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Source: Wildlife Biology, 2019(1) : 1-9

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00528>

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Discriminating different-purpose burrows of the North American badger *Taxidea taxus*

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For many species, burrowing is used for a variety of purposes, such as finding food, sheltering from elements and predators, or raising offspring. For threatened species, differentiating among burrow types allows effective conservation efforts, and provides insight into habitat attributes needed at different stages in their life-history. This study investigated whether burrow characteristics for the North American badger *Taxidea taxus* allowed discrimination among summer, winter and natal burrows, and whether these characteristics reflected different requirements by the animals. Radio-telemetry was used to monitor badgers and classify burrows based on seasonal occupancy. Characteristics relating to thermal and security cover, along with features that could correlate with prolonged usage, were measured across winter, natal and summer burrows. Winter and natal burrows showed greater vegetation cover than summer burrows, potentially indicating increased thermal protection and predator avoidance. However, for winter burrows, greater vegetation cover did not translate into warmer, winter subterranean temperatures compared to summer burrows. Winter and natal burrows also had larger soil fans and, in the case of natal burrows, also had more entrances than summer burrows. These features may be indicative of prolonged usage. All told, it appeared summer burrows were distinguishable from winter and natal burrows based on the dimensions and construction of the burrow, location and surrounding vegetation. However, because badgers are capable of modifying their environment (including existing burrows) it is difficult to make precise predictions of where certain burrow types will occur. Still, the results of this study allow protection efforts or other management considerations to be apportioned more effectively among different burrow types. Comparable work is needed in other regions to understand how burrow characteristics spatially vary in importance.

Keywords: British Columbia, discrimination, natal, rapid assessment, species at risk

The identification of ‘critical habitat’ has become a common focus of conservation planning for many species at risk. However, identification of such may be difficult for species whose requirements change both temporally and spatially, or for those species with large ranges and shifting habitat requirements. One approach to defining critical habitat is to focus on places of residence that are occupied during important periods in a species’ life-history (Canada’s Species at Risk Act 2002). In some cases, identification of critical residences may be relatively straightforward. For example, traditional hibernacula of temperate-zone animals are obvious candidates for conservation (e.g. snake dens and bat caves). However, for other animals, particularly wide-ranging or nomadic species, assigning value to a specific ‘residence’ may be more problematic.

The concept of ‘residence’ is not easily applied to the management of the endangered North American badger *Taxidea taxus jeffersonii* in Canada (Government of Canada 2018a). Burrows occupied during long periods in the winter (Harlow 1981) and during spring natal periods (Messick and Hornocker 1981) are undoubtedly ‘residences’, but it is unclear if these burrows can be differentiated from those used for more transient purposes, such as summer burrows that may be used as little as one night at a time (Messick and Hornocker 1981, Paulson 2007). In fact, for the majority of the year, North American badgers (particularly males) are relatively nomadic in nature, hunting nightly and traveling from burrow to burrow (Sargeant and Warner 1972, Hoodicoff et al. 2009). Thus, labelling summer burrows as a ‘residence’ becomes debatable. Moreover, the availability of burrows does not appear to be limited if given proper soil conditions (Lay 2008), as the animals can readily dig new burrows when needed. All told, the issues confounding the definition of residences for these animals may stall or impede development of conservation efforts, for although burrows

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are often detected without the use of telemetry or other monitoring tools, there is currently no way to rapidly assess their relative importance. Any tool or process that makes this feasible will aid in decisions surrounding land use.

The factors (if any) that characterize different types of badger burrows have not been well studied. There has been previous investigation into badger burrow characteristics (Hoodicoff 2003, Paulson 2007, Huck 2010), and some studies have shown that burrows often are re-used (Messick and Hornocker 1981, Paulson 2007). However, a key question that remains is whether burrows used at different times of the year (e.g. winter or natal burrows) have discriminating characteristics. If such a pattern occurs, it may be driven by the need for different burrow features at different times of the year, such as thermal or security properties. As winter is a critical period for northern mammals (Marchand 1996), burrows used during this time presumably should have characteristics that increase insulation, as reported for other mammalian species (Davis 1996, Hwang et al. 2007, Ross et al. 2010). For example, features such as higher shrub and snow cover may create warmer burrow temperatures (Liston et al. 2002). Conversely, during the natal period (spring), when temperatures are warmer but young are highly vulnerable to predators, reproductive females may seek site characteristics that aid in predator avoidance. To date, there has been no in-depth investigation of fine-scale habitat features of badger winter burrows, much less attempts to discriminate among burrows according to purpose. Only a handful ($n=4$) of natal burrows have been excavated, mapped and described (Lindzey 1978, Weir et al. unpubl.), so there is very little description of external features to aid in rapid assessment or identification.

As part of a larger badger research program (Symes 2013, Klafki 2014), we examined burrow characteristics and usage in an extreme northern population of badgers. We inferred that the relatively harsh environmental conditions in this region would make selection criteria of burrow characteristics (if they exist) more detectable. We hypothesized that 1) burrows used during winter and natal periods would differ from summer burrows in fine-scale vegetation and location characteristics that confer better thermal protection and predator avoidance, and 2) that winter and natal burrows would have construction elements reflecting longer period(s) of occupancy use. Further, we predicted that (A) winter burrows would have greater snow and vegetation cover to aid in thermal insulation, leading to warmer winter temperatures and (B) natal burrows would have greater visual obscurity to aid in predator avoidance. We use the results of our study to comment on the potential for rapid assessment of seasonal-burrow differentiation as a conservation tool. We focused our efforts on examining potential differences at a fourth order (i.e. burrow site) spatial scale (Johnson 1980).

