



## Novel location data reveal spatiotemporal strategies used by a central-place forager

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Central-place foragers in risky landscapes experience conflicting behavioral demands that they must balance by appropriately adjusting how they move throughout their home ranges. We used novel mini-GPS technology and time local convex hull analyses to determine how golden-mantled ground squirrels (*Callospermophilus lateralis*) use a spatiotemporal strategy to optimize foraging early in the year when individuals are in an energy deficit. By using serial correlation from GPS data, we could better understand how individuals use a time management strategy influenced by distance traveled from the burrow, location of food patches, location of refuge patches, and vegetative cover type. Individuals maximized time spent in food patches rather than in travel corridors or at the burrow, suggesting the need to forage was prioritized. Individuals spent more time at patches farther from the burrow relative to nearer patches, potentially as a function of intermittent antipredator vigilance activity and energy optimization. Individuals also had high rates of revisitation, but low visit duration, in risky canopy cover types, suggesting that individuals used areas of low vegetative understory cover to travel efficiently between high-value food patches. Increased predation risk incurred while traveling in these open areas was possibly offset by use of refuges. Understanding these spatiotemporal movement patterns and how they relate to dynamic intrinsic and extrinsic demands has the potential to redefine optimal foraging behavior and better inform management and conservation practices.

Key words: GPS, movement behavior, optimal foraging, small mammal, spatiotemporal

All species must optimize their foraging efforts by balancing the energy gained from food patches with the energetic cost of foraging and associated environmental risks (Brown 1988). Optimality models, such as optimal foraging theory (OFT), attempt to describe the ideal foraging behavior of an individual, such that energy gained in food patches and time devoted to travel and searching for food has been optimized (MacArthur and Pianka 1966; Pyke et al. 1977). As food sources become depleted, OFT predicts that the travel and harvesting costs associated with foraging outweigh the benefits and individuals should cease foraging activity (Pulliam et al. 1982; Brown 1988; Dehn 1990; McNamara and Houston 1992). However, for individuals in risky environments, where to forage and when to stop foraging may be influenced by several dynamic factors such as energetic demands, habitat heterogeneity, predator pressure, and competition (Sih 1980; Kotler et al. 1991). If too much time is allocated to antipredator behavior such as vigilance, for example, individuals may not harvest enough food to meet their energetic needs (Brown 1999). Concurrently, if too

much time is spent traveling through risky matrices, individuals increase their risk of predation (Sih 1980; Bachman 1993; Arenz and Leger 2000). Individuals must optimize their foraging efforts by balancing demands to maximize foraging efficiency while minimizing the associated costs (Newman 1991; Brown 1999).

Species that harvest the same food sources each year have evolved strategies to mediate the associated costs (Schoener 1974; Chesson 2000; Kotler et al. 2002; Kronfeld-Schor and Dayan 2003; Upham and Hafner 2013). Morphological, physiological, and behavioral adaptations caused by competition allow multiple species to partition dietary niches (Thompson 1982; Kotler 1984; Smith 1995). This partitioning causes some species to exploit riskier patch types where they may encounter increased exposure to predators or other stressors (MacArthur and Levins 1964; Wondolleck 1978). For species exploiting riskier patch types, some of these adaptations include larger body size, increased locomotion, increased vigilance during foraging, and foraging within proximity to refuge or shelter

(Bouskila 1995; Ovadia et al. 2001; Doherty et al. 2015). For example, yellow-bellied marmots (*Marmota flaviventris*) spend 63% of their time vigilant to reduce predation risk while foraging (Armitage and Salsbury 2016). Other species, such as degus (*Octodon degas*), increase their travel speed in areas where they perceive a higher risk of predation (Vasquez et al. 2002). Evidence of these adaptive behaviors is reflected in the amount of time an individual may spend in any one patch or how frequently that patch is revisited (Brown and Kotler 2004).

