

Parental care by Black-backed Woodpeckers in burned and unburned habitats of eastern Canada

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Abstract Nest care is an important parental contribution to offspring. In woodpeckers, males often have an equal or greater contribution to parental care, including nest sanitation. The Black-backed Woodpecker (*Picoides arcticus*) is a North American boreal woodpecker for which both parents are highly involved in parental care. By modifying their territory size in optimal and suboptimal habitat (e.g. burned vs unburned habitats), this species seems to have a large tolerance to variation in prey abundance at a landscape scale, and could provide a useful biological model to investigate the adaptability of parent care, particularly to relative contribution of each sex. We investigated sex- and habitat-specific parental care behaviour of Black-backed Woodpeckers at 9 nests by daily monitoring during the nestling period. Specifically, we examined two different aspects of parental care: 1) time spent at the nest, and 2) food delivery. We also compared relative contribution between sexes to nest sanitation. Despite our small sample sizes, our results show that males are more involved in nest sanitation and spend longer at the nest, and both sexes exhibit higher food delivery rates and spend less time at the nest in burned habitat. This latter result may suggest that greater effort is needed to provision Black-backed Woodpecker nestlings in unburned habitat compared to burned habitat.

Keywords: food delivery, nest sanitation, parental provisioning, *Picoides arcticus*, woodpecker

Összefoglalás Az utódgondozás fontos szülői tevékenység. A harkályoknál a hímek szülői ráfordítása gyakran egyenlő mértékű vagy nagyobb a tojókéhoz képest. Ennek egy fontos eleme az odú tisztántartása. Az észak-amerikai, boreális elterjedésű harkályfaj, a feketehátú höcsik (*Picoides arcticus*) esetében mindkét szülő nagy arányban részt vesz az utódgondozásban. A revírek mérete változhat annak függvényében, hogy az adott élőhely optimális vagy szuboptimális-e (pl. leégett vagy le nem égett élőhely). Úgy tűnik, hogy a vizsgált faj jól tolerálja a prédafajok abundanciájának tájfértékű variabilitását. Jó biológiai modellként szolgálhat az utódgondozás adaptibilitásának vizsgálatához, főként az egyes ivarok ráfordítási arányát tekintve. Naponta monitoroztuk a faj ivar- és élőhelyspecifikus utódgondozási viselkedését 9 fészek esetében a fiókanevelés időszakában. Két aspektust vizsgáltunk: 1) a fészeknél töltött időt és 2) a táplálékellátás gyakoriságát. Ezek mellett összehasonlítottuk az ivarok relatív hozzájárulását is az odú tisztántartásához. A kis mintaszám ellenére eredményeink megmutatják, hogy a hímek nagyobb részt vállalnak az odú tisztántartásában, illetve több időt töltenek az odúnál, mint a tojók. Mindkét ivar nagyobb mennyiségű táplálékot hord az odúba, és kevesebb időt tölt a fészeknél a leégett élőhelyen. Az utóbbi eredményből arra következtethetünk, hogy a le nem égett élőhelyen nagyobb mértékű szülői ráfordítás szükséges a feketehátú höcsikektől a leégett élőhelyhez képest.

Kulcsszavak: etetés, fészektisztítás, szülői gondoskodás, *Picoides arcticus*, harkály

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Introduction

Reproductive strategies in birds are globally dichotomous (Ricklefs 1983). Birds with precocial strategies produce young able to walk, thermoregulate and find their food rapidly (Ricklefs 1983). This strategy requires the production of eggs containing sufficient resources for a longer period of development (Gill 2007), and in many cases, only one parent is involved in parental care (Emlen & Oring 1977, Oring 1986). At the opposite end, an altricial strategy produces naked young completely dependent on parents for food, thermoregulation and sanitation (Ricklefs 1983). Eggs contain less resources which results in a shorter incubation period (Gill 2007), but nestlings generally benefit from care by both parents (Lack 1968, Black 1996). For altricial birds generally, most species show greater contributions by females (Clutton-Brock 1991), but in woodpeckers, males have an equal or greater contribution to parental care (Wiktander *et al.* 2000, Michalek & Winkler 2001, Kozma & Kroll 2013) including nest sanitation (Chazarreta *et al.* 2011), and nocturnal incubation, which is generally rare in birds (Ligon 1993).

