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Use of hedgerows by mammals in an intensive agricultural landscape

C. Pelletier-Guittier[a,b,*], J. Théau[a,b], J. Dupras[b,c]

[a] Department of Applied Geomatics, Université de Sherbrooke, 2500 boul. de l'Université, Sherbrooke, QC, Canada
[b] Québec Center for Biodiversity Science (QCBS), 1205 Avenue du Docteur-Penfield, Montréal, QC, Canada
[c] Department of Natural Sciences, Université du Québec en Outaouais, 58 rue Principale, Ripon, QC, Canada

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ABSTRACT

Agricultural intensification causes habitat modification, sometimes leading to habitat loss and subsequent loss of connectivity. Remaining species in these agriculture-dominated landscapes often use hedgerows, such as windbreaks or riparian strips, as movement corridors or even as habitats. However, the understanding of the use of these hedgerows by mammals is limited and could be improved with the use of high-resolution remote sensing data, which are unbiased, detailed and repeatable. The aim of this study was to assess the attributes that affect medium- and large-sized mammals' use of hedgerows, with *in situ* and remotely sensed data (including LiDAR and multispectral images) in an agriculture-dominated landscape in southern Québec. Twenty-three hedgerows were selected and characterized with both field surveys and remote sensing analyses, like LiDAR metrics and vegetation indices. Wildlife frequentation of each hedgerow was measured using camera traps, from late spring to early fall in 2018. 431 mammal detections were obtained among all 23 hedgerows. From this, seven species were recorded, all of them opportunistic and well adapted to agricultural environment. Results showed significant differences in mammal use of hedgerows. Coefficients of the better-ranked models based on AICc indicated a positive relationship between hedgerow length and their use by mammals, and a negative relationship with the hedgerow width. Hedgerow use by mammals also increased as tree cover and understory density increased, and as human disturbance decreased. These results characterized for the first time the variables influencing hedgerow use by a broad set of medium- and large-sized mammal species and confirmed their use as movement corridors and/or habitat. This study also confirmed the complementary usefulness of variables derived from remote sensing combined with field data. The low explanatory power of variables often cited in the literature (e.g. NDVI, gappiness) also highlights the need to further explore their specific influence on mammals. The information provided by this study supports the beneficial role played by hedgerows for wildlife conservation in intensive agricultural landscapes. Management guidelines are provided as well as future research avenues.

1. Introduction

In the past century, the rate of landscape changes has accelerated considerably due to rapid population growth and rising food demand (Firbank et al., 2008). The vast majority of small farm owners turned to bigger and specialized monoculture production to increase crop productivity, leading to a boost in the use of fertilizers and the introduction of alien species, controlling competitors, predators and parasites (Firbank et al., 2008; Jobin et al., 2004; Parcerisas and Dupras, 2018; Stoate et al., 2001).

Land clearing is also often a consequence of agriculture intensification, making the landscape more homogenous and largely composed of crops, with only small and scattered forested habitat patches remaining (Albert et al., 2017; Dupras et al., 2016; Tilman et al., 2011). This habitat loss and fragmentation threatens the survival of many wildlife species and is a limiting factor for the distribution of some species (Fahrig, 2003; Soulé, 1991). The natural or semi-natural patches remaining for wildlife include woodlots, wetlands and "linear habitats", such as hedgerows.

These hedgerows (e.g. windbreaks, vegetated ditches, riparian strips) have in common their narrowness, their length and their position separating two agricultural fields (Pasher et al., 2016; Scholefield et al., 2016). Hedgerows can have several origins, including forest remnant, natural growth after clearing for crops or plantation (Dondina et al., 2016), and functions, such as delineating properties, reducing wind velocity, limiting odors from livestock industry or simply for aesthetic

* Corresponding author at: 2500 Boulevard de l'Université, Faculté des Lettres et Sciences Humaines, Département de Géomatique Appliquée, Sherbrooke. J1K 2R1, QC, Canada.

E-mail addresses: camille.pelletier-guittier@usherbrooke.ca (C. Pelletier-Guittier), jerome.theau@usherbrooke.ca (J. Théau), jerome.dupras@uqo.ca (J. Dupras).

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appeal (Baudry et al., 2000; Grala et al., 2010; Novoa, 2014; Tyndall, 2009).

In addition to their functions for humans, hedgerows can also have functions for wildlife, such as habitat or corridors. Indeed, wildlife use of hedgerows has been studied for almost a century (Alexander, 1932), but ecologists have showed an increasing interest since the 1950s and 1960s (Baudry et al., 2000). Since then, hedgerows have been proven to be useful for almost all taxa in agricultural landscapes (Graham et al., 2018). Even though they are usually only a few meters wide, their vegetation composition makes them much closer to a natural habitat than the surrounding crops (Jobin et al., 1996). Small species such as arthropods, amphibians or micromammals are known to use hedgerows as habitat (Gelling et al., 2007; Maisonneuve and Rioux, 2001; Pollard and Holland, 2006). Even larger species like badgers (*Meles meles*), mongooses (*Hestes ichneumon*) and genets (*Genetta genetta*) were found to have strong habitat preference for hedgerows rather than cultivated fields (O'Brien et al., 2016; Pereira and Rodríguez, 2010). On the other hand, even if they do not meet the year-long needs of large wildlife (Hilty and Merenlender, 2004), they are known to bring a structural and functional connectivity between habitat patches, thereby facilitating fauna dispersal (Dondina et al., 2016; O'Brien et al., 2016; Šálek et al., 2009; Tischendorf et al., 1998). This distinction in hedgerow use (corridor vs. habitat) is not only driven by species size, but also by ecological needs. Specialist species have high requirements, often associated with more intact habitat, while generalist species have a greater adaptability (Devictor et al., 2008). For instance, the American red squirrel (*Tamiasciurus hudsonicus*), a specialist species, can mostly be found in mixedwood forests, whereas the Eastern grey squirrel (*Sciurus carolinensis*) can be found in urban, rural and forested environments (Prescott and Richard, 2014). Some generalist species even use the agricultural matrix as part of their habitat, to feed on the crops for example (Delger et al., 2011).

