It’s a Small World: Evaluating Micro-GPS Technologies and Factors Influencing Habitat Use by Pygmy Rabbits in Idaho

A Thesis

Presented in Partial Fulfillment of the Requirements for the Degree of Master of Science

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

by

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May 2017

Authorization to Submit Thesis

This thesis of Laura A. McMahon, submitted for the degree of Master of Science with a Major in Natural Resources and titled "It's a Small World: Evaluating Micro-GPS Technologies and Factors Influencing Habitat Use by Pygmy Rabbits in Idaho," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

The goals of this research were to 1) evaluate the efficacy of micro-GPS receivers to collect accurate data for habitat selection studies of small mammals, and 2) contrast factors shaping habitat selection across hierarchical behaviors with a two-stage, hurdle modeling approach. We conducted field trials on pygmy rabbits (*Brachylagus idahoensis*) to evaluate GPS performance and to quantify both selection of habitat patches and intensity of patch use. This work suggested that micro-GPS telemetry can be implemented to address fine-scale questions regarding habitat selection, but an understanding of the heterogeneity of the landscape and animal behavior is necessary. At a relatively coarse behavioral level, rabbits selected resources that minimized predation risk, however, at a finer scale, rabbits intensively used patches with increased availability of seasonal forages. The use of micro-GPS receivers and hurdle models provide opportunities for assessing habitat selection at multiple spatial scales and behavioral levels.

Acknowledgements

Many people are responsible for assisting and supporting me throughout my project. First, I would like to thank Dr. Janet Rachlow for her ability to provide advice and direction through a sea storm of problems, while maintaining enthusiasm and a positive outlook. Her passion, support, and mentoring made this thesis possible. Second, I would like to thank my committee members, Drs. Tim Johnson and Ryan Long for their statistical knowledge and support on data analysis, and Dr. Lisa Shipley for her comments shaping the thesis and field sampling support. I would also like to thank the Berklund Foundation for 2 ½ years of funding, which made my participation in this project possible. I would like to thank Dr. Jen Forbey for comments regarding project development. I would also like to thank the many technicians and friends (Miranda Crowell, Megan Whetzel, Steph DeMay, Miriam Hernandez, Charlotte Milling, Mitch Parsons, Nicole Carter, Matt Modlin, Rhianna Hohbein, Ben Shipley, Alex Arnold, Nolan Helmstetter, Sean Alexander, Wes Glisson, John Severson) who worked tirelessly through extreme weather to track rabbits and measure vegetation. For GPS troubleshooting assistance, I would like to thank Quintin Kermeen, Jon Adsem, and John Roth. Funding and other support was provided by the National Science Foundation (DEB-1146166 to Dr. Janet Rachlow, DEB-1146368 to Dr. Lisa Shipley, DEB-1146194 to Dr. Jen Forbey), University of Idaho, Bureau of Land Management, US Forest Service, and Idaho Department of Fish and Game.

Dedication

My parents, Tim and Jeanne McMahon and my sister, Megan McMahon for the unwavering encouragement and support.

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General Introduction

Habitat selection represents an integrated suite of behaviors that animals use to obtain food, water, and cover. Consequently, habitat selection often reflects constraints and tradeoffs that an animal must make among competing resource needs (Godvik et al. 2009). The habitat selection process can be investigated as a binary process (i.e., use-availability designs; Johnson et al. 2006; Godvik et al. 2009) or along a continuum (i.e., variation in use-only; Fauchald and Tveraa 2003; Millspaugh et al. 2006; Nielson and Sawyer 2013). Although use-availability designs characterize the overall process of selecting habitat, use-only approaches better describe the mechanistic drivers behind the behavioral process (Bastille-Rousseau et al. 2010). Combining these approaches using a hurdle model approach can reveal a more comprehensive understanding of habitat selection.

Global positioning systems (GPS) telemetry can provide high-resolution and frequent data on animal locations that are useful for addressing many ecological questions, especially those related to fine-scale patterns of habitat selection, movement, and activity. However, application of GPS technology on small mammals is limited by the size and weight of GPS devices. Over 90% of mammals are < 5 kg (Fleming 1979), and the median mass for 465 species of terrestrial mammals in North America is < 50 g (Brown and Nicoletto 1991). Advances in GPS technology and miniaturization of electronics and batteries now permit micro-GPS (< 20 g) deployment on small mammals weighing < 1 kg. With technological advances, manufacturers are marketing smaller GPS telemetry receivers for wildlife research, but information is minimal regarding the magnitude of errors associated with these micro-GPS receivers in relation to habitat features. Snapshot and traditional GPS receivers differ in the duration of time spent acquiring satellites. Snapshot receivers remain on for < 1 s and require post-processing to generate locations after the receiver has been recovered. Traditional receivers calculate locations on-board, thereby remain powered on for longer durations (< 1 min).

The pygmy rabbit is unique among North American lagomorphs in its extensive and obligate burrowing behaviors (Green and Flinders 1980). Pygmy rabbits are small-bodied leporids in the same family as jackrabbits and hares (*Lepus* spp.) and cottontails (*Sylvilagus* spp.); but unlike these species, the pygmy rabbit has evolved as a sagebrush specialist and burrow obligate (Green and Flinders 1980). This cryptic species is capable of traveling through thick stands of sagebrush to avoid predation (Katzner and Parker 1997; Rachlow et al. 2005) making behavioral and movement observations difficult. Methods employed to investigate the ecology of free-ranging pygmy rabbits have involved the use of camera stations (Larrucea and Brussard 2008, 2009; Lee et al. 2010), radio-telemetry (Katzner and Parker 1997; Sanchez and Rachlow 2008; Estes-Zumpf and Rachlow 2009; Crawford et al. 2010), and genetic analyses (Estes-Zumpf et al. 2010). Although we have learned much about the ecology of pygmy rabbits, many questions remain with respect to fine-scale patterns of habitat use and habitat quality.

The goal of this thesis was to evaluate the efficacy of micro-GPS receivers to collect accurate data for habitat selection studies of small mammals and assess how fundamental resource needs might shape patterns of habitat selection by pygmy rabbits. The use of micro-GPS receivers and hurdle models provide opportunities for assessing habitat selection across multiple scales and hierarchical behaviors. Dissecting behavioral strategies is a critical step in understanding the complex behavioral processes that result in habitat use and distribution of animals across landscapes. Elucidating how animals make choices about habitats across a diversity of spatial and temporal scales has increased understanding of the factors that govern the distribution of populations and movements of individuals. The results of this project will extend these concepts to hierarchical levels of behavior and enhance insights into the processes that shape the patterns we observe. Specific objectives for this research were:

1) Quantify errors associated with micro-GPS receivers;
2) Compare performance of 2 receiver types;
3) Assess the potential for application to small mammals; and
4) Contrast habitat selection at 2 hierarchical behavioral levels.

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Chapter 1: It's a Small World: Evaluation of Micro-GPS Receivers for Tracking Small-Bodied Mammals

Abstract

GPS telemetry markedly enhances the temporal and spatial resolution of animal location data, and recent advances in micro-GPS receivers permit their deployment on small mammals. Whereas traditional GPS receivers calculate locations immediately, one such technological advance, snapshot technology, allows for improved battery life by reducing the time to first fix via postponing the recovery of satellite ephemeris (satellite location) data and processing of satellite signals to estimate locations until the receiver has been recovered from the animal. However, no previous work has employed snapshot technology for a small, terrestrial mammal. We aimed to evaluate performance of two types of micro-GPS (< 20 g) receivers (traditional and snapshot) on a small, semi-fossorial lagomorph, the pygmy rabbit (*Brachylagus idahoensis*). Specifically, we examined the potential for errors to bias conclusions about fine-scale space use and habitat selection by small mammals. During stationary tests of micro-GPS performance, microtopography (i.e., burrows) and satellite geometry had the largest influence on fix success rate (FSR) and location error (LE). Effects of shrub cover varied, but were less pronounced than burrow cover. There was no difference between FSR while animals wore the micro-GPS collars above ground and FSR generated during stationary, above-ground trials, suggesting that animal behavior other than burrowing did not markedly influence micro-GPS performance in our study system. Furthermore, snapshot receivers deployed on animals operated inconsistently due to battery and software failures resulting in highly variable durations of data collection, whereas the traditional receivers consistently performed well. In our study, traditional micro-GPS receivers demonstrated similar FSR and LE to snapshot receivers, albeit traditional receivers collected more precise locations (mean LE = 8.9 m) than snapshot micro-GPS receivers (mean LE = 15.5 m). If problems associated with battery and software failures were resolved, snapshot technology could reduce the tradeoff between fix interval and battery life that occurs with traditional micro-GPS receivers, allowing for more comprehensive evaluation of small mammal movement, activity, and resource selection.

Introduction

GPS telemetry markedly enhances the temporal and spatial resolutions of animal location data. However, until recently, the size and weight of GPS receivers restricted their applications on small species. Although > 90% of mammals weigh < 5 kg (Fleming 1979), relatively few small mammals have been tracked using GPS telemetry. Advances in GPS technologies and smaller, more powerful batteries provide increasing opportunities for collecting GPS locations for small species. Comprehensive studies are needed to evaluate under what conditions micro-GPS receivers can provide the high precision location data necessary to address questions about movement and resource selection at relevant scales for small, mammalian species.

Advances in GPS technology and miniaturization of electronics and batteries now permit GPS deployment on small mammals weighing < 1 kg. To decrease size and weight, lightweight traditional GPS receivers often require small batteries, which leads to a trade-off between the number of locations generated and duration of battery life. Traditional receivers calculate GPS locations in real time, although the amount of time necessary to acquire a location estimate varies (Moriarty and Epps 2015). More frequent locations will deplete batteries more quickly, thereby reducing the duration of data collection. Recent applications of traditional GPS telemetry for mammals < 1 kg have faced such tradeoffs (e.g., Egyptian fruit bats, *Rousettus aegyptiacus* (Tsoar et al. 2011); Madagascar flying foxes, *Pteropus rufus* (Oleksy et al. 2015); gray squirrels, *Sciurus carolinensis* (Stevenson et al. 2013); European hedgehogs, *Erinaceus europaeus* (Glasby and Yarnell 2013); and snowshoe hares, *Lepus americanus* (Feierabend and Kielland 2014)). Snapshot technology, which was originally developed for marine species that only briefly surface above water (Hazel 2009), maximizes the life of small and lightweight batteries, thereby minimizing the tradeoff between battery life and frequency of GPS locations. To accomplish this, the snapshot receiver digitizes and stores raw data (satellite identification and timestamps) from satellite signals in < 1 s, after which the GPS shuts down until its next scheduled fix (Tomkiewicz et al. 2010). The receiver postpones the recovery of ephemeris data (i.e., precise satellite information) and calculation of receiver locations until after recovery of the receiver, when the raw data, in conjunction with post-processing software and downloaded data, are used to estimate GPS locations in a similar manner to traditional GPS receivers.

With technological advances, manufacturers are marketing smaller GPS telemetry receivers for wildlife research. However, limited information is available about the magnitude of errors associated with these micro-GPS receivers in relation to habitat features. No published research has evaluated snapshot GPS collection for small mammals, and we are aware of only two published studies (Tsoar et al. 2011; Glasby and Yarnell 2013) evaluating the performance of micro-GPS receivers (< 20 g) using traditional GPS collection for small mammals. Neither of these studies quantified the influence of habitat characteristics (e.g., vegetation cover or topography) or satellite geometry and availability on successful GPS location estimation and accuracy.

GPS errors typically are associated with environmental characteristics (e.g., terrain, vegetation), satellite acquisition (e.g., number of satellites detected, satellite geometry), and animal behavior. To estimate a location, a GPS receiver must receive satellite signals to triangulate its position, and this reliance on satellites can lead to two common types of performance errors: 1) a reduction in fix success rate (FSR; the number of successful fix attempts divided by the total attempted fixes) when the GPS cannot acquire signals from enough satellites to generate a location estimate; and 2) location errors (LE; the Euclidian distance between each GPS-generated location and the true location), which occur when a GPS receiver inaccurately triangulates a location. Rugged terrain often is associated with poor GPS performance because topography blocks satellite reception, leading to low FSR (Frair et al. 2004; Hebblewhite et al. 2007; Lewis et al. 2007; Adams et al. 2013). Vegetation characteristics, such as canopy closure, can increase LE through multipath error, a result of satellite signals reflecting off of the canopy and woody material (Rempel et al. 1995; Di Orio et al. 2003). The magnitude of location error also is affected by satellite geometry and the number of satellites used to determine a specific location. The GPS receiver computes locations based on the angles of satellites (triangulation), and successful locations are classified as 2-dimensional (2-D) if the GPS exploited 3 satellites or 3-dimensional (3-D) if the GPS used > 3 satellites for these calculations. Location error decreases as the number of satellites used to generate a location increases; for that reason, 3-D fixes are most often associated with smaller location errors (Lewis et al. 2007). Finally, error is introduced when the receiver is worn by an animal. Behavior of the animal (e.g., foraging, resting, burrowing) can reduce FSR or increase LE by altering the angle of the GPS antenna (D'Eon and Delparte 2005) or as a result of use of habitats that are suboptimal for satellite acquisition, such as dense cover, burrows, or tree cavities (Moen et al. 1996; Dussault et al. 1999). Location error can result in biases in research studies by masking habitat selection at fine-scales, especially in heterogeneous landscapes when LE is greater than the selected patch sizes (Visscher 2006; Frair et al. 2010). Likewise, low FSR could bias habitat selection by underrepresenting use of habitat types where the GPS has a lower probability of obtaining a successful location estimate (Frair et al. 2010).

