Using bioacoustics to study vocal behaviour and habitat use of Barred Owls, Boreal Owls and Great Horned Owls

Estudo bioacústico do comportamento vocal e do uso de habitat por coruja-barrada, mocho-funéreo e bufo-real-americano

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ABSTRACT

Bioacoustics is the study of sound produced by animals, and autonomous recording units (ARUs) are increasingly used to research and monitor birds by recording vocalizations because of the benefits of reduced observer bias and the ability to collect data over longer time scales. We used ARUs to study owl vocal behaviour and habitat use by passively recording owls calling during the breeding season. We scheduled ARUs to record for 10 min every hr on a 24-hr basis, and deployed the units at sites throughout northeastern Alberta from mid-March through mid-May in 2013, 2014, and 2015. We scanned all recordings collected using automated recognizers to detect territorial vocalizations of Barred Owls (*Strix varia*), Great Horned Owls (*Bubo virginianus*), and Boreal Owls (*Aegolius funereus*). We found that territorial vocal activity was high for all owls throughout the nocturnal period, with differences between species in the onset and end of vocal activity around sunset and sunrise. Barred Owls called occasionally during daylight hours, but this was infrequent for Great Horned Owls and rare for Boreal Owls. Based on our results, we recommend that surveys for these species start 1 hr after sunset and end 1 hr before sunrise. Locations of owl detections indicated that Barred Owls were more likely to be found calling in mixedwood forests and less likely to be found in more disturbed areas. Boreal Owls were more likely to be found calling in coniferous forests in both disturbed and undisturbed areas, and Great Horned Owls were equally likely to be found calling in all habitats surveyed. This research contributes to our understanding of the behaviour of these owls, demonstrates the utility of new bioacoustic technology, and has practical implications for conducting passive surveys to study and monitor owls.

Keywords: automated species recognition, autonomous recording unit, passive acoustic monitoring, territorial behaviour, vocalizations

RESUMO

A bioacústica é o estudo do som produzido por animais, e as unidades de registo automático (ARUs) são cada vez mais usadas para investigar e monitorizar aves através do registo de vocalizações, devido às vantagens da redução do erro do observador e da capacidade de recolher dados em escalas de tempo alargadas. Utilizámos ARUs para estudar o comportamento vocal de rapinas noturnas e o seu uso de habitat, através de gravações passivas de vocalizações de rapinas noturnas durante a época de reprodução. Configurámos as ARUs para gravar durante 10 minutos por hora durante cada período de 24h, e instalámos as unidades em todo o nordeste de Alberta, de meados de março até meados de maio em 2013, 2014 e 2015. Examinámos todas as gravações recolhidas usando reconhecedores automáticos para detetar vocalizações territoriais de coruja-barrada (*Strix varia*), bufo-real-americano (*Bubo virginianus*) e mocho-funéreo (*Aegolius funereus*). Verificámos que todas as espécies apresentaram elevada atividade vocal territorial durante a noite, embora com diferenças entre si no período de início e de fim da atividade vocal na proximidade do ocaso e do nascer do sol. A emissão de vocalizações durante o dia ocorreu ocasionalmente para a coruja-barrada, ainda menos frequentemente para o bufo-real-americano e raramente no caso do mocho-funéreo. Com base nos resultados, recomendamos que a monitorização destas espécies comece 1 hora após o ocaso e terminem 1 hora antes do nascer do sol. O registo das localizações das aves indicou que a probabilidade de ouvir uma vocalização de coruja-barrada é maior em áreas florestais mistas e menor em áreas mais perturbadas. A probabilidade de ouvir mocho-funéreo é maior em florestas de coníferas, e igual em áreas perturbadas e não perturbadas, enquanto a probabilidade de ouvir o bufo-real-americano é igual em todos os habitats monitorizados. Este estudo contribui para a nossa compreensão do comportamento destas espécies, demonstra a utilidade das novas tecnologias bioacústicas e tem implicações práticas para a realização de gravações passivas para investigar e monitorizar rapinas noturnas.

Palavras-chave: comportamento territorial, monitorização acústica passiva, reconhecimento automático de espécies, unidade de registo automático, vocalizações

Introduction

Bioacoustics is the study of sound produced by animals. The field of bioacoustics has gained momentum in recent years with relatively new technology that is able to record sound autonomously in a variety of environments. Autonomous recording units (ARUs) are increasingly used to monitor and study birds by recording vocalizations; the numerous benefits include reduced observer bias, and the ability to collect data over longer time scales (Shonfield & Bayne 2017a). Several different models of autonomous recording units (ARUs) can be purchased commercially and can be programmed to record on a set schedule. ARUs have a downside that the volume of recordings collected can be very time consuming to process. Automated species recognition is emerging as a valuable tool in the field of bioacoustics and has the potential to efficiently process a large volume of recordings within a manageable timeframe (Knight et al. 2017).