Even though hedgerows are now recognized as wildlife habitat and part of ecological networks (Baudry et al., 2000), in practice their use by fauna is highly uneven, both in diversity and abundance (Dondina et al., 2016; Šálek et al., 2009; Silva and Prince, 2008). Each hedgerow and its surrounding landscape has their unique attributes, affecting the hedgerow's quality as corridor or suitable habitat. Graham et al. (2018) made a review of hedgerow attributes' effects on wildlife habitat provision in the UK and found that height, width, woody biomass, foliar quality and quantity, and gappiness had an effect on species abundance, survival or fecundity. They also concluded that many attributes need to be considered in hedgerow studies because their relationships with wildlife can be complex (i.e. interdependent, synergistic, multi-directional).

Usually, four categories can be drawn to encompass all attributes affecting wildlife use of hedgerows. The first one is the landscape context, including the availability of forested habitat or landscape connectivity (e.g. dense network of connected hedgerows versus isolated hedgerows) (Graham et al., 2018; Lecq et al., 2017). Secondly, the surface area and volume attributes of the hedgerow (e.g. length, width and height measures) can be strongly correlated to species diversity and abundance (Butet et al., 2006; Gelling et al., 2007; Whittingham et al., 2009). This category is probably the one most commonly used to describe the presence of fauna in hedgerows (Graham et al., 2018), equally with the third category, the vegetation characteristics. This can include the type of stand (deciduous, coniferous and mixed), the plant biomass, the presence of gaps in the vegetation or the presence of certain species. For example, Haigh et al. (2012) found that European hedgehogs (*Erinaceus europaeus*) nesting in hedgerows preferred those dominated by *Rubus fruticosus*, a prickly species that is avoided by the hedgehog predators. Finally, some descriptive attributes like the presence of water or the level of human disturbance can also affect the wildlife use of hedgerows. For instance, hedgerows with low human disturbance showed better conservation value for two carnivore species in southern Spain (Pereira and Rodríguez, 2010).

Many studies performed field surveys to obtain these hedgerow attributes (e.g. Deschênes et al., 2003; Morrison et al., 2017), which can be time consuming and limited by the area covered and the sampling design (Huber et al., 2016). However, many attributes can be obtained from remotely sensed data (Betbeder et al., 2014; Vannier and Hubert-Moy, 2014; Wilson et al., 2017). Several technologies are increasingly being used to help describe wildlife habitat, such as high spatial resolution LiDAR data and satellite imagery. LiDAR is widely used to get information about vegetation structure, which is a valuable indicator of both floral and faunal species diversity (Zellweger et al., 2017). Satellite imagery is also used for wildlife habitat description, and it has undergone major improvements in the last few decades. A wide range of sensors now offer images with spatial resolutions of less than 2 m and temporal resolutions close to one day (He et al., 2015). Common use of high-resolution images are vegetation indices, mostly based on visible and near-infrared domains, such as the Normalized Difference Vegetation Index (NDVI). These indices allow to estimate vegetation productivity (health and biomass) (Pettorelli et al., 2011), a good indicator of habitat quality. These two technologies are often underutilised in ecological studies, partly because of their high logistical requirements (i.e. qualified staff, hardware and software) (He et al., 2015; Pettorelli et al., 2014). The few hedgerow studies that used remotely sensed data showed their important complementary value to field data (Betbeder et al., 2015; Dufour et al., 2013; Pasher et al., 2016; Sullivan et al., 2017; Vannier and Hubert-Moy, 2014).

Few studies focused on hedgerows in agricultural landscapes, compared to their adjacent forest patches, even though theses structures can be critical for several species (Gelling et al., 2007; Hinsley and Bellamy, 2000). Moreover, hedgerow's attributes are rarely studied, especially using remote sensing, providing no clear guidelines to land managers regarding conservation practices. Knowledge on these agricultural features is needed and could be improved with additional research and the use of remotely sensed data (Vannier and Hubert-Moy, 2014).

In this study, we assessed the attributes that affect medium- to large-sized mammals' use of hedgerows, in an agricultural landscape in southern Québec (Canada). Unlike most hedgerow studies that focus on a single species or on groups of closely-related taxa (Betbeder et al., 2015; Pereira and Rodríguez, 2010), we chose to focus on a broader set of species, encompassing several functional groups with different requirements. While many have a high dispersion ability (Naughton, 2012), some species are generalists and could use the hedgerows as habitat and/or as corridors, whereas other species are forest specialists and would use them exclusively as corridors or simply avoid them (Devictor et al., 2008). However, this study did not analyse the different use of hedgerows as habitat, movement corridors or both. Finally, we also tested the contribution of remotely sensed attributes to explain the variation in hedgerow use by using remote sensing and field surveys to measure different hedgerow attributes.

2. Material and methods

2.1. Study area

We conducted our research on private properties in the regional county municipality (RCM) of Roussillon, in southern Québec, Canada (Fig. 1). The region was selected for its intensive agriculture landscape and the low number of woodlots. Agriculture covers 73 % of the RCM, and the average area occupied by each farm has grown steadily in the past decade as a result of agricultural intensification (MRC de Roussillon, 2019).