To fill the gap in understanding of micro-GPS performance and its potential to track movement by small mammals, we evaluated performance of two types of micro-GPS telemetry receivers (traditional and snapshot) using stationary tests and field trials on a small (375-450 g), semi-fossorial lagomorph, the pygmy rabbit (*Brachylagus idahoensis*), which inhabits sagebrush steppe environments in the western USA (Green and Flinders 1980). First, we hypothesized that the two types of receivers would have similar FSR, but that traditional micro-GPS would have a lower LE because of extended time to search for satellites. Second, we hypothesized that shrub cover would influence performance of the GPS devices by interfering with the angles of satellite detection. We predicted that shrub cover would be positively correlated with LE and negatively correlated with FSR. Third, we hypothesized that burrowing behavior of rabbits would reduce micro-GPS telemetry performance by obstructing satellite reception, and we expected lower FSR and greater LE when micro-GPS receivers were in burrows of pygmy rabbits. Finally, because previous research has documented that animal behavior influences GPS performance (Graves and Waller 2006; Cargnelutti et al. 2007), we used light sensors paired with GPS collars to identify and screen out location attempts when animals were in burrows to facilitate an evaluation of the influence of behavior on fix success while animals were above ground. We expected to document lower FSR with both technologies from receivers deployed on animals above ground in the field in comparison to results from above-ground stationary tests. We compare our results to data reported from GPS telemetry on large-bodied mammalian species and birds to provide context for considering the scaling of errors with micro-GPS receivers on small species.

Methods

Study Area

We conducted this research at Cedar Gulch (44° 41' N, 113° 17' W), located within the Lemhi Valley in east-central Idaho, USA. The Lemhi Valley runs parallel to the Montana border, and is bounded by the Beaverhead Mountains to the east and the Lemhi Mountain Range to the west. The Cedar Gulch study site has limited topography (elevation ranged between 1,880 and 1,925 m), with higher elevations occurring in the northern region.

The study site encompassed approximately 100 ha of continuous sagebrush-steppe habitat characterized by distinct dome-like mounds of sediments (i.e., mima mounds). At the Cedar Gulch site, the mean diameter of mima mounds was 10.6 m (Parsons et al. 2016) and mounds were separated by 30-50 m. Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) shrubs occurred predominantly clumped on these mounds and also dominated off-mound areas along with low densities of black sagebrush (*A. nova*) and three-tip sagebrush (*A. tripartite*). Compared to the off-mound matrix, mima mounds supported taller and denser shrubs (shrub height = 0.5 – 1.0 m; Parsons et al. 2016), which provided more potential concealment cover for wildlife such as pygmy rabbits than off mounds, creating a heterogeneous landscape lacking in trees and large woody obstructions (Sanchez and Rachlow 2008). At this site, pygmy rabbit burrows occurred almost exclusively on mima mounds. Rabbit burrow systems are simple tunnels consisting of one or more entrances, with the size of the entrance openings varying from 6 to 31 cm (Green and Flinders 1980).

Stationary Tests

We evaluated performance of two types of GPS technology, snapshot and traditional, in stationary tests at randomly located sites throughout our study area. We stratified Cedar Gulch into two strata representing areas on and off of mima mounds and used a stratified random sampling design to identify 20 on- and 20 off-mound test locations (n = 40) for placement of GPS receivers. To facilitate evaluation of the influence of burrows on GPS performance, we constrained our on-mound test sites to mima mounds with rabbit burrows (n

= 195) using a data layer of pygmy rabbit burrow locations within Cedar Gulch. To evaluate the effects of burrowing behavior (i.e., use of underground burrows vs. above-ground locations), we paired 10 of the on-mound locations with a GPS receiver placed in a randomly selected burrow tunnel at a consistent distance of 0.25 m from the burrow entrance. At 0.25 m, the device is completely underground, however, it is near enough to the burrow entrance that it is possible to detect some satellites through the opening. The paired on-mound test site was located on the ground surface directly above the underground receiver. With this configuration, both receivers were located at the same coordinates with the only difference being the separation between above and below ground. All test locations were marked at $\leq$ 3-cm accuracy using a survey-grade GPS unit (Topcon HiPer V, Topcon Positioning Systems, CA, United States, https://www.topconpositioning.com) to provide known references against which to compare GPS-estimated locations (Recio et al. 2011).

We deployed both types of GPS receivers on collars weighing < 15 g. Test receivers were attached with plastic zip-ties to wooden stakes at 8 cm above the ground (approximate height of a GPS collar worn by a pygmy rabbit) for approximately 48-hr periods and were programmed to record a location every 15 min. At a subset of locations, we deployed two receivers simultaneously to evaluate variability in performance between receivers. We tested 18 G10 UltraLITE GPS Loggers (snapshot receivers; Advanced Telemetry Systems, MN, United States, http://atstrack.com) during summer 2015 and 12 FLR V GM502030 Loggers (traditional receivers; Telemetry Solutions, CA, United States, http://www.telemetrysolutions.com) during summer 2016. Snapshot receivers were programmed at the highest sensitivity, allowing the receivers to detect satellites for 512 ms before shutting down. Traditional receivers were programmed to collect satellite information for a maximum of 90 s. Snapshot receivers logged information regarding date, time, latitude, longitude, number of satellites, and dilution of precision (DOP) values including horizontal (HDOP), vertical (VDOP), and positional (PDOP) (Dussault et al. 2001). Traditional receivers recorded date, time, northing, easting, time to fix (TTF) in seconds, type of fix (i.e., 3-D and 2-D), HDOP, and battery voltage. Dilution of precision values measure satellite geometry. Wider spacing of satellites (i.e., more optimal geometry) results in lower DOP (e.g., HDOP) values, which may indicate greater locational precision (Moen et al. 1997; D’Eon et al. 2002).

Stationary tests allowed us to evaluate the influence of a suite of environmental characteristics (shrub canopy, height, and burrow cover) on performance of GPS receivers (Recio et al. 2011). In the field, we quantified vegetation closure measured as the proportion of sky obscured by vegetation or woody material at an approximate 1-m scale using hemispherical photography. Photographs were captured using a smartphone camera equipped with a fish-eye lens, leveled at 8 cm and directed upwards from the test location (Recio et al. 2011). Using the program 'SamplePoint' (Booth et al. 2006), we overlaid a grid with 100 intersections onto each photograph, and classified each intersection within the image as either vegetation or sky. We used the proportion of intersections classified as vegetation as an estimate of vegetation closure. To estimate mean shrub height, we recorded the heights of all shrubs > 8 cm within 1 m of the test location to produce a mean value. We evaluated other shrub characteristics at two extents surrounding test collar locations (6- and 12-m radius buffers) using a shrub data layer classified from 2.74-cm resolution imagery collected from unmanned aerial vehicles. To estimate shrub canopy in the buffered regions surrounding each test location, the number of pixels classified as shrub were summed and divided by the total number of pixels. Because our study site was open and relatively flat with limited terrain obstruction, we did not include variables such as available sky, elevation, or slope in our analyses.

We evaluated errors for each micro-GPS receiver type by calculating FSR and LE (Rempel et al. 1995). Because preliminary analysis of snapshot receivers indicated more variable performance at the start of each stationary test, we used segmented regression to identify a break point in the data that represented the time at which location error stabilized. We excluded the more variable initial fixes from snapshot model development to assess the influence of burrow cover and habitat characteristics. Additionally, we examined if FSR and LE varied by receiver type or burrow cover (i.e., in or out of a burrow).

We modeled FSR and LE separately for both receiver types to identify variables that influenced performance. Models were created based on a priori hypotheses, and we included random effects for receiver and site to account for non-independence among location attempts within devices and/or sites (Hebblewhite et al. 2007) . To assess strength of evidence, we evaluated all models using the corrected Akaike Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002). All statistical analyses were conducted using R 3.2.3 (R Development Core Team 2015). Mixed-effects modeling was conducted in the lme4 package (Bates et al. 2015). We removed models with uninformative parameters (i.e., log-likelihood, LL, was nearly unchanged with the addition of variables) from reported model sets and recalculated model weight (Arnold 2010). For mixed-effects model results, we inferred significance of variables if the 85% confidence intervals for the odds ratios did not overlap one and parameter estimates did not overlap zero (Arnold 2010).

We used mixed-effects logistic regression to model the influence of burrow cover and shrub characteristics on FSR to evaluate the probability of obtaining a successful fix (2-D and 3-D). We fit nine models for each technology type that included an intercept-only null model (Table 1.1). Predictor variables included burrow cover (in or out), vegetation closure, average shrub height within 1 m of the test locations, and shrub canopy cover in each of the two buffers (6 and 12 m). For data derived from snapshot receivers, we included interactions between burrow cover and vegetation closure, shrub height (1 m), and shrub canopy (6 m). Because of small sample sizes, we could not include interactions among variables in our traditional GPS model set.

We modeled LE using mixed-effects linear regression with a log transformation of the response variable to better meet the assumptions of the model (Lewis et al. 2007). We included the same predictors used to model FSR, with the addition of technical variables (number of satellites, HDOP, and TTF). The number of satellites and HDOP were highly correlated, and therefore, were not included in the same models. Time to fix (TTF) was included in modeling LE data from traditional GPS receivers, but was not included in modeling performance of snapshot technology because the snapshot receivers were set to turn on for a standard period of time. We evaluated 19 candidate models with the snapshot GPS data and 20 candidate models with traditional GPS data (Table 1.2).

Initial analyses of FSR and LE with respect to burrow, shrub characteristics, and satellite availability indicated an overwhelmingly strong influence of burrow on error. To determine if the effect of burrow cover masked the influences of vegetation and satellite characteristics, we performed a post-hoc analysis by repeating the logistic and linear mixed-effects models with only data collected from above-ground collected receivers. We revised the original model sets by removing the burrow cover variable.

Field Performance Trials

To evaluate FSR of GPS receivers while deployed on animals, we fitted adult pygmy rabbits weighing > 415 g with GPS receivers attached to a collar. This weight threshold ensured that the collar was ≤ 4% of body mass. Animals were trapped using Tomahawk live traps (Wisconsin, United States) and fitted with GPS collars (snapshot receivers – 10.6 g or traditional receivers – 13.8-15.1 g; Fig. 1.1) with an attached very high frequency (VHF) transmitter (BD-2 – 1.6 g, Holohil Systems Ltd., Ontario, Canada) during winter (January-March) and summer (June-August) of 2015 and 2016. To maximize battery life, snapshot receivers were set to collect one location every 15 minutes and traditional receivers were set to collect one location every hour. Battery life at these respective fix intervals was estimated at 118 days for snapshot receivers and 9-13 days for traditional receivers. The GPS collars remained on individuals for 2-6 weeks, after which the rabbits were trapped to remove the collar and download data. All methods used in this study were approved by the University of Idaho Animal Care and Use Committee (Protocol #2015-12) and complied with the guidelines for use of wild mammals in research published by the American Society of Mammalogists (Sikes and Bryan 2016).

To determine whether failed fixes were influenced by burrow use or other animal behaviors, we attached 1-g light sensors (Intigeo-C65, Migrate Technology, Cambridge, United Kingdom) that logged the highest light levels (lux) every 5 minutes to the collars of a subset of the rabbits. During summer 2015, light sensors were paired with snapshot receivers, and in winter 2016, light sensors were paired with traditional receivers. Because we could only determine burrow use using the light sensor during daylight hours, we focused our analysis on GPS fix-lux pairings between sunrise and sunset. A GPS fix-lux pairing occurred when the GPS location and light reading were obtained within 5 minutes of each other. Because our sampling unit was an individual rabbit, we used a linear mixed-effect model with a random intercept for individual rabbit to make inferences concerning the overall (population mean) lux levels between successfully acquired and missed fixes. To identify lux levels that would indicate when rabbits were underground, we tested light sensor performance at two depths (20 and 30 cm) within burrows and also placed one sensor outside of the burrows, under a shrub. We conducted these trials at two burrow locations during winter and summer. We used lux levels from within the burrows to identify a 95th-percentile threshold for each season to classify each GPS fix-lux pairing as above or below ground. With this method, we aimed to minimize contamination of above-ground GPS fixes with underground fixes to facilitate evaluation of the influence of behavior on fix success while the animal was above ground.

Results

Stationary Performance

Receivers were placed at stationary test locations for an average of 48 hr (range = 46-48) during which we evaluated both FSR and LE relative to habitat parameters. Vegetation closure at these sites ranged from 0-81%. Between June and October 2015, we attempted 126 stationary tests using 18 snapshot receivers, however, the GPS receivers operated for the full 48-hr period during only 87 stationary tests at 37 test sites (31% failure rate). During July and October 2016, we completed 46 stationary tests at the same 37 locations using 12 traditional GPS receivers, all of which successfully recorded locations. Although 10 burrow sites were selected for testing, one burrow collapsed during the first year of sampling and was removed from the analyses, and another burrow was modified by rabbits between the first and second year, resulting in additional entrances. We removed that test site from analyses because the receiver could not be placed 25 cm into a burrow without being < 25 cm from another burrow entrance. As a result, of the 87 snapshot receiver trials, 13 tests were conducted underground in burrows at 9 sites, and of the 48 traditional GPS trials, 7 tests were conducted underground in burrows at 7 sites. Although 8 possible burrow sites were available for traditional tests, only 7 collected usable data because the receiver at the 8th burrow site was visibly disturbed by an animal over the course of the 48-hr trial and was removed from the analysis.