The Black-backed Woodpecker (*Picoides arcticus*) is a boreal woodpecker found exclusively in North America, and produces altricial nestlings where both parents are highly involved in parental care (Dixon & Saab 2001). Black-backed Woodpeckers feed by excavating almost exclusively on dying or recently dead coniferous trees (Tremblay *et al.* 2010, Nappi *et al.* 2015) and eating predominantly wood-boring larvae of Cerambycidae (Murphy & Lehnhausen 1998, Nappi & Drapeau 2009), but also Buprestidae, Curculionidae (Scolytinae) and Tenebrionoidea larva (Ibarzabal *et al.* in prep.). Although Black-backed Woodpeckers occur at high densities in recently burned forests (Hutto 1995, Murphy & Lehnhausen 1998, Nappi & Drapeau 2009), they also occur at low densities in unburned forest stands, where they are mainly associated with mature or old-growth forests (Settington *et al.* 2000, Tremblay *et al.* 2009, 2015), or with forests damaged by insect outbreaks (Goggans *et al.* 1989, Bonnot *et al.* 2008, Rota *et al.* 2014). Home-range sizes of breeding Black-backed Woodpeckers vary considerably from 20 ha in burned habitats (Nappi & Drapeau 2009) to more than 150 ha in old, unburned coniferous forests (Tremblay *et al.* 2009). The principal cause of this variation is prey density and Tremblay *et al.* (2009) showed that Black-backed Woodpecker home range size increased with the distance between preferred foraging habitat patches in unburned habitats. Furthermore, Tremblay *et al.* (2014) report that the amount of old coniferous habitat positively influenced weight gain in Black-backed Woodpecker nestlings.

Since this species seems to have a large tolerance to variation in prey abundance at the landscape level (burned vs. unburned habitats), it could provide a good biological model to investigate the adaptability in parent care, particularly to relative contribution of each sex. It is likely that low resource availability has a greater impact on females since they need to

produce eggs and thus, it is possible that male Black-backed Woodpeckers contribute more to parental care in unburned than in burned habitats. In contrast, when food resources are high, as in a recently burned habitat, females may have a greater ability to contribute equally to parental care.

Only a few studies exist on nestling care by Black-backed Woodpeckers and these tend to report observations from individual nests (Kilham 1966, Short 1974, Kilham 1983). To the best of our knowledge, this study is the first to address parental care by Black-backed Woodpeckers in the context of habitat types that may support different food resource availability. The main objective of this study is to provide insight into the influence of habitat and sex on parental care by the Black-backed Woodpecker in eastern Canada, with a specific focus on three different responses: 1) time spent at the nest, 2) food delivery and 3) nest sanitation.

Material and Methods

Study area

We conducted field work from June 14th to 22nd, 2006 in Québec, eastern Canada (*Figure 1*). The study area was located within the black spruce (*Picea mariana*) moss forest of the Canadian boreal forest ecological domain (Saucier *et al.* 1998). Forest stands were composed mainly of black spruce, or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*) and occasionally, tamarack (*Larix laricina*). The topography is undulating and wildfire is the major natural perturbation. Forest management began at the end of the 1990s and created a mosaic of logged and residual forest blocks across the landscape.

Parental care of Black-backed Woodpecker pairs were observed in two habitat types: burned and unburned forest stands. Burned habitat was created by a wildfire that occurred from May 31th to June 23rd 2005, and 30% of the area was composed of high-severity burn (Ministère des Forêts, de la Faune et des Parcs of Québec) (unpublished data). Salvage logging occurred in the burned habitat and we monitored Black-backed Woodpecker nests in unmanaged sections of high-fire severity areas. Unburned habitat is composed of the inter-persersion of old coniferous stands (>90 years old) and harvested stands (see Tremblay *et al.* 2009, 2015 for more detailed information on habitats).

Nest searching

We used two different methods to locate nests between habitat types, mainly because of relative high and low densities of Black-backed Woodpeckers in burned and unburned habitats respectively. In burned areas, we established transects and played recordings of the Black-backed Woodpecker's rattle call (used in conspecific disputes) (Dixon & Saab 2000) to attract individuals and follow them to their nest. In the unburned habitat, we located birds using roadside surveys with 20 minute (or less if detection occurred) playbacks of Black-backed Woodpecker calls and drumming (Ibarzabal & Desmeules 2006) during the end of

