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RESEARCH ARTICLE

Local habitat association does not inform landscape management of threatened birds

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Abstract

Context Species that use open patches in forested landscapes often select clearcuts. However, it is unknown whether local associations with clearcuts translate to an effect of clearcut amount in the surrounding landscape on occupancy or abundance at local sites. This question is important because forest management decisions are made at landscape scales.
Objectives We examined whether the amount of clearcut in the surrounding landscape influenced site occupancy of two threatened aerial insectivores, Common Nighthawk and Eastern Whip-poor-will. Both species nest in/near clearcuts at a local-scale.
Methods We used acoustic recorders placed on edges of recent clearcuts ($\leq$ 15 years old, n = 49 sites) to measure presence-absence. We estimated occupancy in relation to the proportion of clearcut and open wetland within the surrounding landscapes at spatial extents between 0.5 and 5.0 km.
Results Occupancy of Eastern Whip-poor-will was not related to clearcut amount in the surrounding landscape at any scale. Common Nighthawk occupancy was lower in sites surrounded by landscapes with higher proportion of older (11–15 years old) clearcuts. Both species' occupancy was higher in sites where the surrounding landscapes had higher proportions of open wetland.
Conclusions Two possible mechanisms for our results include multi-scale selection of breeding sites or demographic responses to higher productivity in wetlands than clearcuts; both need further study. Our results show how the association of species with clearcut habitats at a local scale does not necessarily translate to a higher occurrence of those species at the landscape scale at which management decisions are made.

Keywords Aerial insectivore · Scale of effect · Wetlands · Cross-scale extrapolation · Landscape composition · Forest management

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Introduction

The Canadian boreal forest is one of the world's largest forests, interspersed with openings created by lakes, wetlands, recent forest fires and clearcuts

(NRCAN 2017). Faunal community diversity in the boreal forest relies on heterogeneity in forest age and structure (Tews et al. 2004), which was historically maintained by forest fires (Rowe and Scotter 1973). However, a combination of fire suppression and forestry has made clearcutting an important factor contributing to this heterogeneity.

Forest management plans often aim to mimic fires in terms of forest succession, scale, and removal of mature forest (McRae et al. 2001), but evidence is mixed as to whether species respond similarly to clearcutting versus natural disturbances (Smith 2012; Zimmerling et al. 2017). Some research demonstrates initial negative effects of clearcutting on amphibian (Moorman et al. 2011) and cervid species including threatened species like boreal woodland caribou (Hins et al. 2009). However, other research shows that large mammals such as grizzly bears, and some species of birds can respond positively to different successional habitats created by aging clearcuts (Nielsen et al. 2004; Kellner et al. 2016).

To date, most research on clearcuts has examined their effects at local scales (e.g. the use of clearcut patches relative to other patch types), but it is far less clear how the landscape context of a clearcut (i.e. the landscape composition surrounding a clearcut) affects local patch occupancy. Habitat selection by animals is typically a hierarchical process and when different spatial scales are not considered, important habitat associations of species can be missed (Jones 2001). Earlier research shows that although birds select nesting sites based on local characteristics (Robertson 2009), they are also influenced by the landscape context surrounding a potential nesting site (White et al. 2010; Hovick and Miller 2013). Therefore, while species may select clearcut patches for breeding, it is important to understand how the amount of clearcut at a landscape-scale affects local patch occupancy.

Two threatened bird species known to nest in or near clearcuts are Common Nighthawk (hereafter 'nighthawk') and Eastern Whip-poor-will (hereafter 'whip-poor-will') (Cink 2002; Wilson and Watts 2008; Brigham et al. 2011; Tozer et al. 2014; Farrell et al. 2017). Both species are migratory aerial insectivores and have shown marked declines in recent years (Nebel et al. 2010). Data from the North American Breeding Bird Survey indicate that across North America, nighthawks have declined by 4.2% per year since 1968 (Downes et al. 2005), while whip-poor-wills have declined by 3.2% per year since 1970 (Environment Canada 2014c, d). These declines represent population losses of over 75% for both species over the past four decades, however, the mechanisms for these declines are poorly understood (Environment Canada 2015, 2016). Both species are crepuscular and require open areas to forage for insects. They are also known to nest in wooded areas adjacent to openings in the case of whip-poor-will and/or throughout openings in the case of nighthawk (Cink 2002; Russell et al. 2009; Brigham et al. 2011). Previous studies show that nesting sites of both species can be adjacent to or in clearcut, wetland, or recently burned land cover patches (Wilson and Watts 2008; Tozer et al. 2014; Akresh and King 2016; Farrell et al. 2017).

Early successional habitat created by clearcuts or by natural disturbances like fires, is generally thought to have a "lifespan" of 0–15 years following the disturbance event, after which time the area begins to transition into early successional forest (DeGraaf and Yamasaki 2003). Whip-poor-will have been shown to readily nest in < 6 year old clearcuts (Wilson and Watts 2008), and 1–15 year old clearcuts (Tozer et al. 2014; Farrell et al. 2017). However, whip-poor-will have also been shown to avoid nesting near clearcuts < 2 years old (Akresh and King 2016). The clearcut ages favoured by nighthawk for nesting sites are less well understood because studies considered "young" forest stands to be 20–30 years old or had low detectability of the species (Hutto et al. 1993; Stelfox 1995; Kirk and Hobson 2001). However, there is some evidence that nighthawk preferentially nest in or near 4–5 year old clearcuts (Legrand et al. 2007) and 10–20 year old clearcuts (Hutto et al. 1993). Overall it seems both species select clearcuts approximately < 10 years old, with some exceptions.

