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ABSTRACT

Heterogeneous vegetation structure can create a variable landscape of predation risk—a “fearscape”—that influences use and selection of habitat by animals. Mapping functional properties of vegetation that influence predation risk (e.g., concealment and visibility) across landscapes can be challenging. Traditional ground-based measures of predation risk are location specific and limited in spatial distribution. We demonstrate the benefits of terrestrial laser scanning (TLS) to map properties of vegetation structure that shape fearscapes. We used TLS data to estimate concealment of prey from multiple vantage points, representing predator sightlines, as well as visibility of potential predators from locations of prey. TLS provides a comprehensive dataset that allows exploration of how habitat changes may impact prey and predators. Together with other remotely sensed imagery, TLS could facilitate scaling up fearscape analyses to promote management and restoration of landscapes.

Keywords: habitat change, habitat quality, remote sensing, terrestrial laser scanning, viewshed

Animal's Eye-View of Habitat Quality

Animals use habitat (i.e., biotic and abiotic features in their environments, Hall et al. 1997) to meet multiple needs. Habitat quality can be evaluated in the context of fitness or components of fitness such as the degree to which habitat features enhance survival or reproduction (Van Horne 1983, Johnson 2007, Mosser et al. 2009). For prey species, risk of predation strongly shapes use and selection of habitat (Lima and Dill 1990). Understanding how specific habitat features influence predation risk, and thus, how individuals choose those features to reduce risk, is necessary for evaluating habitat quality, for predicting consequences of habitat change, and for guiding conservation and habitat restoration efforts.

In both aquatic and terrestrial systems, vegetation provides an important structural component of the environment that is used by animals to provide shelter from weather conditions (Wiemers et al. 2014), sites for foraging, resting, or reproduction (Squires et al. 2008), and structure that can alter risk of predation (Pierce et al. 2004). Vegetation and other habitat features can impede or enhance a variety of sensory modalities of both prey and predators including hearing, olfaction, and vision (Conover 2007, Slabbekoorn et al. 2010). For example, vegetation can conceal or hide prey, and thereby, reduce the probability that predators will visually detect individual prey (Denno et al. 2005, Camp et al. 2012). In addition to using vegetation to conceal their presence from predators, prey may also select habitat features that enhance their ability to detect predators (Embar et al. 2011, Camp et al. 2013). Early detection can allow prey to employ appropriate anti-predator strategies that increase their probability of survival (Samia et al. 2013). Vegetation structure also can alter risk of predation by facilitating escape of prey (Camacho 2014) or by providing a physical barrier against attack (Wirsing et al. 2007). Heterogeneous vegetation structure can create a spatially variable landscape of predation risk—a "fearscape"—that can influence habitat quality and selection of habitat by prey (Laundré et al. 2001, Arias-del Razo et al. 2012).

Understanding how vegetation functions to alter predation risk is challenging and requires models of habitat relationships at spatial scales that are commensurate with choices made by individual prey. Moreover, evaluating habitat quality within and across landscapes requires measures of habitat heterogeneity at those same spatial scales. Our ability to model predation risk has been hindered by a mismatch between the scales (e.g. plant, patch, habitat, and landscape) at which animals select habitat and the resolution of data on habitat features available across these same spatial scales. For example, one important property that influences predation risk is concealment of prey from predators at the plant scale. Concealment often is assessed by viewing or photographing cover boards or poles at a particular location to estimate how well an animal would be obscured by vegetation from a specific vantage point (Higgins et al. 2012). This approach evaluates concealment of prey from the perspective of a predator at the plant scale. Obtaining a more comprehensive assessment of concealment at larger spatial scales (e.g. patch, habitat, or landscape) would require repeating these measurements from many locations for both prey and predators. Consequently, characterizing predation risk for mobile prey continuously across a landscape is impractical using such an approach. Although habitat data collected through remote sensing techniques such as satellite imagery can be used to estimate vegetation continuously across larger spatial extents, the resolutions of such data are usually coarse relative to the scale at which prey select habitat that provides concealment from predators. Therefore, new techniques are needed to measure and map functional habitat properties at relatively fine scales across landscapes.