Material and methods

Study area

The study area (6377 km²) was located at the north-western extent of North American badger range, namely the Cariboo Region of central interior British Columbia, Canada, near

the town of 100 Mile House. The study area was composed of a matrix of coniferous forest, aspen copses and grassland, much of which has been altered for human use (e.g. pastures). Climate is continental, with warm dry summers and cool winters. Snow cover typically lasts from the beginning of November to the middle of March. The mean total snowfall during winter is 154 cm, and daily temperatures average -4.4°C (Government of Canada 2018b). During the coldest month (January), the mean daily temperature is -7.2°C ($\pm 4.3^{\circ}\text{C}$) with lows of -40°C or colder. A more detailed description of the study area can be found in Symes (2013). Reproducing females typically are restricted to their natal burrows from late-March through April (Klafki 2014).

Badger telemetry

Most of our study animals were live-trapped between 2007 and 2009 as part of an investigation on road mortality of this population (Klafki 2014). These animals all were captured using padded foothold traps (Victor 1½ coil spring) anchored into the ground near active burrows. Trapped animals were restrained using a handling pole and administered Telazol (tiletamine and zolazepam) at a dose of $5\text{--}10\text{ mg kg}^{-1}$ estimated body weight. Once immobilized, body condition was assessed, vital signs monitored and ophthalmic ointment applied. Transmitters (VHF IMP400L Telonics, Mesa, AZ) were surgically implanted in a mobile veterinary field unit or after being transported to a local clinic. To prevent hypothermia, post-operative badgers recovered in a container (modified plastic 2051 barrel) while wrapped in a blanket. Once fully recovered from anesthesia, the animals were released at their burrow and checked frequently thereafter for 48 h to confirm normal behaviour.

Three orphaned siblings were added to our study after their mother was struck and killed by a vehicle. These kits were captured in mid-May 2010 and reared at the BC Wildlife Park (Kamloops, British Columbia). After attaining sufficient size, they animals were implanted with VHF radio transmitters, and seven days later transferred to a soft-release enclosure in the study area (19 July). Within 48 h all three animals left the enclosure via a tunnel they had constructed and were displaying typical badger activities and movements (Klafki and Packham, unpubl.). One sibling was soon killed by a vehicle, while the remaining two were tracked throughout winter. Thus, the final sample of telemetered badgers providing burrow data for this study consisted of 16 animals: 14 live-trapped adults (11♀, 3♂) and the two released orphans (1♀, 1♂). The lack of adult males in our sample may be a product of high male mortality from vehicle collisions (Newhouse and Kinley 2000, Hoodicoff et al. 2009) and/or biased summer captures of resident females rather than wide-ranging, transient males (Klafki 2014). We did not consider the female-bias in our sample to be a substantial detriment, given that the polygynous mating system of badgers lends a greater conservation significance towards females. Moreover, a rapid-assessment tool to distinguish burrow types (if developed) would be used often without knowledge of the sex of the occupant. Consequently, we pooled burrow data collected from all of our badgers, but still calculated mean values ($\pm\text{SD}$) by gender for our measured burrow variables. All telemetered badgers were

located a minimum of once per week during winter in the first three years (2007–2008, 2008–2009, 2009–2010) and approximately once every second day in the fourth winter (2010–2011). These animals also were re-located regularly during the first three summers (\approx every 5 days).

Burrow classification

We defined three different categories of burrows based on previous studies (Hoodicoff 2003, Klafki 2014): SB – summer burrows used between May and October; WB – winter burrows used consecutively for longer than one week between November and February; and NB – natal burrows used by females continually through March and April and confirmed by either the presence of kits or the display of natal-like behavior. Burrows were selected in a randomized block design (block = individual badger). Given NB were less common, the data set was unbalanced.

Burrow characteristics

To determine if snow depth (and its insulating properties) differed among burrow types, we took three measurements (to nearest 0.5 cm), throughout winter at a subset ($n = 104$) of burrows. Measurements were taken within a 5 m radius of the burrow, taking care not to compact the snowpack and to prevent disturbance in case of occupation.

During winter we also collected burrow, subnivean and air temperatures at a random selection of paired SB and WB ($n = 14$) from seven badgers (2♂, 5 ♀). Although SB were not known to be used during winter, this approach provided a comparison of temperatures at used WB versus other available locations (the SB sites). These data were recorded using IButton temperature data loggers (models DS1921G-FS and DS1923) deployed between November 2010 and March 2011. At each burrow site, one data logger was placed in the burrow as far below the surface as possible, another on the ground prior to snowfall (subnivean), and a third attached to a nearby object (i.e. tree or fence post) 1.5 m above the ground (air). Radiation shields (Tarara and Hoheisel 2007) were used to minimize the impact of solar radiation.

Data on other features of the dens (vegetation cover and construction) were collected from all burrows in our dataset following field work each year (22–27 July 2010, 26 June–13 July 2011). This work was conducted when burrows were unoccupied. Following Nudds (1977), we measured average visual obscurity (i.e. horizontal cover; $\pm 5\%$) at 0–0.5 m and 0.5–1.0 m above ground at a distance of 15 m from the main burrow entrance, at each of the four cardinal directions and from an observation height of 1 m.