Using recent satellite imagery (Google Earth, 2017), twenty-three hedgerows were selected on the RCM territory based on the following criteria: (1) presence of agricultural fields on each side; (2) width > 3 m; (3) length > 300 m; and (4) relatively homogenous vegetation. Sampled hedgerows averaged 7 m (4–16 ± 3 SD) and 662 m

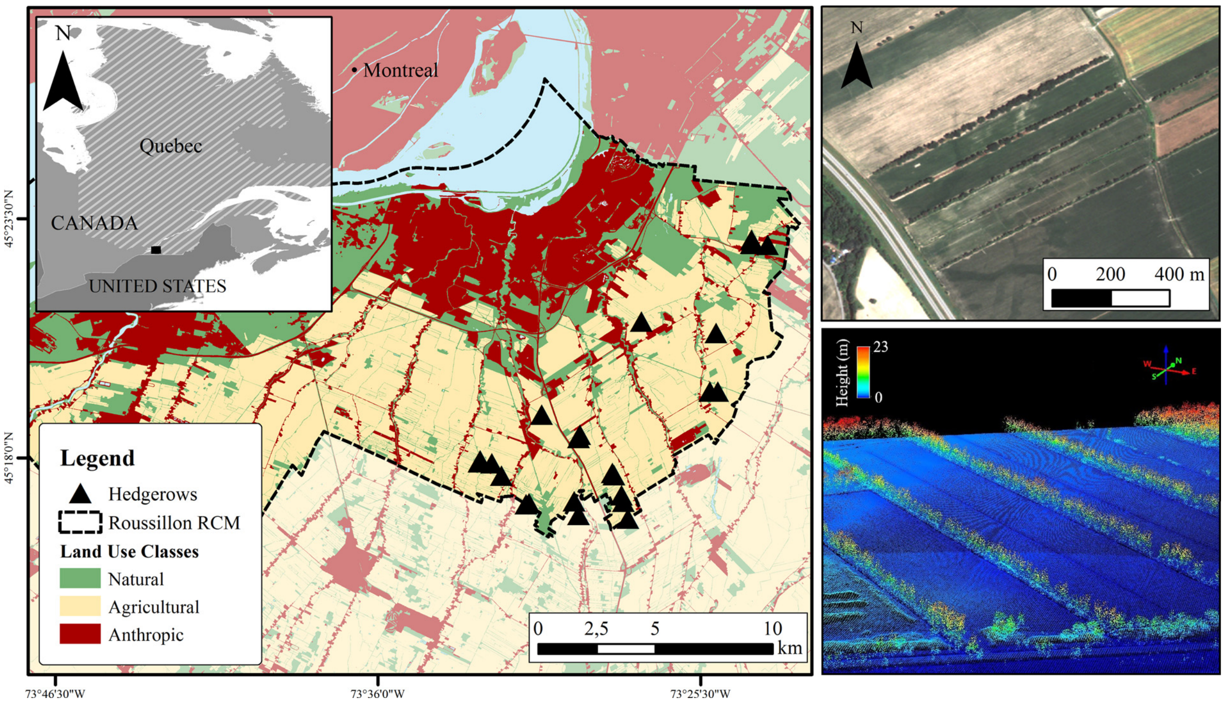

Fig. 1. Location of the study area in the Regional County Municipality (RCM) of Roussillon and selected hedgerows (left). Examples of hedgerows located in the Pleiades-1B multispectral image (top right) and in the LiDAR point cloud (bottom right) used in this study.

(302–1268 ± 309 SD) in width and length, respectively. The crops adjacent to the hedgerows were mostly grains and cereals, but some were vegetables. A majority of the hedgerows were natural (17/23) and the rest were planted (6/23). Most of them ran along drainage ditches, as the law prescribe that a "strip of vegetation at least 3 m wide, measured from the high-water mark, is preserved" (Environment Quality Act, Q-2, r. 35). They also defined current property lines or subdivided parcels with different crops.

2.2. Mammal data collection

Hedgerow use by medium- to large-sized mammals was surveyed using SpyPoint Force 10 infrared-triggered camera traps (GG Telecom, Québec, Canada). Only one camera model was used to avoid differential detection bias (Trolliet et al., 2014). One camera was placed at mid-length of each hedgerow and was attached to an iron post or secured to vegetation so that the infrared beam was set at a height of 0.65 m, as in Meek et al. (2016). Cameras were installed with a 30° angle so they could capture the animals passing through that side of the hedgerow (Fig. 2). They were set to take two pictures per detection to minimize the chances of missing a moving animal (Grift and Ree, 2015).

Hedgerow sampling was conducted over 18 weeks in 2018, from late spring to early fall (May to September). Each hedgerow was monitored for three consecutive weeks in late spring, mid-summer and late summer. This timing was selected so as to include movements from the most active periods of the year for most of our studied species (Naughton, 2012; Prescott and Richard, 2014) and to reduce seasonality biases, which are known to affect the movement behaviours of many species (Vright et al., 1989). The pictures were thoroughly checked to count detections and to identify them at the species level. To segregate independent detections of the same species, individuals detected within a period of 30 min were counted as one (O'Connor et al., 2017; Si et al., 2014).

Fig. 2. Camera-trap disposition in a hedgerow (dashed line). Cameras (black square) were placed at the mid-length of the hedgerow, at a height of 0.65 m and at a 30° angle (dotted line). The background is a pansharpened subset of the Pleiades-1B image used in this study.

2.3. Hedgerow attributes

2.3.1. LiDAR

Discrete-return airborne laser scanning data was acquired in 2017 in leaf-off conditions with horizontal and vertical precisions of 0.15 m. The pulse density was 2 pts/m^2 with a footprint of 0.35 m. The data was already classified into ground and nonground returns, thus the ground class was used to normalize the points elevation to height above ground level. All the processing of point cloud data was made using FUSION (McGaughey, 2018) software packages. Based on the existing literature, five metrics were derived from the LiDAR point cloud: canopy height, structural complexity, canopy cover, gappiness and understory density (see Table 2 for more details) (Davies and Asner, 2014). In ecological studies, these metrics are commonly related to biodiversity and abundance. For example, the canopy height, canopy cover and structural complexity metrics are commonly used with a range of taxa in forested habitat (Davies and Asner, 2014; Flaherty et al., 2014; Melin et al., 2018; Tweedy et al., 2019; Zellweger et al., 2016) but were not previously studied in hedgerows. Their ability to capture vegetation structure was then tested in this particular vegetation configuration. The other two metrics calculated, the gappiness and the understory density, were chosen because of their ability to capture the unique habitat characteristics of hedgerows. The gappiness in vegetation provides information about a hedgerow's continuity, which could affect the animals' movements (Dondina et al., 2016; Gelling et al., 2007; Graham et al., 2018), while the density of the understory vegetation could affect cover, visibility, concealment and resources, such as prey abundance (Dondina et al., 2016; Maisonneuve and Rioux, 2001; Olsoy et al., 2015; Schuttler et al., 2017). Each of these five LiDAR metrics was calculated to obtain a single value for each hedgerow.