A second challenge in evaluating predation risk as a function of vegetation structure is that the degree to which plants provide concealment for prey or facilitate detection of predators by prey likely varies temporally. Changes in plant growth and phenology can alter plant structure and composition (e.g., forest regeneration or loss of seasonal leaves on deciduous shrubs), which can enhance or reduce concealment or detection. Likewise, other seasonal changes in the environment like snow cover and depth can alter vegetation structure available to prey above the snow surface, and consequently, alter the properties of concealment and detection (Mills et al. 2013). The ability to model and evaluate temporal and spatial variation in vegetation structure continuously across a landscape would enhance understanding of how predation risk shapes habitat use and selection by both predators and prey.

Using Terrestrial LiDAR to Map Habitat

Emerging remote sensing technologies are expanding options for mapping habitat features across the landscape that not only address existing mismatches in scales, but also allow greater flexibility in modeling and predicting habitat changes to test a broad range of hypotheses. Airborne- and ground-based light detection and ranging (LiDAR) capture three-dimensional (3-D) structure by emitting a concentrated beam of energy directed at an object. The sensor records the angle and time of flight for each return pulse, which is converted from spherical (r,θ,φ) to Cartesian coordinates (x,y,z). The collection of returns is referred to as a point cloud and ranges from millions to billions of individual points in 3-D. The main benefit of airborne LiDAR is the ability to gather data across broad spatial extents (~10 – 100 km^2), but the point density or resolution is typically relatively low (~1 – 10 pts m^{-2}). In contrast, ground-based LiDAR (also known as terrestrial laser scanning, TLS), generates very high point density (~100 – 1000 pts m^{-2}), but over smaller areas (~0.01 – several km^2). This high point density allows TLS to capture the 3-D physical structure of the surrounding habitat, offering the joint advantages of being comprehensive and scalable within the extent of the coverage (Vierling et al. 2008). By scanning horizontally, TLS also provides a novel method for modeling views from the opposing perspectives of both predator and prey at the plant, patch, and habitat scale.

Our objectives were to 1) validate TLS as a proxy for traditional, field-based estimates of prey concealment, 2) illustrate that with a complete TLS dataset, concealment of prey from predators and visibility of predators by prey can be estimated from any distance, height, or direction at the plant, patch, and habitat scale, and 3) use the sagebrush-steppe (*Artemisia* spp.) community as a model system in which to demonstrate the value of TLS for mapping fearscapes using methods that can be applied to other systems. We selected the sagebrush-steppe as a case study because many endemic prey (e.g., pygmy rabbits [*Brachylagus idahoensis*], greater sage-grouse [*Centrocercus urophasianus*], Piute ground squirrels [*Urocitellus mollis*], songbirds, and reptiles) rely on sagebrush vegetation for refuge from a diversity of terrestrial and aerial predators (e.g., American badgers [*Taxidea taxus*], common raven [*Corvus corax*], and birds of prey, DeLong et al. 1995). Several of these prey and their predators are species of conservation concern and are the focus of land management in the sagebrush-steppe (Connelly et al. 2011). In addition, sagebrush communities have changed extensively over the last century from invasive species, wildfire, and management practices that have altered vegetation structure and composition.

Terrestrial LiDAR Methods and Validation

Our research was conducted at a study site near Magic Reservoir north of Shoshone, Idaho in Lincoln County, 44°14’28” N, 114°19’04” W, elevation 1472 m (Figure 1a). The dominant vegetation type was Wyoming sagebrush (*Artemisia tridentata* subsp. *wyomingensis*), but also included patches of low sagebrush (*A. arbuscula*). The site contained mima-mounds, earthen mounds with relatively large, dense sagebrush and deeper soils that pygmy rabbits use for burrow excavation, foraging, and resting. These mounds are centers of activity for the local pygmy rabbit population, our representative prey species for this study.