Few integrative spatiotemporal methods exist to accurately describe how individuals adapt their behavior to balance risks and costs in dynamic heterogeneous environments. One method involves the collection of activity budgets via direct observation. These studies measure the amount of time spent in discrete behaviors, but are time-consuming and limited by the observer's ability to perceive all activity of any one individual at a time, particularly for secretive species in visually obscured environments (Christiansen et al. 2013). Giving-up densities (GUDs) have also been extensively used to measure trade-offs between behaviors such as foraging effort and predator avoidance by measuring seed density left in patches or experimental seed trays placed at predetermined locations (Brown 1988). However, GUDs do not measure the amount of time individuals spend at a seed tray or how frequently individuals revisit that seed tray, which could have implications for how they potentially reduce their risk of predation. GUDs are founded on the marginal value theorem, an optimality model applied to OFT, which was modified by Brown (1988) to incorporate predation risk, searching and processing costs, thermoregulatory costs, and missed opportunity costs. For example, antipredator behaviors such as vigilance may allow animals to remain in a foraging patch longer than otherwise predicted by optimality models (Nonacs 2001; Price and Correll 2001; Brown and Kotler 2004; Verdolin 2006).

The use of GPS technology has allowed researchers to analyze movement behavior beyond the constraints of direct observation and biases of theoretical models. Regularly collected GPS data have been critiqued for their serial correlation; however, this correlation has more recently been recognized as an important factor in detecting patterns in movement behavior (Boyce et al. 2010; Benhamou 2011). Methods developed in response to the increased demand to incorporate serial correlation, specifically in home range analyses, include Brownian bridge movement models, movement-based kernel density, and time geography density estimation. Another emerging method is the time local convex hull method, or T-LoCoH (Lyons et al. 2013). T-LoCoH is a nonparametric method for aggregating hulls created around each point in a data set. Rather than classifying resource use strictly on static point density, T-LoCoH uses the time stamps from each point collected to supplement the partitioning of patch use by time. This method allows the researcher to infer the amount of time spent in a patch and how many times an individual revisits a patch. These data can be informative when inferring how individuals allocate time to foraging in environments where they experience conflicting demands. Therefore, we use mini-GPS and T-LoCoH to

generate a hypothesis-driven spatiotemporal analysis of individual movement patterns that addresses the limitations of the OFT and existing methodology to describe how animals make real-time decisions in the field.

In the eastern Sierra Nevada Mountains, golden-mantled ground squirrels (*Callospermophilus lateralis*) compete with other granivores for the same limited annual seed source and are subject to risks of predation and starvation (Simberloff and Dayan 1991). *Callospermophilus lateralis* are central-place foragers, storing seeds in 1 burrow throughout the year. They are larger than many competing granivorous rodents and are capable of faster travel speeds between patches and faster harvesting rates, adaptive behaviors found in species using risky patch types (Smith 1995). Time spent traveling between food patches, time spent within food patches, and frequency of revisits to habitat patches can aid in understanding how individuals may be balancing the need to forage, minimize the energetic cost of travel, and avoid predation.

This study was conducted during the first available seed harvest of the year. Antelope bitterbrush (*Purshia tridentata*) is an understory shrub species that grows in clusters where there is little overstory vegetative cover. Because of a lack of other foods available within the study site and the depletion of the larder prior to bitterbrush seed availability, *C. lateralis* individuals were likely in an energy deficit at the beginning of this season. To understand how individuals maximize foraging efficiency, we analyzed their use of time traveling between food patches and refuges, duration of time spent in food patches and refuges, and how often all habitat patches were revisited. To assess the efficacy of the use of novel mini-GPS to analyze such fine-scale spatiotemporal movement behavior, we developed the following basic hypotheses: 1) due to larder depletion and energy deficit, individuals will spend more time in food patches versus patches without food; 2) individuals will frequently revisit corridors identified as open interspaces between food patches, but duration of each visit will be shorter than visits to food patches; and 3) duration of time spent in any patch will decrease with increasing distance from protective cover or shelter (the burrow or other escape refuges such as stumps and boulders).

## MATERIALS AND METHODS

*Study site.*—This study was conducted within a 1.3-km<sup>2</sup> area in the Whittell Forest and Wildlife Area in Little Valley, Washoe County, about 30 km south of Reno, Nevada, United States (39°15'0"N, 119°52'35"W). This study site is owned by the University of Nevada, Reno, and comprises 1,073 ha with elevation about 1,975 m. Dominant woody vegetation includes Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), antelope bitterbrush (*P. tridentata*), greenleaf manzanita (*Arctostaphylos patula*), tobacco bush (*Ceanothus velutinus*), and Sierra bush chinquapin (*Castanopsis sempervirens*). The portion of Little Valley selected for this study had a dominant open tree canopy of Jeffrey pine and a patchy understory of antelope bitterbrush. During the time in which this study was conducted, antelope bitterbrush was the only shrub producing seeds.