Research and monitoring projects focusing on owls frequently use acoustic surveys to determine presence or abundance (Goyette et al. 2011; Rognan et al. 2012) because many owl species are effectively detected by their vocalizations. Owls are especially vocal during the breeding season, and they use territorial vocalizations to attract mates and defend territories from conspecifics (Johnsgard 2002; Odom & Mennill 2010a). Acoustic surveys for owls often broadcast a recorded owl call (Clark & Anderson 1997; Sater et al. 2006; Grossman et al. 2008; Kissling et al. 2010). Broadcasting owl calls can increase the probability of detecting an owl by eliciting territorial individuals to respond (Kissling et al. 2010), but there are drawbacks to this survey method. Call-broadcast surveys are known to draw owls in from a distance (Zuberogoitia et al. 2011), and can also affect detection of other owl species (Crozier et al. 2006; Bailey et al. 2009; Wiens et al. 2011). Thus, this survey method could affect conclusions about habitat associations of owls, and limits the information we can obtain on the natural calling behaviour of different owl species.

Passive acoustic survey methods using recent bioacoustic technology are potentially an efficient approach for studying owls. Passive acoustic surveys using ARUs have been found to be useful for surveying rare and elusive species (Holmes et al. 2014, 2015; Campos-Cerqueira & Aide 2016) and for conducting nocturnal surveys for species such as owls (Rognan et al. 2012). An important benefit of using ARUs for nocturnal owl surveys is that the units can be set up at any time and left out for extended periods. By recording on a set schedule for several days or weeks, this can increase the cumulative detection probability of owls by increasing the number of sampling occasions while still only requiring two visits by field personnel. In this regard, ARUs can reduce the problem of lower detection probabilities of passive surveys and provide data on vocal behaviour and habitat use of owls. For these reasons, using ARUs for passive acoustic surveys appears to be a promising new approach for studying and monitoring owls.

Acoustic datasets collected with ARUs over extended time periods can be large and daunting to process. Automated species recognition of animal vocalizations is changing this. This process involves matching recording segments to a template, often termed a 'recognizer', derived from training data and registering a hit when a similarity threshold is reached. Previous studies have shown that using recognizers can be an effective and efficient tool to process acoustic recordings for birds and amphibians (Buxton & Jones 2012; Frommolt & Tauchert 2014; Taff et al. 2014; Colbert et al. 2015; Holmes et al. 2015; Brauer et al. 2016). We have shown recently that recognizers are highly useful for detecting owls on recordings because of relatively low detection rates of owls from listening to recordings (Shonfield et al. 2018). Owl calls are well-suited to automated species recognition because the calls overlap infrequently with conspecifics (except for some minimal overlap during male-female calling in some species), and very few other species are vocally active at the same time since owls call nocturnally.

There are a few examples in the literature of studies using unsolicited calling behaviour of owls, including Eurasian Eagle-owls *Bubo bubo* (Delgado & Penteriani 2007), Little Owls *Athene noctua* (Zuberogoitia et al. 2008), Tawny Owls *Strix aluco* (Lourenço et al. 2013), and Barred Owls *Strix varia* (Odom & Mennill 2010b). A couple of these studies include descriptions of nightly owl calling patterns (Delgado & Penteriani 2007; Lourenço et al. 2013) but only one study did this over a 24-hr period (Odom & Mennill 2010b).

In this study, we used ARUs to conduct acoustic surveys for owls in northeastern Alberta and processed the recordings using recognizers. We used separate recognizers to identify the calls of three owl species found throughout Canada and the United States: the Barred Owl (*Strix varia*), the Boreal Owl (*Aegolius funereus*), and the Great Horned Owl (*Bubo virginianus*). Our objectives were to document unsolicited vocal behaviour of these species, evaluate owl habitat use, and compare the results from our passive acoustic surveys to accounts of vocal behaviour and habitat use of these owl species in the peer-reviewed literature.

Methods

Study Area

We surveyed for owls in upland forested areas in northeastern Alberta, Canada. Sites were located within an area south of Fort McMurray, north of Lac la Biche and northwest of Cold Lake (see Shonfield & Bayne 2017b for additional details on study area). Forests in the study area were primarily composed of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) trees.

