Premium food for offspring? Black-backed Woodpecker (*Picoides arcticus*) diet during breeding season in eastern Canada

Junior A. Tremblay[a,b], Gabriel L. Fontaine[b], Jean-Pierre L. Savard[a], Jean-Michel Béland[c], Christian Hébert[c], and Jacques Ibarzabal[b]

[a]Environment and Climate change Canada, Wildlife Research Division, 801-1550 ave d'Estimauville (Québec) G1J 0C3, Canada.

[b]Université du Québec à Chicoutimi, Département des sciences fondamentales, 555, boul. de l'Université, Chicoutimi (Québec) G7H 2B1, Canada.

[c]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055, du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, G1V 4C7, Québec City, Canada

Corresponding author :
Junior A. Tremblay
Wildlife Research Division
Environment and Climate Change Canada
801-1550, avenue d'Estimauville
Québec (Québec) G1J 0C3
Telephone 418-649-6260

junior.tremblay@ec.gc.ca

Abstract

Knowledge on the diet of the Black-backed Woodpecker (Picoides arcticus Swainson, 1832) is fragmentary and relies on a limited number of studies. Gaps remain in our understanding of the plasticity of its diet, particularly in the eastern part of its range. The main objective of this study was to assess the diet of Black-backed Woodpeckers in burned and unburned habitats and among sexes and ages in Québec. We collected feces and fecal bags from unburned and burned habitats in the Central Laurentians ecoregion of the eastern boreal shield ecozone, and assessed diets based on identified prey items. Buprestidae and Cerambycidae of the subfamily Lamiinae were predominant prey for adult Black-backed Woodpeckers in burned habitats, and the Pythidae *Pytho niger* (Kirby, 1837) and Lamiinae were the most prevalent prey in unburned habitats. Lamiinae were the most predominant prey items provisioned to nestling in burned habitat while *P. niger* was their predominant food in unburned habitat, followed by Cerambycidae (without Lamiinae) and Lamiinae. Our results present new insights into Black-backed Woodpecker diet where parents feed their offspring with the largest prey available, potentially providing higher fitness for their offspring. Furthermore, our study confirms that Black-backed Woodpeckers, at least in the eastern part of its range, are not restricted to feed on Lamiinae, but are rather opportunistic in taking advantage from resource-pulse interactions provided by recently disturbed habitats, especially from recently burned habitats.

Keywords: Black-backed Woodpecker, Buprestidae, burned habitat, Cerambycidae, Lamiinae, *Picoides arcticus* Swainson 1832, nestling, prey, *Pytho niger* Kirby 1837, unburned habitat

Introduction

Diet studies are important in animal ecology, as food abundance strongly influences animal population density (Ylonen et al. 2003), reproductive output (Htwe and Singleton 2014) and habitat selection (Schoener 1974). Recent technology such as DNA metabarcoding offers promising advances, but it is not yet fully adapted for estimating relative prey abundance within stomach contents or in feces, and the availability of primers restricts its use to well known groups (Valentini et al. 2009; Piñol et al. 2015). Furthermore, DNA-based methods cannot distinguish prey developmental stages (Trevelline et al. 2016), which may be crucial for understanding how prey are captured and for estimating prey nutrient content. However, traditional techniques (i.e. morphology-based identification) may provide the number of prey individuals per sample (Sherry et al. 2016) or the size of prey items (Calver and Wooller 1982).

The Black-backed Woodpecker (*Picoides arcticus* Swainson 1832) is a resident of Nearctic boreal forests where it lives in overmature and old-growth coniferous boreal forests, from Alaska to Newfoundland (Tremblay et al. 2020). It is a common primary excavator of recently dead trees in which it forages and nests (Tremblay et al. 2009, 2010, 2015a Nappi et al. 2015). Black-backed Woodpeckers are opportunistic, taking advantage of resource pulses resulting from natural disturbances such as wildfire (Hutto 1995, Murphy and Lehnhausen 1998, Nappi et al. 2015, Tremblay et al. 2015b) or insect outbreaks (Goggans et al. 1989, Rota et al. 2014).

