

Habitat preferences of adult Canada Jays (*Perisoreus canadensis*) during the post-breeding period in Algonquin Provincial Park, Ontario, Canada

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Abstract

Habitat preferences in animals are often examined during the breeding period when individuals are easier to observe. However, habitat use may change once young become independent and if resource availability shifts with seasonality. While Canada Jays (*Perisoreus canadensis* (Linnaeus, 1766)) in Algonquin Provincial Park, Ontario, Canada, have been studied for several decades, there is no information on habitat use outside of the fall and late-winter nesting period, where they primarily used conifer forests. Using radio telemetry and resource selection functions comparing used versus available habitats, we estimated home-range size and habitat preferences of 12 adult Canada Jays ($n = 334$ locations) in the spring and summer. Mean (\pm SD) home-range size from minimum convex polygons was 84 (± 48 ha) and ranged from 35 to 201 ha. Canada Jays strongly preferred forest–wetland edges, showed a weak preference for coniferous forests, a corresponding weak avoidance of shade-tolerant hardwood forests, and used mixed forest and wetlands in proportion to their availability. Our results suggest that, while adult Canada Jays use multiple types of habitat during the post-breeding period, they also key into forest–wetland edges, likely to take advantage of emergent prey while remaining near forested areas to maximize protection from predators.

Key words: Canada Jay, *Perisoreus canadensis*, boreal forest, forest edge, habitat use, home range, wetlands

Résumé

Les préférences en matière d'habitat des animaux sont souvent examinées durant la période de reproduction, quand l'observation d'individus est plus aisée. L'utilisation de l'habitat peut toutefois changer une fois les jeunes devenus indépendants et si la disponibilité de ressources change avec les saisons. Si les mésangeais du Canada (*Perisoreus canadensis* (Linnaeus, 1766)) dans le parc provincial Algonquin (Ontario, Canada) sont étudiés depuis plusieurs décennies, aucune information n'existe sur leur utilisation de l'habitat en dehors de l'automne et de la période de nidification de la fin de l'hiver, alors qu'ils utilisent principalement des forêts de conifères. En utilisant la radiotélémetrie et des fonctions de sélection de ressources qui comparent les habitats utilisés et disponibles, nous estimons la taille du domaine vital et les préférences en matière d'habitat de 12 mésangeais du Canada adultes ($n = 334$ sites) au printemps et à l'été. La taille moyenne (\pm ÉT) du domaine vital obtenu de polygones convexes minimums est de 84 (± 48 ha), les valeurs allant de 35 à 201 ha. Les mésangeais du Canada présentent une forte préférence pour les bordures entre forêt et milieu humide, une faible préférence pour les forêts de conifères, un faible évitement correspondant des forêts de feuillus tolérants à l'ombre, et ils font une utilisation de forêts mixtes et de milieux humides proportionnelle à leurs disponibilités. Nos résultats indiqueraient que, si les mésangeais du Canada adultes utilisent différents types d'habitat durant la période post-nidification, ils ciblent également les bordures entre forêt et milieu humide, vraisemblablement pour profiter des proies qui en émergent tout à demeurant près de zones boisées pour une protection maximum contre les prédateurs. [Traduit par la Rédaction]

Mots-clés : mésangeai du Canada, *Perisoreus canadensis*, forêt boréale, lisière de forêt, utilisation de l'habitat, domaine vital, milieux humides

Introduction

Habitat selection is the behavioural response of an organism to favour certain resources over others, often leading to a disproportionate use of available habitats (Jones 2001). The habitats a species prefers can change throughout the sea-

sons and as life histories progress (Godbout and Ouellet 2010; Bouyer et al. 2015; McGarigal et al. 2016; Viejou et al. 2018). In many birds, patterns of habitat selection by adults during the breeding season are relatively well understood (Manly et al. 1993; Jones 2001; Arvisais et al. 2004; Wegge et al. 2005;

Grahame et al. 2021; Thomas et al. 2021), but less attention has been given to understanding habitat selection of animals during the post-breeding season (King et al. 2006; Domínguez et al. 2016; McGarigal et al. 2016; Ludwig and Klaus 2017). Since our understanding of a species' life history and ecology relies heavily on the understanding of the habitat types that animals use (Boyce and Waller 2003; Baldwin et al. 2006), a comprehensive understanding of habitat selection throughout species' annual cycle is needed.

The Canada Jay (*Perisoreus canadensis* (Linnaeus, 1766)) is a resident passerine of North American boreal and subalpine ecosystems (Strickland and Ouellet 2020) that caches perishable food items, such as berries, mushrooms, invertebrates, and vertebrate flesh, for both over-winter survival and late-winter/early-spring reproduction (Sechley et al. 2014; Derbyshire et al. 2019; Strickland and Ouellet 2020). At the southern edge of their range in Algonquin Provincial Park, Ontario, Canada (hereafter "APP"), Canada Jays predominantly place their nests within black spruce (*Picea mariana* (Mill.) Britton, Sterns, and Poggenb.) and balsam fir (*Abies balsamea* (L.) Mill.) stands (Strickland and Ouellet 2020) and experimental evidence suggests that coniferous trees are more effective at preserving cached food than shade-tolerant hardwood trees, potentially due to antimicrobial properties of their resin (Strickland et al. 2011; Sechley et al. 2015). In APP, Canada Jays have declined by over 50% in the last two decades (Waite and Strickland 2006) and evidence suggests that increasing fall temperatures and freeze thaw events during the fall are spoiling perishable cached food, which then negatively influences reproductive success and population growth (Waite and Strickland 2006; Sutton et al. 2016, 2021a).