*Animal handling and GPS data.*—During 15–31 July 2014, 6 adult *C. lateralis* (5 male, 1 female) were captured in Tomahawk traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin) and handled in accordance with a protocol approved by the Institutional Animal Care and Use Committee (IACUC, #A07/08-30) that was in keeping with guidelines established by the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2016). To accommodate such a small sample size, individuals were selected based on features that were predetermined to be indicative of the population as a whole within the small study area. Individuals selected had similar availability of relevant habitat features, including food, shelter, slope, aspect, and vegetative species. Individuals also experienced similar exposure to the same predators—primarily red-shouldered hawks (*Buteo lineatus*)—and interspecific competition with the same granivore species—primarily yellow pine chipmunks (*Tamias amoenus*). These features were determined by visual observation and 36 weeks of livetrapping in potential study areas prior to study implementation. All individuals used in the study were all at least 1 year of age and had established home ranges.

Five-gram GiPSy 5 GPS loggers (17 × 12 × 4 mm) supplied by TechnoSmArt Europe Srl (Colleverde, Italy) and 0.8-g VHF transmitters supplied by Advanced Telemetry Systems Inc. (Isanti, Minnesota) were used to record movement behavior of individuals. Individual squirrels on average weighed 165 g when the study was initiated. GPS loggers were attached to squirrels using zip-ties threaded through soft cords of fabric, which were then secured across the neck and chest of individuals. GPS loggers were programmed to collect 1 fix every 10 s only during periods of activity when the squirrel was aboveground. On this schedule, batteries in the loggers lasted 2–3 days. A balance between high resolution data and a short time scale was achieved by determining at what frequency locations needed to be taken to determine fine-scale movement patterns and be representative of foraging behavior during the short peak availability of bitterbrush seeds.

*Distance and vegetative canopy cover type parameter designation.*—A vegetation raster with 1-m resolution was created in ArcMap 10.3 that categorized 3 dominant canopy cover types: open, pine, and antelope bitterbrush. Open canopy was categorized by no overstory and no understory cover. Pine canopy was categorized by a dominant overstory of Jeffrey pine and no understory cover. Bitterbrush canopy was categorized by a dominant bitterbrush understory regardless of whether pine was present as overstory or not. Bitterbrush patches are commonly separated by interspaces of no understory cover and forested overstory cover. Open and pine canopy cover were defined via digitization while bitterbrush cover, burrows, and refuge locations were mapped at the study site using a Trimble GeoExplorer 7x (Trimble, Inc., Sunnyvale, California). One-meter resolution images from the National Agriculture Imagery Program (NAIP) were used to digitize areas of pine canopy cover. In the field, bitterbrush shrubs < 1 m apart were mapped as a continuous stand. Refuge locations consisted of stumps, boulders, and fallen logs under which rodent tunnels were

found. Other studies have identified that *C. lateralis* survival and persistence may be dependent on the presence of these refuge structures (Bartels and Thompson 1993; Smith and Maguire 2004). These locations were mapped as either points (< 1 m in diameter) or polygons (> 1 m in diameter). If refuge locations such as boulders were < 1 m apart, they were mapped as a continuous polygon. Distance to the nearest refuge area was calculated using the Near tool in ArcMap 10.2 for each point from each individual (ESRI 2012). Separate rasters were created for canopy cover and distance to the home burrow. Distance from the home burrow was represented using a Euclidean distance raster with each burrow as the point of origination. Values from these rasters were extracted to each point for each individual. To better understand how food patches and refuge locations may be influencing visit duration and revisitation, densities of bitterbrush and refuge locations were then calculated along a continuous scale of distance from each burrow. Density was determined by creating a 0.5-m point grid in ArcMap 10.2, using the Identity tool to identify points overlapping either bitterbrush or refuge, and using the Near tool to calculate distance from each burrow to each point identified as either bitterbrush or refuge within a 250-m radius from each burrow (the maximum distance any 1 individual travelled during the season).