Technological differences between snapshot and traditional receivers were evident by the types of fixes collected and the variation in data quality at the start of each stationary test. Snapshot receivers only acquired 3-D fixes (> 3 satellites), whereas traditional micro-GPS receivers collected both 3-D and 2-D (3 satellites) fixes. The start of each snapshot stationary test showed greater variability in location errors, and results of the segmented regression analysis suggested that snapshot receivers stabilized and collected more consistent and accurate data after 9.2 ± 0.12 hr (Fig. 1.2). Because of this, we screened the first 37 locations from each snapshot test. No breakpoint was needed for the data recorded by traditional micro-GPS receivers because the data displayed consistent performance across the entire 48-hr testing period (Fig. 1.2).

As expected, micro-GPS performance in our stationary tests was influenced by both burrow cover and receiver type. Above ground, overall FSR was higher ($F_{1, 130} = 1496.00$, $p < 0.001$) and LE values were about 30 times smaller ($F_{1, 123} = 376.49$, $p < 0.001$) than receivers placed in burrows (Fig. 1.3). Additionally, above-ground receivers obtained locations using more satellites ($\bar{x} = 8.1 \pm 0.07$) with lower HDOP values ($\bar{x} = 4.4 \pm 0.02$) than receivers below ground (satellites: $\bar{x} = 6.2 \pm 0.01$; HDOP: $\bar{x} = 9.9 \pm 0.19$). We observed a significant interaction between receiver type and burrow cover on FSR ($F_{1,128} = 12.17$, $p < 0.001$) and LE ($F_{1, 121} = 20.36$, $p < 0.001$). Whereas receiver type within burrows did not significantly influence FSR ($F_{1,18} = 1.66$, $p = 0.21$), it did significantly influence LE ($F_{1, 11} = 5.89$, $p = 0.03$). Below ground, traditional micro-GPS receivers obtained locations with lower LE values ($\bar{x} = 320.2 \pm 264.56$ m) than snapshot receivers ($\bar{x} = 663.7 \pm 175.60$ m). In addition, traditional receivers placed above ground acquired significantly higher rates of successful locations ($F_{1,110} = 13.53$, $p < 0.001$) with lower LE values ($F_{1, 110} = 369.82$, $p < 0.001$) than snapshot receivers. Location errors for snapshot receivers above ground ($\bar{x} = 15.5 \pm 0.27$ m) were almost double that of traditional receivers ($\bar{x} = 8.9 \pm 0.33$ m). Snapshot micro-GPS receivers detected more satellites regardless of placement in or out of a burrow ($\bar{x} = 8.7 \pm 0.01$) than traditional receivers ($\bar{x} = 7.0 \pm 0.02$), although mean HDOP values were lower in traditional ($\bar{x} = 1.6 \pm 0.01$) than snapshot receivers ($\bar{x} = 6.3 \pm 0.02$), suggesting that traditional receivers were using satellites with more optimal satellite geometry.

Burrow cover and vegetation structure influenced FSR for both types of micro-GPS receivers in stationary tests. For snapshot GPS receivers, the top-ranked model contained 100% of the model weight (Table 1.3), and suggested that for receivers above ground, a 5% increase in vegetation closure resulted in a 9% increase in FSR. For receivers in burrows, a

5% increase in vegetation closure decreased the probability of a successful fix by 41% (Fig. 1.4). Model selection for traditional GPS receivers revealed five models with 95% of the cumulative model weight, with the top two models receiving a cumulative weight of 52% (Table 1.3). The top-ranked model suggested that the probability of a successful fix decreased by nearly 100% when below ground and decreased by 38% for every 5% increase in surrounding canopy cover, and the second-ranked model included the effects of burrow cover and shrub height (Table 1.3). That model also suggested that the probability of a successful fix decreased by nearly 100% when below ground and in addition, fix success decreased by 4% for every 1-cm increase in shrub height. Although no single model received overwhelming support, the effect of burrow cover was present in all models indicating that burrows significantly influenced the odds of obtaining a successful fix, whereas surrounding canopy cover, shrub height and other vegetation characteristics (i.e., vegetation closure, surrounding shrub canopy 12-m) had only moderate, non-significant additive influences on fix success.

During stationary tests, LE was influenced by burrow cover, and to a lesser extent, satellite geometry and vegetation. For snapshot GPS receivers, the top model describing the LE had 99% of the model weight and included burrow cover, vegetation closure, their interaction, and HDOP. The interaction (vegetation closure and burrow cover) and HDOP were significant at the 85% confidence level (Table 1.4). Values for LE increased with greater vegetation closure and compounded error for receivers within burrows to augment the magnitude of LE. Finally, satellite geometry (HDOP) was positively correlated with location error. Unlike snapshot receivers, there were four plausible models describing LE for traditional receivers, although the top-ranked model received 40% of the model weight. The top-ranked model included burrow cover and HDOP, whereas the other three competing models included the same two variables with the addition of shrub characteristics (Table 1.4). Similar to snapshot GPS technology, traditional receivers were influenced by being underground, with a larger magnitude of error observed for receivers below ground. Accuracy of traditional GPS receivers declined with larger HDOP values, and that trend was evident in all competing models. The shrub characteristics in the top models had parameter estimates with 85% confidence intervals overlapping 0, suggesting a limited influence on magnitude of LE for traditional GPS telemetry.

Constraining the analysis to data collected from above-ground trials, we observed strong influences of vegetation and satellite availability on LE and FSR for both snapshot and traditional receivers, suggesting that the effect of burrow cover masked the influence of additional variables. For snapshot receivers, the intercept only model for FSR received 35% of the model weight, suggesting vegetation had minimal influence on FSR; however, the top model describing LE had 85% of the model weight and included two significant fixed effects, surrounding shrub canopy (6 m) and the number of satellites. That model suggested that LE values increased by 2.6% for every 5% increase in canopy cover and decreased by 5.0% for every additional satellite used to calculate the location. Unlike snapshot receivers, there were four plausible models describing FSR for traditional receivers, although the two top-ranked models received 81% of the cumulative model weight. The top-ranked model included shrub height, whereas the second-ranked model included only vegetation closure. Both variables significantly reduced the probability of obtaining a fix. Finally, post-hoc model selection for LE of traditional GPS receivers revealed four models with 95% of the cumulative model weight. The top-ranked model received 58% of the model weight and included a significant negative effect of shrub height on LE and a positive relationship between LE and HDOP. The 3 additional models in the 95% confidence set also included a significant positive relationship between HDOP and LE. The effect of HDOP was present in all models indicating that HDOP significantly influenced LE, whereas surrounding canopy cover and vegetation closure had only weak, negative correlations with location error.

Field Performance Trials

The data collected by snapshot receivers deployed on rabbits was limited by receiver failures. We conducted 29 field trials with unique rabbit-GPS receiver pairings (n = 20 individuals); 9 animals were re-fitted with different micro-GPS collars because of receiver malfunctions. Micro-GPS receivers were deployed multiple times over the study period. Deployment of snapshot GPS receivers (n = 29) functioned as expected in only 14% of cases, with malfunctions caused by premature battery failures (n = 18), software failures (n = 4), and unknown causes (n = 3). Snapshot receivers were deployed on animals for an average of 24 ± 1.8 days (range = 5 - 35), but GPS data were acquired for a mean of only 9 ± 1.6 days per animal (range = 0 - 35). The receivers were programmed to attempt 1 fix every 15 min, and in total, they collected 17,723 3-D fixes. Excluding receivers that failed to obtain even a single fix (n = 7), overall 3-D FSR from snapshot receivers on animals averaged $82.0 \pm 4.2\%$. Snapshot receivers used a mean of 8.6 ± 0.02 satellites to estimate GPS locations with an average HDOP of 6.3 ± 0.01.

Traditional GPS receivers operated more consistently than snapshot GPS receivers during field trials with rabbits. We conducted 44 trials with unique rabbit-GPS receiver pairings using 35 individuals (six animals were collared with one or more different GPS receivers following malfunctions). Field trials with traditional GPS receivers were completed as planned in 59% of trials, with most malfunctions related to fatigue of wires connecting the battery and GPS circuit board (n = 14); this occurred only in the initial deployments and was eliminated with a design modification that fixed the battery in place on the collar to minimize friction between the wires connecting the battery and GPS circuit board. We also documented software failure (n = 6) and unknown or user error (n = 2). Traditional GPS receivers were deployed for an average of 14 ± 1.0 days (range = 1 - 36), and the GPS receivers logged location data for a mean of 11.0 ± 1.3 days (range = 0 - 36). Excluding receivers that failed to obtain a single fix (n = 6), overall FSR for all acquired fixes (2-D and 3-D) averaged $80.8 \pm 2.1\%$, and overall 3-D FSR for traditional receivers was $72.4 \pm 2.4\%$. Collecting 1 fix every 60 min, traditional receivers collected a total of 8,903 fixes, 90% of which were 3-D. The mean TTF for all fixes was 43.4 ± 0.2 s. Traditional receivers used on average 5.9 ± 0.02 satellites to estimate a location with a mean HDOP of 1.6 ± 0.02.

Data from light sensors used in conjunction with GPS receivers placed on rabbits suggested that burrow use, but not above-ground behavior, influenced FSR of the GPS receivers. We collected a total of 4,779 fixes with paired data from light sensors for 19 rabbits during summer 2015 and winter 2016. During summer 2015, light sensors were paired with snapshot GPS receivers; during winter 2016, light sensors were paired with traditional GPS receivers. Visual inspection of mean lux levels for missed and successful fixes suggested that lux levels for missed fixes were lower than mean lux levels for successful fixes (Fig. 1.5), indicating that missed fixes were at least partly attributable to burrow use. We removed location data from animals estimated to be in a burrow using seasonal 95% cutoff values generated from light sensor performance tests (summer < 132 lux and winter < 538 lux). The threshold lux levels reflect seasonal differences in natural light, and winter values likely were higher than summer because of light reflected off of snow. Contrary to our expectations, FSR from animals estimated to be above ground was comparable to the FSR for above-ground stationary tests, which suggests that animal behavior did not have a significant effect on FSR when rabbits were above ground (Fig. 1.6).

Discussion

Our study was the first to comprehensively quantify performance measures for micro-GPS telemetry receivers suitable for tracking mammals weighing < 1 kg. Micro-GPS receivers collected data with relatively high FSR and small LE values. Of the two types of micro-GPS receivers that we evaluated, traditional receivers produced more accurate locations than snapshot receivers. Both types of receivers performed poorly when in burrows, and to a lesser extent, when under shrub cover. Fix success rates acquired while animals wore the micro-GPS receivers above ground did not differ from locations acquired during stationary above-ground trials, suggesting that animal behavior other than burrowing did not markedly influence micro-GPS receiver performance in our study system. Our results suggest that micro-GPS receivers are capable of addressing questions about space use and resource selection by small mammals, but that additional techniques might be needed to identify use of habitat structures (e.g., burrows, tree cavities, rock crevices) that could affect micro-GPS performance and bias study results.

Somewhat unexpectedly, the magnitude of LE (8-16 m) and FSR (96 – 100%) that we documented for micro-GPS receivers during stationary tests were similar to those documented for much larger and heavier GPS telemetry receivers used for larger animals in other studies. Although performance reported in the literature for heavier, traditional GPS receivers varies considerably, reviews suggest typical values for FSR around 95% and LE from 10 to 30 m (Cain et al. 2005; Frair et al. 2010). We found only one study that used snapshot GPS telemetry on a terrestrial species (lowland tapirs, *Tapirus terrestris*), and the authors reported similar LE and FSR of their large snapshot GPS receivers to the snapshot micro-GPS receivers used in this study (Tobler 2009). In addition, the micro-GPS receivers that we evaluated generated FSR and LE values similar to other “lightweight” (120-125 g) traditional GPS receivers (Recio et al. 2011; Adams et al. 2013).

Large LE in locations acquired using the snapshot micro-GPS receivers were generated more often at the start of each trial, although traditional micro-GPS receivers collected consistently more accurate data throughout the tests (Fig. 1.2). As expected, the increased TTF for the traditional micro-GPS receivers often allowed those receivers to detect and exploit satellites with more optimal geometry (HDOP), resulting in more accurate location estimates. Although snapshot GPS receivers cannot calculate their own locations, their performance unexpectedly improved over time during the stationary trials (Fig. 1.2), suggesting that those receivers might retain some satellite information through almanac data (i.e., coarse data on the orbits of all GPS satellites). We suspect that the process of obtaining those data, however, might be prolonged due to the restricted durations of time searching for satellites. Removing snapshot data collected during the initial 9 hr of stationary tests eliminated 75% of locations with LE > 300 m. In contrast, traditional receivers collected similarly accurate data from the start of each test (Fig. 1.2), likely as a result of more flexibility in the time allotted to detect and process satellite signals and retain satellite information (Moriarty and Epps 2015).

Burrow cover markedly influenced the performance of micro-GPS receivers. As predicted, receivers below ground were unable to digitize satellite signals because the sky was nearly completely obstructed, resulting in reduced FSR relative to above-ground test locations (Fig. 1.3). Satellite acquisition is necessary to obtain location estimates, and accuracy increases with the number of satellites (Moen et al. 1997) and their spacing (Recio et al. 2011; Adams et al. 2013). Locations collected while underground were subject to limited satellite view, resulting in locations collected with fewer satellites and suboptimal spacing. When a receiver did generate a location while below ground, it was significantly less accurate than the locations generated by the above-ground counterparts (Fig. 1.3). When tracking burrowing animals, biologists will require additional methods to screen location data, including use of additional features such as light sensors or activity sensors, because missed fixes and large location errors can introduce bias into habitat selection studies (Frair et al. 2010).

