

Integrating Data on Sensory Cues into Habitat Ecology

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Abstract

Integrating sensory information into habitat ecology is key to understanding the mechanisms that link an individual's perception to its use of resources. My objective was to further understanding of the mechanistic links between sensory information, habitat, and resource use and also engage students in sensory ecology by: 1) reviewing knowledge about the acoustic ecology of terrestrial mammals; 2) evaluating how diverse environments influence individual access to visual information; 3) testing hypotheses about the influence of visual habitat properties on selection by mammalian prey; and 4) using remote sensing techniques of estimating visual habitat properties to engage undergraduate students in experiential curriculum advancing their knowledge of sensory ecology and habitat selection by wildlife.

To review knowledge about acoustic ecology of mammals, I conducted a systematic review of published literature indexed in the Web of Science. To contextualize all the information in the review, I created a Signaler-Receiver conceptual framework, which orders reviewed information into factors that influence signalers (mammals that emit sound) and receivers (mammals that receive sound). I also identified gaps in knowledge including a heavy emphasis on highly vocal groups. My review is the first to explicitly detail the breadth of factors influencing acoustic behaviors in terrestrial mammals.

To evaluate visual information accessible to individuals as a function of habitat, I collected terrestrial lidar data in four disparate ecosystems (forest, shrub-steppe, prairie, and desert). Within the resulting point clouds, I conducted viewshed analyses. Ecosystem-specific structure and animal position significantly influenced viewsheds demonstrating that visibility is a spatially dynamic visual property that animals can select for when choosing habitats and may also influence resource use within habitats.

To investigate how visual properties of the environment contribute to habitat use, I evaluated habitat selection by pygmy rabbits (*Brachylagus idahoensis*). At patches used by and available to pygmy rabbits, I estimated visibility (using terrestrial lidar) and concealment (using image classification). I also estimated these properties at microsites where I indexed intensity of use by counting fecal pellet density. Pygmy rabbits selected patches with dense and tall vegetation that was associated with small viewsheds, and did not select for concealment. In contrast, at microsites, pygmy rabbits used microsites near their burrows associated with high concealment. This study illustrates how multiple properties of cover influence selection in nuanced ways.

Finally, I designed and implemented an experiential course for undergraduate students at the University of Idaho focused on research assessing visual properties of wildlife habitat. A majority of the course was spent conducting field work. A key feature of the course was introducing students to lidar. Students reported that field work and lidar activities were the most useful for achieving learning goals.

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Dedication

To my parents and brother - Rick Stein, Diane Stein, and Aaron Stein;
my grandparents - Peggy Chasen, Jay Chasen, Lorrie Stein, and Art Stein;
and my friends, especially Rebecca Schroeder, who have always supported me.

Table of Contents

Abstract	ii
Acknowledgments	iv
Dedication	v
List of Tables.....	ix
List of Figures	xi
Statement of Contribution	xv
General Introduction.....	xvi
References	xviii
 Chapter 1: Acoustic Ecology of Terrestrial Mammals: A New Signaler-Receiver Conceptual Framework.....	
Abstract	1
Introduction	1
Methods	3
Results and Discussion.....	4
General Results.....	4
Signaler-Receiver Conceptual Framework.....	5
Conclusions and Future Directions	16
References	19
 Chapter 2: Vegetation and Vantage Point Influence Visibility Across Diverse Ecosystems: Implications for Animal Ecology	
Abstract	30
Introduction	30
Materials and Methods	34
Study Sites.....	34
Data Collection.....	35
Data Analysis	39
Results	40

Discussion	43
References	48
Chapter 3: Under Cover: The Nuanced Influence of Visual Properties on Resource Selection by Prey	54
Abstract	54
Introduction	54
Methods	57
Study Site	57
Habitat sampling.....	58
Concealment estimation	58
Visibility Data Processing	59
Data Analysis	60
Results	61
Path-level habitat selection.....	61
Intensity of Microsite Use	63
Discussion	65
References	68
Chapter 4: Integration of Lidar Remote Sensing into a Multi-modal Experiential Course	72
Abstract	72
Introduction	72
Course Design	74
Research Project	74
Course Delivery.....	74
Post-Course Survey	77
Results from Student Surveys	77
Discussion	78
References	80

Chapter 5: General Conclusion	83
References	86
Appendix A	87
Complete list of reviewed articles.	87
Figures	106
Appendix B.....	107
Tables	107
Appendix C.....	112
University of Idaho Institutional Animal Care and Use Committee Protocol Approval.....	112
Appendix D	113
University of Idaho Institutional Review Board Protocol Approval	113
Lidar Tutorial – Program R Code.....	114

List of Tables

Table 1-1 Examples of factors that may influence the acoustic ecology of mammalian signalers and/or receivers. Two of the mostly commonly described factors in the reviewed literature within each of the Signaler-Receiver Conceptual Framework categories (Fig. 1-2) are presented along with examples of species influenced by those factors with citations.	7
Table 2-1 Examples of behaviors that are influenced by visibility in animals and humans.....	32
Table 2-2 Viewshed Coefficients Across Ecosystems. Difference in viewshed coefficients (ΔVC) at each eye-height, lower and upper confidence limits (LCL and UCL) for 95% confidence intervals, and associated p-values. Where ΔVC is positive, the ecosystem listed first has a larger average VC. Where ΔVC is negative, the ecosystem listed second has a larger average VC.	42
Table 2-3 Coefficients of Variation Across Ecosystems. Difference in coefficients of variation (Δ Coeff. Var.) at each eye-height, lower and upper confidence limits (LCL and UCL) for 95% confidence intervals, and associated p-values. Where Δ Coeff. Var. is positive, the ecosystem listed first has a larger average coefficient of variation. Where Δ Coeff. Var. is negative, the ecosystem listed second has a larger average coefficient of variation.	43
Table 3-1 Correlations among habitat variables (concealment, viewshed coefficient (VC), and vegetation density (Density)) at the patch and microsite scales in habitats used by pygmy rabbits in the Lemhi Valley, USA. Patch scale correlations are above and microsite correlations below the diagonal. Values within cells represent overall, terrestrial, and aerial orientations from top to bottom, respectively. Asterisks denote p-values (* 0.5-0.001, ** <0.001-0.0001, *** <0.0001)..	62
Table 3-2 Competing models of habitat selection at the patch scale and competing models of microsite use by pygmy rabbits in the Lemhi Valley, USA. Parameters include vegetation density (density), shrub height (height), terrestrial viewshed coefficient (VC_t), terrestrial viewshed coefficient of variation (COV_t), terrestrial concealment (conceal _t), aerial viewshed coefficient (VC_a), aerial viewshed coefficient of variation (COV_a), aerial concealment (conceal _a), and distance to burrow (distance). Table includes AIC, ΔAIC , and AIC weight (w_i). Variables that are bolded are significant with 95% confidence.	63
Table 3-3 Standardized model-averaged estimates of parameters across models of habitat selection at the patch scale by pygmy rabbits in the Lemhi Valley, USA.	63
Table 3-4 Standardized model-averaged estimates of parameters across models of microsite use by pygmy rabbits in the Lemhi Valley, USA.....	64
Table 4-1 Targeted learning outcomes for our course.....	77

Table A.B. 1 The viewshed coefficient (VC) models representing viewshed extent. Viewsheds were measured from eye-heights 0.25-50 m in the forest and 0.25-10 m in the other ecosystems. The viewsheds from the highest eye-heights were removed from all models due to lack of variation. <i>P</i> -values are listed on the right of each estimate (95% confidence).	107
Table A.B. 2 The coefficient of variation models representing viewshed variability. Viewsheds were measured from eye-heights 0.25-50 m in the forest and 0.25-10 m in the other ecosystems. The viewsheds from the highest eye-heights were removed from all models due to lack of variation. <i>P</i> -values are listed on the right of each estimate (95% confidence).	107
Table A.B. 3 Difference in viewshed coefficient estimates (ΔVC) in the forest across eye-heights, 95% confidence intervals and their associated <i>p</i> -values. Where ΔVC is positive, the eye-height listed first has a larger average VC. Where ΔVC is negative, the eye-height listed second has a larger average VC.	108
Table A.B. 4 Differences in viewshed coefficient estimates (ΔVC) in the low structure-ecosystems across eye-heights with 95% confidence intervals and their associated <i>p</i> -values. Where ΔVC is positive, the eye-height listed first has a larger average VC. Where ΔVC is negative, the eye-height listed second has a larger average VC.....	109
Table A.B. 5 Difference in coefficient of variation estimates (Δ Coeff. Var.) in the forest across eye-heights, 95% confidence intervals and their associated <i>p</i> -values. Where Δ Coeff. Var. is positive, the eye-height listed first has a larger average coefficient of variation. Where Δ Coeff. Var. is negative, the eye-height listed second has a larger average coefficient of variation.....	110
Table A.B. 6 Differences in viewshed coefficient estimates (Δ Coeff. Var.) in the low structure-ecosystems across eye-heights with 95% confidence intervals and their associated <i>p</i> -values. The eye-height listed first has a larger average coefficient of variation.....	111

List of Figures

- Figure 1-1 Representation of Metatherian and Eutherian mammalian orders in the 228 papers included in the review. The first two orders are the Metatherian orders (dark bars), all others are Eutherian orders (light bars). Inset images depict examples of members of the four most well-represented groups (left to right): Artiodactyla, Carnivora, Rodentia, and Primates. Only orders in reviewed papers are shown. 4
- Figure 1-2 The Signaler-Receiver Conceptual Framework of acoustic ecology in terrestrial mammals. This framework contextualizes the factors that influence signalers and receivers. We define signalers in this framework as individual mammals producing sound and receivers as individuals that may detect any sound. Factors that influence signalers may affect whether calls are emitted and the acoustic structure of the calls; factors that influence receivers may affect whether the sound is detected and how the receiver responds to the sound. We created broad categories of factors that influence both signalers and receivers: environmental factors, social factors, morphological and physiological factors, state-related factors, and other factors. Arrows indicate how factors within that category can influence signalers and receivers as documented by reviewed papers. For example, environmental factors can influence call emission by and call structure of signalers, and whether receivers detect sound and how they respond. Researchers should note that we may not have encountered examples of every factor relevant to this framework (e.g., although no paper documented it, state-related factors may influence detection of sound by a receiver)..... 6
- Figure 1-3 Examples of adaptations for propagation of sound. A) A generalized sound wave with amplitude on the Y axis and time on the X axis. The frequency of a sound wave is measured as cycles/sec (Hz). Low-frequency sounds generally travel farther than high-frequency sounds. Amplitude is related to ‘loudness’; high-amplitude sounds travel greater distances. Many species that produce long-distance calls, such as the African savannah elephant *Loxodonta africana*, produce calls at low frequencies and high amplitude. B) Repeating call structures such as those produced by multiple species of gibbons (family Hylobatidae) also increase the distance over which calls are propagated. 8
- Figure 1-4 Patterns of vocalization as a function of sociality. Generally, species that are more social have a larger vocal repertoire and vocalize at a higher rate than related, but less social species (solid line). For example, Columbian ground squirrels *Spermophilus columbianus* (A; photo by Thomas Quine licensed under CC BY 2.0) are more social and have a larger repertoire than Uinta ground squirrels *Spermophilus armatus* (B; photo by Jacob W. Frank licensed under CC0 1.0), even though they are closely related (positions are relative; Koepl et al. 1978). This pattern does

- not always hold. In rodents that use the subterranean environment, such as those in the genus *Microtus*, asocial species typically have larger call repertoires to overcome the barriers of communication at a distance underground (dashed line; Giannoni et al. 1997). 11
- Figure 2-1 Conceptual representation of hypothesized relationships between visibility (blue spheres) and habitat structure and perspective. (A and B) Ecosystems with extensive vegetation structure (e.g., forests) will afford smaller viewsheds relative to ecosystems with little structure (e.g., prairies). (C) Animal position within habitat structure will influence viewsheds, with visibility generally increasing with eye-height above the ground. 33
- Figure 2-2 (A) Locations of study sites in the western USA. (B) Forest site at the University of Idaho Experimental Forest near Moscow, ID (red dot). (C) Shrub-steppe site in the Lemhi Valley, ID (green dot). (D) Prairie site at the Dave Skinner Ecological Preserve and Thorn Creek Native Seed Farm near Moscow, ID (yellow dot). (E) Desert site at Gold Butte National Monument in southern NV (blue dot). 34
- Figure 2-3 Method for estimating viewsheds. (A) Terrestrial laser scanner (TLS) used to collect data from multiple locations within a plot. (B) Scans gathered using the TLS are stitched together to produce lidar point clouds representing the habitat structure of the entire plot. Displayed is a forest point cloud, in which the color ramp shows relative elevation from low (blue) to high (red). (C) Application of *viewshed3d* to the point cloud from three eye-heights (0.25, 1.5, and 5 m) representative of animal groups that access ecosystems from those heights. The white and blue dots are lidar data points; white points are those at the ends of measured sightlines. Viewshed graphs display the percent of unobstructed sightlines as a function of distance from the animal position. The viewshed coefficient (VC) is calculated as the area under the curve and is a measure of viewshed extent. 38
- Figure 2-4 One complete 12-m radius lidar point cloud from each ecosystem: (A) forest; (B) shrub-steppe; (C) prairie; and (D) desert. The colors of the point clouds indicate the relative elevation of points within that cloud from low (dark blue) to high (red). Topography was not removed. The colored spheres represent the positions of the X,Y,Z vantage points from which viewsheds were calculated, with each color representing a single X,Y location across multiple eye-heights (i.e., Z) ranging from 0.25m to 30m (elevation displayed in scales). 38
- Figure 2-5 Vegetation distribution profiles calculated from the lidar point clouds representing the number of voxels (units of space occupied by some vegetation resolution 5 cm^3 , defined as N in the figure) at each elevation (m) above ground. Note: the y-axis scale differs between the forest and the three low-structure ecosystems (shrub-steppe, prairie, and desert). Mean values (line) and ranges (shaded area) for all plots in each of four ecosystems. 39

Figure 2-6 To determine variability within the viewsheds, whole point clouds were segmented in the azimuth into 20 segments of 18° each. The blue and white points are lidar data points; white points are obstructing individual sightlines. The viewshed coefficients (VC) of these individual segments were calculated and used to determine a coefficient of variation for the viewshed. This was repeated for all vantage points. (A) A full viewshed measured in a forest point cloud. (B) and (C) are adjacent viewshed segments from the same forest point cloud. 39

Figure 2-7 Extent of viewsheds (estimated as the viewshed coefficient, VC) as a function of eye-height across four ecosystems (forest, shrub-steppe, prairie, and desert). Points represent viewsheds at individual vantage points (n = 25 to 45/plot) within multiple plots per ecosystem (n = 5 to 10 plots/ecosystem). Note that the x-axis is on a logarithmic scale. 41

Figure 2-8 Variability of viewsheds (estimated as the coefficients of variation) as a function of eye-height across four ecosystems (forest, shrub-steppe, prairie, and desert). Points represent viewsheds at individual vantage points (n = 25 to 45/plot) within multiple plots per ecosystem (n = 5 to 10 plots/ecosystem). Note that the x-axis is on a logarithmic scale. 41

Figure 3-1 Estimation of concealment. A) A photograph of a sphere at a microsite in a terrestrial orientation. B) Classification of the clipped sphere where blue pixels classify the area removed in the clipping process, red pixels denote the sphere, and green represents habitat structure. Percent concealment of the sphere in this photograph is 35.3%. 59

Figure 3-2 A) Because rabbits may be influenced by predator type (i.e., aerial and terrestrial), we evaluated the overall viewshed (i.e., all available sightlines in all latitudinal and azimuthal directions) and also terrestrial and aerial viewsheds separately by segmenting the lidar point clouds latitudinally 45° from the zenith (denoted by the dashed grey line at 0°). Terrestrial sightlines were defined as those > 45° from the zenith and aerial sightlines were defined as those < 45° from the zenith. B) We used the R package viewshed3d (Lecigne et al. 2020) to measure all sightlines until obstructed by a data point up to 4 m. The red sphere is the position of the animal, and the blue and white points are lidar data points, with white points obstructing sightlines. C) The area under the curve representing percent of unobstructed sightlines as a function of distance was defined as the viewshed coefficient, which describes the spatial extent of all measured sightlines. 60

Figure 3-3 A) Mean (+ 95%CI) concealment, viewshed coefficient, and coefficient of variation (COV) at the paired used and unused patches. B) Mean (+ 95%CI) lidar data points (i.e., vegetation density) and shrub heights at used and unused patches. Asterisks indicate significant differences between the used and unused estimates for that variable according to p-values derived using marginal means from the mixed-effects models. 62

- Figure 3-4 A) Microsite use indexed by density of fecal pellets (number pellets/0.25m²) as a function of visual habitat properties (concealment, viewshed coefficient, and viewshed coefficient of variation (COV)). Lines represent negative binomial quadratic models of each variable. B) Microsite use as a function of vegetation density (indexed by number of lidar data points) and distance to nearest burrow..... 64
- Figure 4-1 A) A photograph of a conifer forest. B) A terrestrial lidar point cloud gathered from a conifer forest composed of ~50 million 3D data points. Inset shows a close-up of one section of the point cloud displaying individual data points..... 73
- Figure 4-2 Students working in the field measuring wildlife habitat. A) A student placing a cube for estimating concealment at the entrance of a midden. B) A student estimating concealment by observing a cube from a 1-m high vantage point. C) Students measuring distance from a midden site to nearest tree (i.e., potential squirrel refuge). D) A lidar scanner set up for data collation at a squirrel midden..... 75
- Figure 4-3 Student interactions with lidar data. A) A point cloud displayed in three-dimensions in CloudCompare as part of the lidar tutorial. B) The same point cloud imported into Program R displaying a measured 'viewshed' (i.e., all measured sightlines and their spatial extents) using computer code provided to students in the tutorial. The blue and white points are lidar data points, the red sphere is the position of the 'animal'. The white points are at the ends of measured sightlines. 76
- Figure A.A. 1 Bar graph displaying the number of reviewed articles published by year..... 106

Statement of Contribution

Although I am first author, each of the four chapters of this dissertation was completed in collaboration with multiple people who have or will appear as co-authors in the published versions.

Chapter 1 was co-written with Dr. Janet Rachlow of the University of Idaho. I was responsible for conceptualizing the project, conducting the literature search, reviewing the selected literature, and writing the manuscript. Dr. Rachlow provided guidance on project conception, the literature search, and edited the manuscript.

Chapter 2 was co-written with Dr. Bastien Lecigne (Université du Québec à Montréal and Jakarta Cartographie), Dr. Jan U.H. Eitel and Dr. Timothy R. Johnson (University of Idaho), Dr. Craig McGowan (University of Idaho and University of Southern California, Los Angeles), and Dr. Janet Rachlow. In addition to conceptualization, I conducted data collection, processing, and analysis, and wrote the manuscript. Dr. Lecigne provided support in lidar data processing. Dr. Eitel provided information on lidar data collection and Dr. Johnson guided data analysis. Dr. McGowan provided the opportunity to gather lidar data at Gold Butte National Monument and assisted with data collection at that site. Dr. Rachlow secured the lidar scanner, guided conceptualization and interpretation, and assisted with data collection. All co-authors provided comments and edits on the manuscript.

Chapter 3 was co-written with Dr. Bastien Lecigne, Dr. Timothy R. Johnson, Dr. Jan U.H. Eitel, and Dr. Janet Rachlow. I conceptualized the project, trapped and collared pygmy rabbits, collected, processed, and analyzed data, and wrote the manuscript. Dr. Lecigne provided support for lidar processing, Dr. Johnson contributed to data analysis, and Dr. Eitel provided support on lidar data collection methods. Dr. Rachlow secured IACUC approval, secured data collection assistance from an undergraduate technician, assisted with data collection, provided guidance on analysis and interpretation, and provided edits on the manuscript. The final manuscript, which will be submitted to an ecological journal, will be edited by all authors but not all have edited this version at the time of submission.

Chapter 4 was co-written with Dr. Karla Eitel (University of Idaho) and Dr. Janet Rachlow. I designed the curriculum, taught the class, guided and managed data collection with students in the field, wrote the student survey, acquired IRB approval, and wrote the manuscript. Dr. Eitel provided guidance on curriculum and survey design as well as the IRB application and also provided comments and edits on the manuscript. Dr. Rachlow contributed to curriculum design, co-taught the class, and provided comments and edits on the survey, IRB application, and the manuscript.

General Introduction

Animals gain information about their environment through multiple sensory modalities (i.e., vision, audition, olfaction) that influence their behavior. Sensory information can induce anti-predator responses (Kawahara and Barber, 2015), detection of resources (Schnitzler and Kalko 2001), and selection of habitat (Kleist et al. 2017). Much research has focused on how availability, distribution, and quality of resources affect movement and space use (Deblinger and Alldrege 1991, Lewis et al. 2011), but less has been directed at understanding the underlying mechanisms that link information available to individuals to decisions about use of those resources. Advancing understanding of what sensory information is available to animals and how animals respond will shed light on the functional links between sensory information, habitat resources, and resource use by animals.

My research included diverse objectives and approaches under the broad umbrella of sensory ecology. The chapters explore existing knowledge about the acoustic ecology of terrestrial mammals, development and application of techniques for assessing visual habitat properties, and curriculum that exposes undergraduate students to those techniques while communicating complex concepts about sensory ecology.

Across taxa, animals use sound to communicate breeding availability (Manno et al. 2017), location at a distance (Harrington and Mech 1983), territory (Conner 1984), predator presence (van der Marel et al. 2019), and to maintain social bonds and group cohesion (Berg 1983). Within bioacoustics, there is a strong focus on highly vocal groups; in mammalogy, a heavy emphasis has been placed on the acoustics of marine mammals and bats (e.g., McCauley 2003, Schnitzler and Kalko 2001). However, these are not the only mammalian groups that rely on sound, and other terrestrial mammals have been less studied. I conducted the first systematic literature review on the acoustic ecology of terrestrial mammals to create a conceptual framework for contextualizing existing knowledge and asking new questions.

An important factor that influences access to both sonic and visual information is habitat structure. Physical objects interact with sound and light waves changing or stopping propagation of waves (e.g., Price et al. 1988, Kükenbrink et al. 2021). Structures block sightlines and alter the area from which visual information can be obtained (Embar et al. 2011). Thus, three-dimensional (3D) habitat structure must be accounted for to achieve a holistic estimate of the visual information available to individuals. Lidar is a remote sensing system that uses emitted laser pulses to measure 3D structures and generates point clouds that are highly accurate computer models of those structures (Davies and Asner 2014). Lecigne et al. (2020) created a package for R, *viewshed3d*, that measures

all the sightlines accessible to an individual from within a point cloud generating a viewshed estimate (i.e., the spatial extent of all sightlines accessible to an individual). At the time I started my dissertation research, the method had only been applied to forest data and no study had assessed the effects of ecosystem-specific habitat structure on viewsheds. To fill this gap, I gathered terrestrial lidar data and assessed access to visual information in four disparate ecosystems representing a gradient of vegetation types: forest, shrub-steppe, prairie, and desert.

Access to visual information can strongly influence prey animals. Predation is the ultimate loss of fitness and exerts strong selection pressure on almost all aspects of prey ecology and behavior including selection of habitat that enhances security from predators (Lima and Dill 1990). Not only can habitat structure influence access to visual information about predators (i.e., visibility), but it can also influence whether an animal is visually hidden from a predator (i.e., concealed; Camp et al. 2012). Animals may enhance their fitness by selecting habitat for one or both of these visual properties (visibility and concealment). Although visibility and concealment are often negatively correlated, they are not directly inverse (Camp et al. 2013), and animals may select for these properties relatively independently, particularly across spatial scales. To evaluate if prey species do select for both properties, I evaluated habitat selection by pygmy rabbits (*Brachylagus idahoensis*) at two spatial scales in the shrub-steppe by indexing visibility using the lidar-viewshed3d method and indexing concealment using image classification.

Although remote sensing technologies, such as lidar, are essential tools to many ecological disciplines, including sensory ecology, undergraduate students typically receive limited exposure during their education. Remote sensing is a new, important, and often underutilized source of data in animal ecology (Davies and Asner 2014), and exposing wildlife students to remote sensing will better prepare them for their careers. Active learning practices enhance student success across STEM disciplines and levels (Freeman et al. 2014) and introduction to remote sensing may similarly be benefited by such practices including experiential learning. To introduce undergraduate wildlife students to remote sensing, I offered an experiential course focused on research assessing properties of wildlife habitat. Students engaged in hands-on lidar data collection and analysis relevant to assessing access to visual information by wildlife. Collectively, my work advances sensory ecology through several approaches including contextualizing existing knowledge on acoustic ecology of terrestrial mammals, expanding and applying new methods of estimating visual habitat properties, and using those methods to communicate complex concepts of sensory ecology to future wildlife professionals.

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Chapter 1: Acoustic Ecology of Terrestrial Mammals: A New Signaler-Receiver Conceptual Framework

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Abstract

1. Mammals use sound for a variety of purposes, such as detecting the presence of others and maintaining social bonds. Much research on mammalian acoustics has been focused on marine mammals and bats; less has considered terrestrial species.
2. Our goal was to review knowledge about the role of acoustics in the behavior and ecology of terrestrial mammals and to develop a conceptual framework that contextualizes the knowledge. The purpose of the framework is to enable researchers to place their work in a broader understanding of the acoustics of terrestrial mammals, as well as to support them to articulate and explore new questions.
3. We conducted a keyword search in Web of Science and removed papers that did not meet our criteria, resulting in 228 reviewed papers. We scored these for keywords and used concept maps to identify broad patterns.
4. Of the 228 papers, 219 were focused on acoustic communication. We therefore structured our Signaler-Receiver Conceptual Framework around factors that influence signalers (i.e., mammals producing sound) and receivers (i.e., mammals receiving sound). Factors that influence signalers were placed into two categories – those that influence call emission and those that influence call structure. Factors that influence receivers also fell into two categories – those that influence detection of sound and those that influence responses to sound. We added an additional receiver category – responses to sound. We present the framework in terms of five types of factors (environmental, social, morphological and physiological, state-related factors, and other) and how they influence both signalers and receivers.
5. Our review is the first to detail the range of factors influencing acoustic ecology of terrestrial mammals, and our framework provides context for the articulation of hypotheses that integrate multiple factors, and so can help researchers place their work in a broader context.

