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LE PIC À DOS NOIR (*PICOIDES ARCTICUS*) : COLONISATION DES BRÛLIS RÉCENTS ET ÉTUDE DE SES DÉPLACEMENTS PAR L'ANALYSE D'ISOTOPES STABLES DE L'HYDROGÈNE





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RÉSUMÉ

Les densités de Pics à dos noir sont largement plus élevées dans les forêts de conifères brûlées qu'en forêts non brûlées. Selon des études récentes, l'espèce pourrait dépendre d'un apport régulier de brûlis récents (i.e. < 5-6 ans) dans le paysage pour maintenir ses populations à des niveaux viables. Pour atteindre ces brûlis, l'espèce effectue sans doute des déplacements importants. Les seules mentions de ce genre de mouvements proviennent de l'Observatoire d'oiseaux de Tadoussac (Québec) où l'on détecte annuellement d'importants déplacements automnaux de juvéniles mais peu de déplacements d'adultes. Ces observations suggèrent les hypothèses suivantes : 1) ce sont principalement les juvéniles qui coloniseront les brûlis récents; et 2) les déplacements des Pics à dos noir sont structurés selon l'âge des individus. Nous avons utilisé le deutérium contenu dans les plumes pour évaluer les distances parcourues annuellement (entre chaque période de mue). Le patron de mue particulier des pics, permet de déterminer l'âge et, selon cet âge, d'échantillonner des plumes d'âge différent sur le même individu. Nos résultats concordent avec la première hypothèse étant donné une différence dans la structure d'âge des pics entre les deux types d'habitats ($\chi = 9.43$, df = 2, P = 0.0088, n = 186). Cependant, cette différence peut être principalement expliquée par un nombre élevé d'oiseaux de troisième année (TY) dans les brûlis. Ceci suggère qu'une part de la colonisation se déroule l'été même du feu par des individus dans leur deuxième année de vie (SY) et par la suite par des juvéniles nés l'année même du feu (automne et hiver).

L'analyse d'isotopes stables d'hydrogène dans les plumes de jeunes encore au nid a révélé la présence d'un gradient latitudinal des isotopes de cet élément dans la région d'étude. Selon cette analyse, les SY (habitats confondus) semblent s'être déplacés au sud des lieux de naissance, pour atteindre les lieux de capture. Ce déplacement concorde avec les données provenant de l'Observatoire d'oiseaux de Tadoussac, qui suggèrent un déplacement automnal de la part de juvéniles de l'année vers le sud. En ce qui concerne les adultes, les TY et les 4Y ont mué au sud de leur aire de distribution au Québec selon les résultats d'analyse isotopique. Cependant, ces résultats impliqueraient un déplacement majeur vers le nord du Québec entre 2003 et 2004, vers les lieux de capture de 2004. Nous croyons qu'un autre phénomène appelé «refroidissement évaporatif» pourrait avoir lieu chez les individus plus âgés capables de voler et de s'alimenter par eux-mêmes. Une différence de métabolisme pourrait être la cause de ces différences de ratios isotopiques entre plumes d'un même individu ou entre groupes d'individus, rendant l'interprétation des signatures isotopiques plus difficile. Quoique peu de femelles de quatre ans (4Y) aient été capturées, nous croyons qu'elles ont tendance à poursuivre leurs déplacements, au-delà de la première année, contrairement aux mâles qui seraient davantage philopatriques à une région (les valeurs δD des plumes nous indiquent une latitude probable) ou un territoire acquis.

AVANT PROPOS

Ce mémoire comporte deux chapitres rédigés sous forme d'articles. En tant que candidat à la maîtrise en ressources renouvelables, j'ai participé à la supervision et à la récolte des données, à la préparation des échantillons en laboratoire, à l'analyse des résultas et à la rédaction de deux articles à titre de premier auteur. Le premier article a été accepté par la revue scientifique arbitrée «Annales Zoologici Fennici»: 1) A comparison of the age class structure of Black-backed Woodpeckers found in recently burned and unburned boreal coniferous forest in eastern Canada. Le deuxième article sera soumis à la revue scientifique arbitrée «Proceedings of the Royal Society B: Biological Sciences» dans les prochains mois: 2) Tracking early post-fire colonisation of boreal forest stands by Blackbacked Woodpeckers using hydrogen stable-isotope ratios. Mon directeur de recherche, le Dr. Jacques Ibarzabal sera coauteur des deux articles étant donné son implication dans l'élaboration de toutes les étapes du projet, tandis que le Dr. Keith A. Hobson sera coauteur du deuxième article pour son implication à l'analyse des résultats relativement aux isotopes d'hydrogène. Finalement, Dr. Jean-Pierre Savard sera aussi co-auteur du deuxième article pour sa participation dans le développement des idées de départ ainsi que pour son implication financière.

J'aimerais d'abord remercier mon directeur, Jacques Ibarzabal, qui a su me guider tout au long de ce projet. Étant un de ses premiers étudiants, je crois avoir bénéficié d'une grande disponibilité de sa part. J'apprécie aussi les opportunités qui m'ont été offertes

grâce à lui pendant ce temps, entre autres de participer à plusieurs congrès. De cette façon, j'ai pu faire reconnaître nos travaux sur le Pic à dos noir à la communauté scientifique ornithologique canadienne et internationale tout en visitant de nouveaux endroits. Justement, pendant ces rencontres, j'ai souvent été interrogé concernant notre efficacité à capturer des pics. Je leur ai répondu que le succès de notre équipe est dû au travail d'excellents techniciens et assistants de terrain possédant la passion pour leur travail. J'aimerais donc remercier à ce titre M. Christophe Buidin et M. Yann Rochepault pour avoir prêté leurs mains résistantes aux attaques de pics emmaillés, crieurs et enragés pendant plusieurs saisons de terrain d'affilée. Ce projet n'aurait pas été possible sans l'aide de plusieurs autres assistants et étudiants dont Simon Boily, Patrice Desmeules, François Gagnon, Lyne Morin et Junior Tremblay. Ce projet n'aurait pas été possible sans l'aide financière du Ministère des Ressources Naturelles et de la Faune, du Consortium de Recherche en Forêt Boréale Commerciale, le programme PAIR (UQAC), ainsi que le Service Canadien de la Faune. J'aimerais aussi remercier Louis Imbeau et Pascal Sirois pour avoir accepté de faire parti du comité de révision pour le dépôt initial de mon mémoire et d'y avoir apporté de commentaires forts pertinents.

J'aimerais finalement remercier mes parents qui m'ont encouragé pour tout et m'inciter à poursuivre mes intérêts en recherche, mes frères, Guillaume et surtout Annick pour toutes les heures de discussion et d'encouragement.

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INTRODUCTION GÉNÉRALE

Dépendance du Pic à dos noir envers les brûlis récents

Le Pic à dos noir (Picoides arcticus) est associé depuis longtemps aux brûlis récents et ce partout dans son aire de répartition (Blackford 1955; Apfelbaum et Haney 1981; Hutto 1995; Murphy et Lehnhausen 1998; Hoyt et Hannon 2002). Cette évaluation est largement basée sur le fait de la rareté générale de l'espèce en forêt non brûlée (Apfelbaum et Haney 1981, Niemi 1978) et à sa forte présence pendant les premières années suivant un incendie forestier (0.25 individus / hectare (Murphy et Lehnhausen 1998)). Au Québec, les chercheurs Imbeau et al. (1999) ainsi que Nappi et al. (2003) ont noté de très fortes densités de Pic à dos noir en brûlis récents. Bien que plusieurs études aient démontré de fortes abondances de ce pic tôt après feu, il faut aussi signaler que son abondance diminue rapidement quelques années après feu (2 à 3 ans; Murphy et Lehnhausen 1998). Le fait que l'espèce est présente dans les brûlis seulement pendant la période de forte abondance de larves d'insectes foreurs laisse croire que l'espèce colonise principalement les brûlis récents pour s'y alimenter (Dixon et Saab 2000; Nappi et al. 2003). D'ailleurs, il a été suggéré que l'arrivée régulière d'individus migrant des brûlis vers les forêts non brûlées entretiendrait une population puits dans ce dernier habitat (Hutto 1995). L'occurrence régulière de feux à l'échelle du paysage serait un facteur important dans le maintien des populations et de ce fait, la lutte contre les incendies forestiers et la coupe de récupération après feu pourraient nuire aux populations sources de Pics à dos noir (Nappi et al. 2004). Actuellement, aucune information ne peut confirmer ou nier cette hypothèse. Cependant, il demeure qu'une activité telle que la coupe de récupération intervient dans le processus de restructuration et de remise en marche naturel d'un écosystème forestier, comme suggéré dans Dellasala et al. (2006).

Historique des mouvements migratoires importants

Le Pic à dos noir est une espèce résidente (non migratrice) qui peut toutefois se déplacer sur de longues distances. Sa présence a déjà été observée à des centaines de kilomètres (West et Speirs 1959, Peterson 1988, Kilham et Foss 1994) au sud-est de son aire de distribution en Amérique du Nord (Fig. 1).



Figure 1. Aire de distribution du Pic à dos noir (*Picoides arcticus*). Birds of north America Online Database (Dixon et Saab 2000).

À plusieurs reprises, l'espèce a été observée au sud de son aire de distribution normale, ce qui démontre son habilité pour effectuer de grands déplacements (Van Tyne 1926, West et Speirs 1959, Yunick 1985, Dixon et Saab 2000). Plusieurs hypothèses ont été proposées pour expliquer ces déplacements sur de longues distances. Axtel (1957) propose que ces déplacements seraient liés à un succès reproducteur important suite à une

abondance de larves d'insectes foreurs (e.x. longicorne noir - Monochamus scutellatus (Say)) après de vastes feux de forêts en Ontario alors que Short (1982) suggère que c'est une diminution de la disponibilité en larves (ex. après leur émergence) qui crée une surpopulation de pic qui est suivie d'un exode vers le Sud. Villard et Schieck (1997) ont observé la présence de Pic à dos noir 10 jours après un incendie en Alberta, ce qui implique que la colonisation ou re-colonisation peut s'effectuer rapidement après un tel événement. Il est difficile de savoir si le Pic à dos noir est en mesure de détecter les brûlis récents éloignés de plusieurs kilomètres, mais nous croyons qu'il peut faire de grands déplacements au travers son aire de distribution. À titre d'exemple, suite à de feux de forêt de grandes superficies à 100-150 km au nord de Thunder Cape en Ontario en 1998 et 1999 (voir Carney 1999 et Escott 2001), plusieurs Pics à dos noir ont été observés à l'Observatoire de Thunder Cape pendant les automnes de 1999 à 2004 (David Hussel, données de Thunder Cape Bird Observatory, comm. pers.). Ces déplacements ayant lieu après l'occurrence des feux suggèrent, tout comme Axtel (1957) et Short (1982), qu'une combinaison de facteurs tels la surpopulation de Pic à dos noir et une diminution de larves d'insectes foreurs contribuent à l'exode de ces pics quelques années après feu.

Depuis 1996, l'Observatoire d'oiseaux de Tadoussac, Québec, a entrepris un programme d'observation et de capture automnal de pics. En moyenne, 158 Pics à dos noir y ont été observés à chaque année entre 1996 et 2005 dont 44 ont été capturés en 2005

(Denault et Drolet 2005). Ce déplacement saisonnier est perçu comme étant un mouvement de dispersion juvénile, puisqu'en moyenne 95 % des individus capturés sont des jeunes de l'année et ne sont pas recapturés les années suivantes.

