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Efficiency of enhanced capture methods and age-class structure of dispersing boreal woodpeckers

Eficiencia de metodos mejorados de captura y estructura de clases de edad de pajaros carpinteros dispersantes

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ABSTRACT. American Three-toed (*Picoides dorsalis*) and Black-backed Woodpeckers (*Picoides arcticus*) are irruptive species for which yearly movements and abundance are linked to higher productivity years due to forest fire or large-scale insect outbreaks in boreal forests. Studies have found that, in Black-backed Woodpeckers, younger birds are the main colonizers of recent burns, and thus related to natal dispersion. However, age structure of dispersing boreal woodpeckers in the fall have yet to be studied. The Observatoire d'oiseaux de Tadoussac is a migration monitoring station located at the southern limit of Québec's boreal forest and where a special effort has been made to count and capture transient boreal woodpeckers in the fall between 2000 and 2006. In this study, we investigated (1) the age structure and sex ratio of dispersing boreal woodpeckers and assessed (2) if the use of enhanced capture methods (ECM) improves their rate of capture and (3) the correlation between capture rates and visual counts. The age structure of Black-backed Woodpecker (1:13.9 [1:4.5–1:64] adult:juveniles ratio) and American Three-toed Woodpecker (1:16.7 [1:4.22–0]) was strongly skewed toward juveniles, and suggests that dispersing individuals were mainly related with post-fledging movements. The use of ECM to capture boreal woodpeckers was an efficient way of capturing these species. This method showed capture rate four times greater than the passive method. Moreover, capture rates were correlated with visual counts. Therefore, our study supports the importance of post-fledging movements in boreal woodpecker population dynamics, and shows that the use of ECM is an efficient method to capture and count these species outside their breeding season.

RESUMEN. Picoides dorsalis y Picoides arcticus son especies irruptivas en las que los movimientos anuales y la abundancia están vinculados con años de mayor productividad debido a incendios forestales o a irrupciones de insectos a gran escala en bosques boreales. Estudios han encontrado que, en Picoides arcticus, las aves más jóvenes son las principales colonizadoras luego de incendios recientes, y esto está así relacionado con la dispersión natal. Sin embargo, la estructura de edades de pájaros carpinteros boreales dispersantes durante el otoño no han sido aún estudiada. El Observatoire d'oiseaux de Tadoussac es una estación de monitoreo de migraciones ubicada en el limite sur del bosque boreal de Quebec en la que un esfuerzo especial ha sido puesto para contar y capturar pájaros carpinteros boreales que se encuentran en dispersión durante el otoño entre los años 2000 y 2006. En este estudio, se investigó (1) la estructura de edades y la proporción de sexos de pájaros carpinteros boreales dispersantes y se evaluó (2) si el uso de métodos mejorados de captura (MMC) incrementa sus tasas de captura y (3) la correlación entre las tasas de captura y los conteos visuales. La estructura de edades de Picoides articus (1:13.9 [1:4.5–1:64] proporción de adultos en relación a juveniles) y la de Picoides dorsalis (1:16.7 [1:4.22– 0]) estuvieron fuertemente sesgadas hacia juveniles, lo que sugiere que los individuos dispersantes estuvieron relacionados principalmente con movimientos de los juveniles luego de que abandonan el nido. El uso de MMC para capturar pájaros carpinteros boreales fue una forma eficiente para capturar estas especies. Este método mostró una tasa de captura cuatro veces mayor que la del método pasivo. Además, las tasas de captura se correlacionaron con los conteos visuales. Así, nuestro estudio soporta la importancia de los movimientos de los juveniles luego de que abandonan el nido en la dinámica poblacional de pájaros carpinteros boreales, y muestra que el uso de MMC es un método eficiente para capturar y contar estas especies fuera de la estación reproductiva.

Key Words: age ratio; American Three-toed Woodpecker; banding; Black-backed Woodpecker; dispersal; mist-netting; population monitoring

INTRODUCTION

Few studies have addressed natal dispersal in small birds even though it is believed to play a major role in population growth and persistence (Wiens et al. 2006, Cox et al. 2014). Dispersal may be especially important for species that occupy a highly specialized niche and that rely on this process to find and colonize new habitat patches (Shitikov et al. 2012). Irruptions are defined as important influxes of individuals that are localized in time and space (Newton 2006). Such movements are usually linked to the exploration of breeding areas of high food availability but can also result from important exoduses due to a lack of food (Bock and Lepthien 1976, Koenig and Knops 2001). Although they are often considered resident species, boreal woodpeckers, such as Black-backed Woodpeckers (*Picoides arcticus*; BBWO) and

