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Influence of habitat type on the decay and disappearance of elk *Cervus canadensis* pellets in boreal forest of northwestern Canada

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Fecal pellet counts are often used to assess trends in ungulate population size and habitat use. However, various factors may influence the physical decay and disappearance of pellets, where disappearance may be a result of physical decay and other factors (e.g. trampling, scattering and concealment by vegetation). Knowing pellet decay and disappearance rates in different habitats is a prerequisite to acquiring reliable information from pellet counts. We examined elk *Cervus canadensis* pellet decay and disappearance of individual pellets and pellet groups in six habitats in the boreal forest of northwestern Canada. We monitored 120 pellet groups deposited in May 2008 at 4, 12, 16 and 28 month intervals (i.e. the end of each of three plant growing seasons) to assess differences in physical decay and disappearance. Pellet decay and disappearance varied among habitats. In moist habitats, pellets showed little sign of decay by the end of our study, likely due to a short plant growing season. In drier, open habitat types, pellet decay was more rapid, likely due to exposure to sun and wind. By the end of our study, the percent of pellets remaining varied from a 14–82% among the sampled habitats. Pellets in moist forest habitats had the lowest decay rates but the highest disappearance rates, whereas those in dry, grassland sites had the highest decay, but the lowest disappearance rates. Our study further demonstrates that ungulate pellet decay and disappearance may differ substantially among habitats, which has important implications for the design of ungulate monitoring programs that utilize pellet counts. We conclude by recommending that fecal accumulation rate (FAR) methods are likely more appropriate in our study area than fecal standing crop (FSC) methods for estimating elk density, because FAR methods are less prone to biases associated with differential pellet decay and disappearance among habitats.

Fecal pellet-group counts have long been a means to achieve a variety of ungulate research and monitoring objectives (Neff 1968, Alves et al. 2013). They have been shown to predict population trends reasonably well, and may be a primary or complimentary method of assessing population status (Bailey and Putman 1981, Forsyth et al. 2007, Acevedo et al. 2010). They may also be used to assess species' distribution and habitat use (Härkönen and Heikkilä 1999, Skarin 2007, Månsson et al. 2011). Compared to other ungulate census and monitoring methods, pellet-group counts may be advantageous because they are relatively cost-effective (Campbell et al. 2004, Rönnegård et al. 2008), and may be particularly useful in habitats where obstruction by vegetation may challenge the ability to use other survey methods (Jordan et al. 1993, Tsaparis et al. 2009).

Approaches to estimate pellet-group density include the fecal accumulation rate (FAR, also known as the clearance plot method), fecal standing crop (FSC), and, more recently, distance-based fecal standing crop strip (FSST) and line transect (FSLT) methods (Marques et al. 2001, Campbell et al. 2004, Alves et al. 2012). Methods based on standing crop measures (FSC, FSST and FSLT) calculate the density of pellet-groups and relate this to their decay and disappearance rates, which is generally obtained in separate trials (Hemami and Dolman 2005). FAR techniques, in contrast, measure the accumulation of pellet-groups over time. FAR techniques do not require the application of pellet decay and disappearance rates, nor distinguishing between new and old pellets, to estimate animal density because plots are cleared prior to the study period; however, knowledge of the decay and disappearance rate is required to set pellet accumulation intervals. Thus, for research and monitoring programs using either FSC or FAR methods it is imperative to take into account possible sources of variation in pellet decay and disappearance rates, otherwise results may be biased (Neff 1968, Marques et al. 2001, Campbell et al. 2004). Unfortunately, many FSC studies assume that pellets decay and disappear at a constant rate, which may lead to incorrect parameter estimates (Campbell et al. 2004, Hemami and Dolman 2004).

Pellet decay is the physical decomposition of pellets from aging and exposure to the elements. Pellet disappearance is the apparent loss of individual pellets or pellet groups irrespective of the mechanism by which the process occurred (Marques et al. 2001). Pellets may disappear because they

physically decay and decompose, become concealed by vegetation, or eaten, buried, trampled or scattered by animals. The disappearance of pellets may vary spatially or temporally, in relation to climate, season or habitat type (Wigley and Johnson 1981, Lehmkuhl et al. 1994, Laing et al. 2003, Persson 2003, Hemami and Dolman 2005).

Estimating pellet disappearance rates has been a relatively active area of research; but variability in results confounds the application of general observations to local conditions. For example, the influence of habitat type on the disappearance of ungulate pellets is somewhat conflicting. Most studies report that pellet disappearance differ significantly among habitat types (Persson 2003, Hemami and Dolman 2005, Skarin 2008, Tsaparis et al. 2009), however several others report that the effect of habitat type is limited (Lehmkuhl et al. 1994, Massei et al. 1998, Theuerkauf et al. 2008). Greater clarity is needed to elucidate if ungulate pellets decay and disappear at different rates in different habitat types.