Introduction

Mammals use sound for a variety of purposes, including communicating breeding availability and facilitating mate choice (Ellis et al. 2011), locating other animals (Harrington & Mech 1983), and

maintaining social bonds and group cohesion (Lemasson et al. 2014). Many predators use sound to detect prey passively (Gannon et al. 2005) or actively through adaptations such as echolocation (Schnitzler & Kalko 2001), and prey species use sound to listen for predators (Randler & Kalb 2020), alert conspecifics (Burke da Silva et al. 1994) and signal to predators (Blumstein 2007). The sounds produced by these animals are not necessarily vocal; sounds may arise from actively moving or hitting objects or surfaces (Rose et al. 2006), hitting parts of the anatomy (Wright et al. 2021), or regular bodily functions (Miura et al. 1988).

The wide occurrence of mammalian sounds has provided opportunities for scientists to use sound as a research tool. Information derived from mammalian sounds has allowed researchers to quantify habitat use (Russo et al. 2003), estimate population size and density (Hansen 2013), and identify individuals (Sadhukhan et al. 2021). Mammalian sounds even provide researchers with clues about phylogeny (Tamura et al. 2018). The wide and varied uses of mammalian sounds in biological research indicate that they are information-rich resources.

Due to human activity, the acoustic habitats of mammals around the world are changing. In many cases, these changes are direct consequences of noise (i.e., biologically irrelevant sounds, often associated with decreased perception of relevant sounds) generated by human activity. Terrestrial sources include outdoor concerts, vehicles, and development (Barber et al. 2011). Alterations of the acoustic habitat can have diverse consequences for species, including masking important signals (Barber et al. 2009, Francis & Barber 2013). To gain a full understanding of the impacts of changing acoustic habitats, it is imperative that the ecological and behavioral significance of sounds is known.

Within bioacoustics (i.e., the study of biological sounds) there is an understandably heavy focus on highly vocal groups. In mammalogy, research has emphasized the acoustics of marine species and bats. Marine mammals, particularly cetaceans, use sound extensively for communication and hunting (Deecke et al. 2005, Erbe et al. 2017). Bats are also extremely vocal and rely on sound for orientation, foraging, and social interactions (Schnitzler & Kalko 2001, 75 Helversen et al. 2003). Several authors have reviewed literature about various aspects of the acoustics of marine mammals and bats (e.g., Jakobsen et al. 2013, Erbe et al. 2017). However, there has been no systematic synthesis of the acoustics of terrestrial mammals.

Our primary goal was to advance understanding of the role of sound in the behavior and ecology of terrestrial mammals by conducting a systematic synthesis of the literature. We aimed to create a framework that contextualizes existing concepts in the research literature relevant to these

taxa. Our intent was to encourage researchers to articulate and explore new questions about the acoustics of terrestrial mammals, and to provide a conceptual structure for doing so.

Methods

We conducted a systematic review of the literature to identify relevant papers. A keyword topic search was conducted using Web of Science in October 2019 with no restrictions on publishing date. We employed a string of keywords in a Boolean search: (acoustics or bioacoustics) and (animal* or wildlife) and (behavior*) and (ecolog*). To this base string, we systematically added “not” statements to remove non-target papers. This conservative method was employed because searching for keywords such as mammal* often excluded known and relevant papers. This refined search returned 1133 papers. To facilitate in-depth review, we reduced the number of papers by about 50% by randomly selecting 600 papers, weighted by decade in proportion to the number of papers identified in that decade, to ensure temporal representation. The remaining papers were not included in the review.

We screened papers to determine their relevance for final review. First, we reviewed titles and removed those that were focused on non-target taxa or on acoustics as a research method. After this process, 435 papers were retained for further consideration. Next, we reviewed the abstracts or, when an abstract was not available, we reviewed the introduction. Any remaining papers that violated the criteria were removed. Unfortunately, a few papers had to be excluded because English copies could not be obtained. Additionally, we removed papers that exclusively reported the physical structure of biological sounds without behavioral or ecological context, and some that were species descriptions that reported that the animals make sound but without description or context. Similar papers that provided behavioral or ecological context were retained. This process resulted in 229 papers selected for in-depth review. Finally, we omitted one of the selected papers that only reported on body size as a proxy for call features, which resulted in 228 papers in the final review (Appendix A). Although we did not include the British spelling of “behaviour” in the keyword search, 44% of the selected papers that included either “behavior” or “behaviour” in the abstracts used the British spelling. Additionally, we did not expressly use PRISMA (Shamseer et al. 2015), but our methods generally align with those guidelines.

Each of the selected papers was read in its entirety and scored for multiple criteria. We recorded notes on taxa, location of the authors’ research institutions, objectives, methods (in particular, acoustics methods), results, and discussions. Throughout this process, we generated a list of key concepts and scored their presence in each paper. If a paper introduced a new key concept, we added it and checked previously reviewed papers. Information from each paper was entered into

detailed concept maps that allowed us to connect ideas regardless of taxa, and so provided the foundation for our final conceptual framework.

Results and Discussion

General Results

The 228 papers included in the review were published over a period of 53 years (1966-2019) in 69 journals and books (Appendix A), and covered species from ten mammalian orders (Fig. 1). There were fewer papers about species within Metatherian orders (2%, $n = 5$) than species within Eutherian orders (98%, $n = 223$), and no papers were focused on Monotremes (Fig. 1.1). A majority (51%, $n = 117$) of reviewed papers was focused specifically on Primates. Although less prevalent, many papers were focused on Rodentia (19%, $n = 43$) and Carnivora (14%, $n = 32$).

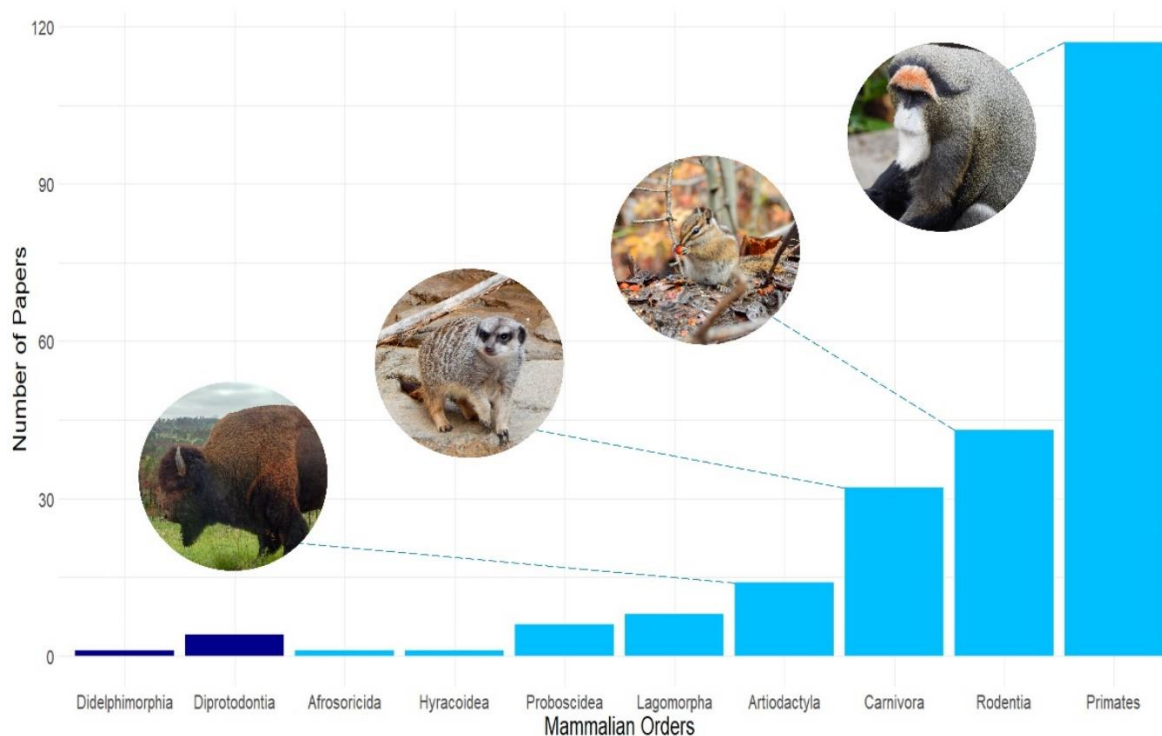


Figure 1-1 Representation of Metatherian and Eutherian mammalian orders in the 228 papers included in the review. The first two orders are the Metatherian orders (dark bars), all others are Eutherian orders (light bars). Inset images depict examples of members of the four most well-represented groups (left to right): Artiodactyla, Carnivora, Rodentia, and Primates. Only orders in reviewed papers are shown.

Acoustic communication was the most frequently covered topic within the review. In total, 96% of papers ($n = 219$) addressed some aspect of acoustic communication. Most of the papers that were not focused on communication concentrated on animal response to sounds, primarily artificial sounds. Papers that were focused on the influence of environmental variables on call structure and

incidence were also common ($n = 77$). Only two papers addressed the influence of environmental variables on calling without addressing any communicative functions of the calls.

Within the topic of communication, papers investigating acoustic call structure and social influence on calls were the most prevalent ($n = 112$ and 109 , respectively). The most common purposes of calls we documented within the review included territory and spacing calls ($n = 76$), alarm calls ($n = 62$), and calls associated with breeding ($n = 49$). These are often conspicuous, which may be connected to their prevalence in this review. Among the least addressed call purposes in the review were coordination of group activity ($n = 7$) and deceptive calling ($n = 12$), which are generally less conspicuous. More surprising was the lack of papers focused on eavesdropping ($n = 6$), which is often cited as a cost of acoustic signaling. Similarly, few papers were focused on the evolution and development of calls.

Signaler-Receiver Conceptual Framework

Most of the reviewed papers ($n = 219$) dealt with acoustic communication to some degree, so we developed a hierarchical Signaler-Receiver Conceptual Framework to contextualize the papers in this review. Our framework first distinguishes between papers that report information associated with individuals emitting a sound (i.e., the signalers) and papers of those receiving a sound (i.e., the receivers; Fig. 2). Although nine papers did not directly address communication, we were able to include them in the framework. Two of these nine papers were focused on variables that alter call emission without discussion of communicative function. The variables they describe are included in the framework as factors affecting signalers. The remaining seven papers addressed responses of animals to non-biological sounds. To accommodate those papers, we defined receivers as individuals receiving and potentially responding to not only biologically relevant sounds, but also other sounds. Thus, the framework we developed contextualizes the entirety of reviewed papers ($n = 228$), and so represents the breadth of the academic literature on the topic of terrestrial mammal acoustics.

We created further subdivisions in the framework that provide context for relationships of mammals to acoustics based on a core concept of information theory (i.e., that all channels of communication contain at least some noise, Shannon & Weaver 1949), and also on a central concept of signal detection theory (i.e., that a receiver's performance is linked to the ability of a receiver to separate a signal from background noise, Wiley 2006). Under these concepts, not only are ecological and environmental constraints defined as noise, but also social and contextual constraints (Smith 1980, Bradbury & Vehrencamp 1998). Thus, the information from the review associated with signalers is divided into two categories that account for the effects of these diverse types of signal noise: factors affecting 1) call emission and 2) the structure of the call. Similarly, information

associated with receivers is primarily divided into two categories: factors affecting 1) whether the sound is detectable and 2) whether and how the receiver responds to the sound. We decided that a third receiver category, responses to sound, also was necessary to contextualize fully all the information in the review (Fig. 1-2). Within each of these categories (except responses to sound), information is further divided into subcategories that include environmental, social, morphological and physiological, situational, and other factors that influence the acoustic behaviors of signalers and receivers (Fig. 1-2, Table 1-1).

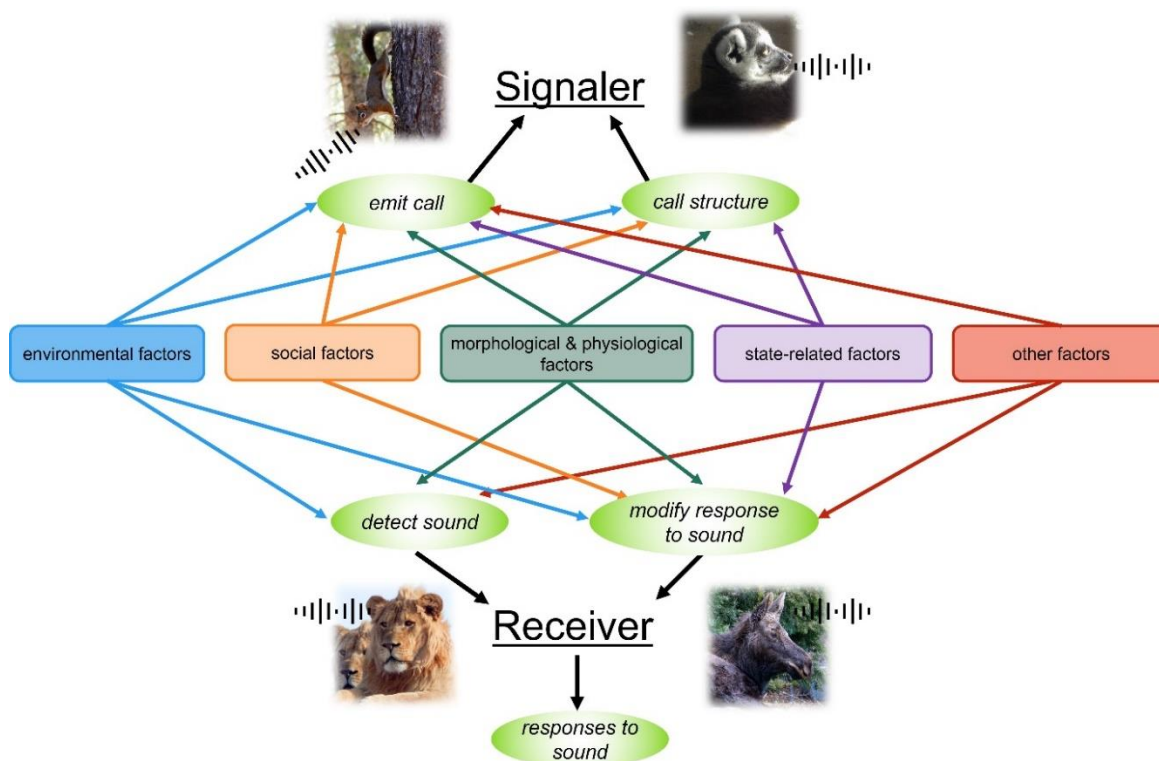


Figure 1-2 The Signaler-Receiver Conceptual Framework of acoustic ecology in terrestrial mammals. This framework contextualizes the factors that influence signalers and receivers. We define signalers in this framework as individual mammals producing sound and receivers as individuals that may detect any sound. Factors that influence signalers may affect whether calls are emitted and the acoustic structure of the calls; factors that influence receivers may affect whether the sound is detected and how the receiver responds to the sound. We created broad categories of factors that influence both signalers and receivers: environmental factors, social factors, morphological and physiological factors, state-related factors, and other factors. Arrows indicate how factors within that category can influence signalers and receivers as documented by reviewed papers. For example, environmental factors can influence call emission by and call structure of signalers, and whether receivers detect sound and how they respond. Researchers should note that we may not have encountered examples of every factor relevant to this framework (e.g., although no paper documented it, state-related factors may influence detection of sound by a receiver).

Although the framework contextualizes the entirety of the reviewed literature, because of the depth of this field and because we needed to eliminate papers for a more thorough review, we expect that we have not encountered or documented every published factor relevant to this framework. For example, no reviewed paper documented that state-related factors may influence detection of sound by receivers (Fig. 1-2). The framework includes factors associated with diverse species,

environments, and contexts, so researchers who use it should expect the relative importance of these factors to depend on the context of their study system.

Table 1-1 Examples of factors that may influence the acoustic ecology of mammalian signalers and/or receivers. Two of the mostly commonly described factors in the reviewed literature within each of the Signaler-Receiver Conceptual Framework categories (Fig. 1-2) are presented along with examples of species influenced by those factors with citations.

Category	Examples of factors	Species	Citation
Environmental	Habitat structure	Marmots <i>Marmota</i> spp. Olive baboon <i>Papio anubis</i>	Blumstein & Daniel 1997 Ey et al. 2009
	Weather	Koala <i>Phascolarctos cinereus</i> African elephant <i>Loxodonta africana</i>	Ellis et al. 2011 Larom et al. 1997
Social	Social structure	Yellow mongoose <i>Cynictis penicillata</i> Ground squirrels <i>Spermophilus</i> spp.	Le Roux et al. 2009 Koepl et al. 1978
	Competition	Rock hyrax <i>Procavia capensis</i> Orangutan <i>Pongo pygmaeus</i>	Demartsev et al. 2016 Mitani 1985b
Morphological and physiological	Sex	Northern muriqui <i>Brachyteles hypoxanthus</i> Collared pika <i>Ochotona collaris</i>	Arnedo et al. 2010 Trefry & Hik 2009
	Body size	Bison <i>Bison bison</i> Fallow deer <i>Dama dama</i>	Berger & Cunningham 1991 Charlton & Reby 2011
State-related factors	Call purpose	Sambirano mouse lemur <i>Microcebus sambiranensis</i> Red fox <i>Vulpes vulpes</i>	Hasiniaina et al. 2018 Newton-Fisher et al. 1993
	Urgency	Meerkat <i>Suricata suricatta</i> Dwarf mongoose <i>Helogale parvula</i>	Hollén & Manser 1993 Collier et al. 2017
Other factors	Sound structure	Domestic goat <i>Capra hircus</i> Cotton-top tamarin <i>Saguinus oedipus</i>	Briefer & McElligott 2011 Matthews & Snowdon 2011
	Habituation to stimuli	Western grey kangaroo <i>Macropus fuliginosus</i> Wolf <i>Canis lupus</i>	Biedenweg et al. 2011 Palacios et al. 2015

We now present an overview of information from the review in the context of the framework we developed, with selected examples. Factors that affect one part of the framework may also influence others (e.g., environmental factors can influence both call emission and reception), so we discuss the framework in terms of these factors and where they fit into the broader conceptual structure.

Environmental Factors

A suite of environmental factors influence propagation of sound through the environment and affect both signalers and receivers. The physical structure of the habitat interacts with soundwaves and alters propagation of sound (e.g., Huisman & Attenborough 1991). For example, leaf width and density of herbaceous vegetation significantly influences attenuation; dense and broad-leaved vegetation contribute to significant decreases in soundwave amplitude at high frequencies (Aylor 1972). Interactions between these environmental factors and physical properties of sound (i.e., frequency, amplitude) have resulted in evolution of call structures that increase propagation within high-structure environments to ensure signals reach intended receivers.

Evolution or alteration of call features to increase propagation relative to habitat structure is most readily demonstrated by papers focused on long-distance calls. Such calls are vocalizations emitted for the purpose of communication across large distances (Mitani 1985a, Garstang et al. 2005, Leblond et al. 2017). Multiple features of long-distance calls enhance call propagation, including low frequencies, slow modulation of frequency and amplitude, and repeating call structures (Fig. 1-3; Wich & Nunn 2002, Brown & Waser 2017). Because low frequency sounds attenuate at a greater distance than high frequency sounds, low frequency is a common feature of long-distance calls. For example, African bush elephant *Loxodonta africana* infrasonic calls are between 14 and 35 Hz in frequency, and elephants can respond to conspecific infrasonic vocalizations > 2 km from the signaler (Langbauer et al. 1991). These same call features are also important in overcoming barriers to acoustic communication in the subterranean environment. Low-frequency sounds that travel more readily through substrates may be achieved by production of seismic or vibrational signals (Heth et al. 1987, Giannoni et al. 1997, Francescoli & Altuna 1998).

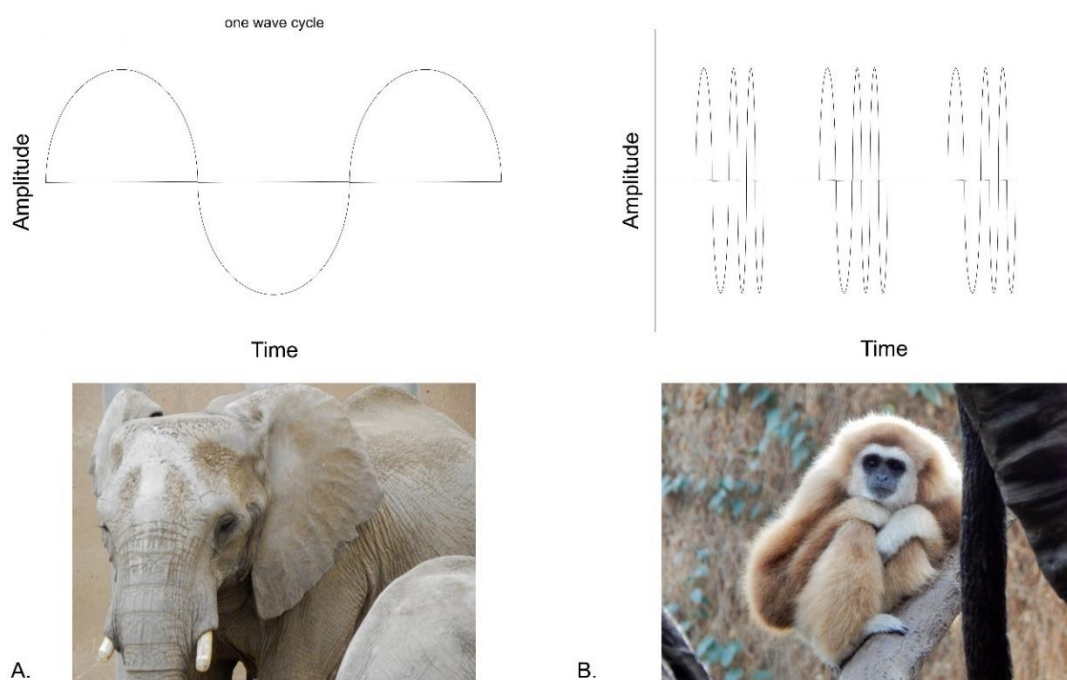


Figure 1-3 Examples of adaptations for propagation of sound. A) A generalized sound wave with amplitude on the Y axis and time on the X axis. The frequency of a sound wave is measured as cycles/sec (Hz). Low-frequency sounds generally travel farther than high-frequency sounds. Amplitude is related to 'loudness'; high-amplitude sounds travel greater distances. Many species that produce long-distance calls, such as the African savannah elephant *Loxodonta africana*, produce calls at low frequencies and high amplitude. B) Repeating call structures such as those produced by multiple species of gibbons (family Hylobatidae) also increase the distance over which calls are propagated.

Habitat structure also can influence how reliant species are on acoustic signaling versus other channels of communication. Physical structures within habitats occlude sightlines and alter visibility (Aben et al. 2018). Where visibility is limited, species may become more reliant on acoustic signals.

Indeed, the presence of long-distance calls in tropical primates has been linked to limited visibility since the 1970s (Waser & Waser 1977). Limited visibility also may cause mammals to increase the rate at which they emit calls. Male Reeve's muntjac *Muntiacus reevesi* increase the rate at which they bark as visibility decreases through the growing season (Yahner 1980). Reliance on acoustic and also tactile and olfactory cues by subterranean rodents is often linked to limited visibility within their environment (Schleich & Francescoli 2018). Limited visibility associated with nocturnality has also been linked to increased reliance on vocal signals (Cox et al. 1988).

Weather factors have major effects on sound propagation. Wind can refract or increase attenuation of sound (Ingård 1953); African savannah elephant infrasonic calls propagate downwind five times further than upwind (Larom et al. 1997). The speed of sound is influenced by air temperature and humidity. Weather variables change with time of day and season, creating dynamic acoustic conditions. As radiation from the sun heats an ecosystem, vertical temperature and humidity gradients can form, which create layers of differential acoustic conditions that may result in 'sound shadows' near the ground (Ingård 1953) and arboreal 'sound windows' where sounds propagate well or even better than expected (Brown & Waser 2017). The position of the signaler and receiver relative to these sound windows and shadows may alter a receiver's ability to detect the sound. When a soundwave moves from one layer of air to another with substantially different characteristics, it may be reflected, refracted, and distorted (Ingård 1953), and so can reach the receiver in a different form than emitted.

Acoustic noise within a habitat also affects acoustic signaling by interfering with or masking signals, but noise is an integral part of the environment. Rainforests generally feature more noise than open habitats (e.g., Waser & Waser 1977), but this is not always the case; Ey et al. (2009) found that the noise hamadryas baboons *Papio hamadryas* contend with in rainforests is less than the noise associated with the savannas within their range. In response to noise, species may alter the incidence and rate of calling (Toarmino et al. 2016, Snowdon 2017). The reviewed papers only addressed differences between noise in rainforests and open habitats, none accounted for noise across other habitat types (e.g., other forest types). However, due to the diverse environmental conditions and biological communities associated with other habitat types, we expect noise level to vary with habitat along with mammal responses. Noise within habitats can increase due to proximity to humans, and mammals may change signaling in response. For example, black-tufted marmosets *Callithrix penicillata* groups near human developments were subject to higher noise and generated longer phoe calls as well as fewer contact calls than groups in habitats far from development (Santos et al. 2017).

Although we have been describing species that evolved call structures and behaviors to optimize transmission, degradation of calls can be beneficial. There is evidence that some species evolved call structures that degrade in consistent ways within their ecosystem. Reliable patterns of call degradation provide useful cues to the receiver about distance to the signaler, which can have strong effects on the receiver's response (e.g., Mendes & Ades 2004, Snowdon 2017).

Observations about the influence of environmental features on calling have led to the acoustic habitat hypothesis, which states that not only are sound-dependent animals shaped by their acoustic habitat, they specifically select for it based on their needs and auditory acuity (Mullet et al. 2017). Although results from some papers in this review support this hypothesis, others do not, providing evidence that environmental factors are context-specific. Indeed, within this review, we have identified additional factors that influence acoustic behaviors (Fig. 1-2, Table 1-1).

Social Factors

The acoustic behaviours of signallers and receivers are influenced by many social factors, including the social organisation of the species and the positions of signallers and receivers within that organisation. The degree of sociality of the species is perhaps the most important social factor that can influence acoustic behaviour. Across taxa, gregarious species are generally associated with higher rates of vocalisation and larger vocal repertoires. In contrast, solitary species typically vocalise at lower rates and have relatively small vocal repertoires (Fig. 1-4; Koepl et al. 1978, Cox et al. 1988, Le Roux et al. 2009). Columbian ground squirrels *Spermophilus columbianus* have more complex social organisation and a larger and more varied vocal repertoire than related ground squirrels (*Spermophilus armatus*, *Spermophilus elegans*, and *Spermophilus richardsonii*; Koepl et al. 1978). This pattern is so pronounced that in species that are difficult to observe, the size and variability of the vocal repertoire has been used as evidence of the social organisation of that species (Cox et al. 1988).

