).

portionally. At forest-grassland complex sites where we could not use a grid design, plots were spaced 100 m apart for a survey effort of ~1 point count station/ha of forest across the entire site. Beetle attack was detected by searching for insect bore holes in the tree bark, and examining trees for changes in foliage colour. Additional vegetation monitoring details are given in Drever et al. (2009).

### 2.3. Population monitoring

To survey woodpecker populations, we counted birds during May and June of each year, from 1997 to 2009, using a combination of point counts (Hutto et al., 1986) and playbacks (Johnson et al., 1981). Point count stations were laid out in the same grid pattern as the vegetation plots: 100 m apart with 7–32 stations at each site (~1 point count station/ha). From 0500 to 0930 h, point counts were conducted at each station, and all birds seen or heard within a 50-m radius of the station for 6-min counts were recorded. During the same surveys, we also used 8-min playbacks of woodpecker calls and drums (calls of all woodpecker species were played twice, each followed by 30 s of listening time) at every second point count station (200 m intervals) following the initial 6-min count. Additional woodpeckers that responded to the playbacks were added to the count. We avoided counting individuals twice by recording the distance and direction of all individuals detected external to our point count circle. Given that woodpeckers have relatively large home range sizes, and on occasion, individuals may have been counted more than once, we used the point count data to assess relative rather than absolute abundance. We surveyed each of 340 stations twice yearly (one playback and one non playback count) for a total of 20 min of survey time per station per year across 20 sites.

### 2.4. Nest location and monitoring

We spent an average of 6–7 h/week searching for nests at each site. Nest finding was facilitated by observations made during point counts/playbacks. Between 1995 and 2004, nest cavities up to 5.2 m high were inspected with a mirror and flashlight after climbing to the cavities with ladders. From 2005, we also used video cameras on extendable poles (Sandpiper Technologies, Manteca, CA), allowing us to check cavities up to 15 m. Nest holes higher than 15 m were also checked by tapping or scratching on the tree to determine the presence of active nests, based on whether an individual looked out of the cavity or flushed, although this method is not as reliable as

visual inspections of cavity interiors. A nest was considered active if  $\geq 1$  egg or nestling was present, if adults were observed feeding nestlings, or if adults were observed entering the cavity with nest material or food on at least two occasions on different days. Nests were monitored every 4–7 days to determine whether nest cavities contained eggs or nestlings. Clutches were considered complete when no further eggs were laid and the same number of eggs was observed during two or more consecutive nest checks. Number of chicks fledged was determined within the last 5 days of the nestling period. Given that some cavities are of an irregular shape and it can be difficult to get a complete count of the nest contents, the counts of eggs and nestlings should be considered minimum estimates. To check for re-nesting attempts, all cavities on all sites, including those cavities used for nesting earlier in the season, were surveyed throughout the breeding season. See Aitken and Martin (2004) for full details.

### 2.5. Data analysis

To estimate the proportion of lodgepole pine trees attacked by mountain pine beetle, we calculated the annual total number of pines with signs of beetle attack and divided this number by the annual total number of pines surveyed.

For each woodpecker species, we calculated the annual mean relative abundance by averaging the number of detections per point count station across all sites in each year. The number of nests found at all sites was totalled annually for each species. We assumed high nest detectability for all species. We calculated mean clutch size and mean number of fledglings per nest as measures of fecundity, with nests pooled into two time periods: before the beetle outbreak (1995–2002) and during the outbreak (2003–2009). We included nests from 1995 and 1996 in the fecundity analysis, but excluded them from the nest count as there was less searching effort in the first 2 years of the study.