Knowledge on Black-backed Woodpecker diet is fragmentary and relies on a limited number of studies. Beal (1911) was the first to publish information on the diet of this woodpecker, based on sampling areas throughout the United States and a few sites from Canada. After examining the stomach contents of 28 Black-backed Woodpeckers, this author reported that the species fed primarily on wood-boring larvae (Cerambycidae; 77%). Murphy and Lehnhausen (1998) supported the association between the Black-backed Woodpecker and wood-boring larvae in a study on the foraging ecology of Nearctic boreal woodpeckers in a one-year-old burn in Alaska. They found that 95% of the prey items in the stomach contents of 13 Black-backed Woodpeckers were larvae of Cerambycidae (mainly *Monochamus scutellatus* (Say 1824) from the Lamiinae sub-family). Since then, it has generally been accepted that the Black-Backed Woodpecker is a wood-boring larvae specialist, closely associated to burned habitat (sensu Hutto 1995). However, in a recent study using DNA metabarcoding, Stillman et al. (2022) showed that Black-backed Woodpecker diet, in Washington and California, was much broader than suggested in previous observational studies even if wood-boring larvae were still the dominant prey. Nevertheless, knowledge of Black-backed Woodpecker diet are based on a limited number of studies, and many gaps remain in our understanding of diet plasticity of these woodpeckers, particularly in the eastern part of their range where diet information is absent.

The main objective of this study was to assess the diet of the Black-backed Woodpecker in burned and unburned habitats, during the breeding season, in the eastern part of the species range. More specifically, we aim to determine how diet composition varies among habitat types and among adults and nestling based on prey item identification.

Materials and methods

Study area

During research projects on the breeding of the Black-backed Woodpecker conducted in 2004 and 2005 (see Huot and Ibarzabal 2006, Tremblay et al. 2009, 2010, 2014, 2015a,b) within the Central Laurentians ecoregion of the eastern boreal shield ecozone, we collected feces opportunistically while handling birds captured (individuals usually defecate upon their release). This area is typically dominated by mature stands of black spruce (*Picea mariana* Mills.) and jack pine (*Pinus banksiana* Lamb.) interspersed with small stands of balsam fir (*Abies balsamea* (L.)

Mill.) and scattered white birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michx.). Unburned samples were collected in 2004 and 2005 from an area located 200 km north of the Lac Saint-Jean mostly dominated by black spruce stands of interspersed recently logged and old residual forested blocks, resulting from commercial timber harvesting (see Tremblay et al. 2009, 2015b for more details). Samples in burned habitat were collected in 2004, one year post-fire in black spruce stands, which were located at ca. 170 km from the unburned sampled area. The fire was ignited accidentally by humans in May 2003 and affected 6735 ha which about 85% of this area has been severely burned (tree canopy completely scorched, and the bark peeling off after being heavily charred; MRNFP 2004).

Woodpeckers were attracted with calls and drumming playbacks and caught in mist nets. As research activities included nest monitoring (Tremblay et al. 2014, 2015a, 2016), we were able to find and collect nestling fecal bags that were dropped a few meters away from the nest by parents (Tremblay et al. 2016). Once collected, feces or fecal bags were immediately stored in a labelled receptacle containing 70% ethanol. Individual feces were teased apart using fine forceps and the material was then sieved through a fine muslin under running water. Arthropod fragments (e.g. head or structural components of the body such as pronotum, elytra, and urogomphy) recovered from samples were observed under a stereomicroscope (50-100x magnification) and first identified at the order level, and then at the family level using the works of Peterson (1960) and Stehr (1991). It was possible to get to the sub-family level for cerambycid larvae using Craighead (1923) and to the species level for Pythidae larvae as a review of the family was available, including larval description, which is unusual (Pollock 1991). Adult Scolytinae (Curculionidae) were identified using Bright (1976). Reference collections of adult and larval arthropods collected at the study sites were also used to facilitate identification, as suggested by Jenni et al. (1990). Considering their numerical response following wildfires (Saint-

Germain et al. 2004) and their historical identification as main prey of the Black-backed-Woodpecker (Murphy and Lehnhausen 1998)), Lamiinae were presented separately from other Cerambycidae sub-families. Other arthropods were identified at the lowest taxonomic level and the frequency of each prey type was estimated on the most conservative basis. For instance, if one feces contained three bark beetle heads and two right elytra, the feces was considered to contain three bark beetles. For larvae, the number of parts or complete pronotums were used for Buprestidae, and the number of urogomphi for Pythidae, as these characters allowed to identify these taxa.