The relative positions of signallers and receivers within a social hierarchy can result in major effects on calls emitted and response to calls. The number of 'girney' calls emitted by and directed at female Japanese macaques *Macaca fuscata* when one individual approaches another is influenced by the relative social ranks of the signaller and receiver. Low-ranking females emit more 'girneys', and these are directed at individuals of higher status (Blount 1985). Receivers moderate their response based on relative social position. Relatively low-ranking receivers move or display a myriad of signals (through any communication channel) that convey submission or aggression. The social rank of the signaller relative to a group can influence the response of the entire group. African wild dogs *Lycaon pictus* attempt to rally and move the group through producing 'sneezes'. Rallies are most

successful when the initiator is dominant (Walker et al. 2017). Changes in social rank influence these patterns. Male lions *Panthera leo* that were previously subordinate substantially increase their rate of roaring after attaining dominance and a pride, whereas previously dominant males lower their rate of roaring (Gray et al. 2017). Signallers and receivers that are ranked similarly may not respond or signal to each other, or their similar ranks may stimulate competition.

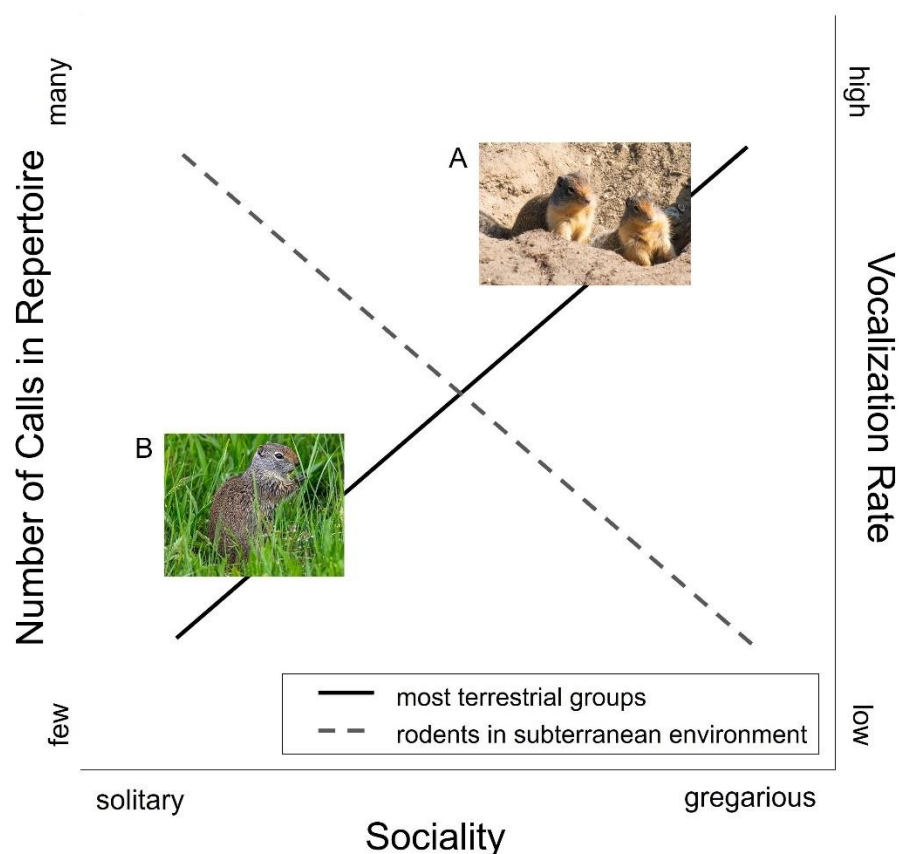


Figure 1-4 Patterns of vocalization as a function of sociality. Generally, species that are more social have a larger vocal repertoire and vocalize at a higher rate than related, but less social species (solid line). For example, Columbian ground squirrels *Spermophilus columbianus* (A; photo by Thomas Quine licensed under CC BY 2.0) are more social and have a larger repertoire than Uinta ground squirrels *Spermophilus armatus* (B; photo by Jacob W. Frank licensed under CC0 1.0), even though they are closely related (positions are relative; Koepl et al. 1978). This pattern does not always hold. In rodents that use the subterranean environment, such as those in the genus *Microtus*, asocial species typically have larger call repertoires to overcome the barriers of communication at a distance underground (dashed line; Giannoni et al. 1997).

Mammals adjust their acoustic behaviours in competitive situations. Competition arises as mammals vie for social position or limited resources. Competition for reproductive females can cause males to alter call structure (Volodin et al. 2019), and mammals in competitive situations may also alter calling rate. Chimpanzees *Pan troglodytes* may actively repress food calls when they come across high-quality food, in order to conceal the information (Kalan & Boesch 2015). Competition also can influence how mammals respond to sound. Depending on the ability of the receiver to

compete with the signaller, individuals approach, retreat, or signal back to the original signaller. For example, in geladas *Theropithecus gelada*, the acoustic quality of loud calls made by males is associated with the relative quality of the male. Leader males (i.e., males that have reproductive access to females) are less likely than bachelor males (i.e., those competing for reproductive access) to approach individuals emitting loud calls, regardless of their acoustic quality. In contrast, bachelor males attend to loud calls of both high and low quality, and approach the source of low-quality calls while signalling threat (Benítez et al. 2017).

Territoriality, a type of competition, has received extensive attention in papers about the acoustics of terrestrial mammals. Territorial mammals often call to signal their presence and the location and ownership of a territory. Conner (1984) found that when an American pika *Ochotona princeps* is removed from its territory, space use by neighbours increases toward the territory of the removed mammal, but only in the absence of playbacks of the individual's territorial calls. In some species, territorial signals may be emitted in pairs or by groups. Duetting is a common behaviour in monogamous arboreal primates that is often used to advertise or defend territories (Tilson & Tenaza 1976, Robinson 1981, Mitani 1985a, Fan et al. 2009). Receivers may respond to territorial calls by approaching the signaller and signalling back. Male rock hyraxes *Procavia capensis* counter-sing in response to songs by conspecific resident males (Demartsev et al. 2016). Territory size and the spatial positions of the signaller and potential receivers also can influence territorial calling, and, in species that maintain relatively large territories, long-distance calls can be employed and acoustically altered to account for territory size (Oliveira & Ades 2004, Rasoloharijaona et al. 2006). Mitani and Stuht (1998) conducted a comparative paper focused on the loud calls of nonhuman primates and found a significant negative relationship between loud-call frequency and home-range size across species, which held after controlling for the potentially confounding effects of body size and phylogeny.

Simply the presence or absence of other animals can alter acoustic behaviours. Male Thomas's langurs *Presbytis thomasi* emit more loud calls upon discovering a model of a predator when in a group than when solitary (Wich & Sterck 2003). Call structure also can change depending on the presence of other animals. Adult black-tailed prairie dogs *Cynomys ludovicianus* emit alarm calls with significantly lower peak frequency when pups are present than when they are absent (Wilson-Henjum et al. 2019). Calling by other individuals can influence responses, including increasing behaviours such as vigilance by receivers, and stimulating the receiver to vocalise in response (e.g., Messeri et al. 1987, Herbinger et al. 2009, Trefry & Hik 2009, Collier et al. 2017).

Morphological and Physiological Factors

Morphology and physiology of signallers and receivers (e.g., body size, reproductive state, age) strongly affect the acoustic ecology of terrestrial mammals. The age of the signaller and receiver can have significant effects on incidence of calling. Some calls are only produced by specific age groups, which can result from behavioural or physical ontogeny as well as learning (Lent 1975, Mausbach et al. 2017, Snowdon 2017). Differences in calling by age are often due to vocal ontogeny, as young mammals have not developed the capability of producing certain sounds, or the sounds are learned rather than innate (Ericson 1975, Mausbach et al. 2017). Differences may also be related to behavioural ontogeny. Meerkat *Suricata suricatta* young display vocal begging behaviours, where the amount of vocal begging directed at a foraging adult is related to the amount of food received. As they age and forage for themselves, this behaviour lessens (Manser & Avey 2000). The age of the signaller also can influence the structure of calls, even if a specific call is emitted by both young and adults; adults usually produce calls at lower frequencies than their young (Newton-Fisher et al. 1993, Hollén & Manser 2007, Matrosova et al. 2007).

A receiver's response to a call also may be influenced by the respective ages of the signaller and receiver. For example, spotted hyena *Crocuta crocuta* whoops carry reliable information about signaller age, and hyenas respond at a higher rate to whoops produced by juveniles than by adult males (Theis et al. 2007). The age of the receiver can alter responses to a sound. Male white-tailed deer *Odocoileus virginianus* respond to antler rattling at different times as a function of their age; young males respond more frequently before the rut, middle-aged males during the rut, and mature males after the rut (Hellickson et al. 2009).

The sex of the signaller and receiver can strongly affect call emission, structure, and response. Across mammalian taxa, certain calls are associated entirely with a particular sex (e.g., Haimoff et al. 1987, Nikol'skii et al. 1990, Steenbeek et al. 1999). Although this is often linked to species that exhibit marked sexual dimorphism, lack of physical sexual dimorphism does not preclude vocal sexual dimorphism. Family-living primates generally show little or no physical sexual dimorphism, yet vocal sexual dimorphism has been documented (Snowdon 2017). These differences in call structure and emission are very important to primate species in which bonded pairs display antiphonal calling (i.e., events in which individuals call in turn; Mendes & Ades 2004, Oliveira & Ades 2004, Rasoloharijaona et al. 2006). In primates that display pair-bond antiphonal calling, the call type and structure of the male and female calls often differ markedly, and together, they advertise territory (Tilson & Tenaza 1976, Robinson 1981, Mitani 1985a, Fan et al. 2009).

The sexual state of the signaller and receiver also plays a role in acoustic behaviour. Individuals that are ready to reproduce may increase their incidence of calling (Berger & Cunningham 1991), use different call structures (Nikol'skii et al. 1990), or produce calls specific to breeding readiness (Le Roux et al. 2009). Sexual selection and male-male competition also influence these behaviours. Male red deer *Cervus elaphus* roar during the rut to attract and defend mates. They extend the neck and lengthen the larynx, causing vocalisations to be emitted at lower, more competitive, frequencies (Volodin et al. 2019). Males may also call to retain females for breeding. For example, regardless of predator presence, male topi antelope *Damaliscus korrigum* emit alarm snorts when females in oestrous move through their territories, causing the females to pause and stand vigilant, thus helping the males to retain the females (Bro-Jørgensen & Pangle 2010). Calling after copulation by males may be associated with mate guarding behaviour (Manno et al. 2007), whereas calling after copulation by females may be related to post-copulatory sexual selection (Maestriperi et al. 2005).

Auditory acuity alters which signals the receiver can detect. Few papers in this review documented the auditory acuity of species but, that is likely the result of our search keywords which did not include a search term for audiogram. The range of frequencies and amplitudes that are detectable vary by species and among individuals. Signal detection range is particularly important for species that use infrasound to communicate, as their calls are often transmitted as vibrational or seismic signals that move through substrates (e.g., Francescoli & Altuna 1998, Schleich & Francescoli 2018). Species that exploit these sounds often use their somatosensory systems for signal detection (Francescoli & Altuna 1998). Similarly, species that communicate via ultrasound must be able to detect extremely high-frequency sounds.

State-related Factors

The situation or stimulating event, as well as the state of the signaller and receiver, can strongly affect acoustic behaviour. A majority, 82% ($n = 187$), of reviewed papers addressed the purpose(s) or function(s) of at least one call, providing rich information about how call purpose influences acoustic behaviour. In addition to primary call purpose, calls may serve other functions, including communication of signaller identity (Chapman & Weary 1990), sex (Nikol'skii et al. 1990), age, reliability (Blumstein 2007), type of predator (Hollén & Manser 2007), competitive ability (Benítez et al. 2017), and location of signaller (Hopkins 2013). Some species emit distinct calls for a singular purpose (Messeri et al. 1987), others have distinct calls for multiple purposes that change with context (Berg 1983), while others emit multiple call types with a single general purpose, whereby the different calls impart additional information (Collier et al. 2017). For example, multiple

prey species have more than one alarm call that conveys information to receivers in addition to general alarm (e.g., Boero 1992, Collier et al. 2017, Snowdon 2017). Meerkats alter their response to alarm calls depending on whether the call signals avian or terrestrial predators. When an avian alarm is sounded, they visually scan the sky; when the call signals a terrestrial predator, they assume an upright posture and scan the surrounding terrain (Manser 1999). Receivers are so tuned to the purpose of calls that studying the response of a receiver is a common method for determining call purpose.

The perceived state of animals, including urgency and safety, can have important effects on acoustic behaviour. The urgency and emotional or motivational state of the signaller may result in altered call structures or in the emission of different call types. Meerkats give distinct calls not only for predator type, but also for level of urgency (high vs. low; Hollén & Manser 2007). Receivers that detect changes in calling associated with situation or state alter their response to the call. In California ground squirrels *Spermophilus beecheyi*, the number of alarm whistles is associated with perception of risk: squirrels are more likely to run to a mound or large burrow upon receiving three to five whistles than upon receiving just one (Leger et al. 1979). Mammals also may delay emitting or fail to emit calls when they perceive themselves to be in danger. Many marmots *Marmota* spp. Do not emit alarm calls unless they are in close proximity to their burrow (Blumstein 2007).

Other Factors Affecting Response to Sound

Two additional factors can affect sound-dependent mammals: the structure of the sound received and habituation to stimuli. Numerous factors have been addressed that alter the structure of a call, and receivers use altered call structures to gather additional information and adjust their responses. Not only are call structures affected by environmental factors, social factors, morphological and physiological factors, and state-related factors, alterations in call structures that reach receivers can change their responses. Changes in receiver behaviour as a result of alterations in call structure have been documented in many terrestrial mammals (e.g., Chapman & Weary 1990, Tooze et al. 1990, Hauser & Marler 1993, Fischer et al. 1998, Blumstein & Munos 2005). Habituation to a stimulus delivered through any sensory modality also can affect mammal responses. For example, Reeve's muntjacs initially bark when presented with a model of a predator, but quickly cease after inspecting the model and habituating to it (Yahner 1980). Experimental studies in the reviewed papers that were focused on response to sound typically employed methods to avoid habituation to sound (Mitani 1985b, Langbauer et al. 1991), but few measured or documented habituation, and none documented habituation to sounds produced by other animals. However, mammals do not always habituate to stimuli. One paper found that western grey kangaroos *Macropus fuliginosus* never habituated to the sound of a bull whip crack (Biedenweg et al. 2011).

Responses to Sound

Responses to sounds by terrestrial mammals include no response, physical movement, alteration of resource use, signalling back, abandoning pursuit, and even altering physical readiness to mate. Responding mammals may approach the sound source, display interest or aggression (Mitani 1985b), or retreat or flee from the sound source (Messeri et al. 1987, Lair 1990). Mammals often alter resource use in response to sound. Common responses to alarm calls include increased vigilance behaviours and decreased foraging (e.g., Jayne et al. 2015, Collier et al. 2017, Dannock et al. 2019). Mammals may also share resources in response to sounds (e.g., sharing food with begging juveniles; Le Roux et al. 2009). In response to calls, receivers may signal back through any communication channel (Herbinger et al. 2009, Trefry & Hik 2009). Alarm calls by prey can convey information to the predator about the fitness of the prey individual and alert the predator that it has been detected, causing the predator to abandon pursuit (Zuberbühler et al. 1999, Blumstein 2007). Breeding calls by male koalas *Phascolarctos cinereus* induce a physiological response in females via induction of oestrous (Ellis et al. 2011).

Conclusions and Future Directions

Our review provides a Signaller-Receiver Conceptual Framework that elucidates patterns applicable to diverse mammalian taxa and can serve as a tool for researchers attempting to advance understanding of the acoustic ecology of terrestrial mammals. Most of the papers we reviewed were focused on one or a few factors that influence acoustic behaviour. Our review is the first to detail explicitly the breadth of factors influencing acoustic behaviour of terrestrial mammals, and the framework we developed highlights interactions among diverse factors that can influence both dissemination and reception of acoustic information. Our framework provides context for and supports articulation of hypotheses that integrate multiple factors relevant to the acoustic behaviour of terrestrial mammals. We encourage researchers to use our framework both to inform their papers and to help place their work in a broader context that facilitates contributions to fundamental advances in the understanding of mammalian acoustics.

Although there is a rich literature on the acoustics of terrestrial mammals, we discovered multiple opportunities for additional research. We present these here but acknowledge that our review is not exhaustive because we randomly selected about half of the papers returned in the initial search to allow in-depth review and analysis. First, we identified a heavy emphasis on highly vocal species; few papers in the review were focused on species with minimal or no vocalisation, even though most terrestrial mammals are likely to be influenced by sounds, whether or not they produce them. For example, the large pinnae of leporids are evidence that they are likely to be strongly influenced by

sound, but no papers in this review were focused on leporids. Second, there was a reporting bias favouring species that produce calls within the range of human hearing. However, multiple species across mammalian families produce calls in frequencies above (ultrasonic) and below (infrasonic) the range of human hearing (e.g., Heth et al. 1987, Hasiniaina et al. 2018). Third, there was a pronounced emphasis on vocal calls; nonetheless, many species use non-vocal auditory signals that influence their interactions (Miura et al. 1988, Giannoni et al. 1997, Rose et al. 2006). Finally, relatively few papers assessed how factors that are known to influence acoustic behaviour are changing or how those changes might influence terrestrial mammals. Environmental changes associated with human activity alter acoustic habitats and influence animal ecology (Francis & Barber 2013). However, few papers in our review explored how the associated changes in relevant ecological factors (e.g., shifts in timing of breeding or migration, or changes in habitat use) might influence acoustic behaviours. Given the widespread and rapid changes threatening mammals worldwide (Bowyer et al. 2019), this research deficiency presents opportunities for advancing understanding of acoustic ecology and developing applications that contribute to conservation of terrestrial mammals.

We also identified several understudied taxa for which papers detailing even basic acoustic behaviours were rare or absent. Most notably, no species of the order Eulipotyphla were the subject of any paper in our review even though the order contains 564 extant described species (Mammal Diversity Database 2022), and only one paper was focused on a species of the order Afrosoricida. Similarly, only one paper assessed the acoustics of a Metatherian species outside the order Diprotodontia. Within well-studied groups, we occasionally found a lack of agreement in terminology, particularly in the naming of specific calls where authors used different terms for what appeared to be the same vocalisation. Authors should make a point of identifying the same calls in previous literature and either use those terms, or clearly redefine them. We recommend reading Lair (1990) who identified and addressed this issue in terminology for red squirrel *Tamiasciurus hudsonicus* calls.

New methods may help advance understanding of the acoustic ecology of mammals. For example, recording equipment is now small enough for researchers to place microphones on animals along with other sensors (Couchoux et al. 2018); recordings from microphones on Canadian lynx *Lynx canadensis* allowed researchers to identify the prey species they captured (Studd et al. 2021). Likewise, advances in technology are allowing expansion of passive acoustic monitoring (i.e., placement of recording equipment in the environment). Data from this method have been integral in estimating populations and understanding patterns of diversity (Marques et al. 2013, Torre et al. 2021), and may also be important in documenting responses to changing environments. Applying

these techniques more broadly requires development of effective and affordable tools. High-quality recording equipment and configurations suited for research can be expensive and may only be suitable for certain environments or taxa (Darras et al. 2019). Less expensive, quality equipment is needed to expand application of these new approaches.

One opportunity for enhancing understanding of mammalian acoustic ecology is better integration of acoustics with the environments in which terrestrial mammals occur. Advances in quantification of three-dimensional (3D) habitat structure, as well as in computing and modelling, have led to the development of programs that map propagation of human sounds through ecosystems (Reed et al. 2012). Although these models are generally only applicable to sounds produced by human technology, they have been useful in understanding the extent of sound pollution and its influence on wildlife (Barber et al. 2011). Broader application requires both access to extensive 3D environmental data, and models that can account for the complexities of animal-derived sounds. Data detailing 3D environmental structure using technologies such as lidar and photogrammetry are increasingly available (D'Urban Jackson et al. 2020). However, modelling the propagation of natural sound presents challenges that stem from its complexity (e.g., modulation of frequency, variation in amplitude, and relative spontaneity). Development of new models that realistically predict propagation of natural sounds within 3D structure will facilitate greater understanding of the influence of environmental factors on the acoustic ecology of diverse species.

Generating and archiving recordings of the acoustic signals of terrestrial mammals will also advance future research. Recording archives 1) give researchers access to acoustic data from diverse groups that can be applied to a wide range of questions and facilitate comparison across groups, and 2) provide benchmarks for understanding changes in acoustic ecology of terrestrial mammals as ecosystems continue to change. Sound libraries offer rich information about the sounds emitted by a multitude of species. However, we are aware of only two mammal-specific sound libraries and those focus on marine mammals (Woods Hole Oceanographic Institution 2022) and bats (Görföl et al. 2022). To our knowledge, there is no recording archive for terrestrial mammals. A comprehensive and accessible sound library focused on these animals would open new avenues for research aimed at advancing their acoustic ecology. Application of the framework we developed in concert with these emerging technologies and methods presents opportunities for future papers that both advance ecological understanding of the acoustics of terrestrial mammals and support development of strategies for management and conservation.

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Chapter 2: Vegetation and Vantage Point Influence Visibility Across Diverse Ecosystems: Implications for Animal Ecology

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Abstract

Visual information can influence animal behavior and habitat use in diverse ways. Visibility is the property that relates 3D habitat structure to accessibility of visual information. Despite the importance of visibility in animal ecology, this property remains largely unstudied. Our objective was to assess how habitat structure from diverse environments and animal position within that structure can influence visibility. We gathered terrestrial lidar data (1 cm at 10 m) in four ecosystems (forest, shrub-steppe, prairie, and desert) to characterize viewsheds (i.e., estimates of visibility based on spatially explicit sightlines) from multiple vantage points. Both ecosystem-specific structure and animal position influenced potential viewsheds. Generally, as height of the vantage point above the ground increased, viewshed extent also increased, but the relationships were not linear. In low-structure ecosystems (prairie, shrub-steppe, and desert), variability in viewsheds decreased as vantage points increased to heights above the vegetation canopy. In the forest, however, variation in viewsheds was highest at intermediate heights, and markedly lower at the lowest and highest vantage points. These patterns are likely linked to the amount, heterogeneity, and distribution of vegetation structure occluding sightlines. Our work is the first to apply a new method that can be used to estimate viewshed properties relevant to animals (i.e., viewshed extent and variability). We demonstrate that these properties differ across terrestrial landscapes in complex ways that likely influence many facets of animal ecology and behavior.

Introduction

Three-dimensional (3D) structure of natural environments is shaped by and responds to diverse ecosystem processes, and consequently, influences organisms in a variety of ways. An early study by MacArthur and MacArthur (1961) demonstrated a functional relationship between the 3D structure of trees and avian diversity. Similarly, Price et al. (2019) documented that 3D structural complexity of cold-water reefs influenced biodiversity and benthic fauna abundance. Three-dimensional habitat structure also can influence patterns of habitat use. For example, terrestrial predators alter use of vegetation structure depending on their hunting strategy. Male lions (*Panthera*

leo), which use an ambush strategy, primarily hunted in areas of high structure relative to their female counterparts, which use a social hunting strategy (Loarie et al., 2013). Likewise, movement decisions by animals can be influenced by habitat structure and mode of locomotion. For example, movement paths of arboreal primates through tree canopies were influenced by 3D connectivity of canopy structure that likely facilitated efficient locomotion (McLean et al., 2016). Even the 3D shape of space between structures may influence animal ecology; foraging success of the predators of mud crabs (*Eurypanopeus depressus*) was influenced by components of 3D interstitial space produced by the spatial arrangement of oyster (*Crassostrea virginica*) shells (Hesterberg et al., 2017).

Anthropogenic alteration of 3D structure also can affect habitat use and subsequent animal fitness. For example, abundance, clutch size, and nesting success of grassland songbirds were influenced by the presence of and distance to human infrastructure (Nenninger and Koper, 2017; Daniel and Koper, 2019). A recognition of the importance of 3D habitat structure to ecology has led to: (1) calls to more broadly integrate 3D components of habitat into studies of wildlife ecology (Davies and Asner, 2014; D'Urban Jackson et al., 2020; Lepczyk et al., 2021); and (2) increased use of remote sensing tools (e.g., photogrammetry, structure from motion, and lidar) to characterize 3D structure in both terrestrial (Ahmed et al., 2014; Olsoy et al., 2015; Adams and Matthews, 2018) and marine environments (Irish and Lillycrop, 1999; Chen, 2019; Lochhead and Hedley, 2021).

Three-dimensional structure can influence perception of the environment by animals and humans by changing accessibility of sensory information, which could have strong effects on fitness (McNamara and Dall, 2010; Munoz and Blumstein, 2012). Interactions with structure by soundwaves alter propagation of sound through an environment and thus the accessibility of sonic information (Aylor, 1972a,b). Similarly, physical elements in the environment such as vegetation or terrain can block sightlines and thus alter the range at which visual information can be gathered (Aspbury and Gibson, 2004; Embar et al., 2011). The area from which visual information is accessible to animals in natural settings has been described as “visibility” or “viewshed” (e.g., Coleman and Hill, 2014; Davies et al., 2016). Although these terms are often applied interchangeably, it is useful to define them separately. Visibility refers to the property of the habitat that relates habitat structure to accessibility of visual information. The viewshed is an estimate of that property, defined as all the spatially explicit sightlines accessible from one vantage point (Aben et al., 2018). Habitat structure can block sightlines in multiple directions, thereby altering an individual’s viewshed (Embar et al., 2011).

