



Clearcut with seed trees in red pine forests associated with increased occupancy by Eastern Whip-poor-wills



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ARTICLE INFO

Article history:

Received 20 January 2014

Received in revised form 16 June 2014

Accepted 17 June 2014

Available online 24 July 2014

Keywords:

Aerial forager

Forest management planning

Goatsucker

Logging

Nightjar

Silviculture

ABSTRACT

Forest management is often used to increase and maintain early-successional forest habitat for breeding birds by emulating natural disturbance with harvesting. However, quantified habitat-use relationships are often lacking, which makes forest management planning challenging for some species. One such species is the Eastern Whip-poor-will (*Antrostomus vociferus*), a crepuscular, insectivorous, neotropical, migrant bird, designated as a species at risk throughout most of its breeding range. Thus, we determined occupancy of Eastern Whip-poor-wills at 37 sampling points in red pine (*Pinus resinosa*)-dominated stands harvested using clearcut with seed trees and in white pine (*P. strobus*)-dominated stands harvested using uniform shelterwood in June 2013 in eastern Algonquin Provincial Park, Ontario. In red pine stands, we found that model-predicted site occupancy increased by 3.3 times from 0.23 where young (<16 years since harvest) clearcuts were absent to 0.76 where young clearcuts were present. Shelterwood harvesting in white pine stands, by contrast, was unassociated with occupancy. Our data suggest that an aggregated mean total of 12 ha of clearcuts per 100 ha (interquartile range: 1.5–18 ha) of mature pine-dominated forest is associated with significantly higher occupancy by breeding Eastern Whip-poor-wills, and that the clearcuts can be composed of various sizes (interquartile range: 3–42 ha) and ages (interquartile range: 5–24 years since harvest). Given that similar relationships have been found by others elsewhere, clearcuts may increase the occupancy and abundance of breeding Eastern Whip-poor-wills in other regions and forest types throughout northeastern North America.

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1. Introduction

Over the past half century early-successional forests have declined in certain regions of northeastern North America (Askins, 2001). In the US Great Lakes states the proportion of timberlands in the seedling–sapling stage declined from 50–60% in the 1950s to 28% in the 1990s (Trani et al., 2001). Similar declines in early-successional forests occurred in most other northeastern US states and adjacent Ontario, Canada (Askins, 2000; Blancher et al., 2007). For instance, mature forests increased at the expense of early-successional forests in New Hampshire from 47% in 1880 to 87% in 1980 (Litvaitis, 1993), while mature forests increased in Ontario south of the Canadian Shield from 10% in 1920 (Larson et al., 1999) to 29% in 2006 (OMNR, 2006).

The causes of declines in early-successional forests depend on various regional pressures (DeGraaf and Yamasaki, 2003). In most of the northeastern US declines are attributed mainly to reforestation of abandoned farms, cleared originally in the 1800s and early 1900s (e.g., Litvaitis, 1993). By contrast, in parts of central Ontario where agriculture has always been largely absent (e.g., Algonquin Provincial Park), declines are attributed mainly to fire suppression (Williams, 2009; Tozer, 2012). Other causes leading to declines in early-successional forests in certain areas include fewer disturbance-creating floods due to storm water management and fewer meadow-creating beavers due to trapping and protection of property (DeGraaf and Yamasaki, 2003).

Early-successional forests have always been present on the landscape due to disturbance, reaching their highest rate of occurrence following European land-clearing for settlement and prior to widespread fire control (Riley, 2013). Evidence suggests, however, that early-successional forest habitats have since declined to a point below their natural rate of occurrence in some regions of

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northeastern North America (Lorimer and White, 2003). For instance, the current extent of early-successional forests in pine-dominated areas in central Ontario is closer to natural levels now than following European settlement and prior to fire suppression, but the extent may have fallen below the natural rate of occurrence by more than a quarter (Elkie et al., 2013).

A consequence of declining early-successional forests has been reductions in certain animal populations, which use them for breeding (e.g., Litvaitis, 2001). Declines have been especially widespread amongst birds (Dettmers, 2003). Populations of 65% of eastern North American shrub–scrub-associated bird species significantly declined between the 1960s and 1990s (Hunter et al., 2001). Compared to any other group of birds, shrubland-dependent breeding birds host the largest proportion of species requiring long-term conservation planning in the northeastern US (45%); grassland birds (40%) and forest birds (34%) score lower (Dettmers, 2003). Although there are many factors involved, population declines of most early-successional forest birds are nonetheless tightly linked temporally with concurrent declines in breeding habitat (Litvaitis, 1993).

To help alleviate bird population declines, forest management can be used as a means to increase and maintain early-successional forest habitat by emulating natural disturbance with harvesting (Thompson and DeGraaf, 2001). Managers have good knowledge of the species that depend on early-successional forests (e.g., Hunter et al., 2001) and the number of years after disturbance during which these species are present (e.g., Thompson and DeGraaf, 2001), but they often lack more-detailed wildlife–habitat relationships for most members of the group (an exception being certain songbirds; e.g., Askins et al., 2007). The absence of quantified habitat relationships for most early-successional forest bird species, such as the habitat quality of different types and characteristics of harvests, makes forest management planning challenging for some species.