Data analyses

Using the R software (version 4.1.1.; R Core Team 2021), Generalized Linear Mixed Models (GLMM) were performed to compare prey abundance according to woodpecker sex/age variable (3 levels; males, females and nestlings), habitat variable (2 levels; unburned and burned forests) and interaction between these two factors. Negative binomial distribution models were used to account for overdispersion (appropriate variance parameterization for count data models) by adding the *theta* parameter. The effect of the year of sampling was tested as a random effect. The *c_hat* function (*AICmodavg* package; Mazerolle 2020) was used to assess overdispersion and *glm.nb* (*MASS* package, Venables and Ripley 2002) was used to produce the negative binomial models. Pairwise comparisons were performed on each model with the estimated marginal means (EMMs) method using the *emmeans* function (Sidak's post-hoc adjustments) (*emmeans*, Lenth 2021).

To test if the diet composition varied between sex/age and habitat, we used a permutational multivariate analysis of variance (PERMANOVA), a multivariate analogue of ANOVA (*adonis* function of the *vegan* package in R). PERMANOVA uses dissimilarity distance-based matrices produced using the Bray-Curtis dissimilarity index (*vegdist* function of the *vegan* package; Oksanen et al. 2022). A significant result indicates that diet varies according to woodpecker sex/age, habitat or both. We also performed permutation tests with pseudo-F ratios on sequential sums of squares of the matrices followed by a multilevel pairwise comparison to evaluate differences in prey assemblages amongst sex/age and habitat groups (pairwise.adonis function; Martinez Arbizu 2020). A permutational analysis of multivariate homogeneity of group dispersions (*betadisper* function of the *vegan* package in R) was also used to verify if within-group dispersion of each group was similar or not (Anderson et al. 2006). We then performed an analysis of variance (ANOVA) on the distances of prey items within a group centroid, followed by pairwise comparisons of group mean dispersion (*permutest* function of the vegan package).

To illustrate how diet composition of adults and nestling Black-backed Woodpeckers vary in burned and unburned forests, we ran a canonical redundancy analysis (*rda* function in the *vegan* package) with permutations of residuals, under a full model for the joint effect of grouping variables (Legendre and Legendre 2012). We tested the rda model significance using the *anova.cca* function of the *vegan* package. We applied a Hellinger-transformation on prey abundances of the original community matrix (*decostand* function of the *vegan* package; Oksanen et al. 2022) to reduce the weight of uncommon prey items (Legendre and Gallagher 2001), and hyper-abundant species that may occur during favorable events (Legendre and Birks, 2012), such as for certain species in recent burned habitat (i.e. *Monochamus scutellatus*; Saint-Germain et al. 2004). We produced a correlation triplot (scaling =2) to show variation in individual diets and their relationships with centroids of their grouping factor (sex/age and habitat). Distance of each centroid to the origin or the length of each eigenvector cannot be compared because they are proportional to their associated specific variances (Zuur et al. 2007). In our correlation triplot, angles between eigenvectors and locations of group centroid and individual diet reflect their correlations. Correlation is completely positive at 0˚, null at 90˚ and completely negative at 180˚. We overlaid data ellipses, assuming a multivariate t-distribution (95% confidence level), on the triplot to visualize prey assemblage variation inside the sex/age grouping. The canonical redundancy analysis highlighted several arthropod clusters that were strongly correlated with the two grouping factors along with the corresponding samples. Subsequently, to prevent collinearity between prey variables in clusters, we merged larvae and adults Scolytinae. The displayed correlation triplot contains therefore only the most significant prey groups (black arrows). Six major prey groups were kept for the triplot: Scolytinae (mostly *Polygraphus rufipennis* (Wood & Bright, 1992) larvae and adults), *Pytho niger* (Kirby, 1837) (Coleoptera: Pythidae; larvae only), Araneae (18% identified at the species level and 82% at the order level), Formicidae (adults), Cerambycidae (mostly Lamiinae larvae of the *Monochamus* genus) and Buprestidae (larvae) (see Appendix for the raw data). We used the *ggplot* function 2 (*ggplot2* package; Wickham 2016) to produce figures.