What remains unclear both from our earlier work (Farrell et al. 2017) and that of others (e.g. Tozer et al. 2014) is whether the known use of clearcuts within forested landscapes translates to greater site occupancy of clearcuts by the species when the surrounding landscape contains a higher proportion of clearcuts. This question is important for management because forestry decisions are made at large spatial extents (OMNRF 2010) and the results of studies showing selection of clearcuts may lead to the assumption that we can enhance the abundance of both species by increasing clearcutting in the landscape. Here we test whether the local-scale association between clearcuts and breeding sites of nighthawk and whip-poor-will are reliable indicators of a positive relationship between clearcut amount in the surrounding landscape and site occurrence for these species. To do this, we used a "focal patch landscape study" design (Brennan et al. 2002). This design involves sampling focal points or patches (here, clearcut edges), and measuring landscape composition (here, clearcut amount) in the landscapes surrounding each focal point (Brennan et al. 2002). This study design is commonly used to estimate the effects of landscape context on species responses (e.g. Lee et al. 2002; Sponsler and Johnson 2015).

We also investigated how both species respond to clearcutting at multiple spatial extents. Often estimates of scale using information on movement ranges of species have been shown to be highly inaccurate (Jackson and Fahrig 2015). Knowing the spatial extent at which species respond to clearcutting (i.e. scale-of-effect) is important to inform management and develop effective recovery strategies (e.g. Environment Canada 2015). Based on previous studies showing their use of clearcut patches at a local-scale (Tozer et al. 2014; Farrell et al. 2017), we predicted that: *sites in landscapes with* (1) *more clearcut and* (2) *more younger clearcut will have higher occupancy of both species*.

Methods

Study region

We conducted field work from May 31 through July 13 2017 in a remote study region north and west of Thunder Bay, Ontario, Canada spanning approximately 29,000 km^2 (Fig. 1). This region included both the Boreal Hardwood Transition and the Boreal Softwood Shield bird conservation regions (Environment Canada 2014a, b) and encompassed five forest management units, which are planning zones defined for the purposes of forest management (OMNRF 2018a). This region is comprised of mainly coniferous and mixedwood stands including but not limited to: black spruce (Picea mariana), jack pine (Pinus banksiana), white birch (Betula papyrifera), and trembling aspen (Populus tremuloides) (OMNRF 2018b). Forestry in this region targets both coniferous and deciduous trees.

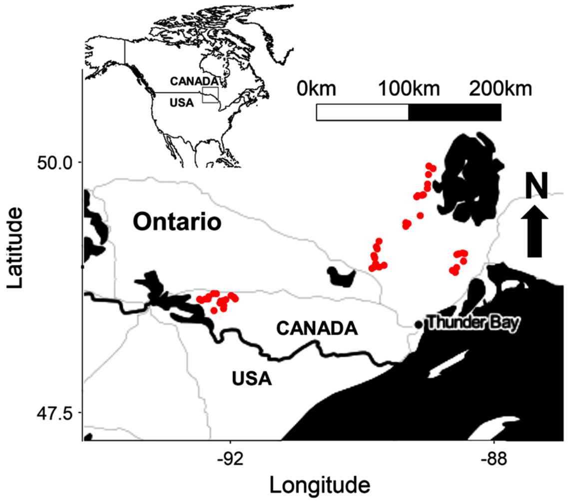

Fig. 1 Distribution of sampling sites for Common Nighthawk and Eastern Whip-poor-will northwest of Thunder Bay, Ontario, Canada. Each dot represents one sampling site on a recent clearcut edge. General location of the study region in North America is represented as the square in the inset image of North America (top left). Other black shapes represent large water bodies in the study region

Site selection

We used recent spatial data from Forest Resource Inventory (FRI) data (OMNRF 2014) to search for road-accessible sampling sites on the edges of recent ($\leq$ 15 years old) clearcuts. FRI data are open-access and are composed of spatial data/metadata pertaining to forestry operations and land cover (OMNRF 2014). We initially selected sixty-nine potential sampling sites without urbanization, agricultural activity, or human settlements within 5 km.

In addition to nesting within or on the edges of clearcut in our study region, both species also readily nest within or on the edges of recently burned stands and open wetlands (Farrell et al. 2017). Although there are no documented cases of either species nesting within a wetland, our results in 2017 (Farrell et al. 2017) as well as others (Raynor 1941; COSEWIC 2007) empirically demonstrate they nest adjacent to wetland edges. We controlled for possible confounding effects of the amount of recent burned stands in the surrounding landscape on nighthawk and whip-poor-will occurrence by selecting landscapes without recent

($\leq$ 15 years old) fire within a 5 km radius. We could not do the same for open wetland amount because of the relatively even distribution of wetlands across our study region. To mitigate the potential confounding effects of open wetlands, we excluded potential sampling sites with high proportions (> 17%) of wetland within a 5 km radius landscape surrounding the site (also see *Scale-of-effect of open wetland* below).

In addition to selecting landscapes without recent burned stands, urban and agricultural land cover, and with < 17% open wetland within a 5 km radius, we also selected clearcuts that were road-accessible. To ensure independence of our sites and avoid pseudoreplication, we selected sites at least 1.4 km apart (maximum 16 km, mean 3.8 km). These distances are farther than documented foraging distances of whip-poor-will (0.13–0.31 km; Cink 2002; Rand 2014) and nighthawk (~ 0.3 km; Brigham and Fenton 1991). Therefore, it is unlikely the same individual was detected at multiple sites, even with the clustered distribution.

Final sampling locations (n = 49), i.e. sites, were on the edges of clearcut patches averaging 95 ha (range 12–364 ha) and were located $\geq$ 100 m from access roads (Fig. 1). We selected a large range of total clearcut amount within the surrounding landscape (5 km radius) of each sampling site: ranging 2–33%.