Le suivi des déplacements par l'analyse d'isotopes stables de l'hydrogène

Diverses techniques comme le marquage-recapture et le suivi par télémétrie sont couramment utilisées pour faire le suivi des déplacements d'oiseaux. Cependant, ces techniques requièrent le marquage d'un nombre très élevé d'individus pour avoir la chance d'en recapturer quelques-uns (capture-recapture), ou bien l'investissement de beaucoup de temps à suivre des individus portant un émetteur (télémétrie). L'utilisation de lourds émetteurs GPS est hors de portée pour toutes espèces de petite taille, ce qui caractérise la plupart des oiseaux forestiers. C'est dans un tel cas que l'analyse d'isotope stables de l'hydrogène devient utile et très pratique dans le suivi des déplacements d'individus étant donné qu'elle est applicable tant à des petits organismes qu'à de grands. Les déplacements observables par cette nouvelle méthode sont dans l'ordre de 1,5 ° de latitude (Meehan et al. 2001), mais cette résolution peut varier selon les processus de fractionnement agissant dans la région étudiée et le régime alimentaire des espèces concernées (Hobson 2005).

L'analyse des isotopes stables de l'hydrogène est possible grâce au fractionnement d'isotopes stables de l'hydrogène présent dans l'eau des précipitations. Dans chaque

événement de précipitations, l'abondance des isotopes stables de l'hydrogène peut différer suite à des processus cinétiques associés à la température, l'évaporation et la condensation (Craig 1961). Étant plus lourd que l'hydrogène (¹H), le deutérium (²H ou D) se condense plus facilement lors d'événements de précipitations et s'évapore moins facilement que sa contrepartie plus légère. En Amérique du nord, une grande proportion de l'eau issue des précipitations provient de l'équateur et est distribuée vers le pôle nord en subissant un fractionnement. Ce processus de fractionnement crée un gradient latitudinal où les précipitations deviennent de plus en plus dépourvues de deutérium partant de la zone près de l'équateur vers le pôle nord (Fig. 2) (Araguas-Araguas et al. 2000).

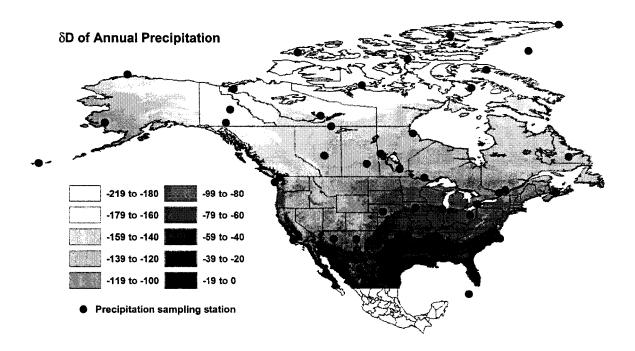


Figure 2. Modélisation du contenu isotopique en hydrogène des précipitations sur une base annuelle et exprimé en ratios δD pour l'Amérique du Nord (lien internet dans Meehan *et al.* 2004). Stations d'échantillonnage de précipitations représentées par points (•).

La figure 2 tient aussi compte d'un autre facteur pouvant influencer indirectement la signature de précipitations, soit l'altitude. Étant donné qu'une augmentation en altitude implique une baisse de température, il en résulte une diminution du contenu en deutérium dans les précipitations en ces lieux (Dansgaard 1964, Ziegler 1988). Aussi, la signature isotopique en hydrogène des précipitations varie selon les saisons en fonction de la température moyenne. Ainsi, les précipitations au cours des mois les plus froids contiennent moins de deutérium que celles qui ont lieu durant les mois chauds de l'année. La régularité de ces facteurs permet la formation de patrons de répartition de deutérium relativement stables à travers le monde.

Le gradient isotopique en deutérium nord-sud s'est avéré utile pour conclure sur les lieux d'origine et les déplacements de plusieurs espèces d'oiseaux migrateurs (Chamberlain et al. 1997, Rubenstein et al. 2002). Les organismes ingèrent les isotopes stables de l'hydrogène contenus dans leur nourriture, ce qui laisse une signature spécifique du lieu d'alimentation dans les tissus formés. Puisque les plumes n'échangent pas d'hydrogène avec le reste du corps une fois qu'elles sont poussées, la kératine qui les constitue est formée d'atome d'hydrogène correspondant au ratio (D/H) de leur lieu de croissance. Il est donc possible de connaître la latitude approximative du lieu de leur formation. La connaissance détaillée du processus de la mue est donc essentielle pour récolter les plumes adéquates et interpréter les résultats.

Le Pic à dos noir ne renouvelle pas toutes ses plumes à chaque année lors de sa mue basale (juillet-septembre), il retient spécifiquement certaines d'entres elles comme beaucoup de non passereaux. Cette mue s'effectue selon des patrons de rétention stables, permettant de déterminer par l'usure des plumes, l'âge des pics jusqu'à trois ou quatre ans (Pyle 1997). Il est donc possible d'évaluer les distances parcourues entre les sites de mues à partir des plumes que l'individu renouvelle annuellement.

Objectifs de l'étude

L'objectif général de l'étude vise à documenter la façon dont le Pic à dos noir colonise les brûlis récents de la forêt boréale québécoise. Plus spécifiquement, le premier chapitre vise à comparer les structures d'âge des populations de Pic à dos noir retrouvées dans les brûlis récents (un an après feu) et dans la forêt non brûlée. Nous voulons ainsi déterminer si les jeunes ont une meilleure capacité de colonisation des brûlis que les adultes. Le deuxième chapitre vise à déterminer la faculté de déplacement des Pics à dos noir et ainsi comprendre ses possibilités de colonisation des brûlis récents. L'examen du contenu en deutérium des plumes permettra de déterminer la provenance des individus en fonction de leur âge, de leur sexe et de l'habitat qu'ils occupent.

CHAPITRE I:

A COMPARISON OF THE AGE-CLASS STRUCTURE OF BLACK-BACKED WOODPECKERS FOUND IN RECENTLY BURNED AND UNBURNED BOREAL CONIFEROUS FORESTS IN EASTERN CANADA

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.

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1.0 Résumé

Black-backed Woodpeckers (*Picoides arcticus*) may depend on recently burned forest patches to maintain viable population levels. We wanted to determine how these habitats are colonized by this species and by which age classes. Data collected at the Observatoire d'oiseaux de Tadoussac (situated on the north shore of the St Lawrence (Québec, Canada)) suggest that an important movement of juveniles occurs during the autumn. It was therefore hypothesised that in the year following fire, burned forest sites would be colonized by a higher percentage of juvenile birds than intact mature stands. In accordance to this hypothesis, there was a difference in woodpecker age structure between the two habitat types ($\chi_2 = 9.43$, df = 2, P = 0.0088, n = 186). However, differences are mainly explained by the higher number of third calendar year birds at burned forest sites, suggesting that a part of the colonization occurs in the same year as the fire by second year birds, rather than by juveniles during the autumn.

1.1 Introduction

Census studies have demonstrated that Black-backed Woodpecker (*Picoides arcticus*) densities are usually much greater in recently burned coniferous forest than in unburned forest (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). Those habitats could be referred to as optimal and suboptimal respectively. These elevated densities in burned areas are usually of limited duration (a few years) and are linked to

outbreaks of woodboring insects (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). This implies that the recurrent occurrence of fire, a natural process in the boreal forest zone, may be a critical element in the maintenance of populations of this species, and that unburned forest might represent a sink habitat (Hutto 1995). While Hutto's hypothesis based mostly on point count data is very plausible, such a statement should ideally be backed by demographical data such as breeding success and mortality rates (Van Horne 1983, Vickery *et al.* 1992).

Although the Black-backed Woodpecker is considered a resident of the boreal forest, it is known to make irregular southward irruptions from its normal northern distribution range. Small groups of individuals have been recorded south to the north-eastern and even mid-eastern United States (Van Tyne 1926, West and Speirs 1959, Dixon and Saab 2000). Between 1950 and 1982, larger invasions lasting several years were recorded in the Maritime Provinces of Canada and in some states of the north-eastern United States (Yunick 1985). Some of these early movements (1950s) were linked to successful breeding following an abundance of wood boring insect larvae after the occurrence of large fires in Ontario (Axtell 1957). By contrast, later irruptions are thought to have been caused by low prey availability or possible overpopulation following such population explosions (Short 1982). Apart from these anecdotal reports, very little information is available on the movement patterns that are characteristic of this species and how individuals compete for space in recently burned and unburned forest.

Field data collected in five consecutive years (2000–2005) by the Observatoire d'oiseaux de Tadoussac, Tadoussac, Québec, Canada (Fig. 3) on Black-backed Woodpeckers migrating southwest along the north shore of the St. Lawrence River, show that 95% of the individuals ringed (n = 343) in the autumn (mid-September to mid-November) are juveniles (hatching year (Observatoire d'oiseaux de Tadoussac, unpubl. data)). This indicates an important dispersal of juveniles of this species during the autumn. It is known for many bird species that yearlings have a general tendency to relocate themselves to unoccupied territories, the distance travelled often depending on the occupancy of suitable territories encountered, habitat suitability and their carrying capacity (Van Balen 1980). Based on the above information, it seems likely that as it is mostly yearlings that disperse during the autumn, that it should be this age class that colonizes recently burned forest areas during the autumn of the year in which the fire occurred.

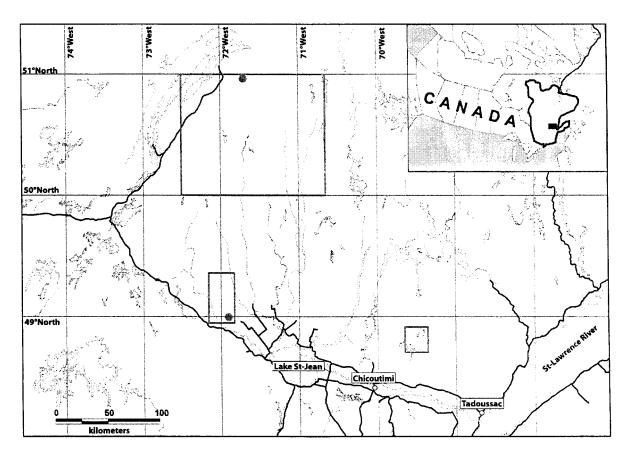


Figure 3. Location of the study area in northern Québec (Canada) with 2002 (49.9° Lat) and 2003 (49.0° Lat) forest burns. Red squares represent sampling areas in unburned forest.

Villard and Schieck (1997) showed that Black-backed Woodpeckers can nest in burned stands during the same year in which the fire occurred. However, the authors did not note the age of the individuals observed during the nesting attempts. If these are 'floaters' (young of the preceding year) that find a nesting territory in a newly burned forest, the colonization could take place much sooner than during the autumn dispersal of juveniles. Few studies are currently available regarding territorial fidelity in the Black-backed Woodpecker, but a few recaptures of banded individuals suggest that site fidelity is

high (Dixon and Saab 2000). This is supported by the fact that other species of the genus *Picoides* also show high site fidelity (e.g., *P. dorsalis* (American Three-toed woodpecker); L. Imbeau, personal communication and *P. tridactylus* (European Three-toed woodpecker) P. Pechacek, personal communication). Therefore, adult birds should dominate the age class structure of unburned forest sites.