To validate the use of TLS to quantify concealment, we compared methods for characterizing how well vegetation would hide prey from the view of a predator (i.e., concealment) using both photographic estimates and TLS. For horizontal concealment (i.e., from the perspective of a terrestrial predator), we placed a 15 cm profile cube representing a prey animal the size of a pygmy rabbit within the habitat near areas of prey activity (i.e., center of active pygmy rabbit burrows) and photographed the cube from a distance of 4 m at a height of 1.5 m above the ground in all four cardinal directions. A digital grid was then placed over each digital photograph of the cube, and the percentage of the cube concealed by vegetation (% concealment) was determined (Camp et al. 2012).

The same centers of activity that were photographed to estimate concealment also were scanned from four sides (NW, NE, SW, SE, Figure 1b) with a Riegl VZ-1000 TLS instrument. The Riegl VZ-1000 has a near-infrared laser (1550 nm) and a range of up to 1400 m for objects with 90% reflectivity or 700 m for objects with 20% reflectivity. The four scans were georeferenced together using reflective targets (Figure 1b). RiSCAN Pro software (Riegl, Horn, Austria) was used to collect, register, and process the TLS point cloud. The profile cube was kept in the same location for both the photographs and TLS. The 3-D point cloud was manipulated to recreate an image with the same lines of sight as the photographs (Figure 2). We estimated percent concealment of the TLS-derived image using the same digital grids used for the field-based photograph. Comparisons between TLS-derived and field-derived concealment methods from the same vantage points were highly correlated (r^2 = 0.85, P < 0.001, Figure 2), which demonstrates that TLS can be used as a proxy for traditional field-based methods for estimating concealment from predators and assessing predation risk. Field-based photographic concealment estimates took approximately 30 min in the field and 2 hr for analysis per patch, while TLS took 2 hr in the field and 2 hr for the same analysis of concealment per patch. TLS data also provides the ability to move beyond assessments at a single location and perspective to modeling concealment for any location from any perspective within the area scanned as described below.

Applications of Terrestrial LiDAR

TLS can create zones of concealment of prey at the patch and habitat scale rather than concealment at a single location (plant scale) from a particular vantage point. Previous work has explored a similar concept by measuring the distance and angle to overhead obstruction of sightlines from the perspective of a prey animal (e.g., “cone of vulnerability”, Kopp et al. 1998). The TLS 3-D structure expands on this approach by providing information throughout the canopy that can be used to calculate fine-scale estimates of concealment from all directions and vantage points. We used TLS to illustrate concealment of prey from terrestrial predators at any given location from within a defined buffer. We used ESRI ArcGIS Spatial Analyst (ESRI, Redlands, CA) to perform viewshed analyses from 100 potential predator locations. The viewshed analysis calculated unobstructed sightlines from which a predator could visually detect a prey at distances of 4 m, 8 m, and 12 m. The 100 viewsheds were summed together, creating a heat map of relative concealment or a fearscape representing prey vulnerability at a patch scale (Figure 3). The TLS-based models showed a general decrease in risk (more blue) as the predator viewed a given location from greater distances (4 m, 8 m, and 12 m). This map illustrates a heterogeneous environment providing locations within a patch of higher concealment (Points 1 and 2) and lower concealment (Point 3) for prey.

Similar analyses can be made to compare viewsheds for terrestrial predators of different sizes and consequently eye-heights (e.g., coyote [*Canis latrans*] vs. weasel [*Mustela* spp.]), in different positions (e.g., standing vs. lying), or with different modes of hunting (e.g., terrestrial vs. aerial predators). If the area of interest is free of occlusion (i.e., no large regions of missing data), then additional TLS scans would not be necessary to complete these new analyses. What would be required is alteration of input parameters, such as a higher inclination angle for avian predators, in GIS software. Additionally, TLS lends itself to highly accurate measurements of canopy cover (e.g., see distribution of shrubs in Figure 3), which is commonly used to assess habitat quality.