Stationary and field data were modeled to assess the influence of vegetation features on micro-GPS performance with and without the influence of burrow cover. Original model results suggested that vegetation characteristics had minimal overall influence on FSR or LE, although shrub cover reduced the performance of snapshot micro-GPS receivers when they were below ground. When snapshot receivers were above ground, shrub cover had limited influence on performance, but because receivers below ground were already subjected to poor satellite reception, receiver performance was more susceptible to the influence of vegetation (Fig. 1.4). Our results for snapshot receivers are consistent with previous research indicating compounding error with vegetation and terrain (Rempel et al. 1995; D'Eon et al. 2002; Frair et al. 2004; Lewis et al. 2007; Sager-Fradkin et al. 2007). Post-hoc analyses reaffirmed that shrub cover had limited influence on FSR, however, these analyses indicated that LE was significantly influenced by increased surrounding canopy cover, although the influence was modest. In contrast, for traditional GPS receivers, our original model results suggested that FSR was only weakly influenced by shrub height, and no shrub characteristics were included in the top-ranked model for LE. We suspect that a similar interaction between vegetation and microtopography might influence the performance of traditional GPS receivers, but we did not have a sufficient sample size to include such interactions in our models because relatively few traditional receivers collected locations while in a burrow. Post-hoc analyses of only the above-ground data indicated significant, although modest, influence of vegetation on FSR and LE. The minimal influence of shrub characteristics on traditional receivers confirms the assertion by Recio et al. (2011) that low vegetation cover is unlikely to significantly affect FSR and LE. Micro-GPS receivers deployed on free-ranging rabbits in our study displayed high FSR (81%), comparable to results reported by Glasby and Yarnell (2013) for traditional micro-GPS receivers (13 g) deployed on European hedgehogs (84.6%), and higher than the 66% FSR reported for traditional GPS receivers (42-52 g) deployed on American martens (*Martes martes*; Moriarty and Epps 2015), which live in heavily forested landscapes. These results support the contention that sagebrush shrub cover had minimal influence on FSR.

In contrast to previous studies on larger mammals, performance of GPS receivers in our study was not markedly influenced by behavior when rabbits were above ground. Research conducted on larger species such as grizzly bears (*Ursus arctos*; Graves and Waller 2006), moose *(Alces alces*; Moen et al. 1996), and white-tailed deer (*Odocoileus virginianus*; Bowman et al. 2000) documented reduced FSR when animals wore traditional GPS collars relative to stationary trials, suggesting that an animal’s activity and movement, such as bedding, can reduce FSR by altering the position or orientation of the collar (Moen et al. 1996; Bowman et al. 2000; D’Eon and Delparte 2005). However, positioning of a GPS collar and body for animals like rabbits may not change much across behaviors like feeding and resting. This difference and the fact that the sagebrush steppe vegetation is open relative to the forested landscapes used by the larger species, could have contributed to the higher fix success documented in our study system.

Our study compared two types of GPS receivers and evaluated the influence of microtopography, vegetation, and satellite geometry on performance. Although previous research has noted differences in performance of GPS receivers among manufacturers (Frair et al. 2004; Hebblewhite et al. 2007; Blackie 2010), neither ATS nor Telemetry Solutions had an equivalent micro-GPS using the alternate technology to compare performance. Functioning of snapshot GPS receivers in our study was highly variable and unpredictable because of battery malfunctions and software problems, although the quality of the location data was similarly accurate to traditional receivers.

Our trials provide data that researchers can use to predict the influence of performance of micro-GPS receivers on studies of space use and habitat selection by small mammals. Large LE values could mask fine-scale patterns in foraging behavior and movement, especially when an animal’s typical movements are small (Bradshaw et al. 2007) or when an animal occupies a highly heterogeneous environment (Visscher 2006). Because small, herbivorous mammals often exploit smaller home ranges (Harestad and Bunnel 1979) or disperse shorter distances (Sutherland et al. 2000) than larger species, assessing the magnitude of LE of micro-GPS receivers is especially important for small mammal research. For example, annual home ranges for pygmy rabbits are typically < 5 ha (Sanchez 2007), orders of magnitude smaller than those of larger, more mobile species that have been the focus of most research using GPS telemetry (e.g., feral cats, *Felis catus*, 270 ha; Recio et al. 2010) or moose (1200 ha; Cederlund and Okarma 1988). Location error can limit the research questions that can be addressed. For instance, at the Cedar Gulch study site, habitat patches associated with mima mounds are on average 11 m in diameter and separated by 30-50 m. If LE was > 20 m, a GPS collared animal located at the edge of one patch, might appear to be using resources in a neighboring patch, resulting in inaccurate estimates of resource use and habitat selection. Our work suggests that micro-GPS telemetry can be used to address fine-scale questions, but an understanding of the heterogeneity of the landscape and animal behavior is necessary.

For burrowing and non-burrowing small mammals, traditional and snapshot GPS-receivers have the ability to produce location data suitable for investigating resource selection and space use. Most large errors that we detected were a result of microhabitat, such as burrows, indicating that small mammals' use of these types of features (e.g., burrows, tree cavities, or rock crevices) might affect the accuracy and subsequent analysis of GPS locations. However, micro-GPS receivers had low FSR below ground, so large location errors as a result of burrow use would be minimized by virtue of the fact that the devices would fail to collect locations. Error could be reduced further for species that use burrows or other cavities by incorporating light or activity sensors to facilitate screening locations when animals occupied such structures. Although we did not test the use of accelerometers and micro-GPS performance, the traditional receivers used in this project incorporated accelerometers that could be used in conjunction with the GPS receiver to attempt a fix only after the receiver surpassed a predetermined movement threshold. Accelerometer-informed GPS data might be beneficial for small species that exploit microhabitat features for resting behaviors by restricting GPS receiver fix attempts at times when the receiver is unlikely to obtain a fix or to generate inaccurate location estimates (Brown et al. 2012; Moriarty and Epps 2015). As receivers improve, snapshot technology could minimize the tradeoff between fix interval and battery life, allowing for more fine-scale evaluation of small mammal movement, activity, and resource selection.

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Table 1.1: The set of candidate models used to evaluate fix success rate (FSR) of two micro-GPS receiver types in stationary tests conducted during 2015-2016. Sample size restrictions precluded models with interactions from the traditional GPS model set. Predictor variables included burrow cover, vegetation closure, shrub height, and surrounding shrub canopy (6 and 12 m).

Model description	Traditional	Snapshot
Burrow	X	X
Vegetation Closure * Burrow		X
Vegetation Closure + Burrow	X	
Vegetation Closure	X	X
Shrub Height	X	X
Shrub Height * Burrow		X
Shrub Height + Burrow	X	
Surrounding Canopy (12 m)	X	X
Surrounding Canopy (12 m) + Burrow	X	X
Surrounding Canopy (6 m)	X	X
Surrounding Canopy (6 m) * Burrow		X
Surrounding Canopy (6 m) + Burrow	X	

X’s indicate inclusion of model in candidate model set for each technology.

Table 1.2: The set of candidate models used to evaluate location error (LE) of two micro-GPS receiver types in stationary tests conducted during 2015-2016. Sample size restrictions precluded models with interactions from traditional GPS model set. Predictor variables included burrow cover, vegetation closure, shrub height, surrounding shrub canopy (6 and 12 m), number of satellites used, and satellite geometry (HDOP).

Model Description	Traditional	Snapshot
# Satellites	X	X
Burrow	X	X
Burrow + # Satellites	X	X
Burrow + HDOP	X	X
Canopy Closure	X	X
Canopy Closure * Burrow		X
Canopy Closure + Burrow	X	
Canopy Closure * Burrow + # Satellites		X
Canopy Closure + Burrow + HDOP	X	
Canopy Closure * Burrow + HDOP		X
HDOP	X	X
Shrub Height	X	X
Shrub Height + Burrow	X	X
Shrub Height + Burrow+ # Satellites	X	X
Shrub Height + Burrow + HDOP	X	X
Surrounding Canopy (12 m)	X	X
Surrounding Canopy (12 m) + Burrow	X	X
Surrounding Canopy (6 m)	X	X
Surrounding Canopy (6 m) * Burrow		X
Surrounding Canopy (6 m) * Burrow + # Satellites		X
Surrounding Canopy (6 m) * Burrow + HDOP		X
Canopy Closure + Burrow + HDOP	X	
Surrounding Canopy (6 m) + Burrow	X	
Surrounding Canopy (6 m) + Burrow + # Satellites	X	
Surrounding Canopy (6 m) + Burrow + HDOP	X	
TTF	X	

X's indicate inclusion in model set for each technology.

Table 1.3: Models in the 95% confidence set explaining fix success rate (FSR) of snapshot and traditional micro-GPS receivers at 37 stationary test sites in Idaho, USA. Each model is described by K, the number of parameters estimated; ΔAICc, the change in AICc; Wt, model weight; LL, log-likelihood. Models are ranked based on the weight of the model.

Micro-GPS	Model	K	AICc	ΔAICc	Wt	LL	Rank
Snapshot							
	Burrow + Vegetation Closure – Burrow X Vegetation Closure*	6	3106.63	0.00	1.00	-1547.3	1
Traditional							
	- Burrow* - Surrounding (6 m) Canopy	5	641.41	0.00	0.26	-315.7	1
	- Burrow* - Shrub Height	4	641.49	0.08	0.25	-315.8	2
	- Burrow*	5	641.52	0.10	0.25	-316.8	3
	- Burrow* - Vegetation Closure	5	642.97	1.55	0.12	-316.5	4
	- Burrow* - Surrounding (12 m) Canopy	5	643.15	1.73	0.11	-316.6	5

*Significant at the 85% confidence level

Table 1.4: Models in the 95% confidence set explaining location error (LE) of snapshot and traditional micro-GPS receivers at 37 stationary test sites in Idaho, USA. Each model is described by K, the number of parameters estimated; ΔAICc, the change in AICc; Wt, model weight; LL, log-likelihood. Models are ranked based on the weight of the model.

Micro-GPS	Model	K	AICc	ΔAICc	Wt	LL	Rank
Snapshot							
	Burrow + HDOP* + Vegetation Closure + Burrow X Vegetation Closure*	8	26288.8	0	0.99	-13136.0	1
Traditional							
	Burrow* + HDOP*	6	12876.5	0	0.40	-6432.3	1
	Burrow* + HDOP* - Vegetation Closure	7	12877.3	0.77	0.27	-6431.7	2
	Burrow* + HDOP* - Surrounding (6m) Canopy	7	12878.1	1.55	0.18	-6432.0	3
	Burrow* + HDOP* - Shrub Height	7	12878.4	1.92	0.15	-6432.2	4

*Significant at the 85% confidence level

Figure 1.1: Micro-GPS receivers deployed in this study: (A) ATS G10 UltraLITE GPS logger (snapshot GPS receivers) weighed 9-10 g and (B) Telemetry Solutions FLR V GM502030 GPS Loggers (traditional GPS receivers) weighed 14-16 g.

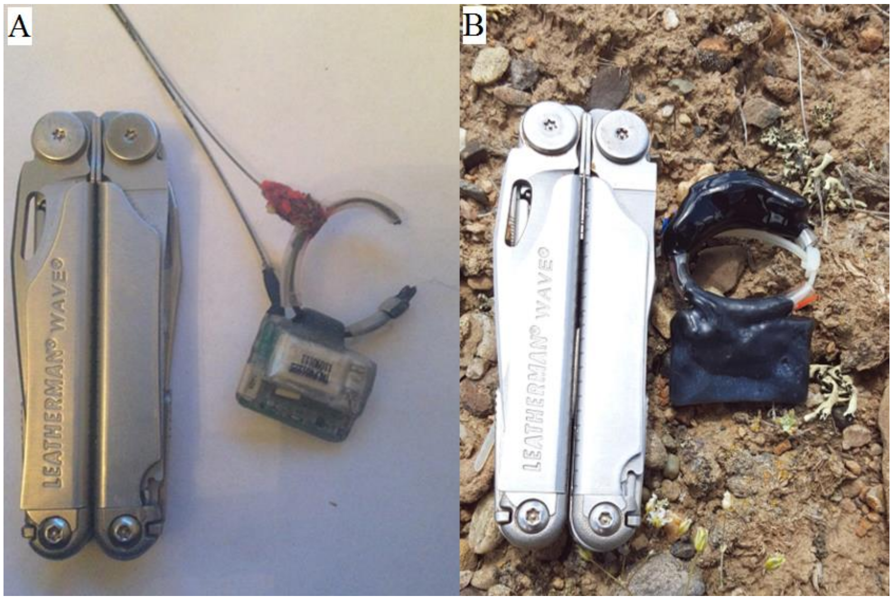


Figure 1.2 Relationship between duration (hr) from the start of stationary tests and micro-GPS accuracy (log of location error [LE]). Traditional micro-GPS receivers (left) displayed consistent performance, whereas snapshot micro-GPS receivers (right) generated large LE values at the start of each stationary test before leveling to a more consistent performance.