Spatial data and land cover analysis

We measured the proportion of clearcut and wetland in the landscape surrounding each sampling site at multiple spatial extents (0.5 to 5.0 km, in increments of 0.5 km) to determine at what scale they most strongly affect occupancy. Because our spatial variables were all proportions of landscapes in certain land cover (values ranging from 0 to 1, landscape with radii of 0.5–5.0 km), we did not need to standardize them. We used land cover data from the FRI to calculate both clearcut (predictor variable) and open wetland (covariate) amount in the landscapes surrounding our sites.

In our analyses, our predictor variables of clearcut amount were either the proportion of total recent clearcut ($\leq$ 15 years old) or the proportion of a specific age-class of clearcut (0–5, 6–10, 11–15, or 16–20 years old; Fig. 2) within landscapes surrounding sampling sites. We computed the proportion of the landscape in recent clearcut as equal to the amount of clearcut $\leq$ 15 years old (km^2)/total landscape size (km^2) at each of the ten spatial scales being examined. We divided all clearcuts into four age-classes (0–5, 6–10, 11–15, 16–20 years old; Fig. 2), and then calculated the proportion of each clearcut age-class in the landscape as equal to the total amount of clearcut in a given age-class (km^2)/total landscape size (km^2), again at each of ten spatial scales. We considered the 16–20 years old age-class to test our assumption that clearcuts older than 15 years are not suitable habitat for either species.

We also calculated the proportion of wetland in the landscape surrounding each sampling site, a covariate in our analyses, using FRI data (proportion of the landscape in open wetland = amount of open wetland (km^2)/total landscape size (km^2) at each of the ten spatial scales previously described.

Bird sampling methodology

We measured occupancy of nighthawk and whip-poor-will using automated acoustic recording units (SM2 and SM4 models, Wildlife Acoustics Inc., Maynard, MA) placed on mature trees within 5 m of the edges of clearcut patches. We conducted sampling from May 31 through July 13, 2017. Because of the large size of our study region (Fig. 1), it was not feasible to sample all 49 sites simultaneously. Instead, each site was sampled for 1 week using a single recorder. At any one time, up to twelve sites were simultaneously sampled. After a week of recording, the recorder was moved to a new site. This process continued until all sites were sampled.

Recorders were deployed at each site for a total of seven nights; however, only data from four nights at each site were used in the analysis. This allowed us to use the four nights with the most favorable sampling conditions, i.e. nights without inclement weather such as rain or high winds, which may have lowered our ability to detect the species. If inclement weather was present in more than 50% of an individual night's recordings, that night was excluded entirely, and the next night was considered. For some sampling periods, weather was generally poor and it was not possible to attain four evenings free of precipitation and wind. To account for this, we used the recording from the evenings with the least amount of precipitation or

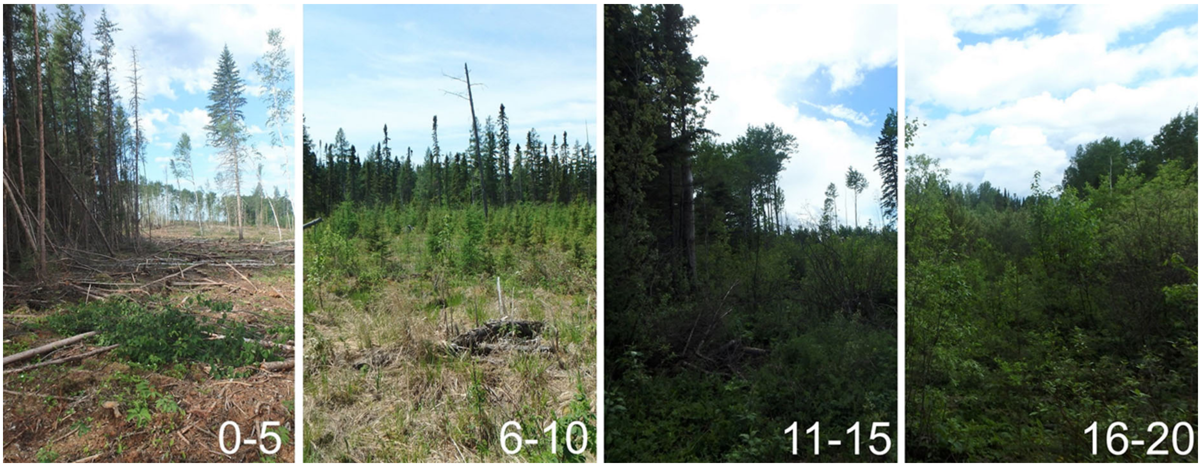

Fig. 2 Example clearcuts of different ages in our study region (0–5, 6–10, 11–15, and 16–20 years old from left to right)

wind and included rain and wind as detection covariates in our models (see below). As both species call at night, each recorder was programmed to turn on for seven 10-min periods throughout the night: (1) 1 h before sunset, (2) at sunset, (3) 1 h after sunset, (4) 2 h after sunset, (5) 2 h before sunrise, (6) 1 h before sunrise, and (7) at sunrise. We used the nighthawk's "peent" and "boom" calls and the whip-poor-will's song to determine the presence of the species. Detection of both species was determined by listening to the first 5 min of each 10 min sample, which represents one detection record in the occupancy models (see below).

Factors affecting detectability

We accounted for five variables that could have influenced the detectability of the two bird species: (1) day-of-year of the recording (where day 1 = May 31 2017 and day 44 = July 13 2017), (2) time of sampling as a categorical variable, (3) rain as a binomial variable (= 1 if rain occurred during the recording period), and (4) wind as a binomial variable (= 1 if wind noise occurred during the sample), all of which have been shown to have some influence on detectability (Farrell et al. 2017). We also included (5) lunar illumination, which has been shown to be positively correlated with the activity level of whip-poor-will and related species in previous studies elsewhere (Mills 1986; Wilson and Watts 2006). This variable was estimated as the % illumination determined using the midpoint latitude/longitude of the study region with the Hoffman MoonCalc tool (Hoffman 2018).