In this study, we characterize Black-backed Woodpecker colonisation of burned forest in the boreal zone of Québec (Canada) one year after fire. We hypothesize that second year birds (age based on calendar year (Pyle 1997)) will be overrepresented in the age structure of recently burned zones in comparison with the age structure found in unburned forest sites. Moreover, if 'floaters' occupied the burned areas during the first summer season after fire, there should be an overrepresentation of three year-old woodpeckers in these sites as compared with that in unburned forest sites.

1.2 Materials and methods

1.2.1 Study areas

Both types of habitat (recently burned and unburned mature forest) were mainly composed of mature stands of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) interspersed with small stands of balsam fir (*Abies balsamea*) and scattered white birch (*Betula papyrifera*).

Since the Black-backed Woodpecker is known to colonize recently burned coniferous forest sites fairly rapidly after the occurrence of fire (Villard and Schieck 1997, Murphy and Lehnhausen 1998), it was important to select sites that burned during the previous summer season in order to have an accurate idea of the age classes colonizing burned sites. Site selection was done on the basis of fire occurrence in mature conifer forest during the 2002 and 2003 spring and summer periods. These years were relatively unproductive in terms of total accessible burned forest areas in northern Québec. Two burned forested areas were chosen: the first, a 2002 burn (1000 Ha), near the Tournemine logging Camp (Chantiers-Chibougamau Ltée; 51.0486°N, 72.6225°W), and the second, a 2003 burn (6500 Ha), near Saint-Thomas- Didyme (48.9958°N, 73.0491°W) (Fig. 3). These burned areas were the only selected sites during these two years because there were relatively few accessible and still unharvested, or only partly harvested, sites at the time scheduled for woodpecker captures one year after the burn. Therefore, birds captured in these two burned sites can be considered as having colonized the sites within the year after the fire event, and should provide an accurate picture of the immediate, "one year after", colonization pattern by Black-backed Woodpeckers of these burned areas. The sampling took place from 10 May-27 June 2003 (2002 burn + unburned), 27 April-8 July 2004 (2003 burn + unburned), and 15 May–10 July 2005 (unburned).

A similar effort was invested in the capture of birds in unburned forest, a habitat known to support much lower Black-backed Woodpecker densities than recently burned

forests (Murphy and Lehnhausen 1998). Sampling for woodpecker age structure in unburned mature forest was done in regions ranging from immediately adjacent to the burned areas and up to several hundred kilometres from them, according to road access, logistics, and the maturity of conifer stands.

1.2.2 Capture methods

If no Black-backed Woodpeckers were seen or heard upon arrival at a given site, vocalisations of this species (Elliott et al. 1997) were played for a maximum of 20 minutes. Following a response, vocalisations were immediately stopped until mist nets were installed. Nets were disposed differently according to site characteristics, tree and snag density, branch layout and wind conditions during capture. Nets were installed in small open areas with few or no perching sites, and surrounded by uncut burned fragments, riparian strips or unburned stands, in order to force low flight altitude by the woodpeckers. In addition, when no snags were available, short snag "look-a-likes" were positioned upright between nets to provide a suitable perching site. Finally, a small speaker playing the rattle call ("pet-pet-wreoo") of a Black-backed Woodpecker (Dixon and Saab 2000) was placed at the base of the snag. Black-backed woodpeckers use this call both agonistically against conspecifics and when establishing territories (Dixon and Saab 2000). Typically, woodpeckers attracted by this method perch at the top of a tree surrounding the open area and then fly in low to investigate the calls and finally end up in one of the mist nets. On certain sites captures were done at the nest cavity.

1.2.3 Molt patterns and ageing

The Black-backed Woodpecker, like most North American (Pyle 1997) and European woodpeckers (Miettinen 2003), is well known to renew its flight feathers in a sequential pattern during each annual molt. Retained feathers are usually paler and more worn than renewed ones, with feathers often showing accelerated wear in areas lacking pigment (white) (Pyle 1997). The age can be precisely determined to up to three years by the examination of primary coverts and secondaries patterns (Pyle 1997). In spring, nestling of the year before are considered as second calendar year birds (SY) and those hatched two years before as third calendar year birds (TY). Thereafter birds showing asymmetrical retention patterns are categorized as being older than three years (ATY).

1.2.4 Statistical analysis

A contingency table analysis using a Pearson chi square test was used to determine whether the age class structure (SY, TY and ATY) obtained from Black-backed Woodpeckers captured both in recently burned and in unburned mature conifer forest were different. A similar contingency table analysis was also used to verify whether inter-habitat variations in the proportion of each sex and in the three age classes occurred.

1.3 Results

Prior to analysis, data from each habitat type were pooled regardless of sampling year since no year effect was found. A total of 186 Black-backed Woodpeckers were captured, 100 at burned forest sites and 86 at unburned forest sites, and their age determined (Fig. 4). Second-year Black-backed Woodpeckers were the most abundant at burned forest sites and ATY were the most abundant at unburned forest sites. We found a significant difference in terms of woodpecker abundance per age class between the two habitat types ($\chi 2 = 9.43$, df = 2, P = 0.0088, n = 186) but this difference was mostly due to the abundance of TY individuals at burned versus unburned forest sites (Fig. 4). No sexwise differences in habitat frequentation were observed ($\chi 2 = 0.041$, df = 1, P = 0.8394, n = 186). On the other hand, we found a difference in the age structure between habitats for males ($\chi 2 = 9.876$, df = 2, P = 0.0072, n = 98), but not for females ($\chi 2 = 3.814$, df = 2, P = 0.1485, n = 88). When assessed independently, the age structure of each sex was markedly different (Fig. 4) indicating that the pooled age structure was mostly influenced by interhabitat differences in the abundance of males of the different age classes.

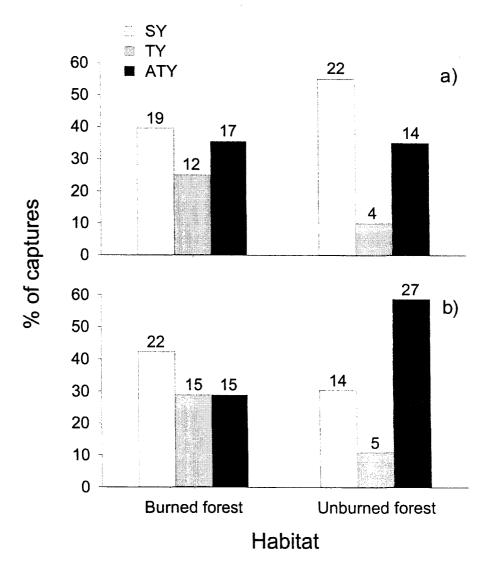


Figure 4. Age structure of Black-backed Woodpecker occupying burned and unburned coniferous forest of Quebec: (a) females and (b) males. Age structure is represented in three classes: birds in their second calendar year (SY), third calendar year (TY) and more than 3 years (ATY). Numbers of individuals caught are presented above each column.

1.4 Discussion

1.4.1 Age class structure

The age structure analysis indicates that the Black-backed Woodpeckers in our study exhibit a different age class structure at recently burned forest sites than at unburned mature conifer forest sites. Contrary to initial expectations, juveniles (SY) were not as abundant at burned sites as initially expected when compared to the other age classes (Fig. 4). In fact, ATY birds were almost as abundant as TY birds at burned forest sites and only a little less than SY. This was unexpected because the only known movements in Québec seem to be by current year birds (Denault et Drolet 2006). In theory, by dispersing after fledging juveniles may, on a regional scale, come into contact with a new territory. Also, if recently burned forest areas are considered as being the best habitat for the Black-backed Woodpecker, individuals should be inclined to respond positively to such disturbances as new territories become available, regardless of whether the individual possesses a territory or not at the time of the fire event. However, the present results suggest another possibility: that these movement of individuals recorded at Tadoussac (see Fig. 3) during the autumn is only a partial representation of what is actually happening in terms of movement of this species throughout the year. It seems logical that a good number of woodpeckers near the burn respond to it by colonizing the area immediately. This input of potentially already established and/or older individuals from near the perturbation further complicates the interpretation of the age class structure observed in both habitat types. It also indicates that Black-backed Woodpeckers of other age classes may move at other periods of the year than the autumn. As many SY birds were captured in unburned forest, results suggest that this age class colonizes both habitats quite readily. For birds caught in burned areas, certain indications, such as the presence of charcoal on the breast and the wear of tail feathers, could provide an estimate of the time an individual has spent in the burned area (J. Ibarzabal, unpubl. data). Interestingly, in late April and early May we caught not only SY birds but also ATY birds with little or no charcoal stains on their breast feathers and with non abraded tails, indicating that they had recently arrived in the burned area. This result suggests the presence of 'floaters' within the population, which move to find new territories or mates at other periods of the year than during the autumn. The proximity to which unburned forest sites may have been to burned sites could have contributed to the observed age class structure in burned forest (St-Thomas-Dydime fire mostly). Captures in burned forest were often close to unburned forest. It is possible that small fires may be more affected than large ones by the incoming of older aged individuals from surrounding unburned habitat.

Furthermore, the present results show a major inter-habitat difference in the abundance of TY birds, with unburned forest being less frequented by this age class than burned forest. As hypothesized before, this finding may be explained by the fact that some woodpeckers that we estimate as yearling 'floaters' (SY by 1 January following their hatching year) could find the burned area during the summer of the year in which the fire occurred (Villard and Schieck 1997). Since woodpeckers were caught the year after the fire

occurred, these birds were now in their third year which makes it plausible that the low presence of these TY birds would be more pronounced in unburned habitat. It is possible that many TY birds found in unburned forest were still without an established territory at the time of the study. If this was the case, it is possible that they were less frequently caught because the playback technique targets territorial individuals. In such a situation, less three years olds would be caught at unburned forest sites because they are not territorial and it may be more difficult to acquire a territory and defend it.

On the other hand, the relatively high abundance of TY birds at the recently burned sites in the present study could indicate that it is easier for an individual of this age class (still relatively young for a woodpecker) to gain access to a territory with high food availability and other possible advantages. While TY birds may be present but simply not responding in unburned forest, this doesn't explain why more SY than TY birds were detected in unburned forest. As individuals get older, experience should lead towards facilitated territory acquisition and the TY birds in our study should be more present than SY birds. As we initially thought, the ATY age class was less important in burned forest than other age classes. Interestingly, they were the most represented age class in unburned forest.

1.4.2 Habitat selection between sexes

Our results show no differences in habitat selection between sexes. This finding is in contrast with the results obtained by Murphy and Lehnhausen (1998), who showed that for Black-backed, Three-toed and particularly Hairy woodpeckers, females were far less numerous than males in the study area. The authors suggested inter-sexual displacement difference between foraging sites and habitats selected by males. In the case of age structure by sex (Fig 4a-b), the difference in the number of ATY males in unburned forest may be due to differences in habitat suitability according to gender, suggesting that for some reason males could have a higher tendency to remain in unburned forest once a territory has been established. Males of other species are known to show greater philopatry to their territory with age than females, notably after reproductive failure (Catchpole 1972). Difficulties in establishing territories may also influence older males to remain on known sites in order to facilitate territory defence (Greenwood and Harvey 1976).