While the ecology of Canada Jays during the winter and breeding period has been well studied, there is currently no information about their home range and habitat use during the spring and summer post-breeding period. Therefore, it is important to study the habitat use of jays outside of the breeding season because this can provide insights into changes in their diet and habitat requirements. In the spring and summer, Canada Jays are presumably exposed to a larger number of avian predators, such as migratory Merlins (*Falco columbarius* Linnaeus, 1758) and Broad-winged Hawks (*Buteo platypterus* (Vieillot, 1823)), who have returned to breed (Martin 1960), although. Although the direct causes of adult mortality in Canada Jays have not been identified, Siberian Jays (*Perisoreus infaustus* (Linnaeus, 1758)), a congener of Canada Jays, use habitats with dense visual cover as protection from *Accipiter* hawks (Griesser et al. 2017). Similar to Siberian Jays, the Canada Jays may seek protection from predators in spring and summer, which could result in their continued preference for dense coniferous stands over shade-tolerant hardwood stands. However, as sources of fresh food become more abundant in the spring and summer and adults are no longer reliant on food cached primarily in coniferous trees, Canada Jays may expand the range of habitats they use. Bogs, marshes, and fens often thaw before forests in the spring and can be productive sites for emerging aquatic invertebrates and vertebrates (Lafleur et al. 1997; Spitzer and Danks 2006; Macdade et al. 2011; Keddy 2016). Canada Jays

are also nest predators of other songbirds (Darveau et al. 1997; Ibarzabal and Desrochers 2004; Strickland and Ouellet 2020) and, as a group, songbirds nest in virtually all habitat types in APP (Martin 1960). The predatory behaviour of Canada Jays may also motivate them to use forest-wetland edges in spring and summer so that they can hunt songbirds and amphibians (Ibarzabal and Desrochers 2004; Tozer and Allen 2004; Murray et al. 2005; Strickland and Ouellet 2020). Canada Jays have been observed to be nest predators of other bird species along habitat edges (Ibarzabal and Desrochers 2004; Tozer and Allen 2004) and may select for the edges of forest-wetland habitats due to the influx of nesting migratory birds in the spring and summer. By using the forest-wetland edge, jays may be able to maximize foraging strategies while also having easy access to protective forest cover.

We examined habitat selection within home ranges of radio-tracked Canada Jays during the post-breeding period (mid-May to late July) in APP. We quantified home-range sizes and land cover types used by Canada Jays during the spring and summer and examined the following hypotheses: (1) the "emergent prey" hypothesis, which suggests that adult Canada Jays select wetland habitats (i.e., submergent and emergent vegetation in open marshes, fens, and bogs) during the post-breeding period due to the emergence of aquatic invertebrates and amphibians; (2) the "predator avoidance" hypothesis, which suggests that adults select for coniferous forest habitats during the post-breeding period because dense conifers can provide protective cover from predators; and (3) the "foraging-predation trade-off" hypothesis, which postulates that adults prefer forest-wetland edges during the post-breeding period to take advantage of habitat where invertebrates, songbirds, and amphibians can occur in high densities along forest-wetland edges while also having protective cover from predators.

Materials and methods

Study site

In 2020 and 2021, we tracked the movement of 12 adult Canada Jays (6 males and 6 females) located along the Highway 60 corridor in APP (48°30'N, 78°40'W). APP is located in the central Ontario transition zone between boreal forest and Great Lakes-St. Lawrence lowlands (Rowe 1972) and is dominated by three major forest types: (1) shade-tolerant hardwood forests, consisting of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), with scattered groves of eastern hemlock (*Tsuga canadensis* (L.) Carrière); (2) mixed forest, consisting of white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), balsam fir and white spruce (*Picea glauca* (Moench) Voss) mixed with paper birch (*Betula papyrifera* Marshall), trembling aspen (*Populus tremuloides* Michx.), large-tooth aspen (*Populus grandidentata* Michx.); and (3) boggy coniferous forests, consisting primarily of black spruce and balsam fir, but also containing patches of tamarack (*Larix laricina* (Du Roi) K. Koch), and eastern white cedar (*Thuja occiden-*

talis L.). Stands consisting almost entirely of black spruce often bordered edges of open, low-lying marshlands that were classified as open wetlands.

Capture and radio telemetry

We captured adult Canada Jays from late April to mid-May in 2020 ($n = 8$) and 2021 ($n = 4$) after the completion of their breeding season (i.e., either after nest failure or after successful fledging) with a walk-in Potter trap baited with suet. Upon capture, individuals were fitted with a 2.5 g radio transmitter (model PipAg393, Lotek Wireless Inc., Newmarket, ON, Canada) attached via a leg-loop harness and then weighed (using 300 g Pesola spring scale; Pesola, Schindellegi, Switzerland). All individuals had been previously captured and fitted with a unique combination of three colour leg bands and a US Fish and Wildlife Service aluminum band. Sexes of all 12 radio-tagged birds were determined by mass ($M \geq 71.5 \text{ g} > F$) and confirmed by observing their breeding behaviour prior to data collection. The adults tracked originated from 12 different breeding territories that spanned the entire study area, represented a range of ages (range 2–9 years old), and composed 36% (12/33) of the breeding adults in the population at the time of sampling. All capture and handling methods were approved by Environment and Climate Change Canada (permit #10416) and the University of Guelph's Animal Care Committee (AUP #4003).