Visibility has far-reaching influence on the ecology and behavior of animals and humans. Visual cues are used to locate resources (Potier et al., 2016), select mates (Detto, 2007), communicate

(Menezes and Santos, 2020), determine movement paths (Aben et al., 2021), and evaluate risk (Potash et al., 2019), or detect danger (Acebes et al., 2013), and consequently they strongly influence space use and habitat selection by animals (Table 2-1). For example, red-capped cardinals (*Paroraria gularis*) spent more time in areas of their territory with high visibility where conspecific invaders were easy to detect (Eason and Stamps, 2001), and anole lizards (*Anolis aenus*) defended smaller territories where visibility was limited, likely due to the increased energetic costs of defending low-visibility territories (Eason and Stamps, 1992). Similarly, locations of leks in ground-displaying birds is constrained by the need for extensive visibility that facilitates attraction of mates and detection of predators (Aspbury and Gibson, 2004; Alonso et al., 2012). The influence of visibility (or lack thereof) on predator-prey interactions is particularly striking. For example, the most important predictor of lion kill sites was the viewshed experienced by the prey; lion kills were twice as likely in areas where the viewshed of their prey was limited (Davies et al., 2016). Multiple studies have documented that African ungulates generally select for habitat with wide-ranging visibility (Riginos and Grace, 2008; Riginos, 2015). Similarly, space use and perceived safety by humans in urban environments are influenced by visibility (Loewen et al., 1993; Haans and de Kort, 2012).

Table 2-1 Examples of behaviors that are influenced by visibility in animals and humans.

Behavior	Taxa	Citations
Resource Detection	black kite (<i>Mivus migrans</i>) and Harris's hawk (<i>Parabuteo unicinctus</i>)	Potier et al., 2016
	great cormorant (<i>Phalacrocorax carbo</i>)	White et al., 2007
	fiddler crab (<i>Uca mjoebergi</i>)	Detto, 2007
Mate Detection and Selection	great bustard (<i>Otis tarda</i>)	Alonso et al., 2012
	greater sage grouse (<i>Centrocercus urophasianus</i>)	Aspbury and Gibson, 2004
	fox squirrel (<i>Sciurus niger</i>)	Potash et al., 2019
Risk Evaluation and Subsequent Space Use	guanaco (<i>Lama guanicoe</i>)	Acebes et al., 2013
	human (<i>Homo sapiens</i>)	Haans and de Kort, 2012
	anole lizard (<i>Anolis aenus</i>)	Eason and Stamps, 1992
Territory Establishment and Defense	red-capped cardinal (<i>Paroraria gularis</i>)	Eason and Stamps, 2001
	western gull (<i>Larus occidentalis</i>)	Ewald et al., 1980
	placid greenbul (<i>Phyllastrephus placidus</i>)	Aben et al., 2021
Movement and Navigation	common swift (<i>Apus apus</i>)	Dokter et al., 2013
	capercaillie (<i>Tetrao urogallus</i>)	Graf et al., 2007

In the study of human sensation and perception, it is well-known that physical position of a person relative to the 3D structure around them influences what can be visually perceived (Gibson, 1979). Lecigne et al. (2020) argued that physical perspective influences the viewshed of wildlife, as well. Accounting for physical position may be important for researchers attempting to determine the influence of viewshed on habitat selection by species with access to different perspectives. For example, we expect that because of their ability to fly, birds can access a wide range of perspectives within their environment, whereas visibility of ground-dwelling species will be constrained to a greater degree by vegetation structure (Fig. 2-1). Additionally, due to diverse ecological drivers,

different ecosystems may have different 3D structures (e.g., forest vs. grassland), and all species are likely influenced by the 3D structures within which they evolved and persist. Non-vegetative 3D structures such as topography and human infrastructure also can influence visibility and subsequent space use (Aspbury and Gibson, 2004; Parsons et al., 2021). Despite the importance of visibility in animal ecology and the expected influence of 3D structure on visibility, no assessment has been conducted to evaluate the influence of ecosystem-specific structure and animal position on visibility.

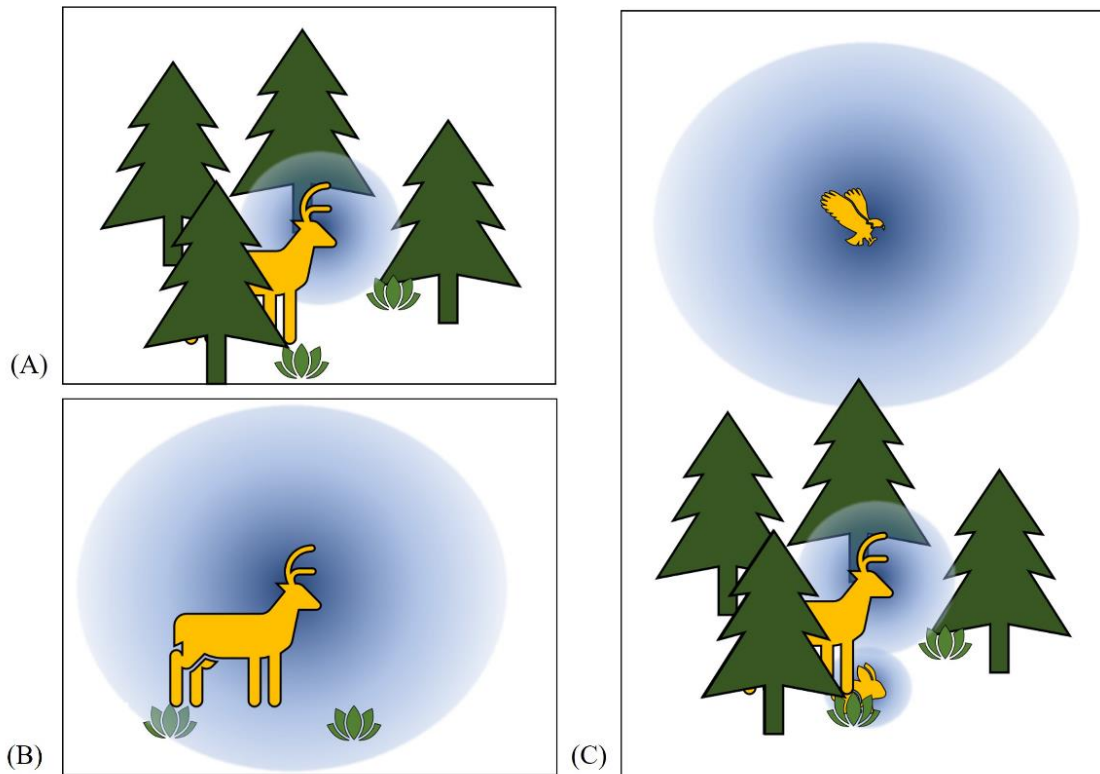


Figure 2-1 Conceptual representation of hypothesized relationships between visibility (blue spheres) and habitat structure and perspective. (A and B) Ecosystems with extensive vegetation structure (e.g., forests) will afford smaller viewsheds relative to ecosystems with little structure (e.g., prairies). (C) Animal position within habitat structure will influence viewsheds, with visibility generally increasing with eye-height above the ground.

The objective of this study was to assess how visibility may change across diverse natural environments as a function of ecosystem type, 3D structure, and perspective within that structure. We quantified fine-scale habitat structure using terrestrial lidar and used the R package *viewshed3d* (Lecigne et al., 2020) to estimate viewsheds within plots sampled at four sites representing disparate ecosystems: forest, shrub-steppe, prairie, and desert. Viewsheds measured within each ecosystem were evaluated relative to habitat structure as well as perspectives (i.e., eye-heights) accessible to native wildlife that inhabit those environments. We expected that both viewshed extent and variability would differ across eye-heights, and that values would differ among ecosystems with contrasting vegetation structure. To our knowledge, this is the first time that these relationships have been

examined in any terrestrial ecosystem. Additionally, this is the first application of the lidar-*viewshed3d* method to ecosystems other than forests. Advancing understanding about how both habitat structure and perspective can influence visibility will increase our ability to assess the mechanisms by which habitat structure influences the ecology and behavior of animals and contribute to more realistic estimates of habitat selection and use.

Materials and Methods

Study Sites

We selected study sites within four ecosystems in the western United States: forest, shrub-steppe, prairie, and desert (Figure 2-2). These ecosystems represent a gradient of vegetation structures from prairie, which has little structure and no canopy, to shrub-steppe and desert, which have moderate structure with a single-layer shrub canopy, to forest, which has relatively dense vegetation structure and a multi-layer arboreal canopy. Within each study site, we selected plots that represented the breadth of vegetative structures within the ecosystem to understand how visibility can change in those ecosystems as a result of ecosystem-specific structures. In the forest, vegetative structure differed among plots to a greater degree than other ecosystems because tree species composition and density varied among forest plots.

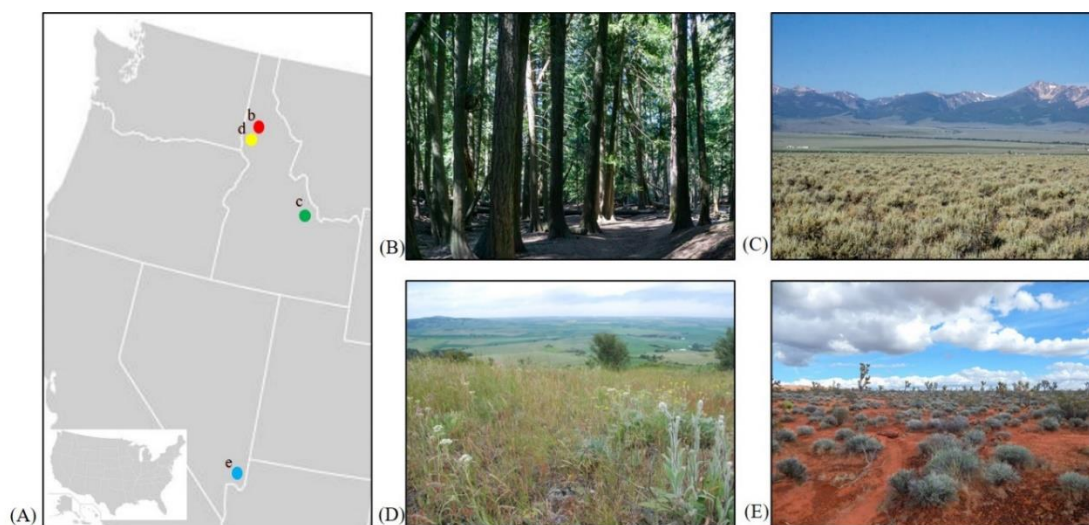


Figure 2-2 (A) Locations of study sites in the western USA. (B) Forest site at the University of Idaho Experimental Forest near Moscow, ID (red dot). (C) Shrub-steppe site in the Lemhi Valley, ID (green dot). (D) Prairie site at the Dave Skinner Ecological Preserve and Thorn Creek Native Seed Farm near Moscow, ID (yellow dot). (E) Desert site at Gold Butte National Monument in southern NV (blue dot).

The forest site was located at the University of Idaho Experimental Forest (UIEF) on Moscow Mountain, Idaho (Figures 2-2 A,B). The UIEF is a temperate coniferous forest with average temperatures ranging from -6°C in winter to 31°C in summer. Precipitation averages 70 cm annually (NOAA, 2021). The UIEF supports ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga*

menziesii), western larch (*Larix occidentalis*), and western red cedar (*Thuja plicata*). Diverse wildlife species are present including snowshoe hares (*Lepus americanus*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*), as well as a variety of birds.

The Lemhi Valley, a high elevation valley situated 1,180 m asl in east-central Idaho was selected as the shrub-steppe site (Figures 2-2 A,C). Average temperatures range from -15°C in winter to 28°C in summer. The area annually receives about 43 cm of precipitation, most of it falling as snow (NOAA, 2021). The site is dominated by Wyoming big sagebrush (*Artemis tridentata*) with a sparse grass and forb understory. This site supports pygmy rabbits (*Brachylagus idahoensis*), American badgers (*Taxidea taxus*), coyotes, American pronghorn (*Antilocapra americana*), and diverse bird species.

We sampled a remnant of the endangered Palouse Prairie ecosystem at the Dave Skinner Ecological Preserve and the Thorn Creek Native Seed Farm near Moscow, Idaho (Figures 2-2 A,D). Being located less than 30 km from the UIEF, this site is subject to the same climate. Palouse Prairie is a short-grass prairie composed of a multitude of small grasses and forbs including plants belonging to the sunflower (*Asteraceae*), bunchflower (*Melanthiaceae*), lily (*Liliaceae*), legume (*Fabaceae*), parsley (*Apiaceae*), rose (*Rosaceae*), broomrape (*Orobanchaceae*), and grass (*Poaceae*) families. Most of the historic extent of Palouse Prairie has been converted into farmland, and the few remaining remnants occur almost exclusively on the tops of ridges that are too rocky for agriculture. The site is regularly utilized by white-tailed deer, American badgers, coyotes, cottontails (*Sylvilagus* spp.), and diverse birds.

We sampled Mojave Desert vegetation at Gold Butte National Monument in southern Nevada (Figures 2-2 A,E). The site receives <2 cm of precipitation annually. Average temperatures vary from -3°C in winter to 36°C in summer (NOAA, 2021). Joshua trees (*Yucca brevifolia*), creosote bushes (*Larrea tridentata*), and white bursage (*Ambrosia dumosa*) are prominent as are a number of cholla (*Cylindropuntia* spp.) and manzanita (*Arctostaphylos* spp.) species. Kangaroo rats (*Dipodomys* spp.), black-tailed jackrabbits (*Lepus californicus*), bighorn sheep (*Ovis canadensis nelson*), coyotes, and desert tortoises (*Gopherus agassizi*) are supported by the site as are numerous bird species.

Data Collection

At each site, we established circular plots with a 12-m radius within which we gathered terrestrial lidar data to compile three-dimensional (3D) point clouds of fine-scale habitat structure. We selected plots within the forested ecosystem ($n = 10$) that encompassed a wide range of stand

types and structures. Plots at the shrub-steppe ($n = 6$) and desert ($n = 5$) sites were selected in areas of known animal activity determined by scat and track identification. Due to the limited extent of the prairie site, we placed plots ($n = 6$) in locations that encompassed only prairie vegetation and no other encroaching ecotypes. We sampled more plots in the forest because of the greater structural diversity relative to the other ecosystems. Plot size was constrained by the limited spatial extent associated with terrestrial lidar, and plot shape was selected reflecting the *viewshed3d* method, which measures sightlines within a sphere (Lecigne et al., 2020).

We collected terrestrial lidar data using a Leica BLK360 Imaging Laser Scanner (Leica Geosystems, St. Gallen, Switzerland) on a tripod typically set at 1.3 m above the ground; we occasionally lowered the height of the tripod and scanner to accommodate uneven terrain or dense vegetation. We completed 15–25 scan locations per plot depending on vegetation density and structure; sites with great vegetation complexity (e.g., forest) required more scans to overcome the increased occlusion from the high level of structure (Van der Zande et al., 2006). The BLK360 is a multiple return scanner that collects data using an 830 nm infrared laser with a beam divergence of 0.4 mrad. The scanner was set to collect data at its standard point density (1 cm at 10 m). Before scanning, we deployed highly reflective targets visible from multiple scan locations.

Within each plot, we stitched individual scans together to create a single large point cloud detailing the structure of the entire plot (Figure 2-3 and 2-4). This process began with the software ReCap Pro v6.0 (Autodesk, San Rafael, CA, United States). Reflective targets provided spatial reference points that the software used to create a rough alignment of scans. We then imported the oriented scans into CloudCompare v2.11.3 (CloudCompare, 2021) and used the iterative closest point (ICP) algorithm tool for fine-scale alignment. The scans were merged into a single point cloud and the reflective targets were removed using the segment tool. Because of relatively large differences in the amount and composition of vegetation across ecosystems (Figure 2-5), resulting point clouds ranged in size from 20 to 97 million points. Lastly, we used ReCap Pro to define the center ground point as 0,0,0; the X,Y orientation was randomly assigned by the program, and Z was designated as elevation above the ground.

We measured 10-m viewsheds within each plot from 5 X,Y locations across multiple Z positions representing eye-heights for diverse wildlife (Figure 2-3 and 2-4). Although the importance of viewshed size and orientation is likely to differ by species, our objective was to examine how these diverse structures and positions within them can influence visibility in general, so we measured all viewsheds to the 10- m maximum constrained by size of the plots to facilitate comparison across vantage points. The first X,Y location was the plot center (X, Y coordinate 0,0). The other locations

were selected using a systematic sampling design applied to locations 2 m from the center location to ensure adequate coverage of the plot. These locations were oriented so that they intersected perpendicular axes that passed through the center of the plot, but the angle of the axes relative to the orientation of the plot was selected randomly for each plot (i.e., at X,Y coordinates: 0,2; 0,-2; 2,0; -2,0). These locations ensured that the 10-m radius viewsheds would not extend beyond the point cloud. The Z positions included terrestrial perspectives at 0.25, 0.75, and 1.5 m from the ground to represent eye-heights of small, medium, and large terrestrial animals. Aerial perspectives were assessed from 5 to 10 m above the ground in the three low-structure ecosystems (shrub-steppe, prairie, and desert), and in the forest, arboreal and aerial vantage points were placed every 5 m (from 5 to 30 m). Before measurement, spheres were projected onto the point clouds at the selected positions and evaluated to ensure they did not occur within a structure (e.g., a tree trunk; Figure 2-4). No selected positions occurred within structures and so no further adjustments to position were required. We did not measure viewsheds from vantage points > 10 m above the ground in the low-structure ecosystems and >30 m in the forest because sightlines measured from higher vantage points were not able to interact with the point clouds since viewsheds were not measured beyond 10 m. This sampling design resulted in estimation of viewsheds at 25 distinct X,Y,Z vantage points within each of the shrub-steppe, prairie, and desert plots and 45 vantage points in each of the forest plots.

We estimated spherical viewsheds at each designated vantage point within each lidar point cloud using the R package *viewshed3d* (Lecigne et al., 2020), which measures 3D sightlines in all latitudinal and azimuthal directions until they are obstructed by any lidar data point (including ground points; Figure 2-3). We set the angular resolution of the sightlines to 0.6° which produced similar viewshed estimates to lower angular resolutions but required fewer computational resources. Measurement of sightlines is reported by the package as a graph of the percent of unobstructed sightlines as a function of distance from the designated vantage point (Figure 2-3). To quantify the size of viewsheds, we calculated the area under the curve to 10 m (maximum radius of the measured viewshed) and defined it as the viewshed coefficient (VC), which is a function of the spatial extent of the viewshed in all directions.

We assessed variation of sightlines within each measured viewshed to describe variability in viewshed composition in addition to viewshed extent (Figure 2-6). Relative to each vantage point, we segmented the point cloud in the azimuth into 20 segments of 18° and estimated the VC of each segment. Next, we calculated the standard deviation and mean VC of these 20 segments to calculate a coefficient of variation for the viewshed at each vantage point within each ecosystem as a descriptive statistic of variation in viewshed composition.

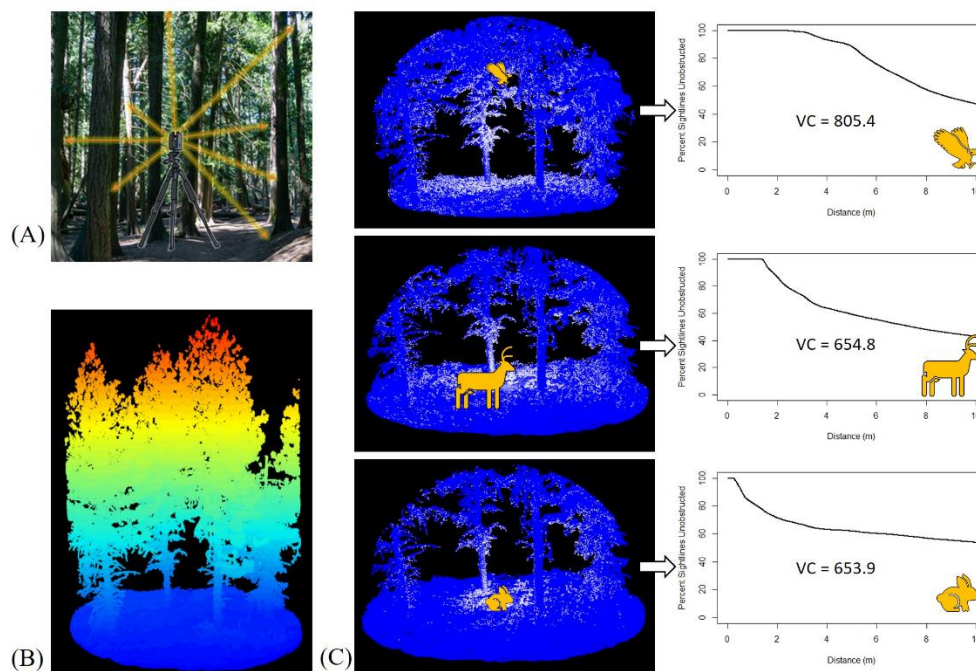


Figure 2-3 Method for estimating viewsheds. (A) Terrestrial laser scanner (TLS) used to collect data from multiple locations within a plot. (B) Scans gathered using the TLS are stitched together to produce lidar point clouds representing the habitat structure of the entire plot. Displayed is a forest point cloud, in which the color ramp shows relative elevation from low (blue) to high (red). (C) Application of *viewshed3d* to the point cloud from three eye-heights (0.25, 1.5, and 5 m) representative of animal groups that access ecosystems from those heights. The white and blue dots are lidar data points; white points are those at the ends of measured sightlines. Viewshed graphs display the percent of unobstructed sightlines as a function of distance from the animal position. The viewshed coefficient (VC) is calculated as the area under the curve and is a measure of viewshed extent.

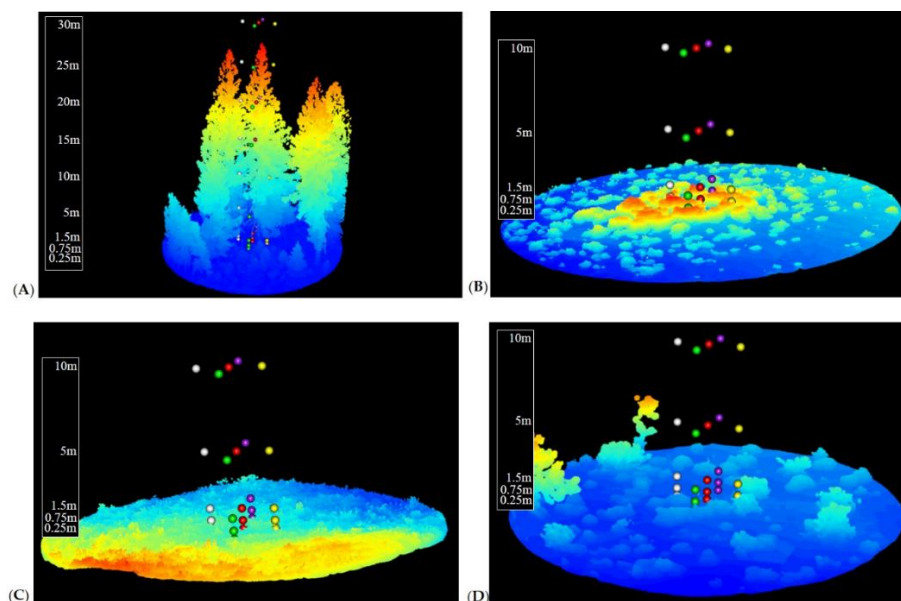


Figure 2-4 One complete 12-m radius lidar point cloud from each ecosystem: (A) forest; (B) shrub-steppe; (C) prairie; and (D) desert. The colors of the point clouds indicate the relative elevation of points within that cloud from low (dark blue) to high (red). Topography was not removed. The colored spheres represent the positions of the X, Y, Z vantage points from which viewsheds were calculated, with each color representing a single X, Y location across multiple eye-heights (i.e., Z) ranging from 0.25m to 30m (elevation displayed in scales).

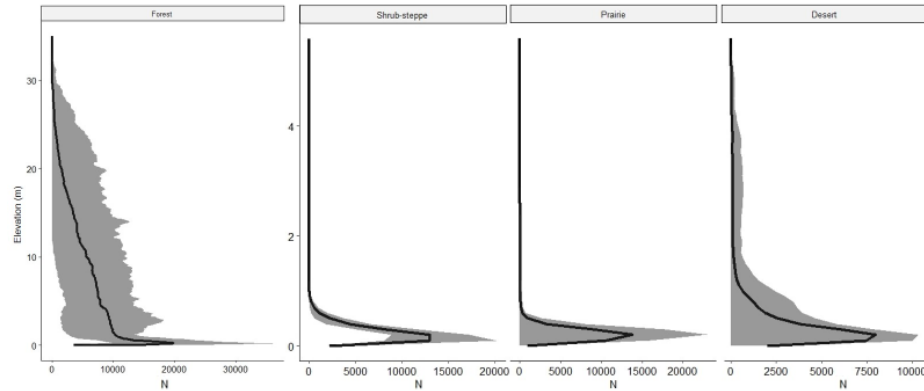


Figure 2-5 Vegetation distribution profiles calculated from the lidar point clouds representing the number of voxels (units of space occupied by some vegetation resolution 5 cm^3 , defined as N in the figure) at each elevation (m) above ground. Note: the y-axis scale differs between the forest and the three low-structure ecosystems (shrub-steppe, prairie, and desert). Mean values (line) and ranges (shaded area) for all plots in each of four ecosystems.

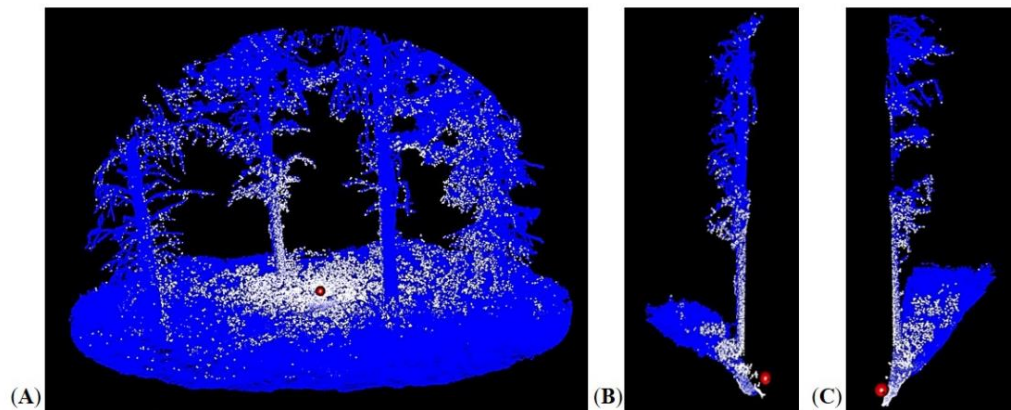


Figure 2-6 To determine variability within the viewsheds, whole point clouds were segmented in the azimuth into 20 segments of 18° each. The blue and white points are lidar data points; white points are obstructing individual sightlines. The viewshed coefficients (VC) of these individual segments were calculated and used to determine a coefficient of variation for the viewshed. This was repeated for all vantage points. (A) A full viewshed measured in a forest point cloud. (B) and (C) are adjacent viewshed segments from the same forest point cloud.