TLS also can be used to investigate tradeoffs between the opposing functional properties of concealment and visibility, both of which influence predation risk and can help to quantify fearscapes. Dense vegetation that provides high concealment also can reduce visibility and increase both perceived and actual risk of predation (Embar et al. 2011, Camp et al. 2013). Although concealment and visibility are inversely related, the correlation is not necessarily one to one, allowing prey to make tradeoffs between the two to gain more of one while giving up relatively less of the other (Camp et al. 2013). For example, areas with similarly high concealment (Points 1 and 2, Figure 3) may have very different levels of visibility (Point 1 = medium visibility, Point 2 = low visibility, Figure 3). The tradeoffs revealed through TLS could be used to predict and explain specific foraging, resting, and movement decisions by both prey and predators. In addition, other functional properties that influence predation risk (e.g., provision of a physical barrier against a predator attack) could be mapped using TLS and tradeoffs evaluated in a comparable manner.

TLS data can be manipulated to simulate changes in vegetation to test hypotheses or make predictions about how animals might respond to real or potential changes in vegetation structure. This tool is particularly valuable given expected changes in habitat associated with climate change or land management practices. As an example of this potential, we used TLS-derived vegetation height rasters to model the availability of vegetation above or below defined snow depths (Figure 4). The predicted changes in vegetation structure allow us to model the distribution of resources to test habitat selection by animals under differing climatic scenarios. Other simulations using TLS could be conducted to predict changes in vegetation structure following shifts in plant compositions and mortality. For example, plant communities in a variety of ecosystems are increasingly altered by fires (Soulard et al. 2013, Wang et al. 2014) and invasion or removal of invasive species (Vilà et al. 2011, Beck et al. 2012). TLS also can be used to predict changes in habitat properties like concealment for prey when new perch sites are introduced in habitats following construction of power lines resulting in novel sightlines for aerial predators. In addition, TLS can model different levels of leaf density that mimic deciduous plants with dense leaves in summer and without leaves in winter, thus capturing how changes in phenology that could influence predation risk in multiple ways. Different levels of concealment and visibility created for the same plant and location based on leaf density could help explain seasonal shifts in habitat use by predators and prey.

Fearscapes derived with TLS can be integrated with remotely collected data on animal locations to better understand factors shaping movement patterns and habitat selection. For example, viewsheds produced by airborne LiDAR were coupled with global positioning system (GPS) locations of lions (*Panthera leo*) to demonstrate that male lions preferred dense vegetation to ambush prey, whereas female lions hunted as groups in the open (Loarie et al. 2013). Within the same system, TLS could further characterize fine-scale habitat selected by prey to conceal or otherwise elude predators. Therefore, TLS coupled with animal movement data could help predict how changes in predator densities might influence foraging behavior of prey (van Beest et al. 2013) and in turn how shifts in foraging by prey might alter the vegetation structure (e.g., behaviorally mediated trophic cascade, Kauffman et al. 2010) and function (e.g., carbon dynamics of habitats, Strickland et al. 2013). By generating quantitative viewsheds from a point, line, or an area, and automatically integrating slope and aspect, TLS provides an unprecedented and sophisticated way to characterize the habitat features shaping the fearscape for wildlife. Because the dataset generated from TLS comprehensively includes vegetation structure and landscape geometry, the dataset is inherently holistic.

Scaling and Implications of Remote Sensing Technology

TLS can be integrated with vegetation maps generated from other remote sensing techniques to scale up fearscape analyses at plant, patch, and habitat scales to larger landscapes. For example, TLS could be linked with imagery from unmanned aerial systems (UAS). Although imagery collected from UAS is currently used to map and monitor forest and rangeland vegetation, these methods have only recently been applied to evaluations of wildlife habitat (Laliberte et al. 2011, Anderson and Gaston 2013). Unlike satellite imagery of vegetation, UAS imagery has the potential to provide fine-scale assessments over relatively large areas. We propose that TLS can be used to validate 3-D digital surface models of vegetation structure constructed using two-dimensional UAS imagery (i.e., structure-from-motion methods, Westoby et al. 2012). Consequently, UAS imagery has the potential to affordably scale up the fearscapes measured at high resolution over smaller extents with TLS to broader landscapes for research or conservation objectives.