Between 26 April–2 August 2020 and 24 April–31 July 2021, we relocated each radio-tagged individual two times per week. Locations of individuals were only taken one time for each visit. To track birds, we used VHF receivers (SRX600; Lotek Wireless Inc., Newmarket, ON, Canada) and three-element Yagi directional antennas (Lotek Wireless Inc., Newmarket, ON, Canada). Birds were tracked at various times during daylight hours. Due to the time it took to get locations and variability of weather conditions, we were unable to limit tracking to a narrow window during the day. In the case of extreme heat, rain, or wind storms, radio tracking was avoided. Via either foot, canoe, or combination of both, we followed signal strength of the radio transmitter until the individual was within sight (10–50 m) and its identity was confirmed through its unique colour band combination. The location of the bird was then recorded using a handheld global positioning system (GPS) with a 5–10 m error (Garmin GPS Map 64st; Garmin International, Inc., Olathe, KS, USA) and a description of the habitat type (coniferous, shade-tolerant hardwood, mixed, or wetland) within a 15–20 m radius of the location was identified and recorded and used to later verify the accuracy of land cover data. After the location was recorded, the radio-tagged bird, its breeding partner, and any accompanying juveniles were observed for approximately 20 min (range 10–30 min, exact time was not recorded) depending on weather conditions. During the time of observation, we recorded any foraging behaviours that occurred. If a foraging event occurred, we attempted to visually identify the prey being consumed via the remains of the food items or by observing the feeding behaviours at close range through binoculars.

Land cover data

APP land cover data were obtained from the Forest Resource Inventory (FRI; [Land Information Ontario 2007](#)). The data were compiled between 2002 and 2004 and included a 100 m grid that was created from the interpretation of aerial survey work ([Land Information Ontario 2007](#)). Land cover polygons in the FRI dataset were reclassified as either coniferous, shade-tolerant hardwood, or mixed forest, based on the tree species composition within each polygon that was included in the land cover data. Similar to previous habitat selection studies ([Ferron and Ouellet 1992](#); [Norris et al. 2002](#); [Arvisais et al. 2004](#)), if a land cover polygon had a coniferous or shade-tolerant hardwood tree species composition of $\geq 70\%$, it was classified as one of these two habitat types, respectively. Stands with tree compositions of $<70\%$ coniferous and $<70\%$ shade-tolerant hardwood species were classified as mixed forest. Habitats with at least 50% of cover types labelled in the FRI dataset as “Forested Treed Muskeg”, “Forested Open Muskeg”, and “Forested Brush and Alder” were defined as wetland based on comparisons made between the land cover data and the habitat observations recorded in the field. Water (i.e., open lakes and rivers) and cleared land (e.g., parking lots, gravel pits) were classified as “other”, although none of these habitats occurred at observed jay locations, but still were present in the land cover of some territories. We then used ArcGIS (Geographical Information Software; ArcMap v.10.0, ESRI, Redlands, CA, USA) to overlay the vector-based land cover data from the FRI with the radio telemetry points. All habitat types assigned to polygons in the land cover data were ground-truthed by comparing classifications to field observations collected on foot.

Resource selection models

Resource selection functions (RSFs) are used to compare “used” locations of where animals are actively found to “available” locations of random points that indicate available habitat ([Manly et al. 1993](#); [Boyce and McDonald 1999](#); [Boyce et al. 2002](#)). We developed resource function models to assess whether adult Canada Jays prefer or avoid the edge/interior of forests that border wetlands (hereafter “forest-wetland edge”) and test for preferences of any of the four classified habitat types (Design I Type A RSF; [Manly et al. 1993](#)). “Used habitat” was defined by the GPS locations of jays taken during radio telemetry. To derive “available habitat”, radio telemetry points of each individual (mean \pm SD = 29 ± 4 points for each individual) were used to calculate home ranges using 100% minimum convex polygons (MCPs; [Johnson and Gillingham 2008](#)). We considered this an accurate representation of habitat types and forest-wetland edges that were potentially available to each adult Canada Jay, with the exception of open water (i.e., large lakes and ponds), which was clipped from the total area of each MCP ([Northrup et al. 2013](#)). To define forest-wetland edges, we used ArcGIS to dissolve all forest habitat types together and then calculated a 10 m buffer (on both sides of the edge) between forest and wetland habitats. We used 10 m as the buffer limit because Canada Jays presumably do not need to fly more than 10 m into a forest for protective cover during a predation attempt. Additionally, beyond 10 m

there is little to no “transition” vegetation between two wetland or forested habitats. We then generated random points within the home range of each individual and, following the suggestions of Nad’O and Kaňuch (2018), each used point was paired with 10 available points. Therefore, we examined resource selection within individual home ranges (third-order selection; DeCesare et al. 2012) and used the findings of individual behaviour to make inferences about the population (Manly et al. 1993). When estimating preference for forest–wetland edge, random points were generated within the 10 m buffer within each individual’s home range.

