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Exploiting the Winter Trophic Relationship between Weasels (*Mustela* spp.) and their Microtine Prey as a Survey Method for Weasels in Meadow Ecosystems

Abstract

Weasels can be important components of grassland and meadow communities where they influence the dynamics of small mammal populations which, in turn, can be keystone species in these communities. We evaluate a method for detecting and identifying two species of North American mustelines (i.e., *Mustela frenata* and *M. erminea*) in mountain meadow systems. It is based on previous knowledge that weasels often co-opt the winter nests of their vole (or lemming) prey and frequently deposit scats there. We exploit this aspect of the predator-prey relationship and describe how, when paired with genetic identification of species from scat, searching after spring melt for weasel scats in winter-constructed vole nests may be an alternative survey method for detecting weasels in meadows. Our work was conducted at the Sagehen Experimental Forest in the Sierra Nevada Mountains. We discovered and examined 90 winter vole nests over four spring seasons, resulting in an average (SD) of 3.31 (1.81) nests found per survey hour per year. From these nests we collected an average of 0.57 (0.37) putative weasel scats per survey hour. Of the seven scats that were verified to be from a weasel, five were from *M. frenata* and two from *M. erminea*. This was a proof of concept effort, to which we conclude that searches of vole nests for scat that can be genetically verified as weasel should have a place in the biologist's toolkit. The method is likely to be the most efficient for obtaining a genetic sample for weasels in mountain meadow systems.

Keywords: weasel, *Mustela*, vole, survey, scat, genetics, DNA

Introduction

Weasels are adapted to hunt small, burrow-dwelling prey, particularly voles and lemmings (King and Powell 2007). These prey species are most common in either grassland, taiga or meadows within forested areas. Montane meadow systems are important biodiversity hotspots and act as regulators of hydrologic processes (Ratliff 1985). Small mammals, in particular voles (*Microtus* spp.), have significant impacts on meadow vegetation, depending on the phase of their population cycle (Krebs and Myers 1974). By specializing on small mammals, weasels influence the dynamics of small mammal populations, which can be dominant or keystone species in montane meadows. Reliable survey approaches are fundamental to understanding the influence of weasels in these small mammal populations within montane meadows.

Most mammalian predators occur at low densities, making it challenging to detect them and monitor their populations (Long et al. 2008). A variety of noninvasive methods (i.e., methods that do not require capture or immobilization) have been used to facilitate the detection of small and intermediate-sized predators, including tracking on natural surfaces (including snow; Franklin et al. 2019), using baited track-receptive surfaces, genetic identification via sources of DNA from hair or feces, and remotely triggered and baited cameras (Long et al. 2008). The small body size of weasels (*Mustela* spp.) results in population densities greater than most of the other members

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of Carnivora (Lindstedt et al. 1986, Carbone and Gittleman 2002), yet weasels are one of the least commonly detected species using the traditional non-invasive methods of cameras, track stations or hair snares (Crooks 2002, Zielinski et al. 2005, Sweitzer and Furnas 2016). Some of this disparity may be because many of the noninvasive survey methods in North America have been designed to maximize the detection of larger species, particularly mesocarnivores such as martens (*Martes americana* and *M. caurina*) and fishers (*Pekania pennanti*) (Zielinski and Kucera 1995). Among the reasons why, historically, weasels have been detected at rates lower than their occurrence may include: 1) track stations and cameras are not always on the ground where weasels could more easily access them, 2) dimensions of hair snares often favor the collection of hair from species of larger body size, and 3) species of weasels, particularly *M. frenata* and *M. erminea*, cannot easily be discriminated using photographs at bait stations (personal observation).

Methods to distinguish the species of weasels from either tracks, photographs, or DNA sources have been underdeveloped compared to larger species of mesocarnivores (Long et al. 2008, but see Gleeson et al. 2010). Although the designs of traditional noninvasive methods could be optimized to improve detectability of weasels, it comes at a cost to maximizing the design for other, larger species for which there may be greater conservation concern.