To understand the influence of vertical structural heterogeneity, we calculated roughness, which is the standard deviation of the canopy heights within 10 m of each X,Y position, using the *lidR* package (Roussel et al., 2020). Roughness was selected as the only structural metric because other standard metrics (e.g., canopy cover, basal area, etc.) were not applicable to the diversity of vegetation structures across the ecosystems we studied.

Data Analysis

Due to the hierarchical structure of the data, linear mixed-effects models were fit to data from each ecosystem. We modeled two viewshed characteristics (VC and the coefficient of variation) as separate response variables to examine the influence of explanatory variables on both the overall extent and variability of the viewshed. Explanatory variables were eye-height above the ground and roughness. Nested random effects were specified with random intercepts for plot and for X,Y location

within each plot. These models were run separately for each ecosystem using the *lme4* and *nlme* packages in R (Bates et al., 2015; Pinheiro et al., 2020). To correct for heteroscedasticity of the response variables, primarily due to relatively small variation among the higher vantage points where there was little vegetation structure, the highest eye-heights in all ecosystems were removed from analysis. Additionally, in the low-structure ecosystem models (shrub-steppe, prairie, and desert), a variance structure was imposed on the 0.25 m eye-heights to allow the response variables to have different error variances than the other eye-heights. We applied logarithmic transformation to coefficients of variation to further account for heteroscedasticity. Eye-height was modeled as a factor with levels of 0.25, 0.75, 1.5, and 5 m in all ecosystems and also 10, 15, 20, and 25 m in the forest to give the models flexibility with respect to the statistical relationship between the response variables and height (Zuur et al., 2009).

We compared modeled VCs and coefficients of variation across vantage points using the *emmeans* and *trtools* R packages (Johnson, 2021; Length, 2021). Additionally, we compared expected VCs and coefficients of variation at each eye-height across ecosystems by calculating a Wald test statistic with 95% confidence. We did not compare viewsheds measured at eye-heights in the forest that were not also measured in the low-structure ecosystems.

Results

As expected, eye-height (i.e., vantage point) strongly influenced both the extent (viewshed coefficient) and variability (coefficient of variation) of viewsheds in all ecosystems. In all models, all eye-heights were significant predictors of both viewshed coefficient (VC) and the coefficient of variation (Appendix B Tables 1, 2). In all VC models, as eye-height increased, the viewshed extent as characterized by the VC, generally increased but the relationships were not linear across the lowest vantage points in any ecosystem nor across the highest vantage points in the forest ecosystem (Figure 2-7). In the low-structure ecosystems, variability in viewsheds, characterized by coefficients of variation, decreased as eye-height increased to heights above the vegetation canopy. In the forest, however, variation in viewsheds was highest at intermediate eye-heights, and markedly lower at the lowest (0.25 m) and highest (>10 m) eye-heights (Figure 2-8).

Roughness was only a significant predictor in the desert VC model and the shrub-steppe coefficient of variation model. However, we retained it in the models to account for large differences in structure for comparisons between ecosystems (Figure 2-5). As expected, roughness was highest and most variable in the forest where average roughness was 16.6 ± 7.7 (standard deviation). Roughness was similar in the three low-structure ecosystems ($\text{roughness}_{\text{shrub}} = 1.6 \pm 0.3$, $\text{roughness}_{\text{prairie}} = 1.9 \pm 0.1$, $\text{roughness}_{\text{desert}} = 1.6 \pm 0.1$).

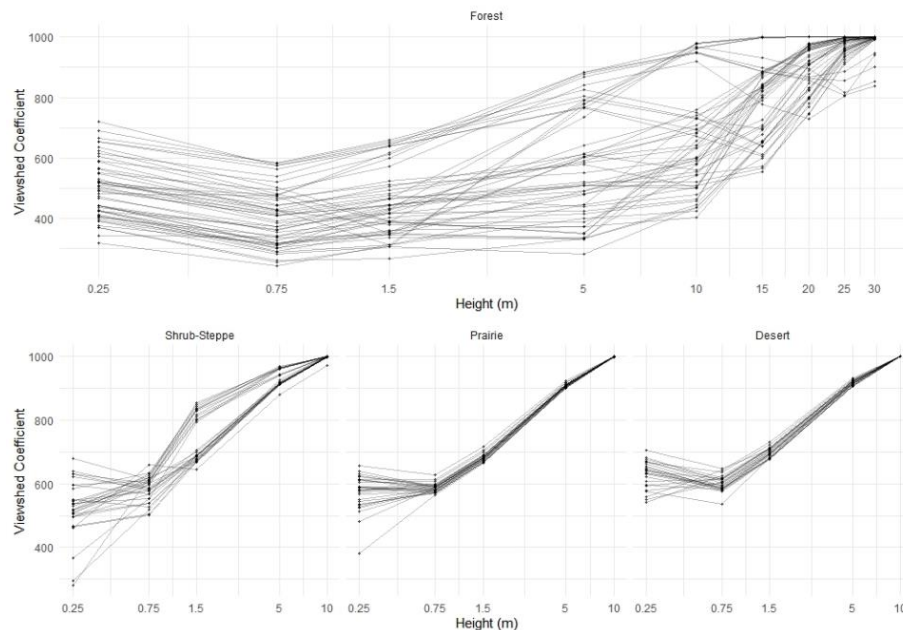


Figure 2-7 Extent of viewsheds (estimated as the viewshed coefficient, VC) as a function of eye-height across four ecosystems (forest, shrub-steppe, prairie, and desert). Points represent viewsheds at individual vantage points ($n = 25$ to 45 /plot) within multiple plots per ecosystem ($n = 5$ to 10 plots/ecosystem). Note that the x-axis is on a logarithmic scale.

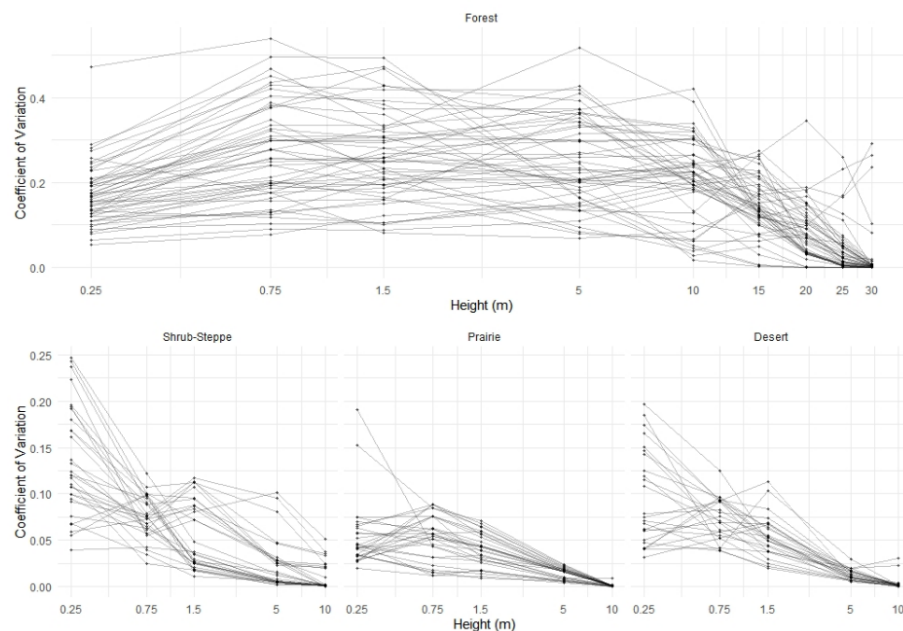


Figure 2-8 Variability of viewsheds (estimated as the coefficients of variation) as a function of eye-height across four ecosystems (forest, shrub-steppe, prairie, and desert). Points represent viewsheds at individual vantage points ($n = 25$ to 45 /plot) within multiple plots per ecosystem ($n = 5$ to 10 plots/ecosystem). Note that the x-axis is on a logarithmic scale.

Our models demonstrate the significant effect that an individual's vantage point may have on the viewshed in the measured ecosystems. Using estimates from the models, we documented that both viewshed extent and variability differed across eye-heights within each measured ecosystem. In the forest, shrub-steppe, and desert, VC differed significantly across all measured eye-heights, and in the

prairie, VC also differed except between the lowest two eye-heights (i.e., at 0.25 and 0.75 m; Appendix B Tables 3, 4). Comparisons of viewshed variability (i.e., coefficient of variation) were significantly different at most eye-heights in the forest (Appendix B Table 5), prairie, and desert, and across all eye-heights in the shrub-steppe (Appendix B Table 6). These results indicate that within the measured ecosystems, movement between vantage points can result in changes in both viewshed extent and composition.

Table 2-2 Viewshed Coefficients Across Ecosystems. Difference in viewshed coefficients (ΔVC) at each eye-height, lower and upper confidence limits (LCL and UCL) for 95% confidence intervals, and associated p-values. Where ΔVC is positive, the ecosystem listed first has a larger average VC. Where ΔVC is negative, the ecosystem listed second has a larger average VC.

Ecosystems	Eye-Height (m)	ΔVC	LCL	UCL	p-value
<i>Desert – Prairie</i>	0.25	-12.3	-62.9	38.2	0.6323
	0.75	-53.6	-104.1	-3.1	0.0376
	1.5	-52.3	-102.8	-1.8	0.0424
	5.0	-59.2	-109.7	-8.7	0.0217
<i>Desert - Shrub-Steppe</i>	0.25	26.2	-21.7	74.1	0.2841
	0.75	-64.6	-106.5	-22.8	0.0025
	1.5	-122.1	-164.0	-80.3	<0.0001
	5.0	-95.1	-136.9	-53.2	<0.0001
<i>Prairie - Shrub-Steppe</i>	0.25	38.5	-31.1	108.1	0.2783
	0.75	-11.1	-76.6	54.5	0.7411
	1.5	-69.8	-135.4	-4.4	0.0369
	5.0	-35.9	-101.4	29.7	0.2839
<i>Desert – Forest</i>	0.25	50.6	-14.0	115.1	0.1246
	0.75	614.3	549.3	679.3	<0.0001
	1.5	665.7	600.7	730.7	<0.0001
	5.0	759.4	694.4	824.3	<0.0001
<i>Prairie – Forest</i>	0.25	62.9	-19.1	144.9	0.1325
	0.75	667.9	627.0	708.7	<0.0001
	1.5	718.0	677.1	758.9	<0.0001
	5.0	818.6	777.7	859.4	<0.0001
<i>Shrub-Steppe - Forest</i>	0.25	24.4	-18.9	67.7	0.2690
	0.75	678.9	601.7	756.2	<0.0001
	1.5	787.8	710.6	865.1	<0.0001
	5.0	854.4	777.2	931.7	<0.0001

The effects of ecosystem-specific habitat structure on the viewshed were more nuanced than the effects of vantage point. Viewshed extent and variability often, but not always, differed across ecosystems when compared at the same eye-heights. The VCs were significantly different in all pairwise comparisons between the forest and low-structure ecosystems except at 0.25 m (Table 2-2). Pairwise comparisons among the three low-structure ecosystems followed a similar pattern, however, the prairie - shrub-steppe comparisons only differed significantly at 1.5 m (Table 2-2). Our results indicate that animals moving between ecosystems with large differences in the amount and type of structure (e.g., between forests and prairies) may encounter viewsheds with very different extents. Coefficients of variation differed significantly at nearly all eye-heights in comparisons between the forest and low-structure ecosystems with exceptions at 0.25 m for the desert and 0.25 and 0.75 m for the prairie (Table 2-3). The coefficients of variation differed significantly at all eye-heights in the

desert - prairie comparison, and at all eye-heights except 0.25 m in the prairie - shrub-steppe comparison. There was no significant difference in coefficients of variation at any eye-height in the desert - shrub-steppe comparison. Differences in the coefficient of variation comparisons across the low-structure ecosystems underscore the influence of diverse habitat structures (Figure 2-5) on viewsheds.

Table 2-3 Coefficients of Variation Across Ecosystems. Difference in coefficients of variation (Δ Coeff. Var.) at each eye-height, lower and upper confidence limits (LCL and UCL) for 95% confidence intervals, and associated p-values. Where Δ Coeff. Var. is positive, the ecosystem listed first has a larger average coefficient of variation. Where Δ Coeff. Var. is negative, the ecosystem listed second has a larger average coefficient of variation.

Ecosystems	Eye-Height (m)	Δ Coeff. Var.	LCL	UCL	p-value
<i>Desert – Prairie</i>	0.25	-0.840	-1.328	-0.352	0.0007
	0.75	-0.994	-1.501	-0.487	0.0001
	1.5	-1.056	-1.563	-0.549	<0.0001
	5.0	-1.506	-2.494	-0.518	0.0028
<i>Desert - Shrub-Steppe</i>	0.25	0.417	-1.391	2.225	0.6511
	0.75	0.781	-1.007	2.570	0.3941
	1.5	0.938	-0.851	2.726	0.3041
	5.0	0.690	-1.098	2.479	0.4494
<i>Prairie - Shrub-Steppe</i>	0.25	1.257	-0.484	2.998	0.1569
	0.75	1.776	0.060	3.491	0.0424
	1.5	1.994	0.279	3.709	0.0227
	5.0	2.196	0.705	3.687	0.0037
<i>Desert - Forest</i>	0.25	-0.952	-2.908	1.004	0.3400
	0.75	-3.416	-5.400	-1.432	0.0007
	1.5	-3.732	-5.716	-1.748	0.0002
	5.0	2.196	0.705	3.687	<0.0001
<i>Prairie – Forest</i>	0.25	-0.112	-2.006	1.782	0.9077
	0.75	-2.422	-4.340	-0.504	0.1332
	1.5	-2.676	-4.594	-0.758	0.0006
	5.0	-3.642	-5.361	-1.923	<0.0001
<i>Shrub-Steppe – Forest</i>	0.25	-1.369	-2.116	-0.623	0.0003
	0.75	-4.197	-5.056	-3.339	<0.0001
	1.5	-4.670	-5.528	-3.811	<0.0001
	5.0	-5.838	-6.694	-4.982	<0.0001

Discussion

Our results clearly demonstrated that both ecosystem-specific habitat structure and physical perspective within that structure can influence the viewshed. Relationships between viewshed extent and variability across eye-heights were consistent in all four ecosystems. Extent of the viewshed generally increased and variability decreased with increasing elevation of vantage points. These patterns were strongly influenced by the occluding vegetation structure and height of the canopy, which was reflected in the contrast between the three low-structure habitats (shrub-steppe, prairie, and desert) and the forest habitat (Figure 2-5). Increased density and diversity of vegetation in the forest resulted in greater variability in viewsheds at all eye-heights below the tree canopy. These results indicate that both vegetation structure and animal position in a landscape may strongly influence the potential viewshed and consequently the visual cues accessible to individual

Although the extent of the viewshed generally increased with increasing eye-height in all ecosystems as expected, this pattern was not uniform. In both the forest and desert ecosystems, VC was larger at 0.25 m than at 0.75 m (Appendix B Table 4). This increased visibility close to the ground may reflect the growth forms of shrubs in these ecosystems (e.g., snowberry in the forest and creosote in the desert) with branches that occlude sightlines at slightly higher eye-heights. In contrast, the VC was significantly smaller at 0.25 m than at 0.75 m in the shrub-steppe site where sagebrush shrubs generally produce branches nearer to the ground. These results demonstrate that perspective, ecosystem-specific structure, and their interactions can influence the extent of viewsheds. It should be noted that a majority of our scans were gathered from above these eye-heights in all ecosystems, and the differences documented in the forest and desert might be partly attributable to occlusion of understory vegetation structure by the mid-level shrub structure. However, such a bias is likely minimal in our samples because of the high point density of our data that clearly identified ground structure under shrubs (Figure 2-7), the lack of this pattern in the shrub-steppe or prairie, and previous studies that indicate that occlusion effects in terrestrial lidar data in forests occur primarily in the arboreal canopy rather than the understory (Chasmer et al., 2006).

Not only did we find that perspective and vegetation structure influenced extent of the measured viewsheds, but both properties also influenced variability of the viewshed (i.e., coefficient of variation). Generally, as eye-height increased, viewshed variability decreased, particularly in the low-structure ecosystems (Figure 2-8). However, this pattern was not as consistent in the forest where variability increased from 0.25 to 0.75 m then remained relatively constant across eye-heights until decreasing at vantage points >10 m (Figure 2-7 and Appendix B Table 2). This zone of relatively high variation in the forest may occur because vegetation from both the understory and overstory occluded sightlines; heterogeneity in either one or both is likely to have a strong influence on variability of the viewshed. Similar to viewshed extent, interactions between perspective and vegetation structure significantly influenced variability of the viewshed. Effects of occlusion due to dense vegetation near the ground in the low-structure ecosystems, and in the highest parts of the arboreal canopy may have influenced these results, although, as with the VC results, the effects of occlusion on variability at the lower eye-heights are likely to be minimal.

Understanding how both viewshed extent and variability differ has important implications for animal ecology. The extent or size of a viewshed provides information about accessibility of visual cues whereas viewshed variability might reveal how other properties associated with 3D habitat structure also influence habitat selection in conjunction with visibility. For instance, selection for concealment (i.e., the property of habitat in which 3D structure hides animals from visual detection

by others), might influence an animal's selection for viewshed variability. Although visibility and concealment often are inversely related, they are not direct opposites, and animals can select for visibility and concealment somewhat independently (Camp et al., 2013). Heterogeneity of 3D structure is likely the primary factor that allows these properties to be decoupled. Thus, selection for viewshed variability may illuminate how animals select for both visibility and concealment simultaneously. We hypothesize that animals with access to vantage points with high variation in both viewshed extent and variability will have greater opportunities to select for visibility within their environments. Although studies have investigated the influence of visibility on medium to large-bodied (Acebes et al., 2013; Riginos, 2015), arboreal (Potash et al., 2019), and aerial species (Eason and Stamps, 2001), our results suggest that small, terrestrial animals may be ideal for studying fine-scale selection for visibility (and other properties of 3D structure) because they appear to have access to relatively large variation in viewsheds, at least in the ecosystems we assessed (Figures 2-7, 2-8). Access to vantage points with high variation in viewsheds also may have implications for biodiversity. High variation in accessible viewsheds may provide opportunities for multiple species with diverse visibility requirements to select for visibility relevant to their needs within the same environment. Because 3D structure can strongly influence multiple aspects of animal ecology including predator-prey interactions (Gibson et al., 2018), reproduction (Nenninger and Koper, 2017), foraging (Hesterberg et al., 2017), communication (Menezes and Santos, 2020), and movement patterns (McLean et al., 2016), it also influences biodiversity in terrestrial (MacArthur and MacArthur, 1961) and aquatic ecosystems (Price et al., 2019). Consequently, access to variable viewsheds may be an additional mechanism by which 3D structure influences biodiversity.

Our work has several limitations and opportunities for advancing understanding and measurement of visibility in ecological systems. First, the scope of this study is limited to four sites that represent specific ecosystems in the United States. Although our results may generally apply to other ecosystems with similar vegetation structures, we expect that differences in ecological drivers and vegetation composition will influence viewsheds differently across other systems, even habitats similar to those we measured. Second, although we could capture point clouds defining all vegetation structure in the shrub-steppe, prairie, and desert ecosystems, the upper canopy in the densest forest plots may not be well represented in our lidar data because it was gathered using a terrestrial laser scanner, which is generally most effective at estimation of structure in forests below the canopy (Chasmer et al., 2006; Hilker et al., 2012). Missing data points in the forest canopy may have caused some inaccuracies in viewsheds measured from the highest vantage points. We recommend that researchers focused primarily on those perspectives consider methods that would allow consistent data collection of structure relevant to those perspectives (e.g., UAV lidar). Additionally, as this study

was focused on visibility as a property of habitat structure, we did not account for species-specific visual acuity. Researchers interested in estimating realized viewsheds (i.e., viewsheds accessible to animals defined by visual acuity) should consider limiting viewsheds to a distance equivalent to that from which the species of interest can gather visual cues. In this study, the size of the viewsheds was set to the spatial extent of our point clouds. If visual acuity is of interest, point clouds should be gathered over spatial extents that allow estimation of viewsheds applicable to the species of interest. Finally, our study was focused on terrestrial visibility purely as a function of 3D structure, and we did not account for factors other than visual acuity that also could influence access to visual information. For example, in aquatic systems, water quality and penetration of light into water layers influences behavior of aquatic animals (Ranåker et al., 2012; Beltran et al., 2021), and similarly in terrestrial systems, precipitation, fog, or pollution also might limit visibility.

Researchers studying specific species also should account for the ecological and evolutionary relevance of visibility to their species when designing studies. For example, Embar et al. (2011) documented that presence of specific predators influenced whether gerbils (*Gerbillus andersoni allenbyi*) perceived greater risk when aerial or terrestrial sightlines were blocked; in the presence of terrestrial predators, occlusion of terrestrial sightlines was associated with elevated risk, however, the relationship was reversed in the presence of aerial predators. These results suggest that researchers interested in selection of viewsheds by prey should consider the ecology of the predators. For example, their studies may benefit from segmenting the point clouds latitudinally into aerial and terrestrial viewsheds (a function that is now available in recent updates of viewshed3d) to estimate relevant sightlines. Likewise, specific portions of viewsheds might have ecological significance for detection of resources or communication with conspecifics, and tailoring the approach to the ecology of the specific system is necessary to achieve robust inferences.

Estimation of viewsheds provides an avenue for advancing understanding of the mechanisms by which 3D habitat structure influences the ecology and behavior of animals. Because ecosystem-specific structure significantly influences the viewshed, it may be an evolutionary driver of animal behavior. Snowshoe hares which evolved in and inhabit forest ecosystems, selected for locations with few sightlines but significant structure that aids in escape (Morris and Vijayan, 2018) in contrast to gerbils in a desert ecosystem that perceived greater risk when sightlines were blocked (Embar et al., 2011). Generally, the desert ecosystem in our study provided larger viewsheds with less variation than the forest (Figures 2-2, 2-4/5, 2-7/8), which might influence evolution of divergent anti-predator strategies. In our prairie site, and likely in most prairies, the primary structure blocking sightlines was created by topographic relief. Terrain also can influence availability of and selection for visibility in

shrub-steppe habitats like those in our study; leks of greater sage grouse (*Centrocercus urophasianus*) were located at sites with enhanced short-range visibility where females could more readily observe potential mates, but leks were characterized by reduced long-range visibility, which could influence detection of predators (Aspbury and Gibson, 2004). Likewise, differences in visibility across ecosystems and perspectives also may shape dynamic habitat use during movement. For example, Aben et al. (2021) reported that visibility influenced where birds flew within 3D space. Visibility afforded as a function of 3D habitat structure may strongly drive the ecology and evolution of animal communication, as well. Habitat structure was a strong evolutionary driver in development of aerial sexual displays in birds; open-habitat passerines had an evolutionary gain of aerial displays six times more frequently than forest passerines (Menezes and Santos, 2020). For example, changes in visibility as a result of 3D structure also can influence use of other communication channels. When visibility was limited by 3D structure and vegetation growth, animals altered the number and acoustic structures of vocal signals (Waser and Waser, 1977; Yahner, 1980; Koda et al., 2008).

Although visibility may strongly influence both terrestrial and aquatic animals, it is not well integrated into studies of animal ecology (Aben et al., 2018). Because visibility can affect multiple aspects of ecology and evolution from resource detection to movement decisions (Table 2-2), the paucity of studies that integrate visibility as an ecologically relevant factor represents a large gap in the animal ecology literature. However, increasing availability of remotely sensed 3D data products (e.g., lidar, structure from motion) may provide resources for addressing this deficit (e.g., D'Urban Jackson et al., 2020; Lepczyk et al., 2021). To date, the viewshed3d method has only been applied to terrestrial lidar data but may be applicable to point clouds gathered by other remote sensing systems. Additionally, the viewshed3d method is not the only approach to estimating visibility. For example, researchers have measured horizontal sightlines from digital surface models derived from airborne lidar data (Davies et al., 2016, 2021). The advantage of the viewshed3d method is its ability to measure sightlines that penetrate gaps in 3D vegetation structure (Lecigne et al., 2020). Our work demonstrates that properties of viewsheds differ among and within landscapes in complex ways, and adds to an emerging understanding of how 3D structure can shape interactions among individuals and between organisms and their environments.

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Chapter 3: Under Cover: The Nuanced Influence of Visual Properties on Resource Selection by Prey

Abstract

Animals at risk of predation select habitat that enhances security from predators. Two properties of cover related to security are concealment (i.e., habitat structure that blocks an individual from detection by others) and visibility (i.e., visual information accessible relative to habitat structure). Although these properties are often negatively correlated, they are not always inverse; animals in habitat with heterogenous structure maybe be able to select for both. We investigated habitat use by pygmy rabbits (*Brachylagus idahoensis*) at two scales (patch and microsite) to evaluate the influence of both structural properties of cover and visual properties (concealment and visibility) on habitat use by prey. We contrasted habitat properties at paired used and unused patches. At each patch, we randomly selected three microsities at which we measured concealment using photographic analyses and viewshed (i.e., visibility) and structural density using lidar. We also measured the heights of the three tallest shrubs. Additionally, at each microsite within used patches, we assessed the density of fecal pellets as an index of intensity of use and also measured distance to nearest burrow. Concealment and visibility were evaluated in three orientations important for assessing predation risk: aerial, terrestrial, and overall. At the patch scale, rabbits selected for structural properties of cover (dense vegetation and tall shrubs), but not visual ones. Pygmy rabbits more intensively used microsities associated with high terrestrial concealment in proximity to burrows. Our results suggested that pygmy rabbits may perceive greater threat from terrestrial as opposed to aerial predators at both scales, and they also indicate a nuanced relationship between properties of cover and habitat use.