Results

Abundance of prey vs Sex/Age and habitat

A total of 69 samples of feces were analyzed from burned habitats (n = 19 for males, n = 26 for females and n = 24 for nestling) and 35 from unburned habitats (n = 13 for males, n = 11 for females and n = 11 for nestling). Buprestidae and Lamiinae were the dominant prey for adult Black-backed Woodpeckers in burned habitats, accounting respectively for 30% and 27% in males and 52% and 22% in females respectively (Table 1). In fact, Buprestidae were a prey almost only in burned habitat, being very rare in the adult diet (only one found) in unburned habitat and completely absent in nestling diet (Table 1; Figure 1). In unburned habitats, *Pytho niger* was the most prevalent prey, accounting for 26% in males and 45% in females. Lamiinae larvae were their second most prevalent prey, accounting for 33% in males and 19% in females (Table 1). Lamiinae was the most prevalent prey item provisioned to nestling in burned habitat (69%), where they were critical for feeding nestling (P=0.003; Figure 1), while *P. niger* (38%) was the predominant prey in unburned habitat, followed by Cerambycidae other than Lamiinae (22%) and Lamiinae (19%; Table 1). The high proportion of Lamiinae among Cerambycidae highlights the importance of this subfamily in the diet of adult and nestling Black-backed Woodpecker (Figure 1e). Although fewer Cerambycidae (including Lamiinae) are found in fecal bags of nestling in unburned habitats than in burned habitats (6.50 vs 16.52 prey/fece or fecal bag; P=0.003; Figure 1), they are significantly more abundant in their diet than in that of their parents (for unburned P_{male}= 0.005; P_{female}= 0.013; for burned P_{male}<0.001; P_{female}<0.001; Table 1; Figure 1). *Pytho niger* was predominant in the diet of adult and nestling Black-backed Woodpeckers in unburned habitat (P<0.001; Figure 2). Formicidae were more numerous in the diet of nestling than of males in unburned habitat (P=0.040). Araneae were significantly more abundant in nestling diet than in male and female diets (P<0.001), particularly in burned habitat.

<Figure 1>

<u>Diet composition vs Sex/Age and habitat</u>

PERMANOVA indicated that prey assemblages differed significantly between burned and unburned habitats as well as between sex/age (Table 2). Prey assemblages of females and males were similar but both differed from nestling (male-female: P=0.940, male-nestling: P=0.003 and female-nestling: P=0.003). Variability in prey assemblages was similar in unburned and burned habitats (df=1, F=1.267, P=0.972), but differed between sexes/ages (df=2, F=2.947, P=0.060).

Nestling showed much lower variability than adults (male-female: *P*=1.000, male-nestling: *P*=0.080, female-nestling: *P*=0.040; Tables 2 and 3).

Habitat and sex/age explained 23% of the variance in prey assemblages and the permutation test for *rda* under reduced model was significant (df=3; F=10.142; *P*=0.001). The 95% confidence interval ellipses are similar in overlap/location and in size, for males and females, according to *adonis* and *betadisper* analyses' results respectively (Figure 2). The ellipse for nestling is much smaller and limited to the lower right quadrant. The unburned habitat centroid is located on the upper right quadrant while the burned habitat centroid is completely opposed (lower left). There is a sparse cluster of unburned samples extending to the upper right, a sparse cluster of the burned samples extending to the left-hand side and a dense cluster of both habitat in the nestling ellipse surrounding (Figure 2).

<Figure 2>

The strongest association with burned habitat belonged to Buprestidae as it was the only prey variable on the left side of the first axis, being therefore the most negatively correlated variable with nestling. Cerambycidae showed a weaker association towards burned habitat but the strongest one in the ordination with nestling. *Pytho niger* was strongly and positively correlated with unburned habitat. Araneae and Formicidae were orthogonal to habitat centroids, indicating an absence of association with habitat type. Formicidae were slightly and positively correlated with nestling while the correlation was strong and positive for Araneae. The Scolytinae tended to be negatively correlated with nestling and burned habitat in general.

Discussion

Our results present new insights on the diet of the Black-backed Woodpecker as they depict newly discovered interactions between sex, age and habitat type where Black-backed Woodpecker parents feed their offspring with the best available food resources and feed themselves on lower quality prey. By feeding their progeny with the largest available prey, adults of the Black-backed Woodpecker provide a “premium” food that may enhance fitness of their offspring by potentially increase growth rate of nestling, consequently enhancing their post-fledging survivorship (*sensu* Tremblay et al. 2014).