Statistical analysis

We conducted analyses in R Version 3.3.3 (R Core Team 2017) and used single season occupancy models from the package 'unmarked' (Fiske and Chandler 2017) to test the effects of clearcuts on our focal species while accounting for detection probability (MacKenzie et al. 2002) and potentially influential variables. All models were ranked using Akaike's Information Criterion corrected for a small sample size (AICc), and the ΔAICc values and Akaike weights (wi) were used to infer support for each of the candidate models (Hurvich and Tsai 1989; Burnham and Anderson 2002; Barton 2018).

Scale-of-effect of open wetland

We conducted multi-scale analyses (Brennan et al. 2002) to empirically estimate the scales of effect at which each species was most influenced by landscape context (proportion clearcuts, proportion each age-class of clearcuts, and proportion open wetlands in the surrounding landscape).

Before testing our predictions on the effect of clearcuts, we wanted to estimate the scale-of-effect of open wetland amount. We first ran a model selection analysis (Online Appendix II) to determine which detection variable(s) affected the occupancy of each of the two species. We then included the top detection variables from this analysis, and ran ten occupancy models, one for each wetland proportion at the ten scales, for each species. We computed AICc values to account for a smaller sample size (Hurvich and Tsai 1989; Barton 2018) and used the change in AICc (ΔAICc) to graphically represent the scale-of-effect (Fig. 3), where the scale-of-effect for open wetland was selected as the scale at which AICc was lowest (Online Appendix III). We then only used the proportion of open wetland at its scale-of-effect as a covariate in the main analyses (below), which focused on testing our expectations about the effects of clearcut proportion.

Other potentially influential variables

In addition to our landscape composition variables—proportion recent clearcut, proportion of four age-classes of clearcut, and proportion open wetland—we considered five local variables that could affect clearcut occupancy including (1) forest type within a radius of 100 m of the acoustic recorder, (2) presence/absence of the other species, i.e. nighthawk or whip-poor-will, (3) size of focal clearcut patch, (4) age of focal clearcut patch, (5) presence/absence of red squirrel (Appendix I). Specifically, to account for differences in forest type surrounding the clearcut patch, we included the forest type within a radius of 100 m of the acoustic recorder (coniferous, mixed-wood, or deciduous) as a covariate. Previous work in the study region found the presence of either nighthawk or whip-poor-will at a site resulted in a significantly higher probability of occupancy by the other species (Farrell et al. 2017). Therefore, we included whether the other species, either nighthawk or whip-poor-will, was detected on our recordings at that site as a binomial variable (1 = yes, 0 = no). Birds can respond to patch size (Lehnen and Rodewald 2009); therefore, we included the area (km^2) of the clearcut patch of the sampling site using the GoogleMaps extension from DaftLogic to delineate patch edges. As described earlier, previous research suggests associations between our focal species and clearcut age-classes. Therefore, we included the age of the sampled clearcut from the FRI data. Finally, we included the occurrence of red squirrels (1 = observed, 0 = not observed), a common avian nest predator (Degregorio et al. 2016; Reitsma et al. 1990) at each site to account for a possible effect of predation pressure on occupancy. We listened for alarm and bark calls of the red squirrel during all bird recordings, as well as during an additional 10 min recording made 3 h after sunrise each day, to determine squirrel presence or absence at each site.

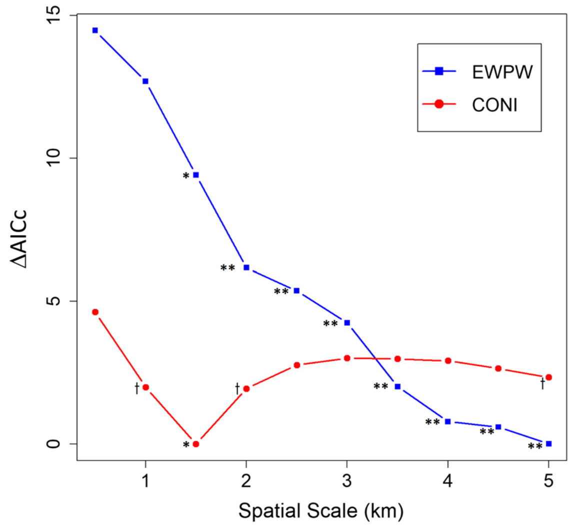

Fig. 3 Strength of relationship between the proportion of open wetland at ten spatial scales (0.5–5 km radius), and the site occupancy of Eastern Whip-poor-will and Common Nighthawk evaluated using the change in Akaike's Information Criterion corrected for small sample size (ΔAICc). The lowest point in these curves represent the estimated scale-of-effect where the relationship is strongest. Significance is indicated with *($p < 0.05$) or **($p < 0.01$) at that spatial scale, with dagger indicating $0.05 < p < 0.1$

Effects of clearcut amount

We conducted two sets of analyses on each species: one for the effect of proportion of the surrounding landscape in recent clearcuts (≤ 15 years old) (prediction 1), and one for the effect of the proportion of the surrounding landscape in each age-class of clearcuts (prediction 2). Each analysis for each prediction was conducted at the ten spatial extents described above. Using two sets of analyses allowed us to sequentially address our predictions rather than combining them in a single analysis. In addition, models containing total clearcut and the sum of the first three clearcut ages (i.e. total clearcut amount), would not converge. Support for our predictions was informed by model selection along with the effect size and confidence intervals for parameter estimates.