Introduction

Cover is an important concept in animal-habitat relationships across taxa, however, the mechanisms underlying selection for cover, and often the property itself, remain poorly described. Cover, which we define as structures within environments (e.g., topography, vegetation, buildings, other animals), potentially provides many functions to wildlife including, physical shelter from the elements (Lambertucci and Ruggiero 2013), protection from predators (Caselli et al. 2017), substrates for occupation (e.g., nests in vegetation and burrows in soil or snow; Onrizal and Bahar 2019, Glass et al. 2022), thermal shelter (Milling et al. 2017), and forage for herbivores (Rettie and Messier 2000). Because of these diverse functions, ecologists have long called for more nuanced assessment of cover to achieve a mechanistic understanding of its importance to wildlife (Elton 1939). However, generalized measures of the amount of cover are still common even though they provide limited information on why animals select for that cover.

A key function of cover for prey species is contribution to security from predation. Predation shapes almost all aspects of prey ecology and behavior (Lima and Dill 1990), and consequently prey select for habitat that facilitates security by providing physical protection (Lambertucci and Ruggiero 2013), facilitating escape (Morris and Vijayan 2018), making the individual difficult to detect or discern (Gotmark et al. 1995, Dimitrova and Merilaita 2009), and facilitating detection of predators (Aspbury and Gibson 2004, Acebes et al. 2013). Cover can contribute to security by influencing both concealment and visibility. Concealment refers to the property of habitat whereby structure blocks an individual from visual detection by others (Mysterud and Ostbye 1999). Sites that confer concealment can prevent an individual from being detected by potential predators, thus preventing a predation attempt from occurring. Animals may also select habitat for visibility, which is a property describing the visual information accessible to an individual as a function of habitat structure (Aben et al. 2018). Access to visibility allows prey to detect a potential predator and engage in behaviors that reduce predation risk including fleeing or seeking refuge (Camp et al. 2012) and producing alarm calls that signal conspecifics (Le Roux et al. 2009) or predators (Blumstein 2007). Although there has been a heavy emphasis in the literature on concealment, for some species, visibility may be more important than concealment for avoiding injury or mortality (Embar et al. 2011).

Because concealment and visibility are related to visual information relative to the surrounding habitat, they may be correlated with each other. Camp et al. (2013) documented that concealment and visibility were inversely related, but they also documented relatively high variation among sites, suggesting that animals might not be subject to a direct tradeoff between the two visual properties. Although related to habitat structure, the two properties differ in that concealment is influenced by the size and position of the animal's body relative to habitat structure (Campos et al. 2009), whereas visibility can change as a function of the position of the individual's eye relative to fine-scale three-dimensional structure (Stein et al. 2022). Therefore, these visual properties might be decoupled in habitats with dense heterogeneous structure that provides concealment but also visibility via fine gaps in the vegetation structure. For example, Stein et al. (2022) demonstrated that habitat with dense and heterogeneous structure was correlated with highly variable sightline lengths. Consequently, although both properties are influenced by habitat structure, animals might not be constrained to selecting for only one of these visual properties.

Because perception of predation risk is influenced by the ecology of the prey and their predators, animals might select for concealment and visibility in specific orientations. For example, in the presence of barn owls (*Tyto alba*), gerbils (*Gerbillus andersoni allenbyi*) perceived the highest risk in areas with limited aerial visibility, and in the presence of red foxes (*Vulpes vulpes*), they

perceived the highest risk in areas with limited terrestrial visibility (Embar et al. 2011). Similarly, Potash et al. (2019) found that perception of risk by fox squirrels (*Scuirus niger*) was associated canopy openness (i.e., aerial structure), which may be related to high risk from avian predators. Despite these findings, previous studies have rarely considered orientation of cover, and fewer have estimated both concealment and visibility in multiple orientations.

Because cover can provide multiple functions of differential importance, animals may select habitat for cover properties differently across spatial scales. Scale-dependent habitat selection has been documented in many taxa (e.g., Yan et al. 2013, Atuo and O'Connell 2017) and has traditionally been connected to level of need in which animals select resources to satisfy critical requirements at larger spatial scales (Kotliar and Wiens 1990). For example, cover provides both security and forage for caribou (*Rangifer tarandus*); at the seasonal home-range scale caribou selected habitat types associated with decreased wolf (*Canis lupus*) presence, but at the daily home-range scale, caribou selected habitat with higher quality forage (Rettie and Messier 2000). Thus, scale should be considered as an important influence on how animals select for properties of cover.

Our objective was to investigate how different properties of cover associated with security influence habitat use by prey at two spatial scales. Like all leporids, pygmy rabbits (*Brachylagus idahoensis*) are subject to intense predation by a suite of avian and terrestrial predators that strongly influence their habitat selection and so are an ideal model to investigate selection for secure properties of cover. Although pygmy rabbits strongly select for dense vegetation structure, both concealment and visibility can influence their perception of risk (Camp et al. 2012). Pygmy rabbits are endemic to the sagebrush-steppe of the western USA and excavate burrows that are used as thermal shelter and predation refuges (Camp et al. 2012, Milling et al. 2017). However, they frequently rest above ground, even during thermal extremes, and selection of habitat outside the burrow is influenced by perception of predation risk (Milling et al. 2017). McMahon et al. (2017) documented that at the patch scale, pygmy rabbits selected and more intensely used patches with habitat structure associated with security including dense herbaceous vegetation, tall shrubs, high aerial concealment, and presence of burrows. Evaluation of microsite use during experimental trials with captive pygmy rabbits revealed a preference to feed at sites closer to burrows and with greater structure in the terrestrial orientation but not the aerial orientation (Crowell et al. 2016). Perception of risk also was influenced by distance to burrows for free-ranging rabbits (Camp et al. 2012).

Because habitat selection can differ markedly across scales, we evaluated hypotheses about habitat use by free-ranging pygmy rabbits at microsites and within broader habitat patches. At the patch-scale, we hypothesized that structural properties of cover would influence habitat use, and we

predicted selection for patches vegetation with relatively dense structure and with taller shrubs than generally available which contribute to multiple functions of cover. We also hypothesized that visual properties of cover would influence selection because perception of risk is influenced by concealment and visibility (Camp et al. 2012). We expected rabbits to select for greater concealment and also select for higher visibility if a strong negative relationship between the two properties did not force a tradeoff. Because we expected that structural properties of cover and concealment would be strongly selected at the patch scale, we hypothesized that rabbits would more intensely use microsites with relatively high visibility to facilitate detection of predators. Burrows represent security from most predators, and we expected that proximity to burrows also would influence use of microsites. Finally, because pygmy rabbits have a diverse suite of avian and terrestrial predators, we explored whether the orientation of visual properties of cover (terrestrial, aerial or overall) also influenced habitat use. Ecological knowledge of the mechanistic links between the functional properties of cover and selection of habitat by wildlife may be advanced by a better understanding of the perceptual cues used by prey to select secure habitat.

Methods

Study Site

We conducted our study during June-July in 2021 and 2022 in the Lemhi Valley located in east-central Idaho, USA. The Lemhi Valley is a high elevation valley 1,180 m a.s.l. that annually receives 43 cm of precipitation, primarily in the form of snow (NOAA 2023). Wyoming big sagebrush (*Artemis tridentata*) is the dominant shrub, but other sagebrush species are also present including three-tip sagebrush (*A. tripartita*) and black sagebrush (*A. nova*). Green rabbitbrush (*Chrysothamnus viscidiflorus*) and rubber rabbitbrush (*Ericameria nauseosa*) are common sub-shrubs, and the sparse understory contains numerous forbs (e.g., buckwheat; *Eriogonum* spp) and grasses (e.g., fescue; *Festuca* spp.). In addition to pygmy rabbits and other prey species, the site supports diverse terrestrial predators including badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and long-tailed weasels (*Mustela frenata*), and numerous avian predators (e.g., hawks, *Buteo* spp.; northern harriers, *Circus cyaneus*; and short-eared owls, *Asio flammeus*). At our study site, small topographic mounds called ‘mima mounds’ support relatively dense vegetation growth that creates habitat patches where pygmy rabbits excavate burrows and focus above-ground activity (Parsons et al. 2016). Individual rabbits use burrow systems within multiple mima mounds within their home ranges simultaneously, and the ranges of individuals and their associated mounds overlap (Estes-Zumpf and Rachlow 2009, Sanchez et al. 2009).

Habitat sampling

We collected estimates of habitat properties within patches of habitat associated with mima mounds that were used by rabbits and within paired, unused patches. In 2021, as part of another study, we trapped pygmy rabbits using wire-box traps and fitted them with radio telemetry collars. Rabbits were tracked to a patch that we identified as active both by the presence of the rabbit and the presence of fresh pellets and open burrows (Sanchez et al. 2009). The nearest patch with no evidence of activity (i.e., no pellets or evidence of digging) was identified as the paired, unused patch. We did not encounter any instances in which there were two unused patches equidistant from the used patch. During 2022, we conducted burrow surveys to identify pairs of actively used patches and nearby unused patches that were not sampled during 2021. Within each patch, we measured the heights of the three tallest shrubs and gathered data on visual properties at three randomly selected microsites. We also counted fecal pellets within a 0.25m² plot to index intensity of microsite use and recorded distance to the nearest burrow. Microsite measurements were also gathered at 26 additional used patches as part of the other study.

Concealment estimation

We used image classification to assess concealment of a red sphere approximately the size of a pygmy rabbit placed on the ground at each microsite (Fig 3-1). We photographed the sphere from a distance of 4 m in each of the cardinal directions at a height of 1 m above the ground following previous methods (e.g., Camp et al. 2013). We also photographed the sphere from above from a height of 1.3 m. Each photograph was first cropped to fit the sphere. We used ENVI (Classic 5.6.2) to conduct a supervised maximum likelihood classification with three classifications: sphere, structure, and cropped area outside of the sphere. Pixels representing each category were counted to estimate percent concealment of the sphere using the following equation: $(\text{structure}/\text{sphere} + \text{structure}) * 100$. In photographs with high occlusion of the sphere that prevented us from identifying the edges for cropping, we used an alternate approach in which we classified the photograph into two categories, sphere and everything else. We then compared the classification to a reference photograph of an unobstructed sphere gathered in the field. To estimate percent concealment, the following equation was used $((\text{sphere}_{\text{reference}} - \text{sphere}_{\text{test}}) / \text{sphere}_{\text{reference}}) * 100$. Because this method might lead to higher errors, we used the former method when possible. The second method was only required for <5% of the photographs.

To account for the potential effects of predation risk by different predators on selection, we calculated concealment in terrestrial, aerial, and overall orientations. Terrestrial concealment for the microsite was defined as the average concealment of the four photographs gathered in the cardinal

directions. Aerial concealment was defined as the concealment of the photograph taken above the sphere, and overall concealment was calculated by averaging the values of all five photographs.

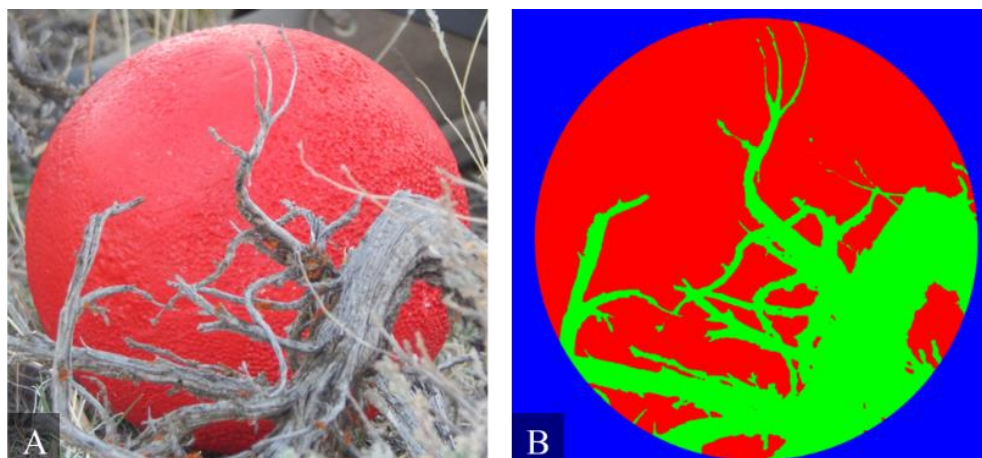


Figure 3-1 Estimation of concealment. A) A photograph of a sphere at a microsite in a terrestrial orientation. B) Classification of the clipped sphere where blue pixels classify the area removed in the clipping process, red pixels denote the sphere, and green represents habitat structure. Percent concealment of the sphere in this photograph is 35.3%.

Visibility Data Processing

To gather data for estimating visibility, we placed a Leica BLK360 Terrestrial Laser Scanner (TLS) at each microsite and collected lidar data at a point density of 0.1 m at 10 m. Each lidar point cloud was imported into Program R, and the packages *lidR* (Roussel et al. 2020) and *viewshed3d* (Lecigne et al. 2020) were used to process the point cloud and generate visibility estimates. Viewshed3d measures the length of sightlines in all directions until they are obstructed by a data point and displays the data as a graph of the percent of unobstructed sightlines as a function of distance from the observer. Stein et al. (2022) defined the area under this curve as the viewshed coefficient (VC), a quantitative description of the volume of the spherical 3D viewshed (Fig. 3-2). Using each TLS scan, we measured an overall spherical viewshed to 4 m (i.e., the distance from which the concealment photographs were gathered). We also estimated variation in the viewshed by segmenting it in the azimuth and calculating the coefficient of variation (COV) among segments (Stein et al. 2022).

As with concealment, we calculated estimates of terrestrial and aerial viewsheds by segmenting each viewshed latitudinally (Fig. 3-2). From these segmented clouds, we generated aerial and terrestrial VCs and associated COVs. In addition to visibility analyses, we used the lidar data to index vegetation density by counting the number of lidar points within 4 m of each microsite (we included both vegetation and ground points in this count).

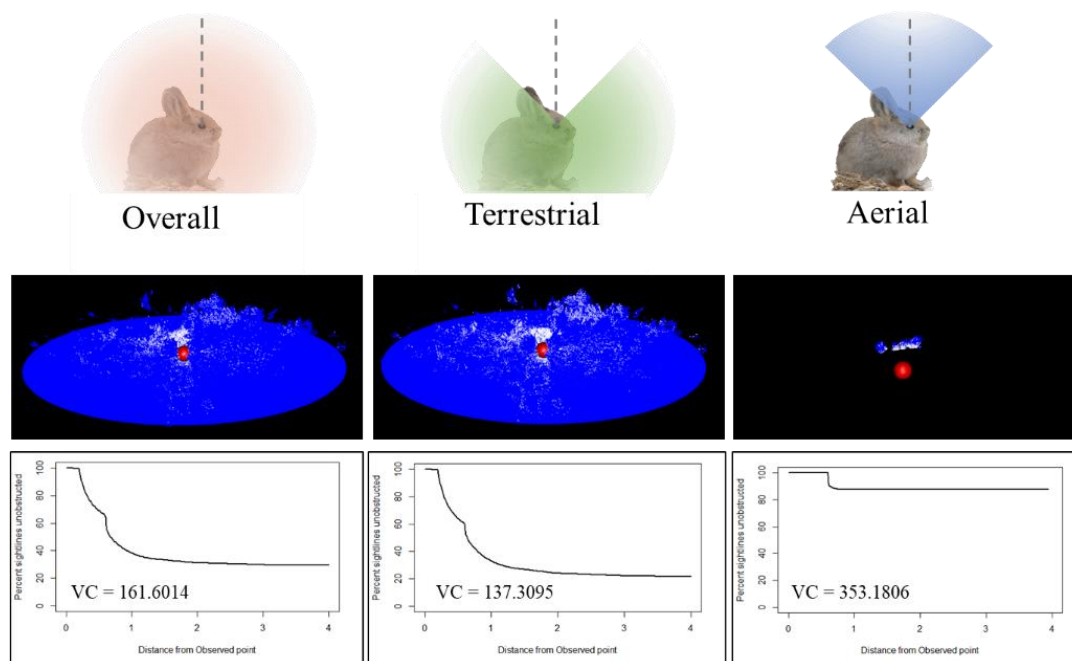


Figure 3-2 A) Because rabbits may be influenced by predator type (i.e., aerial and terrestrial), we evaluated the overall viewshed (i.e., all available sightlines in all latitudinal and azimuthal directions) and also terrestrial and aerial viewsheds separately by segmenting the lidar point clouds latitudinally 45° from the zenith (denoted by the dashed grey line at 0°). Terrestrial sightlines were defined as those $> 45^\circ$ from the zenith and aerial sightlines were defined as those $< 45^\circ$ from the zenith. B) We used the R package *viewshed3d* (Lecigne et al. 2020) to measure all sightlines until obstructed by a data point up to 4 m. The red sphere is the position of the animal, and the blue and white points are lidar data points, with white points obstructing sightlines. C) The area under the curve representing percent of unobstructed sightlines as a function of distance was defined as the viewshed coefficient, which describes the spatial extent of all measured sightlines.

Data Analysis

At the patch scale, we evaluated habitat selection with mixed-effects models in two ways. First, patch use was set as a predictor for each variable (i.e., vegetation density, shrub height, and concealment, VC, and COV in each orientation) and patch was set as the random effect. This allowed us to estimate the mean response of each variable at the used and unused patches and to compare them using marginal means (Length 2021). Second, we assessed habitat selection for patches by contrasting used and unused patches using logistic regression with use as the response, the habitat variables as predictors, and patch as the random effect. Because of the large size of the lidar points clouds, we applied a logarithmic transformation to density to aid interpretation. We generated suites of models that included estimates of terrestrial, aerial or overall visual properties of cover as well as structural properties (vegetation density and height), and we used an information theoretic approach to evaluate the weight of evidence for models using Akaike's Information Criterion (AIC; Akaike 1974). We generated standardized model averages for parameter estimates from competing models ($< \Delta AIC 2$) using the *MuMIn* R package (Burnham and Anderson 2002).

At the microsite scale, we evaluated intensity of use to assess properties that influence habitat use. We modeled intensity of use by fitting negative binomial linear mixed-effects models with pellet density as the response, the habitat properties as predictors (including distance to burrow), and patch as the random effect. Before calculating the models, all variables were scaled to the proportion of their maximum values. The negative binomial method was employed to correct for over dispersion of the data. As with the patch-level analyses, we generated suites of models, used AIC to assess strength of support for each model, and generated model-averaged parameter estimates from the competing models.

Results

Path-level habitat selection

We conducted measurements at 30 pairs of habitat patches at which some but not all properties of cover associated with security differed between used and unused patches. As expected, structural properties of cover (vegetation density and shrub height) were greater within used than unused patches (Fig. 3-3). Contrary to our predictions, concealment did not differ between used and unused patches at any orientation (overall, terrestrial, or aerial), and the size of viewsheds (VC) was significantly smaller within used relative to unused patches across all orientations (Fig. 3-3). Concealment and VC were weakly but significantly negatively correlated only in the overall orientation (Table 3-1) suggesting that a tradeoff was not required between the two visual properties. Although viewshed size was smaller, viewshed variability (COV) was significantly greater at used patches in the overall and terrestrial orientations (Fig. 3-3). We did note a strong negative correlation between vegetation density and VC in the terrestrial and overall orientations (Table 3-1).

Patches of habitat selected by pygmy rabbits were characterized by dense vegetation, tall shrubs (mean height 99 ± 3 cm), and relatively small terrestrial viewsheds. All three variables (density, shrub height, and terrestrial VC) were included in all six of the competing models, and the former two variables were significant across all models (Table 3-2). Model-averaged parameter estimates indicated that vegetation density and shrub height were the most influential variables (Table 3-3). Terrestrial VC was the next most influential variable. Although the model-averaged parameter estimate was marginally insignificant, terrestrial VC was a significant variable in three of the six competing models indicating that used mounds were associated with smaller terrestrial viewsheds (Table 3-2). Selection for large viewsheds in the overall and terrestrial orientations may be constrained by the strong negative relationships between vegetation density and VC (Table 3-1).

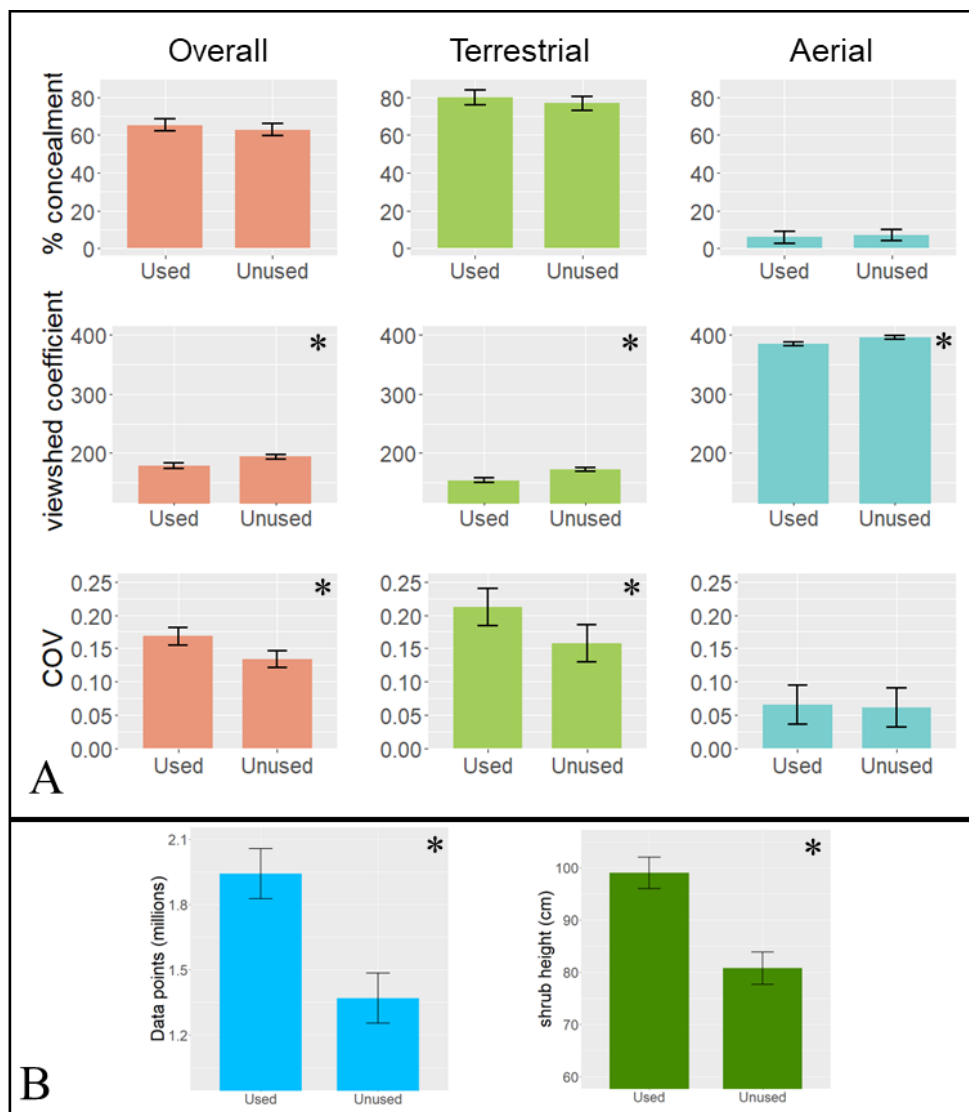


Figure 3-3 A) Mean (+ 95%CI) concealment, viewshed coefficient, and coefficient of variation (COV) at the paired used and unused patches. B) Mean (+ 95%CI) lidar data points (i.e., vegetation density) and shrub heights at used and unused patches. Asterisks indicate significant differences between the used and unused estimates for that variable according to p-values derived using marginal means from the mixed-effects models.

Table 3-1 Correlations among habitat variables (concealment, viewshed coefficient (VC), and vegetation density (Density)) at the patch and microsite scales in habitats used by pygmy rabbits in the Lemhi Valley, USA. Patch scale correlations are above and microsite correlations below the diagonal. Values within cells represent overall, terrestrial, and aerial orientations from top to bottom, respectively. Asterisks denote p-values (* 0.5-0.001, ** <0.001-0.0001, *** <0.0001).

	Concealment (%)	Viewshed (VC)	Density
Concealment (%)	X	-0.278* 0.084 -0.118	-0.002 0.024 -0.165*
Viewshed (VC)	-0.007 -0.037 -0.117	X	-0.730*** -0.324*** -0.054
Density	-0.137 -0.029 -0.278*	-0.849*** -0.856*** -0.408**	X

Table 3-2 Competing models of habitat selection at the patch scale and competing models of microsite use by pygmy rabbits in the Lemhi Valley, USA. Parameters include vegetation density (density), shrub height (height), terrestrial viewshed coefficient (VC_t), terrestrial viewshed coefficient of variation (COV_t), terrestrial concealment ($conceal_t$), aerial viewshed coefficient (VC_a), aerial viewshed coefficient of variation (COV_a), aerial concealment ($conceal_a$), and distance to burrow (distance). Table includes AIC, Δ AIC, and AIC weight (w_i). Variables that are bolded are significant with 95% confidence.

		K	AIC	ΔAIC	w_i
<i>Patch</i>	density + height + VC_t + COV_t	4	85.48	0	0.31
	density + height + VC_t + COV_t + conceal_a	5	86.65	1.17	0.18
	density + height + VC_t	3	87.01	1.53	0.15
	density + height + VC_t + COV_t + conceal_t	5	87.36	1.88	0.12
	density + height + VC_t + COV_t + COV_a	5	87.41	1.93	0.12
	density + height + VC_t + COV_t + VC_a	5	87.41	1.93	0.12
<i>Microsite</i>	conceal _t + distance + conceal _t *distance	4	894.10	0	0.40
	conceal_t	2	895.05	0.95	0.25
	conceal_t + distance	3	895.43	1.33	0.21
	conceal _t + distance + conceal _t *distance + VC_t	5	896.08	1.98	0.15

Table 3-3 Standardized model-averaged estimates of parameters across models of habitat selection at the patch scale by pygmy rabbits in the Lemhi Valley, USA.