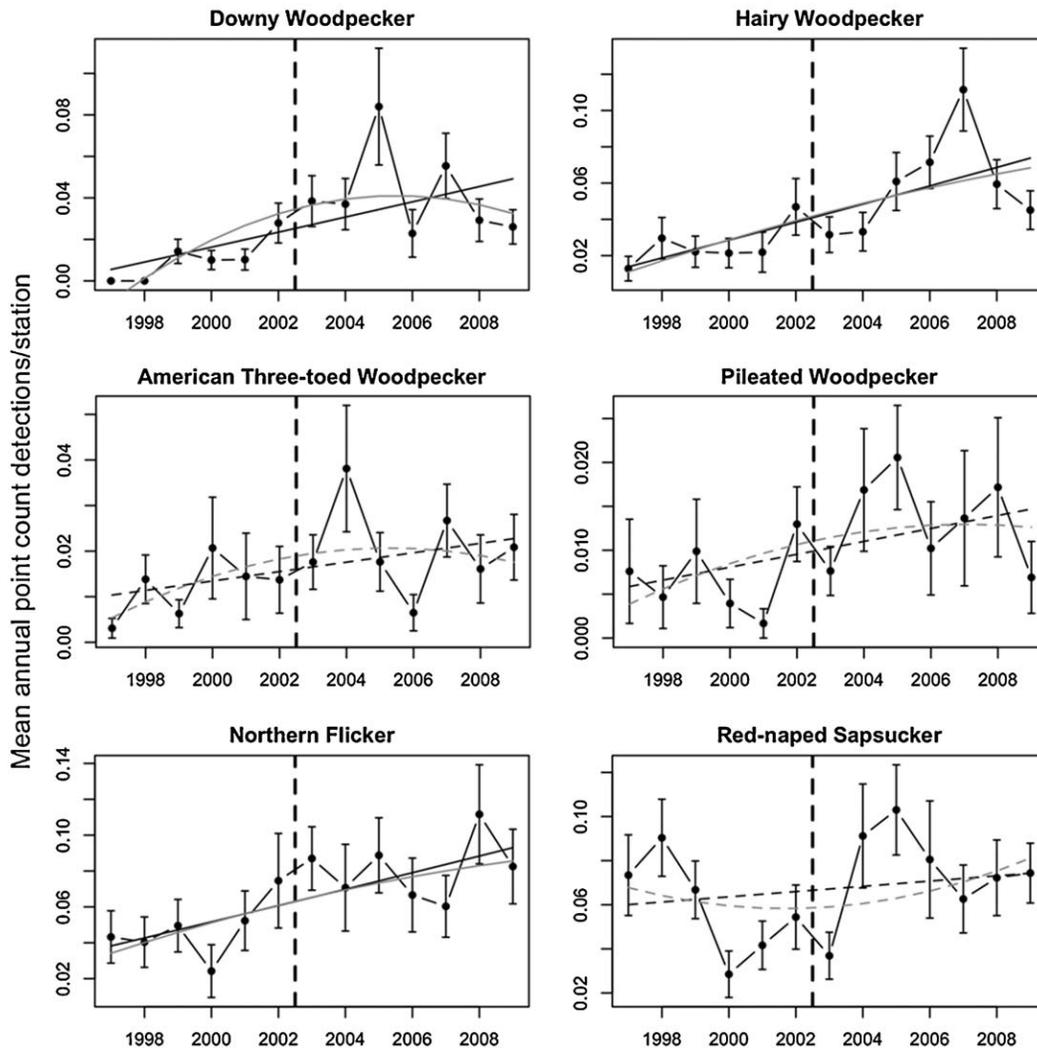
We estimated a temporal trend in abundance using linear regressions, where log-transformed relative abundance (number of detections per point count station+1) was set as the dependent variable, and year as the independent variable that was able to represent the progression of the mountain pine bark beetle epidemic and secondary beetle infestations. We also considered quadratic responses in changes in relative abundance over time, and these quadratic models produced the same qualitative results as linear models (see Section 3), so we focus on results from simpler linear regression analyses.

We used general linear models to test for differences in fecundity measures before the beetle outbreak and during outbreak conditions, with fecundity measure as the dependent variable and outbreak period ('pre-outbreak' and 'outbreak') as the independent variable. For each model, we assessed statistical assumptions of non-heteroscedasticity and normality of residuals, and found no departures from these assumptions. Data were analyzed using the statistical software R 2.9.2 (R Development Core Team, 2010).

## 3. Results

### 3.1. Mountain pine beetle attack

We surveyed a total of 15,752 tree-year measurements (8911 trees) for beetle attack at 20 sites from 1997 to 2009. The proportion of pine with signs of beetle attack increased gradually from 1997 to 2002 (Fig. 1). Then the rate of increase in proportion of beetle-attacked pine increased steeply in 2003, peaked in 2004, and by 2006, almost all of the pine trees at our sites had been attacked by beetles.



**Fig. 2.** Mean number ( $\pm$ SE) of woodpecker detections per station for six woodpecker species during two rounds of point counts/playbacks at 20 sites in interior British Columbia, 1997–2009. An outbreak of mountain pine bark beetles increased slowly until 2002, and rose steeply to peak outbreak conditions in 2003 and 2004. The vertical dashed line indicates the beginning of outbreak conditions. Simple linear regression lines are shown in solid black for species with significant trends ( $\alpha < 0.05$ ) and in dashed black for non-significant trends. Quadratic trends are shown in grey lines. Scales are variable for the vertical axes and indicate different densities for the species.