In burned habitats, nestling were mainly fed on larvae of Lamiinae, a sub-family to which belong the genus *Monochamus*, which were the largest in size in our study. *Monochamus scutellatus* adults are roughly 2.5 times larger than those of *Melanophila acuminata* (DeGeer, 1774) (respectively 13-40 mm vs 7-13 mm long, according to Evans (2014)), the most prevalent prey on which fed adults in our study. Moreover, Lamiinae larvae are found at high density in burned trees during the first two years after wildfire (Saint-Germain et al. 2004). They were likely the greatest source of protein to feed nestling of the Black-backed Woodpecker in burned habitats of our study. As comparison, the size of Scolytinae larvae and adults ranges from 2 to 5 mm (Bright 1976) and they are thus considered as a low-quality food. Moreover, Scolytinae are much less abundant after severe wildfire than Lamiinae and Buprestidae, but they can be very abundant in dying or recently dead trees of natural forests. This suggests that they are highly-sensitive to the quality of subcortical tissues and that wildfire strongly affects it (Hébert 2023).

Our study support that the Black-backed Woodpecker, at least in the eastern part of its range, is not restricted to feed on Lamiinae (*Monochamus spp.*) but is rather opportunistic in benefiting from resource-pulse interactions provided by recently disturbed habitats, especially recently burned habitats (Tremblay et al. 2015a). Hence, the previous conception of the Black-backed Woodpecker being a *Monochamus* (Lamiinae) specialist may have been biased by studies focusing on adults delivering prey to their offspring at the nest, especially in burned habitats. To a lesser extent, our results indicate a similar pattern in unburned forests, as Lamiinae are also among the most predominant prey provisioned to nestling along with *Pytho niger* and other Cerambycidae. Mature larvae of Lamiinae range from 38-51 mm in length with up to 9.5 mm wide (Wilson 1975), but mature larvae of the genus *Pytho* can be also large, ranging from 20-40 mm in length with up to 5 mm wide (Pollock 1991).

Our study reports for the first time that *Pytho niger* is a predominant prey in the diet of both adult and nestling Black-backed Woodpeckers in unburned forests. It has been possible to identify this beetle at the species level because we had a relatively recent monograph on the genus *Pytho* (Pollock 1991), in which keys and drawings allow identifying larvae, which is rather rare in Coleoptera. Only nine species belong to the genus *Pytho* in the world. Larvae are found underneath loose bark of conifer trees that died 3-4 years before and which maintain a certain degree of humidity (Pollock 1991). In fact, *Pytho* is a secondary colonizer of dead conifers that have been initially attacked by primary phloeophagous or xylophagous insects (Scolytinae, Buprestidae, Cerambycidae). Hence, *Pytho* are found within a fairly narrow range of decay, and dead trees remain suitable to host this species for a limited time, only 4-10 years (Pollock 1991). Moreover, *Pytho* is nearly always found in the boles of fallen trees, and rarely in snags (Pollock 1991). For instance, *P. niger* has been found in burned logs of black spruce fell on the ground 2-5 years before in eastern boreal forest (C. Hébert, unpublished results). Accordingly, Black-backed Woodpeckers have been observed foraging on downed woody debris in unburned forests, from 16% (Tremblay et al. 2010) to 41% (Villard 1994) of their time, while Tremblay et al. (2010), in a study within our study area, reported that large logging residues in recent cutblocks were also occasionally foraged by the species.

For populations of Black-backed Woodpecker in unburned forests, rapidly finding recently dead trees requires time and energy (Tremblay et al. 2009, 2014, 2016). Dense and productive old-growth forests are preferred by foraging Black-backed Woodpeckers as the recurrent and significant inputs of new and often large snags in these stands ensure the temporal stability of foraging resources (Martin, Tremblay et al. 2021), and likely of *P. niger*. However, densities of *P. niger* in unburned forest stands may not be comparable to densities of Lamiinae in recently burned habitats which may explain why *P. niger* is a less predominant prey provisioned for nestlings in unburned habitats than Lamiinae are in recent burns.