One such species is the Eastern Whip-poor-will (*Antrostomus vociferus*), a crepuscular, insectivorous, neotropical, migrant bird, designated as a species at risk throughout many parts of its breeding range due to steep population declines (Cink, 2002). Although the causes are unknown, habitat loss and degradation, vehicle collisions, and changes in food supply related to pesticides and climate change may explain population declines (COSEWIC, 2009). Eastern Whip-poor-wills call most frequently during periods when the moon is >50% illuminated (Wilson and Watts, 2006), presumably because they time breeding to coincide with the full moon, which likely assists with sit-and-wait capture of large back-lit insects (Mills, 1986). Foraging individuals appear to concentrate along the edges of forest clearings, including those created by harvesting (Cink, 2002), presumably because insects back-lit by moonlight are easier to locate in the open conditions found there (Mills, 1986). Very little is known regarding relationships between occurrence of Eastern Whip-poor-wills and different types of harvesting, partly due to lack of correctly-timed surveys. A study in North Carolina was an exception, which found that the relative abundance of Eastern Whip-poor-wills on moonlit nights was seven times higher along the edges of regenerating loblolly pine (*Pinus taeda*) clearcuts than within forests (Wilson and Watts, 2008).

We determined occupancy of Eastern Whip-poor-wills in red pine (*Pinus resinosa*)-dominated stands harvested using clearcut with seed trees and in white pine (*P. strobus*)-dominated stands harvested using uniform shelterwood in eastern Algonquin Provincial Park, Ontario, Canada. We predicted that occurrence of Eastern Whip-poor-wills, measured via an established monitoring protocol (Bird Studies Canada, 2013), would increase most in the presence of clearcuts (see also Wilson and Watts, 2008), and would also increase, but to a lesser degree, with increasing amounts of shelterwood harvesting. We based our predictions on the premise that

larger openings in the canopy formed by clearcut harvesting would provide superior foraging habitat because large insects would be maximally back-lit by moonlight, followed by smaller canopy openings formed by shelterwood harvesting (Mills, 1986).

2. Methods

2.1. Study area

Our study was conducted during June 2013 in the eastern portion of Algonquin Provincial Park, Ontario, Canada (45°55'N, 77°55'W). The canopy trees within 500 m of sampling points were comprised of stands dominated by white pine (53%); white pine mixed with other conifers and hardwoods (16%); red pine (*P. resinosa*; 12%); jack pine (*P. banksiana*; 3%); and various combinations of red oak (*Quercus rubra*), black spruce (*Picea mariana*), white birch (*Betula papyrifera*), sugar maple (*Acer saccharum*), white spruce (*P. glauca*), and other less common hardwoods and conifers (16%) (based on Forest Resource Inventory information, Ontario Ministry of Natural Resources). The entire study area was high-graded for super-canopy white pine in the mid-to-late 1800s, and for hardwoods in the early 1900s (Lloyd, 2006). Since 1975, the study area has been managed using a mix of predominantly shelterwood in white pine-dominated stands, and to a lesser extent, clearcut with seed trees in red pine-dominated stands to achieve diverse silvicultural goals and objectives (Lloyd, 2006; OMNR, 1998, 2004, 2010, 2013a). Shelterwood in white pine stands consisted of a series of up to 4 cuts at ~20 year intervals, increasingly and uniformly thinning out the stand with each cut, but providing a seed source and maintaining optimum light levels (i.e., 40–50% direct sunlight) for white pine regeneration below; after the final cut a new young stand of pine was left to grow to a point where the cycle could be repeated (OMNR, 1998). Clearcut with seed trees in red pine stands consisted of removing all mature trees except seed-producing red pines spaced uniformly as close as tree-length apart, but providing nearly full sun for optimum red pine regeneration below (OMNR, 1998).

2.2. Sampling points

We surveyed Eastern Whip-poor-wills at 37 points placed at least 750 m apart along 4 roadside routes throughout the study area in June 2013 (Fig. 1). Routes were as far apart as possible given availability of navigable roadways, and were part of a larger network of randomly-placed Eastern Whip-poor-will sampling points throughout southern Ontario (Bird Studies Canada, 2013). We limited our analysis to data from 4 routes located within the eastern portion of Algonquin Park because we were able to acquire harvesting information since 1970 for this area.

2.3. Whip-poor-will surveys

Surveys occurred 0.5 h after sunset and 0.5 h before sunrise between 17 June and 30 June 2013. Conditions were calm (wind < 11 km/h) with no precipitation and little cloud cover, such that the moon was always visible and > 60% illuminated to maximize detection probability (Mills, 1986). We conducted two 3-min point counts at least 7 days apart at each point. One of us (H. K.) conducted all of the surveys. The survey protocol is described in more detail in Bird Studies Canada (2013).