**Table 1**

Temporal trends in relative abundance (mean number of detections per point count station) of six woodpeckers in interior British Columbia, Canada, 1997–2009.

	Intercept	Slope	t (slope)	P (slope)	R <sup>2</sup>
Downy woodpecker	-7.07	0.0035	2.59	<b>0.025</b>	0.32
Hairy woodpecker	-9.54	0.0048	3.54	<b>0.005</b>	0.49
American three-toed woodpecker	-2.02	0.0010	1.62	0.133	0.12
Pileated woodpecker	-1.45	0.0007	1.94	0.080	0.19
Northern flicker	-8.52	0.0043	3.73	<b>0.003</b>	0.52
Red-naped sapsucker	-2.16	0.0011	0.70	0.497	0.04

Significant P values are bolded. N = 13 years.

**Table 2**

The number of woodpecker nests found annually at 20 sites in interior British Columbia over 13 years increased with the progression of the mountain pine bark beetle epidemic that reached outbreak conditions in 2003 and peaked in 2004 (Drever and Martin, 2010; Norris and Martin, 2010).

Species	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
Downy woodpecker	0	1	4	5	5	4	4	8	10	8	17	14	11	91
Hairy woodpecker	1	1	2	4	3	5	1	7	9	12	11	6	6	68
American three-toed woodpecker	0	1	3	2	2	3	7	8	7	9	10	5	4	61
Pileated woodpecker	0	3	2	2	2	3	1	2	3	2	4	3	2	29
Northern flicker	11	15	15	16	23	22	26	30	27	32	27	33	40	317
Red-naped sapsucker	10	19	18	10	10	14	18	27	30	32	32	34	30	284
Annual total	22	40	44	39	45	51	57	82	86	95	101	95	93	850

**Table 3**

Fecundity variables (mean per nest) for six woodpeckers across 12 uncut and 8 cut sites in interior British Columbia, Canada, 1997–2009. Critical values (*F*) and *P* values are the results of a linear model comparing fecundity measures from nests at uncut and cut sites.

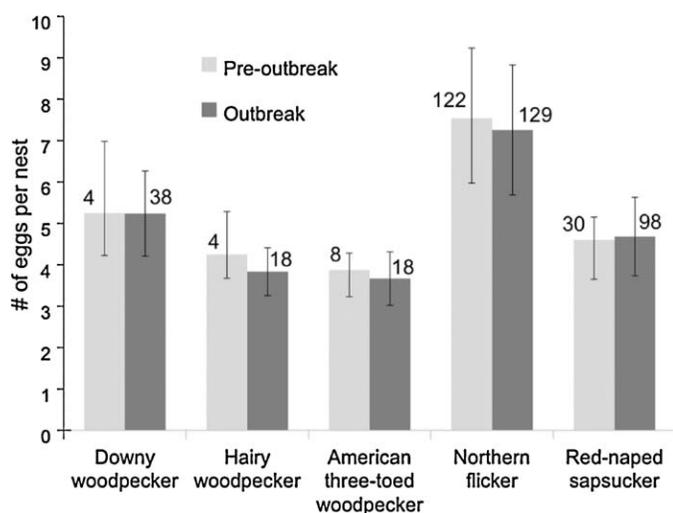
	Mean ( $\pm$ SE)		<i>F</i> ( <i>P</i> )
	<i>N</i>		
	Uncut	Cut	
<b>Clutch size</b>			
Downy woodpecker	5.81 $\pm$ 0.18 23	5.43 $\pm$ 0.18 26	2.150 (0.150)
Hairy woodpecker	4.00 $\pm$ 0.26 4	4.08 $\pm$ 0.17 28	0.075 (0.788)
American three-toed woodpecker	3.49 $\pm$ 3.94 14	3.60 $\pm$ 0.20 14	1.802 (0.192)
Pileated woodpecker	4.33 $\pm$ 0.54 4	4.00 $\pm$ 0.67 6	0.150 (0.724)
Northern flicker	7.56 $\pm$ 0.12 154	7.47 $\pm$ 0.24 37	0.125 (0.724)
Red-naped sapsucker	4.59 $\pm$ 0.10 78	4.88 $\pm$ 0.11 88	3.717 (0.056)
<b>Number of fledglings</b>			
Downy woodpecker	4.17 $\pm$ 0.21 21	4.15 $\pm$ 0.20 21	0.005 (0.945)
Hairy woodpecker	3.00 $\pm$ 0.46 5	3.14 $\pm$ 0.17 12	0.084 (0.774)
American three-toed woodpecker	2.86 $\pm$ 0.24 16	2.43 $\pm$ 0.24 10	1.581 (0.220)
Pileated woodpecker	2.50 $\pm$ 0.18 3	3.00 $\pm$ 0.14 2	4.800 (0.060)
Northern flicker	5.70 $\pm$ 0.14 185	5.70 $\pm$ 0.28 47	0.000 (0.996)
Red-naped sapsucker	3.54 $\pm$ 0.10 76	3.60 $\pm$ 0.10 72	2.830 (0.658)