Similarly, the larger scale and lower 3-D resolution from airborne LiDAR could be augmented with targeted data acquisitions from TLS to fill in the gaps of resolution in areas of high heterogeneity (e.g., Murgoitio et al. 2013). Leveraging data collection for comprehensive land management analyses will reduce total costs. Both TLS and ALS have a relatively large upfront cost and require extensive training to perform data processing and analysis. ALS data collection should be considered when there is a need for data over large extents. For projects that require fine-scale spatial or temporal resolution (e.g., repeat scans of the same feature) for vegetation that is relatively small or sparse, then TLS should be considered. Furthermore, the same TLS dataset that was collected for evaluating fearscapes as demonstrated here can be leveraged and used for quantifying fuel loads with biomass measurements (Olsoy et al. 2014) or inventorying vegetation (Moskal and Zheng 2012). Thus, TLS facilitates comprehensive assessments of habitat and, specifically, vegetation structure that can enhance land managers' ability to monitor and restore changing landscapes. Integration of TLS, UAS, airborne LiDAR, and animal location data represents an exciting new area of research and development for understanding, mapping and managing habitat quality for wildlife.

As with all emerging technology, there are benefits and limitations. The most informative future studies of habitat quality and use by wildlife will integrate existing on-ground techniques with TLS and other remote sensing techniques (e.g., UAVs, ALS). The particular suite of techniques that will result in the most useful information is dependent on the particular questions asked and the study system. Lastly, remote sensing techniques like TLS require expensive equipment and a higher level of expertise than ground-based techniques. The costs of remote sensing are highly variable depending on the size of the study site, as well as the type of sensor. Upfront costs of TLS sensors range from $12,000 for basic models (Eitel et al. 2013) to over $200,000 for some commercial units. In general, analysis of data requires a moderate to high level of expertise in GIS and remote sensing theory and software (e.g., ESRI ArcGIS, RiSCAN Pro, ENVI). As such, we encourage wildlife biologists to establish collaborations with those labs using remote sensing technology where discussions related to specific habitat features or wildlife of interest can help direct the integration of the remote sensing, wildlife and conservation fields.