As described in the wetland scale-of-effect analysis, we identified top candidate models by first running a set of models that only included variables influencing detection probability of each species (Online Appendix II) and then adding our main variables and covariates to our top detection models to test our two predictions. This model fitting procedure ensured that models were not overfit: i.e. the largest number of variables in a single model was five. Therefore, for a sample size of 49 sites we typically had more than ten samples per variable. We also note that the sample size for detection probability, where we had five potentially influential variables, is much higher than for occupancy because it incorporates the number of samples within each site (12) times the number of sites (49), i.e. 588 samples.

To test our first prediction, that occurrence of the two species would be higher in sites surrounded by more clearcut, we used the proportion of total recent clearcut ($\leq$ 15 years old) at each of our ten spatial scales. We ran models including each scale's total clearcut proportion and the covariates (proportion open wetland, red squirrel presence etc.) by themselves and in combination with each other (see Online Appendix IV). We determined the top model based on the lowest AICc value and report model coefficients, AICc values and Akaike's weight from the top models of this analysis (Table 1).

To test our second prediction, that occurrence of the two species would be higher in sites surrounded by more younger clearcuts, we conducted a set of analyses using the proportions of the four age-classes of clearcuts at each spatial scale. Because of the large number of variables (listed in Online Appendix I) we wanted to first determine the scale-of-effect of the age-classed clearcut variables. To do this, we first ran ten models: where each model included all four age-specific clearcut variables measured at the same spatial scale (i.e. clearcuts 0–5 + clearcuts 6–10 + clearcuts 11–15 + clearcuts 16–20 years old, all at one scale, for each of the 10 scales from 0.5 to 5.0 km) (Online Appendix V). We then selected the top model at the estimated scale-of-effect as indicated by the lowest AICc, and all subsequent analyses only used clearcut proportions at this scale. We then ran models including each one of the four clearcut age-classes (at the scale-of-effect) and the covariates by themselves and in combination with each other, and determined the top model based on the lowest AICc value (Table 1; Online Appendix V).

Model Support and Fit

For each species, we examined model fit using a parametric bootstrap test on top models from the total clearcut analysis. We simulated 200 data sets using the "parboot" function of 'unmarked' (Fiske and Chandler 2017) and refit the model to the data and examined model fit using a Chi squared fit statistic. This allowed us to compare how simulated data, made from our top models, differed from our observed data. We used $p > 0.05$ to indicate an adequate fit (Fiske and Chandler 2017). The observed data did not differ significantly from the simulated bootstrapped distributions ($p = 0.244$ and $p = 0.239$, for nighthawk and whip-poor-will, respectively), indicating good model fit for both species.

Results

We detected nighthawk at 33/49 sites and whip-poor-will at 14/49 sites (Fig. A9). The mean probability of detection for nighthawk was 0.29 ± 0.01 with a probability of occupancy of 0.67 ± 0.07. The mean probability of detection for whip-poor-will was 0.27 ± 0.02 with a mean probability of occupancy of 0.29 ± 0.06 (Online Appendix VI). Detectability of both species varied most with time of day (Table 1; Online Appendix II). Detectability of nighthawk was significantly higher 2 h after sunset and at sunrise and significantly lower an hour before sunset and 2 h before sunrise (Online Appendix II). Detectability of whip-poor-will was significantly higher 1 h before sunrise and significantly lower during sunset. Whip-poor-will detectability was also negatively affected by the presence of rain. Detectability of both species was not significantly related to lunar illumination (%) (Online Appendix II).

The scale-of-effect of the proportion of the landscape in open wetland was 1.5 km for nighthawk and 5.0 km for whip-poor-will (Fig. 3; Online Appendix III). The scale-of-effect for total recent clearcut ($\leq$ 15 years old) was estimated at 5 km for both species (Table 1; Online Appendix IV). The scale-of-effect for clearcut in the models including variables for the separate clearcut age-classes was estimated at

Table 1 Top models investigating the effect of total clearcut amount (39 models) and age-classed clearcut amount (42 models) on Common Nighthawk and Eastern Whip-poor-will occupancy at boreal forest sites in northwestern Ontario

Common Nighthawk					Eastern Whip-poor-will				
Model	AICc	ΔAICc	w_i	K	Model	AICc	ΔAICc	w_i	K
Total clearcut analysis (39 models)									
ForestType	1010.99	0.00	0.26	4	wetland_5 km	407.63	0.00	0.47	5
ForestType + wetland_1.5 km	1011.44	0.45	0.21	5	wetland_5 km + CCUT_5 km	410.80	3.17	0.10	6
ForestType + CCUT_5 km	1012.42	1.43	0.13	5	wetland_5 km + CONI	410.92	3.29	0.09	6
Age-specific clearcut analysis (42 models)									
ForestType + CCUT_11–15(0.5 km)	1009.99	0.00	0.07	5	wetland_5 km	407.63	0.00	0.47	5
ForestType	1010.99	1.00	0.04	4	wetland_5 km + CCUT_6–10(5.0 km)	409.55	1.92	0.18	6
ForestType + CCUT_0–5(0.5 km)	1012.94	2.95	0.30	5	wetland_5km + CCUT_0–5(0.5 km)	409.67	2.04	0.17	6

Top detection variables for Common Nighthawk (time) and Eastern Whip-poor-will (time and rain) were included in models but are not shown

ΔAICc change in Akaike's Information Criteria corrected for small sample size, *wi* Akaike weights, *K* number of model parameters, *ForestType* dominant tree type of old growth forest at edge of clearcut (i.e. coniferous/deciduous/mixed), *wetland_Xkm* proportion of wetland within a given km radius, *CCUT_5 km* proportion of total clearcut amount (0–15 years old), *CCUT_0-5/6-10/11-15/16-20 (Xkm)* proportion of age-specific clearcut amount (0–5, 6–10, 11–15, 16–20 years old) within given radius (Xkm)

0.5 km for nighthawk and 5.0 km for whip-poor-will. We checked for correlations among our predictor variables (Online Appendix VII) and found in general, the spatial predictor variables in our best models had low correlations to each other and to latitude. However, there was a correlation between wetland amount and longitude, with more wetland in the more western landscapes (Online Appendix VII).