1.4.3 Conclusion

Contrary to our expectations, age structure between theoretically optimal and suboptimal habitats (burned and unburned sites) shows little contrast. Even if the annual northsouth autumn migration contributed to the colonization of burned forest areas, age structure
suggests that colonization can begin during the year in which the fire occurred by SY birds.
Furthermore, the finding that males were represented in such different numbers per age

class and habitat in comparison to females was not expected. We believe that these results will help in understanding to what extent the Black-backed Woodpecker can use unburned forest habitat. Although there are indications suggesting that recently burned areas offer better habitat for population maintenance (Hutto 1995), the presence of young and old age classes in unburned forest point to the fact that it could also be an alternative habitat for this species. These results give the first overview of the abundance of this species per age class in two different habitats and, therefore, offer one of the few detailed insights into habitat frequentation by this species. Future studies should focus on movement analysis by age class to determine the habitat colonization capacity of Black-backed Woodpeckers and to determine site fidelity. Ideally, burned forest colonization by Black-backed Woodpeckers should be examined during the same year as fire occurrence in order to determine arrival dates by floaters. Forest fires would have to occur before mating season as individuals become much more difficult to capture after this period.

CHAPITRE II:

TRACKING EARLY POST-FIRE COLONISATION OF BOREAL FOREST STANDS BY BLACK-BACKED WOODPECKERS USING HYDROGEN STABLE ISOTOPE RATIOS

Huot, M., Ibarzabal, J., Savard, J.-P. L. and K. A. Hobson 2007: Tracking early post-fire colonisation of Boreal forest stands by Black-backed Woodpeckers using hydrogen stable isotopes. *Oecologia*.

2.0 Résumé

The presence of an annual juvenile Black-backed Woodpecker autumnal migration along the St-Lawrence north shore (Observatoire d'oiseaux de Tadoussac – OOT, Québec, Canada) led us to study movement history in a species closely associated to recently burned conifer forests. We used hydrogen stable isotopes in feather samples to evaluate movement history between molts, as this woodpecker's particular molt patterns allow age determination and the sampling of differently aged feathers on the same individual. Since juveniles are the only ones showing movement at the survey site (OOT), we assumed that adults should show signs of stabilisation in their feather δD values. The sampling of hatchling feathers allowed not only the confirmation of the presence of a latitudinal hydrogen isotope gradient in our study area, but also that second year individuals moved a significant distance southwards from their birth grounds to reach capture sites. On the other hand, three (TY) and four (4Y) year old individuals seem to have underwent their 1st (TY and 4Y) and 2nd (4Y) molts south of the species' normal distribution range, only to return north many hundred kilometres to their capture sites. These results lead us to believe that evaporative cooling may be causing different hydrogen isotope fractionation rates in adults than juveniles. Finally, the examination of sequential feather δD values between 4Y females and males indicate that females may not stabilize their movements as males do after their first molt.

2.1 Introduction

The Black-backed Woodpecker (BBWO) (*Picoides arcticus*) is associated to recently burned forest habitat throughout it's distribution range (Fig 1, Dixon and Saab 2000) (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). It has even been suggested that the species may be dependent to fire and that the regular emigration of individuals from recent burns to unburned conifer forest, when conditions become less suitable, could be the key to maintaining population levels in unburned forest at viable levels (Hutto 1995). In this situation, recent burns and unburned forest are considered by Hutto (1995) as being source and sink habitats, respectively.

In the past, the species has been shown to be present and to nest within a matter of days after a fire (Villard and Schieck 1997), but also to be in important breeding density the year following a fire (Murphy and Lenhausen 1998, Nappi *et al.* 2003, J. Ibarzabal, unpublished data). These events demonstrate the species' ability to colonize and use recent burns fairly rapidly after fire occurrence and that recent burns are a sought-after habitat.

This ability to colonize recent burns brings up the question as to the origins of individuals having emigrated into them. In fact, few records on breeding site fidelity are available but Dixon and Saab (2000) report a case where a few banded individuals were seen nesting in the same area for five consecutive years after a 500 ha fire that occurred in 1995 in south-western Idaho (U.S.). Other species of the genus *Picoides* also show high site

fidelity e.g., P. dorsalis (American Three-toed Woodpecker); L. Imbeau, personal communication and P. tridactylus (European Three-toed Woodpecker) P. Pechacek, personal communication). On the other hand, the Black-backed Woodpecker is capable of long distance movements throughout its distribution range in the north and mid-eastern United States (Van Tyne 1926, West and Speirs 1959, Yunick 1985, Dixon and Saab 2000). Larger winter invasions were recorded in the Maritimes provinces of Canada as well as in the north-eastern United-States (Yunick 1985). These movements have shown to be a few hundred km south of their distribution range, and may be due to successful breeding after a high abundance of wood-boring beetle larvae following the occurrence of forest fires (Axtell 1957) or an exodus caused by a low availability of prey a few years after the occurrence of wide scale forest fires (Short 1982). This is a typical response for a resident avian species, where a constant compromise is made between the potential lack of food during winter, which favours dispersion, and the lack of breeding sites, feeding sites and the global knowledge of the territory, which enhance site fidelity (Lundberg 1979). In theory, older individuals with an already acquired territory may be more prone to limiting their movements while juveniles, who do not hold territories, could undertake dispersal movement after fledging to ensure their needs are met. If they are less dominant than adults, they could be forced to disperse further before finding a suitable territory (Ellsworth and Belthoff 1999).

From recent capture data obtained by the Observatoire d'oiseaux de Tadoussac, Tadoussac, Quebec (2000-2005, unpublished data), we have an indication that fall dispersion movement implies near exclusively juveniles since mostly yearling birds (n = 343, 95 %) are seen passing through the area from mid-September to mid-November each year. Considering this, dispersal movements allowing colonisation of recently burned areas should be age class dependant. Thus, long distance movement should be done by juveniles whereas adults should colonize from nearby areas.

Several studies have used the North American latitudinal gradient of hydrogen stable isotopes to infer molting locations of migratory birds by determining the δD values of feathers known to have been grown on molting grounds (Chamberlain et al 1997, Hobson and Wassenaar 1997, Hobson et al. 2003). Hobson et al. (2003) have also demonstrated that δD values obtained after analysing feathers from hummingbirds of the Columbian Andes also became more negative with an increase in altitude. Since these isotopes are taken in by animals as food and water, the quality of results can be influenced negatively if individuals feed at different locations during feather growth. This has proven to be problematic in raptor studies were captured individuals had possibly been using endogenous reserves accumulated while in migration during their feather renewal period (Meehan et al. 2003). So far, use of hydrogen stable isotope analysis has also mostly been limited to migratory species in North America that execute important movements to and from their breeding and wintering grounds each year even though resolution is estimated to be 1.5 ° of latitude (Meehan 2001). Thus, in the case of a non-migratory species feeding near exclusively on insects locally produced, determining molt locations by hydrogen stable isotope analysis is possible. As Black-backed Woodpeckers are well known to

undergo annual partial molts, stable retention patterns are created, permitting 1) to age individuals up to three years, and 2) to observe up to three differently aged feathers on these old individuals at the same time (Pyle 1997). Therefore, having the possibility to associate a feather to a particular molt year allows the determination of the approximate region where each feather was grown, but also where the individual was at time of molt. Evaluating the distance between molt locations can thereafter be done by calculating the difference between feather δD values associated to each molt year or individual age.

In this study, our first objective was to determine whether the deuterium gradient in northern Québec was sufficiently present to allow the differentiation of individuals within relatively close sampling locations (in the order of 100 to 200 km). Secondly, we looked at whether individuals that have colonized selected recent fires one year after occurrence and ones captured in unburned forest originate from near or distant areas according to δD values of feathers grown during the previous year's molt. This was done while considering for age and sex. We also verified whether movement patterns done by each age class (two year old; SY, three year old; TY and after three year old; ATY) differed according to age and gender (age based on calendar year (Pyle 1997)). Finally, we determined whether older individuals are being philopatric to their territory at time of capture.

2.2 Materials and methods

2.2.1 Study area

Captures for feather sampling took place from 15 May - 23 June 2003 and 27 April - 8 July 2004 in a study area located West and North of Lake Saint-Jean (Québec) (Fig. 5). Sampling was done near roadside of both recently burned and unburned forest. Both types of habitat (recently burned and unburned mature forest) were similar in terms of tree species present. Black Spruce (*Picea mariana*) and Jack Pine (*Pinus banksiana*) stands were most abundant on almost all sites, interspersed with small stands of Balsam Fir (*Abies balsamea*), Trembling Aspen (*Populus tremuloides*) and scattered White Birch (*Betula papyrifera*) in areas of regeneration.

For the duration of the study, we worked in two recently burned forest areas according to their availability and their accessibility. One occurred in 2002 (1 000 ha) and the second in 2003 (6 500 ha). These burned areas were still only partly harvested at scheduled time of woodpecker captures one year later in spring. Since density was high in recently burned forests, Black-backed Woodpeckers were captured at sites often less than 500 m apart. In unburned forests, the density was lower and time necessary for detection (and capture) was longer (Ibarzabal and Desmeules 2006). We attempted to attract and capture them at every kilometre and since we had only approximately 30% of response to our playbacks (personal data), we used a larger area to catch them in comparison to burned areas. Moreover, sampling was concentrated in areas surrounding several logging company

camps for logistical reasons and to allow the use of newly constructed roads leading to uncut forest. Since few forest fires occurred in the region shortly prior to the study, the majority (ca. 90%) of SY, TY and ATY captures in recent burns took place in two small burned forest areas west of Lake St-Jean, while those in unburned forest were in a larger area approximately 200 kilometers north of Lake St-Jean. Nestling captures in burned forest took place only in the southern fire west of lake St-Jean (St-Thomas-Didyme 2003 fire sampled in 2004) and not the 2002 burn sampled in 2003 due to a lack of forest fires during and previous to the sampling years. Meanwhile, captures in unburned forest took place in the unburned region north of Lake St-Jean in 2004 mostly because unburned forest suitable for Black-backed Woodpeckers was inaccessible to us and/or not present in the southern sampling region of Saint-Thomas-Didyme.

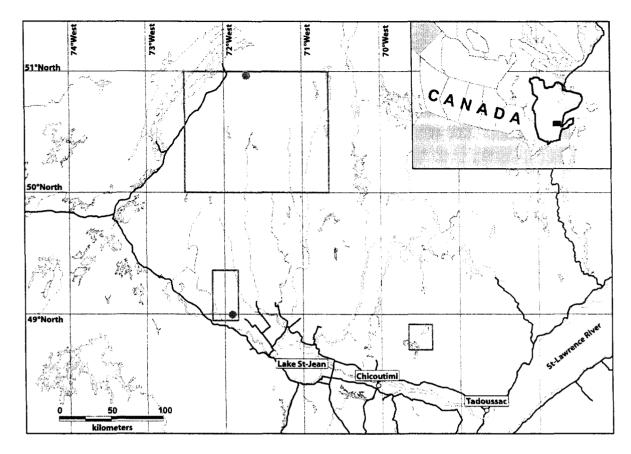


Figure 3. Location of the study area in northern Québec (Canada) with 2002 (49.9° Lat) and 2003 (49.0° Lat) forest burns. Red squares represent sampling areas in unburned forest.

2.2.2 Capture methods

Mist nets were installed to capture individuals in areas recently cleared after fire but still surrounded by uncut burned fragments or beside forest access roads in unburned mature forest. Black-backed Woodpecker vocalisations (Elliot *et al.* 1997) were played in vicinity of the nets to induce territorial responses (Huot and Ibarzabal 2006). In order to obtain samples from nestlings after having searched for nests, we proceeded by drilling a hole using an 18V wireless drill equipped with a 4 inch hole saw, the top being

approximately 1 to 2 inches below cavity entrance. This procedure allowed us clear access to nestlings (Ibarzabal and Tremblay 2006). All openings were immediately resealed after manipulations and all handling steps were done according to animal care committee approbation (# 0351).