*T-LoCoH and statistical analysis.*—Time local convex hull was used to design methods to measure revisitation rates and visit duration using GPS data. T-LoCoH is not a method that is entirely preconfigured, meaning much of the analysis requires appropriate knowledge of the study subject and how it uses its habitat in order to design code and obtain meaningful results. All code was run in program R version 3.1.2 (R Development Core Team 2011) using the T-LoCoH package (Lyons and Getz 2014). T-LoCoH operates similarly to the previously developed local convex hull method, in that it designs hulls around clusters of points defined by the analyst using either the *k* (nearest neighbor), *r* (fixed radius), or *a* (adaptive radius) method. Distinctively, T-LoCoH uses time to also define how nearest neighbors are selected and how hulls are sorted. This method is accomplished by using time-scaled distance, which incorporates the use of a spatiotemporal scaling parameter (for additional information, see Lyons et al. 2013).

To begin the analysis, the analyst selects a scaling parameter *s*, which determines to what degree temporal influence is used to define nearest neighbors that are used to create local hulls. A hull is a polygon that contains one parent point and its neighbors that are determined to be most similar to each other in terms of time and space. Values of *s* increasing from zero indicate an increase in the amount of temporal influence. It is generally suggested to select a value of *s* so that 40–80% of hulls created are time-selected (Lyons and Getz 2014). In that analysis, we selected values of *s* closest to 60% for each individual. Additionally, nearest neighbor selection is determined using either the *k*, *r*, or *a* method, as mentioned above. Therefore, we used the *a*, or adaptive, method to construct hulls. In this method, the cumulative distance (meters) between a parent point and its neighbors is defined and used to construct hulls. This method is recommended because it minimizes

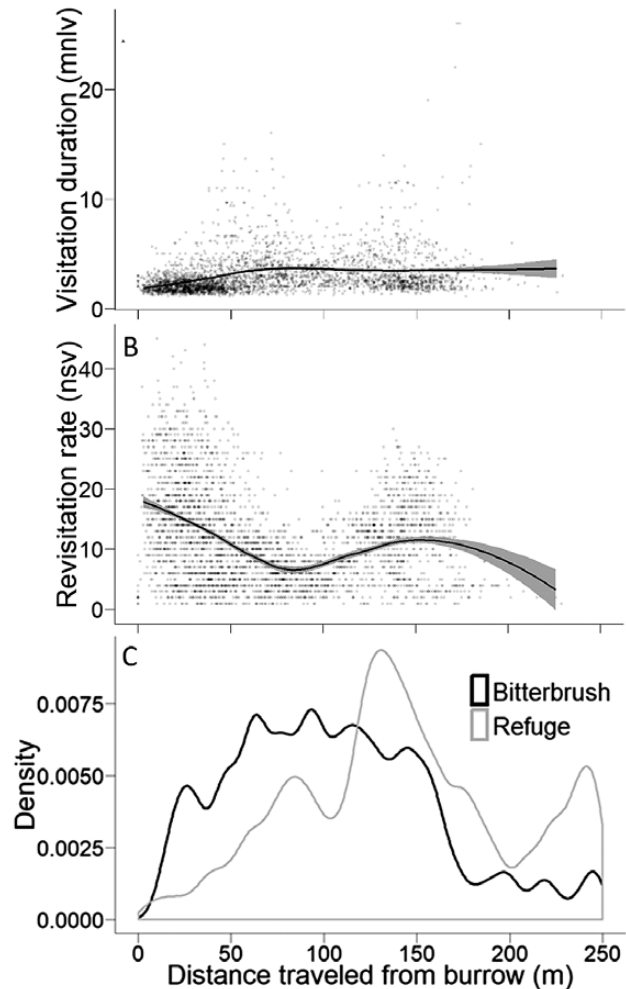


spurious massive hulls or extremely small hulls that are a result of defining a set number of neighbors to be included in the creation of a hull, as occurs in the commonly used  $k$  method. Values of  $a$  (meters) are determined via visual analysis of hulls generated and using knowledge of the study subject. We selected a cumulative distance value for each unique individual that was largely dependent on the size of the area used by each individual, the dispersion of points within that area, and if those hulls minimized encompassing widely scattered outlying data points while also covering holes within the core areas of activity.