Acoustic Surveys

We conducted passive acoustic surveys for owls using a commercially available ARU: the SM2+ Song Meter (Wildlife Acoustics Inc., Maynard, Massachusetts, USA). We programmed each ARU to record in stereo format at 44.1 kHz with a 16-bit resolution. We tested each ARU and both microphones prior to deployment to identify any units with non-responsive channels or degraded microphones. We used gain settings of 48 dB for both the left and right channel microphones. We installed ARUs at each site for approximately two weeks in late winter/early spring, when owls are actively calling (Clark & Anderson 1997; Kissling et al. 2010). We conducted surveys at 54 sites in 2013, in 2014 we surveyed 27 of the same sites and added 18 new sites, and in 2015 we surveyed 35 sites that were surveyed in one or both of the previous two years. In 2013 ARUs were out and recording between 18 March and 18 May, in 2014 ARUs recorded between 21 March and 6 May, and in 2015 ARUs recorded between 24 March and 5 May. We attached ARUs at a height of approximately 1.5 m on trees with a smaller diameter than the width of the ARU (18 cm).

At each site, we deployed five ARUs in a square formation, with one at each corner spaced 1.6 km apart, and one in the center positioned 1.2 km from each corner (hereafter each individual location with an ARU is referred to as an 'ARU station'). The spacing of ARU stations is similar to the spacing of point count stations used in traditional owl surveys with broadcast calls (e.g. Morrell et al. 1991; Kissling et al. 2010). As part of a study looking at the effects of industrial noise on owls, some of the ARUs we deployed were located close to noise sources (e.g. compressor stations) or near roads. We found that owls were not strongly avoiding noise sources or roads (Shonfield & Bayne 2017b), however there were some effects on detection probability of owls, particularly for Boreal Owls. To minimize potential effects of noise masking on the results reported here, we only included ARUs with an estimated relative noise level less than 90 dBA (see Shonfield & Bayne 2017b for details on how sound measurements were made from recordings).

Processing Recordings

We used the program Song Scope 4.1.3A (Wildlife Acoustics Inc., Maynard, Massachusetts, USA) to build recognizers to detect owl territorial calls: the two-phrased hoot of the Barred Owl (Odom & Mennill 2010b), the staccato song of the Boreal Owl (Bondrup-Nielsen 1984), and the territorial hoot of the Great Horned Owl (Kinstler 2009). Song Scope uses hidden Markov models to match recording segments to a recognizer template derived from training data and registers a hit when a similarity threshold is met (Wildlife Acoustics 2011). For each detected vocalization, Song Scope provides two values: a quality value (between 0.0 and 99.9) that indicates where the vocalization fits within a statistical distribution of parameters from the training data used to build the recognizer, and a score value (between 0.00 and 99.99) indicating the statistical fit of the vocalization to the recognizer model (Wildlife Acoustics 2011). A minimum quality and minimum score threshold are set by the user each time a recognizer scans a set of acoustic data. Based on our previous work with these recognizers (Shonfield et al. 2018) we used a minimum quality setting of 50 and a minimum score setting of 60 when scanning recordings. See Shonfield et al. (2018) for further details on how we built these recognizers in Song Scope and their overall performance.

The results from each recognizer had a number of false positives (i.e. hits that were not the target owl species), so trained observers verified all hits generated by the program before compiling the data. After removing stations with an estimated relative noise level greater or equal to 90 dBA, we compiled data from 236 ARUs deployed in 2013, 191 ARUs deployed in 2014, and 150 ARUs deployed in 2015. We calculated the number of 10-min recordings with an owl calling for each hour of the day to obtain an estimate of vocal activity across a 24-hr period for each species. In addition, we calculated the time to sunrise and sunset for each recording with an owl calling based on the longitude and latitude of the ARU station and the date of the recording. We binned the data by hour relative to sunrise and sunset times to summarize the vocal activity data and quantify how often owls call in daylight and darkness, especially since hours of daylight change markedly in our northern study area during the period we surveyed. The range of sunrise times varied from 07:34 hr during the start of our surveys in mid-March, to 04:54 hr in mid-May. Sunset times varied from 19:42 hr at the start of our surveys in mid-March to 21:52 hr in mid-May.

Habitat Use Analysis

We used an occupancy modelling approach to evaluate habitat use by owls. Occupancy modelling uses repeat observations to estimate detectability and account for imperfect detection when estimating the probability of a species occupying a site or patch (MacKenzie et al. 2002). To build our models to evaluate habitat use, we first extracted variables on forest composition, forest age, and human disturbance in ArcGIS 10.3.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA). We used an 800-m radius buffer around each ARU station, approximating the maximum detection radius of an ARU to detect owls calling (Yip et al. 2017). For forest composition, we calculated the proportion of coniferous forest present weighted by area from the Alberta Vegetation Inventory (AVI) within each 800-m buffer. We also calculated mean forest age weighted by area from the AVI layer. For human disturbance, we calculated the proportion of human footprint in the buffer area from Alberta Biodiversity Monitoring Institute's Human Footprint layer 2012 version 3 (http://www.abmi.ca/home/data-analytics). Disturbances in this layer include linear features (roads, seismic lines, pipelines, transmission lines and railways), industrial and resource extraction features (well pads, compressor stations, processing plants, mines and other facilities), and forest cut blocks.