In contrast, Buprestidae larvae were almost only found in adult woodpecker diet sampled in one-year burned habitats. In a study sampling insects in recently burned boreal forests and unburned ones in which trees were girdled, Boucher et al. (2012) reported Buprestidae (11 species) only from the burned site, with the exception of one individual. Similarly, Jeffrey (2013) noted that the strongest abundance of several species of Buprestidae, such as the fire associated *Melanophila acuminata* (Evans 1966), occurred within a one-year window post-fire, such as in our study. It is possible that Black-backed Woodpecker adults preferentially selected buprestid larvae over Lamiinae larvae for their own use in burned habitats because buprestids were easier to collect as they feed just beneath bark while Lamiinae feed much deeper into the wood and are thus less accessible. However, no buprestid was found in young feces; adults may have preferred to feed their young with Lamiinae larvae as these are larger and likely provide more protein to ensure optimal growth of the young. Nevertheless, we cannot eliminate the likelihood that buprestid larvae were less accessible at the time of feeding the young. Indeed, for a given woodpecker pair, adult feces were collected almost only at the time of their capture, i.e. 2-3 weeks before we were able to collect young feces. This time lag in the acquisition of feces could have caused some prey, such as buprestids (especially species with a one-year cycle), to complete their immature development and disperse when becoming imago. They would then no longer be accessible to feed the young. Further studies with concomitant sampling for adults and nestlings would help to better understand prey partitioning between these two age classes.

All other types of prey were found in both habitats. Formicidae and Aranae, which are present in the diet of both adults and nestlings in both habitat types, seem to be a stabilizing force by always providing abundant and accessible food sources. The observed sizes of Formicidae and Aranae are mostly larger than Scolytinae, but smaller than those of Cerambycidae, Buprestidae and Pythidae. Thus, Formicidae and Aranae can be qualified as medium-quality food. In unburned habitat, Formicidae were significantly more abundant as prey provisioned to nestling than in the diet of males, females being intermediate. Moreover, *Pytho niger* was less prevalent in male diet than in females and nestling ones, but the reverse was true for Scolytinae which were nearly absent from the prey provisioned to nestling. This suggests that males may forage preferentially on snags, in which Scolytinae are found, but females may rather forage more on fallen trees where *Pytho niger* and Formicidae live. These results suggest that nestling are mainly provisioned in prey by females which was not reported as being an important variable influencing food deliveries by parents within the study area (Tremblay et al. 2016). However, in a study based on observations at a single Black-backed Woodpecker nest during five consecutive days, Short (1974) report that female fed nestlings more frequently than male in unburned habitats in northeastern United States. Additionally, it is possible that even if *Monochamus* larvae is the premium food, the diversity of food provided to nestling could be important to ensure adequate growth and development. For instance, Deblauwe and Janssens (2008) found that Great Apes ate a wide range of ant and termite species despite their low energy contribution, probably due to their nutritional supplement of specific nutrients.

Our results suggest that the diet of the Black-backed Woodpecker, known as a wood-boring specialist, is broader (i.e. more plastic) than previously thought, and support recent DNA metabarcoding analyses (Stillman et al. 2022), especially in the absence of major insect pulse from wildfires. Furthermore, our study stresses the need for future research on the diet of the Black-backed Woodpecker at different stages of the life-cycle and life-stage in order to better understand the implications of their diet on fitness and survivorship, and to assess the relationship of prey biomass ingested by the Black-backed Woodpecker and their contribution the individual energetic budget.

Acknowledgements

This paper could not have been completed without the hard work of all field assistants who worked on the different sites and projects throughout the years (C. Buidin, P. Desmeules, F. Gagnon, M. Huot, and Y. Rochepault). G. Fontaine would like to give special thanks to M.-H. St-Laurent for his assistance with early drafts of the manuscript, and to M. Huot and F. Gagnon for data and help throughout this study. Thanks to Abitibi Consolidated Inc., Bowater Inc. (both regrouped now as Resolute Forest Products), and Chantier Chibougamau Ltd for access to research sites, data and financial as well as technical help. We also wish to thank the Consortium de recherche sur la forêt boréale commerciale and the Ministère des Ressources Naturelles et de la Faune for their financial support.

Competing Interests

There is no competing interests for all authors

Data availability

Data available upon request.

References

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics, **62**(1): 245--253.

Beal F.E.L. 1911. Food of the woodpeckers of the United States. U.S.D.A. Biological Survey Bulletin **37**.