¹Observatoire d'oiseaux de Tadoussac, Cooporation Explos-Nature, ²André Desrochers laboratory, Université Laval, ³Environment and Climate Change Canada, ⁴Département des sciences du bois et de la forêt, Université Laval, ⁵Department of Physiology and Cell Biology College of Medicine, The Ohio State University Columbus, ⁶Department of Fisheries Wildlife and Conservation Sciences, Oregon State University, ⁷Département des sciences fondamentales Université du Québec à Chicoutimi American Three-toed Woodpeckers (*P. dorsalis*; ATTW), irrupt south of their respective ranges in certain winters but not necessarily synchronously (Tremblay et al. 2020a, 2020b). These irruptions are thought to be associated with an important increase in boreal woodpecker's productivity originating from wildfires or large-scale insect outbreaks (West and Speirs 1959, Yunick 1985). In Black-backed Woodpeckers, colonization of recent burns is predominantly done by second year (SY) birds and thus related to natal dispersion (Huot and Ibarzabal 2006, Tremblay et al. 2015, Siegel et al. 2016). Whether irruptions of boreal woodpeckers indeed result from post-fledging movements remains to be determined however, as no study has yet documented the age and sex of individuals involved in such events.

For species such as boreal woodpeckers, ATTW and BBWO, who have juveniles that are not readily distinguishable from adults in the field, capturing individuals and aging them with moult patterns can contribute to a better understanding of the movements of the different age classes (Pyle 1997, Froehlich 2003, Johnson et al. 2011). Although mist netting remains the most prevalent capture method for forest birds, its capture efficiency varies greatly among species (Jenni et al. 1996, Remsen and Good 1996, Dunn and Ralph 2004) and habitats (Dunn and Ralph 2004). Standardized mist-netting operations using standard 30 mm mist-net to capture passerines in migration, are not efficient at capturing larger woodpeckers because of their body size (Wang and Finch 2002). In addition, because of their behavior and preferred habitat, visual migration counts are not always possible, meaning that bird counts acquired through capture could prove a useful tool for population management (Dunn and Ralph 2004).

Few techniques have been developed to improve the capture rates of woodpeckers undergoing dispersal or migration. Most methods for capturing nesting woodpeckers are inappropriate for documenting woodpecker's dispersal and migration movements. Capturing boreal woodpeckers is particularly challenging outside of the breeding season because capture rates using mist nets for these birds are typically low, and boreal woodpeckers seldom visit feeders. This has led some authors to capture individuals using netguns as a last resort (Lehman et al. 2011). The use of audio lures to increase detection rate in audio/visual inventory is frequently used on different woodpecker species (Kosinski et al. 2004, Michalczuk and Michalczuk 2006, Wynia et al. 2019, and others). Yet, this technique is seldom used for large-scale capture operations. In addition, its efficiency at increasing capture rate has not been quantified.

In this study, we investigated the efficiency of a new capture technique specifically targeting this group of species and the ageclass structure of dispersing boreal woodpeckers. We captured boreal woodpeckers using either enhanced capture methods (EMC) including playback of their calls broadcasted from within a mist net enclosure where dead snags were planted or with standard passive mist-netting. We then examined the age-class structure of two woodpecker species (Black-backed and American Three-toed Woodpeckers) caught using EMC, evaluated the capture rates of both methods, and finally compared the capture rates using EMC with standardized visual counts to assess the capacity of the former to estimate dispersal intensity. Because EMC may attract specific population classes (Whalen and Watts 1999, Lecoq and Catry 2003), we assessed whether capture rates using EMC differed from a 1:1 sex ratio (F:M) or from the expected productivity of 1:1.5 (adult:juvenile; Nappi and Drapeau 2009, Tremblay et al. 2015). We hypothesized that capture sex ratio using EMC would be unbiased because in both species, both sexes show aggressive behaviors against intruders or counterparts (Lawrence 1967). We hypothesized that capture rates would be biased toward juveniles because irruptions are thought to be driven by natal dispersal and post-fledging movements (Huot and Ibarzabal 2006, Tremblay et al. 2015, Siegel et al. 2016).

METHODS

Study site

The village of Tadoussac, located on the north shore of the St. Lawrence River at its confluence with the Saguenay River (Fig. 1), lies along an important southward migration corridor for raptors (Berthiaume et al. 2009) as well as for passerines and transient boreal woodpeckers (Savard and Ibarzabal 2001). A seasonal banding station, the Observatoire d'oiseaux de Tadoussac (OOT; 48°09'N, 69°42'W; Fig. 1) was set up in 1994 to monitor and study fall migrating birds. The immediate area around the capture site (250 m radius) is covered by a very low density of jack pines (Pinus banksiana), spruces (Picea spp.) and balsam fir (Abies *balsamea*) over sandy naked soil. At a broader scale, the site is characterized by mix of deciduous and coniferous forest stands. This site, and its surroundings (> 10 km) is not proper for boreal woodpeckers because the site does not contain mature trees or recently burned areas, therefore the number of individuals that are not transient is null or limited.