We measured additional vegetation cover surrounding the burrow in a nested plot design, similar to standard Provincial forestry practices (RISC 2007). Percent cover ($\pm 5\%$) of canopy, shrub, bare ground, coarse woody debris (> 10 cm in diameter), and litter were visually estimated within 2 m and the number of trees were recorded within 5.64 m of the main burrow entrance. Plot radius differed from snow depth measurements as caution was taken not to compact snow in potentially occupied WB.

We recorded the presence of ‘infrastructure’ (e.g. roots, stumps, coarse woody debris), noted surrounding coarse-level

vegetation community (i.e. coniferous, deciduous, mixed-wood, open [pasture or grassland], and disturbed), measured slope and aspect, and classified the topographic position of the burrow (crest, upper, mid, lower, toe, depression or level).

Finally, we measured construction elements thought to indicate length of use, namely the number of entrances, and the maximum width and length of any associated soil fan. We defined the main entrance as having the largest soil fan, badger tracks (if present), an absence debris and no loss of integrity (e.g. caved-in or filled with soil). We also measured dimensions of the burrow (e.g. minimum width and height of entrances), and classified soil texture according to (Thien 1979).

Data analysis

R Statistical Software ver. 3.5.2 (www.r-project.org) was used for data analysis. Linear mixed effects (LME) models were used to test the hypotheses that WB and NB differed in fine-scale vegetation characteristics that aid in thermal protection and predator avoidance, and construction elements that may indicate length of stay. Fixed effects included snow depth, temperature, horizontal, vegetation cover, number of entrances, entrance dimensions and maximum width and length of soil spoils. Models accounted for random effects caused by individual badgers and were built using package nlme in R (Pinheiro et al. 2018). We used log-likelihood ratio tests of independence (G-tests) without correction to examine frequencies of different burrow types for categorical data (i.e. habitat, presence of infrastructure, soil texture). We considered differences significant when $p < 0.05$.

We investigated the potential to create a rapid-assessment tool by examining potential differences in thermal protection, predator-avoidance and constructability characteristics among burrow types in a linear discriminate analysis (LDA). Due to the high dimensionality of the dataset, candidate variables for multivariate analysis were limited to those that were continuous, not categorical (Quinn and Keough 2009).

Data exploration followed Zuur et al. (2009a, b) and McGarigal et al. (2000) to ensure assumptions of analyses were met. Variables not fitting normal distributions were transformed when possible using arcsine or log transformations (Quinn and Keough 2009). Following transformations, covariates displayed univariate normality and homogeneity of variances. However, multivariate normality and equal variance–covariance matrices were not detected. Although LDA is robust to violations of multivariate normality and unbalanced designs, we still treated the results as descriptive and exploratory (Williams 1983, McGarigal et al. 2000). Subsequent examination of the resultant discriminant scores revealed no departures from normality or linearity. Nevertheless, covariance matrices differed among burrows; therefore, we refitted the data in a quadratic discriminant analysis (QDA). For highly correlated variables ($r > 0.7$), only that which best discriminated among burrows in the LME models were retained. Covariates were fit in a forward, stepwise selection process using Wilk’s Lambda criterion in package klaR (Weihs et al. 2005). LDA and QDA were conducted using the package Mass (Venables and Ripley 2002). Overall correct classification was estimated using both

re-substitution and jackknife leave-one-out cross validation (LooCV) approaches. Model performance was estimated using Cohen's Kappa (McGarigal et al. 2000).

Results

Burrow characteristics

Thermal characteristics (snow depth, temperatures and shrub cover)

Our final dataset consisted of 139 burrows (SB: $n=90$, NB: $n=13$, WB: $n=36$) from 16 telemetered badgers. Snow depths at NB were significantly less than other burrows (mean NB: 22.6 ± 2.2 ; $F_{2, 296} = 5.9$, $n=104$, $p < 0.01$); however, there was no difference between WB (mean: 28.2 ± 1.4 cm) and SB (mean: 28.0 ± 0.9 cm). There was a significant difference in shrub cover among burrow types ($F_{2, 121} = 7.8$, $n=139$, $p < 0.001$; Table 1); WB had roughly twice as much shrub cover ($16.5 \pm 2.8\%$) as SB ($7.6 \pm 1.1\%$). However, NB did not differ from WB and were found to have a moderate amount of shrub cover (mean: $12.1 \pm 3.2\%$). Similar patterns occurred for canopy cover and number of trees in proximity to the burrow (p 's < 0.001 ; Table 1). WB also had twice the amount of coarse woody debris and litter cover as SB ($F_{2, 121} = 11.1$, $n=139$, $p < 0.001$ and $F_{2, 119} = 3.5$, $n=139$, $p < 0.05$ respectively; Table 1); however, NB did not differ from WB and SB.

During winter, subnivean and burrow temperatures at both WB and SB reflected a relatively warm and stable thermal environment compared to ambient air temperature (Fig. 1). However, there was a significant difference in subnivean (WB mean: $-4.3 \pm 0.1^\circ\text{C}$, SB mean: $-3.3 \pm 0.1^\circ\text{C}$; $F_{1, 1378} = 34.9$, $n=14$, $p < 0.0001$) and within-burrow temperatures (WB mean: $-2.1 \pm 0.1^\circ\text{C}$, SB mean: $-0.2 \pm 0.1^\circ\text{C}$; $F_{1, 1181} = 593.3$, $n=14$, $p < 0.0001$) between these two burrow types. Although WB were buffered against colder fluctuating ambient air, temperatures inside WB burrows and WB subnivean sites were less stable than those at corresponding SB sites (Fig. 1).