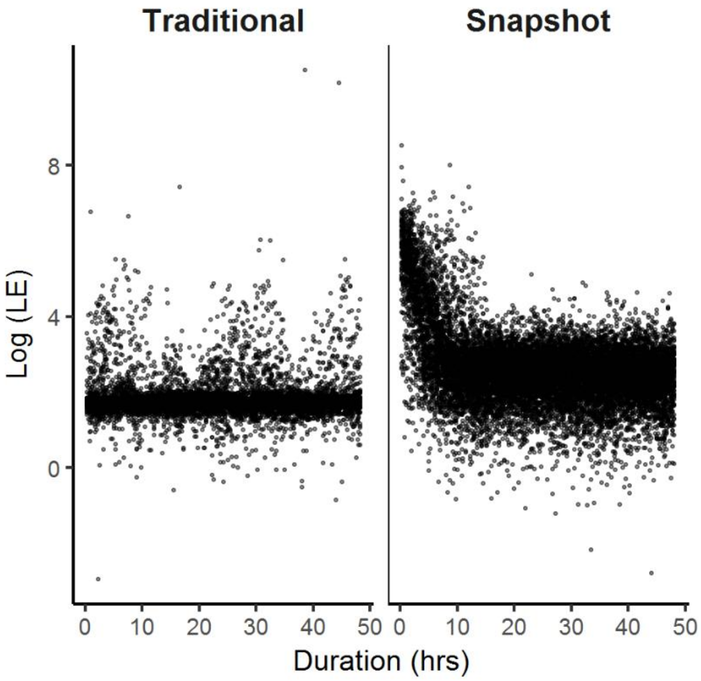


Figure 1.3: Performance of micro-GPS receivers during stationary tests for locations in burrows and above ground. Mean values (±SE) of (A) fix success rate (%) and (B) location error (m) for traditional and snapshot micro-GPS receivers placed on the ground surface and in burrows at a depth of 25 cm.

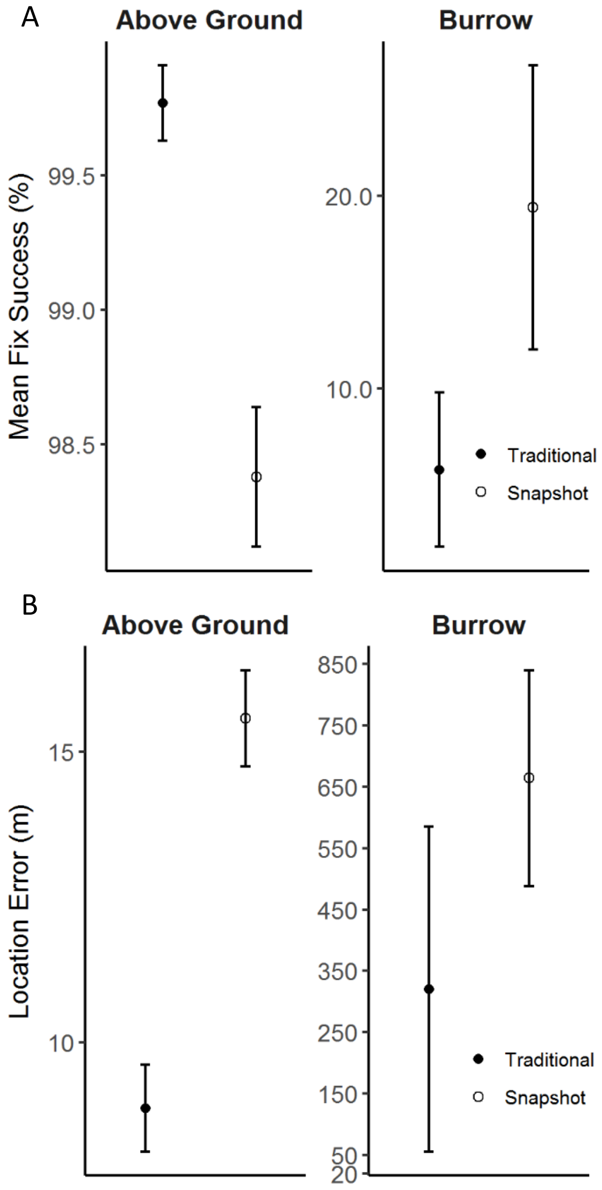


Figure 1.4: Predicted probability of obtaining a successful fix by a snapshot micro-GPS receiver. Performance of snapshot micro-GPS receivers varied as a function of vegetation closure and location in a burrow vs. above ground. Predicted probabilities were generated from the top-ranked model while holding the random effects to zero. The shaded regions are the 95% confidence bounds.

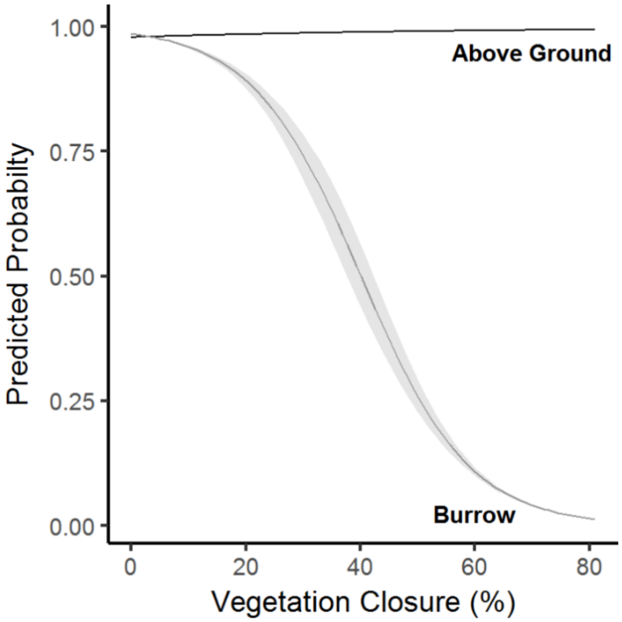


Figure 1.5: Mean (+SE) light values (lux) relative to micro-GPS receiver performance. When collars with both micro-GPS receivers and light loggers were deployed on free-ranging pygmy rabbits, successfully acquired locations (Success) had greater light levels than missed fixes (Fail) supporting the contention that burrow use reduced satellite reception and micro-GPS receiver performance. Trials for each technology were conducted during different seasons (snapshot trials during summer and traditional trials during winter) when variation in natural light levels differed markedly.

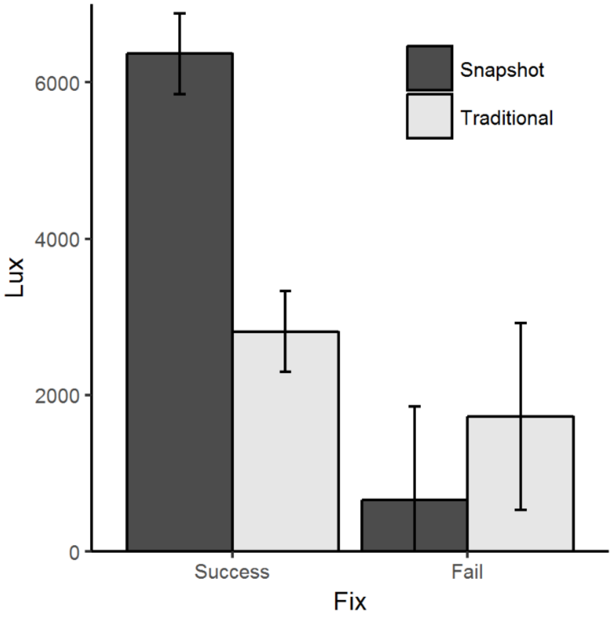
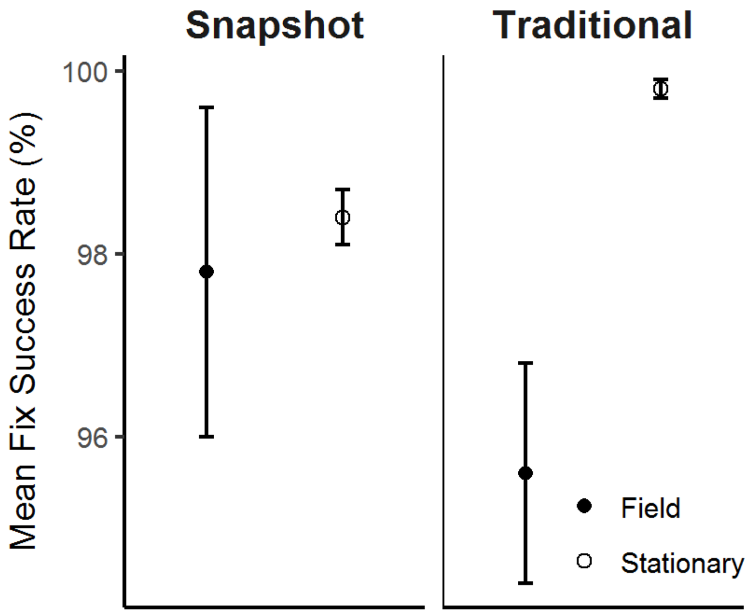


Figure 1.6: Mean fix success rates (±SE) of micro-GPS receivers during deployment on free-ranging pygmy rabbits (field) while estimated to be above ground and during stationary tests (stationary). Fix success was relatively >95% during field trials suggesting that animal behavior while above ground did not strongly influence micro-GPS performance.



Chapter 2: Safety First: Habitat Selection Differs Across Hierarchical Behaviors

Abstract

When animals select habitats, they integrate a suite of behaviors that are influenced by multiple competing resource requirements. Resources that influence decisions about habitat use are likely to differ across spatial scales and hierarchical behaviors. At coarser scales, animals are expected to select resources that are critical to fitness, and at finer scales, to intensively use resources that enhance fitness. Our goal was to contrast habitat selection at 2 hierarchical behavioral levels to test hypotheses about resources that shape habitat use. We applied a two-stage hurdle approach to quantify both selection and intensity of use of resource patches by a burrowing herbivore, the pygmy rabbit (*Brachylagus idahoensis*). We expected security from predation to influence selection of patches, and forage availability to influence intensity of use of selected patches. We monitored locations of adult rabbits fitted with radio collars during winter and summer. We measured vegetation, burrow characteristics, and security properties within patches that were used and unused by rabbits, and we quantified habitat features surrounding patches in a GIS. Selection of habitat patches from available patches was largely influenced by security resources (presence and proximity of burrows, shrub height, and woody ground cover) during both seasons. In contrast, intensity of patch use was influenced by forage availability, and consequently, differed between seasons. During winter, sagebrush is the primary forage, and greater sagebrush canopy within a patch was associated with increased intensity of use. During summer, rabbits more intensively used patches with greater availability of herbaceous forage. Prey species respond to limiting factors other than predation when predation risk is minimized, and greater priority is assigned to alternative factors (e.g., forage). Elucidating how animals make choices about habitats across a diversity of spatial and temporal scales has increased understanding of the factors that govern distribution of populations and movements of individuals. By extending these concepts to hierarchical behaviors, we can enhance insights into the processes that shape the patterns we observe.

Introduction

Animals select habitat across spatial and temporal scales, but their choices about resources also occur across hierarchal behaviors. Although the habitat selection process represents an integrated suite of behaviors that are influenced by multiple stimuli, constraints, and tradeoffs (Johnson 1980; Orians and Wittenberger 1991; Mayor et al. 2009), resource selection can be evaluated at various behavioral resolutions. Hierarchal behaviors can be identified by distinguishing multiple steps in the selection process. For example, *selection* defined as the process of choosing resources for use, might be a first step or higher order behavior, and variation in *intensity of use* of selected resources (based on frequency or duration of use) might represent a secondary step in the selection process. The latter is akin to Johnson's (1980) 4th order of habitat selection.

Resources that influence decisions about space use differ across spatial scales and are likely to vary in a similar manner across hierarchal behaviors. At coarse spatial scales, individuals are expected to select resources that address the greatest threats to fitness (e.g., avoiding predation; Rettie and Messier 2000, Spencer 2002). At finer scales, individuals are expected to use more intensively resources that enhance fitness (e.g., accelerate growth or increase fecundity; (Rettie and Messier 2000; Payer and Harrison 2003; Gaillard et al. 2010). Hierarchical spatial and temporal scaling is an arbitrary construct used to examine processes such as habitat selection (e.g., Turner et al. 1989; Wiens 1989; Mayor et al. 2009), and by applying hierarchy theory to behaviors, we propose that, like coarse spatial scales, first-step behaviors (e.g., selection) might constrain secondary-step behaviors (e.g., intensity of use).

Assessing variation between selection of habitat and intensity of habitat use requires a combination of quantitative approaches. Analysis of resource selection in a use-availability framework facilitates an understanding of factors that contribute to selection of resources, but not to variation in intensity of their use (Johnson 1980). In contrast, use-only approaches like Resource Utilization Functions (RUFs) and First-Passage Time (FPT) model intensity of use of selected resources, but do not address the process of selection in relation to resources that were not used (i.e., available, but not selected; Millspaugh et al. 2006; Freitas et al. 2008). Because use-availability designs characterize the overall process of selecting habitat and use-only approaches describe the mechanistic drivers behind the behavioral processes driving intensity of use, combining these models can reveal a more comprehensive understanding of habitat selection (Bastille-Rousseau et al. 2010). A hurdle model is a two-stage modeling process that provides flexibility to assess factors that contribute to both coarse and fine-scale processes (Wenger and Freeman 2008; Santini et al. 2015). The “hurdle” component of the model separates zero and non-zero data by first estimating the probability of a non-zero count (i.e., probability of selection). If the hurdle is crossed (non-zero count), a truncated count model is used to describe the non-zero values (Zurr et al. 2009). Previous applications of hurdle models in wildlife ecology have included evaluation of variables that influence animal presence-absence and abundance (Heinänen et al. 2008; Eskelson et al. 2009). To evaluate habitat characteristics influencing both selection and intensity of resource use in a hurdle model framework, binary data for selection and count data representing intensity of use can be modeled separately (Martin et al. 2005).