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Figure Captions

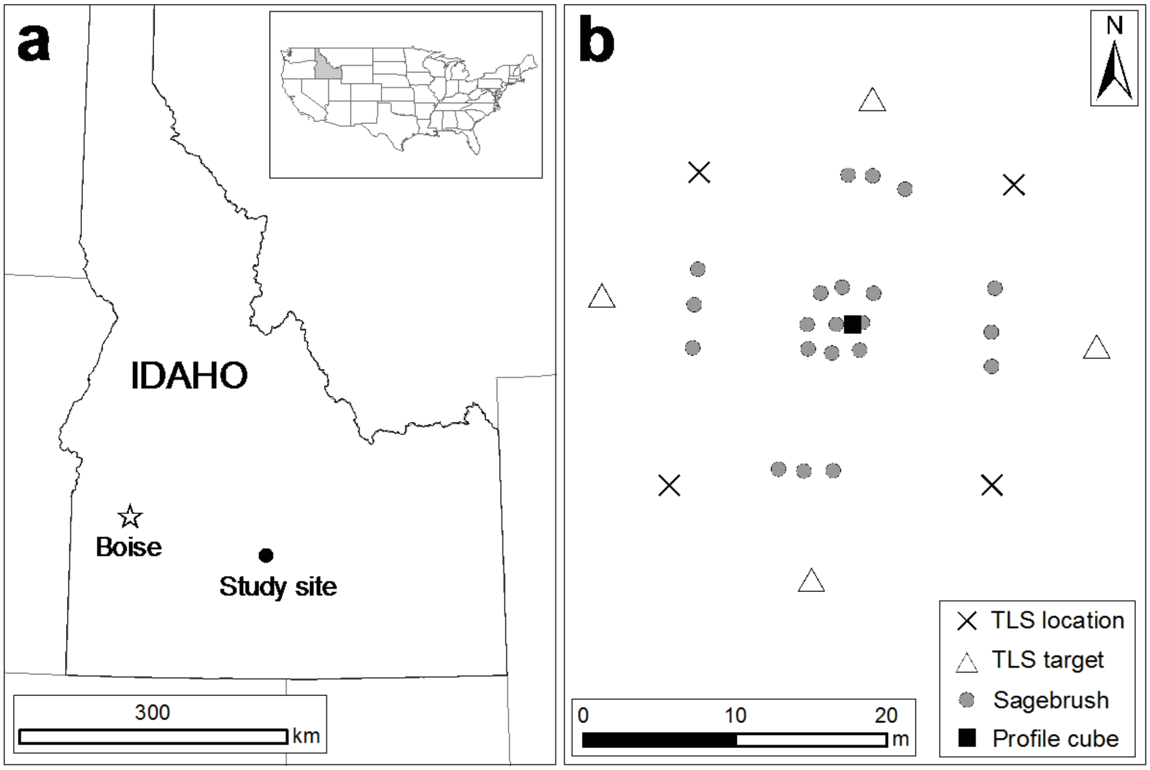

Figure 1. (a) Map showing the location of the study site in Idaho near Magic Reservoir (inset of Idaho in USA). (b) A typical example of the study design with the focal center of activity by prey in the middle and a profile cube placed on that center of activity. TLS reflective targets are placed in the four cardinal directions (N, E, S, W), and the four TLS scan positions are located in the NW, NE, SW, and SE corners.