Lastly, an inter-visit gap (IVG) value was assigned to define which points were considered revisits. We chose an IVG of 60 s based on field observation of individuals foraging in the field as well as calculated velocity and distance traveled between sequential GPS points. Therefore, separate visits were identified when an individual left a hull and then returned after a period of at least 60 s had passed. Rates of revisitation (number of separate visits to a hull: nsv) as well as visit duration (mean number of locations per visit to a hull: mnlv) were then assigned to each point within each hull. These values were used to determine if distance parameters to the burrow and refuge locations were correlated with high or low occurrences of revisitation using Spearman's correlation coefficient. An interaction effect of distance traveled from the burrow and distance traveled from refuge was also incorporated to determine if refuge served as a moderator to increase or decrease revisitation rates as distance from the burrow increased. To determine if there was a difference in revisitation and visit duration among vegetative canopy cover types, generalized linear mixed effects models were used, with individual squirrel as the random effect. Variation among individuals for both visit duration and revisitation rate was calculated using the rptR package in R (Stoffel et al. 2017).

## RESULTS

**Distance parameters.**—Correlation coefficients were weak overall, but displayed distinctly different patterns between revisitation rate and visit duration. As individuals traveled farther from the burrow, visit duration weakly increased (Spearman's rank correlation:  $r_{3169} = 0.35$ ,  $P < 0.001$ ), while revisitation rate weakly decreased (Spearman's rank correlation:  $r_{3169} = -0.23$ ,  $P < 0.001$ ). Revisitation rate showed a weak, but negative correlation with distance to refuge (Spearman's rank correlation  $r_{3169} = -0.18$ ,  $P < 0.001$ ), indicating that revisitation was somewhat less likely the farther the site was from refuge locations. There was no significant correlation between visit duration and distance from refuge (Spearman's rank correlation:  $r_{3169} = 0.0004$ ,  $P = 0.84$ ). Small correlation factors were likely due to the nonlinear nature of the variable distance to burrow, given that individuals concentrated efforts in 2 dominant locations: directly adjacent to the burrow, and approximately 150 m from the burrow (Figs. 1A and 1B). There was a significant but weak negative correlation between visit duration (mnlv) and revisitation rate (nsv) across all patches, showing that as visit duration increased, revisitation rate decreased (Spearman's rank correlation:  $r_{3169} = -0.34$ ,  $P < 0.001$ ).



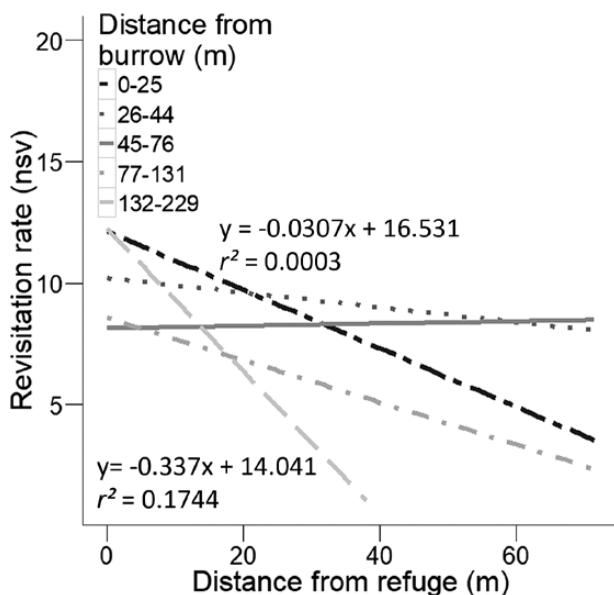
**Fig. 1.**—A) Visit duration (mean number of locations per visit: mnlv), B) revisitation rate (number of separate visits: nsv), and C) density of bitterbrush and refuge locations correlated to distance *Callospermophilus lateralis* ( $n = 6$ ) traveled from the burrow (m) in the Whittell Forest and Wildlife Area 15–31 July 2014. Best-fit lines in A) and B) were generated using the nonparametric loess smoothing technique, a locally weighted regression method.

Bitterbrush patches and refuge locations followed a bimodal distribution as distance from the burrow increased. Bitterbrush density was highest 50–100 m from the burrow, consistent with the highest values of visit duration (Fig. 1C).

Density of refuges peaked at 125–150 m from the burrow consistent with a peak in revisitation rate. To investigate if refuge served as a moderator of distance traveled from the burrow, a linear regression model was used to test for an interaction effect of distance traveled from the burrow and distance traveled from the refuge. Because of non-normality, data were transformed using the Box–Cox power transformation methodology prior to use in linear mixed models (Box and Cox 1964). The interaction of distance traveled from refuge and distance traveled from the burrow was significant (linear regression model:  $\beta_{3169} = -0.0004$ ,  $P < 0.001$ ,  $r^2 = 0.22$ ). Best-fit linear trend lines revealed that as distance from the burrow increased, distance traveled from refuge locations better explained revisitation rate

(Fig. 2). In other words, at greater distance from the burrow, revisitation rates dropped with increasing distance from refuge.