Visual obscurity

Horizontal cover (0.5–1 m height) was significantly greater at NB and WB (mean: $59.1 \pm 6.9\%$ and $51.0 \pm 4.7\%$ respectively; Table 1) than SB ($33.1 \pm 2.9\%$; $F_{2, 121} = 9.6$, $n=139$, $p < 0.001$) when observed at a height of 1 m. Despite having

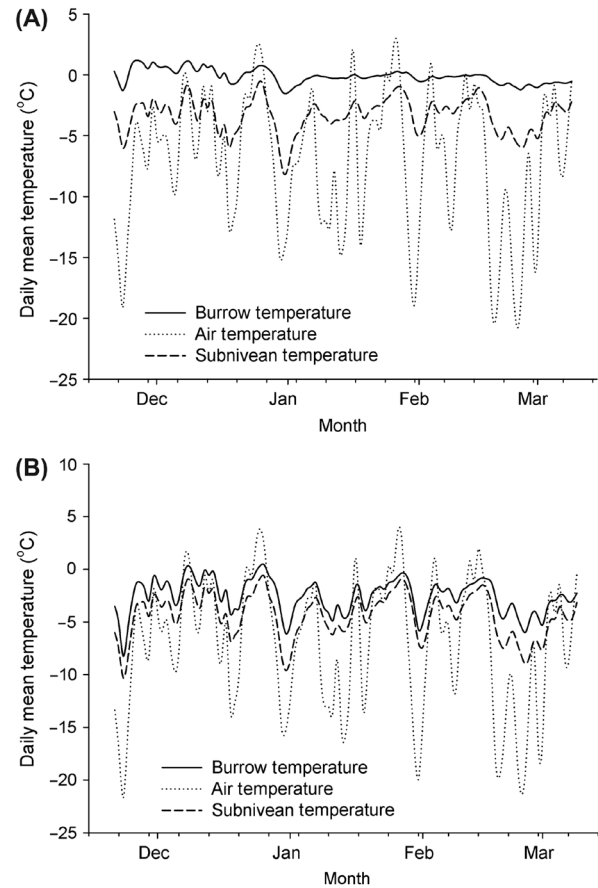


Figure 1. Daily mean temperatures at burrow, subnivean and air sites at (A) summer ($n=7$) and (B) winter burrows ($n=7$) of the North American badger between November 2010 and March 2011. Note burrow and subnivean temperatures are more stable (i.e. less variable) at summer burrows (A) than winter (B).

less horizontal cover, SB had twice as much grass cover than WB and NB ($F_{2, 121} = 16.8$, $n=139$, $p < 0.001$; Table 1). Horizontal cover at the 0–0.5 m height was not significant ($F_{2, 121} = 1.9$, $n=133$, $p = 0.16$).

Other burrow metrics (location, construction and dimensions)

There were significant differences in characteristics that might indicate length of stay. NB had significantly more entrances (mean: 4.6 ± 0.6 ; Table 1) than WB and SB (mean: 2.1 ± 0.1 and 2.1 ± 0.3 respectively; $F_{2, 121} = 8.3$, $n=139$, $p < 0.001$).

Table 1. Mean (\pm SE) values for measurements that significantly differed among types of burrows for the North American badger. WB = winter burrow, NB = natal burrow, SB = summer burrow. ^{a, b} Means with the same letters are not significantly different ($p > 0.05$).

| Characteristic | Variable | NB ($n=13$) | SB ($n=90$) | WB ($n=36$) | df | F | p |
|--------------------|----------------------------|----------------------|-------------------|--------------------|--------|------|--------|
| Thermal | % Shrub cover | $12.1 \pm 3.2^{a,b}$ | 7.6 ± 1.1^a | 16.5 ± 2.8^b | 2, 121 | 7.8 | <0.001 |
| | % Canopy cover | 22.6 ± 6.9^a | 7.3 ± 1.9^b | 19.8 ± 4.9^a | 2, 120 | 8.5 | <0.001 |
| | % Coarse woody debris | $10.2 \pm 7.5^{a,b}$ | 4.4 ± 1.4^b | 24.0 ± 5.5^a | 2, 121 | 11.1 | <0.001 |
| | No. trees | 6.4 ± 2.1^a | 2.7 ± 0.6^b | 7.3 ± 1.7^a | 2, 121 | 11.4 | <0.001 |
| | % Litter cover | $12.9 \pm 4.4^{a,b}$ | 12.2 ± 1.5^a | 20.6 ± 3.4^b | 2, 119 | 3.5 | <0.05 |
| Predator avoidance | % Grass cover | 25.0 ± 5.2^a | 52.5 ± 2.9^b | 26.8 ± 4.1^a | 2, 121 | 16.8 | <0.001 |
| | Visual obscurity (0.5–1 m) | 59.1 ± 6.9^a | 33.1 ± 2.9^b | 51.0 ± 4.7^a | 2, 121 | 9.6 | <0.001 |
| Length of stay | No. of entrances | 4.6 ± 0.6^a | 2.1 ± 0.1^b | 2.1 ± 0.3^b | 2, 121 | 15.3 | <0.001 |
| | Soil fan length (cm) | 207.1 ± 18.3^a | 121.1 ± 5.9^b | 167.9 ± 11.1^a | 2, 119 | 16.7 | <0.001 |
| | Soil fan width (cm) | 195.6 ± 19.6^a | 120.6 ± 6.5^b | 153.1 ± 10.3^a | 2, 119 | 10.1 | <0.004 |

Moreover, soil fan length and width were greater at NB and WB compared to SB (p 's < 0.01; Table 1).