Visual counts

We counted dispersing woodpeckers daily between 2000 and 2003 and over hourly periods from 2004 until 2006 following Explos-Nature protocols (Côté and Dumas 2022). We used two sites for visual counts, one located on the marine terraces (Dionne and Occhietti 1996) bordering the St. Lawrence River and the other located 800 m inland from the first. Counts were performed

Fig. 1. Location of the visual migration count sites at the Observatoire d'oiseaux de Tadoussac, Tadoussac, Québec, Canada.



simultaneously at the two sites by the same two observers who alternated between the sites every day for the entire season. Counts started each day at 08:00 and stopped at around 14:00, usually from mid-August until mid to late November. All birds actively moving south that were detected and properly identified, either by sight or by ear, were recorded. The observation point closer to the shore was located at 130 m from the mist net locations (slightly more inland) so that the observers could not see either the nets or the birds therein (Fig. 1). These daily counts were used to estimate dispersal intensity.

Mist netting

Mist netting was performed concurrently with visual counts (i.e., 2000–2006) using two methods: (1) passive mist netting involving one to eight nets set at different locations, depending on financial resource capacity, and (2) EMC where birds were actively attracted with playbacks broadcasted from within one to three net enclosures planted with dead snags depending on years and weather. Although the location of the passive nets did change at a local scale between years, the EMC locations remained the same but were discontinued after 2006.

Passive mist netting

Passive capture effort (hours of activity × length of nets in meters) included a varying number of mist nets set from mid-August/late September until late September/late October of each year, with up to 71 days of mist netting per season. Although some changes in net locations occurred between years, nets were always positioned in known woodpecker and passerine trajectories to optimize the capture of transient individuals. Passive nets were at least 150 m away from active enclosures to limit the impact of the active systems on their capture rates. No passive captures were made in 2003 and 2004. Primarily aimed at capturing passerines, nets were 9 to 12 m long with a mesh size of 30 mm. Nets ranged from 20 to 30 cm from the ground to a maximum height of 2.6 to 2.7 m. Passive netting began 30 min before sunrise and continued for 7 hours, weather permitting.

Enhanced capture methods (EMC)

The net enclosure consisted of four mist nets forming a closed squared area. Nets (Avinet 110/2) were 9 m long by 2.8 m high with a mesh size of 60 mm. Nets ranged from 20 to 30 cm from the ground to a maximum height of 2.6 to 2.7 m. Trees within the enclosure were kept at or below the nets' height so that birds flying on and off these trees were more likely to be captured. Two to three snags were planted vertically in the ground within the enclosure as perching areas to encourage woodpeckers to enter the enclosure. These planted snags were kept at or below the height of nets to lower birds' flight altitude. In the center of the enclosure, we installed a sound broadcasting system comprising two speakers set off the ground and opposite each other (Ibarzabal and Desmeules 2006). The broadcasting unit could produce sounds having an amplitude of 100 dB, although we always kept the amplitude lower (at approximately 75 dB) to avoid sound saturation. We continuously broadcasted a single track consisting of a mix of calls and drumming of Black-backed and American Three-toed Woodpeckers for a period of up to seven hours; playbacks generally began 30 min after sunrise, depending on field conditions. Both the call and drumming soundtracks were from the 1997 Stokes field guide to bird songs (Stokes et al. 1997). EMC effort varied from year to year but usually spanned from mid-September until early November.

Statistical analyses

The capture rate (captures/net meters-hour) was modeled using negative binomial models for each species. A set of two candidate models was designed for model selection based on AICc (Burnham and Anderson 2002) to quantify the effect of EMC on capture rate. The first model only included the effect of dispersal intensity (observed transient individuals divided by the visual count effort in time) on capture rate (H_0), while the second model included both the dispersal intensity and the enhanced capture effort (H_1). Both candidate models contained an offset of the natural logarithm of capture effort. We compared both candidate models based on their AICc. The objective behind the previous model selection is to provide an order of magnitude of the efficiency of the EMC on boreal woodpeckers' capture rate. Despite smaller mesh size, passive netting is still efficient at capturing transient boreal woodpeckers.