We adapted existing ecological knowledge about North American weasels and their prey to propose a new noninvasive method for detecting weasels in meadow systems, based on knowledge gained about the habits of weasels hunting vole (*Microtus* spp.) or lemming (*Lemmus* spp., *Dicrostonyx* spp.) in their winter runways and nests. In northern latitudes and higher elevations microtine rodents and lemmings create winter nests of thatch beneath the snow associated with their subnivean runways (Criddle 1926, Criddle 1947, Fitzgerald 1977, MacLean et al.1974, King and Powell 2007). All three species of North American weasels (*M. nivalis, M. erminea, M. frenata*) can eat a wide variety of prey (King and Powell 2007) but they hunt either vole or lemming prey—and occasionally pocket gophers (*Thomomys* spp.) and ground squirrels (*Citellus* spp.)—in their runways, tunnels or subterranean or subnivean nests. After killing their prey, weasels will often take advantage of their prey's nests by hunting from these nests for days or weeks (Polderboer et al. 1941, Polderboer 1942, Zielinski 2015). Nests that were used by a weasel during the preceding winter can be identified by examining the characteristically domed thatch nests in spring, immediately after snow melt. Those occupied by a weasel often have rodent hair plastered to the inside surface of the nest, presumably placed by a weasel (Fitzgerald 1977). More importantly, however, weasel scats are often deposited at one or more of the nest's entrances or exits (Polderboer et al. 1941, Polderboer 1942, Fitzgerald 1977).

The habit of weasels occupying the nests, and leaving evidence of their use, provides an opportunity to develop a new survey method to detect weasels. Vole nests are conspicuous after snow melt, so a search for them can be more efficient than a general search for weasel scat. The ability to distinguish weasel scats using genetic methods (Riddle et al. 2003) makes searching for small mammal nests during spring an efficient new protocol for surveying for the presence of weasels, particularly in meadow and other open-canopy ecosystems. We conducted searches for weasel scats in vole nests in a meadow system in the Sierra Nevada and used genetic methods to identify weasel species. We did not attempt to compare the method with more established methods used to detect weasels (e.g., camera, track station, hair snare) nor did we attempt to apply the method to individual identification necessary for estimating population size. Our objective was to demonstrate proof of concept of this new approach and to establish a foundation for future, more quantitative work. In addition, we wanted to confirm that specific elements of the protocol would be successful, such as confirming that DNA could be extracted from scats that may have been deposited in a wet, subnivean environment up to 6 months prior to their collection and analysis.

Methods

The study area was located in Placer County, California, in the Truckee Ranger District of the Tahoe National Forest. Specifically, we worked at a meadow complex associated with the Sagehen Experimental Forest, described in Adams et al. (2003). This location has a long history of studies of long-tailed and short-tailed weasels and martens (*Martes caurina*) (Fitzgerald 1977, Zielinski et al. 1983, Martin and Barrett 1991, Spencer et al. 1983, Moriarty et al. 2011). We used Station Meadow due to its proximity to the field station, which occurs at about 1900 m elevation. This meadow is approximately 14 ha, but most of our searches for vole nests in the spring were focused on approximately 50% of the area where grasses and forbs occurred. With a few exceptions, this area was searched in either April or May, depending on date of snow melt, in 2012, 2013, 2016 and 2017. A single search occurred in a small portion of nearby Kiln Meadow in 2012 only. Drought resulted in low snow levels which prevented searches from being conducted in 2014 and 2015. During these years most of the meadow areas had little to no snow (Figure 1). This left much of the meadow area uncovered, or with snow considered too shallow to provide a thermal refuge (MacLean et al. 1974, Pauli et al. 2013).

Forests surrounding Station Meadow were dominated by mature stands of white fir (*Abies concolor*) and lodgepole pine (*Pinus contorta*). Summer day temperatures average 24–27 °C, though temperatures at night may fall below freezing. Most of the annual precipitation comes as snow between October and May and single snowfalls may be up to 100 cm deep. Meadows typically become free of snow in either April or May depending on snowfall the previous winter. The maximum annual snow depth varied significantly within the sampling period, from lowest in 2014 and 2015, during the California drought, to highest in 2017 (Figure 1).