We applied a two-stage hurdle approach to test hypotheses about hierarchical behaviors (i.e., selection and intensity of use of resource patches) by a specialist herbivore in a highly heterogeneous environment. The pygmy rabbit (*Brachylagus idahoensis*) is a sagebrush (*Artemisia* spp.) habitat specialist that occurs only in the sagebrush-steppe of the western USA. Predation is a primary cause of mortality for the species throughout the year (Crawford et al. 2010; Price et al. 2010), and like many lagomorphs, predation likely represents a strong evolutionary force that has shaped their morphology and behavior (Lima and Dill 1990). Sagebrush shrubs create habitat structure that provides security from aerial and terrestrial predators, and other vegetation and woody material on the ground also provide concealment and reduce perceptions of predation risk by this species (Camp et al. 2012). During winter, the height and structure of shrubs above the snow surface is reduced, which likely diminishes concealment (Olsoy et al. 2015), however, snow also can provide additional cover because pygmy rabbits readily create and use subnivian tunnels (Katzner and Parker 1997). Pygmy rabbits also are obligate burrowers that excavate and use burrow systems that serve as effective refuges from all but a few predators.

Because predation is the overriding proximate cause of mortality for pygmy rabbits, we hypothesized that resources that decrease risk of predation would be selected strongly throughout the year (Crowell et al. 2016). We predicted that selection of habitat patches during both summer and winter would be positively influenced by shrub canopy cover, shrub height, and presence of woody debris at the ground level. Additionally, we expected that pygmy rabbits would select for patches of sagebrush with excavated burrow systems, especially those that were proximal to other burrow systems. To account for snow cover, we predicted that rabbits would select for relatively tall sagebrush during winter because tall shrubs would provide greater concealment above the snow surface.

Diets of pygmy rabbits differ between seasons, and consequently distribution of available forage also changes seasonally. Herbaceous vegetation comprises approximately 50% of the diet of pygmy rabbits during summer, whereas the winter diet is almost exclusively sagebrush (Thines et al. 2004; Shipley et al. 2006). We hypothesized that forage availability would influence intensity of patch use, and because of seasonal differences in diet, we expected that the factors that influence intensity of use would differ between winter and summer. We predicted that intensive patch use during winter would be influenced by availability of sagebrush shrubs, and consequently, would be similar to selection of patches. In contrast, during summer, we predicted that intensity of patch use would be positively related to abundance of herbaceous forage (e.g., grasses and forbs) as well as sagebrush shrubs. Finally, if habitat parameters associated with security (e.g., presence of burrows and features that provide concealment from predators) strongly influence selection of patches, then we expected that these factors might be less influential in shaping intensity of use of selected patches because individuals addressed security requirements at a coarser behavioral level. An understanding of how resources shape the distribution and movements of animals across a landscape requires integration across behaviors as well as spatial and temporal scales (Bélisle 2005).

Methods

Study Area

We conducted research at Cedar Gulch (44° 41' N, 113° 17' W), located within the Lemhi Valley in east-central Idaho. The region is composed of a mix of private and public lands and supports seasonal cattle grazing and alfalfa (*Medicago sativa*) production. The Cedar Gulch study site encompassed approximately 100 ha of continuous sagebrush-steppe habitat characterized by mima mounds, distinct dome-like mounds of sediments. At Cedar Gulch, the mean diameter of mima mounds was 10.6 m (Parsons et al. 2016), and Wyoming big sagebrush (*Artemisia tridentate* spp. *wyomingensis*) shrubs occurred predominantly clumped on these mounds. Sagebrush shrubs are typically taller and denser on mima mounds compared to the off-mound matrix (Parsons et al. 2016), and vegetation between mounds was relatively sparse and short, creating a highly heterogeneous landscape. Black sagebrush (*A. nova*) and three-tip sagebrush (*A. tripartite*) were distributed less commonly throughout Cedar Gulch. Grasses and forbs occurred seasonally throughout the study area at relatively low densities.

Sagebrush shrubs created overstory and vertical habitat structure that provide both cover and forage for pygmy rabbits, and a suite of other species. Pygmy rabbits experience high rates of predation, and several species of terrestrial and avian predators occurred at the study site including American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), red foxes (*Vulpes vulpes*), northern harriers (*Circus cyaneus*), short-eared owls (*Asio flammeus*), and great horned owls (*Bubo virginianus*). Additionally, 3 other lagomorphs occurred at relatively low densities at Cedar Gulch: mountain cottontails (*Sylvilagus nuttallii*), white-tailed jackrabbits (*Lepus townsendii*), and black-tailed jackrabbits (*L. californicus*).

The climate of the Lemhi Valley was typical of high-elevation sagebrush-steppe habitats. Winters are characterized by freezing temperatures (daily average = -7.1 °C; Western Regional Climate Center 1965-2006), and average snowfall is approximately 44 cm with a majority of snow falling between December and March (Western Regional Climate Center 1965-2006). Most rainfall occurs during late spring and early summer, although the majority of summer is dominated by warm (daily average = 26°C) and dry periods (Western Regional Climate Center 1965-2006).

Capture and Radio telemetry

We radio-tagged adult pygmy rabbits during winter (January-March) and summer (June-August) of 2014 and 2015. Animals were trapped in box traps (Tomahawk Live Traps, Wisconsin, United States) set at burrow entrances. We handled rabbits in a mesh bag, recorded weight, identified sex, and attached a very high frequency (VHF) radio-collar to adults (> 400 g). We collected location data on rabbits for 4-6 weeks, after which the rabbits were trapped to remove the collar. To identify individuals that might be recaptured in subsequent seasons, we implanted all study animals with passive integrated transponder (PIT) tags following collar removal.

Individuals were radio tracked daily during daylight hours, and we approximated their location to minimize animal disturbance. We used VHF homing techniques to find the location of the animal from a distance of ≥ 40 m. To approximate the coordinates of the animal location, the observer recorded his or her location using a handheld GPS unit and then estimated the distance and orientation to the animal using a range finder and compass. Because of the highly heterogeneous distribution of vegetation, animal locations could be estimated within 10 m, which is consistent with the scale at which we assessed habitat use. All methods used in this study were approved by the University of Idaho Animal Care and Use Committee (Protocol # 2015-12) and are in compliance with the guidelines for use of wild mammals in research published by the American Society of Mammalogists (Sikes and Bryan 2016).

Habitat and burrow characteristic sampling

We defined habitat patches as areas of dense sagebrush where rabbits tend to cluster activity at. To evaluate factors shaping both selection of habitat patches and intensity of patch use, we sampled habitat features at used and available patches. Most animal locations were within the relatively dense vegetation on mima mounds, although rabbits occasionally exploited sagebrush patches that were not associated with mounds. We identified patches used by individuals via radio telemetry, and we sampled a minimum of 4 used patches per individual (unless the animal was located at fewer patches, in which case, we sampled all patches used by that individual). For each rabbit, we randomly selected the same number of available patches for sampling. Available mounds had no documented use by the individual to which it was assigned. If use was documented after sampling, a new patch was selected as a replacement available mound. We identified activity areas for each individual by buffering used patches by 75 m, and we randomly selected patches from those areas (ArcView 10.3, ESRI, Redlands, CA). We restricted sampling to vegetated areas (mima mounds and dense patches of vegetation) because such areas are used extensively by pygmy rabbits for burrowing, foraging, and resting (Estes-Zumpf and Rachlow 2009).

At each used and available patch, we quantified habitat features within the patch and in the surrounding area. At each sampling location, we established 2 perpendicular transects lines that intersected at the center of the patch, with the first line set in a random direction (Parsons et al. 2016). Transect lengths varied based on the width and length of the patch, and because most habitat sampling occurred on mima mounds, we used the edge of the mound to establish the patch boundary. At patches without clear boundaries, transect length was determined using the average diameter (11 m) for mima mounds at this study site (Parsons et al. 2016). Along these transects, we measured shrub canopy of live and dead sagebrush and rabbitbrush using the line-intercept method (Canfield 1941). On each of the 4 resulting transect segments, we randomly placed a 0.5 x 0.5-m quadrat. Within these quadrats, we measured the closest rooted Wyoming big sagebrush (> 15 cm) to the center of the quadrat, on which we measured height of the tallest branch. To determine ground cover within the quadrats, we used cover classes to estimate the cover of grass, forbs, and woody debris (0 [0%], 1 [0-5%], 2 [5-25%], 3 [25-50%], 4 [50-75%], 5 [75- 95%], and 6 [95-100%]; Bonham 1989). Finally, at each of the 4 quadrats, we estimated concealment of a rabbit-sized animal from terrestrial and aerial predators by viewing a 15 x 15-cm cube placed at the center of the quadrat from a height of 1 m at a distance of 4 m in the 4 cardinal directions and from a height of 1.5 m directly above the cube (Camp et al. 2013).

At each sampled patch, we measured burrow system characteristics using field measurements and a data layer generated in a GIS. If a burrow system was present in a patch, we counted the number of open burrow entrances and estimated terrestrial and aerial concealment at up to 3 entrances, using the methods described previously. We used a GIS data layer of burrow locations generated during annual burrow surveys at Cedar Gulch (Sanchez et al. 2009; Parsons et al. 2016) to calculate the distance (m) to the nearest neighboring burrow system, and burrow system density within a 50-m radius surrounding the center of each sampled patch. We evaluated surrounding shrub canopy within 50 m of patches using a shrub data layer classified using unsupervised classification from 2.74-cm resolution imagery collected from unmanned aerial vehicles (UAVs). To estimate shrub canopy in the buffered regions surrounding each test location, the number of pixels classified as shrub were summed and divided by the total number of pixels using ArcGIS 10.3 (ESRI, Redlands, CA). To fill in missing values that resulted from selected and available mounds falling outside the region where UAV-derived vegetation data were available ($n = 19$), we used a shrub data layer classified from 0.5-m resolution NAIP imagery. Although the resolutions differed, shrub cover estimates derived from both data layers were positively and significantly correlated ($n = 435$, $r = 0.63$, $p < 0.001$).

During both seasons and years, we distributed sampling effort temporally over the course of the season to capture conditions as the animals experienced them. However, during winter, significant snow accumulation and creation of subnivean tunnels by rabbits, made it impossible to sample habitat characteristics without substantial disturbance that could influence habitat use by rabbits and potentially bias our results. Consequently, we measured snow depth over the course of the season coincident with use of the patches, but shrub and burrow characteristics were measured in March when much of the snow had melted. We calculated available shrub height above the snow by subtracting the average snow depth of the patch from the average shrub height.

Data Analysis

We evaluated the influence of habitat characteristics on both selection of habitat patches and variation in intensity of patch use. We grouped habitat variables into 3 categories for variable reduction (burrow characteristics, vegetation, and security properties; Table 2.1), and ran models for both selection and intensity of patch use with all possible combinations of single-category variables. We used the variables from the top model in each single-category model set to select variables for construction of a final set of candidate models describing hypothesized selection or intensity of patch use. The final model set included the 3 most plausible models generated from our single-category analyses, and combinations of variables from each category (i.e., burrow – security, burrow – vegetation, security – vegetation, and burrow-security-vegetation) and an intercept-only model. To assess strength of support, we evaluated all models using Akaike Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002).

Because we expected that seasonal differences in resource distribution and animal behavior would influence habitat selection, we modeled data separately for winter and summer. We did not include concealment variables (i.e., terrestrial and aerial concealment, percent woody debris) in the winter models because we assumed these variables would change over the course of the season as snow depth fluctuated. Additionally, we could not sample these properties without destroying characteristics of the patch. Instead, we used shrub height above snow to represent potential concealment during winter.

To evaluate the influence of burrows, vegetation resources, and security variables on selection of patches and intensity of patch use, we employed a hurdle-model approach using conditional logistic regression to test hypotheses about selection and zero-truncated Poisson regression to evaluate variation in intensity of use (Eskelson et al. 2009). Because we sampled the same number of used and available patches per animal, we employed conditional logistic regression because it is appropriate for matched designs (Compton et al. 2002; Boyce 2006). To account for individual variation, our models incorporated individual as a stratifying variable (Lendrum et al. 2012), and therefore, the models described the difference between available and used locations for each animal. To assess the relative importance of burrow, vegetation, and security on intensity of use, we removed locations with no use (i.e., available patches with no VHF locations) and employed a zero-truncated Poisson (ZTP) regression model (Zurr et al. 2009). The response variable for our ZTP model was the total count of VHF locations per individual at each sampled patch. In addition, we included a random effect for individual in the ZTP regression models to account for individual differences in factors influencing intensity of use (Duchesne et al. 2010). An offset term was included in the models to account for the number of days that each individual was monitored. For ease of interpretation, we exponentiated all parameter estimates to generate odds ratios for the conditional logistic regression output and incident rate ratios for the ZTP output. We inferred variable significance if the 85% confidence intervals for the odds and incident rate ratios did not overlap one (Arnold 2010). All statistical analyses were conducted using R 3.2.3 (R-Core Team 2015). Conditional logistic regressions were run using the survival package (Therneau 2015), and mixed-effect zero-truncated Poisson regression models were conducted in the glmmADMB package (Skaug et al. 2016). Mean values are presented with standard errors.

Results

Pygmy rabbits used multiple habitat patches and burrow systems during both summer and winter. We monitored daily movements of 29 pygmy rabbits during winter (14 females and 15 males) and 13 rabbits (9 females and 4 males) during summer. Most (n = 49) were tracked for a single season, but 3 individuals were recaptured and contributed data to 2 consecutive seasons. Rabbits were tracked for an average of 39 ± 0.8 days, and we collected 37 ± 1.0 locations per animal, for a total of 1580 telemetry locations. During winter, 89 ± 2.3% of locations were within patches that contained burrow systems, and rabbits exploited an average of 6 different habitat patches (range = 2-11). During summer, use of patches with burrow systems declined (only 62 ± 6.1% of locations were within patches that included burrows), and although rabbits exploited an average of 9 different habitat patches (range = 2-14), only 4 of those typically had burrow systems. We sampled a suite of habitat variables at 458 patches during winter (n = 288) and summer (n = 170), half of which were used and half of which were available (Table 2.2).