Capture biases per species for sex and age ratios were investigated using *t*-tests. Using simple linear models, we found no significant effect of capture effort either on sex or age ratio therefore, no capture effort was included in these analyses. The null hypothesis for the *t*-tests was a theoretical 1:1 ratio of female:male, which is accepted as the normal ratio for the wild population (Clutton-Brock 1986), and a ratio of 1:1.5 adult:juvenile. Our use of the 1:1.5 ratio is conservative as the highest observed productivity ranges from 2 to 3 juveniles per couple (Nappi and Drapeau 2009, Tremblay et al. 2015). All analyses were conducted using R 3.6.3 (R Core Team 2020); models were made using glm.nb from the MASS package (Venables and Ripley 2002).

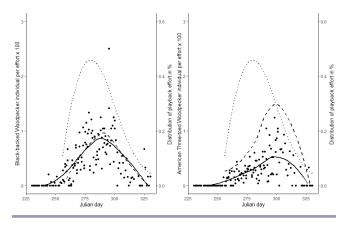
RESULTS

Standardized visual counts from 2000 to 2006 recorded averages of 205.4 \pm 30.4 ind. yr⁻¹ for the Black-backed Woodpecker and 114.3 \pm 25.6 ind. yr⁻¹ for the American Three-toed Woodpecker. Distribution of capture efforts in relation to visual counts indicated a relatively good coverage of the dispersing window (Fig. 2). Black-backed Woodpecker captures averaged 0.7 \pm 0.5 ind. yr⁻¹ without EMC and 69.3 \pm 9.3 ind. yr⁻¹ with EMC. American Three-toed Woodpecker captures averaged 0.6 \pm 0.4 ind. yr⁻¹ without EMC and 93.6 \pm 21.7 ind. yr⁻¹ with EMC. For the Black-backed Woodpecker, capture rate using EMC is positively correlated to visual counts across years (0.71, p=0.071; Fig. 3). For the American Three-toed Woodpecker, the correlation between capture rate using EMC and visual counts was strong (0.97, p < 0.001; Fig. 3).

The proportion of adults in both species was low (Table 1). Blackbacked Woodpecker caught using EMC were biased in favor of juveniles. The average captured age ratio was 1 adult for 13.9 juveniles (ratio of 0.07 ± 0.03 , p < 0.001; Table 1). The same pattern was found for the American Three-toed Woodpecker, with a ratio of 1 adult for 16.7 juveniles (ratio of 0.06 ± 0.04 , p < 0.001; Table 1). The observed sex ratio using EMC capture did not differ significantly from the 1:1 ratio for both species and all age classes, where the average captured Black-backed Woodpecker sex ratio was 1.26 females for 1 male (p = 0.06, df = 6), and was 0.75 female for 1 male (p = 0.1, df = 6) for American Three-toed Woodpecker (Table 1).

The addition of an EMC factor to the baseline model containing only dispersal intensity improved the model, increasing the log-likelihood by 279.43 (Δ AICc = 554.15) for the Black-backed Woodpecker and by 14.73 (Δ AICc = 24.73) for the American

Fig. 2. Average daily count (observation and capture) across the years of Black-backed Woodpecker (*Picoides arcticus*) and of American Three-toed Woodpecker (*P. dorsalis*) and the relative distribution of playback effort. Solid line and dots = 100*visual counts divided by observation effort, dashed line = 100*playback captures/playback effort, dotted line = relative distribution of playback effort (in %).

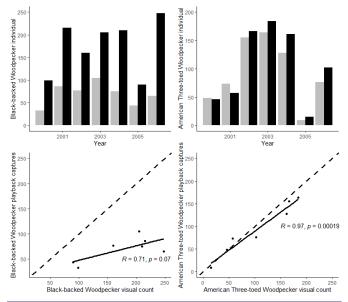


Three-toed Woodpecker (Table 2). Indeed, the number of captures was positively affected by EMC; EMC had an additive effect on the average number of captures of 4.5 ± 0.5 (p < 0.001) for the Black-backed Woodpecker and 4.6 ± 0.6 (p < 0.001) for the American Three-toed Woodpecker.

DISCUSSION

Our main objectives were to investigate the efficiency of EMC calls in capturing woodpeckers and to determine the population structure of Black-backed and American Three-toed Woodpeckers during fall movements at the OOT, located at the southern limit of Québec's boreal forest. Although our experimental design does not permit to quantify the effect of the different mesh size used, the use of EMC within an enclosure greatly increased capture rate by an additive effect of > 4 for both species. The proportion of individuals caught (BBWO = 1:13.9 and ATTWO = 1:16.7) differed from the expected productivity of both species (1:1.5; adult:juveniles; Nappi and Drapeau 2009, Tremblay et al. 2015), supporting our hypothesis that most individuals caught during the fall are juveniles likely dispersing (i.e., post-fledging movements).