Voles can occur in other habitats but they largely favor open, grassland or meadow habitats (Randall 1978). The dominant species of vole in the meadows in our study area is the montane vole (*Microtus montanus)* which creates the runways

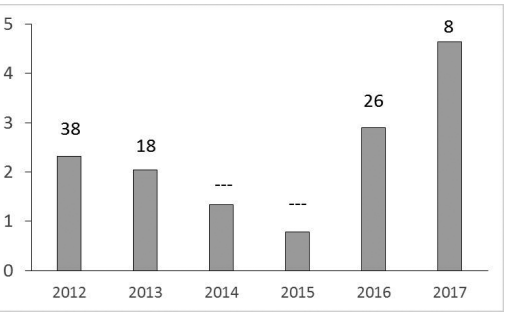

Figure 1. Maximum annual snowpack (meters) during 2012–2017. Snowpack data were provided by the Central Sierra Snow Laboratory (UC Berkeley) and were collected at Donner Summit, approximately 8 km SW of Station Meadow. At 2150 m elevation, the summit has greater snowpack than Station Meadow (on the east side of the summit at 1940 m) but the relative ranking by year would be the same. Numbers above each bar are the number of vole nests discovered each year at Station Meadow, located at the Sagehen Experimental Forest, Nevada County, California. No nest searches were conducted during 2014 and 2015 as drought during those winters caused snowpack to be so low that it was unlikely that voles were building subnivean nests.

and subnivean grassy nests that are identifiable in the spring after snowmelt (Fitzgerald 1977). Long-tailed voles (*M. longicaudus)* are uncommon, occur largely in areas with sparse grass, and do not use runways or create subnivean nests (Jenkins 1948). Populations of long-tailed (*Mustela frenata*) and short-tailed (*M. erminea*) weasels occurred in the meadow system in the mid-1970s and were assumed to still occur there.

Two people usually conducted nest searches by either traversing adjacent parallel transect lines that were approximately 10–20 m apart or by dividing a search area in half and each person would search half of the total area. The former method was applied to the largest, unbroken portion of the meadow and the latter was applied to smaller portions or outpockets of the meadow. Nests discovered were carefully examined for evidence of weasel occupancy: the presence of typically musteline scat or rodent hair plastered to the interior walls (Fitzgerald 1977). Scats were placed in small paper bags in the field and within one week were shipped to the USDA National

Genomics Center for Wildlife and Fish Conservation in Missoula, Montana for genetic analysis.

Genomic DNA was extracted from scat samples using the QIAGEN Qiamp DNA Stool Mini Kit (Qiagen, Valencia, CA) according to manufacturer's instructions. To determine species, we amplified the left domain of the control region of mitochondrial DNA (mtDNA) using primers L15926 and H16498 (Kocher et al. 1989, Shields and Kocher 1991). Reaction volumes of 30 µL contained 50–100 ng DNA, 1x reaction buffer (Life Technologies, NY), 2.5 mM MgCl2, 200 µM each dNTP, 1 µM each primer, 1 U Amplitaq Gold polymerase (Life Technologies, NY). The PCR program was 94 °C/5 min, [94 °C/1 min, 55 °C/1 min, 72 °C/1 min 30s] x 34 cycles, 72 °C/5 min. The quality and quantity of template DNA were determined by 1.6% agarose gel electrophoresis. PCR products were purified using ExoSap-IT (Affymetrix-USB Corporation, OH) according to manufacturer's instructions.

Reactions were sequenced at Eurofins Genomics (Louisville, KY) using standard Sanger sequencing protocols. DNA sequence data were viewed and aligned with Sequencher (Gene Codes Corp., MI). DNA species identification was performed using a BLAST search of reference sequences available on Genbank (National Center for Biotechnology Information). Weasel samples were genotyped with microsatellite loci used in previous mustelid studies (Mer022, Mer041, Mer082, Mer095, Mvis002, Mvis020, Mvis022, Mvis072 [Fleming et al. 1999], Mvi87 [O'Connell et al. 1996]). Sex identification was performed using an SRX/SRY analysis (DBY7Ggu; Hedmark et al. 2004) along with internal controls for DNA quality. The reaction volume (10 mL) contained 1.0 mL DNA, 1x reaction buffer (Applied Biosystems), 2.0 mM $MgCl_2$, 200mM of each dNTP, 1mM reverse primer, 1mM dye-labeled forward primer, 1.5 mg/mL BSA, and 1U Taq polymerase (Applied Biosystems). The PCR profile was 94 °C/5 min, [94 °C/1 min, 55 °C/1 min, 72 °C/30s] x 45 cycles. DNA from scat samples was amplified using the multi-tube approach (Eggert et al. 2003, McKelvey and Schwartz 2004). The resultant products were visualized on a LI-COR DNA analyzer (LI-COR Biotechnology). Data were error checked using program Dropout (McKelvey and Schwartz 2005).