Selection of habitat patches from available patches was largely driven by security resources during both winter and summer. As expected, strong selection for burrows within the patches and in the surrounding area was evident during both seasons (Table 2.3). Model results suggested that for each additional burrow entrance, the odds of selection increased by a factor of 4.3 during winter and 1.6 during summer (Fig. 2.1 and 2.2). Additionally, security variables that might enhance concealment at a patch were positively associated with selection. Although there were 4 competing models in the candidate set describing winter patch selection, the significant positive influence of the number of burrow entrances within a patch and density of burrow systems in the surrounding area was evident in all models (Table 2.3). The top-ranked model suggested a significant association between height of sagebrush shrubs above the snow and patch selection, indicating selection for vegetation that might be strongly associated with concealment cover. Like winter, selection of habitat patches during summer was consistently associated with burrows (within patches and in surrounding areas) and vegetation characteristics (i.e., shrub height; Fig. 2.2). In addition, rabbits selected patches with additional security cover provided by woody debris. Summer patch selection was best described by 2 similar, top-ranking models that collectively received 81% of the model weight. Both models included burrow characteristics and security cover provided by woody debris (Table 2.3).

In contrast to selection of patches, intensity of patch use was influenced by forage availability, and consequently, differed between seasons. During winter, rabbits more intensively used patches with greater sagebrush canopy. A 5% increase in sagebrush canopy was associated with an 11% increase in intensity of patch use (Fig. 2.3). Because sagebrush is the primary winter food source for this species, greater cover of sagebrush provides both forage and security. Consistent with selection of patches, presence of burrow systems also significantly influenced intensity of use (Fig. 2.3). Winter intensity of use was best described by 2 similar models that collectively received 100% of the model weight (Table 2.4). During summer, rabbits more intensively used patches with greater availability of herbaceous forage, which comprises about half of their summer diet. A 5% increase in cover of grasses and forbs resulted in a 15% increase in patch use (Fig. 2.4). Security variables also influenced intensity of patch use. Although presence of burrows did not significantly influence use of patches, rabbits intensively used habitat patches with greater aerial concealment that were surrounded by more burrow systems (Table 2.4). Surprisingly, surrounding shrub canopy was negatively associated with patch use. Intensity of use during summer was described best by 2 models that held 88% of the model weight, which was almost evenly distributed between both models (Table 2.4).

Discussion

Our work suggested that animals met diverse fundamental resource needs by selecting habitat differently across hierarchical behaviors. Selection of habitat by pygmy rabbits at a relatively coarse behavior (i.e., selection of patches for use) was best explained by resources that provided security from predation. In contrast, intensity of use of selected patches was positively associated with seasonal diet and forage availability (sagebrush during winter and herbaceous forage during summer). Quantifying resource use at each scale independently facilitated testing hypotheses about the mechanisms influencing the habitat selection process.

During both seasons, pygmy rabbits demonstrated strong selection for habitat patches that reduced risk of predation. Choice of patches on the landscape was predominately shaped by the presence of burrow systems, and selected patches tended to have taller shrubs than available patches. Similar summer habitat associations have been documented for this species (Gabler et al. 2001; Heady and Laundré 2005; Schmalz et al. 2014). Few studies of winter habitat selection have been published, however, Katzner and Parker (1997) reported that pygmy rabbits in a heavy snow year restricted use to the tallest patches of sagebrush. During winter, tall shrubs provide the only structure that can conceal rabbits above the snow surface. Species that experience high rates of predation might select habitats at coarse spatial scales to minimize predation risk (Rettie and Messier 2000; Apps et al. 2001). Our work suggests that selection at coarse hierarchical behaviors by pygmy rabbits was influenced by similar factors.

In contrast to selection of patches, intensity of patch use was influenced by parameters reflecting availability of season-specific forage. During winter, rabbits intensively exploited patches with more burrow entrances and greater shrub canopy cover (Fig. 2.3). The diet of pygmy rabbits is comprised predominately of sagebrush during winter (Thines et al. 2004), and shrub canopy cover within the patch likely reflects the biomass of available forage more than other sagebrush characteristics that we evaluated such as shrub height. These resources allowed animals to satisfy the heightened energy requirements associated with winter temperatures (Katzner et al. 1997), while also maintaining proximity to refuges from thermal extremes and predators (Kinlaw 1999). Although the shrub canopy also provides cover from predators, it was not strongly correlated with measures of concealment from either the aerial or terrestrial perspectives, and neither of those concealment properties was supported in models explaining intensity of patch use of during winter. However, the multiple functions provided by sagebrush make it impossible to disentangle the complementary properties of forage and security during winter. Intensity of patch use during summer, however, more clearly reflected the influence of forage on behavior. The summer diet of pygmy rabbits includes a large proportion of grasses and forbs (Thines et al. 2004), and as expected, use increased at patches with higher cover of herbaceous plants. At our study site, these plants are low-growing and relatively sparsely distributed, and consequently, provide little concealment cover for rabbits. Counterintuitively, intensity of patch use during summer also increased at patches that were surrounded by less canopy cover. This could reflect selection for patches that provided greater visibility of the surrounding landscape (Camp et al. 2012). Alternatively, the result might be an artifact of the highly patchy landscape.

Despite differences between hierarchical behaviors and seasons, pygmy rabbits consistently demonstrated a strong association with burrows. This species is an obligate burrower unlike other North American lagomorphs, and burrows facilitate heat dumping during summer (Long et al. 2005) and reduce metabolic costs associated with low winter temperatures (Kinlaw 1999). In addition, burrows provide protection from most predators (Camp et al. 2012), and proximity to burrows was a key factor in selection of resting locations by rabbits at our study site (Milling et al. *in review*). Although patch-level burrow characteristics did not significantly influence intensity of patch use during summer, patches that were surrounded by elevated burrow densities were used more intensively (Fig 2.4). Availability of multiple burrow systems likely enhances opportunities for forging while maintaining the relative safety of nearby refuges (Wilson et al. 2012; Crowell et al. 2016).

The hierarchical behaviors we examined differ fundamentally from the spatial or temporal scales commonly used to frame habitat selection studies. In fact, the responses we measured at both behavioral levels were at the same spatial (i.e., patch) and temporal scales, and the same data were included in both analyses (with the exception that unused patches were not included in the intensity estimates). Decisions made by animals across hierarchical behaviors undoubtedly occur simultaneously, and in a way, the separation of behavioral levels for analyses parallels delineation of spatial scales associated with analyses of habitat selection (Johnson 1980; Turner 1989; Boyce 2006). By modeling the data as 2 processes, however, we were able to detect the influence differing resources on selection of habitat patches and intensity of patch use. Identifying and examining behavioral responses at hierarchical levels can facilitate understanding about animal choices and advance our ability to link resource use to components of fitness.

Our work aimed to address fundamental resource needs that shape patterns of habitat selection by pygmy rabbits (i.e., security and forage), but we acknowledge that other factors also can influence selection. We did not include the effect of sex in our models because of sample size limitations, and although behavioral patterns differ between males and females, especially during the summer reproductive season (Heady and Laundré 2005; Burak 2006; Sanchez and Rachlow 2008), security and forage are essential for all individuals, especially for species that are subject to high rates of predation. Nonetheless, examination of more complex models that include sex and other habitat resources and potential constraints on selection (e.g., population density or interspecific interactions) would enhance understanding of habitat relationships for this species. Finally, we examined habitat selection at 2 hierarchical behaviors, but selection also likely occurs at other behavioral levels. For example, intensity of use could be characterized at a finer resolution by distinguishing frequency of repeated use from longer vs. shorter durations of use. Availability of GPS locations collected at short time intervals could provide the data needed to evaluate such fine-scale behavioral processes.

Dissecting behavioral strategies is a critical step in understanding the complex behavioral processes that result in habitat use and distribution of animals across landscapes. Elucidating how animals make choices about habitats across a diversity of spatial and temporal scales has increased understanding of the factors that govern distribution of populations and movements of individuals (Johnson et al. 2002; Mayor et al. 2009). By extending these concepts to hierarchical behaviors, we can enhance insights into the processes that shape the patterns we observe.

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Table 2.1: Habitat characteristics measured during winter and summer (2015-2016) in Idaho, USA. Variables were grouped into 3 categories (burrow characteristics, vegetation, and concealment cover) for variable selection. Some variables were included only in summer (S) or winter (W) models.

Burrow Characteristics	Vegetation	Concealment Cover
Distance to Neighboring Burrow	Patch Shrub Canopy	Terrestrial Concealment (S)
Number of Burrow Entrances	Shrub Height	Aerial Concealment (S)
Surrounding Burrow Density	Surrounding Shrub Canopy	Woody Debris Cover (S)
	Grass Cover (S)	Snow Depth (W)
	Forb Cover (S)	
	Shrub Height above Snow (W)	

Table 2.2: Habitat characteristics used to evaluate selection of habitat patches by pygmy rabbits, *Brachylagus idahoensis*, in Idaho, USA, during winter and summer (2015-2016). Values for each season represent averages across all used (winter: n = 144; summer: n = 85) and available (winter: n = 144; summer: n = 85) patches sampled during that season.

Vegetation parameter	Winter				Summer			
	Used		Available		Used		Available	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
# Burrow Entrances	2.7	0.15	0.3	0.07	1.5	0.21	0.4	0.12
Surrounding Burrow Density [a]	2.8	0.12	1.9	0.12	2.7	0.16	2.5	0.14
Distance to Neighboring Burrow (m)	37.9	1.59	38.7	1.06	32.7	1.05	36.4	1.23
Snow Depth (cm)	19.9	1.52	21.0	1.60	-	-	-	-
Shrub Height above Snow (cm)	30.5	1.87	23.0	1.91	-	-	-	-
Surrounding Shrub Canopy (%) [a]	18.4	1.04	17.5	0.95	16.5	0.34	16.3	0.63
Patch Shrub Canopy (%)	45.9	0.94	50.2	0.90	48.3	1.14	51.5	1.02
Shrub Height (cm)	50.5	0.97	43.9	0.97	52.2	1.48	46.9	1.26
Grass Cover (%)	-	-	-	-	10.0	0.75	9.2	0.84
Forb Cover (%)	-	-	-	-	2.5	0.77	2.5	0.63
Patch Terrestrial Concealment (%)	-	-	-	-	76.4	1.31	74.7	1.43
Patch Aerial Concealment (%)	-	-	-	-	20.7	1.42	19.8	1.47
Woody Debris (%)					4.0	0.78	3.0	0.70

[a] Variables recorded in a 50-m radius surrounding the center of the habitat patch.

Table 2.3: Model selection results for the 95% confidence set of models describing selection of habitat patches by pygmy rabbits, *Brachylagus idahoensis*, in Idaho, USA, during winter and summer (2015-2016). Selection models were analyzed with conditional logistic regression using individual as the stratifying variable. Parameters are: K, the number of parameters estimated; ΔAICc, the change in AICc; and Wt, model weight.

Season	Variables	K	AICc	ΔAICc	Wt	Rank
Winter						
	BurrowDensity* + # BurrowEntr* + ShrubHtAboveSnow* - PatchCanopy	4	147.78	0.00	0.56	1
	BurrowDensity* + #BurrowEntr*	2	149.83	2.05	0.20	2
	BurrowDensity* + #BurrowEntr* - SnowDepth	3	150.12	2.34	0.17	3
	BurrowDensity* + #BurrowEntr* - SnowDepth + PatchCanopy	4	152.12	4.34	0.06	4
Summer						
	BurrowEntr* - NearestBurr* + WD* + ShrubHt* - PatchCanopy	5	168.73	0.00	0.45	1
	BurrowEntr* - NearestBurr* + WD*	3	169.20	0.47	0.36	2
	BurrowEntr* - NearestBurr* + ShrubHt* - PatchCanopy*	4	170.94	2.22	0.15	3

*Significant at the 85% confidence level

BurrowDensity, density of burrow systems within 50 m; #*BurrowEntr*, number of burrow entrances at patch (0 = no burrow system); *NearestBurr*, distance (m) to the nearest neighboring burrow system; *ShrubHtAboveSnow*, shrub height (cm) above the snow; *ShrubHt*, shrub height (cm) on the patch; *PatchCanopy*, total percent canopy cover on the patch, includes living and dead canopy cover; *SnowDepth*, depth (cm) of snow at patch; *WD*, % woody debris cover.

Table 2.4: Model selection results for the 95% confidence set of models describing intensity of use of habitat patches by pygmy rabbits, *Brachylagus idahoensis*, in Idaho, USA, during winter and summer (2015-2016). Models were analyzed with zero-truncated Poisson regression with an offset to account for the number of days the animal was tracked and a random variable to account for individual-level variation. Parameters are: K, the number of parameters estimated; ΔAICc, the change in AICc; and Wt, model weight.