2.4. Analyses

Harvesting was characterized within 500 m buffers around each point using a geographic information system. We selected for

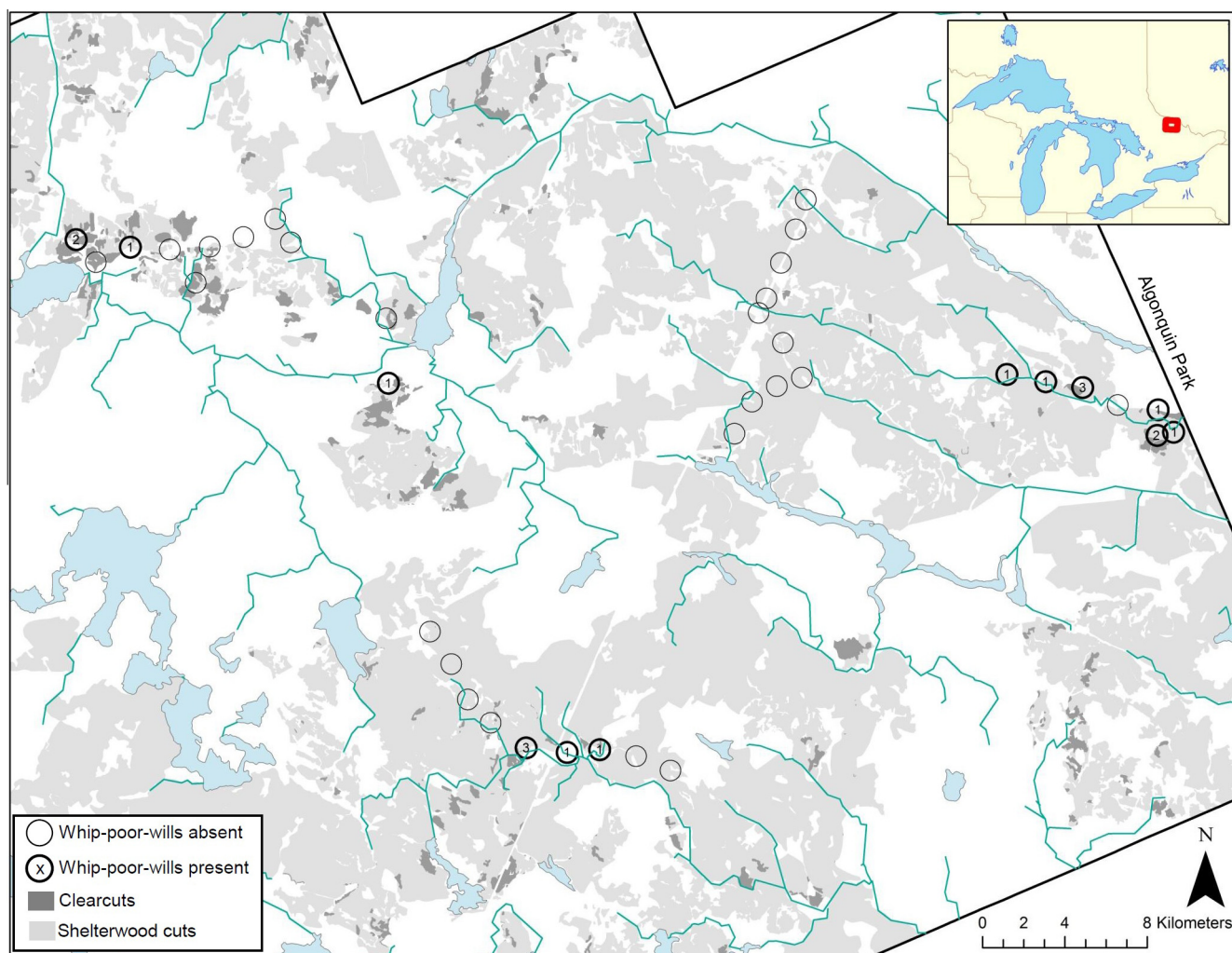


Fig. 1. Distribution of sampling points ($n = 37$ points) showing 500-m radius circles where Eastern Whip-poor-wills were detected (present; $n = 12$ points) or were not detected (absent; $n = 25$ points) on moonlit nights along roadside routes in eastern Algonquin Provincial Park, Ontario, Canada, June 2013. The maximum number (1, 2, or 3) of Eastern Whip-poor-wills detected on one or the other of two survey visits is shown for points where birds were detected. Also shown are areas logged with clearcut with seed trees (clearcuts) and uniform shelterwood (shelterwood cuts) since 1970.

analysis 37 points with largely non-overlapping buffers (Fig. 1) where we had access to spatial harvesting information since 1970. Harvesting data prior to 1970 were unavailable.

The response variable was the presence or absence of Eastern Whip-poor-wills within 500 m of each survey point (hereafter “site occupancy”). We used single-season site occupancy models to simultaneously evaluate variables affecting detection probability via a detection sub-model and site occupancy via an occupancy sub-model (MacKenzie et al., 2002), and an information theoretic approach via Akaike’s information criterion (AIC) to select best approximating models among sets of candidate models (Burnham and Anderson, 2002). We tested the fit of our global model with a parametric bootstrap and associated χ^2 statistic to ensure that our explanatory variables as a group reliably predicted the response variable; P -values >0.05 indicated adequate fit (Fiske and Chandler, 2014).