To analyze habitat use we only used unique ARU locations with an estimated relative noise level less than 90 dBA. Given these criteria, we included 236 stations surveyed in 2013 and 74 stations surveyed in 2014 in this analysis. We compiled detection histories for each ARU station from the presence/absence data for each owl species derived from the recognizers. We defined each 'sampling occasion' in our detection history as a 24-hr period (a total of 24 ten-min recordings processed by the recognizers). We had a total of nine sampling occasions in our detection history because ARUs were deployed for a minimum of nine days. Stations with ARUs that failed at some point during the deployment (n = 5) and did not record for all nine days were indicated in the detection history as 'missing observations' on days that they did not record. An advantage of occupancy modeling is that it can account for 'missing observations' (MacKenzie et al. 2002).

Owl occupancy was modeled using 'single species single season' occupancy models (MacKenzie et al. 2002) using the package 'unmarked' (Fiske & Chandler 2011) in R version 3.4.3 (R Core Team 2017) with RStudio version 1.1.383 (RStudio Team 2017). We ran models with proportion coniferous forest, proportion disturbed by humans, and mean forest age as continuous predictor variables for the occupancy parameter to evaluate habitat use by owls. For Barred Owls, we included a quadratic term for proportion coniferous forest, since previous research indicates they prefer mixedwood forests (Mazur et al. 1998; Livezey 2007; Russell 2008). For Boreal Owls and Great Horned Owls, we did not include a quadratic term for proportion coniferous forest since Boreal Owls prefer coniferous forests (Hayward et al. 1993; Lane et al. 2001) and Great Horned Owls are found in a wide variety of forest types (Johnsgard 2002). We included Julian date as a predictor variable for the detection probability parameter, as the probability of detecting owls calling could change as the breeding season progresses. In the occupancy modelling literature, time of day is often included as a survey-specific variable in the detection parameter to account for differences in detectability at different times of day. We did not include time of day in our models because we surveyed during all hours and then pooled the detections on a daily basis for this analysis. Since owls are unlikely to be found consistently within the area around a single ARU station due to movement, and the same owl could be found at more than one station within a site on different sampling occasions, the occupancy estimates from these models should be interpreted as an estimate of owl 'use' (MacKenzie 2006).

We included a null model (with no variables), a global model (with all variables), and models fitted for all possible combinations of variables (proportion coniferous, proportion disturbed, forest age, and Julian date) without interactions. We used an information-theoretic approach (Burnham & Anderson 2002) for model selection. We ranked models using Akaike's Information Criteria (AIC), and made model-averaged predictions using the R package 'MuMIn' (Barton 2017). Model averaging of top models can be a robust method to obtain parameter estimates and predictions, and is recommended when the weight of the top model is less than 0.9 (Grueber et al. 2011). Models within 2 ΔAIC were chosen as the top model set for model averaging (Burnham & Anderson 2002).

Figure 1 - Daily vocal activity (estimated by the number of recordings with an owl calling) for Barred Owls (BADO), Boreal Owls (BOOW), and Great Horned Owls (GHOW). Hours are using the 24-hr clock, with the zero hour being midnight. The vertical dashed lines indicate the range of sunrise and sunset times during the survey period.

Figura 1 - Atividade vocal diária (estimada a partir do número de gravações contendo rapinas noturnas a vocalizar) para coruja-barrada (BADO), mocho-funéreo (BOOW) e bufo-real-americano (GHOW). As horas seguiram o formato de relógio de 24 horas, com a hora zero sendo a meia-noite. As linhas tracejadas verticais indicam o intervalo de horas do nascer do sol e do ocaso durante o período da monitorização.