There are two main explanations for the observed age ratio bias toward juveniles. First, juveniles, through a higher attraction or a lack of experience, are caught more often in nets; this has been observed for passerines (Brotons 2000, Oñate-Casado et al. 2021). Because of the proximity of the visual count site (~100 m, in their flight trajectory), we believe that the high juvenile ratio in American Three-toed Woodpecker captures is likely not linked to EMC bias, as EMC captures represent an average of 82% of the individuals observed through the dispersing counts. We believe it is the same situation for Black-backed Woodpecker, but with an average of 33% of observed individuals caught, we cannot rule out a potential bias of EMC on the high juvenile ratio. However, no field cue led us to believe we may have experienced such bias. Another possible explanation is that most individuals caught and **Fig. 3.** Correlation between visual counts and captures (passive and active) for Black-backed Woodpecker (*Picoides arcticus*; left) and American Three-toed Woodpecker (*P. dorsalis*; right). Top figures: black columns = visual counts, grey columns = captures. Bottom figures: dashed line 1:1 correlation, solid line: observed correlation, black dots: observed data.



observed at the study site are juveniles undergoing natal dispersal, with adults less likely to disperse. Indeed, it is possible that these surpluses of dispersing individuals originate from high productivity breeding seasons linked to natural disturbances such as forest fire or spruce budworm outbreaks; both disturbances create suitable habitat for these species (Tremblay et al. 2020a, 2020b). Variations in standardized capture rates from one year to another may reflect vearly variations in productivity and newly created habitats by natural disturbances. Black-backed Woodpecker abundance and productivity are closely linked to pulsed resource interactions resulting from recently burned stands (Tremblay et al. 2015). Indeed, recent burns provide a high-quality habitat available for only a short period (Saab et al. 2007, Hutto and Patterson 2016, Tingley et al. 2018); however, these ephemeral habitats are likely responsible for a large output of juveniles in the population (Nappi and Drapeau 2009). Accordingly, younger individuals are predominant in recently burned habitats, suggesting colonization via natal dispersal (Huot and Ibarzabal 2006, Tremblay et al. 2015, Siegel et al. 2016). Future analysis could use data collected at bird observatories such as the OOT, i.e., population structure and abundance, and link the data to the frequency, intensity, size, and distribution of natural disturbances in boreal forests. Unfortunately, little is known with regard to the American Three-toed Woodpecker demographic response to natural disturbances, especially in the eastern part of its range (Tremblay et al. 2020b), making it difficult to interpret the variations in productivity observed at our study site. Observed fluctuations in age ratios and abundance may yield interesting insights into the species' breeding ground productivity and annual demography. Indeed, the species could also benefit from natural

Table 1. Black-backed Woodpecker (*Picoides arcticus*; BBWO) and American Three-toed Woodpecker (*P. dorsalis*; ATTW) population structure of dispersing individuals. Sex ratio is female/ male, age ratio is juvenile/adult. Comparisons were made using *t*-test based on all the captures from both techniques. For year's line, numbers in brackets represent the total number of individuals captured.

	Sex ratio (fe	emale:male)	Age ratio (adult:juveniles)		
	BBWO	ATTW	BBWO	ATTW	
2000	0.89 (36)	1.07 (48)	0.24 (36)	0.26 (48)	
2001	1.15 (86)	0.23 (74)	0.05 (86)	0.03 (72)	
2002	1.48 (77)	1.09 (155)	0.05 (77)	0.03 (155)	
2003	1.69 (105)	0.65 (163)	0.03 (105)	0.006 (162)	
2004	1.34 (75)	1.10 (128)	0.09 (75)	0.11 (128)	
2005	1.32 (44)	0.67 (10)	0.05 (44)	0 (9)	
2006	1.03 (67)	0.55 (79)	0.02 (67)	0.01 (79)	
Mean	1.26 (277:213)	0.75 (283:374)	0.07 (27:403)	0.06 (21:622)	
SE	0.12	0.14	0.03	0.04	
DF	6	6	6	6	
p-value	0.06	0.1	< 0.001	< 0.001	

Table 2. Binomial negative model comparison results for Blackbacked Woodpecker (*Picoides arcticus*; BBWO) and American Three-toed Woodpecker (*P. dorsalis*; ATTW) capture rates when adding a playback factor to the observed dispersion intensity.

Species	Model	K	AICc	∆AICc	AICcWt	Log- likelihood
BBWO	Dispersal + playback	4	71.39	0	1	-28.84
	Dispersal	3	625.54	554.15	0	-308.27
ATTW	Dispersal + playback	4	89.56	0	1	-37.92
	Dispersal	3	114.30	24.73	0	-52.65

forest disturbances, but in lesser magnitude than the Black-backed Woodpecker (Tremblay et al. 2020b). It should be acknowledged that population structure studies using EMC capture data should be taken with caution because biases are well known in different species (Schaub et al. 1999) and results could change according to location and time. Accordingly, we used a conservative test, and our results still show strong and significant differences in age ratio.