We considered two explanatory variables that might explain site occupancy: proportion of the landscape within 500 m of each point that was harvested with shelterwood since 1970 (hereafter “% shelterwood”) and presence of clearcuts within 500 m of each point that were harvested ≤ 16 years prior to our study (i.e., harvested in 1997 or after; hereafter “presence of young clearcuts”). We chose 16 years since harvest as a cut-off for clearcuts because a previous study suggested that Eastern Whip-poor-wills

were less common in clearcuts older than 17 years since harvest (Wilson and Watts, 2008). We chose presence of clearcuts rather than proportion of clearcuts in the buffer because 15 of 37 (41%) points had no clearcuts in the buffer, and where clearcuts were present in the buffer, there was limited variation in the proportion (median = 12%; first, third quartile = 3, 20%). Similarly, we chose proportion of shelterwood rather than presence of shelterwood in the buffer because shelterwood cutting was present in the buffers of all but one of the points. Thus, we felt that variation in habitat conditions across points was better described using presence for clearcuts and proportions for shelterwood.

We also considered % shelterwood and presence of young clearcuts as variables that might explain detection probability. We did not consider wind (range: 0–11 km/h), date (17–30 June), temperature (7–22 °C), noise level (slight-moderate; Bird Studies Canada, 2013), moon illumination ($>60\%$), or cloud cover (0–50%) because there was not enough meaningful variation in these variables to influence detection probability due to our strict field survey criteria described above.

We evaluated a total of 9 models, which included various combinations of % shelterwood and presence of young clearcuts in the detection and occupancy sub-models. Given that our sample size was 37, we limited the number of variables in each model, such that the total number of estimated parameters was ≤ 4

(Burnham and Anderson, 2002). Consideration of models with larger numbers of estimated parameters might have led to over-fitting and weak inferences. Because of this limitation, we were unable to evaluate a full global model that included all of the detection and occupancy probability covariates that we considered. Instead, we selected one of the most highly-parameterized models in our set as our global model, which we identify in Table 1.

We considered models with AICc values within seven of the best model (lowest AICc value) to have support, i.e., models with $\Delta AICc < 7.0$ were considered important (Burnham et al., 2011).

We used model-averaged parameter estimates and unconditional standard errors to address model-selection uncertainty (Burnham and Anderson, 2002). To assess support for our predictions we examined model-averaged parameter estimates and associated confidence limits for each explanatory variable included in the supported set of models; variables with 85% confidence limits that did not overlap zero were considered important (Arnold, 2010). We predicted site occupancy with associated 95% confidence intervals as a function of each important explanatory variable using the best model that included the variable.

We generated box-and-whisker plots summarizing the area and years since harvest of clearcuts of any age within 500 m of points where Eastern Whip-poor-wills were detected compared to clearcuts within 500 m of points where Eastern Whip-poor-wills were not detected. We tested the statistical significance of the differences in these metrics using independent two-sample *t*-tests. We also translated the total area of clearcuts within 500 m of points where Eastern Whip-poor-wills were detected to ha of clearcuts per 100 ha of forest. Area and years since harvest of clearcuts were not considered as explanatory variables in our occupancy models described above, because their inclusion resulted in numerous zero values for points lacking clearcuts and because we limited the number of covariates in models due to sample size constraints. Nonetheless, we included this information to assist forest managers in the field.

All analyses were conducted using the R programming language (R Development Core Team, 2013); models were fitted using package *unmarked* (Fiske et al., 2014) and model-averaged estimates and AICc tables were generated using package *AICcmoadv* (Mazerolle, 2013).

3. Results

We detected Eastern Whip-poor-wills at 12 of 37 (32%) sampling points (Fig. 1), with an overall mean relative abundance of 0.6 ± 0.2 (mean \pm 95% confidence intervals) individuals per point (range: 0–3 individuals per point). Using the best model described

Table 1
Model selection results for 9 candidate models explaining detection probability and site occupancy of Eastern Whip-poor-wills during surveys on moonlit nights along roadside routes in eastern Algonquin Provincial Park, Ontario, Canada, June 2013. K = number of parameters; LL = log likelihood; AICc = Akaike's information criterion; w = Akaike weight.

Model ^a	K	LL	AICc	$\Delta AICc$	w
$p(\cdot) \psi(CC)$	3	-33.4	73.5	0	0.36
$p(CC) \psi(\cdot)$	3	-33.8	74.3	0.9	0.23
$p(CC) \psi(CC)$	4	-33.3	75.8	2.3	0.11
$p(\cdot) \psi(CC + SH)^b$	4	-33.3	75.9	2.4	0.11
$p(CC + SH) \psi(\cdot)$	4	-33.8	76.8	3.4	0.07
$p(\cdot) \psi(\cdot)$	2	-36.5	77.3	3.9	0.05
$p(\cdot) \psi(SH)$	3	-35.5	77.7	4.2	0.04
$p(SH) \psi(\cdot)$	3	-36.3	79.4	6	0.02
$p(SH) \psi(SH)$	4	-35.2	79.7	6.2	0.02

^a p = probability of detection; ψ = probability of occupancy; CC = presence of <16 year-old clearcuts within 500 m; SH = % shelterwood within 500 m.

^b Global model, see methods—analysis for details.

in further detail below, the probability of detecting an Eastern Whip-poor-will during a single 3-min point count at an occupied sampling point was 50% ($\pm 15\%$ SE). Young clearcuts were present at 14 sampling points and absent at 23. Median % shelterwood across the 37 sampling points was 51 (inter-quartile range: 46; range: 0–100).