2.2.3 Molt patterns, ageing and gender determination

Unlike most passerines, non-passerines like the Black-backed Woodpecker experience partial molts on an annual basis. In this situation, stable molt patterns allow ageing up to three years of age, where thereafter birds showing unknown retention patterns are categorized as being older than three years (ATY) (Pyle 1997). Although still unofficial, it might be possible to age certain individuals BBWO to four years of age (in spring) if specific symmetrical retention patterns are found on each wing. Of those captured, we identified a number of individuals showing these symmetrical patterns and included them in movement analyses. Finally, distinguishing males from females is easily done as males have a prominent yellow patch on the center of the crown while females lack this feature (Dixon and Saab 2000).

2.2.4 Feather sampling to determine philopatric tendencies

In SY birds, one mid-secondary or primary covert feather was sampled by cutting one to two cm from the tip. Since TY individuals typically retained feathers in their mid

secondaries and inner primary coverts, one renewed feather and one retained feather were sampled either in primary coverts or secondaries as pairs, whichever showed the clearest contrast for comparison. Finally, ATY birds showing symmetrical retention pattern were sampled in the same way as TY birds, except that three samples were taken if feathers showed different wear patterns. For all age classes, feathers showing the least color change from black to black-brown were considered the newest, according to the species molt patterns suggested by Pyle (1997). We obtained an estimate of movement between spring 2003 and 2004 in all individuals by collecting nestling feathers throughout the sampling sites and comparing their δD values to recently renewed feathers of captured Black-backed Woodpeckers. Furthermore, the two and three feather sets obtained from TY and 4Y individuals allowed us to have a clearer idea on whether individuals are being philopatric to their capture site after initial juvenal dispersal.

2.2.5 Isotope analysis

All samples were cleaned using a 2:1 chloroform / methanol solution to remove surface oils and contaminants prior to sample weighing. Thereafter, feather samples were left to dry under a fume hood for at least 48 hours. Small amounts of feather material weighing $350 \pm 10 \,\mu g$ were compacted into $3.5 \, x$ 5.0 mm silver capsules (Costech Analytical). Analyses were done by the Colorado Plateau Stable Isotope Laboratory (CPSIL) in spring 2004. Feather samples and standards were left in slightly open trays at the CPSIL for 48 hours to allow for equilibration with ambient moisture. Standards were

previously analysed (CPSIL lab 2004) for their % in exchangeable hydrogen content via steam equilibration with vapour of known isotopic content (Wassenaar and Hobson 2003). Samples were pyrolysed at 1400 °C in a Thermo-Finnigan TC / EA using a glassy carbon furnace and analysed for their stable hydrogen isotope ratios through an interfaced Thermi-Finnigan Delta Plus XL isotope ratio mass spectrometer via a continuous flow of helium. Feather non exchangeable hydrogen δD values were obtained after normalizing them to the VSMOW (Vienna Standard Mean Ocean Water) scale using calibrated keratin standards (Wassenaar and Hobson 2003). Routine checks with standards of known δD values were included in daily analyses to check on day-to-day performance and sample reproducibility. These checks revealed an external repeatability of better than ± 2.0 % for feather δD values.

2.2.6 Statistical analyses

2.2.6.1 Influence of latitude and habitat type on feather δD values

In order to determine the presence of a sufficient gradient over our sampling locations, we used a regression between the nestling feather δD values and nest's latitude. We then determined if captures in recent burns were situated in different latitudinal zones than those done in unburned forest through a T-test. Finally, we verified via a T-test whether habitat type alone could have an effect on all 19 juvenile feather δD values (burned and unburned sites – south and north respectively) as they are the basis of our feather comparisons.

2.2.6.2 Comparing latest movements to capture habitat

 δD values of feathers grown at the previous molt (newest feather - δD_{nf}) were compared to those of the nearest nest (nearest nest – δD_{nn}) (maximum distance of 25 km) for all age classes (SY, TY and ATY) to verify distance travelled within last year to reach capture site in all individuals. In this analysis, all ATY, regardless of whether they were 4Y or not were pooled together (see Table 1 for sample sizes as captures where not balanced by age, sex and habitat). We chose to reduce bias related to distance by excluding individuals captured further than 25 km to a nest for this analysis. These differences are represented as "feather comparisons" as suggested in Meehan *et al.* (2003). We used three-way ANOVA

to look at feather comparisons according to age, capture habitat, and sex. Using a square root transformation of feather difference values, plus a value of 30 (sqrt (dDdiff + 30)) for negative feather comparison values, normality assumptions were verified using the Shapiro-Wilk statistic. Variance homogeneity was verified by plotting residual vs predicted values after selection of the compound symmetric covariance structure (based on log likelihood values). Mean comparisons were done using Tukey's HSD *a posteriori* test on significant parameters.

Table 1. Summary of Black-backed Woodpecker sample sizes within each habitat, age and sex category. -; unsexed hatchling

Capture habitat	Sex	Age					Total (excluding HY)
		HY	SY	TY	4Y (sym)	ATY (asym)	
Burned forest	F		22	12	7	2	43
c	M		25	13	6	6	50
	-	12					
Unburned forest	F		18	3	2	7	30
	M		12	5	4	12	33
	-	7					
Total (excluding HY)			77	33	19	27	156

2.2.6.3 Movement patterns in older individuals according to age, habitat and gender

In TY and 4Y individuals, we used a repeated measures model (Proc Mixed, SAS Institute 1996) to determine whether feather age, capture habitat or sex had any influence on feather δD values for each age group. Normality assumptions were verified using the Shapiro-Wilk statistic and variance homogeneity was verified by plotting residual vs predicted values after selection of the compound symmetric covariance structure (based on log likelihood values). Mean comparisons were done using Tukey's HSD a posteriori test on significant parameters.

2.3 Results

2.3.1 Influence of latitude and habitat type on feather δD values

A δD / latitude gradient was found across the nest sites located in unburned forest north of lake St-Jean, showing a strong correlation to expected (from Meehan *et al.* 2004 dataset) precipitation δD_p values (Fig. 6). The latitude gradient covered by these samples (7 samples total) represents a spread of 0.54° latitude, indicating the possibility of using δD values to follow inter-annual movement of Black-backed Woodpeckers in the sampling region. On the other hand, nest sites located in the 2003 Saint-Thomas-Didyme forest fire area were excluded from the regression as nestling (12 samples total) feather δD values

0

corresponded very poorly, but consistently to δD_p values by an average of 20.9 % inferior values (values not shown).

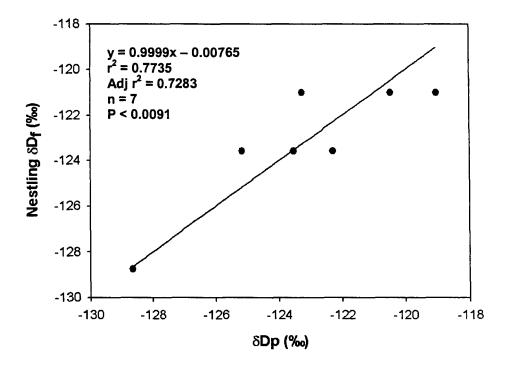


Figure 6. Regression model for the regression fit between 7 nestling δD_f values and interpolated δD_p values from natal areas where feathers were grown.

Individuals captured in recent burns were captured at a different latitude than that of those captured in unburned forest (t = 13.04, df = 135, P < 0.0001). This result clearly indicates that burned and unburned capture sites were distributed unevenly across the study area, as explained earlier. Also, we observed that juvenile feather δD values between burned and unburned forest were significantly different in their departure from expected precipitation δD values extrapolated from the Meehan (Meehan *et al.* 2004) map (Fig. 7)

(t = 15.54, df = 21, P < 0.0001). The juveniles (12 total) captured in recently burned forest had over-depleted feather δD values by a mean of - 20.9 ‰, while juveniles sampled in unburned forest had values very similar to those of expected precipitation δD values from the same Meehan (Meehan *et al.* 2004) dataset.

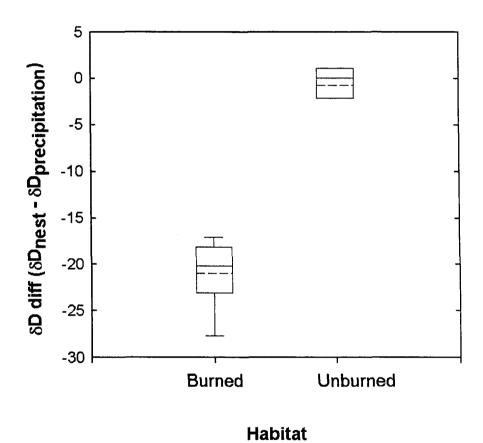


Figure 7. δD value differences (δD diff) between nestling feathers collected in recently burned and unburned forest and expected precipitation δD values extrapolated from Meehan's dataset (Meehan *et al.* 2004) (shown with standard error, mean (dash) and median (solid)).

2.3.2 Comparing latest movements to capture habitat

Results of the three-way ANOVA using nearest nest associations indicate that feather comparisons varied significantly only according to age in individuals $(F_{2,125} = 67.35, P < 0.0001; \text{ Table 2, figure 8})$. A Tukey's HSD multiple comparisons test shows that the $\delta D_{\text{feather}}$ $-\delta D_{\text{nest}}$ difference was significantly greater for TY and ATY individuals than SY individuals (Fig. 8.). Feather comparisons were not different between habitats $(F_{1,125} = 0.01, P = 0.9246; \text{ Table 2})$. As capture habitat, sex was not systematically related to movement amplitude in δD values $(F_{1,125} = 0.31, P = 0.5816; \text{ Table 2})$ nor any interaction term (Table 2).

Table 2. Three-way ANOVA table showing the effect of age, habitat and sex on feather δD value differences calculated between a feather from the most recent molt to a nestling feather less than 25 kilometres apart (δD feather $-\delta D$ nest) in all two year (SY), three year (TY) and four year (4Y) old Black-backed Woodpeckers captured (Proc Mixed, Sas Institute). *; significant, ***; highly significant.

Variable	Num. df	Denom. df	F	<i>P</i> > F
Age	2	125	67.35	< 0.0001 ***
Sex	1	125	0.31	0.5816
Habitat	1	125	0.01	0.9246
Age * Sex	2	125	0.72	0.4887
Age * Habitat	2	125	1.12	0.3303
Sex * Habitat	1	125	0.00	0.9924
Age * Sex * Habitat	2	125	1.61	0.2037

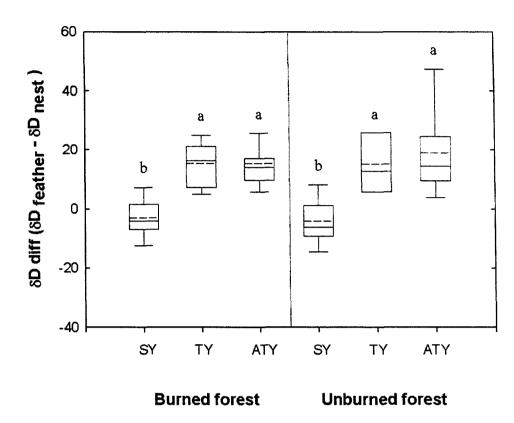


Figure 8. δD value differences (δD diff) between SY, TY and ATY individuals' latest molt feathers and the nearest nestling's feather of Black-backed-woodpeckers captured in recently burned and unburned forest (shown with standard error, mean (dash) and median (solid). δD_{diff} ($\delta D_{feather}$ - δD_{nest})

2.3.3 Movement patterns in older individuals to age, gender and habitat

The repeated measures ANOVA for TY birds (Table 3.) revealed that only the feather variable varies in its δD value between molt years (P < 0.0001). Feathers acquired at nest show values more depleted in deuterium than ones acquired at first molt (fig. 9). In 4Y birds, δD values also vary only according to molt year and only when sex is taken into consideration with the "feather * sex" interaction term (P = 0.0465). *A posteriori* T-tests on this interaction term revealed 1) that feathers acquired at nest (juvenile) were significantly different in their δD value to those acquired at 2^{nd} molt in 4Y females (P = 0.0075), 2) that male nest feathers (juvenile) were different in their δD values to those of 2^{nd} molt females' and 3) that male 2^{nd} molt feathers were different in their δD values to those of 2^{nd} molt females' (see figure 10). These results suggest that 4Y females had a different overall feather δD pattern between molt years than males as age increases in individuals. Males seem to have remained at similar latitudes throughout their life, contrary to females that show movement.