### 3.2. Population abundance

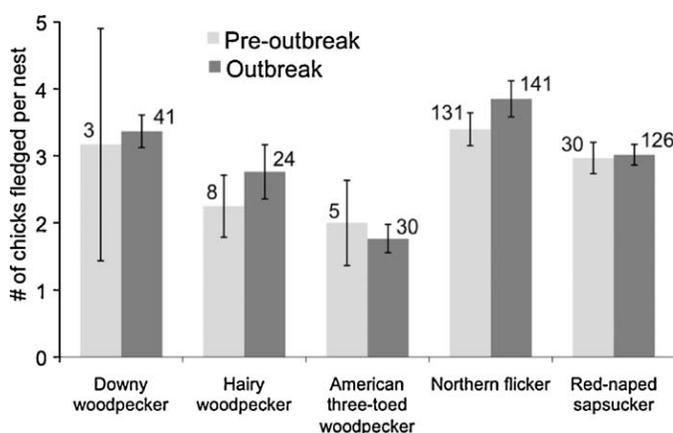
A total of 8719 point counts at 340 stations was conducted at 20 sites surveyed from 1997 to 2009, from which woodpecker relative abundance (total number of detections per point count) was calculated for 13 years. The most frequently detected species were red-naped sapsucker, northern flicker, hairy and downy woodpeckers, while American three-toed and pileated woodpeckers were less common (Fig. 2). Black-backed woodpeckers (*Picoides arcticus*) were also detected, but were rare and were not included in this analysis. We found strong and significant positive numerical increases for downy woodpeckers, hairy woodpeckers,

and northern flickers (Table 1). Although abundances of pileated woodpeckers, American three-toed woodpeckers, and red-naped sapsuckers also had positive trends over time (Fig. 2), these trends were not significant. All six woodpeckers showed patterns of abundance consistent with linear increases (Fig. 2). We also report the results of our quadratic analysis of woodpecker abundance across time (Fig. 2), which produced the same qualitative results as the linear analysis.

We found a total of 850 nests at 20 sites during the study, 1997–2009 (Table 2). Number of nests increased gradually from 1997 to 2007, with a relatively large increase in 2004, and then declined in 2008 and 2009. During pre-outbreak conditions, 1997–2002, we found between 22 and 51 nests annually. Nest den-



**Fig. 3.** Average clutch sizes ( $\pm$ SD) for five woodpecker species before an outbreak of mountain pine beetles (1995–2002) and during the outbreak (2003–2009) at 20 sites in interior British Columbia. Sample sizes are shown above each bar. None of the differences between pre-outbreak and outbreak conditions for species were significant, showing a lack of positive response to mountain pine beetle infestation.



**Fig. 4.** Average number of chicks fledged/nest ( $\pm$ SD) for five woodpecker species before an outbreak of mountain pine beetles (1995–2002) and during the outbreak (2003–2009) at 20 sites in interior British Columbia. Sample sizes are shown above each bar. None of the differences between pre-outbreak and outbreak conditions for species were significant, showing a lack of positive response to mountain pine beetle infestation. There were insufficient data to analyze differences in downy woodpecker fledglings/nest.

sity increased from 57 nests in 2003 to over 80 nests in 2004 and 2005 coincident with sharply increasing detections of bark beetles (Table 3). The number of nests increased to higher levels from 2005 to 2009 with numbers between 93 and 101 from 2006 to 2009 (Table 2). American three-toed woodpeckers and red-naped sapsuckers were important contributors to the increase in nest abundance, despite their non-significant trends in point count detections.

### 3.3. Fecundity

We obtained data on clutch size from 479 nests and number of chicks fledged per nest from 539 nests. Pileated woodpeckers were excluded from the fecundity analysis because of low sample sizes. We detected no functional response to the mountain pine beetle outbreak for any of the six woodpecker species. Analysis of variance tests of both fecundity variables (clutch size and mean number of fledglings/nest) comparing pre-outbreak and outbreak periods failed to detect a difference in mean fecundity for any of the five species examined (Figs. 3 and 4).