Results

We spent approximately seven person hours per year (about 28 hours total over four years) searching the same 14 ha area in Station Meadow. We discovered and examined 90 winter vole nests over four springs, resulting in an average (SD) of 3.31 (1.81) nests found per person survey hour (Table 1). Sixteen nests (17.8%) contained scats that we estimated in the field were from a weasel, based on their association with the nest and their morphological characteristics. Our survey effort resulted in an average (SD) of 0.57 (0.37) putative weasel scats per person survey hour, or one weasel scat sample per two person hours of effort.

Nine of 16 samples (56.3%) were of sufficient quality DNA to obtain an identification. Two of these were identified as non-target species (one "mole" and one *Microtus* sp.) and 7 (43.7 %) were identified as weasel. Five of the seven weasel scats were attributed to *M. frenata* and two to *M. erminea*. Four of the five *M. frenata* scats were determined to be from one or more females and one from a male, and the *M. erminea* scats were attributed to one or two females.

All five of the scats identified as *M. frenata* were collected in 2013 and both of the scats identified as *M. erminea* were collected in 2016. We expended 28 person hours of effort (about 14 person hours in 2012 and 2013 combined) before we documented the presence of *M. frenata* in the meadow system. Approximately 21 person hours (seven each in 2012, 2013 and 2016) of effort occurred before we documented *M. erminea*.

Discussion

As proof of concept we demonstrated that exploiting the winter nest-building habit of voles, and the strong relationship between weasel and vole predation (MacLean et al. 1974, Fitzgerald 1977) can be a way to survey high-elevation meadows for the occurrence of long-tailed or short-tailed weasels. This unique survey method has the advantage of focusing scat searches in locations where there was a high likelihood of

TABLE 1. Number of winter vole nests, number of nests with putative weasel scat, number of nests where *Mustela* spp. were confirmed and number of scats with poor DNA or were identified via genetic methods as another taxon (one each of *Microtus* sp. and "mole") at Station Meadow at Sagehen Experimental Forest, Placer County, California. Sampling occurred during four springs (April or May depending on rate of snow melt) over a 6-year period. Drought conditions in 2014 and 2015 precluded sampling.

Spring of Year	Number of winter vole nests found	Number (%) of nests with putative weasel scat	Number (%) of nests with confirmed weasel scat	Number of scats that could not be identified as *Mustela* spp.
2012	38	1 (2.6)	0 (0)	0
2013	18	7 (38.9)	5 (27.8)	4
2016	26	5 (19.2)	2 (7.7)	3
2017	8	3 (37.5)	0 (0)	3
Total	90	16 (17.8)	7 (7.8)	10

finding weasels (i.e., in association with winter vole nests). The method relies on the presence of winter vole nests in meadows so is not applicable in other habitats (e.g., slash plies; Lisgo et al. 2002, Jedrzejewski et al. 1995). In fact, we deliberately chose a study site where the likelihood of finding nests and weasels was high. The method would also be less effective in drought years where the winter snowpack is not deep enough to cover and insulate subnivean nests. This is one of the shortcomings compared to other survey methods, like baited track stations/cameras, scat detection dogs (Long et al. 2008) or weasel-specific hair snaring devices (e.g., Gleeson et al. 2010).

Vole-assisted scat surveys, however, have advantages over baited stations (track plate, camera or hair snare) which require much more effort and costly equipment, to establish and check. The method would appear to be more efficient and costly than invasive methods that require capture, which necessitate the purchase of a large number of traps that are checked once or twice daily. Invasive methods that necessitate the capture of weasels in traps also entail risks of injury to weasel and handler. Certainly scat detection dogs (MacKay et al. 2008, Long et al. 2007) could be more efficient than the approach described herein, because dogs can be used to search all areas of each meadow (not exclusively in vole nests) and can be applied in other habitats that weasels may use, as well as seasons other than winter. It can be expensive, however, to train service dogs to find *Mustela* spp. scats and to deploy them in the field especially because weasel scats are so small. Our approach may be as efficient as scat transects with scat dogs because the relative ease of visually finding vole nests allows us to target scat collection to the few locations where scat searches would be most productive. Finally, like scat detection dogs, we are collecting evidence of where the target species chose to occur, instead of attracting the species to a detection location from an unknown distance. Therefore, these data could be used to develop species distribution or habitat suitability models, but generally not for population estimation.