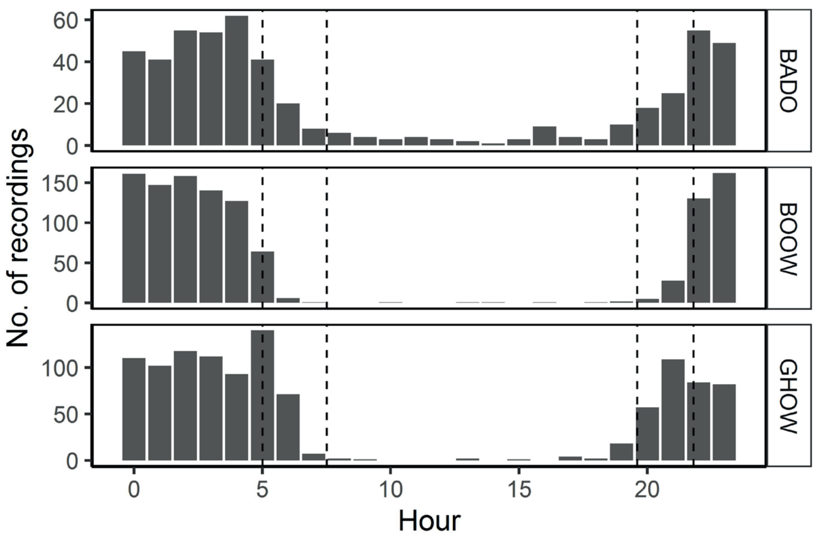
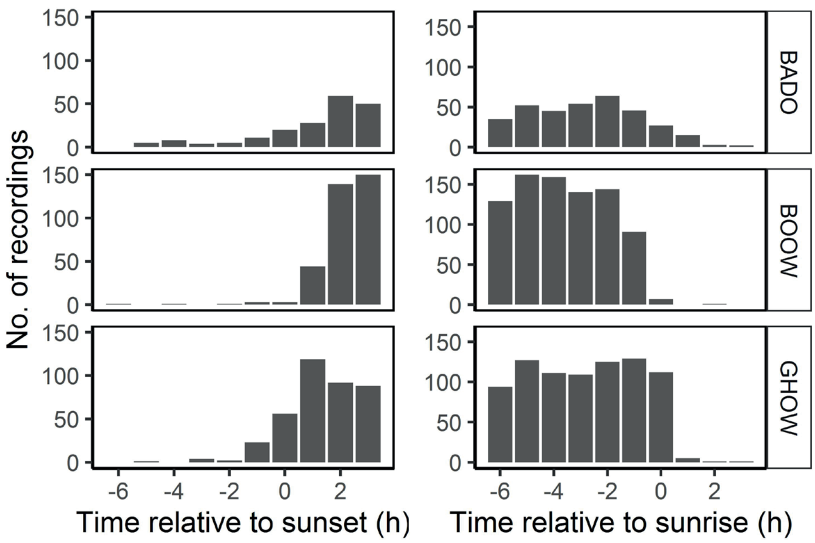


Figure 2 - Daily vocal activity (estimated by the number of recordings with an owl calling) relative to sunset and sunrise times for Barred Owls (BADO), Boreal Owls (BOOW), and Great Horned Owls (GHOW). Negative numbers indicate hours prior to sunset/sunrise, zero indicates the hour of sunset/sunrise, and positive numbers indicate hours after sunset/sunrise.

Figura 2 - Atividade vocal diária (estimada a partir do número de gravações contendo rapinas noturnas a vocalizar) em relação ao ocaso e nascer do sol para coruja-barrada (BADO), mocho-funéreo (BOOW) e bufo-real-americano (GHOW). Os números negativos indicam horas antes do ocaso/nascer do sol, zero indica a hora do ocaso/nascer do sol e números positivos indicam horas após o ocaso/nascer do sol.



Results

Vocal Activity

Over the three years that we surveyed for owls using ARUs, we collected a very large acoustic dataset: 125,844 10-min recordings in 2013; 84,518 10-min recordings in 2014; and 53,791 10-min recordings in 2015. The recognizers scanned all recordings and detected Barred Owls calling on a cumulative total of 548 recordings over all three years, Boreal Owls were detected calling on 1,178 recordings, and Great Horned Owls were detected calling on 1,202 recordings.

While all three species showed a strong nocturnal pattern in their calling activity, Barred Owls had a tendency to call more during daylight hours than the other two species (Fig. 1). For Barred Owls, 10% of recordings with vocalizations were during daylight hours between 08:00 hr and 19:00 hr. For Great Horned Owls, only 2.5% of recordings with vocalizations were between 08:00 hr and 19:00 hr. Boreal Owls were more strictly nocturnal in their vocal behaviour than the other two species, with only 0.7% of recordings with vocalizations between 08:00 hr and 19:00 hr.

We found there were differences between species in their onset and end of vocal activity around sunset and sunrise. Barred Owls showed a steady increase in the hours before sunset, and a steady decrease in the hours after sunrise (Fig. 2). The other two owl species showed more abrupt changes in vocal activity, for example Boreal Owls rarely vocalized at sunset but showed a marked increase in vocal activity two hours after sunset (Fig. 2). Great Horned Owls on the other hand often called at sunset, and their vocal activity peaked an hour after sunset (Fig. 2). At sunrise Great Horned Owls continued to call frequently, and then an hour after sunrise this activity dropped off markedly, in contrast Boreal Owls decreased their vocal activity an hour before sunrise and then their activity dropped off at sunrise (Fig. 2).