Earlier, we documented that woodpecker richness and abundance either increased or did not change in response to forest harvest treatments at our sites (Drever et al., 2008; Drever and Martin, 2010). Because both timber harvest and the beetle outbreak had positive effects on woodpecker densities, we examined whether there was an influence of harvesting on woodpecker fecundity. Similar to responses to the beetle outbreak, we found no significant differences in mean clutch size or number of chicks fledged per nest between cut and uncut sites (Table 3).

## 4. Discussion

The large-scale outbreak of mountain pine beetles in interior British Columbia was a food pulse for many woodpeckers at our sites, providing us with the opportunity to investigate mechanisms of population regulation in woodpeckers in a temporal sense, thus controlling for differences that might be due to geographic or ecosystem variation. Of the two responses to resource pulses suggested by Ostfeld and Keesing (2000), our results indicated that woodpeckers regulate numerically rather than reproductively during a resource pulse. The changes in woodpecker abundance may result from improved survival of both adults and juveniles, or immigration of adults to our sites, or a combination of both. Woodpeckers are generalist predators and the strong numerical responses of woodpeckers we observed to the beetle outbreak are consistent with results from other studies that found woodpecker densities increased during insect outbreaks (Bonnot et al., 2008; Koplín, 1969; Saab et al., 2007; Yeager, 1955). Some woodpecker species, including black-backed and Lewis' woodpeckers (*Melanerpes lewis*), rely on and congregate at recently burned patches of forest (Bonnot et al., 2008; Saab et al., 2007). This pattern suggests that woodpeckers are able to adapt to changes in the geographical distribution of food by dispersing widely to areas of high food availability. It also provides evidence that food supply affects population density and may be a limiting factor. While fire creates a dual resource pulse of insects and nest sites in snags for burn-specialist woodpeckers, the mountain pine beetle outbreak did not affect the quaking aspen trees that predominantly were used as nest sites by the six woodpecker species at our sites (90%; Aitken and Martin, 2004).

Several of our sites were harvested during the study, but harvested sites can have elevated insect abundances after cutting, and thus an increased food supply for woodpeckers (Conner and Crawford, 1974). Earlier, we documented that woodpecker richness and abundance either increased or did not respond to forest har-

vest treatments at our sites (Drever et al., 2008; Drever and Martin, 2010). Abundances of all woodpeckers were higher at sites that were clear-cut with reserves than at uncut sites, with statistically significant differences for all species except red-naped sapsucker. Forest cutting therefore likely contributed to the increase in food supply and thus added to our test of woodpecker response to a food pulse. Thus, we cannot entirely separate the effects of timber harvest from the beetle outbreak, but because both were effects with year-round consequences and both had positive effects on woodpecker densities, this study remains a viable test of woodpecker responses to a food pulse. Other factors, including climate warming (Dawson et al., 2008), may have also affected the population trends of woodpeckers, for example, due to milder winter temperatures affecting overwinter survival. Thus, not all of the numerical responses we observed may have been related to food supply.

The lack of change in clutch sizes and fledging success throughout the food pulse created by the mountain pine bark beetle confirmed that many woodpeckers are indeed conservative in their annual reproduction (Winkler et al., 1995). There was no evidence of re-nesting in any of the six species throughout the study, except after failure in the early stages of a first nest. Because of their generalist foraging habits and ability to extract beetle larvae in the sapwood of trees, many woodpeckers have access to a comparatively stable food (Wiebe et al., 2006). In contrast, during the winter, weaker excavators and non-excavators must broaden their foraging habits (Conner, 1981) or migrate, both of which may result in higher winter mortality and to compensate, those species have evolved higher or more flexible clutch sizes (Martin and Li, 1992; Ricklefs, 2000; Wiebe, 2006). Thus, seasonal stability of woodpecker food supply appears to be an important factor influencing their reproductive response to annual variation in prey abundance. However, this conservative reproductive trend need not be the case for all woodpecker species. Acorn woodpeckers (*Melanerpes formicivorus*) in California and black-backed woodpeckers in Quebec responded to high food levels by significantly increasing their offspring fledging rates, and to a lesser extent, their clutch sizes (Nappi and Drapeau, 2009; Koenig, unpubl. data).