Capturing woodpeckers can be challenging; this heightens the difficulty in obtaining sufficient data and metrics to fully understand woodpecker biology, ecology, and population dynamics. Boreal species are a particular challenge to survey and capture (Lehman et al. 2011), in part because of the limited largescale movements of adults (Tremblay et al. 2020a, 2020b). The net enclosure system proved useful and efficient for capturing large numbers of dispersing boreal woodpeckers and yielded data on population size not obtained through passive mist netting. Indeed, from 2000 to 2006, 78% of all American Three-toed Woodpeckers and 36% of Black-backed Woodpeckers in North America were banded at the OOT (Bird Banding Office, unpublished data). Black-backed Woodpeckers capture representation at the OOT is underestimated as an additional 216 captures were made from 2003 to 2006 through research projects during the breeding season (Huot and Ibarzabal 2006, Tremblay et al. 2009). In addition, our study shows that the number of captured individuals using EMC is strongly correlated with visual counts. Hence, long-term capture with EMC could prove useful in providing accurate species population trends for boreal woodpeckers, two species known to be challenging for monitoring efficiently with other techniques, in sites that are not fit for visual counts.

Previous studies on owls and passerines using playbacks to lure the birds into mist nets show sex biases to be common (Schaub et al. 1999, Whalen and Watts 1999). These and other studies consistently document higher capture rates for males than females. Our captures were not significantly skewed toward females nor males for both species. The lack of a strong bias could be explained by the fact that woodpeckers are a group where both sexes are known to be aggressive against intruders or counterparts (Lawrence 1967).

Our data quality on passive netting fluctuated in part because of differences in effort between years. In addition, certain locations for passive nets were more successful than others, and we therefore relocated the nets to the same area the following year, whereas some nets were moved between years; however, the net enclosures used the same type of nets and the same locations. A more constant effort in passive capture both in location and in capture effort would provide a better comparison between both methods. Nevertheless, we believe that using the effort in terms of net length × hours partially corrects for any bias from all net locations not being the same. Another possible bias in our study was differences in net mesh size. Because we also wished to capture passerines with the passive netting, we used a mesh size of 30 mm, whereas the mesh used in the enclosure was 60 mm, which is better adapted for capturing woodpeckers. Indeed, smaller mesh sizes are appropriate for passerines, although sturdier and larger woodpeckers could bounce off the nets (Jenni et al. 1996). Unfortunately, our design does not allow us to fully distinguish between the specific effects of mesh size and EMC. Despite different mesh size, our passive nets proved efficient at capturing boreal woodpeckers where 1.0% of the captures of Black-backed woodpeckers and 0.6% of American Three-toed woodpeckers originated from them. These observations suggest passive nets were not entirely ineffective at catching larger birds, despite their smaller mesh size. Because boreal woodpeckers fly mostly above the canopy while dispersing, they are less likely to be caught in passive nets set below the canopy. Therefore, we believe that even if the EMC effects could be overestimated because we could not control for mesh size, EMC likely still had a significant positive effect on the capture rate. The potential of this method to be replicated at other bird banding locations is very high, and we recommend using such a method as a means of increasing our knowledge of fall movements by woodpeckers and their population dynamics on a year-to-year basis.

In conclusion, our observations of the skewed age-class structure toward juveniles of the Black-backed Woodpecker and the American Three-toed Woodpecker highlight the importance of juveniles in irruptive events of boreal woodpeckers, and possibly for other specialist species. Moreover, bird numbers captured each year at the net enclosure were positively correlated to the numbers detected during visual observations, therefore supporting our hypothesis that EMC capture, if highly standardized, can be used as an effective population monitoring tool.

Author Contributions:

All the authors contributed to the research presented in this manuscript, read and reviewed the manuscript and accepted its submission.

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Data Availability:

Data and code underlying the analysis are available upon request with the coresponding author.

LITERATURE CITED

Berthiaume, É., M. Bélisle, and J. P. Savard. 2009. Incorporating detectability into analyses of population trends based on hawk counts: a double-observer approach. Condor 111:43-58. <u>https://doi.org/10.1525/cond.2009.080081</u>

Bock, C. E., and L. W. Lepthien. 1976. Synchronous eruptions of boreal seed-eating birds. American Naturalist 110:559-571. https://doi.org/10.1086/283091

Brotons, L. 2000. Attracting and capturing Coal Tits *Parus ater*: biases associated with the use of tape lures. Ringing and Migration 20:129-133. https://doi.org/10.1080/03078698.2000.9674234

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Clutton-Brock, T. 1986. Sex ratio variation in birds. Ibis 128:317-329. <u>https://doi.org/10.1111/j.1474-919X.1986.tb02682.</u> X

Côté, P., and P. A. Dumas. 2022. Protocole de suivi de la migration des oiseaux par les relevés visuels quotidiens. Corporation Explos-Nature, Les Bergeronnes, Québec, Canada.

Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg. 2014. Post-fledging survival in passerine birds and the value of postfledging studies to conservation. Journal of Wildlife Management 78:183-193. <u>https://doi.org/10.1002/jwmg.670</u> Dionne, J.-C., and S. Occhietti. 1996. Aperçu du Quaternaire à l'embouchure du Saguenay, Québec. Géographie Physique et Quaternaire 50:5-34. <u>https://doi.org/10.7202/033072ar</u>

Dunn, E. H., and C. J. Ralph. 2004. Use of mist nets as a tool for bird population monitoring. Studies in Avian Biology 29:1-6.

Froehlich, D. 2003. Ageing North American landbirds by molt limits and plumage criteria. A photographic companion to the identification guide to North American birds, Part I. Slate Creek Press, Bolinas, California, USA.

Huot, M., and 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., and D. A. Patterson. 2016. Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire. International Journal of Wildland Fire 25:1074-1085. <u>https://doi.org/10.1071/WF15228</u>

Ibarzabal, J., and P. Desmeules. 2006. Black-backed Woodpecker (*Picoides arcticus*) detectability in unburned and recently burned mature conifer forests in north-eastern North America. Annales Zoologici Fennici 43:228-234.

Jenni, L., M. Leuenberger, and F. Rampazzi. 1996. Capture efficiency of mist nets with comments on their role in the assessment of passerine habitat use. Journal of Field Ornithology 67:263-274.

Johnson, E. I., J. D. Wolfe, T. Brandt Ryder, and P. Pyle. 2011. Modifications to a molt-based ageing system proposed by Wolfe et al. 2010. Journal of Field Ornithology 82:422-424. <u>https://doi.org/10.1111/j.1557-9263.2011.00345.x</u>

Koenig, W. D., and J. M. H. Knops. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. Journal of Animal Ecology 70:609-620. <u>https://doi.org/10.1046/j.1365-2656.2001.00516.x</u>

Kosinski, Z., M. Kempa, and R. Hybsz. 2004. Accuracy and efficiency of different techniques for censusing territorial Middle-spotted Woodpeckers *Dendrocopos medius*. Acta Ornithologica 39:29-34. <u>https://doi.org/10.3161/068.039.0108</u>

Lawrence, L. K. 1967. A comparative life-history study of four species of woodpeckers. Ornithological Monographs 5:1-156. https://doi.org/10.2307/40166747

Lecoq, M., and P. Catry. 2003. Diurnal tape-luring of wintering Chiffchaffs results in samples with biased sex ratios. Journal of Field Ornithology 74:230-232. https://doi.org/10.1648/0273-8570-74.3.230

Lehman, C. P., D. C. Kesler, C. T. Rota, M. A. Rumble, E. M. Seckinger, T. M. Juntti, and J. J. Millspaugh. 2011. Netguns: a technique for capturing Black-backed Woodpeckers. Journal of Field Ornithology 82:430-435. <u>https://doi.org/10.1111/j.1557-9263.2011.00347.x</u>

Michalczuk, J., and M. Michalczuk. 2006. Reaction to playback and density estimations of Syrian Woodpeckers *Dendrocopos syriacus* in agricultural areas of south-eastern Poland. Acta Ornithologica 41:33-39. <u>https://doi.org/10.3161/068.041.0109</u> Nappi, A., and P. Drapeau. 2009. Reproductive success of the Black-backed Woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? Biological Conservation 142:1381-1391. https://doi.org/10.1016/j.biocon.2009.01.022

Newton, I. 2006. Advances in the study of irruptive migration. Ardea 94:433-460.

Oñate-Casado, J., M. Porteš, V. Beran, A. Petrusek, and T. Petrusková. 2021. An experience to remember: lifelong effects of playback-based trapping on behaviour of a migratory passerine bird. Animal Behaviour 182:19-29. <u>https://doi.org/10.1016/j.anbehav.2021.09.010</u>

Pyle, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, California, USA.

R Core Team. 2020. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.