Variable	Estimate	Standard Error	p-value
Vegetation density	3.1737	1.0495	0.0025
Shrub height	3.8700	0.8814	<0.0001
Terrestrial VC	-2.8766	1.5819	0.0690
Terrestrial COV	-2.1634	1.8451	0.2410
Terrestrial Concealment	0.0246	0.2104	0.9069
Aerial VC	-0.0542	0.6192	0.9303
Aerial COV	-0.0431	0.4976	0.9309
Aerial Concealment	0.1192	0.4076	0.7700

Intensity of Microsite Use

Intensity of use, as indexed by counts of fecal pellets, varied markedly across microsites and was generally associated with higher concealment, relatively small viewsheds, and close proximity to burrows. We measured 126 microsites at which fecal pellet density ranged from 0-1841 pellets/0.25 m². However, only two microsites contained >1000 pellets, and we removed those two because they strongly influenced results. Consequently, pellet density for plots in the analysis ranged from 0-724 pellets/0.25 m². Intensity of use as a function of visual properties of cover contrasted between terrestrial and aerial orientations. Greater use was associated with relatively high values of concealment and low values of VC in the terrestrial orientation, with opposing trends in the aerial orientation (Fig. 3-4A). Microsites closer to burrows and with intermediate values of vegetation density also experienced higher use (Fig. 3-4B). Visual properties of cover (concealment and VC) were not correlated in any orientation, but vegetation density was strongly and negatively correlated with VC in all orientations (Table 3-1).

Multivariate analyses revealed that intensity of use of microsites increased with higher values of concealment and closer proximity to burrows. Terrestrial concealment was retained in all four of the competing models and was significant in two (Table 3-2). Likewise, distance to burrow was significant in two of the three competing models in which it appeared. A marginally insignificant interaction between these two variables also was retained in two models. The interaction between

terrestrial concealment and distance to burrow was positive indicating higher use of microsites with less concealment near burrows and greater concealment further from burrows. However, model-averaged parameter estimates were not significant for any variables, suggesting relatively weak influence (Table 3-4). Contrary to our hypothesis, viewshed size did not exert significant influence in the competing models.

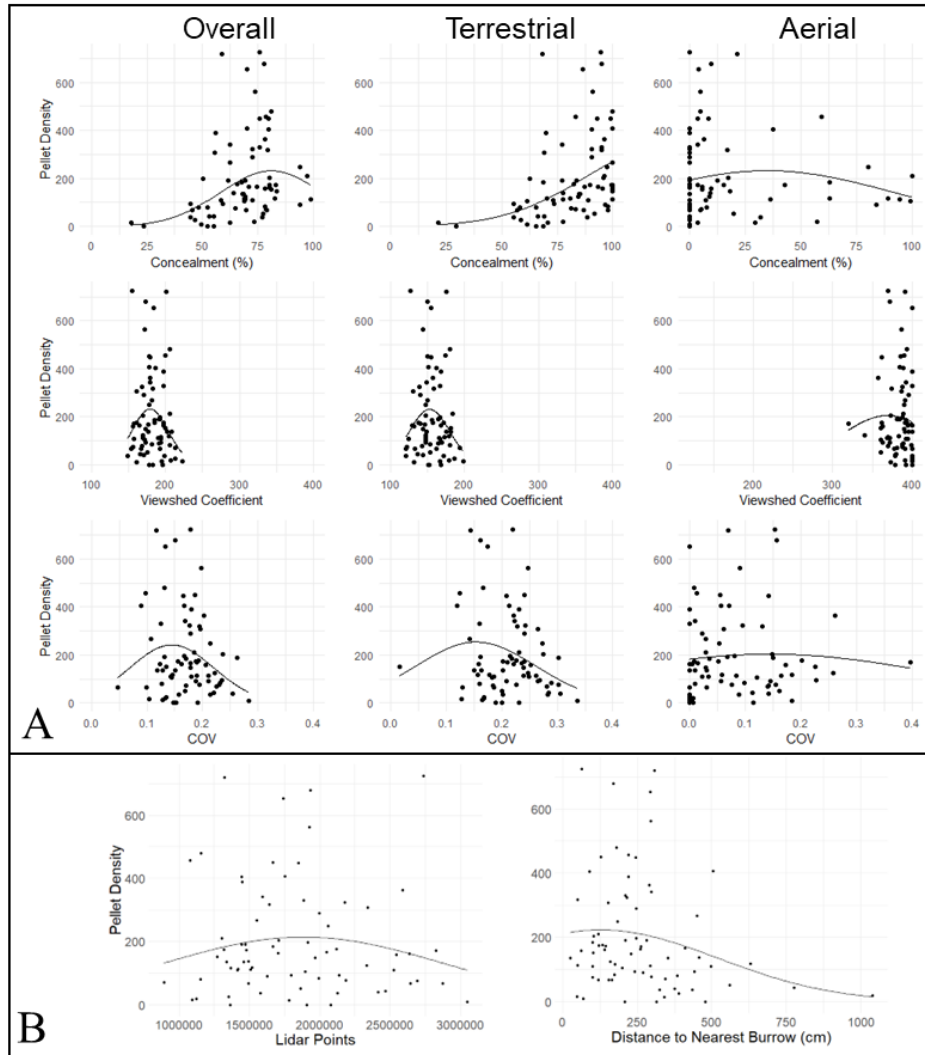


Figure 3-4 A) Microsite use indexed by density of fecal pellets (number pellets/0.25m²) as a function of visual habitat properties (concealment, viewshed coefficient, and viewshed coefficient of variation (COV)). Lines represent negative binomial quadratic models of each variable. B) Microsite use as a function of vegetation density (indexed by number of lidar data points) and distance to nearest burrow.

Table 3-4 Standardized model-averaged estimates of parameters across models of microsite use by pygmy rabbits in the Lemhi Valley, USA.

Variable	Estimate	Standard Error	p-value
Terrestrial Concealment	2.1091	1.9864	0.2924
Distance to Burrow	-5.4872	5.7700	0.3450
Terrestrial Concealment * Distance to Burrow	5.7307	6.7037	0.3961
Terrestrial VC	-0.0280	0.4888	0.9552

Discussion

Our analysis identified diverse functional properties of cover associated with security of a small mammalian prey species. We documented that structural properties, and not visual ones, shaped selection of habitat patches, whereas a visual property and proximity of refuges influenced intensity of use of microsites within patches. Vegetation density and shrub height strongly influenced selection of habitat patches, and although smaller viewsheds also were selected, our estimate of viewshed volume (VC) was strongly and negatively correlated with vegetation density, suggesting that selection for viewsheds was constrained by the tradeoff with vegetation density. In contrast, intensity of microsite use was linked with greater concealment (a visual property) and proximity to burrows. Our data also suggest that an interaction between these two variables influenced microsite use, such that greater use occurred at sites closer to burrows with lower levels of concealment and at sites farther from burrows with greater concealment. Collectively, these results suggest that selection for ‘cover’ can be complex, supporting the need to consider multiple functional measures of cover in studies of animal-habitat relationships.

Contrary to our expectations, viewshed size did not appear to drive habitat selection at either the patch or microsite scales. Although viewsheds were significantly smaller within used compared to unused patches, this relationship was likely driven by the strong negative correlation between vegetation density and VC (Table 3-1). Indeed, vegetation density was the most influential variable in selection of habitat patches by rabbits. We had expected that an inverse relationship between concealment and visibility might constrain selection for both properties, as documented in other studies (Camp et al. 2013), but our data did not support this tradeoff. Likewise, viewshed did not appear to influence intensity of use of microsites by rabbits.

Interactions among properties of cover also might influence selection across heterogeneous habitats. In our examination of intensity of microsite use, we documented a strong effect of burrow proximity, but we also found that use was associated with high terrestrial concealment. Although the interaction term was not significant in the model-averaged estimate, the interaction between terrestrial concealment and distance to burrow had a large effect size in the model based on standardized parameters (Table 3-4). The positive interaction suggests that further from the burrow pygmy rabbits used sites with greater terrestrial concealment and used sites with less terrestrial concealment close to the burrow. This interpretation is consistent with previous work that indicated that pygmy rabbits perceived less risk near the burrow and also selected more strongly for secure habitat properties (including concealment) when further from the burrow (Camp et al. 2012, Crowell et al. 2016).

At both scales, we found that pygmy rabbits used habitat associated with visual properties almost exclusively in the terrestrial orientation. Crowell et al. (2016) also documented that pygmy rabbits in experimental arenas foraged more intensively at sites with high levels of terrestrial structure. Pygmy rabbits, like many small prey species, have a diverse suite of terrestrial and avian predators. In our study site, both patches and microsites were associated with relatively low values of aerial concealment and high values of aerial visibility (Fig. 3-3A and 3-4A). The lack of variation in the aerial orientation might have reduced opportunity for selection for or against these visual properties. This result contrasts with McMahon et al. (2017) who documented selection for aerial concealment at the patch-scale at the same site although they also documented selection for dense vegetation and tall shrubs consistent with our study. An elevated perception of predation risk from terrestrial predators could be a function of greater presence of those species (Embar et al. 2011) or greater risk posed by mammalian predators.

Selection for either concealment or visibility rather than both properties might be related to the anti-predator strategy of prey and the hunting strategy of predators. For example, concealment decreased predation risk for desert cottontails (*Sylvilagus audubonii*), which rely on crypsis, but not for black-tailed jackrabbits (*Lepus californicus*), which instead rely on detection and escape (Wagnon 2020). At the microsite scale, pygmy rabbits seem to employ an adaptable anti-predator strategy where selection for concealment is mediated by distance to burrow, which reflects their reliance on both concealment and access to refuge. Additionally, predation strategy may influence selection for visual properties by prey because concealment may decrease detection of prey by coursing predators (Lone et al. 2014) whereas visibility might increase detection by prey of ambush predators (Acebes et al. 2013, Davies et al. 2016). We documented that pygmy rabbits selected for vegetation structure at the patch scale and concealment at the microsite scale, which might indicate greater perceived risk from coursing predators by pygmy rabbits.

Several factors could influence interpretation of our results. Although we used a new and comprehensive measure of the viewshed, methodological differences between our estimates of visibility and concealment could influence our results. Unlike viewshed, in which we were able to estimate sightlines in all directions, our method of estimating concealment was constrained to data gathered in limited directions and at a single distance. Thus, concealment was not indexed as holistically as viewshed, which may have limited our ability to detect correlations between the visual properties. Indeed, previous studies that estimated these properties in more analogous ways found a stronger correlation between the two (Camp et al. 2013). Additionally, although, measures of fecal pellet density are a common tool for assessing habitat use by leporids (e.g., Mills et al. 2005), it is a

coarse index of intensity of use. Finally, pygmy rabbits are considered ecosystem engineers that significantly alter vegetation structure (Parsons et al. 2016). As such, our measurements of both structural and visual properties of cover are potentially influenced by pygmy rabbit activity.

In addition to creating structure that protects and hides pygmy rabbits from predators, vegetation potentially serves multiple other functions. Sagebrush shrubs, which form the majority of the vegetation structure in the sagebrush-steppe ecosystem at our study site, likely provide thermal shelter, concealment, and forage as well as security (Camp et al. 2017, Milling et al. 2017). Disentangling these relationships requires independent measures of their functional properties, and subsequent examination of the correlations among them. Some properties are likely to covary (e.g., forage availability and concealment; McMahan et al. 2017), while others might exhibit relationships that differ across seasons. For example, dense vegetation that provides shade might result in thermally moderated microclimates during summer, whereas open areas that allow penetration of sunlight might create more suitable microclimates during winter (Milling et al. 2017). These relationships underscore the need to define and measure explicit properties of cover.

Our study highlights the importance and some of the challenges of identifying and measuring functional properties of cover. As might be expected, rabbits selected for structural functional properties, but not always in the ways we expected. Competing needs associated with functions provided by cover likely resulted in nuanced selection within and between different spatial levels of habitat selection. Broad measures of cover cannot account for these subtly different needs, and so are limited in their ability to inform why and how animals choose cover. Studies linking the functional properties of cover with their ecological significance are needed to develop mechanistic understandings of wildlife-habitat relationships.

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Chapter 4: Integration of Lidar Remote Sensing into a Multi-modal Experiential Course

A version of this chapter is in review for publication as: Stein, R.M., Eitel, K., Rachlow, J.L. (*in review*) “Integration of lidar remote sensing into a multi-modal experiential course” *Journal of College Science Teaching*.

Abstract

Lidar remote sensing, which uses laser pulses to measure three-dimensional structure, has become essential across natural science disciplines. However, undergraduate students typically receive limited exposure to these technologies and rarely have opportunities to experience them. Experiential and multi-modal courses may be ideal for introducing students to remote sensing. We offered an experiential course to undergraduate students at the University of Idaho focused on research assessing properties of wildlife habitat. A majority of course time was spent in the field, but students also participated in online class activities. A key feature of this course was introducing students to lidar through an experiential curriculum that included an introductory lecture, data collection in the field, and a tutorial on visualizing and analyzing the data. Students reported that field work and lidar activities were the most useful for achieving learning goals. Our course demonstrates that multi-modal experiential courses may be effective settings to introduce students to remote sensing.

Introduction

Remote sensing technologies are becoming ubiquitous in the natural sciences and in daily life. Technologies classified as remote sensing are those that gather information at a distance, usually by measurement of reflected light (Jensen, 2007). Data gathered by remote sensing are used for a variety of applications such as weather prediction (Thies & Bendix, 2011), precision agriculture (Sishodia et al., 2020), and forest management (Piermattei et al., 2019).

One remote sensing technique that is becoming increasingly important is lidar, which uses emitted laser pulses to measure three-dimensional (3D) structures in the environment. Data from these measurements are aggregated into highly accurate, 3D computer models (Fig. 1; Stein et al., 2022). Because lidar provides highly accurate 3D data, it has become an important tool for a variety of applications including mapping bathymetry (i.e., measurement of water depth) and topography of coastal environments (Irish & Lillycrop, 1999), evaluating carbon sequestration in forests (Hudak et al., 2012), mapping pollution of aerosols in the atmosphere (Sheng et al., 2018), and mapping important aspects of 3D habitat structure for both vertebrates (Vierling et al., 2013) and invertebrates (Vierling et al., 2011). Lidar is also becoming more common in daily life; both the iPhone12 Pro

(Apple, 2020) and Google StreetView (Russell, 2022) have integrated lidar and is an important tool in the advancement of self-driving cars (Gomes et al., 2023).

Despite the growing importance of lidar in the natural sciences and everyday life, most undergraduate students receive limited exposure to this technology. Experiential courses may be ideal for introducing lidar and other remote sensing techniques to students by providing hands-on experience with data collection and analysis. Experiential courses and participation in authentic research experiences provide students with a myriad of benefits. Some of these benefits, such as increased knowledge about the nature of science (Burnette & Wessler, 2013), increased analytical and technical skills (Feinstein et al., 2013), and increased science identity (Brownell et al., 2012), may positively influence learning about remote sensing. Additionally, because remote sensing includes both field and data analysis components, it may be ideal for multi-modal courses (i.e., courses that are conducted in multiple formats), which are becoming more common approaches to learning at the college level.

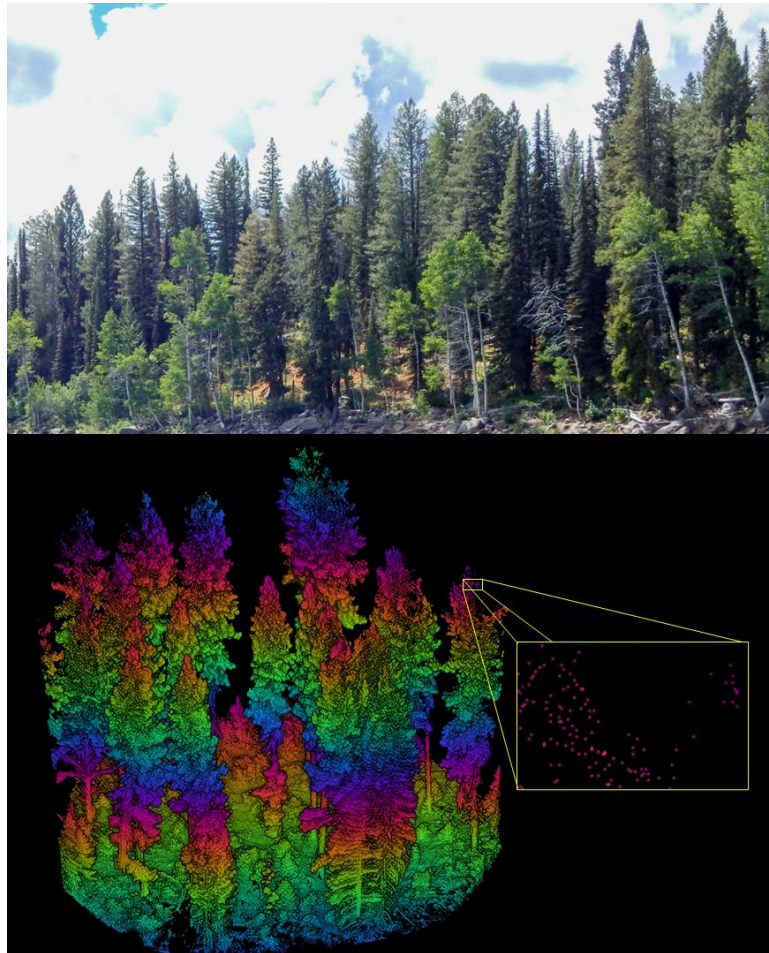


Figure 4-1 A) A photograph of a conifer forest. B) A terrestrial lidar point cloud gathered from a conifer forest composed of ~50 million 3D data points. Inset shows a close-up of one section of the point cloud displaying individual data points.

We designed and implemented an experiential course that engaged undergraduate students at the University of Idaho in wildlife research and integrated lidar data collection and analysis. Our objectives in integrating lidar were to: 1) provide students with a foundational understanding of lidar relevant to multiple ecological applications; 2) give students experience collecting lidar data in a field setting; and 3) engage students in lidar data visualization and analysis.

Course Design

Research Project

The course was designed to engage students in our research focused on understanding factors that influence habitat selection by American red squirrels (*Tamiasciurus hudsonicus*). Habitat structure can influence the security of wildlife by creating refuges and by affecting the functional properties of *visibility* (i.e., visual information accessible to an animal) and *concealment* (i.e., how well an animal is hidden from view). Animals may enhance their security by selecting for these habitat properties (Camp et al., 2012). Red squirrels are a small territorial mammal subject to predation by a suite of predators. A central feature of their territory is the midden, a single larder where they store food (Elkins, 2017). Middens are associated with increased presence of some predators (Pearson & Ruggiero, 2001) and competitors that pilfer stored food (Gerhardt, 2005). Thus, selection of secure midden sites is crucial for minimizing risk of predation and competition. Our research objective was to evaluate the influence of access to refuge, visibility, and concealment on placement of red squirrel middens at the University of Idaho Experimental Forest (UIEF) near Moscow, Idaho, USA. The local nature of the project made it ideal for engaging students in ecological research because it increased accessibility and relevance of the project. Additionally, because the project involved only habitat measurements, it was a good way to involve students in wildlife research without the potential ethical and safety concerns associated with students directly handling wildlife.

Course Delivery

Our delivery of the course was multi-modal and included in-person field work and online lectures, assignments, and live discussion. Each student participated in two days of field work, at the start of which we discussed the signs associated with squirrel middens (e.g., canopy cover, squirrel presence, pinecone litter) and introduced the field equipment (i.e., data sheets, lidar scanner, concealment cube, meter tapes and sticks). We then searched for middens as a class and, upon discovering one, gathered data. At each midden site, the students assisted with lidar data collection for visibility analysis (Stein et al., 2022), estimated concealment visually using concealment cubes (Camp et al., 2012), measured distance to the nearest tree (i.e., nearest refuge), and recorded

qualitative notes on midden construction and primary tree species in the surrounding forest. Once students were familiar with the methods, they led the search for middens and subsequent data collection (Fig. 4-2).



Figure 4-2 Students working in the field measuring wildlife habitat. A) A student placing a cube for estimating concealment at the entrance of a midden. B) A student estimating concealment by observing a cube from a 1-m high vantage point. C) Students measuring distance from a midden site to nearest tree (i.e., potential squirrel refuge). D) A lidar scanner set up for data collation at a squirrel midden.

To provide a holistic understanding of the project, students viewed online lectures and completed associated activities. Students watched two lectures on 1) secure properties of habitat and 2) lidar and its use in the project. The lidar lecture introduced students to basic lidar function, the importance of 3D habitat structure to wildlife, applications of lidar in ecology, and application of lidar to our specific project.

In addition to the introductory lecture, students also completed a tutorial in which they visualized and analyzed lidar data gathered from the UIEF (Fig. 4-3). Students were provided two single-scan lidar point clouds. Using CloudCompare (v2.11.3), an open-source software, students practiced manipulating the 3D point clouds. Students then imported the point clouds into Program R (v4.1.1), an open-source statistical software, for analysis. They used two packages in Program R, *viewshed3d* (Lecigne et al., 2020) and *lidR* (Roussel et al., 2020), to estimate visibility by animals within the measured ecosystems using computer code that we provided (Fig. 4-3, Appendix D).

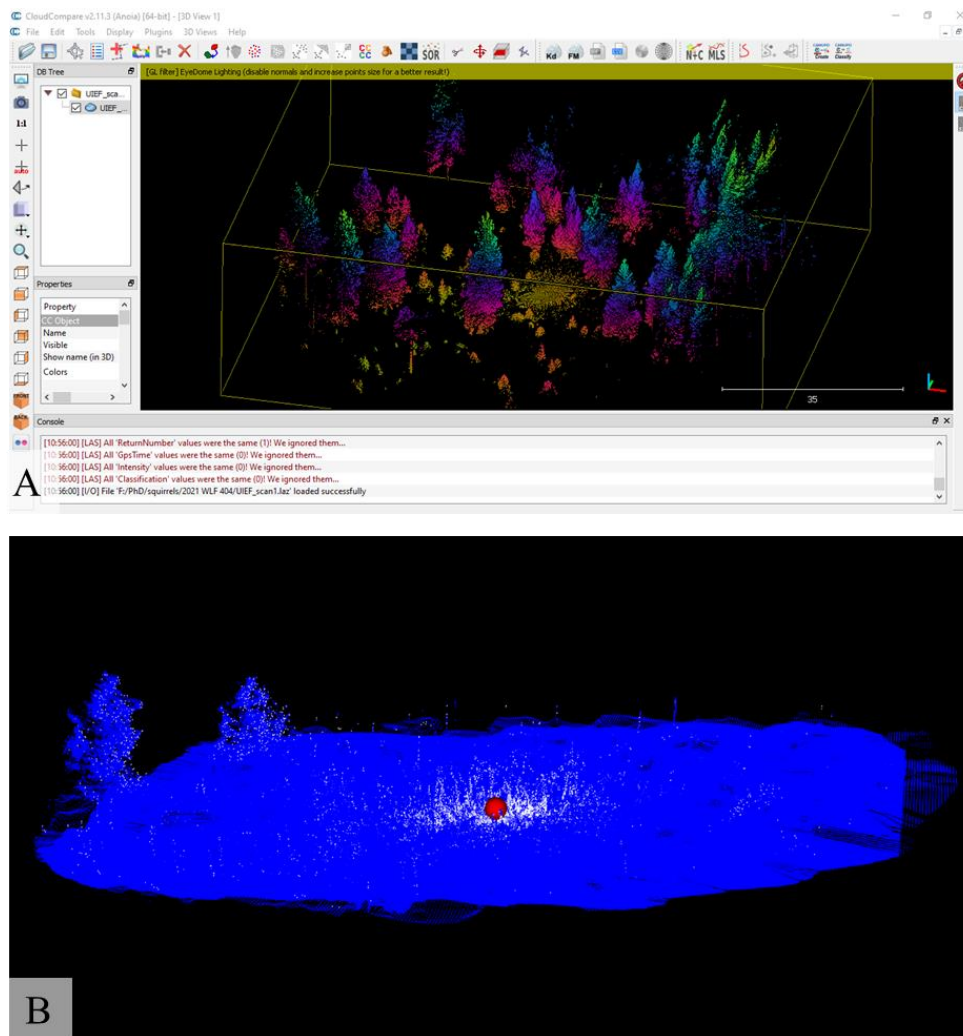


Figure 4-3 Student interactions with lidar data. A) A point cloud displayed in three-dimensions in CloudCompare as part of the lidar tutorial. B) The same point cloud imported into Program R displaying a measured ‘viewshed’ (i.e., all measured sightlines and their spatial extents) using computer code provided to students in the tutorial. The blue and white points are lidar data points, the red sphere is the position of the ‘animal’. The white points are at the ends of measured sightlines.

We also conducted one online live discussion of primary research literature. Students were assigned 2-3 relevant articles to read within one of 3 categories (functional habitat properties, perceptions of risk, and red squirrel ecology). During the online class discussion, students assigned

papers within a category presented information from their articles as a group to the other students. The class discussed challenges with the research and worked together to “redesign” the study during which each group served as experts in their assigned literature category.

Post-Course Survey

At the end of the course, all students (n = 11) completed a survey in which they assessed the effectiveness of each activity at helping them achieve learning outcomes and personal goals. To assess students’ abilities to apply concepts and methods learned in the course to a novel situation, we presented students with a scenario about a different prey animal and asked them to write a hypothesis about selection of secure habitat by that animal and to describe their methods. Finally, students were given the opportunity to provide additional comments. Surveys were anonymous and approved by the University’s Institutional Review Board (IRB 015216).

Results from Student Surveys

Students ranked class activities from most useful to least useful for achieving learning outcomes. Field work activities were ranked by students as most useful for achieving every learning outcome (Table 4-1). Rankings of other activities varied by learning outcome. For example, students ranked the lidar tutorial as the second most useful (after field work) for increasing understanding of the concept of visibility, and they ranked the lecture on secure properties of habitat second for increasing understanding of concealment (Table 4-1).

Table 4-1 Targeted learning outcomes for our course.

Learning Outcome	Description
<i>Functional Habitat Properties</i>	Students will understand the functional properties of habitat and their influence on wildlife
<i>Perceptions of Risk</i>	Students will understand factors that influence how wildlife perceive risk
<i>Understanding of Visibility</i>	Students will understand factors that influence visibility and associated habitat selection
<i>Visibility Measurement</i>	Students will gain skills in measuring visibility
<i>Understanding of Concealment</i>	Students will understand factors that influence concealment and associated habitat selection
<i>Concealment Measurement</i>	Student will gain skills in measuring concealment

We scored students on appropriate application of the concepts of visibility and concealment as well as data collection methods in their responses to the novel ecological scenario. Most students (82%) correctly applied the concept of concealment, and fewer (64%) correctly applied the concept of visibility, although some students only addressed concealment in their response. However, most included appropriate methods for estimating both concealment and visibility in their study design. A majority of students discussed lidar, but not always in reference to visibility. One student did not explicitly mention lidar but did appropriately apply ideas related to 3D visibility estimation.