2.3.2. Satellite

The multispectral image (Pleiades-1B) was acquired in July 2018, when vegetation is at its peak. This sensor has a very high spatial resolution of 2 m and 0.5 m for multispectral and panchromatic bands, respectively. All the spectral bands were acquired (near infrared: 750 − 950 nm, red: 600 − 720 nm, green: 490 − 610 nm, blue: 430 − 550 nm, panchromatic: 480 − 830 nm). Preprocessing of the image consisted of radiometric corrections, which included normalizing the solar illumination conditions according to the sensor settings and time of acquisition. The following five vegetation indices were calculated (Table 1) and averaged for each hedgerow: NDVI, Modified Soil Adjusted Vegetation Index 2 (MSAVI2), Atmospherically Resistant Vegetation Index (ARVI), Enhanced Vegetation Index 2 (EVI2) and Green NDVI (GNDVI) (see Table 2 for more details). These indices were chosen for their correlation with the quantity and health of the vegetation (Eckert, 2012; Santos et al., 2016; Sarker and Nichol, 2011; St-Louis et al., 2009; Yang et al., 2017), which is a good proxy for habitat quality (Hurlbert and Haskell, 2003; Zellweger et al., 2013). More particularly, a high and healthy plant biomass supports a greater species diversity and abundance by providing food, shelter and habitat (Hurlbert and Haskell, 2003; Pettorelli et al., 2011). In addition to these five vegetation indices, their individual coefficients of variation were calculated to provide information about the vegetation heterogeneity, which usually affects species diversity and abundance (Duro et al., 2014; Rocchini et al., 2010). The proportion of pixels with NDVI values above 0.6 was also calculated for the hedgerows to capture the amount of lush vegetation (i.e. very dense and healthy vegetation), which could affect mammals in terms of diversity, abundance, body mass or even migration (Oindo and Skidmore, 2002; Pettorelli et al., 2011; Weier and Herring, 2010). Finally, the Pleiades image was pansharpened and used to measure the width and length of the hedgerows.

2.3.3. Land cover

A recent land cover map produced by the *Ministère de l'Environnement et de la Lutte contre les changements climatiques* was used to obtain some landscape attributes (Bentrup, 2008; ECCC and MDDELCC, 2018; Yaap et al., 2016). This layer is derived from several existing layers focused on agriculture, hydrological features, wetlands, forests and roads, and is also implemented by photo-interpretation (ECCC and MDDELCC, 2018). The availability of forested habitat surrounding the hedgerows and the connectivity were both derived from this land cover map (see Table 2).

Table 1
Vegetation indices selected in this study.

Indices	Formula	Author
ARVI	$\frac{\rho_{nir} - (\rho_{red} - \gamma(\rho_{blue} - \rho_{red}))}{\rho_{nir} + (\rho_{red} - \gamma(\rho_{blue} - \rho_{red}))}$	Kaufman and Tanré (1992)
EVI2	$2.5 * \frac{\rho_{nir} - \rho_{red}}{\rho_{nir} + 2.4 * \rho_{red} + 1}$	Jiang et al. (2007)
GNDVI	$\frac{\rho_{nir} - \rho_{green}}{\rho_{nir} + \rho_{green}}$	Gitelson et al. (1996)
MSAVI2	$\frac{2 * \rho_{nir} + 1 - \sqrt{(2 * \rho_{nir} + 1)^2 - 8 * (\rho_{nir} - \rho_{red})}}{2}$	Qi et al. (1994)
NDVI	$\frac{\rho_{nir} - \rho_{red}}{\rho_{nir} + \rho_{red}}$	Rouse et al. (1974)

ρ = spectral reflectance of: nir (near-infrared band), red (red band), green (green band) and blue (blue band); γ = atmospheric correction factor.

2.3.4. Field data

In addition to the geospatial data, other attributes were measured *in situ* during summer 2018. First, hedgerows were assigned a culture intensity class (Boutin and Jobin, 1998; Prevedello and Vieira, 2010) and a human disturbance class (Pereira and Rodríguez, 2010). The presence of water was also noted, as well as the origin of the hedgerow and the type of stand (Dondina et al., 2016; Maisonneuve and Rioux, 2001). The lateral cover (%) in tree, shrub and grass was visually estimated to identify gaps in hedgerows ground vegetation which are known to affect many species (Gelling et al., 2007; Hinsley and Bellamy, 2000; Silva and Prince, 2008). All the attributes used in the analyses as predictors, including *in situ* attributes, are listed and detailed in Table 2.

2.4. Statistical analyses

All of the statistical analyses were made in R (R Core Team, v 3.6.0). The combined mammal species' detections were used, as the detection rates were too low to perform within-species analyses.

Variable collinearity was first examined by constructing a Pearson's correlation matrix and calculating variance inflation factors (VIF), where all covariates were required to have a VIF < 2 (Zuur et al., 2009). When a strong correlation was found ($r^2 > 0,5$; $p < 0.05$), only one variable was kept according to the best ecological knowledge from the literature (see Table 2). All continuous independent variables were standardized using an autoscaling procedure.

Using the R package lme4 (Bates et al., 2015), generalized linear mixed models (GLMM) were used to determine hedgerow attributes that affect mammal abundance, with hedgerows' ID as a random effect. The negative-binomial distribution was used for the models due to overdispersion issues (Lindén and Mäntyniemi, 2011). An offset was also used to account for the reduced proportion of sampled areas in wider hedgerows (Sullivan et al., 2017). A set of nine candidate models were constructed to explain the variability in hedgerow use, based on the results or hypotheses from pertinent studies that describe possible wildlife preferences in hedgerows. The best approximating models were selected using an Akaike Information Criterion corrected for small sample sizes (AICc) selection approach (Burnham and Anderson, 2002), using the R package AICmodavg (Mazerolle, 2019). Models with ΔAICc $\leq$ 2 were considered to be top models, and the calculated Akaike weights (w_i) indicate the relative support of each model (Burnham and Anderson, 2002). Finally, the significance of the fixed effects of the best model was estimated with the package lmerTest (Kuznetsova et al., 2017).