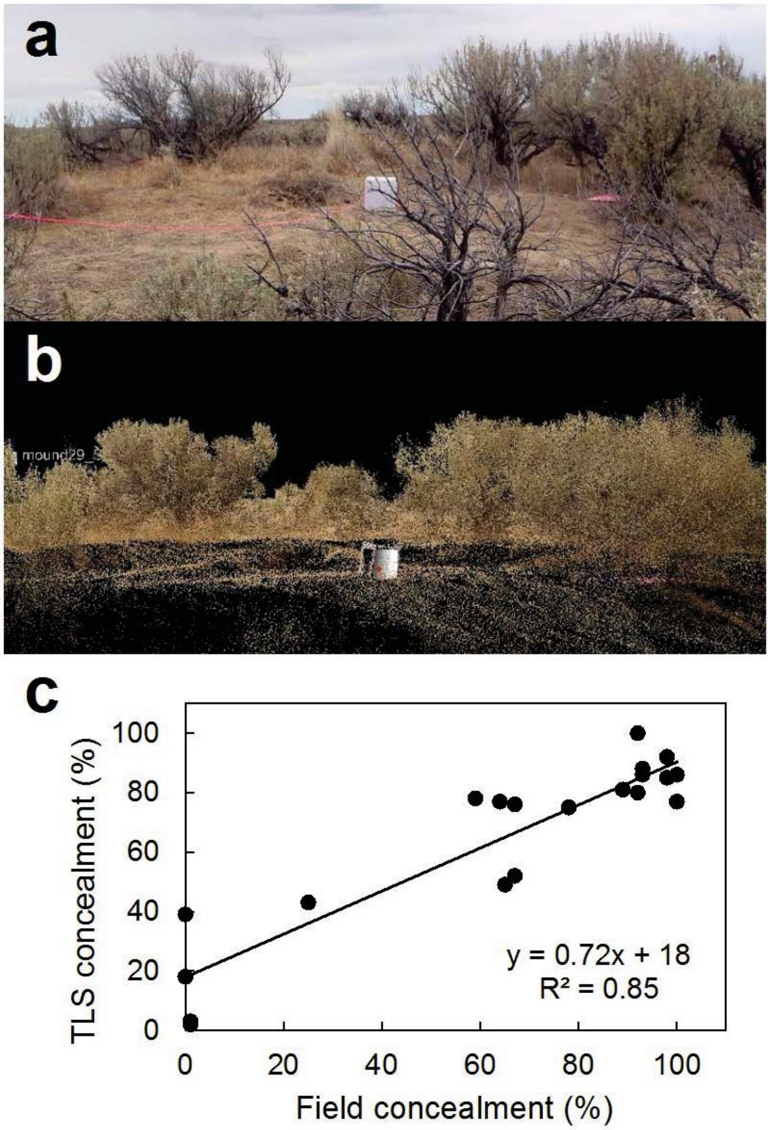

Figure 2. Comparison of (a) a photograph used to estimate field concealment of a profile cube (described in Figure 1), and (b) the TLS point cloud used to estimate TLS concealment of the same profile cube at the same distance and vantage point. c) Relationship between estimates of TLS-derived and field-derived concealment of a profile cube (n = 20).