The global model fit the data adequately ($P = 0.1$, Table 1), with support for all of the models (all $\Delta AICc < 6.2$ and $w > 0.02$; Table 1). Confidence limits around model-averaged parameter estimates from the detection probability sub-model included zero for % shelterwood and presence of young clearcuts (Table 2), suggesting that these variables were unimportant for explaining detection probability. By contrast, confidence limits around model-averaged parameter estimates from the occupancy sub-model included zero only for % shelterwood, suggesting that presence of young clearcuts was the only important variable explaining site occupancy (Table 2).

Using the best model, which included only presence of young clearcuts in the occupancy sub-model, site occupancy increased by 3.3 times from 0.23 at points where young clearcuts were absent to 0.76 at points where young clearcuts were present (Fig. 2). However, a model that included only presence of young clearcuts in the detection sub-model and a model that included only presence of young clearcuts in both the detection and occupancy sub-models were also highly ranked ($\Delta AICc < 2.3$ and $w > 0.11$; Table 1), suggesting that presence of young clearcuts in the detection sub-model might also be important, even though the model-averaged parameter estimate overlapped zero, albeit only slightly (Table 2). Thus, we also calculated occupancy as a function of presence of young clearcuts using the third-best model, which included presence of young clearcuts in both the detection and occupancy sub-models, but we obtained predictions and associated errors that were nearly identical to those presented above using the best model, so we used the results from the best and simpler model for inference (Fig. 2).

Clearcuts of any age were present within 500 m at 10 of 12 (83%) points where Eastern Whip-poor-wills were detected. By contrast, clearcuts of any age were present at only 12 of 25 (48%) points where Eastern Whip-poor-wills were not detected. Twenty clearcuts within 500 m of points where Eastern Whip-poor-wills were detected were significantly larger by 14 ha, on average, than 30 clearcuts within 500 m of points where Eastern Whip-poor-wills were not detected ($t = 2.2$, $df = 48$, $P = 0.02$; Fig. 3). By contrast, there was no significant difference in the number of years since harvest between clearcuts within 500 m of points where Eastern Whip-poor-wills were detected compared to clearcuts within 500 m of points where Eastern Whip-poor-wills were not detected ($t = 1.2$, $df = 48$, $P = 0.26$; Fig. 3).

There was the equivalent of an aggregated total of 12 ± 9 ha (mean \pm 95% CIs) of clearcuts per 100 ha (inter-quartile range: 1.5–18 ha) of forest surrounding sampling points where Eastern

Table 2

Model-averaged parameter estimates (Est.; logit scale), associated 85% confidence limits (85% CIs), and relative importance values calculated as cumulative Akaike weights (Σw) for variables used to model detection probability and site occupancy of Eastern Whip-poor-wills during surveys on moonlit nights along roadside routes in eastern Algonquin Provincial Park, Ontario, Canada, June 2013.

Variable	Detection probability			Site occupancy		
	Est.	85% CIs (lower, upper)		Est.	85% CIs (lower, upper)	
SH ^a	0.00	-0.03, 0.03	0.11	0.02	-0.03, 0.03	0.17
CC ^a	1.56	-0.09, 3.21	0.41	2.26	0.30, 4.22	0.58
Intercept	-0.39	-2.15, 1.38	-	-0.86	-2.43, 0.72	-

^a CC = presence of <16 year-old clearcuts within 500 m; SH = % shelterwood within 500 m.

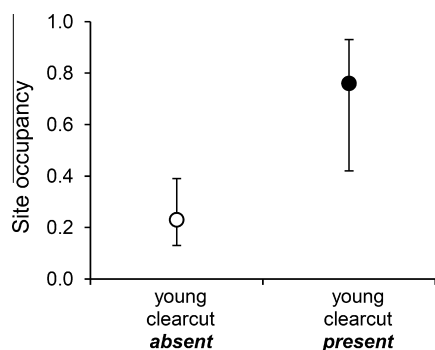


Fig. 2. Site occupancy of Eastern Whip-poor-wills within 500 m of sampling points on moonlit nights along roadside routes in eastern Algonquin Provincial Park, Ontario, Canada, June 2013, as a function of the presence of young (<16 year-old) clearcuts. Shown are predictions from the best model that included presence of young clearcuts. Error bars are 95% confidence intervals.

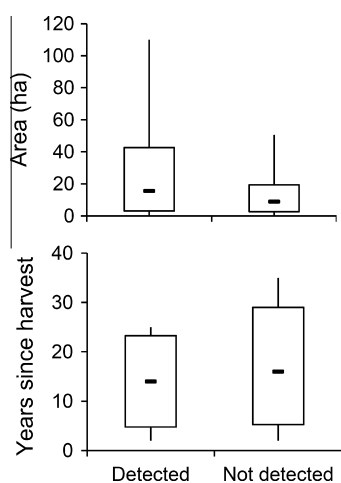


Fig. 3. Size and age of clearcuts within 500 m of sampling points where Eastern Whip-poor-wills were detected ($n = 20$ clearcuts surrounding 12 points), or were not detected ($n = 30$ clearcuts surrounding 25 points), during surveys on moonlit nights along roadside routes in eastern Algonquin Provincial Park, Ontario, Canada, June 2013. Shown are box-and-whisker plots, whiskers indicating the range.