An additional explanation of the lack of change in fecundity is that the woodpecker populations were tracking food abundance. If the amount of food per pair of woodpeckers remained stable, then fecundity would not change. However, under outbreak conditions, the mountain pine beetle escapes regulation by its natural predators, including woodpeckers. Given the sharp increase in mountain pine beetle abundance during the outbreak years, it is unlikely that food per breeding pair remained constant, despite the increased density of woodpeckers at our sites.

Compared to the lack of changes in fecundity in woodpeckers, other cavity-nesting birds known to feed on mountain pine beetle (red-breasted nuthatch [*Sitta canadensis*] and mountain chickadee [*Poecile gambeli*]) showed large increases in clutch size and an increased tendency to re-nest (both replacement clutches and second broods), leading to "boom-and-bust" population dynamics at our study sites (Martin et al., 2006; Norris and Martin, 2008, 2010). Both species increased in abundance, resulting in very high densities. Nuthatches experienced a dual resource pulse of food and nest cavities that were excavated by the increased downy woodpecker populations (Norris and Martin, 2008). Nuthatches that reused downy woodpecker cavities, rather than excavating fresh cavities, initiated nests earlier and laid larger clutches (Norris and Martin, 2010). Thus, downy woodpeckers and red-breasted nuthatches, despite both being small, resident excavators, had very different fecundity responses to the food resource pulse.

Migratory woodpecker species also increased numerically during the study period. Despite leaving the beetle outbreak region during the winter, northern flickers demonstrated a significant increase in abundance and red-naped sapsuckers had a non-

significant increase. Relative to northern flickers, changes in red-naped sapsucker abundance were more variable and less correlated with beetle trends (their abundance was high in 1998 and dropped in 1999–2000 after we detected increases in mountain pine beetle abundance). Strong cyclical population fluctuations have been observed elsewhere in red-naped sapsuckers (Walters et al., 2002). Thus, we cannot assess whether the strong increase in sapsucker abundance from 2004 to 2006 was part of an unrelated population cycle, or was enhanced by the food pulse (Fig. 2). Where knowledge of summer and winter food supply is available, as well as woodpecker survival rates, comparing responses by migrant and resident woodpeckers to a food pulse may further illuminate the roles of summer and winter food supply in population regulation.

Changes in clutch size could have been masked by lower fecundity in first year recruits. Reproductive success increases with age in many bird species (Martin, 1995), and if the increased density of birds represented an influx of young birds, then the average clutch size or number of fledglings/nest may not have changed. If this were the case, we should have observed increased variation in clutch size during the beetle outbreak, which was not readily apparent (Figs. 3 and 4). Alternatively, the overall population may be limited in abundance by food supply while breeding pair fecundity is constrained by other factors. Constraints on time spent guarding nestlings and foraging may limit the amount of food a pair can provision nestlings (Martin, 1992). Further research into adult return and immigration rates, as well as foraging habits of woodpeckers is needed in order to fully address these hypotheses.

Overall, we found that woodpeckers responded numerically in response to the massive mountain pine beetle outbreak but maintained their fecundity. We were able to provide multi-species tests of fecundity-related demographic traits based on variation over time at the same sites, in contrast to previous tests based on vital rates for different geographic sites (Koenig, 1984; Ricklefs, 1980; Wiebe et al., 2006). We suggest that woodpecker populations are regulated numerically, probably through a combination of immigration and adult/juvenile survival. The continued growth of woodpecker populations after the peak of bark beetle infestation in 2004 indicates a sustained increase in food supply likely due to secondary infestations by other bark and wood-boring insect species. In post-burn forests, woodpecker populations typically remain high 2–5 years after the burn, relying on secondary insect attack (Koplin, 1972; Murphy and Lehnhausen, 1998). In mature conifer and mixed forests, insect outbreaks and fire are the two major disturbance processes; and especially so in the Montane Cordilleran region of interior British Columbia (Lindenmayer et al., 2008; Klennner et al., 2008). This mountain pine beetle epidemic was unusual in its severity and extremely widespread scale and has created a landscape of standing dead trees (Safrañik and Wilson, 2006). Our results show that this forest continues to provide good woodpecker habitat for up to 5 years after the beginning of the outbreak. The long-term effects of the mountain pine beetle epidemic on woodpecker populations in these mixed forests remain unknown.