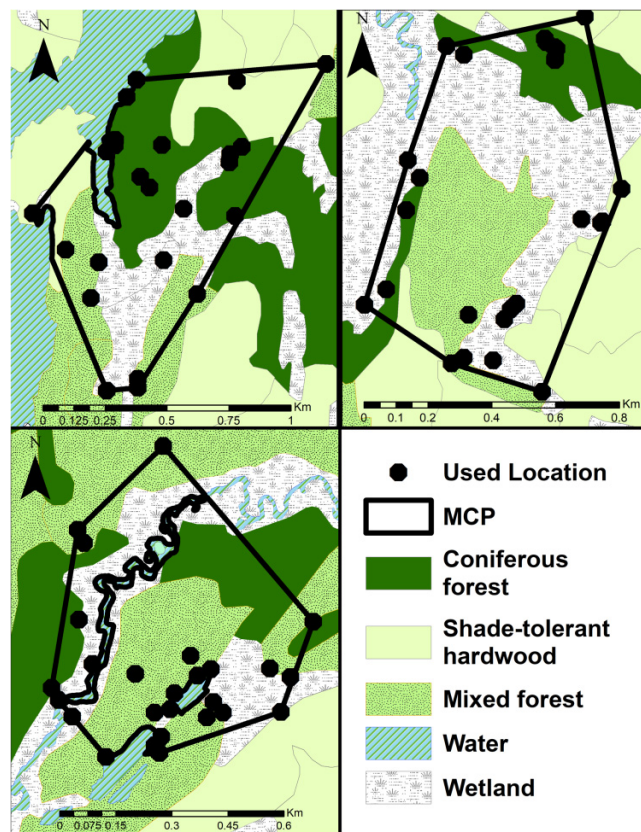
To estimate the probability that a given habitat type or forest–wetland edge was preferred by Canada Jays, we used binomial generalized linear mixed models (GLMMs; Duchesne et al. 2010) with a logit link function. We constructed separate GLMMs for each habitat type (coniferous, shade-tolerant hardwood, mixed, wetland) and forest–wetland edge to eliminate issues related to multicollinearity and model convergence. For models that examined habitat type and edge preferences, we included a binomial variable (1 = used, 0 = available) as the response variable. For each habitat or edge model, the GLMM included a binomial predictor variable indicating if the location was within or outside of the specified habitat (1 = within given habitat type, 0 = outside habitat type) or forest–wetland edge (1 = forest–wetland edge, 0 = non-forest–wetland edge). To account for the multiple locations taken from each individual, we also included individual ID as a random effect in all GLMMs. The output of the RSF model is the coefficient of selection estimate (β value), whereby a positive value (up to 1) indicates preference for a habitat type and a negative value (down to -1) indicates avoidance. The α value for all models was set at 0.05.

Results

We collected 204 radio telemetry locations of eight Canada Jays in 2020 and 130 locations of four Canada Jays in 2021 ($n = 334$ total; Fig. 1). The mean (\pm SD) home-range size, as estimated by MCPs, was 84 ha (\pm 48 ha), and ranged from 35 to 201 ha (Fig. 1). Of the 12 individuals tracked, 3 adults were accompanied by a dominant juvenile fledgling through June and July. However, we did not observe any notable differences in home-range size or habitat selection amongst these three individuals. Random points generated within each MCP suggested that shade-tolerant hardwood forest (38%) and wetland habitats (25%) were most abundant habitat types, whereas coniferous (21%) and mixed (17%) forest habitats were in lower abundance (Fig. 2). Forest–wetland edges made up 20% of random locations within home range MCPs. Results from the GLMMs indicated that Canada Jays had a weak preference for coniferous forest (26% of used locations), a stronger preference for forest–wetland edges (30% of used locations), a weak avoidance of shade-tolerant hardwood forests (32% of used locations), and used mixed forest and wetland habitats in proportion to their availability (Table 1, Fig. 2).

Observations of radio-tracked Canada Jays generally supported the notion that wetlands, and to a lesser extent coniferous and mixed forests, were productive habitats for foraging (Table 2). Canada Jays were often seen foraging on

Fig. 1. Maps of 3 of the 12 individual Canada Jays (*Perisoreus canadensis*) that were radio-tracked in Algonquin Provincial Park, Ontario, Canada, between late April and early August. The black outline represents the home range of the individual calculated as a minimum convex polygon (MCP). Each black dot corresponds to used locations of adult Canada Jays. Map produced with ArcGIS Desktop 10.7.1 (ESRI 2015) using the NAD83 projection and UTM coordinate system (Zone 17T). Land cover data used for maps were from the Forest Resource Inventory (Land Information Ontario 2007). [Colour online.]



invertebrates with 22, 9, and 3 observations of jays consuming invertebrates in coniferous forests, mixed forests, and wetlands, respectively. In May 2020, one pair of Canada Jays was observed killing and consuming an adult American Toad (*Anaxyrus americanus* (Holbrook, 1836)) along the forest–wetland edge, with the toad being eaten from an opening beneath the throat, suggesting the jays were avoiding the parotid toxin glands behind the toad’s eyes. During spring and summer, Canada Jays were also observed consuming adult Red-backed Salamanders (*Plethodon cinereus* (Green, 1818)) and Spotted Salamanders (*Ambystoma maculatum* (Shaw, 1802)) along forest–wetland edges (Table 2). Additionally, Canada Jays were seen hunting and killing Black-capped Chickadees (*Poecile atricapillus* (Linnaeus, 1766)), Magnolia Warblers (*Setophaga magnolia* (A. Wilson, 1811)), and White-winged Crossbills (*Loxia leucoptera* J.F. Gmelin, 1789) at forest–wetland edges. Lastly, in mid-late summer, we observed three instances of Canada Jays foraging and consuming mushrooms such as *Boletus* sp. and fly amanita (*Amanita*

Fig. 2. Proportion of habitat types that occurred at used and available locations ($n = 334$ used, 3340 available) within the home ranges of Canada Jays (*Perisoreus canadensis*) tracked during the post-breeding season (i.e., spring–summer) in Algonquin Provincial Park, Ontario, Canada, in 2020 and 2021. The data included in this figure include five separate analyses that each individually tested for preferences of coniferous forest, mixed forest, shade-tolerant hardwoods, open wetlands, and forest-wetland edges. Thick lines in boxes represent the median, upper and lower limits indicate the standard error, and vertical lines are the standard deviation. The * above a given box plot indicates statistically significant selection according to resource selection function models ($\alpha = 0.05$). Canada Jay graphic was created by Shelby Bohn. [Colour online.]