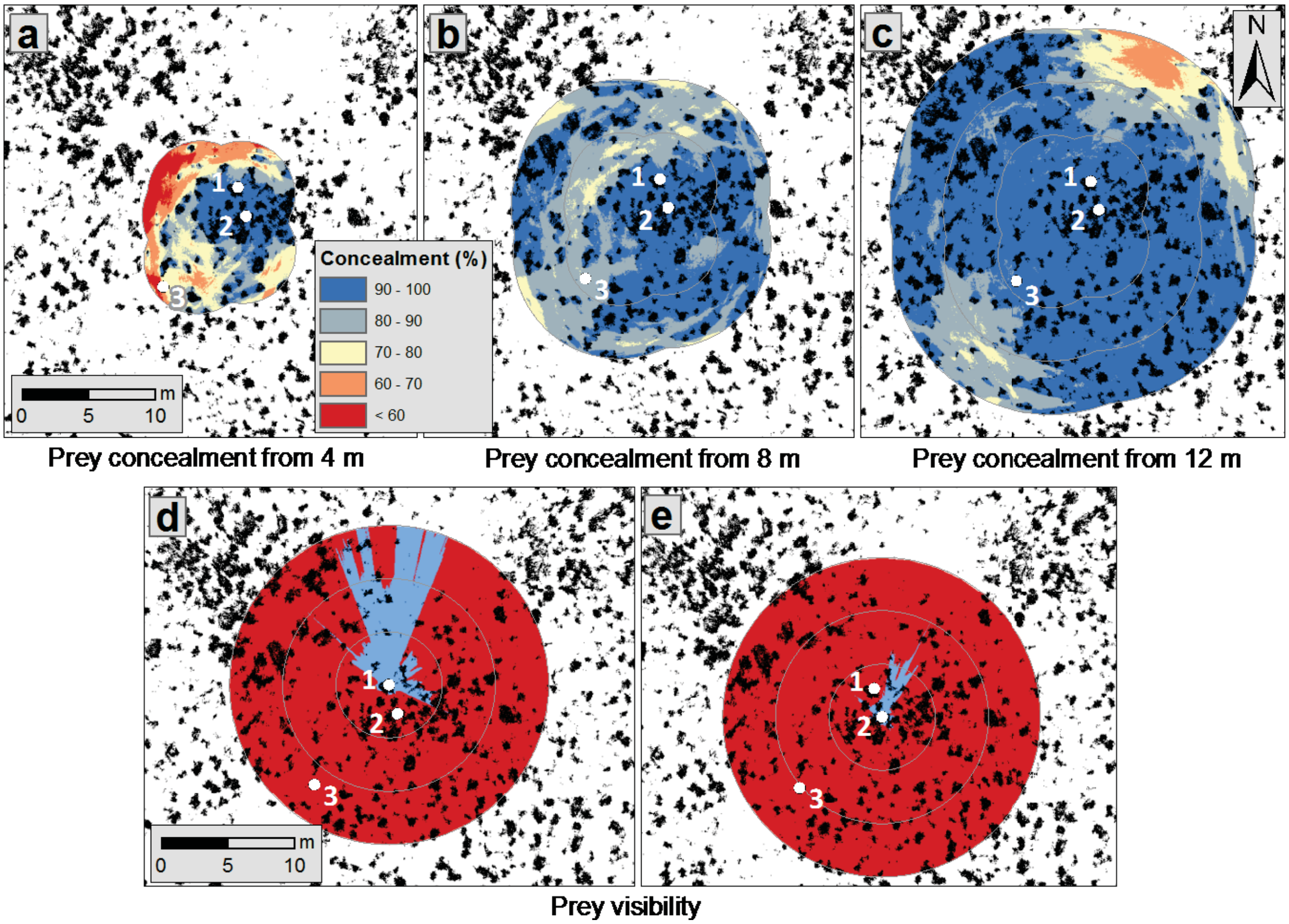

Figure 3. Top panel: map of horizontal concealment (one property of a fearscape) around a burrow system at (a) 4 m, (b) 8 m, and (c) 12 m representing the center of activity of prey. Points 1 and 2 show areas of high concealment, while Point 3 shows relatively lower concealment at all distances. Bottom panel: two different perspectives of prey locations within a patch with similar concealment (Points 1 and 2 in top panel) but differing visibility: (d) high visibility at Point 1, and (e) low visibility at Point 2. The black pixels represent shrubs within the habitat (> 0.5 m vegetation height) measured with TLS, and the grey lines indicate distances of 4 m, 8 m, and 12 m from the center of activity.

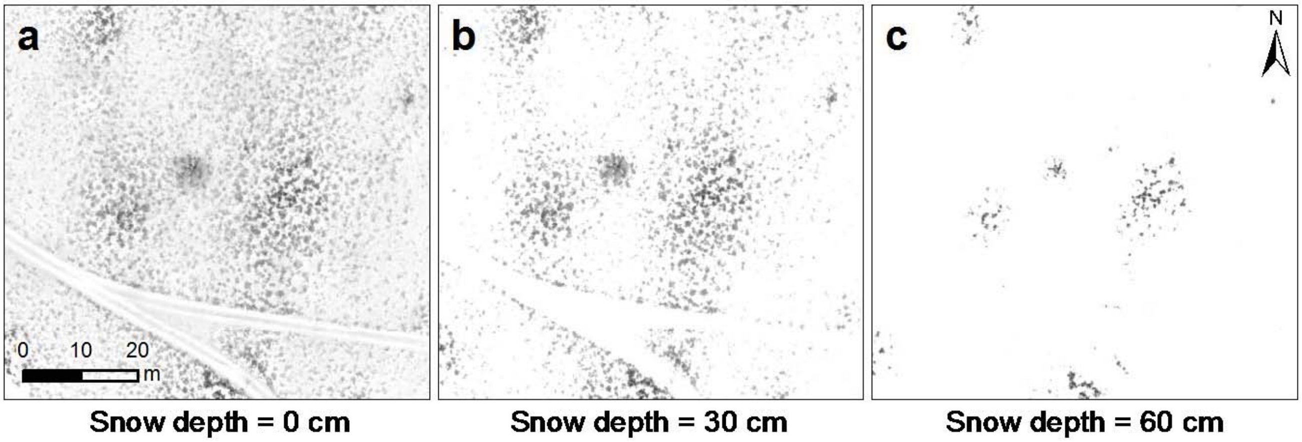

Figure 4. Models of available vegetation (grey pixels) above the snow surface that is a cover and food resource for animals at different snow depths: (a) 0 cm, (b) 30 cm, and (c) 60 cm using the TLS dataset.