We also found a significant difference in vegetative communities among burrow types ($G_8 = 15.9$, $n = 139$, $p < 0.05$ – Fig. 2). Winter burrows were found more often than expected in forested (coniferous, deciduous and mixed) and less often than expected in open communities (grasslands and pastures). Conversely, SB showed the opposite pattern (Fig. 2). NB were found more often than expected in deciduous and mixed and less often than expected in open communities (Fig. 2). Nearly 35% of burrows contained infrastructure consisting of tree roots (the most common feature), followed by anthropogenic wood piles, coarse woody debris, stumps and boulders. Compared to SB, WB and NB more often involved one or more of these infrastructure types ($G_2 = 27.1$, $n = 139$, $p < 0.001$ – Fig. 3).

Burrows occurred on flat or gentle slopes ($x = 23.4 \pm 1.4^\circ$, range 0 – 90°), and there was no difference between types ($F_{2, 121} = 0.73$, $n = 139$, $p = 0.49$). Similarities among burrow types also were seen for slope positioning ($G_{16} = 13.6$, $n = 139$,

$p = 0.6$) and soil texture ($G_{18} = 25.0$, $n = 139$, $p = 0.1$). There did not appear to be a difference between male and female burrow characteristics (Table 2).

Linear and quadratic discriminant analysis

The linear discriminant analysis resulted in two discriminant functions, with the first (LD1) explaining 67% of the total between-group variation, and the second (LD2) explaining 33% (Table 3). Squared canonical correlation was 0.35 for LD1 and 0.21 for LD2; both linear discriminants were significant (LD1: $F_{2, 130} = 36.2$, $n = 139$, $p < 0.001$; LD2: $F_{2, 130} = 18.1$, $n = 139$, $p < 0.001$).

Plotted discriminant scores appeared to show moderate success in differentiating burrow types (Fig. 4). In LD1, structure coefficients indicated that maximum fan length contributed most to the first discriminant function (Table 3). The largest contributors of LD2 were litter cover, number of entrances and percent coarse woody debris (Table 3).

The overall correct classification rate when using re-substitution showed reasonable success with 77% of

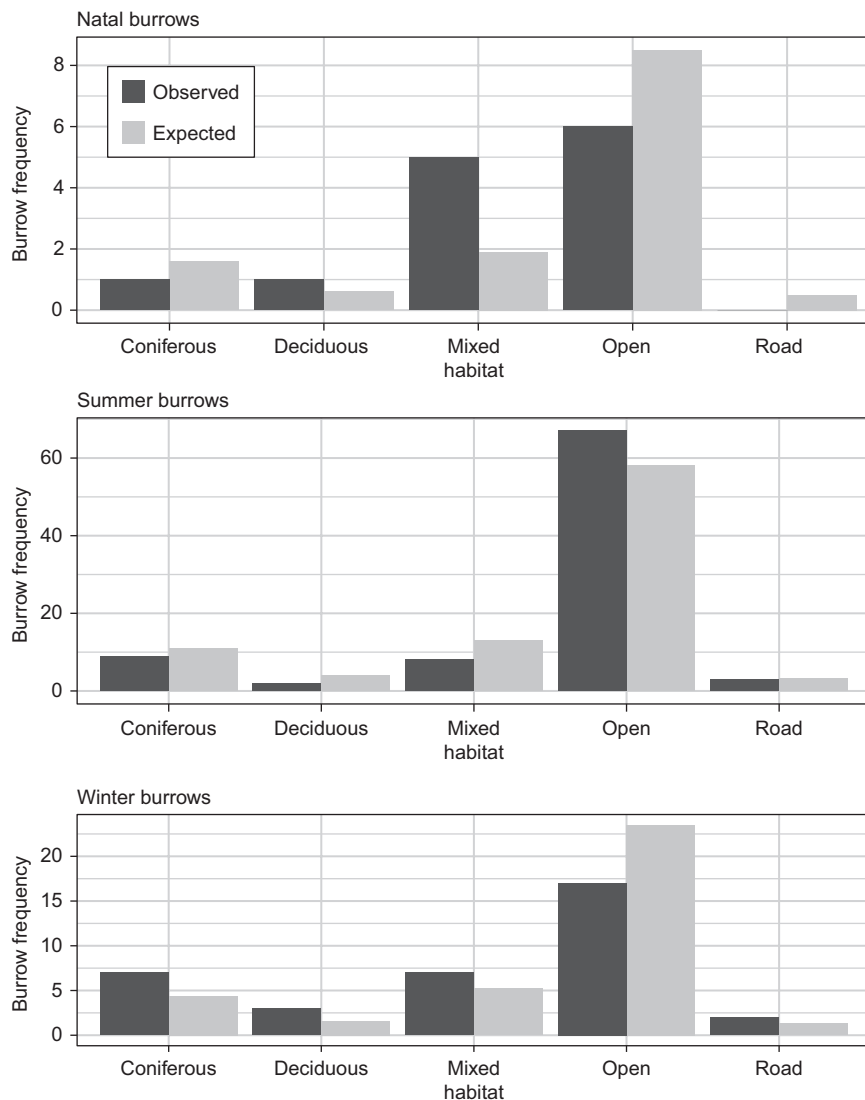


Figure 2. Frequency of North American badger seasonal burrows types in coarse-scale vegetation communities in the Cariboo Region of British Columbia, Canada, between 2009 and 2011. Sample sizes: winter (WB): $n = 36$, natal (NB): $n = 13$, summer (SB): $n = 90$.