Habitat Use

We surveyed for owls between March 18 and May 18, and included date as a predictor for the detection probability parameter in our occupancy models to evaluate habitat use. We found that date did not have a strong effect on detection of Barred Owls or Great Horned Owls (Figure 3). There was an effect of date on detection probability of Boreal Owls, with later dates leading to greater detection probability for this species (Fig. 3).

Forest composition varied between stations from 0% to 100% coniferous forest with a mean of 50%. Proportion of the area disturbed by humans varied from 0% to 94% with a mean of 18%. For Barred Owls the top model included forest composition and human disturbance as predictor variables for occupancy (Table 1). For Boreal Owls the top model included forest composition as a predictor variable for occupancy, and date as a predictor variable for detection probability (Table 1). For Great Horned Owls the top model was the null model with no predictor variables for occupancy or detection probability (Table 1). Occupancy of stations (hereafter 'use') by Barred Owls was highest when the forest was a mix of deciduous and coniferous trees and declined with increasing disturbance by humans (Fig. 3). Forest composition and human disturbance had no effect on Great Horned Owl habitat use (Fig. 3). There was no effect of human disturbance on use by Boreal Owls, but there was a weak trend for them to use more coniferous forests (Fig. 3).

There was limited variation in forest age at the locations surveyed, mean forest age around each ARU ranged from 21 to 153 yr (overall mean of 93 yr), 97% of stations were surrounded by mature forest (50+ yr old), and 84% of stations were surrounded by old forest (80+ yr old). We found no effect of forest age on owl habitat use for any of the three species (Figure 3).

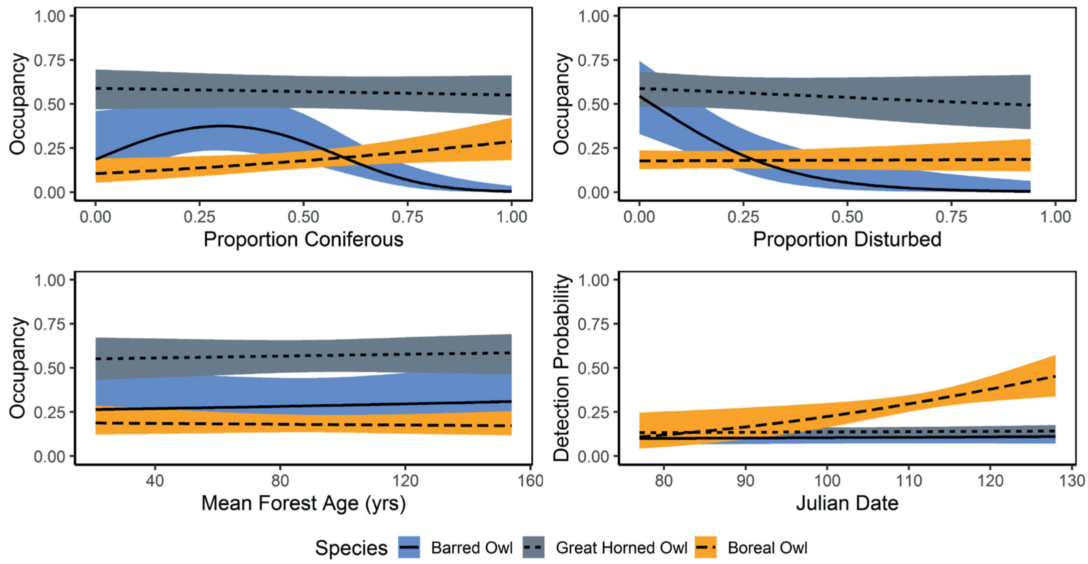
Table 1 - Occupancy models for each of the three owl species. Models are ranked by AIC weights (w_i). K is the number of parameters. We report only those models with strong support ($\Delta AIC \leq 2$) that made up our top model set for each species. Mean forest age (Age), proportion coniferous forest (Con) and proportion of the area disturbed by humans (Dist) were included as predictor variables for the occupancy parameter (Psi). Julian date (Date) was included as a predictor variable for the detection probability parameter (p).

Tabela 1 - Modelos de ocupação para cada uma das três espécies de rapinas noturnas. Os modelos são classificados por pesos de AIC (w_i). K é o número de parâmetros. Reportamos apenas os modelos com forte suporte ($\Delta AIC \leq 2$) que compunham o nosso modelo de topo para cada espécie. A idade média da floresta (Age), a proporção de floresta de coníferas (Con) e a proporção da área afetada pelo homem (Dist) foram incluídas como variáveis preditivas do parâmetro de ocupação (Psi). A data juliana (Date) foi incluída como uma variável preditiva para o parâmetro de probabilidade de deteção (p).