Season	Variables	K	AICc	ΔAICc	Wt	Rank
Winter						
	#Entrances* - NearestBurr - ShrubHtAboveSnow + PatchCanopy*	6	1213.77	0.00	0.52	1
	#Entrances* - NearestBurr* + PatchCanopy* - SnowDepth	6	1213.89	0.12	0.48	2
Summer						
	BurrowDensity + Herb* - SurrCanopy* + AerialConc*	6	539.89	0.00	0.45	1
	Herb* - SurrCanopy* + AerialConc*	5	540.00	0.11	0.43	2
	BurrowDensity* + Herb* - SurrCanopy*	5	543.26	3.37	0.08	3

*Significant at the 85% confidence level

#Entrances, number of burrow entrances*; NearestBurr*, distance (m) to the nearest neighboring burrow system; *BurrowDensity*, Burrow density within 50 m of mound; *ShrubHt*, height (cm) of sagebrush shrubs at patch; *ShrubHtAboveSnow*, height (cm) of sagebrush above snow; *AerialConc*, aerial concealment on the patch; *PatchCanopy*, total percent canopy cover on the patch, includes living and dead canopy cover; *SurrCanopy*, surrounding (50 m) canopy cover; *Herb*, % herbaceous cover

Fig 2.1: Odds ratios (± 85% CI) for parameter estimates generated from the 2 top models (ΔAIC ~ 2) describing selection of habitat patches by pygmy rabbits, *Brachylagus idahoensis*, (n = 29) during winter in Idaho, USA (2015-2016).

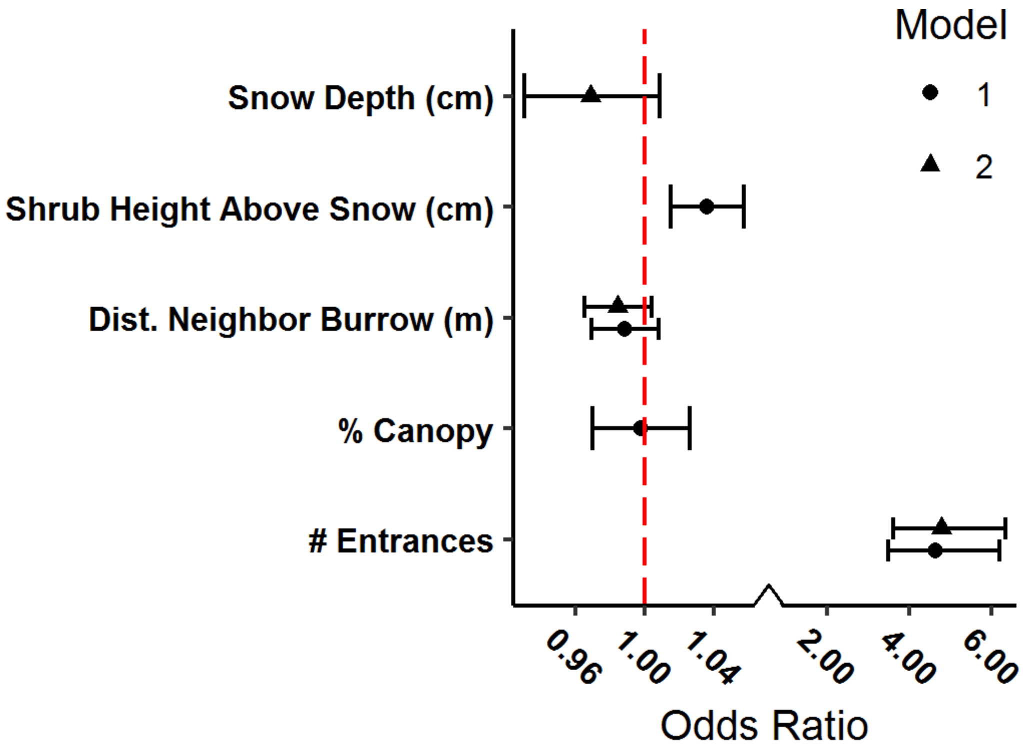


Fig 2.2: Odds ratios (± 85% CI) for parameter estimates generated from the 2 top models (ΔAIC < 2) describing selection of habitat patches by pygmy rabbits, *Brachylagus idahoensis*, (n = 13) during summer in Idaho, USA (2015-2016).

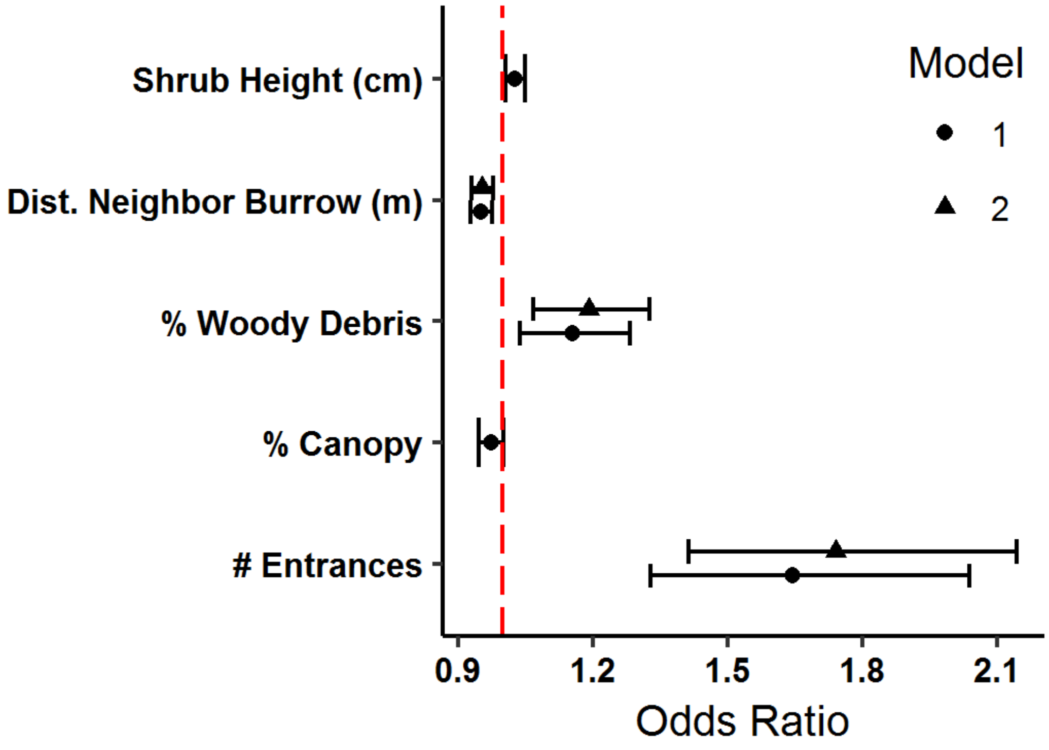


Fig 2.3: Incident rate ratios (± 85% CI) for parameter estimates generated from the 2 top models (ΔAIC < 2) describing intensity of habitat patch use by pygmy rabbits, *Brachylagus idahoensis*, (n = 29) during winter in Idaho, USA (2015-2016).

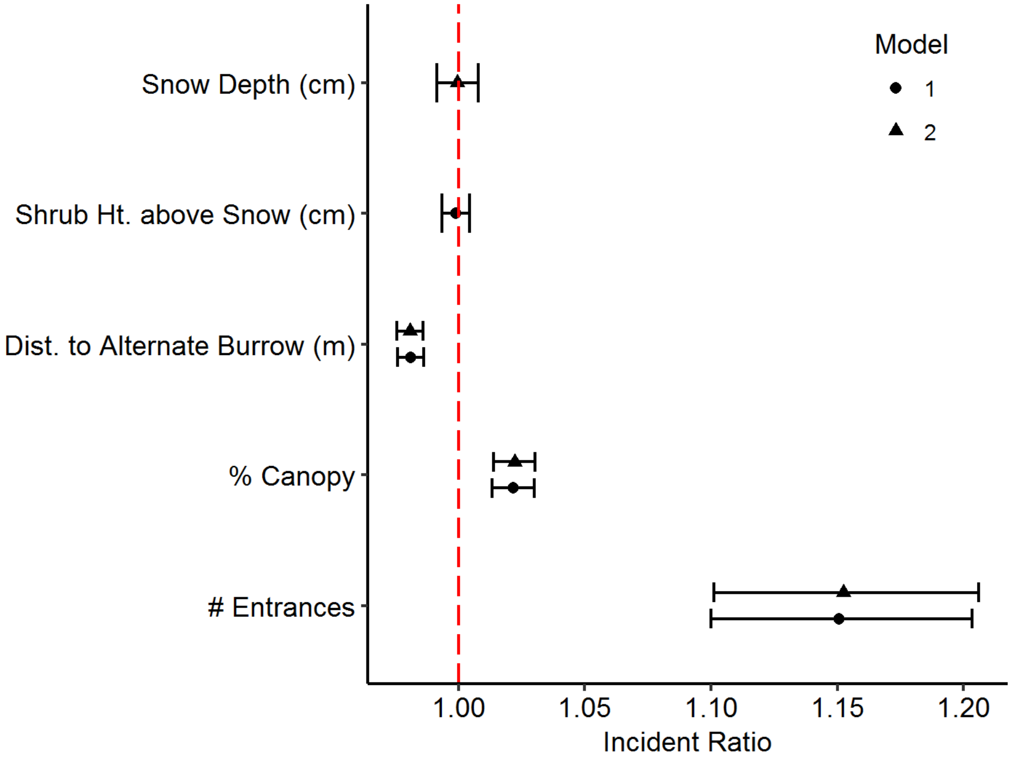
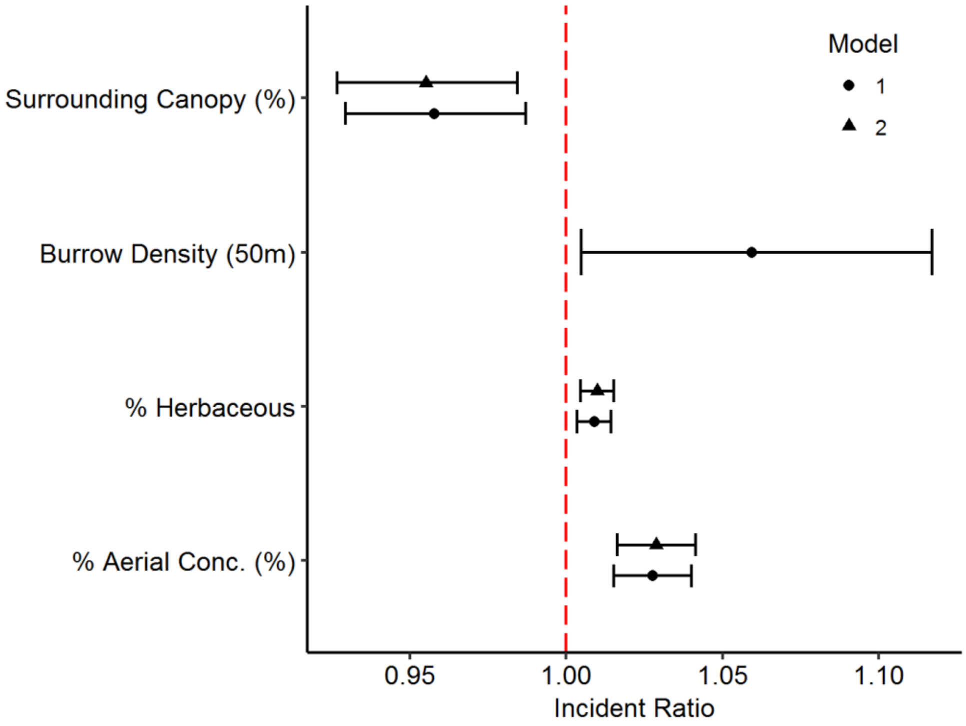


Fig 2.4: Incident rate ratios (+ 85% CI) for parameter estimates generated from the 2 top models (ΔAIC < 2) describing intensity of habitat patch use by pygmy rabbits, *Brachylagus idahoensis*, (n = 13) during summer in Idaho, USA (2015-2016).



General Conclusion

Habitat selection can be investigated using a variety of data sources and analytical methods. Previous research suggests that GPS telemetry can be used on large-bodied animals to advance the understanding of difficult to study species (Hebblewhite and Haydon 2010). Our work likewise suggests that micro-GPS receivers (< 20 g) also can be deployed on cryptic small mammals to address questions about habitat selection, and additionally, that habitat selection can be investigated as hierarchical behaviors to better understand factors shaping the habitat selection process.

Our work suggests that micro-GPS receivers (< 20 g) have the capacity to collect fine-scale location data suitable for habitat selection studies of small mammals. We compared 2 micro-GPS receivers: snapshot and traditional receivers using stationary and field deployments. Testing indicated similar error between receiver types; however, operational battery life was highly variable for snapshot receivers. Our results suggested that for small mammals, traditional and snapshot GPS-receivers have the ability to produce location data suitable for investigating resource selection and space use; however, an understanding of habitat heterogeneity and animal behavior is necessary before deployment. As receivers improve, snapshot technology could minimize the tradeoff between fix interval and battery life, allowing for more fine-scale evaluation of small mammal movement, activity, and resource selection.

Additionally, we investigated habitat selection by pygmy rabbits across hierarchical behaviors using a hurdle-model approach to evaluate habitat selection as a binary process (i.e., selection) and along a continuum (i.e., intensity of use). Our results suggested that selection was influenced by variables that improved security and decreased perceptions of risk; however, intensity of use was influenced by forage availability, in addition to security variables. Dissecting behavioral strategies is a critical step in understanding the complex behavioral processes that result in habitat use. By analyzing habitat selection in 2 stages, we can identify factors that shape behavioral choices.

The results from this thesis expand our understanding of the technological abilities of micro-GPS receivers and how factors shaping selection and intensity of use can differ.

Micro-GPS receivers provide opportunities to collect accurate location data on small, difficult to study mammals. Use of GPS data can aid in detecting variable habitat use by pygmy rabbits and other small mammals. Investigating selection and intensity of use as 2 processes provides opportunities to expand upon our understanding of the functional links between the animal and its environment.

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