## Acknowledgments

We thank numerous field assistants who have collected data over the years. Funding for this research was provided by the Sustainable Forest Management Network, Forest Renewal BC, FIA Forest Science Program of BC, Environment Canada, and the Natural Sciences and Engineering Research Council of Canada (NSERC) Special Strategic Grant. Tolko Industries Limited (Cariboo Woodlands) provided logistical and financial support from 1996 to 2003. We thank Karen Wiebe for discussions of the ideas in this paper. Walter Koenig, Michael Murphy, Peter Attiwill, and 2 anonymous reviewers provided constructive comments. Edworthy was supported by

NSERC Canada Postgraduate Scholarship, Science Horizons Internship (Environment Canada), and a Junco Technologies Award of the Society of Canadian Ornithologists.

## Appendix 1

Summary of site characteristics at 20 study sites in interior British Columbia. Each point count station represents approximately 1 ha of surveyed area.

Site ID	Number of point count stations	Harvested?	Composition
7M	15	N	Mixed conifer (with Aspen)
LT2	20	N	Douglas fir leading
MC	15	N	Pine leading
RC	8	N	Aspen groves
RL	14	N	Mixed conifer
RP	12	N	Pine leading (with Aspen)
SC	26	N	Aspen groves
SHAC	23	N	Mixed conifer
SW	15	N	Mixed conifer (with Aspen)
TO	16	N	Mixed conifer (with Aspen)
YY	20	N	Mixed conifer (with Aspen)
D1	20	Y	Douglas fir leading
CT	7	Y	Mixed conifer (with Aspen)
D2	22	Y	Spruce leading
FO	15	Y	Pine leading
KN	15	Y	Pine leading
LT1	10	Y	Pine leading
MM	22	Y	Mixed conifer (with Aspen)
MX	32	Y	Mixed conifer
SHCC	13	Y	Mixed conifer (with Aspen)

## References

- Aitken, K.E.H., Martin, K., 2004. Nest site availability and selection in aspen-conifer groves in a grassland landscape. *Can. J. Forest Res.* 34, 2099–2109.
- Aitken, K.E.H., Wiebe, K.L., Martin, K., 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. *Auk* 119, 391–402.
- Amman, G.D., Ryan, K.C., 1991. Insect Infestation of Fire-injured Trees in the Greater Yellowstone Area. U.S. Department of Agriculture, Forest Service Intermountain Research Station, USA.
- Arcese, P., Smith, J.N.M., 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *J. Anim. Ecol.* 57, 119–136.
- Ashmole, N.P., 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b, 458–473.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., Taylor, S.W., 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 29, 427–441.
- BCMFR, 2007. Mountain pine beetle action plan: sustainable forests, sustainable communities. Annual progress report 2006/2007 [Online]. Available at [http://www.for.gov.bc.ca/hfp/mountain.pine.beetle/MPB-Annual\\_Report\\_20070917.pdf](http://www.for.gov.bc.ca/hfp/mountain.pine.beetle/MPB-Annual_Report_20070917.pdf). Accessed April 2010.
- Bonnot, T.W., Rumble, M.A., Millsbaugh, J.J., 2008. Nest success of black-backed woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. *Condor* 110, 450–457.
- Both, C., 1998. Experimental evidence for density dependence of reproduction in great tits. *J. Anim. Ecol.* 67, 667–674.
- Conner, R.N., 1981. Seasonal changes in woodpecker foraging patterns. *Auk* 98, 562–570.
- Conner, R.N., Crawford, H.S., 1974. Woodpecker foraging in Appalachian clearcuts. *J. Forest.* 72, 564–566.
- Dawson, R., Werner, A.T., Murdock, T.O., 2008. Preliminary analysis of climate change in the Cariboo-Chilcotin area of British Columbia. In: Pacific Climate Impacts Consortium. University of Victoria, Victoria, BC, 49 pp.
- Drever, M.C., Martin, K., 2010. Response of woodpeckers to changes in forest health and harvest: implications for conservation of avian biodiversity. *Forest Ecol. Manage.* 259, 958–966.
- Drever, M.C., Aitken, K.E.H., Norris, A.R., Martin, K., 2008. Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol. Conserv.* 141, 624–634.
- Drever, M.C., Goheen, J.R., Martin, K., 2009. Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology* 90, 1095–1105.
- Greenwood, J.J.D., Baillie, S.R., 1991. Effects of density dependence and weather on population changes of English passerines using a non-experimental paradigm. *Ibis* 133, 121–133.
- Hutto, R.L., 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conserv. Biol.* 9, 1041–1058.