SPECIES	MODEL	K	AIC	ΔAIC	w_i
Barred Owl †	Psi(Con + Con^2 + Dist),p(.)	5	556.57	0.00	0.47
	Psi(Con + Con^2 + Dist),p(Date)	6	557.97	1.40	0.23
	Psi(Age + Con + Con^2 + Dist),p(.)	6	558.26	1.69	0.20
Boreal Owl	Psi(Con),p(Date)	4	844.19	0.00	0.40
	Psi(Age + Con),p(Date)	5	846.02	1.84	0.16
	Psi(Con + Dist),p(Date)	5	846.12	1.93	0.15
Great Horned Owl	Psi(.),p(.)	2	1484.39	0.00	0.17
	Psi(Dist),p(.)	3	1485.11	0.71	0.12
	Psi(.),p(Date)	3	1485.57	1.18	0.09
	Psi(Con + Dist),p(.)	4	1486.01	1.62	0.07
	Psi(Age),p(.)	3	1486.03	1.64	0.07
	Psi(Con),p(.)	3	1486.09	1.70	0.07
	Psi(Dist),p(Date)	4	1486.27	1.88	0.06
	Psi(Age + Dist),p(.)	4	1486.30	1.91	0.06

Figure 3 - Model averaged predictions from occupancy models (models within 2 ΔAIC of the top model; Table 1) for all three owl species. Occupancy estimates are shown as a function of forest composition (proportion coniferous forest), landscape disturbance (proportion of the area disturbed by humans resulting in loss of forest cover), and forest age. Detection probability estimates are shown as a function of Julian date (day 80 is March 21 and day 130 is May 10). The solid or dashed lines are the model averaged predictions, and the grey bands are the 95% confidence intervals.

Figura 3 - Previsões do modelo-médio dos modelos de ocupação (modelos dentro de 2 ΔAIC do modelo de topo; Tabela 1) para as três espécies de rapinas noturnas. As estimativas de ocupação são apresentadas em função da composição da floresta (proporção de floresta de coníferas), alteração da paisagem (proporção da área perturbada pelo homem resultando em perda de cobertura florestal) e idade da floresta. As estimativas de probabilidade de deteção são apresentadas como uma função da data juliana (o dia 80 é 21 de março e o dia 130 é 10 de maio). As linhas contínuas ou tracejadas são as previsões do modelo-médio e as faixas cinzas são os intervalos de confiança de 95%.



DISCUSSION

The vocal activity of these three owl species was predominantly nocturnal; however, there were some differences in vocal activity patterns between species, particularly in the onset and end of vocal activity around sunset and sunrise. Barred Owls were most active at night but called more frequently during daylight hours than the other two species. This is consistent with results of a passive acoustic study on vocal behaviour of Barred Owls that found they called throughout the day, though they were more vocally active at night with the peak from 02:00 hr to 05:00 hr (Odom & Mennill 2010b). We similarly found that Barred Owl vocal activity peaked from 02:00 hr to 04:00 hr. We also found that Barred Owls showed a more gradual increase in vocal activity in the hours leading up to sunset, and in the hours after sunrise compared to other two owl species that showed more abrupt changes in vocal activity around sunset and sunrise.

Boreal Owls were almost exclusively nocturnal in their calling behaviour, and rarely vocalized during daylight hours. Boreal Owls did not often vocalize in the hour when the sun rose or set, but showed a large increase in vocal activity one and two hours after sunset and prior to sunrise. We could not locate any published accounts of the daily vocal activity patterns of Boreal Owls obtained from passive acoustic surveys. A study on Boreal Owl vocalization behaviour in Wyoming using call-broadcast surveys found that they were most vocal within the first hour after sunset (Clark & Anderson 1997). We noted some vocal activity in the first hour after sunset, but much greater activity two hours after sunset. Our results suggest if conducting passive surveys, it would be preferable to survey for Boreal Owls starting 2 hours after sunset.

Vocal activity of Great Horned Owls was mostly nocturnal, and they only infrequently called during daylight hours. Onset and end of vocal activity for Great Horned Owls appeared to be timed with when the sun set and rose, and they did not vocalize very often in the hour prior to sunset or in the hour after sunrise. There appear to be no published accounts of the daily vocal activity patterns of Great Horned Owls obtained from passive acoustic surveys. A study using broadcast calls for Great Horned Owls in Pennsylvania, found their vocal activity peaked from 0:00 hr to 02:00 hr (Morrell et al. 1991). We found that the vocal activity of Great Horned Owls was high during this period, but was also high throughout the night and that passive surveys for Great Horned Owls could occur anytime from an hour after sunset to sunrise.