3. Results

3.1. Mammal detections

We caught a total of 431 medium- to large-sized mammals over 1572 trap-days. Seven species of interest were recorded, while bird, domestic animal and arthropod detections were excluded from the analysis. These species represent about two-thirds of the medium- to large-sized mammals that are likely to be present in this particular agricultural landscape (Prescott and Richard, 2014). The detected species were, in descending order, white-tailed deer (*Odocoileus virginianus*) (n = 225), raccoon (*Procyon lotor*) (n = 85), coyote (*Canis latrans*) (n = 64), red fox (*Vulpes vulpes*) (n = 31), stripped skunk (*Mephitis mephitis*) (n = 9), eastern grey squirrel (n = 4) and eastern cottontail (*Sylvilagus floridanus*) (n = 2).

Table 2
Synthesis of all the attributes used as predictors to describe the medium- to large-sized mammals use of hedgerows.

Attributes	Source	Type	Description
Canopy height[1]	LiDAR point cloud	Continuous	Mean canopy height calculated from the 95th percentile
Canopy cover[1]	LiDAR point cloud	Continuous	Mean canopy cover calculated from the percentage of points above 1.37 m
Structural complexity[1]	LiDAR point cloud	Continuous	Mean structural complexity calculated from the standard deviation of the points
Gappiness	LiDAR point cloud	Continuous	Mean gappiness calculated from the percentage of points under 1 m
Understory density	LiDAR point cloud	Continuous	Mean understory cover calculated from the percentage of points between 1 and 3 m
ARVI[1]	Pléiades multispectral image	Continuous	Mean value of the ARVI formula calculated for every pixel in the hedgerow
EVI2[1]	Pléiades multispectral image	Continuous	Mean value of the EVI2 formula calculated for every pixel in the hedgerow
GNDVI[1]	Pléiades multispectral image	Continuous	Mean value of the GNDVI formula calculated for every pixel in the hedgerow
MSAVI2[1]	Pléiades multispectral image	Continuous	Mean value of the MSAVI2 formula calculated for every pixel in the hedgerow
NDVI	Pléiades multispectral image	Continuous	Mean value of the NDVI formula calculated for every pixel in the hedgerow
Coefficient of variation of each vegetation index[1]	Pléiades multispectral image	Continuous	Ratio of the standard deviation of the index to the mean of the index (calculated for the five indices)
Amount of lush vegetation[1]	Pléiades multispectral image	Continuous	Percentage of pixels in the hedgerow with an NDVI value > 0.6
Width	Pléiades multispectral image	Continuous	Mean width of the hedgerow in meters
Length	Pléiades multispectral image	Continuous	Length of the hedgerow in meters
Forested habitat availability	Land cover map	Continuous	Amount of habitat (forest or wetlands) around the hedgerow (ha/10 km^2)
Connectivity[1]	Land cover map	Continuous	Amount of other hedgerows around each hedgerow (ha/10 km^2)
Culture intensity	Field survey	Categorical	(1) Intense: intensive cultures[2] on both sides of the hedgerow, (2) Medium: intensive cultures on one side of the hedgerow, (3) Low: extensive cultures[2] on both sides of the hedgerow
Presence of water	Field survey	Categorical	(1) Presence: a ditch or a stream (2) Absence: no ditch or stream
Origin	Field survey	Categorical	(1) Planted: the trees in the hedgerow were planted in clear rows by the producer, (2) Natural: the hedgerow is a forest remnant or grew naturally
Human disturbance	Field survey	Categorical	(1) High: humans were recorded on camera trap pictures fifteen days or more in the hedgerow, (2) Medium: humans were recorded between one and fifteen days in the hedgerow, (3) Low: Humans were never recorded in the hedgerow
Tree cover	Field survey	Continuous	Percent tree cover estimated visually
Shrub cover[1]	Field survey	Continuous	Percent shrub cover estimated visually
Grass cover[1]	Field survey	Continuous	Percent grass cover estimated visually

[1] Variables removed from the full model after collinearity analysis.
[2] Intense crops included corn, soybean, wheat and vegetables while extensive cultures include pastures and perennial cultures because they are more diverse and undergo fewer treatments (Boutin and Jobin, 1998).

Most detections (81 %) were made at night and all the species detected are common in agroecosystems (Fig. 3). The white-tailed deer was particularly abundant in the hedgerows, representing 52 % of the detections.

Even though all the hedgerows were used by mammals for their movements, 35 % of them (n = 8) had less than 10 detections. In terms of species richness, no hedgerow had detections of all species, but two of them recorded six species. Also, 26 % of the hedgerows only recorded white-tailed deer. On average, each hedgerow had 19 detections and 2.4 species. Image analysis showed that most of the mammals were walking in the hedgerow, although some were eating, sleeping and even having interactions with conspecifics.

3.2. LiDAR metrics and vegetation indices

Four of the five selected LiDAR metrics (canopy height, canopy cover, structural complexity and gappiness) were strongly correlated ($R^2 > 0.6$, p-value < 0.02), given that they were all calculated from the same base dataset. Even if it is possible to keep correlated variables (see Schooler and Zald, 2019), we chose to avoid collinearity issues and following skewed results. Of the four correlated metrics, only the gappiness was used in model creation, as it is more specific to hedgerow-type habitat. The understory cover, which did not have collinearity issues, was also used in the model creation. The vegetation indices derived from the satellite image were also strongly correlated ($R^2 > 0.98$, p-value < < 0.05), as well as their coefficient of variation and the amount of lush vegetation, and so only the NDVI was kept in the analysis for its common use in habitat description (Neumann et al., 2015; Pettorelli et al., 2016, 2011; Vihervaara et al., 2017).