Boucher, J., Azeria, E. T., Ibarzabal, J., and Hébert, C. 2012. Saproxylic beetles in disturbed boreal forests: temporal dynamics, habitat associations, and community structure. Ecoscience, **19**(4): 328-343.

Bright D.E. 1976. The bark beetles of Canada and Alaska. The insects and arachnids of Canada, part 2. Agriculture Canada. Direction de la recherche. Ottawa.

Calver, M.C., and Wooller, R.D. 1982. A technique for assessing the taxa, length, dry weight and energy content of the arthropod prey of birds. Wildlife Research, **9**(2): 293-301.

Craighead F.C. 1923. North American Cerambycid larvae : a classification and the biology of North American Cerambycid larvae. Entomological bulletin **23.**

Deblauwe I., and Janssens G.P.J. 2008. New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. American Journal of Physical Anthropology, **135**(1): 42-55.

Evans, W.G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). Ecology, **47**(6): 1061-1065.

Evans, A.V. 2014. Beetles of eastern North America. Princeton University Press.

Goggans, R., Dixon, R.D., and Seminara, L.C. 1989. Habitat use by three-toed and Black-backed Woodpeckers. USDA Deschutes National, Oregon. Technical Report **87-3-02**.

Hébert, C. 2023. Forest arthropod diversity. Chapter 3, *in* Handbook of Forest Entomology, Springer. *In Press*.

Htwe, N.M., and Singleton, G.R. 2014. Is quantity or quality of food influencing the reproduction of rice-field rats in the Philippines? Wildlife Research, **41**(1): 56-63.

Huot, M., and Ibarzabal, J. 2006. A comparison of the age-class structure of black-backed woodpeckers found in recently burned and unburned boreal coniferous forests in eastern Canada. Annales Zoologici Fennici, **43**: 131-136.

Hutto, R.L. 1995. Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forest. Conservation Biology, **9**(5): 1041–1058.

Jeffrey, O. 2013. Effets des coupes de récupération sur les successions naturelles de coléoptères saproxyliques le long d’une chronoséquence de 15 ans après feu en forêt boréale commerciale. Master’s Thesis, Université Laval, Canada.

Jenni, L., Reutimann, P., and Jenni-Eiermann, S. 1990. Recognizability of different food types in faeces and in alimentary flushes of Sylvia warblers. Ibis, **132**(3): 445-453.

Legendre P., and Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia, **129**(2): 271-280.

Legendre, P., and Birks, H.J.B. 2012. From classical to canonical ordination. In Tracking environmental change using lake sediments. Springer, Dordrecht.

Legendre, P., and Legendre, L. 2012. Numerical ecology. Elsevier.

Lenth, R.V., Buerkner, P., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., and Singmann, H. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.0.

Martin, M., Tremblay, J. A., Ibarzabal, J., and Morin, H. 2021. An indicator species highlights continuous deadwood supply is a key ecological attribute of boreal old-growth forests. Ecosphere, **12**(5): e03507.

Martinez Arbizu, P. 2020. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4

Mazerolle, M.J. 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1

Ministère des Ressources naturelles, de la Faune et des Parcs (MRNFP). 2004. Insectes, maladies et feux dans les forêts québécoises en 2003. Direction de la conservation des forêts, Division des relevés et des diagnostics. 53p.

Murphy, E.C., and Lehnhausen, W.A. 1998. Density and Foraging Ecology of Woodpeckers Following a Stand-Replacement Fire. Journal of Wildlife Management, **62**(4): 1359–1372.

Nappi, A., Drapeau, P., and Leduc, A. 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? Forest Ecology and Management, **346**: 10–21.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Sólymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker,B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Beatriz, H., Evangelista, A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J.F., and Weedon J. 2022. vegan: Community Ecology Package. R package version 2.6-2.

Peterson A. 1960. Larvae of insects: an introduction to Nearctic species. 4th ed. Columbus, Ohio.

Piñol, J., Mir, G., Gomez-Polo, P., and Agustí, N. 2015. Universal and blocking primer mismatches limit the use of high-throughput DNA sequencing for the quantitative metabarcoding of arthropods. Molecular ecology resources, **15**(4): 819-830.