**Vegetative canopy cover type.**—Generalized linear mixed model fit with a Poisson distribution indicated a significant relationship between revisitation rate (number of separate visits: *nsv*) and vegetative canopy cover type (generalized linear regression model [GLM]:  $\beta = 2.07297$ ,  $SE = 0.24877$ ,  $P < 0.001$ ). Post hoc Tukey's multiple comparison test revealed no significant differences in revisitation rate (*nsv*) among bitterbrush, open, and pine canopy types. Nevertheless, bitterbrush had the lowest overall revisitation rate (mean  $\pm$  *SD*,  $9.64 \pm 7.94$  *nsv*,  $n = 6$ ) in comparison to open ( $12.28 \pm 7.46$  *nsv*,  $n = 6$ ) and pine ( $11.63 \pm 8.17$  *nsv*,  $n = 6$ ) vegetative canopy cover types (Fig. 3). The proportion of variation explained by differences among individuals indicated repeatability of rate of revisitation among individuals (repeatability [*R*] =  $0.499 \pm 0.144$ ). Generalized linear mixed model fit with a Gaussian distribution and log link also indicated a significant relationship between visit duration (mean number of locations per visit: *mnlv*) and vegetative canopy cover type (GLM:  $\beta = 1.06875$ ,  $SE = 0.13249$ ,  $P < 0.001$ ). Post hoc Tukey's multiple comparison test revealed the visit duration (*mnlv*) differed significantly between all vegetative canopy cover types ( $P < 0.01$ ). Bitterbrush had the highest visit duration ( $4.01 \pm 2.76$  *mnlv*,  $n = 6$ ) in comparison to open ( $3.11 \pm 2.01$  *mnlv*,  $n = 6$ ) and pine ( $2.84 \pm 1.54$  *mnlv*,  $n = 6$ ) vegetative canopy types. The

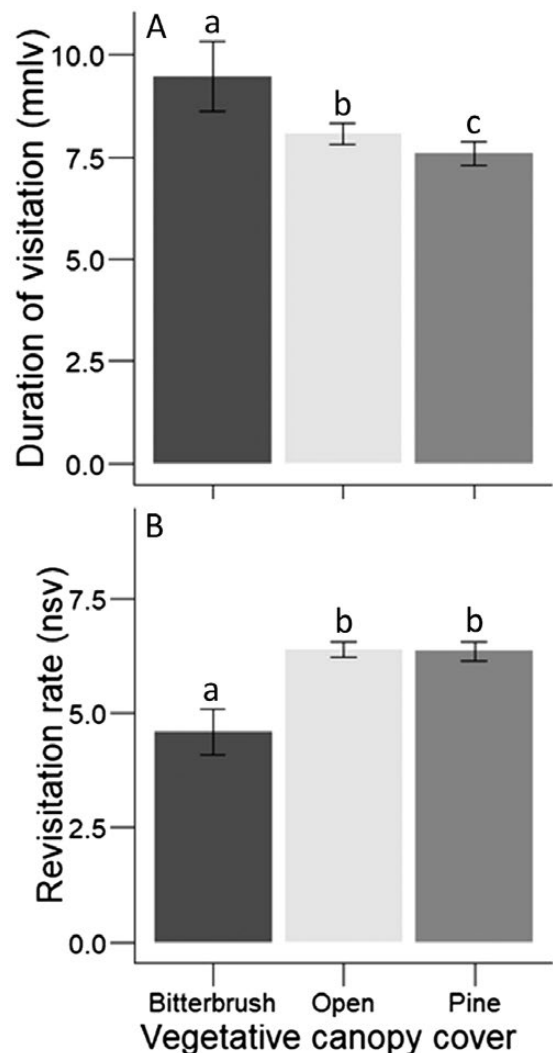


**Fig. 2.**—The effect of the interaction of distance traveled from the burrow (m) and distance traveled from points of refuge (m) on revisitation rate (number of separate visits to a hull: *nsv*) of *Callospermophilus lateralis* ( $n = 6$ ) to habitat patches in the Whittell Forest and Wildlife Area 15–31 July 2014. Each trend line represents binned values for distance traveled from the burrow in ascending order (0–229 m). The trend line equation in the upper right corresponds to closest distance from the burrow (0–25 m) and the trend line in the lower left corresponds to greatest distance from the burrow (132–229 m). The larger  $r^2$  value represented by the trend line corresponding to greatest distance from the burrow indicates a greater influence of distance traveled from refuges on revisitation rate.