Whip-poor-wills were detected. These clearcuts were composed of various sizes (27 ± 13 ha [mean \pm 95% CIs]) and ages (14 ± 4 years since harvest).

4. Discussion

We found that occurrence of Eastern Whip-poor-wills increased by 3.3 times where young clearcuts were present. Others have also found that occurrence of breeding Eastern Whip-poor-wills increases with increasing amounts of human-created early-successional forested habitat in other regions and forest types (e.g., loblolly pine forest in North Carolina, Wilson and Watts, 2008; mixed white and pitch [*Pinus rigida*] pine-oak [*Quercus*] forest in New Hampshire; Hunt, 2013). These results may not be surprising considering that foraging Eastern Whip-poor-wills are suspected to benefit from back-lit conditions created by moonlight (Mills, 1986). It is possible that insects, such as large moths and beetles, which are preferred prey, are more easily located during sit-and-wait foraging under these conditions (Mills, 1986). Presumably this was also the case in this study, where canopy openings created by clearcut with seed trees may have created superior back-lit foraging conditions on moonlit nights relative to closed-canopy forests (see also Wilson and Watts, 2008).

Superior foraging conditions in open areas with associated backlighting may also partly explain higher occupancy and abundance of other Caprimulgids in various open anthropogenic habitats. For example, high numbers of Common Nighthawks (*Chordeiles minor*) feeding over urban areas (Brigham et al., 2011), particularly where insects are attracted to and illuminated by street lights (e.g., Shields and Bildstein, 1979), and various South American species feeding over road corridors and clearings above dwellings amongst dense closed-canopy forests (Ingels et al., 1999). Regardless of the mechanism, our results suggest that clearcut with seed trees in red pine-dominated stands increases occupancy of breeding Eastern Whip-poor-wills in pine-dominated forests in central Ontario.

We measured occupancy of singing Eastern Whip-poor-wills. Due to challenging logistics, we were unable to collect data on more direct measures of habitat quality, such as productivity and survivorship. Measuring productivity of Eastern Whip-poor-wills requires fitting birds with radio-transmitters, to locate nests that are almost impossible to find due to camouflaging by incubating or brooding adults. Measuring survivorship requires uniquely color-marking captured individuals for recapture in subsequent years. Both of these techniques are time consuming and relatively expensive. For example, two studies captured and attached transmitters to 8 and 15 Eastern Whip-poor-wills, respectively, over 5 collective field seasons, impressive totals considering the logistics involved, but illustrative of the challenges preventing necessary sample sizes for studies such as ours (Garlapow, 2007; Hunt, 2013). In most cases, however, occupancy is a reliable measure of breeding habitat quality, an assumption that is probably also true in this study (Bock and Jones, 2004). Nonetheless, information on productivity and survivorship of Eastern Whip-poor-wills from territories associated with clearcut and shelterwood harvesting versus territories unassociated with these types of harvesting would be beneficial, and is an area for future research.

As with most early-successional forest breeding bird species, Eastern Whip-poor-wills were more abundant in central Ontario following European settlement than they are now (e.g., Tozer, 2012). Extensive open areas, which provided high-quality foraging habitat, were created by fires ignited by humans and lightning (e.g., Tozer and Strickland, 2012). For instance, in an area immediately southwest of our study area, observers described the Eastern Whip-poor-will as “locally abundant” in 1908 (Cooper, 1917) and as “the one bird that best typifies the [area]” during the late-1930s (Miller, 1962). Miller, (1962) even commented that while camping in the area “[the reoccurring noise each night from close-calling birds] grew so irritating that I used to step out [of our tent] and fling stove wood at [them]. . .”. This is remarkable considering that Eastern Whip-poor-wills, which are now designated as threatened in Ontario (OMNR, 2013b), have been completely absent as breeders from the area of Miller’s description since the early-1990s (Tozer, 2012).

Since the 1920s, there has been increasingly effective fire suppression and gradual disappearance of suitable clearings for foraging Eastern Whip-poor-wills (Tozer and Strickland, 2012). There has also been a parallel decline in Eastern Whip-poor-will numbers during the same time period. For instance, the average annual amount of burned land in Algonquin Park where our study took place decreased from 6500 ha during the 1920s and 1930s, to 500 ha between the 1940s and 1970s, to only 25 ha since 1980 (Runge, 1976; Cumming, 2005; summarized in Williams, 2009). Consistent with the reduction in fire-created openings, the number of 10×10 km breeding bird atlas squares occupied by breeding Eastern Whip-poor-wills in Algonquin Park declined from 20 out of 70 (29%) in the early 1980s to 9 out of 70 (13%) in the early 2000s (Tozer, 2012).