- Hutto, R.L., Pletschet, S.M., Hendricks, P., 1986. A fixed-radius point-count method for nonbreeding and breeding season use. *Auk* 103, 593–662.
- Johnson, R.R., Brown, B.T., Haight, L.T., Simpson, J.M., 1981. Playback recordings as a special avian censusing technique. *Stud. Avian Biol.* 6, 68–75.
- Klenner, W., Walton, R., Arsenault, A., Kremsater, L., 2008. Dry forests in the southern interior of British Columbia: historic disturbances and implications for restoration and management. *Forest Ecol. Manage.* 256, 1711–1722.
- Koenig, W.D., 1984. Geographic variation in clutch size in the northern flicker (*Colaptes auratus*): support for Ashmole's hypothesis. *Auk* 101, 698–706.
- Koplin, J.R., 1969. The numerical response of woodpeckers to insect prey in a sub-alpine forest in Colorado. *Condor* 71, 436–438.
- Koplin, J.R., 1972. Measuring predator impact of woodpeckers on spruce beetles. *J. Wildl. Manage.* 36, 308–320.
- Kreisel, K.J., Stein, S.J., 1999. Bird use of burned and unburned coniferous forests during winter. *Wilson Bull.* 111, 243–250.
- Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. *Salvage Logging and its Ecological Consequences*. UBC Press, Vancouver, British Columbia.
- Martin, T.E., 1992. Interaction of nest predation and food limitation in reproductive strategies. *Curr. Ornithol.* 9, 163–197.
- Martin, K., 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. *Am. Nat.* 35, 340–348.
- Martin, K., Aitken, K.E.H., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106, 5–19.
- Martin, K., Eadie, J.M., 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecol. Manage.* 115, 243–257.
- Martin, T.E., Li, P., 1992. Life-history traits of open- vs. cavity-nesting birds. *Ecology* 73, 579–592.
- Martin, K., Norris, A.R., Drever, M.C., 2006. Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: implications for critical habitat management. *B.C.J. Ecosys. Manage.* 7, 10–24.
- Meidinger, D., Pojar, J. (Eds.), 1991. *Ecosystems of British Columbia*, B.C. Ministry of Forests Special Report Series No. 6, Victoria, BC.
- Murphy, E.C., Lehnhausen, W.A., 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *J. Wildl. Manage.* 62, 1359–1372.
- Nappi, A., Drapeau, P., 2009. Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? *Biol. Conserv.* 142, 1381–1391.
- Norris, A.R., Martin, K., 2008. Mountain pine beetle presence affects nest patch choice of red-breasted nuthatches. *J. Wildl. Manage.* 72, 733–737.
- Norris, A.R., Martin, K., 2010. The perils of plasticity: dual resource pulses increase facilitation but destabilize populations of small-bodied cavity-nesters. *Oikos* 119, 1126–1135.
- Ostfeld, R.S., Keesing, F., 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* 15, 232–237.
- Paine, T.D., Raffa, K.F., Harrington, T.C., 1997. Interactions among *Scolytid* bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* 42, 179–206.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R 2 Foundation for Statistical Computing, Vienna, Austria (Version 2.9.2).
- Ricklefs, R.E., 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97, 38–49.
- Ricklefs, R.E., 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 102, 9–22.
- Saab, V., Russell, R., Dudley, J.G., 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *Condor* 109, 97–108.
- Safranyik, L., Wilson, W.R., 2006. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada.
- Walters, E.L., Miller, E.H., Lowther, P.E., 2002. Red-naped sapsucker (*Sphyrapicus nuchalis*). In: Poole, A. (Ed.), *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca [Online] Available at <http://bna.birds.cornell.edu/bna/species/663b/articles>. Accessed April 2010.
- Wiebe, K.L., 2006. A review of adult survival rates in woodpeckers. *Ann. Zool. Fenn.* 43, 112–117.
- Wiebe, K.L., Moore, W.S., 2008. In: Poole, A. (Ed.), *Northern Flicker (Colaptes auratus)*, *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca [Online] Available at <http://bna.birds.cornell.edu/bna/species/166a/articles>. Accessed April 2010.
- Wiebe, K.L., Koenig, W.D., Martin, K., 2006. Evolution of clutch size in cavity-excavating birds: the nest site limitation hypothesis revisited. *Am. Nat.* 167, 343–353.
- Winkler, H., Christie, D., Nurney, D., 1995. *Woodpeckers: A Guide to the Woodpeckers of the World*. Houghton Mifflin, Boston.
- Yang, L.H., Bastow, J.L., Spence, K.O., Wright, A.N., 2008. What can we learn from resource pulses. *Ecology* 89, 621–634.
- Yeager, L.E., 1955. Two woodpecker populations in relation to environmental change. *Condor* 57, 148–153.