Our objective here was not to conduct a quantitative comparison to evaluate the costs and benefits of different survey methods. We only wished to demonstrate proof of concept, not to compare our method with established methods to detect uncommon species or to estimate their occupancy or abundance. A number of such studies have been conducted comparing various methods of detection for other species of mustelids (e.g., Long et al. 2007, Moriarty et al. 2018, Croose et al. 2019). Although methods varied, these studies suggest that scent detection via scat detection dog was generally the most cost-effective detection method compared with methods that use bait to attract the target species to a camera station, tracking surface or hair snare. Insofar as our method also relies on finding scats for genetic identification, we suspect that if it were to be compared to other detection methods it may also be more cost effective than traditional methods that rely

on attracting subjects to a bait. However, using multiple detection methods simultaneously seems to generate the best estimates of abundance in other mustelid species (e.g., Moriarty et al. 2018, Croose et al 2019).

We sought to test the approach in a location where we were reasonably confident that at least one species of weasel was present (Fitzgerald 1977). This was necessary to evaluate all elements of our protocol, from searching for scats to genetic confirmation. Consequently, the method was not evaluated at a study site where the occurrence of weasels was unlikely or unknown, a bias that may have affected the detection characteristics of our small sample (e.g., time until first detection, success of amplifying DNA in scat samples that had been exposed to freeze-thaw conditions).

There are reasons that the efficiencies of our method will not be achieved. There will be some years when vole nests are rare and, thus, fewer weasel scats will be collected and it may take > 1 year (i.e., ≥ 2 spring surveys) to verify the presence of a weasel species. We verified the presence of *M. frenata* in our second year of surveys, but it was not until our third spring survey that we verified *M. erminea*. This was a long time, but we used only about 7 person hours of search effort per year, resulting in a total of 14 and 21 total person hours to detect *M. frenata* and *M. erminea*, respectively. This amounts to only 1–3 field days, depending on whether one or two field personnel are involved. Moreover, if vole winter nests are abundant, searching a meadow for scats can effectively sample the use of the meadow by weasels over the entire duration of the preceding winter. There may be several months during the winter over which scats can be deposited prior to their collection in the spring. This advantage should not be discounted. Another advantage of our survey method is that it focuses the search in high-probability areas (i.e., winter nests) rather than less efficient random scat transect surveys.

A total of 17.8% of the 90 nests we found had evidence of weasel occupation. This compares favorably with earlier research conducted on vole-weasel ecology in the same meadow system (Fitzgerald 1977). Fitzgerald (1977) examined a greater number of nests (n = 4,016) but after 4 years of intensive field work, he found 16.8 nests per year with evidence of weasel occupation. MacLean et al. (1974) found as many as 35% of winter lemming nests suggested predation by least weasels (*M. nivalis*).

Although we were pleased with the relatively high proportion of nests that had weasel scats, we were disappointed with the number of scats with DNA of such poor quality that species could not be determined. Seven of 16 (43.7%) of the samples that we assumed were weasel scat when they were collected in the field had poor-quality DNA that prevented confirmation of species. Success for obtaining DNA from scats is highly variable (Schwartz and Monfort 2008). The relatively high percent of samples with inadequate DNA quality for genetic analysis may be because the scats we collected were deposited ≥ 6 months prior, during a period of temperature and moisture fluctuations in the surface and subsurface environment; conditions known to increase the probability of failure (Brinkman et al. 2010). New adaptations of qPCR assays for use with non-invasive genetic samples collected from carnivores have been shown to improve the success rate of species identifications from these types of samples (Franklin et al. 2019). Although these assays have not yet been developed for weasels, they have been developed for confamilial species including fisher, marten, and wolverine. We anticipate they will be available for weasels soon.

Our study was a proof of concept effort, to which we conclude that searches of vole nests for scat that can be genetically verified as weasel should have a place in the biologist's toolkit. This method certainly will not replace previous methods based on baiting a subject to a track or camera station or that use trained scat detector dogs. It may, however, be useful when weasels are the only target species and when neither funding nor time is available to mount a larger, multiple species carnivore survey. Furthermore, although the method requires the participation of a technically trained geneticist, it is amenable to participation of citizen scientists who can easily be trained to identify winter vole nests and weasel

scats therein. Importantly, the method described here is ineffective without snow deep enough to insulate voles' above-ground nests. Due to climate change, less snow is predicted to fall in the Sierra Nevada in the future (Dettinger et al. 2018). This may jeopardize the predator-prey system, and the nesting habits of the voles, upon which our survey method depends.

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