proportion of variation explained by differences among individuals indicated repeatability of visit duration among individuals, though not as strongly as visitation rate ( $R = 0.375 \pm 0.135$ ).

## DISCUSSION

Animals maximize their fitness largely depending on strategies that optimize their foraging efforts in environments associated with dynamic risks and costs. *Callospermophilus lateralis* must maximize its foraging efficiency by appropriately allocating time within, traveling through, and revisiting a mosaic of habitat types that are not equally accessible from the burrow and are associated with varying levels of energy expenditure and risk of predation. *Callospermophilus lateralis* may use a spatiotemporal strategy that allows them to mitigate risks and costs while foraging. In support of our first hypothesis, individuals spent greater relative durations of time in locations away from



**Fig. 3.**—Relationship of vegetative canopy cover type with A) visit duration (mean number of locations per visit within an inter-visit gap of 60 s: *mnlv*), and B) revisitation rate (number of separate visits to a hull after an inter-visit gap of 60 s: *nsv*) for *Callospermophilus lateralis* ( $n = 6$ ) in the Whittell Forest and Wildlife Area 15–31 July 2014.

the burrow and in food patches, indicating they may be increasing foraging efforts in a time when food stores in the larder are low. Concurrently, individuals spent more time in patch types such as bitterbrush canopy cover in comparison to more open canopy cover types including pine and areas of no overstory cover. Revisitation rates to the latter patches were higher, however, which is consistent with our second hypothesis. This may indicate a prioritization of bitterbrush canopy cover, while other habitat patches served as frequented corridors despite potential increased risk of predation. We were not able to support our third hypothesis stating duration of time decreased as distance from refuge locations increased; however, individuals revisited areas nearer to refuges more frequently than areas farther from refuges, suggesting individuals may be using areas of refuge as protective cover when away from their burrow.

Antelope bitterbrush was the primary source of food available during the study and was the first seed source available to individuals following winter torpor. For these reasons, *C. lateralis* may choose to prioritize foraging efforts by maximizing time in food patches. Other species have been shown to maximize foraging efforts over other activities, even in risky patches, when their energetic demands are high (Brown 1989; Kotler et al. 1991). Prioritization of foraging activity over other behaviors often occurs due to life history patterns such as reproduction or limited temporal availability of food (MacWhirter 1991; Brown 1999; Carter and Goldizen 2003). Nevertheless, though foraging activity is prioritized, *C. lateralis* may also use strategies to mitigate associated risks and costs. To account for potential increased risk of predation, other wildlife species interrupt foraging within and travel between food patches with episodes of vigilance, use indirect routes to remain close to protective cover, or alter their travel speed (Thompson 1982; Kotler 1984; Brown 1999). *Callospermophilus lateralis* adjusted rates of revisitation and visit duration relative to locations of refuge, vegetative canopy cover type, and distance traveled from the burrow in ways that suggest use of such strategies to dually reduce predation risk and the energetic cost of travel.

Foraging within proximity to a refuge allows animals to mitigate predation risk while also extending the length of time they can spend in a food patch away from a central burrow or nest (Abu Baker et al. 2015). Refuges have been used by many small mammals to facilitate use of patch types that may expose the individual to higher predation risk (Kotler et al. 1991; Sutherland and Dickman 1999). In contrast, some studies have concluded that refuge in the form of dense shrub cover is disadvantageous because it restricts the ability of the individual to detect predators and retreat to the shelter of a burrow (Schooler et al. 1996; Wheeler and Hik 2014). The latter studies have primarily identified refuges in terms of vegetative cover, whereas this study strictly identified refuges as stumps and boulders. These features were chosen after several weeks of direct observation of individuals standing vigil on and fleeing to them. *Callospermophilus lateralis* showed greater revisitation rates in areas of higher concentration of refuge locations when farther from the burrow, indicating these patches could be important to facilitate travel between food patches when retreat to the burrow is difficult.