Tests of the predictions

The proportion of the surrounding landscape in recent clearcut was not a strong predictor of site occupancy for either species (Fig. 4; Table 1). The effects of the separate clearcut age-class variables were also not strong, apart from a negative effect of the amount of clearcuts 11–15 years old at the smallest scale (within 0.5 km) on the site occupancy of nighthawk (Fig. 4; Table 1; Online Appendix V). For whip-poor-will, none of the four age-classes of clearcuts was included in the top model (Fig. 4; Table 1; Online Appendix V).

Effects of other variables

Although our results did not support our predictions for positive effects of clearcut amount in the surrounding landscape on nighthawk and whip-poor-will site occupancy, other variables were influential. The best model for nighthawk site occupancy contained only local forest type with significantly higher occupancy in clearcuts abutted by coniferous forest compared to those with deciduous and mixed wood. The second best model included open wetland in the surrounding landscape within 1.5 km of the site, and was only 0.45 AICc units higher than the best model, potentially suggesting a weak but positive effect of the proportion of open wetland at 1.5 km (Table 1; Online Appendices IV, V). Whip-poor-will showed a positive, significant relationship with proportion of open wetland in the surrounding landscape within 5.0 km (Table 1; Online Appendices IV, V). We detected red squirrels at 28/49 sites but neither species responded to red squirrel presence or to local clearcut size or age, and neither species was influenced by the presence of the other bird species.

Discussion

We found no support for either of our predictions that local occupancy of both nighthawk and whip-poor-will was higher in sites surrounded by landscapes with more total clearcut and younger clearcut amount. Although the amount of clearcut 11–15 years old was in the top model for nighthawk, the relationship was negative, opposite to our expectation. In contrast, we did find positive effects of open wetland amount in the surrounding landscape on site occupancy of both species, with a stronger effect for whip-poor-will (Fig. 4). Together, the lack of a landscape-scale effect of clearcut amount combined with the positive effect of open wetland amount has important implications

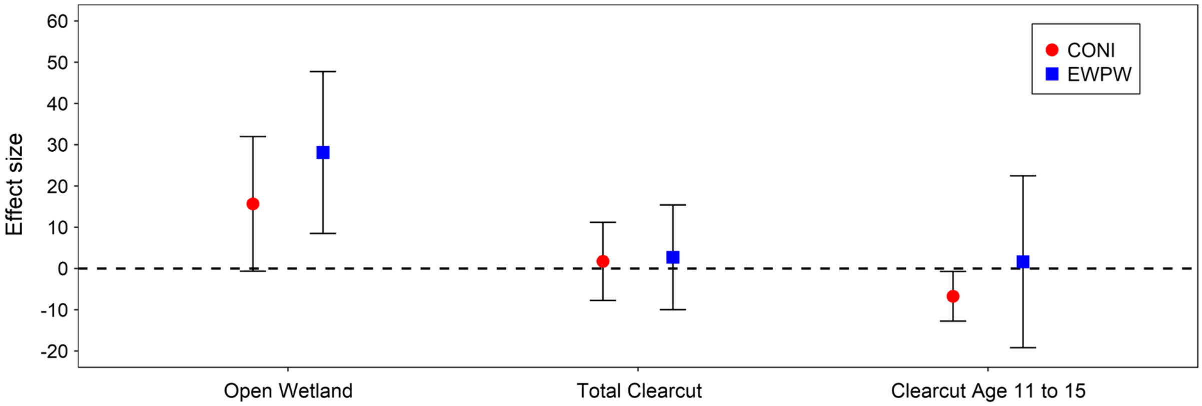

Fig. 4 Effect sizes (model coefficients) and 95% confidence intervals for the influence of the proportion of open wetland, the proportion of total recent (≤ 15 years old) clearcut and the proportion of 11–15 year-old clearcut in surrounding landscapes at their scales of effect on Common Nighthawk and Eastern Whip-poor-will occupancy

for management of these species, elaborated upon below.

The lack of effect of clearcut amount in the surrounding landscape was unexpected given the documented local associations of both species with clearcuts; it highlights the challenge of predicting effects of landscape composition based on local habitat associations (Fahrig et al. 2019). Results of studies showing selection of clearcuts at the local-scale (Tozer et al. 2014; Farrell et al. 2017) may lead to the interpretation that we can enhance the abundance of the species when landscapes contain more clearcutting (landscape-scale). We show here that this is not true as we found no effect of the amount of clearcutting in the surrounding landscape on the local site occupancy by either species. Although unexpected, this mismatch between local and landscape-level habitat associations has been observed in other bird species both within (Tremblay et al. 2009) and outside of (Naugle et al. 1999) the boreal forest. For example, Tremblay et al. (2009) found Black-backed Woodpeckers (*Picoides arcticus*) were frequently observed in open clearcuts at the local-scale but were more strongly associated with old-growth forest at the landscape-scale.

We suggest three possibilities for our observed mismatch between local and landscape-level habitat associations: i.e. why occupancy of both species was positively affected by the proportion of wetland but not by the proportion of clearcut in the landscapes surrounding breeding sites, despite having similar site occupancy of clearcuts and wetland patches (Farrell et al. 2017).