3.3. Explanatory model of wildlife frequentation of hedgerows

The best regression model describing mammal abundance had moderate explanatory power ($R^2 = 0.23$) (Table 3). This model had a high AICc weight which suggests that it is the most parsimonious among the candidate models set (Burnham and Anderson, 2002).

Most of the fixed effects in the best model had a significant effect on the number of mammal detections (P-values were estimated using lmerTest package) (Table 4). This dependant variable is defined as the number of individuals, all species combined, that visited a particular hedgerow during a week (n = 275). The length (Fig. 4A), the tree cover (Fig. 4C) and the understory density (Fig. 4D) had a positive effect on the number of mammal detections, while the width (Fig. 4B) had a negative effect. Hedgerows with high human disturbance had significantly lower mammal detections than medium and low disturbance levels (Fig. 4E).

4. Discussion

The purpose of this study was, firstly, to investigate medium- and large-sized mammals' use of hedgerows, secondly, to examine local or landscape attribute effects on hedgerow use, and finally, to test the contribution of remotely sensed attributes in this analysis. This research did provide quantifiable evidence that medium- and large-sized

Fig. 3. Camera trap pictures of the four most-detected species in the studied hedgerows: white-tailed deer (*Odocoileus virginianus*), upper left; coyote (*Canis latrans*), upper right; red fox (*Vulpes vulpes*), bottom left; raccoon (*Procyon lotor*), bottom right.

Table 3
Set of candidate models examining the effect of hedgerow characteristics on the number of medium- to large-sized mammal detections. Models are ranked using Akaike's Information Criterion corrected for small sample size (AICc). The model AICc weight (w_i) is shown with the coefficient of determination (R^2). Hedgerow's ID was included as a random effect in each model.

Candidate models	AICc	w_i	R^2
HD + LT + WD + TC + UD	824	0.85	0.23
CI + FH + GA + HD + OR + TC + WA + WD	828	0.14	0.20
CI + HD + NDVI + WD	835	> 0.01	0.21
Null	836	> 0.01	0.23
GA + LT + NDVI + WD	836	> 0.01	0.24
CI + FH + OR + WA	836	> 0.01	0.21
FH + GA + TC	840	> 0.01	0.22
GA + NDVI + UD	841	> 0.01	0.23
FH + GA + TC + UD + WD	842	> 0.01	0.22
FH + GA + NDVI + WD	842	> 0.01	0.23

CH canopy height, *CI* crop intensity, *HA* habitat availability, *HD* human disturbance, *LT* length, *NDVI* normalized difference vegetation index, *OR* origin of the hedgerow, *ST* stand type, *TC* tree cover, *WA* presence of water, *WD* width.

Table 4
Best abundance model of the use of hedgerows by medium- and large-sized mammals in southern Québec. SE: standard error of estimates. The reference "Human disturbance" level was maximal.

Components (Random effects)	Values	% of variance	P-value
Hedgerows' ID	0.060	6.680	0.253
Residual variance	0.834	93.320	–
Predictors (Fixed effects)	**Estimate**	**SE**	**P-value**
(Intercept)	−2.273	0.354	< 0.001
Tree cover	0.410	0.131	0.002
Length	0.426	0.115	< 0.001
Width	−0.145	0.133	0.276
Understory density	0.072	0.131	0.585
Human disturbance-min	1.252	0.393	0.001
Human disturbance-med	1.677	0.399	< 0.001

mammals in an agricultural context use hedgerows. Seven species were detected in the hedgerows, and they seemed to favor some attributes, both local (from the hedgerows) and from the landscape.

4.1. Mammals use of hedgerows

Species from the Carnivora order (raccoon, coyote, red fox and striped skunk) were quite common, which could be explained by the absence or low density of large carnivores such as bobcats (*Lynx rufus*) or wolves (*Canis lupus*) in our study site. Because the larger species are more vulnerable to extinction in fragmented landscapes, there is often an increase in the number of smaller predators (Crooks and Soulé, 1999; Schuttler et al., 2017). This lack of large carnivores could also explain the abundance of bigger prey, in our case, the white-tailed deer. Another explanation for the high detection number of deer is their adaptation to agricultural landscapes, their diet now largely consisting of corn (Delger et al., 2011). White-tailed deer are the most abundant species of large herbivore in North America (Gonzalez et al., 2013). They play a role in vegetation depredation, transmission of Lyme disease and chronic wasting disease (Clements et al., 2011), and they were the most popular game species in Québec, in 2018 (MFFP, 2018). Information about their movements and habitat preferences is therefore very useful for management practises in this context of overabundance.

Other species, like the grey squirrel and the cottontail were not very common, possibly because camera traps tend to get triggered by larger animals. This could also be a result of the large number of coyotes and red foxes who feed on these two species (Naughton, 2012).

Another aspect identified by the camera trapping was that no forest specialist species, like fishers (*Martes pennanti*), American red squirrels or moose (*Alces alces*) (Naughton, 2012), were captured in the hedgerows. Given that forest patches are very scarce on our study site, the density of these mammals is probably very low or null in some cases. Moreover, even if they are present on the territory, forest specialist species likely do not use hedgerows for their movements because of their higher requirements than generalist species. Their needs in terms