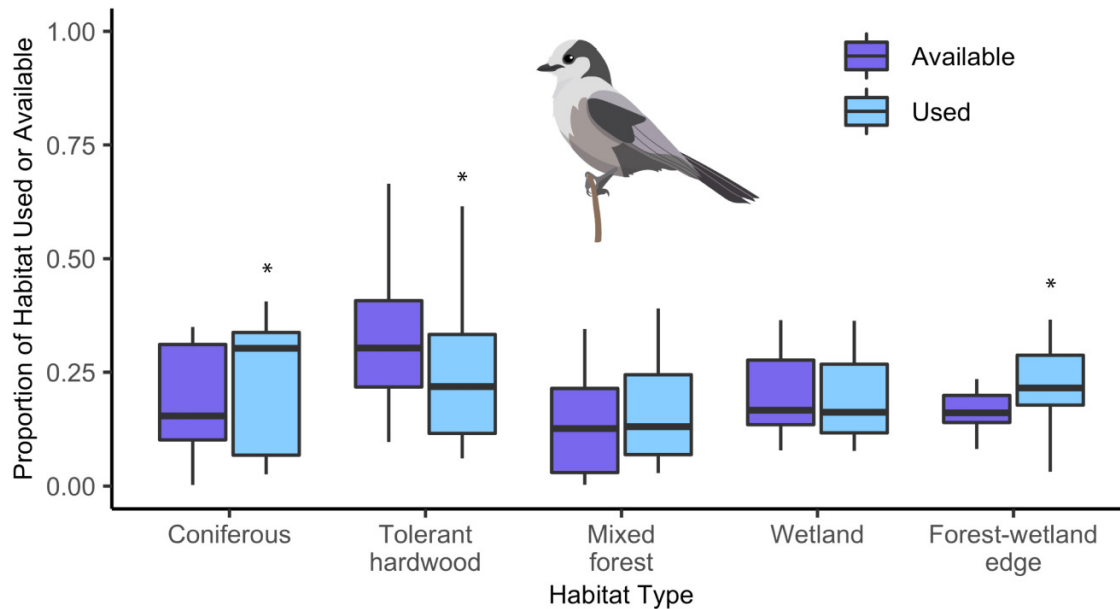


Table 1. Selection coefficient (β) and 95% confidence intervals (CI) estimated from a binomial logistic regression model for Canada Jay (*Perisoreus canadensis*) habitat selection for land cover types and edge/interior in the 2020 and 2021 post-breeding seasons in Algonquin Provincial Park, Ontario, Canada.

Habitat feature	Feature type	Selection coefficient (β)	2.5% CI	97.5% CI	p value
Land cover	Coniferous	0.274 ± 0.13	0.011	0.528	0.03*
	Shade-tolerant hardwood	-0.247 ± 0.12	-0.490	-0.009	0.04*
	Mixed	0.098 ± 0.15	-0.203	0.385	0.51
	Wetland	-0.039 ± 0.13	-0.308	0.219	0.76
Forest-wetland edge	Edge	0.498 ± 0.06	0.243	0.746	0.009*

Note: Positive β estimates indicate selection for that habitat type and negative values indicate avoidance (* represents significance at α threshold of 0.05). Confidence intervals for a habitat type that overlaps with zero suggest a lack of evidence for either a preference or an avoidance of that habitat type.

muscaria (L.) Lam.) in mixed forest types. These results demonstrate that Canada Jays repeatedly exhibit active hunting in spring and summer, a behaviour that has only been observed a few times before in this species (Tozer and Allen 2004; Murray et al. 2005).

Discussion

Our results support the hypothesis that Canada Jay habitat use during the spring and summer is at least partially driven by a trade-off between the benefits of foraging in productive areas and the risk of predation. We suggest that the statistical preference of Canada Jays for forest-wetland edges is also biologically significant given that adults use wetland habitat to search for, and capture, a variety of prey items. At

forest-wetland edges, we observed radio-tracked Canada Jays feeding on invertebrates, songbirds, larval salamanders, and even American Toads, all of which have been previously documented prey items (Ouellet 1970; Ibarzabal and Desrochers 2004; Tozer and Allen 2004; Murray et al. 2005; Strickland and Ouellet 2020). At the same time, forest-wetland edges would provide easy access to protective cover from visual predators, such as Northern Goshawks (*Accipiter gentilis* (Linnaeus, 1758)), Red-tailed Hawks (*Buteo jamaicensis* (Gmelin, 1788)), Broad-winged Hawks, and Merlins, all of which have been observed to hunt Canada Jays (Strickland and Ouellet 2020). Predation threat is likely higher during the spring and summer and this is supported by the lower survival rates of Canada Jays in APP during this time compared to the fall and winter (Norris et al. 2013). Remaining close to or within the dense

Table 2. Novel foraging observations of adult Canada Jays (*Perisoreus canadensis*) while they were radio-tracked during the post-breeding season (April–August 2020, 2021) in Algonquin Provincial Park, Ontario, Canada.