The point follows, however, that Eastern Whip-poor-will populations may currently be returning to levels closer to those found prior to European settlement, implying that clearcut with seed trees as a means to maintain open foraging habitat in the absence of fire may not be important. However, despite the challenges with estimating historical landscape patterns, the current amount of suitable Eastern Whip-poor-will foraging habitat in central Ontario may be less than that found prior to settlement. For example, the amount of suitable Eastern Whip-poor-will foraging habitat in Algonquin Park may be ~36% less than the lower end of the best estimate of the range of natural variation (amounting to a shortage of at least ~8000 ha based on the “pre-sapling” class for the “young” forest indicator in Ontario’s Landscape Tool; Elkie et al., 2013). Therefore, clearcut with seed trees in red pine-dominated stands may provide habitat to support populations of Eastern Whip-poor-wills at levels more consistent with those found historically.

Acknowledgements

Assistance for this project was provided by the Government of Ontario. Myles Falconer, Audrey Heagy, Ron Tozer, and two anonymous reviewers provided helpful comments that improved the manuscript. We thank Jennifer Hillyer and the Algonquin Forestry Authority for assistance with GIS data.

References

- Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike’s information criterion. *J. Wildl. Manag.* 74, 1175–1178.
- Askins, R.A., 2000. *Restoring North America’s Birds: Lessons from Landscape Ecology*. Yale University Press, New Haven, CT.
- Askins, R.A., 2001. Sustaining biological diversity in early successional communities: the challenges of managing unpopular habitats. *Wild. Soc. Bull.* 29, 407–412.
- Askins, R.A., Zuckerberg, B., Novak, L., 2007. Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland birds in southern New England? *For. Ecol. Manag.* 250, 137–147.
- Bird Studies Canada, 2013. Ontario Whip-poor-will Project. Bird Studies Canada, Port Rowan, Ontario, Canada, <<http://www.birdscanada.org/birdmon/wpwi>>.
- Blancher, P., Cadman, M.D., Pond, B.A., Couturier, A.R., Dunn, E.H., Francis, C.M., Rempel, R.S., 2007. Changes in bird distributions between atlases. In: Cadman, M.D., Sutherland, D.A., Beck, G.G., Lepage, D., Couturier, A.R. (Eds.), *Atlas of the Breeding Birds of Ontario, 2001–2005*. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature, Toronto, Ontario, Canada, pp. 32–48.
- Bock, C.E., Jones, Z.F., 2004. Avian habitat evaluation: should counting birds count? *Front. Ecol. Environ.* 2, 403–410.
- Brigham, R.M., Ng, J., Poulin, R.G., Grindal, S.D., 2011. Common nighthawk (*Chordeiles minor*). In: Poole, A. (Ed.), *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Cink, C.L., 2002. Eastern Whip-poor-will (*Antrostomus vociferous*). In: Poole, A. (Ed.), *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY.
- Cooper, J.M., 1917. Birds of Lake Onigamis region, Que., and Algonquin park. *Ont. Ottawa Nat.* 30, 123–129.
- COSEWIC, 2009. COSEWIC assessment and status report on the Eastern Whip-poor-will *Caprimulgus vociferus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON. <http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_whip-poor-will_0809_e.pdf>.
- Cumming, G.H., 2005. *Forest Management Plan for the Algonquin Park Forest Management Unit, Southern Region*. Algonquin Forestry Authority, Huntsville, Ontario, Canada.
- DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *For. Ecol. Manag.* 185, 179–191.
- Dettmers, R., 2003. Status and conservation of shrubland birds in the northeastern US. *For. Ecol. Manag.* 185, 81–93.
- Elkie, P.C., Smiegielski, A., Elliott, J., Kushneriuk, R., Rempel, R.S., 2013. Ontario’s Landscape Tool User’s Manual, Version 2013. Ontario Ministry of Natural Resources, Policy Division, Forests Branch, Policy Section, Guides Unit, Sault Ste. Marie, Ontario, Canada. <<http://www.olt.tbaytelirectit.com/OLTUsersManual.pdf>>.
- Fiske, I., Chandler, R., 2014. Overview of Unmarked: An R Package for the Analysis of Data From Unmarked Animals. <<http://cran.r-project.org/web/packages/unmarked/vignettes/unmarked.pdf>>.
- Fiske, I., Chandler, R., Miller, D., Royle, A., Kery, M., 2014. Package Unmarked. <<http://cran.r-project.org/web/packages/unmarked/unmarked.pdf>>.
- Garlapow, R.W., 2007. Whip-poor-will Prey Availability and Foraging Habitat: Implications for Management in Pitch Pine/Scrub Oak Barrens Habitats. M.Sc. Thesis, University of Massachusetts Amherst, Amherst, MA.
- Hunt, P., 2013. Habitat use by Eastern Whip-poor-will (*Antrostomus vociferous*) in New Hampshire with recommendations for management. Report to the New Hampshire Fish and Game Department Nongame and Endangered Wildlife Program, New Hampshire Audubon, Concord, NH.