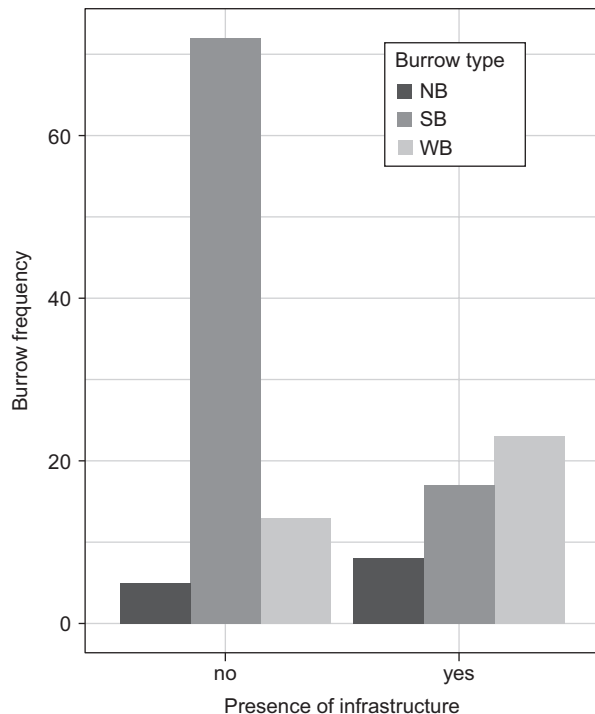


Figure 3. Frequency of North American badger seasonal burrow types with and without additional infrastructure (i.e. roots, stumps, coarse woody debris, woody debris piles, etc.) in the Cariboo Region of British Columbia, Canada, between 2009 and 2011. Sample sizes: winter (WB): $n = 36$; natal (NB) $n = 13$; summer (SB) $n = 90$.

the burrow types correctly identified (Table 4). With the more conservative approach (LooCV), slightly fewer classifications were correctly predicted (74%). Cohen's Kappa scores for both performance classifications showed only moderate agreement for both the re-substitution method (Cohen's Kappa: 0.51, 95% CI=0.35–0.66) and the LooCV method (Cohen's Kappa: 0.46, 95% CI=0.30–0.62). SB were classified correctly more often than WB or NB (Table 3). When the data were refit to a QDA, classification improved to 82% showing substantial agreement (Cohen's Kappa: 0.63, 95% CI=0.50–0.77) for the resubstituting with lower success (70%) and only fair agreement (Cohen's Kappa: 0.38, 95% CI=0.22–0.54) for the LooCV method.

Table 2. Mean (\pm SE) values for measurements taken at male and female burrows for the North American badger. WB=winter burrow, SB=summer burrow.

| Variable | SB | | WB | |
|------------------------------|-------------------|---------------------|------------------|---------------------|
| | Male ($n = 18$) | Female ($n = 72$) | Male ($n = 9$) | Female ($n = 27$) |
| No. entrances | 1.9 (0.3) | 2.2 (0.2) | 2.8 (0.8) | 1.9 (0.3) |
| Soil fan length (cm) | 135.6 (17.1) | 117.4 (6.0) | 184.0 (20.6) | 162.3 (13.1) |
| Soil fan width (cm) | 127.4 (16.9) | 118.8 (7.0) | 167.8 (19.3) | 148.1 (12.2) |
| No. trees | 2.0 (0.9) | 2.9 (0.8) | 12.3 (4.3) | 5.6 (1.8) |
| % canopy cover | 11.1 (5.8) | 6.3 (1.9) | 29.1 (11.3) | 16.6 (5.3) |
| % coarse woody debris | 2.2 (1.2) | 4.9 (1.7) | 41.7 (11.8) | 18.0 (5.9) |
| % shrub cover | 6.8 (3.0) | 7.8 (1.1) | 10.0 (2.0) | 18.6 (3.6) |
| % litter cover | 11.3 (3.4) | 12.4 (1.7) | 22.1 (6.4) | 20.1 (4.1) |
| % grass cover | 36.3 (5.3) | 57.1 (3.3) | 17.4 (5.6) | 29.9 (5.0) |
| Visual obscuration (0.5–1 m) | 35.3 (7.1) | 32.5 (3.2) | 38.4 (8.3) | 55.2 (5.5) |

Discussion

Winter burrows, insulation and thermal environment

Winter burrows (WB) differed from SB in fine-scale vegetation characteristics (e.g. shrub cover, canopy cover, coarse woody debris) that were thought to provide increased thermal protection. Moreover, WB were found more often than expected in wooded environments. However, the greater amounts of cover detected at WB did not appear correlated with increasing subterranean temperatures, by aiding in snow accumulation. Compared to SB sites, snow depth was not significantly deeper at WB, and temperatures recorded inside unoccupied burrows were colder (although the average difference of 1.9°C between burrow types may not be ecologically meaningful). Regardless, the environment within the WB was warm and stable compared to outside air temperatures, similar to that reported for winter setts of Eurasian badgers (Moore and Roper 2003, Sidorchuk and Rozhnov 2008). Of course, burrow temperatures almost certainly rise when a badger is present (Moore and Roper 2003), and how thermal properties of the different burrow types respond to this effect was beyond the scope of this study.