The first possibility is that both species may use different criteria for habitat selection at different scales. Avian habitat selection at broader landscape scales is often different from territory/nest selection at the local-scale (Jones 2001) as birds often respond simultaneously to different local and landscape habitat characteristics (Lee et al. 2002; Pickens and King 2014; Jedlikowski et al. 2016). Habitat selection at multiple scales could explain our results, if for example, birds returning to breeding areas in spring initially select landscapes containing high wetland cover, but then do not differentiate between types of open cover for breeding territories at a local-scale (e.g. Farrell et al. 2017). Thus, although both species use clearcuts for breeding locally, this explanation would suggest that they do not view clearcut as equal to wetland when make settlement decisions at the landscape-scale.

A second possible explanation for our results is related to reproductive success. While clearcuts provide nesting sites for these species, they may be of lower quality than natural open habitat types (e.g. wetlands or recent burns). Because both nighthawk (Poulin et al. 1996) and whip-poor-will (Cink 2002) exhibit site fidelity, this effect could result in lower reproductive success and thus fewer returning individuals to sites in landscapes with high amounts of clearcut, in comparison to sites in landscapes with high amounts of wetland in succeeding years.

Third, it is also possible that the amount of potential clearcut habitat exceeds what the population can use in the study area. In this case, each species may utilize clearcuts but as the amount of clearcutting in the landscape increases there would be a negative relationship between the amount of clearcutting and the probability of detecting an individual at any one clearcut patch. While we did not observe such a negative relationship between whip-poor-will occupancy and clearcut amount, we did observe a decline in clearcut patch occupancy for nighthawks as the amount of older clearcuts increased at the landscape scale. These three possibilities require further investigation.

As alluded to above, while we did not examine the effects of patch type or landscape context on reproduction in this study, we suggest this is an important area for future research given research on other species. For example, reproductive success of eagle-owl (*Bubo bubo*) and ovenbird (*Seiurus aurocapilla*) is lower in clearcuts than in other open habitat types (Shin and Yoo 2016) including wetlands (Streby and Andersen 2013). Also, Hollander et al. (2011) found that nest success and offspring quality of the red-backed shrike, (*Lanius collurio*) which preferentially nests in clearcuts, were lower in clearcuts compared to agricultural nesting sites and that clearcuts were acting as ecological traps. The possibility of similar effects on nighthawk and whip-poor-will needs to be investigated further.

Given the positive effect of wetland amount in the surrounding landscape on both species, we suggest that open wetlands are particularly important to nighthawk and whip-poor-will in the boreal forest because of their value as habitat for insect prey. Wetlands, unlike clearcuts, do not undergo herbicide application and are known to host high insect diversity and abundances (Spitzer and Danks 2006). The idea that wetlands are important prey habitat for whip-poor-will and nighthawk is supported by Alexander and Cresswell (1990) who found European Nightjars (*Caprimulgus europaeus*), a close relative of both species, foraged 3–5 times more frequently in wetlands compared to other open habitat types, including clearcuts despite the small amount of wetland in their study region (Alexander and Cresswell 1990). In clearcut, herbicide application lowers the abundance of insects like lepidopterans and coleopterans (Chaundry-Smart et al. 2012; Iglay et al. 2012; Stark et al. 2012), which are key prey for our two species (Garlapow 2007; English et al. 2017; Knight et al. 2018). In our study region, herbicides are commonly applied to clearcuts (Thompson and Pitt 2011).

An alternative explanation for the positive response we observed for both species to open wetland in the landscape is that it is a statistical artefact. Our sites were clustered in the western and eastern range of our study region. The western landscapes, where whip-poor-will site occupancy was higher, also had a higher proportion of open wetland than the eastern landscapes (see Online Appendices VII and VIII). Therefore, the positive responses of the whip-poor-will to open wetland amount in the surrounding landscape may be a response to longitude. However, we think this is unlikely as nighthawk, a species known to select similar habitat to whip-poor-will, did not show higher occupancy in the western landscapes, yet still responded positively to open wetland amount. In addition, this explanation seems unlikely because open wetland amount consistently had positive effects at multiple scales for both species (Figs. 4, 5; Online Appendix III) unlike clearcut amount, which showed little influence. Thus, it is likely that occupancy is indeed higher for both species at sites in landscapes with higher amounts of wetland (Fig. 6).

The positive responses of both species to open wetland amount are particularly striking given the small range of wetland amount within our selected landscapes (1–17%) and given the documented similarity between clearcut and wetland site occupancy in this region (Farrell et al. 2017). The positive response to wetland amount is a novel finding, largely because habitat effects on these species have not been extensively studied in the boreal forest nor has most research examined the value of wetland habitat for these species. Two studies outside of the boreal forest had similar results, finding a weakly positive effect of wetland amount (English et al. 2017) and amount of open area including wetlands (Purves 2015) on whip-poor-will abundance. Our previous work also found that both species were as likely to occur in wetlands as they were in clearcut or burned stands (Farrell et al. 2017). Taken together the results of these studies strongly suggest the importance of wetland for these species, suggest future work should focus on habitat associations with wetlands at landscape scales, and emphasize the need to investigate the benefits of wetlands to reproduction.