Location within study area	Date	Food item	Habitat type	Notable behaviours	Observed caching?
Arowhon Road	14 May 2020	American Toad (<i>Anaxyrus americanus</i>)	Coniferous forest (interior)	Jays were seen killing and consuming the toad. Eaten from beneath the throat	No
North Madawaska River	19 May 2020	Spotted Salamander (<i>Ambystoma maculatum</i>)	Coniferous forest (forest–wetland edge)	One jay was seen perched and then dove to capture a salamander in the <i>Sphagnum</i> and then ate it	No
Bluebird Lake	6 July 2020	<i>Boletus</i> sp.	Mixed forest (interior)	Jays observed pecking at and eating mushroom	No
Wolf Howl Pond	9 July 2020	<i>Craterellus</i> sp.	Coniferous forest (interior)	Jays observed pecking at and eating mushroom	Yes
Leaf Lake Ski Trail	20 July 2020	Magnolia Warbler (<i>Setophaga magnolia</i>)	Coniferous forest (interior)	Aerial pursuit of adult warbler resulting in capture and consumption	No
Bat Lake	24 May 2021	Spotted Salamander	Coniferous forest (forest–wetland edge)	Jay was seen plucking a salamander from underneath leaf litter and then ate it	No
Bat Lake	31 May 2021	Red-backed Salamander (<i>Plethodon cinereus</i>)	Mixed forest (forest–wetland edge)	Jay picked up prey from leaf litter on a cold morning	No
Beaver Pond Trail	7 June 2021	Chestnut-sided Warbler (<i>Setophaga pensylvanica</i> (Linnaeus, 1766))	Mixed forest (forest–wetland edge)	Jay was seen sitting on branch eating freshly killed adult warbler	No
Sunday Creek	19 June 2021	White-winged Crossbill (<i>Loxia leucoptera</i>)	Coniferous forest (forest–wetland edge)	Jay was seen sitting on branch eating freshly killed juvenile crossbill	No
Mizzy Lake Trail	1 July 2021	Black-capped Chickadee (<i>Poecile atricapillus</i>)	Coniferous forest (interior)	Aerial pursuit of juvenile resulting in capture and consumption	No
Mizzy Lake Trail	30 July 2021	Fly amanita (<i>Amanita muscaria</i>)	Mixed forest (forest–wetland edge)	Jay seen consuming and pulling apart mushroom	Yes

forest cover may serve to improve spring/summer survival of Canada Jays similar to the way dense cover benefits other boreal birds (Wegge et al. 2005; Griesser et al. 2017). The reluctance of Canada Jays to spend time in open habitats during the spring and summer is indirectly supported by a previous study that found no evidence of preferential foraging of quail eggs by Canada Jays in clear-cut areas within boreal forest (Darveau et al. 1997).

While there was a preference for wetland-forest edges, our results also suggest that Canada Jays used a variety of habitat types during the post-breeding period. Although we found evidence that jays weakly preferred coniferous stands and weakly avoided shade-tolerant hardwood stands (Table 1, Fig. 2), we suspect this is because coniferous stands are the most common forest type bordering wetlands in APP while shade-tolerant hardwoods are the least common. Assuming that these patterns result more from sampling bias than active preference, it appears that adult Canada Jays used a wider variety of habitats during the post-breeding period compared to during the fall and winter when they are strongly associated with coniferous forests, which are used for storing cached food and nesting (Sechley et al. 2014; Derbyshire et al. 2019; Strickland and Ouellet 2020). It is perhaps unsurprising that jays would expand their habitat use after the breeding period given their generalist diet and the availability of

fresh food (Ouellet 1970; Potter et al. 2015; Strickland and Ouellet 2020; Freeman et al. 2021). Canada Jays have been documented to consume arthropods, berries, fungi, and vertebrate flesh scavenged from carrion or through predating amphibians and birds (Ouellet 1970; Freeman et al. 2021). Even during the relatively short duration that this study took place, Canada Jays were observed capturing and consuming a variety of food items such as songbirds, amphibians, insects, and fungi across different habitats (Table 2). Thus, while jays may key into forest–wetland edges because of their productivity and protective cover, it is apparent that they also take advantage of a broader range of habitats during the spring and summer.

While we assessed the use of broadly classified habitat types within Canada Jay territories, it is important to note that classification of habitats at a finer scale was limited by the resolution of the land cover data. The FRI data that were used in this study are coarse with land cover within ~20 m not distinguishable due to the resolution of the original imagery. Because of this, small strips of land cover, particularly along the boundary of habitat types are not well defined. For example, the boundary along forested spruce stands and open marshes often has sparse trees, which is not reflected in the land cover data. This may have led to underestimates of where coniferous forests stop and open wetlands begin. Ad-

ditionally, the tree species composition listed for a given plot in the land cover data may not reflect the tree species composition at the exact location at which the Canada Jays were observed. Future research should attempt to more clearly define habitat types and classify different forest types according to aerial imagery and normalized difference in vegetation indices.

Of the Canada Jay's three distinct forms (van Els et al. 2012), the continent-spanning boreal morphotype is invariably associated with black or white spruce (Graham et al. 2021). In APP, however, at the southern edge of their range in eastern North America, Canada Jays originally showed no obvious habitat preference. They even occurred, and indeed were first studied (Rutter 1969), in park forests that were overwhelmingly dominated by hardwoods, albeit with narrow coniferous ribbons along lakeshores, creeks, and the edges of beaver ponds. Since the 1980s, however, Canada Jays have declined by over 50% in APP and now persist only in forested spruce bogs and mostly coniferous forests indicating that Canada Jays have largely been extirpated in low-quality territories and are now only found in higher quality habitats (Strickland et al. 2011; Sutton et al. 2021b). Our results suggest that, while boreal Canada Jays are highly dependent on conifers during the fall and winter, in APP they take advantage of a wider range of habitats during the spring and summer, particularly forest-wetland edges that appear to serve as productive foraging areas for this generalist species.