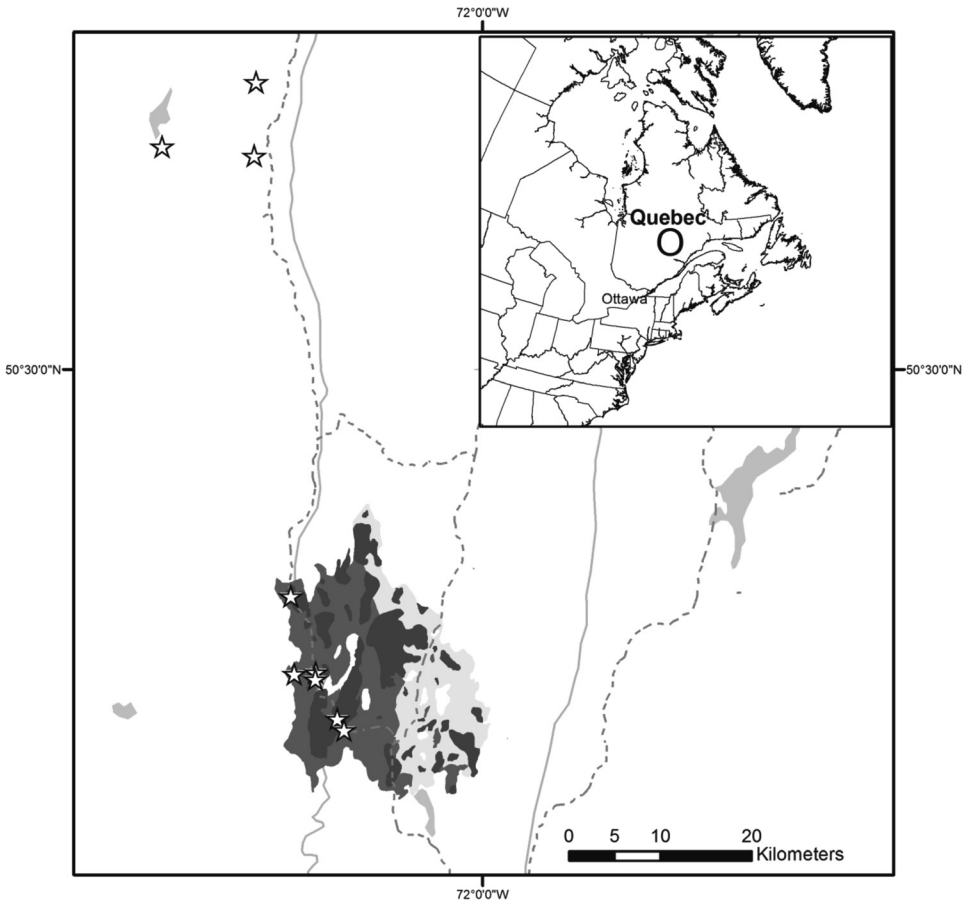


Figure 1. Location of the study area and nests (white stars) investigated for parental care by Black-backed Woodpecker in eastern Canada. Burned habitat was classified according to the burn severity and color intensity is related to fire severity

1. ábra A fekete hátú hőcsik szülői utódgondozásáról szóló vizsgálatban a vizsgált terület és a költőodúk (fehér csillagok) elhelyezkedése Kelet-Kanadában. A leégett élőhelyen az erdőtüz intenzitását a különböző árnyalatok jelölik

May through the first third of June. We used mist nets to capture woodpeckers and we fitted a 2.3g radio-transmitter (Model PD-2, Holohil Systems Ltd., Carp, Ontario) at the base of the two central rectrices on individuals showing signs of breeding (i.e. a brood patch). Nests of released birds were located using telemetry by homing methods (Mech 1983).

We recorded nest location coordinates using a global positioning system (GPS Garmin Legend, Garmin Corporation, Olathe, Kansas), and we marked the location using flagging tape placed at least 3m from the nest tree. Age of nestlings was monitored using a wireless camera mounted on a telescopic pole and images were captured on a video recorder for later visualizations. We developed, during our global study on Black-backed Woodpecker (Tremblay *et al.* 2014, 2016), a developmental chart of nestlings based on nest histories

and nestling observations from 37 nests (unpublished data) which enabled us to age nestlings precisely. Nests in unburned habitat were at least 20 km from those in burned habitat (Figure 1).

Observations at nest

One observer was hidden at about 20 m from the nest and recorded time (hour/minute/second) for each arrival and departure of a woodpecker; sex was determined by the yellow crown of the male. Nestlings were aged between 8 and 21 days during observation periods, and weather conditions were favourable (no precipitation and mean min.-max. temperature of 9.6 and 22.4 °C; Environment Canada 2013). Time spent at the nest was split between time spent outside and inside the cavity. Food deliveries and nest sanitation were noted for all visits. Two different individuals made these observations from 06.00 to 16.00, and observations were recorded on a dictaphone to enhance recording speed, and ensure we did not miss any behavioral event. From these observations, we determined the following parental care measures: time spent at nest (outside, inside the nest, and total), rate of food delivery (number of food delivery per hour), nest sanitation (% of visits with transportation of fecal bag), number of visits/hour, and interval duration between consecutive visits.

Statistical analysis

We used a combination of linear models and descriptive statistics to assess the relative influence of variables that may influence parental care of Black-backed Woodpeckers. Time spent at nest and rate of food delivery were examined using a generalized linear mixed model where woodpecker ID was included as a random variable to account for replicate observations per individual. After a preliminary exploratory analysis, we limited our set of explanatory variables to three (“habitat type”, “number of nestlings” and “sex”) in order to be parsimonious. We specifically used GLMM for zero-truncated count data using *glmer.nb* function in the *lme4* package (Bates *et al.* 2015). This approach is suitable when the data cannot include zero. As “Time spent at nest” showed some evidence of over-dispersion, we subsampled with a cut-off value of 500s. Homogeneity of residuals was assessed by plotting residuals against fitted values, and normality of residuals was checked by visual inspection.