*Callospermophilus lateralis* also revisited open and pine canopy cover more frequently than bitterbrush canopy cover types, but spent less time in these patches per visit. As mentioned above, dense understory vegetation can pose more of a predation risk to some small mammal species in comparison to open habitat. Additionally, traveling through open understory decreases movement path tortuosity, increasing energetic efficiency of travel (Wilson et al. 2013). Although we did not measure travel speed, other larger rodent species frequently use habitat types with a more open understory to increase travel speed, thereby allowing them to reduce predation risk and energy expended while traveling through corridors between food patches. Kenagy and Hoyt (1989) found that the closely related Cascade golden-mantled ground squirrel (*Callospermophilus saturatus*) traveled greater distances during the day at their maximum aerobic speeds while moving around their home ranges. This travel speed was made possible by the frequent use of open habitat and was found to be more energetically efficient than traveling the same distances at a walking speed. Yellow-bellied marmots (*M. flaviventris*) ran fastest across low grasses and bare ground while traveling between food patches (Blumstein et al. 2004). Degus (*Octodon degus*) traveled 1.82 times faster in open habitat as compared to shrub habitat (Vasquez 2002). *Callospermophilus lateralis* may similarly be using patch types with no overstory vegetative cover as energetically cost-effective corridors while also adjusting their travel patterns to remain near refuges to reduce predation risk.

The duration of time *C. lateralis* spent at any one patch increased at distances away from the burrow, particularly around 75 m. Optimality models indicate that energetic cost of travel increases with distance traveled, suggesting it is more efficient to remain in distant patches longer to maximize energy intake (Orians and Pearson 1979). However, this feature of optimality models has been refuted in recent studies (Nonacs 2001; Barrette and Giraldeau 2008). These studies suggest that an increase in time allocation is not strictly a function of increasing travel distance and amount of food harvested. Individuals may also increase bouts of antipredator vigilance the farther they travel from protective cover, which also contributes to an increase in duration of time spent at greater distances (Cassini 1991; Brown 1999; Brown and Kotler 2004). Seed harvest may contribute to greater time allocation; however, time spent at any distance from a central location is influenced by many more factors than the availability of food along a travel continuum.

New mini-GPS technology is an exciting breakthrough in movement analyses for small mammals. Spatiotemporal data allow researchers to address questions regarding time management in movement behavior free from the assumptions and limitations of optimality models. Previous methods, such as GUDs and observational studies, are much more limited in their ability to capture these fine-scale movement patterns due to limited windows of time for observation and potential observer interference (Verdolin 2006). Nevertheless, use of this technology is not without its drawbacks. GPS technology is still costly and, if not entirely cost-prohibitive, sample size is often sacrificed for more data per individual and greater data precision (Hebblewhite and Haydon 2010). Additionally, true behavior cannot be explicitly explained, only inferred from patterns identified in data clusters



(Davis et al. 1999; Cagnacci et al. 2010). Greater behavior-specific knowledge can be achieved through use of biosensors such as accelerometers, but comes at an additional financial cost (Cooke et al. 2004). Supplementing GPS data with other methods, such as direct observation of individuals, is therefore still valuable to support inferences drawn from analyses.

Spatiotemporal GPS analyses can be an important tool for testing the assumptions of optimality models such as OFT and their reliability in predicting how animals budget time while foraging. Habitat use is much more than which resources are selected and where, but how and when those resources are utilized in space. External factors such as predator pressure, energetic investment, exposure to abiotic elements in unsuitable matrices, and competitive interactions are all important to consider when uncovering how animals use habitat (Bonenfant and Kramer 1995; Fuller and Harrison 2010; Harvey and Fortin 2013). Incorporating this knowledge into conservation and management objectives is still a burgeoning concept, but its importance has been highlighted in recent years (Martin 1998; Sutherland 1998; Caro 2007; Wildermuth et al. 2013). Temporal data may allow us to expand our knowledge of spatial patch use, leading to better-informed inferences about core habitat requirements, corridor use, and potential risks to species survival. This new knowledge could additionally help parameterize individual-based models to assess habitat use and effects of habitat change or disturbance on species behavior and distribution (Pauli et al. 2013). In an era of unprecedented environmental change, having such complete, accurate descriptions of habitat use is imperative for successful conservation efforts.

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