Had snow depths been lower at the WB sites, one could postulate that the wooded habitat (higher cover) resulted in increased snowfall interception (D'Eon 2004). However, our data provide support for neither of these arguments. Increased cover around burrows in forest habitats may confer advantages we did not test for, such as improved winter hunting opportunities (cf. Squires et al. 2010) or increased wind interception (Liston et al. 2002) that would favour above-ground foraging. Detailed prey surveys or wind measurements would be needed to test this, but snow tracking of the study animals has shown that winter forays tend to occur in proximity of their burrows (Symes 2013).

Natal burrows and predator avoidance

Natal burrows had greater amounts of horizontal cover than SB and this could provide thermal or predator protection. Greater horizontal cover creates greater visual obscurity, providing cover for young animals similar to that seen in other species (Pruss 1999, Martorello and Pelton 2003, Hwang et al. 2007, Organ et al. 2008). However, Huck (2010) reported less visual obstruction at badger reproductive burrows as compared to random sites, although only

Table 3. Structure coefficients showing the correlation between two linear discriminant functions (LD1 and LD2) and seven variables used to measure differences among types of badger burrows. Variables with larger coefficients are those that contributed more to the discriminatory power of the function.

| Variable | LD1 coefficient | T statistic | p-value | LD2 coefficient | T statistic | p-value |
|-----------------------|-----------------|-------------|---------|-----------------|-------------|---------|
| Grass cover % | 1.296 | 12.11 | <0.001 | -0.312 | -1.83 | 0.07 |
| Number of entrances | -1.826 | -4.59 | <0.001 | -4.835 | -12.35 | <0.001 |
| Max. soil fan length | -8.604 | -10.70 | <0.001 | -0.434 | -1.97 | 0.05 |
| Coarse woody debris % | -1.911 | -6.50 | <0.001 | 2.403 | 4.73 | <0.001 |
| Litter cover % | -1.190 | -2.64 | <0.01 | 6.182 | 3.67 | <0.001 |
| Canopy cover % | -0.402 | -6.90 | <0.001 | -1.639 | -0.64 | 0.52 |
| Shrub cover % | -0.455 | -6.84 | <0.001 | 0.169 | 2.74 | <0.01 |

two of the 14 burrows in her study were confirmed natal burrows, and no data were collected on other burrow types.

Winter and natal burrows and length of stay

Soil fans at NB and WB were larger than at SB. Although this has been suggested for NB by others (Huck 2010), until the present study it has not been explicitly tested. Larger soil fans, as seen in the NB and WB of our study, may be an indication of the depth, length of stay, frequency of use or the number of badgers utilizing the burrow concurrently. For example, enlargements of the main chamber or regular

clearing of waste during long occupations would result in larger soil fans. Regardless, NB (and to some extent WB) sites had soil fans over 1.5 times the size of SB, providing a simple discriminating tool for field use.

Similarly, the greater number of multiple entrances to NB have been reported for other species, and this too may serve in predator evasion (Ross et al. 2010). Here again, our results differed from those seen elsewhere (Utah/Idaho and southern British Columbia) for the North American badger: both Lindzey (1978) and Weir et al. (unpubl.) reported natal burrows possessing only a single entrance, although the combined sample sizes of those studies were few (n = 4). It is quite possible that multiple entrances to burrows are a result of repeated, multi-year or lengthy occupations by family groups or even unrelated badgers, rather than planned, deliberate construction on the part of reproductive females.

Other metrics differentiating burrows

The higher proportion of WB and NB sites located in wooded habitats likely explains some of the vegetative and structural differences among burrow types (i.e. number of trees, percent canopy cover, shrub cover, coarse woody debris, litter cover and presence of additional infrastructure). In British Columbia, it is not uncommon for badgers to use forested habitats (Hogg 2007). Similarly, we have also observed females establish burrows in urban areas and along the margins of a major highway (Symes et al. unpubl.). The use of atypical vegetative communities such as forests

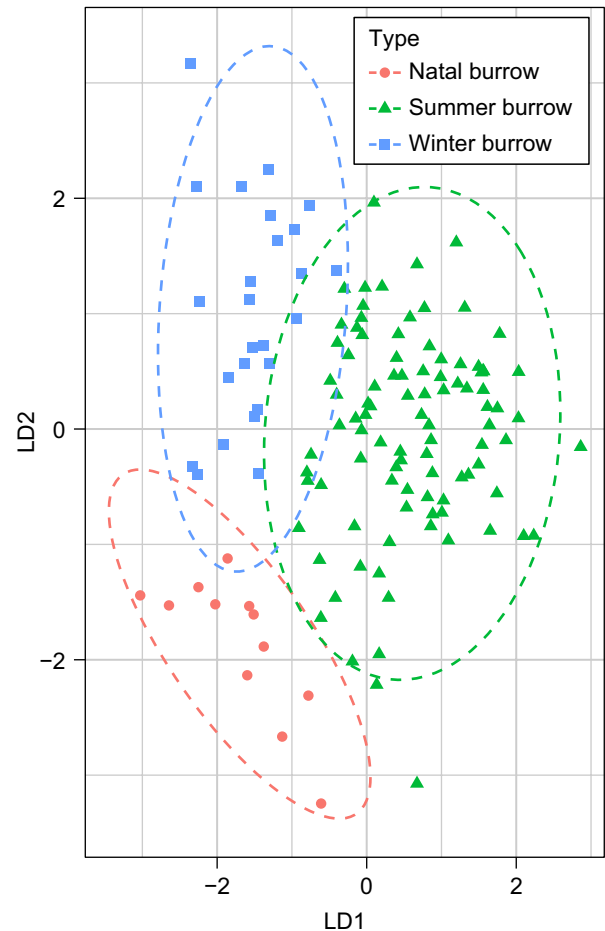


Figure 4. Individual scores of linear discriminant functions 1 and 2 (LD1 and LD2) showing differentiation among winter (n = 34), natal (n = 12) and summer (n = 87) burrows of the North American badger in British Columbia, Canada.