Considering our low sample size, we limited our set of biologically relevant models to single variables and an intercept-only model, resulting in a set of 4 models. We used Akaike’s Information Criterion (AIC) to evaluate the set of candidate models (Burnham & Anderson 2002). For each model, we calculated ΔAIC as the difference between that model and the model with the lowest AIC value in the candidate set. We also examined the AIC weights (w_i), which are a measure that indicates the probability that the model is the best in the set. We assumed all models within 2 ΔAIC units of the top model as having support but we also considered support for each variable by comparing it against the same null model with only an intercept. In this case, when that model has a lower AIC despite the additional parameter we can infer support for the inclusion of that variable (Burnham & Anderson 2002).

We only report descriptive statistics to compare time spent at nest between sexes and habitats, between the time spent inside and outside the nest, rates of food delivery in relation to the number of nestlings and between habitats, nest sanitation between habitats, and lastly, duration of intervals between consecutive visits between habitats. For each comparison we report the mean \pm SE and 95% confidence limits uncorrected for repeated measurements.

All statistical tests were done using R version 3.2.0 (R Core Team 2015).

Results

Parental care of 9 Black-backed Woodpecker pairs were monitored in this study; 6 pairs in burned (2.9 ± 0.2 nestlings/nest) and 3 pairs in unburned forests (2.3 ± 0.3 nestlings/nest), for a total of 41.2 and 40.3 hours of observation in each habitat respectively and a total of 710 observations.

A model with sex was the most supported model for time spent at nest with an AIC weight of 0.66, although habitat also had a weaker influence with a drop in AIC of 1.92 units relative to the intercept only model (*Table 1*). Visit durations were longer in males (79.4 ± 8.7 sec) than in females (29.4 ± 3.3 sec) (*Table 2*), primarily because females do not enter the nest cavity as often as males. It seemed to have two peaks of time spent at nest during the day, one on the morning and the other in the afternoon (*Figure 2*). Time spent at the nest tended to be higher in unburned (97.9 ± 13.7 sec) than in burned habitat (36.5 ± 3.4 sec) (*Table 2*).

Model	log(L)	AIC	Δ AIC	w_i	K	Variance of the random factor
<i>Time spent at nest</i>						
Sex	-3122.24	6252.47	0	0.66	2	0.390
Habitat	-3123.40	6254.78	2.31	0.21	2	0.444
Intercept-only	-3125.35	6256.70	4.23	0.08	1	0.558
Number of nestlings	-3124.86	6257.71	5.24	0.05	2	0.526
<i>Rate of food delivery</i>						
Number of nestlings	-419.62	847.23	0	0.66	2	0.110
Habitat	-420.31	848.63	1.40	0.33	2	0.139
Intercept-only	-424.99	855.98	8.75	0.01	1	0.328
Sex	-424.96	857.92	10.69	<0.01	2	0.328

Table 1. Model selection results for parental care of 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during the nestling period. Analyses were conducted using generalized linear mixed-effects models (GLMM for zero-truncated count data) which contained "woodpecker ID" as a random effect to control for repeated observations

1. táblázat A modell szelekció eredményei 9 feketehátú hócsik költőpár esetében (6 pár a leégett, 3 pár a le nem égett élőhelyen) a fiókanevelési időszakban. Az analízisek során általánosított lineáris kevert modellt alkalmaztunk (GLMM for zero-truncated count data), amely tartalmazta az egyedek azonosítóját „woodpecker ID”, mint random hatást az ismételt megfigyelések figyelembe vételére

Response variables	Mean	SE	95% Confidence limits	
			Lower	Upper
<i>Interval durations between visits (minutes)</i>				
Burned	8.2	0.5	6.8	9.6
Unburned	17.6	1.2	12.3	22.9
<i>Nest sanitation (%)</i>				
Female	1.1	0.6	0.7	1.6
Male	27.8	2.4	26.0	29.7
<i>Rate of food delivery (visits per hour)</i>				
2 nestlings	2.0	0.4	0.0	3.9
3 nestlings	5.5	0.5	4.1	6.9
Burned	5.3	0.6	3.8	6.8
Unburned	2.4	0.3	1.0	3.7
<i>Time spent at nest (seconds)</i>				
Female	29.4	3.3	21.8	37.0
Male	79.4	8.7	59.2	99.5
Burned	36.5	3.4	27.9	45.2
Unburned	97.9	13.7	39.0	156.7
Inside	86.9	11.3	60.8	113.0
Outside	35.6	3.4	27.8	43.4

Table 2. Mean, SE and 95% Confidence limits of response variables investigated in parental care of 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during nestling period

2. táblázat 9 pár feketehátú höcsik (6 pár a leégett, 3 pár a le nem égett élőhelyen) szülői utódgondozását leíró változók átlaga, standard hibája és 95%-os konfidencia-intervallumai a fiókanevelési időszakban

Time spent inside the cavity (86.9 ± 11.3 sec) was significantly longer than time spent on the nest tree (35.6 ± 3.4 sec) (*Table 2*).