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References

- Arvisais, M., Lévesque, E., Bourgeois, J.-C., Daigle, C., Masse, D., and Jutra, J. 2004. Habitat selection by the wood turtle (*Clemmys insculpta*) at the northern limit of its range. *Can. J. Zool.* **82**(3): 391–398. doi:10.1139/z04-012.
- Baldwin, R.F., Calhoun, A.J.K., and deMaynadier, P.G.. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog, *Rana sylvatica*. *J. Herpetol.* **40**: 442–453. doi:10.1670/0022-1511(2006)40[442:CPFASW]2.0.CO;2.
- Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R.C., Odden, J., and Linnell, J.D.C. 2015. Eurasian lynx habitat selection in human-modified landscape in Norway: effects of different human habitat modifications and behavioral states. *Biol. Conserv.* **191**: 291–299. doi:10.1016/j.biocon.2015.07.007.
- Boyce, M.S., and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. *Trends. Ecol. Evol.* **14**: 268–272. doi:10.1016/S0169-5347(99)01593-1.
- Boyce, M.S., and Waller, J.S. 2003. Grizzly bears for the Bitterroots: predicting potential abundance and distribution. *Wildl. Soc. Bull.* **31**: 670–683.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., and Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. *Ecol. Modell.* **157**: 281–300. doi:10.1016/S0169-5347(99)01593-1.
- Darveau, M., Bélanger, L., Huot, J., Mélançon, É., and Debellefeuille, S.. 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. *Ecol. Appl.* **7**(2), 572–580. doi:10.1890/1051-0761(1997)007[0572:fpatro]2.0.co;2.
- DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., et al.. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecol. Appl.* **22**(4): 1068–1083. doi:10.1890/11-1610.1.
- Derbyshire, R., Norris, D.R., Hobson, K.A., and Strickland, D. 2019. Isotopic spiking and food dye experiments provide evidencethat nestling Canada Jays (*Perisoreus canadensis*) receive cachedfood from their parents. *Can. J. Zool.* **97**(4): 368–375. doi:10.1139/cjz-2018-0158.
- Domínguez, J., Carbonell, R., and Ramírez, A. 2016. Seasonal changes in habitat selection by a strict forest specialist, the middle spotted woodpecker (*Leitopicus medius*), at its southwestern boundary: implications for conservation. *J. Ornithol.* **158**(2): 459–467. doi:10.1007/s10336-016-1415-6.
- Duchesne, T., Fortin, D., and Courbin, N. 2010. Mixed conditional logistic regression for habitat selection studies. *J. Anim. Ecol.* **79**(3): 548–555. doi:10.1111/j.1365-2656.2010.01670.x.
- ESRI. 2015. ArcGIS desktop. Environmental Systems Research Institute, Redlands, CA.
- Ferron, J., and Ouellet, J.-P. 1992. Daily partitioning of summer habitat and use of space by the snowshoe hare in southern boreal forest. *Can. J. Zool.* **70**(11): 2178–2183. doi:10.1139/z92-294.
- Freeman, N.E., Newman, A.E.M., Sutton, A.O., Kyser, T.K., and Norris, D.R. 2021. Causes and consequences of variation in diet composition of nestling Canada Jays. *J. Avian Biol.*, **52**(1): e02623. doi:10.1111/jav.02623.
- Godbout, G., and Ouellet, J.P. 2010. Fine-scale habitat selection of American marten at the southern fringe of the boreal forest. *Ecoscience*, **17**: 175–185. doi:10.2980/17-2-3288.