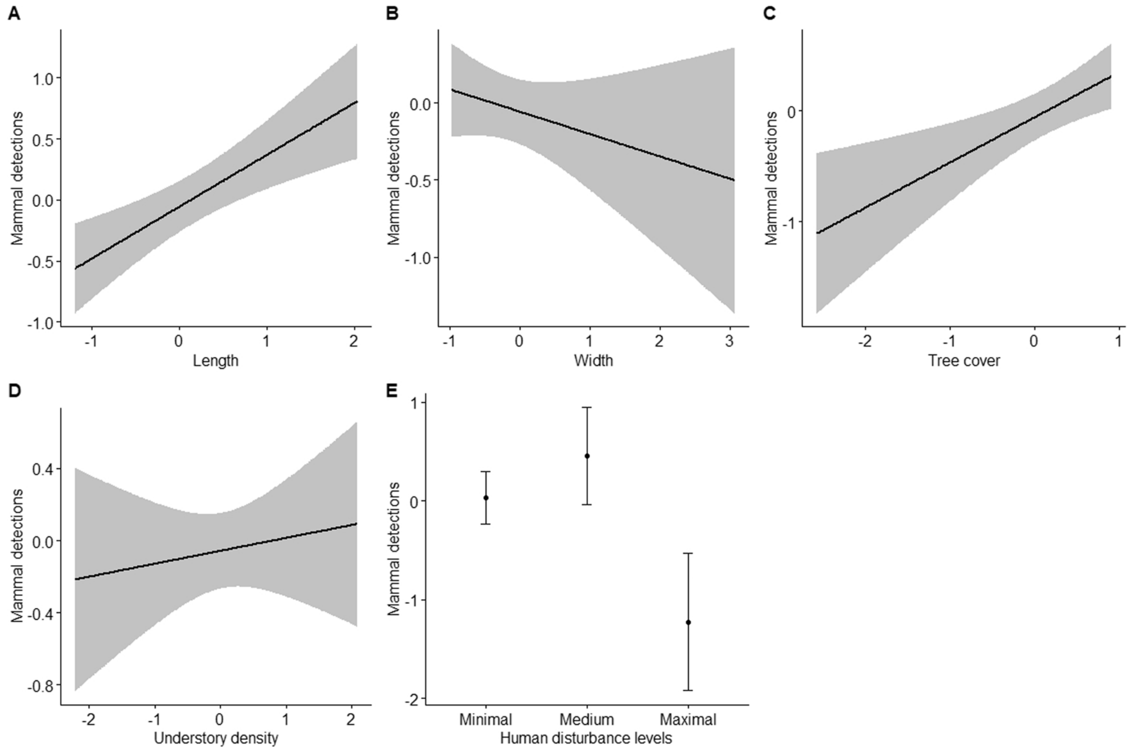

Fig. 4. Relationship between the mammal detections in hedgerows and the A) Length of the hedgerows, B) Width of the hedgerows, C) Tree cover in the hedgerows, D) Understory density in the hedgerows, and E) Human disturbance in the hedgerows among 23 detection sites in southern Québec, 2018. Black lines represent the effect of a variable obtained from our GLMM when all the other independent variables equal their average value. Light grey areas are the 95 % confidence intervals. All continuous predictors are standardised and mammal detections are log-transformed.

of hedgerow dimensions or vegetation cover are probably rarely met. The fisher, for example, prefers old-growth forest with dead trees on the ground (Buskirk and Powell, 1994), which was never seen in the studied hedgerows. Therefore, these results cannot determine if generalist or specialist species use hedgerows as corridors. In this study's context, hedgerows are probably used as habitat by generalist species, although we cannot exclude that they may use them as corridors to some extent.

Furthermore, the fact that the mammals detected in the hedgerows were not only walking or running, but also eating, sleeping and interacting with other conspecifics shows that hedgerows are probably part of a network of resource patches, including forests and crop fields (Hinsley and Bellamy, 2000). Although we have ignored the respective importance of hedgerows compared to forests or crops, these results surely reinforce the importance of hedgerows for medium- and large-sized mammals in our intensive agricultural landscape. It also shows that generalist species can display preferences for some attributes in this kind of environment (Derugin et al., 2016).

4.2. *Effect of hedgerow attributes on mammals' use*

The fauna detected also showed preference patterns in hedgerow use. The best regression model supports that structural attributes of hedgerows are important when describing mammal frequentation (Table 4). Indeed, the length and the width both affected the use of hedgerows, the first positively and the second negatively. Whether hedgerows are used as corridors, habitat, or both, a larger area is often associated with increased abundance and species richness (Červinka et al., 2013; Hilty and Merenlender, 2004; MacArthur and Wilson, 1967; Spackman and Hughes, 1995). Surprisingly, our results suggest, although with a non-significant coefficient, that narrower hedgerows could benefit mammals. Few studies found a negative effect of width on wildlife (Červinka et al., 2013; Sinclair et al., 2005) or even no effect of the width (see the Hazel Dormouse (*Muscardinus avellanarius*) in Dondina et al., 2016; Hilty and Merenlender, 2004). The vast majority of research found a positive effect of the width on animal diversity or abundance (Dondina et al., 2016; Gelling et al., 2007; Hilty et al., 2006; Spackman and Hughes, 1995). The hedgerows under study were all quite similar in terms of width, except for two wider ones. Therefore, it is possible that our small sample size combined with a narrow range of widths could explain the negative (non-significant) effect observed. On the other hand, we found a positive effect of the length of the hedgerow on mammal detections. Long hedgerows are often associated with larger crop fields. Therefore, this effect could be linked to matrix avoidance, in the sense that during longer movements, mammals would look for cover, which can be found in hedgerows. Generalist species, such as white-tailed deer, use crop fields for feeding, but like any prey species, tend to avoid long exposure in open environments (Camp et al., 2013). This positive effect of length could also be explained by our particular location, where forest is so scarce that hedgerows are probably a part of these generalist species' habitat (Butet et al., 2006; Gelling et al., 2007). Thus, a longer hedgerow would mean more habitat available for wildlife. A larger habitat area is also often more complex, meeting more niche requirements and yielding more resources (Weibull and Östman, 2003).