Table 4. Predicted success of classification using linear discriminant analysis to classify seasonal North American badger burrows using re-substitution and leave-one-out-cross-validation methods for both linear discriminant analysis (LDA) and quadratic discriminant analysis (QDA).

| Method | Burrow type | Predicted | Actual | Success (%) | |
|--------|--------------------------------|-----------|--------|-------------|----|
| LDA | Re-substitution | natal | 7 | 12 | 58 |
| | | summer | 78 | 87 | 89 |
| | | winter | 17 | 34 | 50 |
| | Leave-one-out Cross-validation | natal | 7 | 12 | 58 |
| | | summer | 77 | 87 | 89 |
| | | winter | 15 | 34 | 44 |
| QDA | Re-substitution | natal | 8 | 12 | 67 |
| | | summer | 79 | 87 | 91 |
| | | winter | 22 | 34 | 65 |
| | Leave-one-out Cross-validation | natal | 4 | 12 | 33 |
| | | summer | 74 | 87 | 90 |
| | | winter | 15 | 34 | 44 |

may be a product of the small, patchy and possibly limited habitat at the range periphery compared to more homogeneous habitat at the core of badger range.

It may be that the infrastructure present at WB and NB sites is more a consequence of burrow selection at the stand/habitat level, rather than specific selection by the badger excavating the burrow. Features such as roots, stumps, and CWD likely are more prevalent in wooded habitats. Still, additional infrastructure may facilitate access the soil (Vleck 1979) or support burrows once they are constructed (i.e. denning bears: McLoughlin et al. 2002). An interesting observation was that badgers in our study often had WB and NB sites within woody debris piles (both natural and anthropogenic). This is a phenomenon reported for other mustelids during winter (Wilson and Carey 1996, Liso et al. 2002). Regardless of why these burrow types are associated with additional infrastructure, this provides another characteristic that can be factored into the identification of seasonal burrows.

Burrow discrimination

The strongest discriminators of burrow type were the size of the soil fan, the number of entrances and litter cover. Additional categorical variables that appear to aid in the differentiation of burrows include the presence of additional infrastructure and more frequent occurrence in wooded habitats. Overall, the results of this study suggest that both WB and NB may be distinguished from SB by certain features, namely the dimensions and construction of the burrow, and the location and vegetation surrounding it.

Although the discriminant analysis was successful at differentiating SB from NB and WB, the LDA and QDA were relatively weak at differentiating NB and WB. From a conservation viewpoint, however, NB and WB sites likely will be assigned greater value than SB, making their joint discrimination still important. It appears as though some SB, such as those that are heavily-used, have intermediate characteristics (Symes 2013). This is not surprising, given that there is likely a continuum of differences among burrow types. Burrows that are heavily-used that share intermediate characteristics may be contributing to misclassifications. Further study is warranted and perhaps a more accurate model can be developed with more data.

As with any study on a wide-ranging animal, care must be taken in extrapolating results from one location to another, especially across distances and ecosystems (Constible et al. 2009). This is the first detailed study to focus on burrow characteristics for the North American badger, and parallel work is needed to corroborate our findings elsewhere in the species' range. It also is important to realize that the characteristics recorded for any burrow (including the surrounding area) at any one time may not necessarily reflect those present during establishment. During the history of the burrow, entrances may have filled in, soil fans decreased and settled, and vegetation cover altered through succession or other mechanisms. Moreover, burrows may be used differently by various individuals or used in multiple seasons (winter, natal or summer), and so burrow types may not be mutually exclusive. This is the typical situation facing wildlife professionals who must categorize a burrow without knowledge of its previous usage. Another point to consider

is that many burrowing animals, like badgers, can significantly modify their environment. As this study was descriptive and exploratory in nature, we caution against assuming that an animal has 'selected' a burrow for any particular suite of characteristics. To determine the significance of features such as horizontal cover, snow cover, multiple entrances and large soil fans, further studies comparing known NB, WB and SB are needed over a broader geographic range.

The characteristics identified in this study provide managers with a tool (albeit limited at this stage) to discriminate burrows: they do not necessarily predict where the animals are likely to occur.

Acknowledgements – Thanks are extended to Jonquil Crosby, Cara Lamont, Michael Packham, Hamish Nicolson, Kayla Straume and Cristen Symes, who all assisted with winter field work. Similarly, Nicole Heim contributed to early examination of seasonal burrows. In addition, we thank Melvin Louis and the Canoe Creek First Nation for providing support through the field season.

Funding – The British Columbia Ministry of Transportation and Infrastructure, the British Columbia Ministry of Environment, the Natural Sciences and Engineering Research Council of Canada and the Habitat Conservation Trust Fund provided funding and support for this project.

Permits – We conducted this work under British Columbia Ministry of Environment permit number WL10-65208. All protocols for capturing, handling and researching badgers were approved by the Thompson Rivers University Animal Ethics Committee (protocol no. AUP 2009-30R).

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