Pollock D.A. 1991. Natural history, classification, reconstructed phylogeny, and geographic history of *Pytho* Latreille (Coleoptera: Heteromera: Pythidae). Memoirs of the Entomological Society of Canada **154**: 3-104.

R Core Team 2021. R: A Language and Environment for Statistical Computing. Version 4.1.1. Vienna, Austria.

Rota, C.T., Rumble, M.A., Millspaugh, J.J., Lehman, C.P., and Kesler, D. C. 2014. Space-use and habitat associations of Black-backed Woodpeckers (*Picoides arcticus*) occupying recently disturbed forests in the Black Hills, South Dakota. Forest Ecology and Management, **313**: 161-168.

Saint-Germain, M., Drapeau, P., and Christian, H. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biological Conservation, **118**: 583–592.

Schoener, T.W. 1974. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences of the United States of America, **71**(10): 4169–4172.

Sherry, T.W., Johnson, M.D. Williams, K.A., Kaban, J.D., McAvoy, C.K., Hallauer, A.M., Rainey, S., and Xu, S. 2016. Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations. Journal of Field Ornithology **87**: 273 –292.

Short, L.L. 1974. Habits and interactions of North American Three-toed Woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). American Museum Novitates **2547**: 1–42.

Stehr, F.W. 1991. Immature Insects: Kendall/Hunt Dubuque, Iowa.

Stillman, A.N., Caiafa, M.V., Lorenz, T.J., Jusino, M.A., and Tingley, M.W. 2022. DNA metabarcoding reveals broad woodpecker diets in fire-maintained forests. Ornithology, **139**(2): 1–14.

Tremblay, J.A., Ibarzabal, J., Dussault, C., and Savard, J.-P.L. 2009. Habitat requirements of breeding black-backed woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. Avian Conservation and Ecology, **4**(1).

Tremblay, J.A., Ibarzabal, J., and Savard, J.-P.L. 2010. Foraging ecology of Black-backed Woodpeckers (*Picoides arcticus*) in unburned eastern boreal forest stands. Canadian Journal of Forest Research, **40**(5): 991-999.

Tremblay, J.A., Ibarzabal, J., Savard, J.-P.L., and Wilson, S. 2014. Influence of old coniferous habitat on nestling growth of black-backed woodpeckers *Picoides arcticus*. Acta Ornithologica, **49**(2).

Tremblay, J.A.., Savard, J.-P L., and Ibarzabal, J. 2015a. Structural retention requirements for a key ecosystem engineer in conifer-dominated stands of a boreal managed landscape in eastern Canada. Forest Ecology and Management, **357**: 220–227.

Tremblay, J.A., Ibarzabal, J., and Savard, J.-P.L. 2015b. Contribution of Unburned Boreal Forests to the Population of Black-Backed Woodpecker in Eastern Canada. Ecoscience, **22**(2–4).

Tremblay, J.A., Ibarzabal, J., Saulnier, M.-C., and Wilson, S. 2016. Parental care by Black-backed Woodpeckers in burned and unburned habitats of eastern Canada. Ornis Hungarica, **24**(1), 69–80.

Tremblay, J.A., Dixon, R.D., Saab, V.A., Pyle, P., and Patten, M.A. 2020. Black-backed woodpecker (*Picoides arcticus*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Trevelline, B.K., Latta, S.C., Marshall, L.C., Nuttle, T., and Porter, B.A. 2016. Molecular analysis of nestling diet in a long-distance Neotropical migrant, the Louisiana Waterthrush (*Parkesia motacilla*). The Auk: Ornithological Advances, **133**(3): 415-428.

Valentini, A., Pompanon, F., and Taberlet, P. 2009. DNA barcoding for ecologists. Trends in Ecology and Evolution, **24**(2): 110–117.

Venables, W.N., and Ripley, B.D. 2002Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilson, L.F. 1975. White-Spotted Sawyer. U.S. Department of Agriculture, Forest Service, Forest Pest Leaflet 74.

Ylönen, H., Jacob, J., Runcie, M.J., and Singleton, G.R. 2003. Is reproduction of the Australian house mouse (*Mus domesticus*) constrained by food? A large-scale field experiment. Oecologia, **135**(3): 372-377.

Zuur, A., Leno, E.N., Smith, G. M. 2007. Analyzing Ecological Data. Springer New York.