Students were asked to reflect on why they registered for the class and were given an opportunity to provide additional comments. All students indicated that when they registered for the course, they were either hoping to gain experience in field work or learn about lidar. All eleven students indicated that they did gain the knowledge or skills they had hoped for during registration.

Discussion

Students consistently reported that the field work and lidar class activities were the most useful to achieving learning outcomes and supporting their personal goals. One student stated, “Seeing how all of the pieces fall together at the end was very helpful. I have a base understanding for lidar, viewshed..., and overall experimenting now.” Student responses indicated that integration of lidar remote sensing into an experiential course can be an effective approach to both introduce students to lidar and advance other learning outcomes. Although the primary purpose of the course was to provide students with knowledge about and experience measuring functional properties of wildlife habitat, survey responses showed that the lidar activities were perceived by the students as some of the most useful for achieving learning outcomes, including advancing their understanding of visibility. These results demonstrate that remote sensing curricula can be effectively integrated into an experiential course to advance multiple learning outcomes.

Although the lidar tutorial was more of a “cookbook” style activity (i.e., students followed step-by-step directions to carry out a “tried and true” task), which many authors argue against (e.g., Feinstein et al., 2013; Holt et al., 1969), given the complexity of lidar analysis and multi-modal nature of the course, providing students with working computer code in addition to field work and the lecture appeared to be affective. Multiple students commented on how the multi-pronged approach helped them understand lidar. One student stated,

In this class I was looking to get a general idea of not only how to use lidar in the field but how to analyze the data after collection. With those goals in mind, I was able to do this by first collecting the data in the field and... then pairing that with actually running through the lidar tutorial it really gave me a good understanding about how lidar can be used.

However, one student commented that the usefulness of the lidar tutorial was limited because they could not recreate the computer code or execute analyses on their own, which lends support to arguments against cookbook style activities. Given that most students responded positively to the tutorial, but always in context of field work, we argue that an occasional cookbook style activity for

introduction of complex remote sensing analyses may be useful if paired with other, more active learning lessons.

We integrated one remote sensing technology into our course, however, a plethora of others could be incorporated in a similar fashion. A key feature of our course was providing students with the opportunity to gather lidar data in the field. Handheld spectrometers, thermal imagers, and cameras or sensors mounted on drones also could provide students with hands-on data collection field experiences. However, most remote sensing technologies do not include field-based data collection. For example, information from the NASA and USGS Landsat satellite is extremely valuable for answering a multitude of questions but the data are gathered automatically. Instructors interested in integrating these types of remote sensing products might consider engaging students in ‘ground validation’, a common practice in which remote sensing data are calibrated using data collected on the ground (Jensen, 2007). Including ground validation would enable hands-on field work relevant to the remote sensing technology and, because it is used in data calibration, could lead to a deeper understanding of the sensor.

Visualizing and analyzing remote sensing data can be complex and require resources (i.e., sensors and commercial programs) that may not be readily accessible. Although they should be used sparingly, ‘cookbook’ style tutorials like ours can be a means of simplifying the process and making the analysis accessible to students. Oftentimes, advanced sensors are not accessible for use in single classrooms, in part due to the high cost of sensors. Instructors can overcome this by 1) collaborating with other instructors and researchers who have access to sensors; 2) using freely available data products such as those provided by Landsat; or 3) using accessible cameras, such as phone cameras, for coarser measurements. Associated analysis programs can similarly be inaccessible, and instructors may increase accessibility by using open-source software such as ImageJ (Gomes et al., 2023). The costs of lidar and other remote sensing technologies are decreasing yearly, which will make those technologies more accessible for education in the future. We encourage instructors to consider integrating hands-on remote sensing into their experiential and multi-modal courses to advance multiple learning outcomes and to introduce students to technology that is increasingly relevant to their daily lives.

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Chapter 5: General Conclusion

Behaviors connected to fitness including resource selection are strongly influenced by access to and perception of sensory information. Thus, there is increasing interest in understanding wildlife ecology through the lens of sensory ecology. I aimed to advance the field of sensory ecology by: 1) reviewing and contextualizing existing knowledge about the acoustic ecology of terrestrial mammals; 2) evaluating the influence of three-dimensional habitat structure on access to visual information by individuals; 3) assessing habitat selection by prey species as a function of visual properties of habitat; and 4) engaging undergraduate students in experiential curriculum focused on remote sensing methods for quantifying visual habitat properties.

Although there has previously been a heavy focus on bats and marine mammals in the study of mammalian bioacoustics, I found a deep literature on the acoustic ecology of terrestrial mammals. My review is the first to detail the breadth of factors influencing the acoustic behavior of terrestrial mammals. The Signaler-Receiver Conceptual Framework (Figure 1-2) developed from the reviewed literature documents the diversity of factors that influence both signalers (mammals that emit a sound) and receivers (mammals receiving a sound). The Framework not only contextualizes existing knowledge, but also provides context for creation of new hypotheses. The literature review also highlights gaps in knowledge including a lack of research on species that are less vocal or use infrasound and ultrasound, and how changing ecosystems are influencing acoustic behavior. Additionally, although there is a plethora of information on certain orders including Primates and Carnivora, other orders, such as Eulipotyphla, have received little attention. The Signaler-Receiver framework may be applied in conjunction with emerging methods and tools (e.g., Reed et al. 2012, Couchoux et al. 2018) to fill persisting gaps in knowledge.

Both sound and light waves interact with three-dimensional (3D) habitat structures (Price et al. 1988, Kükenbrink et al. 2021), influencing access to sensory information by wildlife. Structure blocks sightlines and alters the area from which visual information can be gathered (Embar et al. 2011). Additionally, position relative to habitat structure can influence what is visually perceived in humans (Gibson, 1979), although it has not been as well assessed in wildlife. I gathered data in four ecosystems (forest, shrub-steppe, prairie, desert) and documented that ecosystem-specific structure and animal position significantly influenced the viewsheds (i.e., all sightlines accessible to an individual and their spatial extents) in those environments. Generally, as animal height from the ground increased, viewshed size increased and variability decreased. However, the multi-layered canopy structure associated with the forest resulted in a decrease in viewshed size and greater variability at intermediate eye-heights likely as a result of sightline interaction with both the shrub

and tree canopies. Understanding both viewshed size and variability may have important implications for animal ecology. Viewshed size provides information about the spatial extent of accessible information whereas variability may provide information about how animals manage selection for visibility in addition to other properties of 3D structure. Visibility can influence resource detection (Potier et al. 2016), movement decisions (McLean et al. 2016), and anti-predator strategies (Embar et al. 2011), and yet it is not well integrated into studies of animal ecology (Aben et al. 2018). My results demonstrate that visibility is a spatially dynamic visual property that is variable both within and between landscapes.

Prey species may reduce predation risk by selection of habitat that provides visibility and concealment (Camp et al. 2012). I investigated habitat selection at two scales (patch and microsite) by pygmy rabbits (*Brachylagus idahoensis*), which are small leporids at risk of predation. Pygmy rabbits selected habitat patches associated with taller and more dense vegetation that were also associated with smaller viewsheds in the terrestrial orientation. In contrast, pygmy rabbits more intensively used microsites near their burrow and those associated with high terrestrial concealment. Because viewshed size was negatively and significantly correlated with vegetation density, the nearly significant selection for small terrestrial viewsheds at the patch scale may be a consequence of the strong selection for dense vegetation. However, previous studies have found that pygmy rabbits preferentially select cover in the terrestrial orientation (Crowell et al. 2016), and indeed, at the microsite scale, rabbits selected habitat associated with terrestrial concealment although they did not select for dense vegetation. Collectively, these results may indicate that pygmy rabbits perceive higher predation risk from terrestrial predators. My results demonstrate the importance of measuring the properties of interest rather than a generalized measure of cover and indicate that there is a nuanced relationship between habitat structure and predation risk.

I introduced undergraduate students to lidar remote sensing within an experiential course focused on measuring visual properties of habitat used by red squirrels (*Tamiasciurus hudsonicus*). In post-class surveys, students reflected that field work and class activities focused on lidar were most useful in achieving learning outcomes (including advancing understanding of functional properties of wildlife habitat), as well as advancing their personal goals. Integration of lidar into experiential courses may effectively introduce students to lidar and also advance other learning outcomes. Although some authors argue against ‘cookbook’ style activities (Holt et al. 1969, Feinstein et al. 2013), such as the lidar tutorial I developed, our results indicated that paired with hands-on activities and in the context of the complexity of lidar analyses, an occasional ‘cookbook’ activity may be effective. Integrating remote sensing into this course advanced multiple learning outcomes relevant to

wildlife ecology and also to students' everyday lives, and consequently, I encourage instructors to consider integration of remote sensing into ecological courses.

Although the chapters within this dissertation had very different objectives, together they further the field of sensory ecology in multiple directions. My dissertation research advanced fundamental understanding of access and response to visual and acoustic information, advanced methods of estimating access to visual information, and highlighted opportunities for integrating new technologies into questions about animal ecology as well as college education. This dissertation contributes to fundamental understandings of wildlife-habitat relationships through the lens of sensory ecology, a field increasingly important for predicting responses of wildlife to changing environments and developing effective management and conservation strategies.

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Appendix A

Complete list of reviewed articles.

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Figures

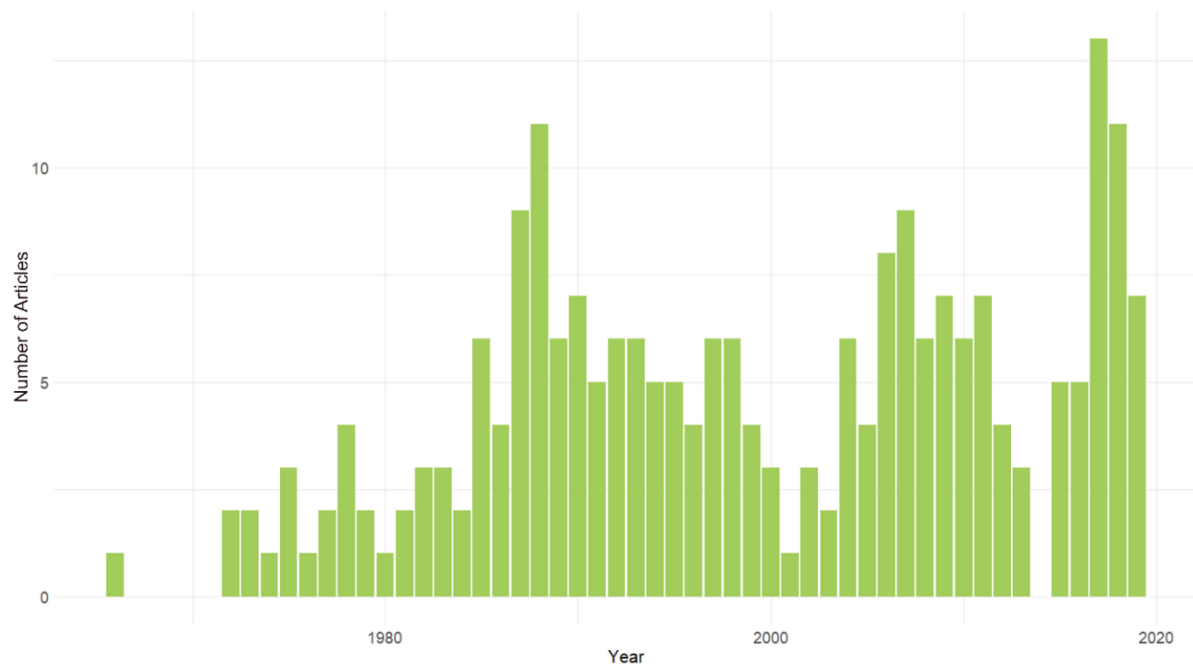


Figure A.A. 1 Bar graph displaying the number of reviewed articles published by year.

Appendix B

Tables

Table A.B. 1 The viewshed coefficient (VC) models representing viewshed extent. Viewsheds were measured from eye-heights 0.25-50 m in the forest and 0.25-10 m in the other ecosystems. The viewsheds from the highest eye-heights were removed from all models due to lack of variation. *P*-values are listed on the right of each estimate (95% confidence).

	Forest	<i>p</i>-value	Shrub-steppe	<i>p</i>-value	Prairie	<i>p</i>-value	Desert	<i>p</i>-value
Intercept	497.5	<0.0001	521.9	<0.0001	560.4	<0.0001	548.0	<0.0001
0.75 m	-94.6	<0.0001	584.3	<0.0001	573.3	<0.0001	519.7	<0.0001
1.5 m	-49.7	0.0168	738.2	<0.0001	668.4	<0.0001	616.0	<0.0001
5.0 m	77.0	0.0002	931.4	<0.0001	895.6	<0.0001	836.4	<0.0001
10.0 m	167.9	<0.0001	-	-	-	-	-	-
15.0 m	289.8	<0.0001	-	-	-	-	-	-
20.0 m	402.7	<0.0001	-	-	-	-	-	-
25.0 m	466.1	<0.0001	-	-	-	-	-	-
roughness	-0.1	0.9762	0.0	0.9996	7.2	0.6472	50.6	0.0466

Table A.B. 2 The coefficient of variation models representing viewshed variability. Viewsheds were measured from eye-heights 0.25-50 m in the forest and 0.25-10 m in the other ecosystems. The viewsheds from the highest eye-heights were removed from all models due to lack of variation. *P*-values are listed on the right of each estimate (95% confidence).

	Forest	<i>p</i>-value	Shrub-steppe	<i>p</i>-value	Prairie	<i>p</i>-value	Desert	<i>p</i>-value
Intercept	-1.860	<0.0001	-3.229	<0.0001	-1.972	0.0506	-2.812	0.0077
0.75 m	0.431	0.0027	-3.767	<0.0001	-1.991	0.0471	-2.985	0.0047
1.5 m	0.419	0.0036	-4.251	<0.0001	-2.257	0.0249	-3.313	0.0018
5.0 m	0.356	0.0132	-5.482	<0.0001	-3.286	0.0013	-4.792	<0.0001
10.0 m	0.094	0.5130	-	-	-	-	-	-
15.0 m	-0.352	0.0142	-	-	-	-	-	-
20.0 m	-0.860	<0.0001	-	-	-	-	-	-
25.0 m	-1.968	<0.0001	-	-	-	-	-	-
roughness	0.001	0.9415	0.684	0.0176	-0.588	0.2626	0.196	0.7594

Table A.B. 3 Difference in viewshed coefficient estimates (ΔVC) in the forest across eye-heights, 95% confidence intervals and their associated p -values. Where ΔVC is positive, the eye-height listed first has a larger average VC. Where ΔVC is negative, the eye-height listed second has a larger average VC.

Eye-Heights	ΔVC	LCL	UCL	p-value
0.25-0.75	94.6	53.9	135.3	<0.0001
0.25-1.5	49.7	9.0	90.3	0.0168
0.25-5	-77.0	-117.7	-36.3	0.0002
0.25-10	-167.9	-208.6	-127.2	<0.0001
0.25-15	-289.8	-330.5	-249.2	<0.0001
0.25-20	-402.7	-443.4	-362.0	<0.0001
0.25-25	-466.1	-506.8	-425.5	<0.0001
0.75-1.5	-45.0	-4.3	-2.2	0.0304
0.75-5	-171.6	-212.3	-130.9	<0.0001
0.75-10	-262.5	-221.8	-12.7	<0.0001
0.75-15	-384.4	-425.1	-343.8	<0.0001
0.75-20	-497.3	-538.0	-456.6	<0.0001
0.75-25	-560.7	-601.4	-520.1	<0.0001
1.5-5	-126.6	-167.3	-86.0	<0.0001
1.5-10	-217.6	-258.3	-176.9	<0.0001
1.5-15	-393.5	-380.2	-298.8	<0.0001
1.5-20	-452.3	-493.0	-411.6	<0.0001
1.5-25	-515.8	-556.5	-475.1	<0.0001
5-10	-90.9	-131.6	-50.3	<0.0001
5-15	-212.9	-253.5	-172.2	<0.0001
5-20	-325.7	-366.4	-285.0	<0.0001
5-25	-389.2	-429.8	-348.5	<0.0001
10-15	-121.9	-162.6	-81.3	<0.0001
10-20	-234.8	-275.5	-194.1	<0.0001
10-25	-298.2	-338.9	-257.5	<0.0001
15-20	-112.8	-153.5	-72.2	<0.0001
15-25	-176.3	-217.0	-135.6	<0.0001
20-25	-63.5	104.2	-22.8	0.0022

Table A.B. 4 Differences in viewshed coefficient estimates (ΔVC) in the low structure-ecosystems across eye-heights with 95% confidence intervals and their associated p -values. Where ΔVC is positive, the eye-height listed first has a larger average VC. Where ΔVC is negative, the eye-height listed second has a larger average VC.

Ecosystem	Eye-Height	ΔVC	LCL	UCL	p-value
<i>Shrub-Steppe</i>	0.25-0.75	-62.5	-97.3	-27.7	0.0004
	0.25-1.5	-216.3	-251.1	-181.6	<0.0001
	0.25-5	-409.6	-444.4	-374.8	<0.0001
	0.75-1.5	-153.9	-172.5	-135.2	<0.0001
	0.75-5	-347.1	-365.8	-328.4	<0.0001
	1.5-5	-193.2	-211.9	-174.6	<0.0001
<i>Prairie</i>	0.25-0.75	-12.9	-30.9	5.0	0.1587
	0.25-1.5	-108.0	-125.9	-90.0	<0.0001
	0.25-5	-335.2	-353.2	-317.3	<0.0001
	0.75-1.5	-95.1	-97.4	-92.8	<0.0001
	0.75-5	-322.3	-324.6	-320.0	<0.0001
	1.5-5	-227.2	-229.5	-224.9	<0.0001
<i>Desert</i>	0.25-0.75	28.3	9.6	47.2	0.0031
	0.25-1.5	-68.0	-86.8	-49.2	<0.0001
	0.25-5	-288.3	-307.1	-269.5	<0.0001
	0.75-1.5	-96.4	-102.3	-90.4	<0.0001
	0.75-5	-316.7	-322.6	-310.7	<0.0001
	1.5-5	-220.3	-226.2	-214.4	<0.0001

Table A.B. 5 Difference in coefficient of variation estimates (Δ Coeff. Var.) in the forest across eye-heights, 95% confidence intervals and their associated p -values. Where Δ Coeff. Var. is positive, the eye-height listed first has a larger average coefficient of variation. Where Δ Coeff. Var. is negative, the eye-height listed second has a larger average coefficient of variation.

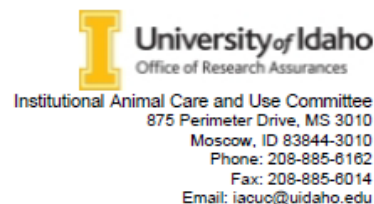
Eye-Heights	Δ V Coeff. Var.	LCL	UCL	p-value
0.25-0.75	-0.4306	-0.7121	-0.1491	0.0027
0.25-1.5	-0.4187	-0.7002	-0.1372	0.0036
0.25-5	-0.3561	-0.6376	-0.0746	0.0132
0.25-10	-0.0940	-0.3755	0.1875	0.5130
0.25-15	0.3522	0.0707	0.6337	0.0142
0.25-20	0.8583	0.5702	1.1465	<0.0001
0.25-25	1.9663	1.6761	2.2564	<0.0001
0.75-1.5	0.0119	-0.2696	0.2934	0.9338
0.75-5	0.0745	-0.2070	0.3560	0.6039
0.75-10	0.3366	0.0551	0.6181	0.0191
0.75-15	0.7828	0.5013	1.0643	<0.0001
0.75-20	1.2889	1.0008	1.5771	<0.0001
0.75-25	2.3969	2.1067	2.6870	<0.0001
1.5-5	0.0626	-0.2189	0.3441	0.6630
1.5-10	0.3247	0.432	0.6062	0.0238
1.5-15	0.7708	0.4894	1.0523	<0.0001
1.5-20	1.2770	0.9889	1.5652	<0.0001
1.5-25	2.3849	2.0948	2.6751	<0.0001
5-10	0.2621	-0.0194	1.825	0.0680
5-15	0.7083	0.4268	0.9898	<0.0001
5-20	1.2144	0.9263	1.5026	<0.0001
5-25	2.3224	2.0322	2.6125	<0.0001
10-15	0.4461	0.1646	0.7276	0.0019
10-20	0.9523	0.6642	1.2404	<0.0001
10-25	2.0602	1.7700	2.3504	<0.0001
15-20	0.5062	0.2180	0.7943	0.0006
15-25	1.6141	1.3239	1.9043	<0.0001
20-25	1.1079	0.8128	1.4031	<0.0001

Table A.B. 6 Differences in viewshed coefficient estimates (Δ Coeff. Var.) in the low structure-ecosystems across eye-heights with 95% confidence intervals and their associated p -values. The eye-height listed first has a larger average coefficient of variation.

Ecosystem	Eye-Height	Δ Coeff. Var.	LCL	UCL	p-value
<i>Shrub-Steppe</i>	0.25-0.75	0.5375	0.2544	0.8207	0.0002
	0.25-1.5	1.0218	0.7386	1.3049	<0.0001
	0.25-5	2.2527	1.9696	2.5359	<0.0001
	0.75-1.5	0.4843	0.1363	0.8322	0.0064
	0.75-5	1.7152	1.367	2.0632	<0.0001
	1.5-5	1.2309	0.8830	1.5789	<0.0001
<i>Prairie</i>	0.25-0.75	0.0193	-0.2109	0.2495	0.8695
	0.25-1.5	0.285	0.0550	0.5153	0.0152
	0.25-5	1.3141	1.0839	1.5442	<0.0001
	0.75-1.5	0.2659	0.1730	0.3587	<0.0001
	0.75-5	1.2948	1.2019	1.3876	<0.0001
	1.5-5	1.0289	0.9360	1.1218	<0.0001
<i>Desert</i>	0.25-0.75	0.1733	-0.0625	0.4091	0.1498
	0.25-1.5	0.5012	0.2654	0.7371	<0.0001
	0.25-5	1.9797	1.7438	2.2155	<0.0001
	0.75-1.5	0.3280	0.1546	0.5013	0.0002
	0.75-5	1.8064	1.6330	1.9798	<0.0001
	1.5-5	1.4784	1.3050	1.6518	<0.0001

Appendix C

University of Idaho Institutional Animal Care and Use Committee Protocol Approval



Date: May 20, 2021
To: Janet L. Rachlow Witham
From: University of Idaho Institutional Animal Care and Use Committee
Re: Protocol IACUC-2021-31 *Evaluating habitat selection by pygmy rabbits*

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on 05/20/2021.

This protocol was initially submitted for review on: 05/19/2021 03:20:22 PM PDT
The original approval date for this protocol is: 05/20/2021
This approval will remain in effect until: 05/19/2022
This protocol may be continued by annual updates until: 05/19/2024

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol, you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Sincerely,

University of Idaho Institutional Animal Care and Use Committee

Appendix D

University of Idaho Institutional Review Board Protocol Approval



November 09, 2021

To: Janet L. Rachlow Witham

Cc: Rachel Stein

From: University of Idaho Institutional Review Board

Approval Date: November 09, 2021

Title: Are experiential field work courses mutually beneficial to students and researchers?

Protocol: 21-205, Reference: 015216

Exempt under Category 1 at 45 CFR 46.104(d)(1).

On behalf of the Institutional Review Board at the University of Idaho, I am pleased to inform you that the protocol for this research project has been certified as exempt under the category listed above.

This certification is valid only for the study protocol as it was submitted. Studies certified as Exempt are not subject to continuing review and this certification does not expire. However, if changes are made to the study protocol, you must submit the changes through [VERAS](#) for review before implementing the changes. Amendments may include but are not limited to, changes in study population, study personnel, study instruments, consent documents, recruitment materials, sites of research, etc.

As Principal Investigator, you are responsible for ensuring compliance with all applicable FERPA regulations, University of Idaho policies, state and federal regulations. Every effort should be made to ensure that the project is conducted in a manner consistent with the three fundamental principles identified in the Belmont Report: respect for persons; beneficence; and justice. The Principal Investigator is responsible for ensuring that all study personnel have completed the online human subjects training requirement. Please complete the *Continuing Review and Closure Form* in VERAS when the project is completed.

You are required to notify the IRB in a timely manner if any unanticipated or adverse events occur during the study, if you experience an increased risk to the participants, or if you have participants withdraw or register complaints about the study.

IRB Exempt Category (Categories) for this submission:

Category 1: Research, conducted in established or commonly accepted educational settings, that specifically involves normal educational practices that are not likely to adversely impact students' opportunity to learn required educational content or the assessment of educators who provide instruction. This includes most research on regular and special education instructional strategies, and research on the effectiveness of or the comparison among instructional techniques, curricula, or classroom management methods.

Lidar Tutorial – Program R Code

```
###Import packages
library(viewshed3d)
library(lidR)
library (pracma)

###Read in lidar file
tls <- lidR::readLAS("TLS file", select="xyz")

###clean the point cloud
angle <- 0.6
tls <- viewshed3d::denoise_scene(tls,method="sd",
                                filter=6)

###classify the points as either ground or vegetation
tls <- lidR::classify_ground(tls, lidR::csf(rigidness = 1L,
                                           class_threshold = 0.2,
                                           sloop_smooth = FALSE))

center <- c(0,0,0)
position=data.frame(X = center[1], Y = center[2], Z = center[3])

###reconstruct ground
tls <- viewshed3d::reconstruct_ground(tls,
                                     position = center,
                                     ground_res = 0.05,
                                     angular_res = angle,
                                     method="knnidw",
                                     full_raster = TRUE)

###view point cloud
lidR::plot(tls)
```

```
###calculate viewshed
view.data <- viewshed3d::visibility(data = t1s,
                                   angular_res = angle,
                                   scene_radius = 4,
                                   store_points = TRUE)
plot(view.data$visibility$r,view.data$visibility$visibility,
     type="l",ylim=c(0,100),lwd=4, xlab = "Distance (m)", ylab = "Percent Sightlines Unobstructed",
     cex.lab = 1.8)
viewshed_coefficient <- trapz(view.data$visibility$r,view.data$visibility$visibility)
viewshed_coefficient

###view viewshed
x=lidR::plot(view.data$points,color="Visibility",
             colorPalette = c("blue","white"))
lidR::add_treetops3d(x,sp::SpatialPointsDataFrame(position,position),
                    radius=0.2,col="red")
```