- Graham, B.A., Cicero, C., Strickland, D., Woods, J.G., Dohms, K.M., Szabo, I., and Burg, T.M. 2021. Cryptic genetic diversity and cytonuclear discordance characterize contact among Canada jay (*Perisoreus canadensis*) morphotypes in western North America. *Biol. J. Linn. Soc.* **132**(4): 725–740. doi:10.1093/biolinnean/blaa223.
- Grahame, E.R.M., Martin, K.D., Gow, E.A., and Norris, D.R. 2021. Diurnal and nocturnal habitat preference of Eastern Whip-poor-wills (*Antrostomus vociferus*) in the northern portion of their breeding range. *Avian Conserv. Ecol.* **16**: 14. doi:10.5751/ACE-01929-160214.
- Griesser, M., Mourocq, E., Barnaby, J., Bowgen, K.M., Eggers, S., Fletcher, K., et al. 2017. Experience buffers extrinsic mortality in a group-living bird species. *Oikos*, **126**(9): 1258–1268. doi:10.1111/oik.04098
- Ibarzabal, J., and Desrochers, A. 2004. A nest predator's view of a managed forest: gray jay (*Perisoreus canadensis*) movement patterns in response to forest edges. *Auk*, **121**(1): 162–169. doi:10.1093/auk/121.1.162.
- Johnson, C.J., and Gillingham, M.P. 2008. Sensitivity of species-distribution models to error, bias and model design: an application to resource selection functions for woodland caribou. *Ecol. Modell.* **213**: 143–155. doi:10.1016/j.ecolmodel.2007.11.013.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk*, **118**(2): 557–562. doi:10.1093/auk/118.2.557.
- Keddy, P. 2016. *Wetland ecology: principles and conservation*. Cambridge University Press, New York.
- King, D.I., Degraaf, R.M., Smith, M.L., and Buonaccorsi, J.P. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J. Zool.* **269**(4): 414–421. doi:10.1111/j.1469-7998.2006.00158.x.
- Lafleur, P.M., McCaughey, J.H., Joiner, D.W., Bartlett, P.A., and Jelinski, D.E. 1997. Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland. *J. Geophys. Res. Atmos.* **102**: 29009–29020. doi:10.1029/96JD03326.
- Land Information Ontario 2007. Forest Resources Inventory (FIM v1)-Package-S. Ontario GeoHub[Online]. Available from <https://geohub.lio.gov.on.ca/datasets/forest-resources-inventory-status/explore> [accessed 6 June 2022].
- Ludwig, T., and Klaus, S. 2017. Habitat selection in the post-breeding period by Hazel Grouse *Tetrastes bonasia* in the Bohemian Forest. *J. Ornithol.* **158**: 101–112. doi:10.1007/s10336-016-1365-z.
- Macdade, L.S., Rodewald, P.G., and Hatch, K.A. 2011. Contribution of emergent aquatic insects to refueling in spring migrant songbirds. *Auk*, **128**(1): 127–137. doi:10.1525/auk.2011.10186.
- Manly, B.F.J., McDonald, L.L., and Thomas, D.L. 1993. *Resource selection by animals: statistical design and analysis for field studies*. 1st ed. Chapman and Hall, London, UK.
- Martin, N.D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. *Ecology*, **41**: 126–140. doi:10.2307/1931946.
- McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., and Cushman, S.A. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol.* **31**: 1161–1175. doi:10.1007/s10980-016-0374-x.
- Murray, M.P., Pearl, C.A., and Bury, R.B. 2005. Apparent predation by gray jays, *Perisoreus canadensis*, on long-toed salamanders, *Ambystoma macrodactylum*, in the Oregon Cascade Range. *Can. Field-Nat.* **119**: 291–292. doi:10.22621/cfn.v119i2.116.
- Nad'ou, L., and Kaňuch, P. 2018. Why sampling ratio matters: logistic regression and studies of habitat use. *PloS One*, **13**(7). doi:10.1371/journal.pone.0200742.
- Norris, D.R., Flockhart, D.T.T., and Strickland, D. 2013. Contrasting patterns of survival and dispersal in multiple habitats reveal an ecological trap in a food-caching bird. *Oecologia*, **173**: 827–835.
- Norris, D.R., Theberge, M.T., and Theberge, J.B. 2002. Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. *Can. J. Zool.* **80**: 866–872. doi:10.1139/z02-067.
- Northrup, J.M., Hooten, M.B., Anderson, C.R., and Wittemyer, G. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, **94**: 1456–1463. doi:10.1890/12-1688.1.
- Ouellet, H. 1970. Further observations on the food and predatory habits of the gray jay. *Can. J. Zool.* **48**: 327–330. doi:10.1139/z70-053.
- Potter, D., Obbard, M., and Howe, E. 2015. Ontario wildlife food survey, 2014. Science and Research Technical Report TR-01. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, Ontario, Canada.
- Rowe, J.S. 1972. Forest regions of Canada. *Can. Dep. Environ. For. Serv. Publ. No.* 1300.
- Rutter, R.J. 1969. A contribution to the biology of the Gray jay (*Perisoreus canadensis*). *Can. Field-Nat.* **83**: 300–316.
- Sechley, T.H., Strickland, D., and Norris, D.R. 2014. Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. *J. Avian Biol.* **45**: 85–93. doi:10.1111/j.1600-048X.2013.00296.x.
- Sechley, T.H., Strickland, D., and Norris, D.R. 2015. Linking the availability of cached food to climate change: an experimental test of the hoard-rot hypothesis. *Can. J. Zool.* **93**(6): 411–419. doi:10.1139/cjz-2015-0016.
- Spitzer, K., and Danks, H.V. 2006. Insect biodiversity of boreal peat bogs. *Annu. Rev. Entomol.* **51**(1): 137–161. doi:10.1146/annurev.ento.51.110104.151036.
- Strickland, D., and Ouellet, H. 2020. Canada jay (*Perisoreus canadensis*), version 1.0. In *Birds of the World*. Edited by P. G. Rodewald. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.gryjay.01.
- Strickland, D., Kielstra, B., and Norris, D.R. 2011. Experimental evidence for a novel mechanism driving variation in habitat quality in a food-caching bird. *Oecologia*, **167**: 943–950. doi:10.1007/s00442-011-2040-y.
- Sutton, A.O., Strickland, D., and Norris, D.R. 2016. Food storage in a changing world: implications of climate change for food-caching species. *Clim. Change Responses*, **3**(1): 12. doi:10.1186/s40665-016-0025-0.
- Sutton, A.O., Strickland, D., Freeman, N.E., and Norris, D.R. 2021a. Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine. *Global Change Biol.* **27**: 983–992. doi:10.1111/gcb.15445.
- Sutton, A.O., Strickland, D., Freeman, N.E., and Norris, D.R. 2021b. Environmental conditions modulate compensatory effects of site dependence in a food-caching passerine. *Ecology*, **10**: e03203. doi:10.1002/ecy.3203.
- Thomas, J.P., Larter, N.C., and Jung, T.S. 2021. Individual-based season habitat selection in a forest-dwelling population of reintroduced bison *Bison bison*. *Wildl. Biol.* **2021**(3): wlb-00852. doi:10.2981/wlb.00852.
- Tozer, D.C., and Allen, M.L. 2004. Adult gray Jay captures an adult black-capped chickadee. *Wilson J. Ornithol.* **11**: 357–359.
- Van Els, P., Cicero, C., and Klicka, J. 2012. Phylogeography of a widespread boreal bird, the gray jay (*Perisoreus canadensis*). *Mol. Phylogenet. Evol.*, **63**: 456–465.
- Viejou, R., Avgar, T., Brown, G.S., Patterson, B.R., Reid, D., Rodgers, A.R., et al. 2018. Woodland caribou habitat selection patterns in relation to predation risk and forage abundance depend on reproductive state. *Ecol. Evol.* **8**: 5863–5872. doi:10.1002/ece3.4124.
- Waite, T.A., and Strickland, D. 2006. Climate change and the demographic demise of a hoarding bird living on the edge. *Proc. R. Soc. London, Ser. B*, **273**(1603): 2809–2813. doi:10.1098/rspb.2006.3667.
- Wegge, P., Ostad, T., Gregersen, H., Hjeljord, O., and Sivkov, A.V. 2005. Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. *Can. J. Zool.* **83**: 1547–1555. doi:10.1139/Z05-157.