The understory density attribute was also positively correlated with the number of detections, although non-significantly. Because the effect was not significant, it could mean that it favours some species and disadvantages others. The relation between an individual's behaviour and its cover is complex because it is a compromise between visibility and concealment (Camp et al., 2013; Olsoy et al., 2015). Furthermore, an increased understory density could provide more resources (Boutin and Jobin, 1998), but it could also discourage some species to use a hedgerow if the shrubs are prickly (Haigh et al., 2012). These findings also raise the potential implications of hedgerow maintenance practices, which often limit the density of shrubs and saplings by cutting or herbicide spraying (Jobin et al., 2001; Vickery et al., 2009). These changes in vegetation density could thus modify the availability and quality of mammal species' habitats. The tree cover also positively affected the mammal detections in our study. This is consistent with the literature on this subject, usually demonstrating that the more trees there are in a hedgerow, and the bigger they are, the better the habitat (Dondina et al., 2016; Maisonneuve and Rioux, 2001). This can be explained by the stronger resemblance to a forest (Hinsley and Bellamy, 2000).

Finally, our best regression model indicated that human disturbance at its highest level negatively affected the mammal detections in the hedgerows. The hedgerows used as trails by humans, or hedgerows next to "U-Pick" fields were significantly less used than others. Even if some species are more adapted to anthropic landscapes, mammals still display human avoidance behaviours, possibly because they perceive them as potential predators (Gill et al., 1996; Hebblewhite and Merrill, 2008). This avoidance was also found with wolves and weasels (*Mustela nivalis*) towards towns or roads (Červinka et al., 2013; Thurber et al., 1994). Despite the facts that the human presence was strictly during the daytime and that the hedgerow use was higher during the night, they could still avoid these spots due to smell or past encounters (Apfelbach et al., 2005; Hansen et al., 1984).

We should note that an extended period for the camera trap survey, encompassing all the seasons, could lead to new conclusions about the attributes influencing mammals in their hedgerow use. Indeed, mammals can have completely different habitat requirements and preferences during other seasons (Bixler and Gittleman, 2000; Smith, 1991). White-tailed deer are particularly known to change their range between summer and winter to get more vegetation cover, among other factors (Naughton, 2012). Similarly, a larger dataset would allow species-specific analyses, which could lead to species-specific conclusions.

4.3. Contribution of remotely sensed attributes

Three variables derived from remotely sensed data were included in the best performing model: hedgerow length and width, and understory density. Length and width can both be measured using field surveys, but remote sensing allows a faster and easier way to estimate these attributes, while offering the same precision. The understory density is derived from the LiDAR dataset, and even though it could be visually estimated with field work, LiDAR brings a more repeatable, unbiased, and verifiable metric. This could partly explain why the shrub cover estimated during field work was not correlated with this remotely-sensed variable. Our work demonstrates that this technology can help derive new explanatory variables rapidly, and at relatively low cost, to study wildlife habitat use for conservation.

The NDVI (satellite image) was not included in this model, indicating a lower explanatory power compared to the other variables. Several factors could explain this situation. One limitation of NDVI, or of any vegetation index based on near-infrared, is the reflectance saturation in this wavelength when the leaf-area index (LAI) is high (Asrar et al., 1984; Birky, 2001). As many of the studied hedgerows had very dense vegetation (i.e. high LAI), it is possible that the mean values for most of these hedgerows reached a plateau. Also, our satellite image was acquired at mid-summer, when LAI is maximal, further increasing the saturation effect (Wang et al., 2005). Moreover, the assumption that NDVI can help predict wildlife abundance is based on the fact that it provides information about food availability: directly on vegetation resources and indirectly on prey abundance (Owen, 1988; Pettorelli et al., 2011). The NDVI therefore might not necessarily reflect the real food availability for omnivores or carnivores, which represented 44 % of our total detections. According to Pettorelli (2013), the number of studies that found this assumption to be true for mammalian omnivores are fewer than the ones failing to find such a relation, it therefore needs to be further explored.

Regarding the presence of only one LiDAR metric in the final model, the lack of specific knowledge on the relationship between hedgerow structure and large mammals' needs could have lead to a disconnection between the metrics we chose and what mammals actually require (Schooler and Zald, 2019). Indeed, even if the chosen metrics are supposed to capture all the key elements of habitat structure (Davies and Asner, 2014; Graham et al., 2018), most of the studies showing an effect of these structural variables on wildlife were not conducted on our targeted species (Bae et al., 2014; Garcia-Feced et al., 2011; Goetz et al., 2007; Palminteri et al., 2012). Moreover, we chose to keep only two out of five metrics to avoid collinearity issues. This conservative approach possibly accentuated the disconnection between the chosen metrics and the mammals' requirements.

Finally, a single sensor cannot provide information on significant vegetation-related variables for all mammal species. The use of multiple and complementary sensors, as well as field data, is needed to better represent the range of attributes with which to model mammal use of hedgerows (Vogeler and Cohen, 2016).

5. Conclusions

To our knowledge, this study investigated for the first time hedgerow use by all medium- and large-sized mammals likely to use them in a highly intensive agricultural landscape. The results showed the importance of hedgerows for wildlife, with all the studied hedgerows being used as habitat or movement corridors. They also highlight the fact that hedgerow attributes, such as human disturbance, vegetation characteristics and their local structure, can affect their use by mammals, showing that even generalist species display preferences in their use of hedgerows. Both field data and remotely sensed data were important to describe hedgerow use, proving their complementary power. These findings also confirm the benefits of hedgerows for mammal communities in intensive agricultural landscapes. Efforts in these landscapes for wildlife preservation should therefore concentrate on protecting existing hedgerows and/or creating new ones. It should be noted that a large part of the variation in mammal detections in hedgerows remained unexplained by the best model, suggesting that preferences for certain attributes could be species-specific. Further studies regarding the use of hedgerows by wildlife should also investigate the differential use of the agricultural matrix and hedgerows, for example, by using networks of camera traps. Finally, higher sampling sizes will be crucial to better understand the role of hedgerow and landscape attributes on each medium- and large-sized mammal species in intensive agriculture landscapes.

Author contributions

CPG performed the data collection and analysis and wrote the first draft of the manuscript. CPG and JT created the experimental design and the results' interpretation. All authors contributed to manuscript revision and read and approved the submitted version.

Declaration of Competing Interest

None

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