Models with number of nestlings and habitat had the highest support for food delivery rate of Black-backed Woodpecker pairs with an AIC weight of 0.66 and 0.33 respectively (*Table 1*). Indeed, food delivery rates tended to be higher for nests with 3 nestlings (5.5 ± 0.5 deliveries/hour/adult) than for nests with 2 nestlings (2.0 ± 0.4 deliveries/hour/adult), and to be different among habitats with a mean of 5.3 ± 0.6 and 2.4 ± 0.3 deliveries/hour/adult in burned and unburned habitats respectively (*Table 2*). Accordingly, interval durations between visits were significantly different among habitats with a mean of 8.2 ± 0.5 and 17.6 ± 1.2 min between visits in burned and unburned habitats respectively (*Table 2*). Parents had food in most of the visits in both habitats (97.1% and 94.1% of the visits in burned and unburned habitats respectively).

Males removed fecal bags more frequently ($27.8 \pm 2.4\%$ of visits) than females ($1.1 \pm 0.6\%$) (*Table 2*), where males removed almost exclusively fecal bags (98 removals by males and only 4 by females).

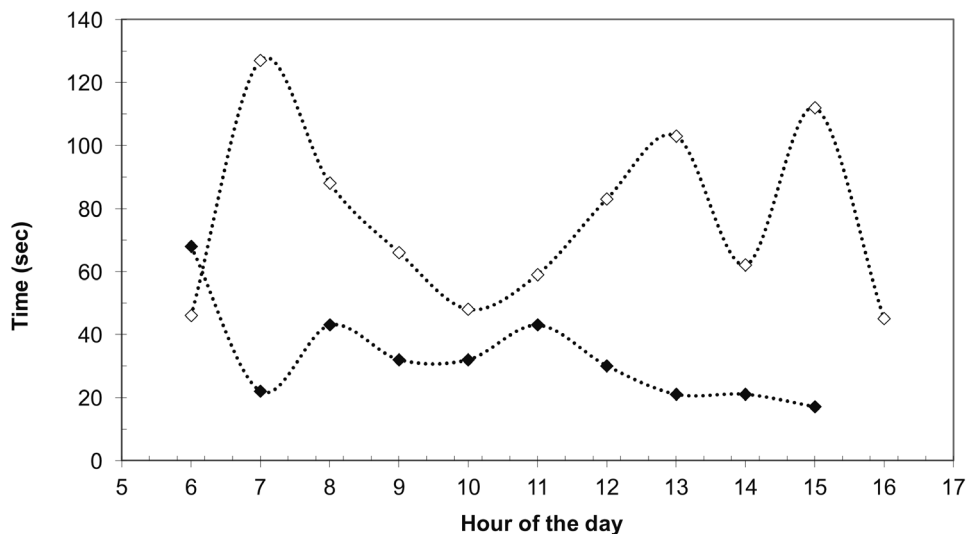


Figure 2. Mean time passed at nest (sec) during hour of the day by 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during nestling period (white: males, black: females)

2. ábra A nap adott órájában a 9 pár (6 pár a leégett, 3 pár a le nem égett élőhelyen) feketehátú hősík által, fiókanevelési időszakban, a fészeknél eltöltött átlagos idő (másodpercben) (fehér négyzet: hímek, fekete négyzet: tojók)

Discussion

Our study is based on a limited sample size, but offer first insights into the relative influence of both parental sex and habitat on parental care by Black-backed Woodpecker. Further research with larger sample sizes is needed to verify our results and to investigate the patterns we found in greater detail. Our results show that the sexes differ in the parental contribution to nest care in this species with males being more involved in nest sanitation and time spent at the nest. We also found that habitat is an important variable in explaining rates of food delivery, after taking into account the number of nestlings in the cavity.