Table 3. Effect of feather age (juvenile, 1st or 2nd molt), habitat and sex on sequentially retained feather's δD values in three year (TY) and four year (4Y) old Black-backed Woodpeckers using a repeated measures analysis (TY and ATY analysed separately) (Proc Mixed, Sas Institute). *; significant, ***; highly significant.

Age	Variable	Num. df	Denom. df	F	P > F
TY	Sex	1	29	1.15	0.2920
	Habitat	1	29	0.69	0.4124
	Feather	1	29	23.93	< 0.0001 ***
	Sex * Habitat	1	29	0.11	0.7458
	Sex * Feather	1	29	0.00	0.9812
	Habitat * Feather	1	29	0.07	0.7946
	Sex * Habitat * Feather	1	29	0.73	0.4013
ATY	Sex	1	15	1.86	0.1924
	Habitat	1	15	2.06	0.1713
	Feather	2	28	2.45	0.1046
	Sex * Habitat	1	15	4.22	0.0577
	Sex * Feather	2	28	3.43	0.0465 *
	Habitat * Feather	2	28	1.48	0.2454
	Sex * Habitat * Feather	2	28	0.64	0.5348

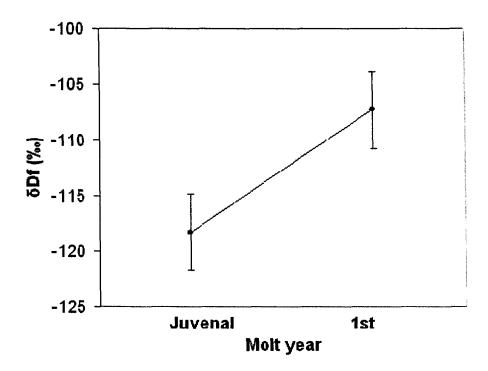


Figure 9. Retained juvenile and 1^{st} sequential molt feather δD values of TY old Black-backed woodpeckers captured in burned and unburned forest. Mean group values are shown along with 95% confidence error bars.

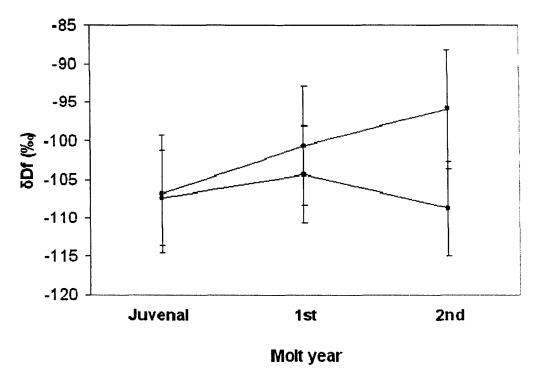


Figure 10. Retained juvenile, 1st and 2nd sequential molt feather δD values of 4Y (symmetrical ATY) old Black-backed woodpecker males (M) and females (F) captured in burned and unburned forest. Mean group values are shown along with 95% confidence error bars.

2.4 Discussion

2.4.1 Presence of the hydrogen isotope gradient

Our results demonstrate the possibility of using sequentially retained feathers to estimate annually averaged movements between molts on the same individual. We had initial worry that the latitudinal hydrogen isotope gradient might not be sufficiently pronounced to detect bird movement in the order of a few hundred km over our study area but the nestling samples (Fig. 6) confirmed the gradient's latitudinal influence on feather δD values even if the nestlings samples only ranged over 0.54 degrees of latitude. The slope equation we obtained resembles ones obtained in studies at similar latitudes in Hobson and Wassenaar (1997; $\delta D_f = -31 + 0.9 \delta D_p$), Wassenaar and Hobson (2000; $\delta D_f = -31 + 0.9 \delta D_p$) $27.4 + 1.1 \delta D_p$) and Meehan et al. (2001; $\delta D_f = -34 + 1.0 \delta D_p$). However, as nestling feather samples collected in the Saint-Thomas-Didyme 2003 forest fire were more depleted in deuterium than predicted by an average of - 20.9 ‰ (Fig. 7), their feather δD values were excluded from the regression model. This large difference in observed versus predicted δD_f values is an indication that either the habitat in which individuals are captured or particular meteorological processes are having an unexpected effect on δD_f values in the area surrounding Lake-St-Jean. The species' "resident" status (Dixon and Saab 2000) implies that individuals do not usually undergo long migrations prior to the breeding period, meaning that ingested food items such as white-spotted sawyer (Monochamus scutellatus (Say)) and other wood boring insect larvae (Dixon and Saab 2000) should not differ much in their δD value during the summer feather renewal period. In this case, nestlings are bound to have δD_f values very near those characteristic of their nest's location since variation inherent to migratory behaviour is at a minimum. Adding a station to the global network in precipitation sampling in this habited region could help resolve the issue where δD_f values are more depleted than the prediction model suggests for the area. The departure from the prediction model when the Saint-Thomas-Didyme nestlings are included in the regression model could be caused by dryer conditions in the recent burn. Nestlings in the northern unburned forest region could have been under average meteorological conditions (i.e. temperature, precipitation, evaporation), as those with which the interpolated δD_p values were created.

2.4.2 Comparing movements to age

While comparing the movement done by different age classes to reach capture site (since the most recent molt), we based ourselves on the δD values of nestling's feathers located nearby each adult's capture site to estimate relative movements that may have been done during each individual's last year. In this manner, we have determined that adults (TY and ATY) were prone to have come from further away than juveniles to reach capture site (burned and unburned forest (Fig. 8.)). These results seem opposed to those obtained from the comparisons between juvenal, 1^{st} and 2^{nd} molt feathers in a same individual (Fig. 9 and 10). Movement seems important between the birth year and the 1^{st} molt, while it seems to stabilise itself thereafter. More so, movement between these adults' (both TY and ATY)

newest feather and nearest nest δD value seems to average around a 16 % δD difference and indicates that the majority of adults have come from the species' southernmost distribution range area after their most recent molt to colonize the capture site. Again, we obtain an opposite results (Fig. 9 and 10) where it is clearly shown that when TY and 4Y feathers are taken on a same individual and that their δD ratios are compared, the juvenal feathers show an average 5-10 % depletion in deuterium, indicating that they were grown at a more northern location than their associated adult feathers. Therefore, the combination of results where 4Y have stabilised their movements but have moved to reach their capture site is contradictory. These leads us to believe that other factors may be responsible for such observed differences in feather δD values and this must be discussed before interpreting other results about movement by age, sex, habitat of capture and the interpretation of colonization of a new habitat or philopatry.

The problem arises from the fact that we are comparing the most recent feathers from captured individuals to feather δD value that we consider as being representative of each individual's capture site i.e. a feather from an immobile juvenile Black-backed Woodpecker captured in a cavity at less than 25 km from the concerned individual. Our feather comparison test revealed that SY birds grew their first plumage at similar latitude to that of the feather from the nearest nest situated no further than 25 km (Fig. 8) by the -4 ‰ difference value. Also, TY and ATY (with asymmetrical and symmetrical 4Y) adults seem to have travelled over a more important distance than SY birds to reach their northern capture site, which is shown in the 16 ‰ δD differences by feather comparison to each

individual's nearest associated nest site. As stated earlier, the averaged newest feather δD values in these adults indicate a molt location in the southernmost portion of the species' distribution range of eastern Canada and north-eastern United-States. Since the species is known to make irregular irruptions to these regions (West and Spears 1959, Yunick 1985), a move to northern latitudes is possible. Were such a move executed by a small portion of the population, variance might be expected to be greater than it is and feather δD values should resemble those of nestlings more than they do in our data. This unimodal response and the fact that juveniles are normally more mobile than adults (Observatoire d'oiseaux de Tadoussac, unpublished data) gives us reason to believe that adults (TY and 4Y) are experiencing something else in addition to the latitudinal hydrogen stable isotope gradient that nestling Black-backed Woodpeckers are not.

Duxbury *et al.* (2003) have experimented on Peregrine falcon and Japanese quail juveniles by giving them food and water sources of known hydrogen isotopic content in order to monitor changes in δD values through sequential plumage stages. They determined that for these species, differences in isotope profiles can show up between juvenile (e.g. down) and mature plumage stages after an initial diet change. The use of endogenous resources to produce eggs can be problematic as the parent's tissues may be enriched or depleted in deuterium relatively to the δD values present in food items at the nest site, especially if feeding has occurred at a different location than nesting. This could be the case in the Black-backed Woodpecker where juvenile feathers (not down but fully functional flight feathers) could be different in hydrogen isotope signature than adult feathers if the

female parent used endogenous reserves during egg formation and juveniles were later fed food items differing in their isotope signature to that of the parent's reserves. Such an explanation was suggested in Meehan *et al.* (2003), where adults Cooper's hawks (*Accipiter cooperi*) had consistently less depleted feather values than their offspring's even though the selected adult feathers were thought to have been renewed at or near their nest site. In trying to relate to these results, since the adult Black-backed Woodpecker is not known to migrate over large distances anytime preceding, during or after its breeding period, endogenous reserves should be similar throughout these periods, assuming that similar food items are consumed during these periods. These reserves and food item's δD signature should therefore be reflected in the nestling's feathers δD ratios.

Results showing that adults all seem to be coming from the species' southern distribution limit after experiencing one (TY) or two (4Y) molts suggest that evaporative cooling may be affecting adults in our study. Wolf and Martinez del Rio (2000) were among the first to discuss of deuterium enrichment of body water over source water, using Schoeller *et al.* (1986)'s work to support their idea that the degree of body-water deuterium enrichment increases with the rate of fractionated evaporative water losses. While evaporative cooling is largely used by desert animals as a way to evacuate certain heat, it is also used during periods of increased physical exertion. This physiological adaptation to elevated stress (e.g. heat, flight, territory defence and physical exertion) could explain such constant significant δD differences we observed between nestling and adult feathers. Nestlings fed at the nest should not have particularly elevated metabolism due to physical

activity compared to parents participating in the feeding of their young. Weathers et al. (1990) have shown that nestling Acorn Woodpeckers (Melanerpes formicivorus) develop endothermy at three weeks of age and depend mostly upon others to maintain a correct body temperature below this age. This suggests that their metabolic rate stays relatively unaugmentable as a response to low temperatures until three weeks old. The authors showed that field water efflux rate of nestlings more than doubled its initial rate from birth to adult. size. As feathers grow fully during a similar but shorter time period in Black-backed woodpeckers (fledging occurs at 20-22 days), our nestling δD_f values may well have been influenced by different water efflux rates than adults, explaining such marked differences in δD_f values between the two age groups. Even though nestlings located in cavities exposed to direct sunlight (e.g. recent burns) may be advantaged over individuals located in more shaded environments (e.g. unburned forest) as they could survive without parental warmth for longer periods of time, they should not be able to increase their metabolic rate until their first set of feathers has almost finished growing (3 weeks). On the other hand, a higher metabolic rate may be indirectly caused by increased cavity temperatures in recent burns, possibly by an increase in habitat temperature and/or an increase in the number of hatchlings per nest, explaining the more depleted δD_f values in nestlings captured in recent burns. It is also possible that metabolism can be kept low in hatchlings by procuring a part of required heat source from nest congeners.