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildl. Soc. Bull.* 29, 440–455.
- Ingels, J., Oniki, Y., Willis, E.O., 1999. Opportunistic adaptations to man-induced habitat changes by some South American Caprimulgidae. *Rev. Brasil. Biol.* 59, 563–566.
- Larson, B.M., Riley, J.L., Snell, E.A., 1999. The Woodland Heritage of Southern Ontario: a Study of Ecological Change, Distribution, and Significance. Federation of Ontario Naturalists, Don Mills, Ontario, Canada.
- Litvaitis, J.A., 1993. Response of early successional vertebrates to historic changes in land use. *Cons. Biol.* 7, 866–873.
- Litvaitis, J.A., 2001. Importance of early successional habitats to mammals in eastern forests. *Wildl. Soc. Bull.* 29, 466–473.
- Lloyd, D.L., 2006. Algonquin Harvest: The History of the McRae Lumber Company. Robert D. McRae, Whitney, Ontario, Canada.
- Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *For. Ecol. Manag.* 185, 41–64.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Mazerolle, M.J., 2013. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). Version 1.33. R Foundation for Statistical Computing, Vienna, Austria. <<http://CRAN.R-project.org/package=AICcmodavg>>.
- Miller, R.B., 1962. *A Cool Curving World*. Longmans Canada, Toronto, Ontario, Canada.
- Mills, A.M., 1986. The influence of moonlight on the behavior goatsuckers (*Caprimulgidae*). *Auk* 103, 370–378.
- Ontario Ministry of Natural Resources, 1998. A silvicultural guide for the Great Lakes St. Lawrence Conifer Forest in Ontario. Ontario Ministry of Natural Resources, Queen’s Printer for Ontario, Toronto, Ontario, Canada. <http://www.mnr.gov.on.ca/stdprodconsume/groups/lr@mnr/@forests/documents/document/stdprod_100104.pdf>.
- Ontario Ministry of Natural Resources, 2004. Ontario Tree Marking Guide, Version 1.1. Ontario Ministry of Natural Resources, Queen’s Printer for Ontario, Toronto, Canada. <http://www.mnr.gov.on.ca/stdprodconsume/groups/lr@mnr/@forests/documents/document/mnr_e000526.pdf>.
- Ontario Ministry of Natural Resources, 2006. State of the Forest Report, 2006. Ontario Ministry of Natural Resources, Queen’s Printer for Ontario, Toronto, Ontario, Canada. <http://www.mnr.gov.on.ca/en/Business/Forests/2ColumnSubPage/STEL02_179267.html>.
- Ontario Ministry of Natural Resources, 2010. Forest Management Guide for Conserving Biodiversity at the Stand and Site Scales. Ontario Ministry of Natural Resources, Queen’s Printer for Ontario, Toronto, Ontario, Canada. <http://www.mnr.gov.on.ca/stdprodconsume/groups/lr@mnr/@forests/documents/document/stdprod_109196.pdf>.
- Ontario Ministry of Natural Resources, 2013a. Forest Management Guide for Great Lakes-St. Lawrence Landscapes. Ontario Ministry of Natural Resources, Queen’s Printer for Ontario, Toronto, Ontario, Canada. <<http://www.mnr.gov.on.ca/stdprodconsume/groups/lr@mnr/@forests/documents/document/260036.pdf>>.
- Ontario Ministry of Natural Resources, 2013b. Species at risk in Ontario (SARO) list. <http://www.mnr.gov.on.ca/en/Business/Species/2ColumnSubPage/MNR_SAR_CSSR_SARO_LST_EN.html>.
- R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <<http://www.R-project.org/>>.
- Riley, J., 2013. *The Once and Future Great Lakes Country: an Ecological History*. McGill-Queen’s rural, wildland, and resource studies, vol. 2. McGill-Queen’s University Press, Montreal and Kingston, Canada.
- Runge, R.A., 1976. Deer, fire, and logging: resource management and planning in Algonquin Provincial Park. M.Sc. thesis, University of Waterloo, Waterloo, Ontario, Canada.
- Shields, W.M., Bildstein, K.L., 1979. Birds versus bats: behavioral interactions at a localized food source. *Ecol.* 60, 468–474.
- Thompson III, F.R., DeGraaf, R.M., 2001. Conservation approaches for woody, early successional communities in the eastern United States. *Wildl. Soc. Bull.* 29, 483–494.
- Tozer, R., 2012. Birds of Algonquin Park. Custom Printers, Renfrew, and The Friends of Algonquin Park, Whitney, Ontario, Canada.
- Tozer, R., Strickland, D., 2012. *Pictorial History of Algonquin Provincial Park*. The Friends of Algonquin Park, Whitney, Ontario, Canada.

- Trani, M.K., Brooks, R.T., Schmidt, T.L., Rudis, V.A., Gabbard, C.M., 2001. Patterns and trends of early successional forests in the eastern United States. *Wild. Soc. Bull.* 29, 413–424.
- Williams, J.S., 2009. Moving towards sustainable forest management. In: Euler, D., Wilton, M. (Eds.), *Algonquin Park: The Human Impact*. OJ Graphix, Espanola, Ontario, Canada, <<http://www.algonquin-eco-watch.com/book.html>>.
- Wilson, M.D., Watts, B.D., 2006. Effect of moonlight on detection of Whip-poor-wills: implications for long-term monitoring strategies. *J. Field Ornithol.* 77, 207–211.
- Wilson, M.D., Watts, B.D., 2008. Landscape configuration effects on distribution and abundance of Whip-poor-wills. *Wilson. J. Ornithol.* 120, 778–783.