Black-backed Woodpeckers showed high rates of food delivery with more than 94% of visits with prey in both habitats of the study area. Recently burned habitats are known to have a high density of xylophagous insect larvae (Saint-Germain *et al.* 2004, Boulanger & Sirois 2007) that offers abundant foraging opportunities for woodpeckers such as the Black-backed Woodpecker, and prey availability influences rate of food delivery (Naef-Daenzer *et al.* 2000). Such greater abundance of prey may explain the higher rates of food delivery by Black-backed Woodpeckers observed in burned habitat, where rates were more than 2 times higher in burned habitat. However, in burned habitat food delivery rates observed in this study are lower than those reported for the species by Short (1974) in an unburned habitat of northeastern United States (NY) where a mean of 12.4 feedings/hour was observed during 5 consecutive days at a single nest (perhaps 5 nestlings based on Short (1974). This may be explained by the fact that observations of Short (1974) come from forest stands flooded

by recent damming activities by beaver, where favorable habitat conditions may have been generated for wood-boring larvae (Soto *et al.* 2002). Nevertheless, times between visits were longer in unburned habitats as prey may be spatially more dispersed. In an exploratory study, Tremblay *et al.* (2014) reported that amount of unburned old coniferous habitat (food availability) within the home range positively influenced weight gain in Black-backed Woodpecker nestlings. Consequently, interval durations between visits and rates of food delivery may reflect more dispersed food availability in the home range. More studies should be done to examine this relationship.

In our study, the number of nestlings seemed to influence rate of food delivery by Black-backed Woodpecker parents, following by habitat. Accordingly, we observed a higher rate of food delivery for nests with more nestlings with 4.0 and 11.0 deliveries/hour for nests containing 2 and 3 nestlings respectively. This rate corresponds to 2.0 and 3.7 feedings/nestling/hour. These results are quite surprising as we expected to observe a decrease in food delivery rate/nestling with an increase in the number of nestlings per nest as reported for Northern Flickers (*Colaptes auratus*) (Gow *et al.* 2013). No comparable study exists for the Black-backed Woodpeckers. Kozma and Kroll (2013) studied provisioning rates for Hairy (*Picoides villosus*) and White-headed Woodpeckers (*Picoides albolarvatus*), two species that take advantage of burned habitats and frequently feed on wood-boring larvae (Raphael & White 1984, Covert-Bratland *et al.* 2006, Kozma & Kroll 2013) as in the Black-backed Woodpecker. For these two species, mean provisioning rates of about 4 and 3.5 feedings/nestling/hour were observed in nests with 2 and 3 nestlings respectively for Hairy Woodpeckers and about 3.6 and 3.0 feedings/nestling/hour in nests with 2 and 3 nestlings respectively for White-headed Woodpeckers. Thus, the rate of food delivery we observed for Black-backed Woodpecker nests with 3 nestlings is comparable with Hairy and White-headed Woodpeckers while delivery rates for nests with 2 nestlings was lower. This difference may be explained by habitat types as 2 of 3 nests monitored in unburned habitat had 2 nestlings while 5 of 6 nests monitored in burned habitat had 3 nestlings although this interaction did not perform well in our model selection. We have previously found that productivity per nest in the Black-backed Woodpecker is on average 0.9 nestlings/nest higher in burned than in unburned habitats (Tremblay *et al.* 2016).

Studies on food deliveries by Black-backed Woodpecker report that females feed nestlings more frequently than males (Kilham 1966, Short 1974; two and one nest respectively). Sex was not an important variable influencing food deliveries in our study, but was important for time spent at nest and nest sanitations were almost exclusively made by males. Indeed, females rarely entered the cavity and our results show that visits inside the cavity were about 2.5 times longer than visits where the parent remained at the cavity entrance. Time spent inside the nest may not only include time searching for fecal sacs, but also other activities such as pecking walls inside the cavity to add fresh layers of woodchips to cover debris/feces, to stimulate nestling defecation (Backhouse 2005), or thermoregulate when nestlings are too young to thermoregulate themselves. Our results are congruent with those of Short (1974) reporting, for one nest, that the female removed fecal sacs on only 3 percent of her 234 visits, and the male remove 12 times more sacs overall than the female. An important variable that may explain the predominance of males in nest sanitation is the aggressiveness

of nestling Black-backed Woodpeckers. Indeed, during our study nestlings had attacked parents in many occasions and were also reported in other studies (Short 1974, Kilham 1983). Such aggressiveness does not seem to be a frequent behavior in woodpeckers, and was not reported in American Three-toed Woodpecker (*Picoides dorsalis* – reported as *P. tridactylus* at this time) nestlings by Short (1974).

Although time spent at the nest/visit was longer by a factor of 2.7 in unburned habitat, mean time spent at the nest/hour (time spent at nest/visit*nb of visits/hour) was shorter by only a factor of 1.2 in unburned habitat (4.2 min/hour vs 3.4 min/hour in unburned and burned habitats respectively). Thus parents may compensate for their fewer visits in unburned habitat by a longer duration of the visit and total time spent at nests were comparable between both habitats.