Woodpecker species which are more likely to excavate for extracting insect larvae from hardwood than other birds may be more prone to higher physical stress than

previously thought for non-migratory birds. As molting in adults usually occurs in July-September, after the breeding period but when juveniles may still be dependent on their parents, it is possible that increased metabolic rates could be a result of raising their young. Unfortunately, we have no way of knowing exactly which adults were breeding except a handful for which nests were monitored. It is most likely that not all were reproducing in 2004, which means that not all adults necessarily had an increased metabolic rate due to raising their young, causing evaporative cooling. The difference in juvenile and adult feather δD values is quite generalized, suggesting that adult metabolism is more elevated than nestlings' during and perhaps outside the breeding period or at least while young are being raised, as suggested in McKechnie *et al.* (2004) and Meehan *et al.* (2003).

We consider the δD_{diff} value of approximately -4 ‰ in SY individuals (Fig. 8) to represent a small southwards movement to reach their capture location. This trend seems to follow the one observed at the Tadoussac Bird Observatory. The difference between an adult's (TY and ATY) HY feather to that of the 1st molt is in the order of 12 ‰. We can assume that if these two cohorts have traveled similar distances during juvenal dispersal, that the difference caused by a different isotopic fractionation rate between juveniles and adults is in the order of 12 to 16‰ in favour of adults. This difference could be the result of high skin and lung evaporation rates (Marder *et al.* 2003) in individuals unprotected by the nest cavity i.e. adults, leading to more elevated water losses outside of the cavity and to the accumulation of deuterium in the body tissues.

Our results on movements by different age classes indicate that juveniles have moved during their first year to becoming SY by the -4 ‰ difference to nearby nest feather δD values. Since we are uncertain if differences in juvenal and 1^{st} molt δD_f values in TY and 4Y are due to evaporative cooling, we cannot say for sure whether there was movement or not in these two older age classes. If future analyses reveal no metabolic difference between nestlings and adults, it implies, although unlikely, that the Black-backed Woodpeckers in our study have undergone important northward movements to reach their capture sites near Lake St-Jean (Saint-Thomas-Didyme) and 200 km north of it.

2.4.3 Movement by sex

Our data indicates that sexes may go about differently in their annual movements, but only in older individuals (Table 2; Fig. 9 (TY) and 10 (4Y – symmetrical ATY)) as males were more prone to limiting their year to year long distance movements than females (Fig. 10). The fact that 4Y old females had a tendency to change year to year molt locations compared to males made us think that the species may behave in a similar ways to certain Fennoscandian owls where females and juveniles are more prone to executing regular movements throughout their life as opposed to males whom often remain on an already acquired territory for reproductive or territory defence reasons (Lundberg 1979). This hypothesis has been further developed in Huot and Ibarzabal (2006) where older females (TY and ATY) were less abundant in unburned forest than males while being (females) abundant in all age classes in recently burned areas. Unless males are differently affected

by physical exertion than females or simply that sexes feed on different food items differing in their isotope signature, there should not be any differences in evaporative cooling rates between sexes. Data from the Tadoussac bird observatory Black-backed woodpecker capture program indicate that sexes are equally represented in birds captured, although these are HY individuals in majority (95%). Unfortunately, we could not capture additional older age class individuals, limiting the use of this data to make generalizations on Black-backed woodpecker between years based on sex. Nevertheless, females are showing less philopatry to a given area or latitude between years than males. Moreover, the stable and large differences in juvenile – adult feather δD ratios suggest that we should be careful in establishing movement patterns using the juvenile to 1^{st} and 2^{nd} feather δD value comparisons. This also applies to other studies using HY and feathers from subsequent molts in between-year bird movement and migration studies.

2.4.4 Movement by habitat of capture

While our results do not indicate differences in movement tendencies in individuals present in recently burned forest and unburned forest at time of capture, we believe that differences in habitat quality may influence movement rates as 4Y females in this study were more prone to moving than males (despite low sample numbers). In Huot and Ibarzabal (2006), the age class structure of Black-backed Woodpeckers found in unburned forest in the same capture areas as this study (fig. 1) were in favour of old (ATY, some of which were 4Y) males over females (also shown in table 1). In addition, younger females

(SY) comprised of a larger percentage of captures than males of the same age in the unburned habitat. As they, we believe that females may be more mobile than males in a habitat considered as being of secondary value (Hutto 1995), while males are more prone to limiting their movements and investing in territory defence once a suitable one has been located. This may be why less older aged (TY and ATY) females are seen in our unburned forest sites.

Considerations as to whether similar deuterium fractionation rates occur between recently burned forest and unburned forest of the same type are not to be neglected as all unburned forest nestling δD_f values corresponded fairly well to the predicted model (Fig. 7), in contrary to the recently burned forest nestling feather samples. A way to resolve this situation would be to increase resolution of the interpolated δD in precipitation map to the studied area by augmenting the number of samples taken from precipitation for hydrogen isotope analysis. Knowing this makes it difficult to analyse movement in an individual that may have frequented both habitats during it's lifetime without supplemental knowledge of what causes such differences in isotopic signatures between habitats.

2.4.5 Colonization VS Philopatry

The juveniles captured in our study seem to have executed a southward movement which could correspond to juvenal dispersion, allowing for the colonization of new territories among recently burned forest. Similarly, females seem to continue moving after their first year. The only individuals that are showing philopatry to a given latitude, based on non-different δD_f values between molts, are males 4Y (Fig. 9). However, these movement trends in females and males should only be considered as indicative and be interpreted with caution since sample sizes were small.

2.4.6 Conclusion

Our study shows that it is possible to recreate the movement history of adult Black-backed Woodpeckers by the sampling of feathers of multiple ages on the same individual. Many other bird species are known to experience stable feather retention patterns, therefore allowing for similar studies to be carried out. This opens possibilities towards the monitoring of bird movements throughout years without having to rely on extensive recapture programs. However, correctly ageing of captured individuals remains the key factor in obtaining the correct movement readings, along with sturdy knowledge of the time period in which feathers are renewed. While we have shown that the species undergoes initial movements at young age, our study identifies two possible sources of variation in deuterium "cycling" within individuals, the first being an individual's age where nestlings

may differ from flying adults in their metabolism and the second being that burned habitat seems to produce over-depleted δD_f than unburned habitats. Future work should be focused on determining the cause and reason for the amplitude of variation in feather δD values we found in adults and juveniles or between habitats as in-between year feather comparisons are possible only if fractionation rates are known.

CONCLUSION GÉNÉRALE

Cette étude jette un éclairage nouveau sur la compréhension des mécanismes de colonisation du Pic à dos noir en forêt récemment brûlée. L'analyse des structures d'âge entre les deux habitats révèle que les SY se retrouvent en brûlis presque autant qu'en forêt non brûlée. Nous avons déterminé que la colonisation du brûlis se fait probablement l'année même du feu, au moins par les SY grâce à l'analyse isotopique. Les SY pourraient être nés l'année même du feu en sa localité ou à proximité, ce qui est soutenu par l'examen du contenu en deutérium de leurs plumes lorsque comparées aux valeurs δD de plumes de juvéniles situés dans des nids à proximité des sites de capture. Cette analyse démontre cependant qu'il y a eu un déplacement vers le sud de petite envergure par la différence de valeur δD entre plumes de SY et d'individus dans des nids à proximité (Fig. 8 : -4‰). Ils sont soit issus d'individus ayant hâtivement colonisé le feu ou venus de nids localisés à faible distance du brûlis. Ainsi, il est possible de croire qu'ils aient un fort potentiel de dispersion pendant la première année. Ce comportement est probablement observé en partie à l'Observatoire d'oiseaux de Tadoussac à chaque automne. La plus faible proportion de TY en forêt non brûlée pourrait signifier que l'habitat n'est pas aussi sélectionné que la forêt récemment brûlée et que les SY s'y retrouvant n'y restent pas nécessairement jusqu'à l'atteinte de trois ans.

L'importante proportion d'individus matures (TY, ATY et 4Y) retrouvée en brûlis récents suggère qu'ils s'y sont déplacés peu de temps après l'évènement et que cette classe

d'individus peut demeurer ou redevenir mobile quelques années après dispersion initiale, si elle a eu lieu. D'ailleurs, des traces de leur récente arrivée, un an après feu, ont été observées sur leur plumage ventral. La majorité des individus capturés en forêt non brûlée avaient des plumes de poitrine blanches, tandis que des traces de suie ont été remarquées sur beaucoup d'individus capturés en forêt récemment brûlée. Ainsi, des individus ayant une poitrine non souillée serait probablement issus de forêt non brûlée peu de temps avant la période de capture printanière. Il est envisageable de croire que les individus plus âgés (ATY et 4Y) sauraient mieux en mesure de tirer profit d'un territoire en forêt non brûlée que les jeunes (SY et TY), de part leur forte présence dans cet habitat. Le plus faible nombre de captures de femelles âgées en forêt non brûlée. D'ailleurs, l'analyse isotopique supporte cette hypothèse, malgré le nombre de captures peu élevé.

De plus, l'analyse isotopique indique que les TY et les 4Y sont revenus à la latitude de leur site de naissance pendant l'année avant (les TY) et après (les 4Y) la 2e mue, ceci après s'être déplacés au sud de leur aire de distribution pendant leur première année. Quoique ces derniers résultats soient plausibles, ils laissent croire qu'une telle indication de déplacement « en masse » effectué par la majorité des individus dans l'année avant leur première mue soit plutôt due à un autre phénomène.

En général, les résultats de l'analyse isotopique laissent croire qu'il existe un phénomène de refroidissement évaporatif, causé par une différence de métabolisme, entre

juvéniles au nid et adultes (SY, TY et ATY). En utilisant un plus grand volume d'eau dû à un métabolisme plus élevé, les individus impliqués accumuleraient plus rapidement les isotopes lourds de l'hydrogène tel le deutérium qui transitent dans leur corps. Si ce mécanisme est en action, ces mêmes individus verraient la signature isotopique de leurs plumes semblable à celle de plumes ayant été formées par des individus situés à des latitudes inférieures qu'eux. Les valeurs de ratio isotopique seraient moins négatives qu'elles ne devraient l'être pour le lieu de formation, l'écart étant dépendant du métabolisme.