Remsen, J. V., and D. A. Good. 1996. Misuse of data from mistnet captures to assess relative abundance in bird populations. Auk 113:381-398. <u>https://doi.org/10.2307/4088905</u>

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109:97-108. <u>https://doi.org/10.1093/condor/109.1.97</u>

Savard, J.-P. L., and J. Ibarzabal. 2001. Le suivi des oiseaux de la forêt boréale à l'observatoire d'oiseaux de Tadoussac, une opportunité unique au Québec. Le Naturaliste Canadien 125:47-52. https://www.researchgate.net/profile/Jean-Pierre-Savard/publication/237304091 Le suivi des oiseaux de la foret boreale a 1% 27observatoire d%27oiseaux de Tadoussac une opportunite – unique au Quebec/links/0c960533b0b4c9ca47000000/Le-suivi-des-oiseaux-de-la-foret-boreale-a-lobservatoire-doiseaux-de-Tadoussac-une-opportunite-unique-au-Quebec.pdf

Schaub, M., R. Schwilch, and L. Jenni. 1999. Does tape-luring of migrating Eurasian Reed-Warblers increase number of recruits or capture probability? Auk 116:1047-1053. <u>https://doi.org/10.2307/4089684</u>

Shitikov, D., S. Fedotova, V. Gagieva, D. Fedchuk, E. Dubkova, and T. Vaytina. 2012. Breeding-site fidelity and dispersal in isolated populations of three migratory passerines. Ornis Fennica 89:53-62. https://doi.org/10.51812/of.133792

Siegel, R. B., M. W. Tingley, R. L. Wilkerson, C. A. Howell, M. Johnson, and P. Pyle. 2016. Age structure of Black-backed Woodpecker populations in burned forests. Auk 133:69-78. https://doi.org/10.1642/AUK-15-137.1

Stokes, D., L. Stokes, and L. Elliot. 1997. Stokes field guide to bird song: eastern region (Audio CD). Hachette Audio, New York, New York, USA.

Tingley, M. W., A. N. Stillman, R. L. Wilkerson, C. A. Howell, S. C. Sawyer, and R. B. Siegel. 2018. Cross-scale occupancy dynamics of a postfire specialist in response to variation across a fire regime. Journal of Animal Ecology 87:1484-1496. <u>https://doi. org/10.1111/1365-2656.12851</u> Tremblay, J. A., R. D. Dixon, V. A. Saab, P. Pyle, and M. A. Patten. 2020a. Black-backed Woodpecker (*Picoides arcticus*), version 1.0. In P. G. Rodewald, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. <u>https://doi.org/10.2173/bow.bkbwoo.01</u>

Tremblay, J. A., J. Ibarzabal, C. Dussault, and J.-P. L. Savard. 2009. Habitat Requirements of Breeding Black-Backed Woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. Avian Conservation and Ecology - Écologie et conservation des oiseaux 4(1):2. <u>https://doi.org/10.5751/</u> <u>ACE-00297-040102</u>

Tremblay, J. A., J. Ibarzabal, and J.-P. L. Savard. 2015. Contribution of unburned boreal forests to the population of Black-backed Woodpecker in Eastern Canada. Écoscience 22:145-155. <u>https://doi.org/10.1080/11956860.2016.1169386</u>

Tremblay, J. A., D. L. Leonard Jr., and L. Imbeau. 2020b. American three-toed Woodpecker (*Picoides dorsalis*), version 1.0. In P. G. Rodewald, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. <u>https://doi.org/10.2173/</u> bow.attwoo1.01

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA. https://doi.org/10.1007/978-0-387-21706-2

Wang, Y., and D. M. Finch. 2002. Consistency of mist netting and point counts in assessing landbird species richness and relative abundance during migration. Condor 104:59-72. <u>https:// doi.org/10.1093/condor/104.1.59</u>

West, J. D., and J. M. Speirs. 1959. The 1956-1957 invasion of Three-toed Woodpeckers. Wilson Bulletin 71:348-363.

Whalen, D. M., and B. D. Watts. 1999. The influence of audiolures on capture patterns of migrant Northern Saw-whet Owls. Journal of Field Ornithology 70:163-168.

Wiens, J. A., B. R. Noon, and R. T. Reynolds. 2006. Post-fledging survival of Northern Goshawks: the importance of prey abundance, weather, and dispersal. Ecological Applications 16:406-418. https://doi.org/10.1890/04-1915

Wynia, A. L., V. Rolland, and J. E. Jiménez. 2019. Improved campephiline detection: an experiment conducted with the Magellanic Woodpecker. Ecology and Evolution 9:11724-11733. https://doi.org/10.1002/ece3.5671

Yunick, R. P. 1985. A review of recent irruptions of the Blackbacked Woodpecker and Three-toed Woodpecker in eastern North America. Journal of Field Ornithology 56:138-152.