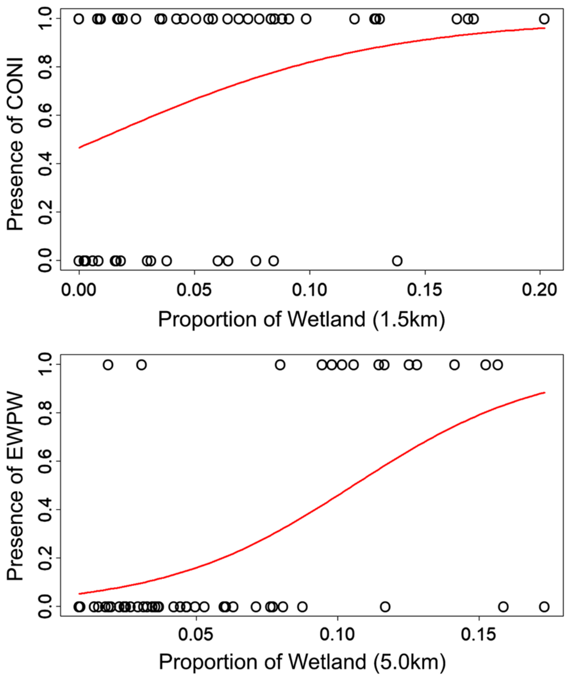

Fig. 5 Presence (1) and absence (0) of Common Nighthawk (top panel), and Eastern Whip-poor-will (bottom panel) in northwestern Ontario, Canada, May–July 2017, as a function of proportion of open wetland within a radius of 1.5 km and 5.0 km respectively (the scale-of-effect: Fig. 3, Online Appendix III). Each point represents data from one sampling site

Species occupancy probability

We found the mean probability of occupancy of nighthawk and whip-poor-will to be 0.67 and 0.27 respectively. Our estimate for nighthawk is higher than that for previous studies (0.43, Stenger et al. 2011; 0.48, Farrell et al. 2017). However, the estimate for whip-poor-will is lower than in our previous study

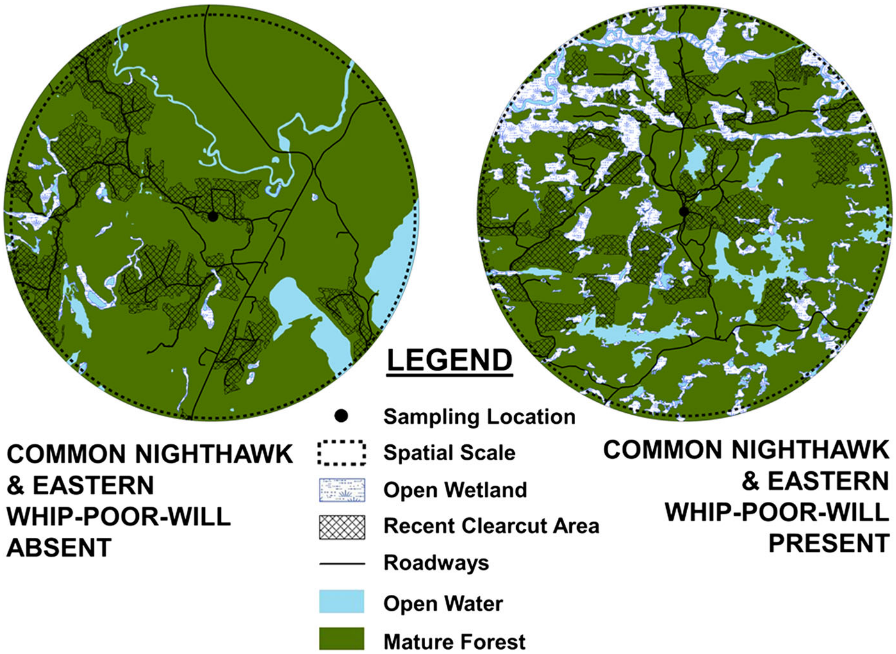

Fig. 6 Two sample landscapes (5.0 km radius). The left image shows a landscape with recent clearcut surrounding a site where neither Common Nighthawk nor Eastern Whip-poor-will was detected. The right image shows a landscape also with recent clearcut, but with a much higher proportion of open wetland area surrounding a site where both species were detected. We found both species responded positively to open wetland area on a landscape-scale, but not to clearcut area

of site occupancy probability on edges of clearcuts, open wetlands and burned stands in the same region, where the mean occupancy on clearcut and wetland edges was 0.36 and 0.40 respectively (Farrell et al. 2017). Our estimate of whip-poor-will site occupancy in this study was also lower than other studies in more southern landscapes in eastern Ontario (0.76, Tozer et al. 2014) and in the southern U.S.A. (0.75, Twedt 2015). The fact that we studied whip-poor-will at the northern part of its range may explain why we observed lower site occupancy estimates than other studies at more southern latitudes. However, it does not explain why our site occupancy estimate for whip-poor-will is lower than our recent work in this study region (Farrell et al. 2017). One possibility is year-to-year fluctuations in population size. For example, occupancy probability on the breeding grounds in a given year might be related to fluctuations in the quality of winter habitat during the previous non-breeding season (Wilson et al. 2011; Rushing et al. 2016). Together, differences in site occupancy reported here with the results of Farrell et al. (2017) using data collected only 2 years previous to our sampling stresses the necessity of monitoring both species in the north to document year-to-year variability in population size and to uncover the drivers of this variability.

Conclusions

In conclusion, and in contrast to our predictions, nighthawk and whip-poor-will occupancy were not significantly higher at sites surrounded by landscapes with more clearcut, irrespective of clearcut age. This central finding indicates how local-scale associations of species with an anthropogenic cover type like clearcutting does not indicate higher amounts of that cover type will be beneficial at broader landscape scales. In contrast, site occupancy of both species, but especially whip-poor-will, showed positive responses to the proportion of open wetland in the surrounding landscape. We suggest that the lack of positive response to clearcut amount in the surrounding landscape, combined with the positive effect of wetland amount in the surrounding landscape, may result from one or all three mechanisms suggested: particularly multi-scale habitat selection and reproductive success. Further work is needed to test each idea. Research should also explicitly address how the demography of these species is affected by clearcutting at multiple spatial scales, and to compare demographic rates in clearcut with rates from open wetland and burned stands, before concluding that clearcut land cover has a neutral effect on either species in the boreal forest. Our results emphasize that we cannot necessarily scale up local habitat associations to broader landscape context effects. Our results also highlight the importance of wetlands for the persistence of these two species-at-risk in the boreal forest.

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