Notre étude démontre qu'il demeure incertain que l'espèce se déplace suffisamment pour que l'analyse d'isotopes stables de l'hydrogène puisse détecter les déplacements, sauf chez les SY. Ce résultat est d'ailleurs appuyé par les données de capture à l'Observatoire d'oiseaux de Tadoussac. Notre étude démontrerait cependant qu'il y existe une certaine stabilité dans la différence de signature isotopique entre juvéniles au nid (HY ou plumes de SY acquises au nid) et adultes (TY et 4Y). Il serait donc possible d'établir une relation entre les deux et mettre au point un facteur de conversion de valeurs δDf , permettant une certaine comparaison de plumes acquises au nid et celles d'adultes datant de la 1ere ou 2e mue. Idéalement, la prochaine étape serait de faire des captures-recaptures avec des individus sédentaires issus de nids connus. En récoltant et comparant la signature isotopique de leurs plumes juvéniles avec leurs plumes de première mue pendant l'automne des années suivantes, il serait possible de connaître les effets d'un métabolisme plus actif chez les adultes que les jeunes au nid et d'éliminer ou non le déplacement comme

évènement pouvant expliquer la différence de signature isotopique observable entre plumes juvéniles au nid et adultes. De plus, l'évaluation du taux métabolique chez diverses classes d'âge permettrait la comparaison fiable entre plumes de différents âges (sur un même oiseau ou non). Si le Pic à dos noir n'obtenait pas ses premières plumes au nid, i.e. lorsqu'il est relativement inactif, une comparaison directe des ratios isotopiques de plumes d'adultes et de juvéniles au nid pourrait être faite. Sans ceci, nous resterons dans le doute quant à ses déplacements interannuels, du moins ceux ayant lieu avant la première mue, considérant que le niveau d'activité moyen entre différentes classes d'âges devrait demeurer semblable après le départ du nid.

Pour terminer, il faut souligner que les résultats de ces deux études suggèrent que les brûlis récents tels que ceux étudiés ici, ainsi que les forêts non brûlées en forêt boréale sont deux habitats d'une importance significative pour le Pic à dos noir par son taux de fréquentation et d'utilisation. D'autre part, les difficultés que nous avons éprouvé à capturer des individus en forêt non brûlée n'impliquent pas que l'espèce ne peut y survivre à long terme sans l'apport de feux dans le paysage, mais elle témoigne du fait de sa plus faible densité dans cet habitat. D'autres études axées sur l'acquisition de paramètres démographiques tel le succès reproducteur, l'utilisation de l'habitat à différentes échelles spatiales et les taux de mortalités dans ces deux habitats pourraient apporter des outils additionnels permettant une meilleure détermination de la qualité d'un habitat. Ces données supplémentaires, ajoutées à celles figurant dans ce mémoire, permettront de mieux comprendre la dynamique de population du Pic à dos noir et du même coup de mesurer

l'impact de l'exploitation des brûlis récents pour la conservation de cet emblème de la forêt boréale.

RÉFÉRENCES

- Alderfer, J. 2006. Complete birds of North America. Washington, D. C., National Geographic Society.
- Apfelbaum, S. et A. Haney 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83: 347–354.
- Araguas-Araguas, L., Froeiilich, K. et K. Rozanski 2000. Deuterium and oxygen-18 isotope composition of precipitation and atmospheric moisture. Hydrological Processes 14: 1341-1355.
- Axtell, H. H. 1957: The Three-toed Woodpecker invasion. Audubon Outlook 6: 13–14.
- Blackford, J. L. 1955. Woodpecker concentration in burned forest. The Condor 57: 28-30.
- Carney, M. 1999. What was found in the burn. Federation of Ontario Naturalists. Seasons;
 Winter: 26-31
- Catchpole, C. K. 1972: A comparative study of territory in the reed warbler (*Acrocephalus scirpaceus*) and sedge warbler (*A. schoenonaenus*). Journal of Zoology 166: 213–231.
- Chamberlain, C. P., Blum, J. D., Holmes, R. T., Feng, Xiahong, Sherry, T. W. et G.R. Graves 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109: 132-141.
- Craig, H. 1961. Isotopic variations in meteoric waters. Science 133: 1702-1703.
- Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus XVI 4: 436-468.

- Dellasalla, D. A., Karr, J. R., Schoennagel, T., Perry, P., Noss, R. F., Lindenmayer, D., Beschta, R., Hutto, R. L., Swanson, M. E. et J. Evans 2006. Post-fire logging debate ignores many issues. Science 314 (5796): 51-52.
- Denault, S. et B. Drolet 2006. Rapport d'activité de la saison 2005. Observatoire d'oiseaux de Tadoussac, Explos-Nature, Les Bergeronnes (Québec). VII-46p + annexes.
- Dixon, R. D. et V. A. Saab 2000: Black-backed Woodpecker (*Picoides arcticus*). In: Poole,
 A. and Gill, F. (eds), *The Birds of North America*, no. 509. The Birds of North America, Inc., Philadelphia.
- Duxbury, J. M., Holroyd, G. L. et K. Muehlenbachs 2003. Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope-base maps for tracking migratory birds. Isotopes in Environmental and Health Studies 39(3): 179-189.
- Elliott, L., Stokes, D. et L. Stokes 1997: Stokes field guide to bird songs: eastern region. —

 Time Warner Audio-Book.
- Ellsworth, E. A. et J. R. Belthoff 1999. Effects of social status on the dispersal behaviour of juvenile western screech-owls. Animal behaviour 57: 883--892.
- Escott, N. G. 2001. A concentration of Black-backed Woodpeckers in Thunder Bay District. Ontario Birds 12 (3): 119-129.
- Greenwood, P. J. et P. H. Harvey 1976: The adaptive significance in breeding area fidelity of the Blackbird (*Turdus merula* L.). *J. Anim. Ecol.* 45: 887–898.

- Hobson, K. A. et L. I. Wassenaar 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109: 142-148.
- Hobson, K. A., Wassenaar, L. I., Milá, B., Lovette, I., Dingle, C., et T. B. Smith 2003.

 Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorian hummingbird community. Oecologia 136: 302-308.
- Hobson, K A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. Diversity and Distributions 11: 157–164.
- Hoyt, J. S. et S. J. Hannon 2002. Habitat associations of Black-backed and Three-toed Woodpeckers in the boreal forest of Alberta. *Can. J. For. Res.* 32: 1881–1888.
- Huot, M. et J. Ibarzabal 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 forests. Conservation Biology 9:
 1041–1058.
- Ibarzabal, J. et P. Desmeules 2006. Black-backed woodpecker (*Picoides* arcticus) detectability in unburned and recently burned mature conifer forests in eastern Canada. *Annales Zoologici Fennici* 43: 228-234.
- Ibarzabal, J. et J. Tremblay 2006. The hole saw method for accessing woodpecker nestlings during developmental studies. *Annales Zoologici Fennici* 43: 235-238.

- Imbeau, L., Savard, J-P. L. et R. Gagnon 1999. Comparing bird assemblages in successional black-spruce stands originating from fire and logging. Canadian Journal of Zoology 77: 1850–1860.
- Kilham, L. et C. R. Foss 1994. Black-backed Woodpecker *Picoides arcticus*. Pp. 138–139 in Atlas of breeding birds in New Hampshire (C. Foss, ed.). Audubon Society of New Hampshire/Arcadia, Dover.
- Lundberg, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. Oecologia (Berl.) 41: 273--281.
- Marder J, Withers PC, et R. G. Philpot 2003. Patterns of cutaneous water evaporation by Australian pigeons. Israel Journal of Zoology 49 (2-3): 111-129 2003.
- McKechnie, A. E., Wolf, B. O. et C. Martínez del Rio 2004 Deuterium stable isotope ratios as tracers of water resource use: an experimental test with rock doves. Oecologia 140: 191–200.
- Meehan, T. D., Lott, C. A., Sharp, Z. D., Smith, R. B., Rosenfield, R. N., Stewart, A. C. et R. K. Murphy 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's hawks migrating through the Florida Keys. The Condor 103: 11-20.
- Meehan, T.D., Rosenfield, R.N., Atudorei, V. N., Bielefeldt J., Rosenfield L. J., Stewart A.C., Stout W. E., et M. A. Bozek 2003. Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's Hawks. Condor 105:567–572

- Meehan, D., T., Giermakowski, J. T. et P. M. Cryan. 2004. Gis-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. Isotopes in Environmental Health Studies 40(4): 291-300.
- Miettinen, J. 2003: Age determination in woodpeckers. Forschungsbericht 48: 127–131.
- Murphy, E. C. et W. A. Lehnhausen 1998: Density and foraging ecology of woodpeckers following a stand replacement fire. Journal of Wildlife Management 62: 1359–1372.
- Nappi, A., Drapeau, P. et J-P. L. Savard 2004. Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? The Forestry Chronicle 80 (1): 67-74.
- Nappi, A., Drapeau, P., Giroux. J-F. et J-P. L. Savard 2003. Snag use by foraging Black-backed Woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. Auk 120: 505-511.
- Niemi, G. J. 1978. Breeding birds of burned and unburned areas in northern Minnesota.

 Loon 50: 73-84
- Peterson, M. C. 1988. Black-backed Woodpecker *Picoides arcticus*. Pp. 238–239 *in* The atlas of breeding birds in New York state (R. F. Andrle and J. R. Carroll, eds.). Cornell Univ. Press, Ithaca, NY.
- Pyle, P. 1997: Identification guide to North American birds. Part 1: Columbidae to Ploceidae. Bolinas, CA, Slate Creek Press.

- Rubenstein, D. R., Chamberlain, C. P., Holmes, R. T., Ayres, M. P., Waldbauer, J. R., Graves, G. R. et N. C. Tuross. 2002. Linking Breeding and Wintering Ranges of a Migratory Songbird Using Stable Isotopes. Science 295: 1062-1065.
- Schoeller, D.A., Leitch, C.A., et C. Brown 1986 Doubly labelled water method: in vivo oxygen and hydrogen isotope fractionation. American Journal of Physiology 251: R1137-R1143.
- Short, L. L. 1982: Woodpeckers of the world. Delaware Museum of Natural History

 Monograph Series no. 4.
- Van Balen, J. H. 1980: Population fluctuations of the Great Tit and feeding conditions in winter. *Ardea* 68: 143–164.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.
- Van Tyne, J. 1926: An unusual flight of arctic Three-toed Woodpeckers. The Auk 43: 469–474.
- Vickery, P. D., Hunter, M. L. J. et J. V. Wells 1992. Is density an indicator of breeding success? The Auk 109: 706-710.
- Villard, M.-A. et J. Schieck 1997: Immediate post-fire nesting by Black-backed Woodpeckers, *Picoides arcticus*, in Northern Alberta. Canadian Field Naturalist. 111: 478–479.
- Wassenaar, L. I. et K. A. Hobson 2000. Stable carbon and hydrogen isotope ratios reveal breeding origins of Red-winged Blackirds. Ecological Applications 10: 911 916.

- Wassenaar, L. I. et K. A. Hobson 2003. Comparative equilibration and online technique for determination on non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39(3): 211-217.
- Weathers. W. W., Koenig, W. D. et M. T. Stanback 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. The Condor 92: 341-359.
- West, J. D. et J. M. Speirs 1959. The 1956–1957 invasion of Three-toed Woodpeckers. Wilson Bulletin 71: 348–363.
- Wolf B.O. et C. Martínez del Rio 2000. Use of saguaro fruit by whitewinged doves: isotopic evidence of a tight ecological association. Oecologia 124:536–543
- Yunick, R. P. 1985: A review of recent irruptions of the Black-backed Woodpecker and

 Three-toed Woodpecker in eastern North America. Journal of Field Ornithology

 56: 138–152.
- Ziegler, H. 1988. Hydrogen isotope fractionation in plant tissues. Stable Isotopes in Ecological Research. P. W. Rundel, J. R. Ehleringer, and K. A. Nagy. New York, Springer Verlag.