Understanding vocal activity patterns of owls is important because many monitoring and research projects rely on detecting the vocalizations of owls to collect data on presence or absence of owl species and to provide insight on their habitat use. Based on our results, we would suggest that the optimal survey time for these three owl species is between an hour after sunset to an hour before sunrise. Studies that have collected data using acoustic surveys (either with or without a broadcast call) on one or more of the three owl species we studied, typically start either at sunset (Laidig & Dobkin 1995; Clark & Anderson 1997), or a half-hour or an hour after sunset (Lane et al. 2001; Grossman et al. 2008; Kissling et al. 2010; Munro et al. 2016) and end anywhere from 5 hours after sunset to sunrise. Thus, our recommendation is not very different from the survey times that owl researchers are already using. But seeing as there are so few published accounts with detailed descriptions of owl daily vocal activity patterns, and even fewer based on passive acoustic surveys, we believe the information provided here will be useful as justification for the methods of future owl research projects.

In addition to understanding daily vocal activity patterns of these owls, it is also important to understand seasonal vocal activity patterns. While it was not one of our objectives to document vocalization behaviour across the breeding season, we did include date as a variable for the detection probability parameter in our occupancy models to evaluate habitat use. We sampled within a date range that we believed would correspond to when these owls were most vocally active, and this assumption was supported by studies using a similar range of dates for surveys of these owl species in the boreal forest (Bondrup-Nielsen 1984; Clark & Anderson 1997; Grossman et al. 2008). We found no effect of date on the detection probability of Barred Owls and Great Horned Owls, suggesting that this range of dates was within the period when these species are vocally active. For Boreal Owls, we found a higher detection probability with later dates, suggesting that surveys for this species could be more effective if they occurred in the second half of our survey period (from April into May). More research using ARUs is needed to know when in the season vocalizations taper off for these three owl species.

The forest composition of locations we surveyed varied in the amount of deciduous and coniferous forest, and varied in how disturbed they were by humans. Results from telemetry studies of Barred Owls in northern Alberta and northern Saskatchewan suggest they prefer older mixedwood forests in the northern boreal forest (Mazur et al. 1998; Russell 2008). A study in northern Alberta using call-broadcast surveys found that Barred Owls were most likely to occur in landscapes with >66% forest cover (Grossman et al. 2008). We did not find an effect of forest age, but we suspect this was due to the fact that most locations surveyed were in mature forest. Similar to previous studies using telemetry or call-broadcast methods, the results from our passive acoustic surveys are in support of Barred Owls preferring mature mixedwood forests, and suggest they are sensitive to human disturbance that results in the loss of forest cover.

Great Horned Owls are considered a generalist species and are found in a wide range of habitats throughout North America (Johnsgard 2002; Bennett & Bloom 2005). We found that Great Horned Owls were equally likely to use all habitats we surveyed, and that forest composition, forest age and human disturbance had no effect on their habitat use. Similarly, a study in New Jersey, USA, found that Great Horned Owls were not associated with any particular habitat type (Laidig & Dobkin 1995). Great Horned Owls may be more tolerant to disturbance, as they are often associated with heterogeneous landscapes. A previous study found Great Horned Owls were prevalent in landscapes with intermediate levels of forest cover (Grossman et al 2008). Our results are in support of Great Horned Owls being habitat generalists and relatively tolerant to human disturbance.

We found a weak trend for Boreal Owls to use areas with more coniferous trees, but no effect of forest age, and no effect of human disturbance on probability of habitat use. Long-term studies of Boreal Owls in Finland have established this owl to be closely associated with old-coniferous forests (Korpimäki and Hakkarainen 2012). A study tracking Boreal Owls with telemetry found they inhabit mixed-conifer, spruce-fir and Douglas fir forests in Idaho, western Montana, and northwestern Wyoming (Hayward et al 1993). Another study using passive acoustic surveys in Minnesota found Boreal Owls used older mixedwood forests (Lane et al 2001). Not many studies have examined the effects of disturbance on Boreal Owls, but one study using telemetry and call-broadcast surveys found sites occupied by Boreal Owls contained a greater proportion of disturbed areas (clearcuts, forest stands with silviculture treatments, and forest stands with wind or insect mortality) than unoccupied sites (Munro et al. 2016).

We found that using new bioacoustics tools, ARUs in combination with recognizers, was effective in surveying for owls to obtain data on vocal behaviour and habitat use. These tools allowed us to efficiently conduct passive surveys for three owl species, and this approach is likely to be useful for studying many other owl species that vocalize frequently. One of the benefits of this approach is that it is less invasive and requires less time in the field compared to studies using telemetry or call-broadcast survey methods. This research contributes to our understanding of the vocal behaviour of these owls, and can serve to inform owl researchers designing survey protocols.

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