Conclusion

Although our study is based on limited sample size and needs to be supported by further studies, it represents one of the only existing studies on parental care in Black-backed Woodpecker. Overall, our results show that males are more involved in nest sanitation and time spent at the nest, and both sexes exhibit higher food delivery rates and seemed to spend less time at the nest per visit in burned habitat. Parent activities while away from the nest are unknown but our results suggest that raising nestlings, at least feeding them, in unburned habitat requires greater effort than in burned habitat, ultimately leading to fewer fledged young than in burned habitat (Tremblay *et al.* 2016). With our limited data, we observed difference in parental care between sexes, except for food delivery, but our results gave no indication of female disengagement, neither in burned habitat, a high food resource habitat for Black-backed Woodpecker, nor in unburned habitat, a lower resource habitat. Nevertheless, more intensive studies are needed to support our findings, acknowledging that it may be challenging to monitor more nests of Black-backed Woodpecker in unburned habitats during the same breeding season.

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References

- Backhouse, F. 2005. Woodpeckers of North America. – Firefly Books, Buffalo & New York
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B. & Grothendieck, G. 2015. Linear mixed-effects models using Eigen and S4. <http://lme4.r-forge.r-project.org/>
- Black, J. M. 1996. Introduction: pair bonds and partnership. – In: Black, J. M. (ed.) Partnership in birds: the study of monogamy. – Oxford University Press, Oxford, pp. 3–20.
- Bonnot, T., Rumble, M. A. & Millspaugh, J. J. 2008. Nest success of Black-backed Woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. – *The Condor* 110: 450–457. DOI: 10.1525/cond.2008.8460
- Boulanger, Y. & Sirois, L. 2007. Postfire succession of saproxylic arthropods, with emphasis on Coleoptera, in the north boreal forest of Quebec. – *Environmental Entomology* 36: 128–141. DOI: 10.1603/0046-225X-36.1.128
- Burnham, K. P. & Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. – Springer Verlag, New York
- Chazarreta, M. L., Ojeda, V. S. & Trejo, A. 2011. Division of labour in parental care in the Magellanic Woodpecker *Campophilus magellanicus*. – *Journal of Ornithology* 152: 231–242. DOI: 10.1007/s10336-010-0570-4
- Clutton-Brock, T. H. 1991. The evolution of parental care. – Princeton University Press, Princeton
- Covert-Bratland, K. A., Block, W. M. & Theimer, T. C. 2006. Hairy Woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. – *Journal of Wildlife Management* 70: 1379–1392. DOI: 10.2193/0022-541X(2006)70[1379:HWWEIP]2.0.CO;2
- Dixon, R. D. & Saab, V. A. 2000. Black-backed Woodpecker (*Picoides arcticus*). – In: Gill, F. B. & Poole, A. (eds.) *The Birds of North America* 509. Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologist's Union, Washington DC.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. – *Science* 197: 215–223.
- Environment Canada 2013. Canadian climate data web site. <http://www.climate.weatheroffice.ec.gc.ca>, downloaded 14.08.2013.
- Goggans, R., Dixon, R. D. & Seminara, L. C. 1989. Habitat use by Three-toed and Black-backed Woodpeckers. – USDA Deschutes National, Oregon
- Gill, F. B. 2007. Ornithology, 3rd ed. – W. H. Freeman, New York
- Gow, E. A., Musgrove, A. B. & Wiebe, K. L. 2013. Brood age and size influence sex-specific parental provisioning patterns in a sex-role reversed species. – *Journal of Ornithology* 154: 525–535. DOI: 10.1007/s10336-012-0923-2
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement in northern Rocky Mountain (USA) conifer forests. – *Conservation Biology* 9: 1041–1058. DOI: 10.1046/j.1523-1739.1995.9051033.x-1
- Ibarzabal, J. & Desmeules, P. 2006. Black-backed Woodpecker (*Picoides arcticus*) detectability in unburned and recently burned mature forests in north-eastern North America. – *Annales Zoologica Fennici* 43: 228–234.
- Kilham, L. 1966. Nesting activities of Black-backed Woodpeckers. – *The Condor* 68: 308–310.
- Kilham, L. 1983. Life history studies of woodpeckers of Eastern North America. – *Publications of the Nuttall Ornithological Club* 20: 1–240.
- Kozma, J. M. & Kroll, A. J. 2013. Nestling provisioning by Hairy and White-headed Woodpeckers in managed ponderosa pine forests. – *Wilson Journal of Ornithology* 125: 534–545. DOI: 10.1676/12-188.1
- Lack, D. 1968. Ecological adaptations of breeding in birds. – Methuen Publishing, London
- Lawrence, L. K. 1967. A comparative life-history study of four species of woodpeckers. – *Ornithological Monographs* 5: 1–156.
- Ligon, J. D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. – In: Power, D. M. (ed.) *Current Ornithology*. Vol. 10. – Plenum Press, New York, pp. 1–46.
- Mech, L. D. 1983. Handbook of animal radio-tracking. – University of Minnesota Press, Minneapolis
- Michalek, K. G. & Winkler, H. 2001. Parental care and parentage in monogamous Great-spotted Woodpeckers (*Picoides major*) and Middle-spotted Woodpeckers (*Picoides medius*). – *Behaviour* 138: 1259–1285. DOI: 10.1163/15685390152822210
- Murphy, E. C. & Lehnhausen, W. A. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. – *Journal of Wildlife Management* 62: 1359–1372. DOI: 10.2307/3802002
- Naef-Daenzer, L., Naef-Daenzer, B. & Nager, R. G. 2000. Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food

- availability. – *Journal of Avian Biology* 31: 206–214. DOI: 10.1034/j.1600-048X.2000.310212.x
- Nappi, A. & Drapeau, P. 2009. Reproductive success of the Black-backed Woodpecker (*Picoides arcticus*) in burned boreal forests: Are burn source habitats? – *Biological Conservation* 142: 1381–1391. DOI: 10.1016/j.biocon.2009.01.022
- Nappi, A., Drapeau, P. & Leduc, A. 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? – *Forest Ecology and Management* 346: 10–21. DOI: 10.1016/j.foreco.2015.02.028
- Oring, L. W. 1986. Avian polyandry. – In: Johnston, R. F. (ed.) *Current Ornithology*. Vol. 3. – Plenum Press, New York, pp. 309–351.
- R Core Team 2015. <http://www.R-project.org>.
- Raphael, M. G. & White, M. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. – *Wildlife Monographs* 86: 1–66.
- Ricklefs, R. E. 1983. Avian postnatal development. – In: Farner, D. S., King, J. R. & Parkes, K. C. (eds.) *Avian Biology*, Vol. 7. – Academic Press, New York, pp. 1–83.
- Rota, C. T., Millspaugh, J. J., Rumble, M. A., Lehman, C. P. & Kesler, D. C. 2014. The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of Black-backed Woodpeckers in the black hills, South Dakota. – *PLoS One* 9: e94700. DOI: 10.1371/journal.pone.0094700
- Saint-Germain, M., Drapeau, P. & Hébert, C. 2004. Comparison of Coleoptera assemblages from recently burned and unburned black spruce forests of northeastern North America. – *Biological Conservation* 118: 583–592. DOI: 10.1016/j.biocon.2003.10.007
- Saucier, J. P., Bergeron, J. F., Grondin, P. & Robitaille, A. 1998. Les zones de végétation et les domaines bioclimatiques du Québec [Vegetation zones and bioclimatic domains of Quebec]. – Ministère des Ressources naturelles du Québec, Sainte-Foy (in French)
- Setterington, M. A., Thompson, I. D. & Montevecchi, W. A. 2000. Woodpecker abundance and habitat use in mature balsam fir forests in Newfoundland. – *Journal of Wildlife Management* 64: 335–345. DOI: 10.2307/3803231
- Short, L. L. 1974. Habits and interactions of North American Three-toed Woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). – *American Museum Novitates* 2547: 1–42.
- Soto, G. E., Vergara, P. M., Lizama, M. E., Celis, C., Rozzi, R., Duron, Q., Hahn, I. J. & Jiménez, J. E. 2002. Do beavers improve the habitat quality for Magellanic Woodpeckers? – *Bosque* 33: 271–274. DOI: 10.4067/S0717-92002012000300007
- Tremblay, J. A., Ibarzabal, J., Dussault, C. & Savard, J-P. L. 2009. Habitat requirements of breeding Black-backed Woodpeckers in unburned boreal forest. – *Avian Conservation and Ecology* 4(1): 2. <http://www.ace-eco.org/vol4/iss1/art2/>
- Tremblay, J. A., Ibarzabal, J. & 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: 991–999. DOI: 10.1139/X10-044
- Tremblay, J. A., Ibarzabal, J., Savard, J-P. L. & Wilson, S. 2014. Influence of old coniferous habitat on nestling growth of Black-backed Woodpeckers *Picoides arcticus*. – *Acta Ornithologica* 49: 273–279. DOI: 10.3161/173484714X687172.
- Tremblay, J. A., Savard, J-P. L. & Ibarzabal, J. 2015. 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. DOI: 10.1016/j.foreco.2015.08.024
- Tremblay, J. A., Ibarzabal, J. & Savard, J-P. L. 2016. Demography of the Black-backed Woodpecker in unburned boreal forest stands in eastern Canada. – *Ecoscience*, in press
- Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser-spotted Woodpecker *Dendrocopos minor*. – *Journal of Avian Biology* 31: 447–456. DOI: 10.1034/j.1600-048X.2000.310003.x