Our aim was to estimate the influence of habitat type on the physical decay and disappearance of elk *Cervus canadensis* pellets in semi-arid boreal forest of northwestern Canada. No studies have examined habitat influences on the decay and disappearance of ungulate pellets in the boreal forest of northwestern North America. Several studies have examined ungulate pellet decay in coastal environments in northwestern North America (Harestad and Bunnell 1987, Lehmkuhl et al. 1994); however, those ecological regions have a much more mild and wet climate than interior boreal forests. As such, results from those studies, although geographically proximate, are likely not applicable to boreal forest. Estimating ungulate population trends without consideration to temporal or habitat-based differences in pellet decay and disappearance could lead to unreliable information from which to manage populations.

Locally, elk populations occur at low densities in a remote, forested region that is challenging to survey using standardized aerial methods (Skalski et al. 2005, McIntosh et al. 2009). As such, data from pellets may provide a cost-effective means to monitor populations, through either pellet-group counts (Rowland et al. 1984, Edge and Marcum 1989), or the use of pellets to obtain DNA mark–recapture estimates (Harris et al. 2010, Poole et al. 2011). In our study area, elk use a variety of habitats (Strong et al. 2013) and we were interested in the influence that habitat type may have on pellet decay and disappearance, which may affect recommendations for developing protocols for using pellets to monitor populations. More broadly, elk provide a good model for examining the influence of habitat on the decay and disappearance of ungulate pellets over time, because elk pellets are morphologically and compositionally similar to those of other Holarctic cervids, such as moose *Alces* spp., deer – e.g. *Odocoileus* spp., *Dama dama*, *Capreolus capreolus*, or caribou *Rangifer tarandus*, allowing for results to be applicable to a broader suite of ungulates.

In our study, we expected overall to observe low rates of physical decay of pellets due to the cold, dry climate (Skarin 2008). Similar to other studies (Hemami and Dolman 2005, Tsaparis et al. 2009), our study was conducted in an area of relatively high habitat heterogeneity and we expected that pellets would disappear quicker in some habitats than others, depending on the relative degree of moisture. Specifically, we believed that pellets would decay and disappear more rapidly in moist habitats (e.g. closed canopy conifer forests) than in drier habitats (e.g. grasslands and deciduous forests) because moist habitats would promote rapid decomposition and concealment by more vigorous vegetation growth.

Material and methods

Study area

Our study was conducted within a broad valley bordering the Takhini River in southwestern Yukon, Canada, approximately 50 km west of the city of Whitehorse (60°71′61″N, 135°05′50″W). The valley is within the rain shadow of the Coast Mountains and, accordingly, the climate is semi-arid (Yukon Ecoregions Working Group 2004). Precipitation ranges from 200–325 mm, with up to 50% falling as snow, with snow cover persisting from mid-October to mid-April. The mean annual temperature is –5°C (Yukon Ecoregions Working Group 2004). A stand-devastating fire burned most of the valley in 1958. Prior to fire, the valley was predominantly covered by white spruce *Picea glauca* forest (Keenan and Cwynar 1992). Post-fire regeneration has been exceedingly poor. Vegetation in much of the valley primarily consists of trembling aspen *Populus tremuloides* stands and grassland, interspersed by small stands of lodgepole pine *Pinus contorta* and regenerating white spruce. The current vegetation of the burn resembles aspen parkland, a dry vegetation zone that forms the transition between boreal forest and grassland in the Northern Great Plains (Hogg and Wein 2005, Strong et al. 2013). Mature stands of white spruce persist in areas unaffected by fire.

The elk population in the study area was estimated at about 200 animals, and used a range of approximately 1144 km^2, with most locations of 15 radio-collared elk being found within a 95 km^2 'core use' area (Strong et al. 2013). Strong et al. (2013) reported that most radio-telemetry locations of elk in the core use area were found in parkland-type habitats (e.g. open aspen forests, grassy meadows and south-facing slopes), while use of closed-canopy forests occurred at a more limited extent. Winter diet of elk in the study area was reported by Jung et al. (2015) and was primarily comprised of grasses (37.4%) and shrubs (i.e. sage *Artemisia frigida*; 26.1%), with more minor components of sedges (15.7%), conifer (14.4%), forbs (5.8%), and mosses and lichens (0.6%). Elk in our study area also occasionally depredated nearby agricultural fields during winter, accessing hay as supplemental forage.

Pellet decay and disappearance

We experimentally established pellet sample plots among six distinct habitat types used by elk in our study area (Strong et al. 2013), including: 1) wet conifer, which consisted of poorly-drained white spruce stands where the forest floor was largely a mat of moss, 2) dry conifer, which were upland stands of mature lodgepole pine or white spruce with a sparse understory, 3) dense aspen stands, where stem density and canopy closure was high, 4) open aspen stands, which represented an aspen parkland type, with low stem densities and canopy closure, 5) dry grass meadow on level slopes,

and 6) dry grass slope, which were grasslands on steep south-facing slopes, at low elevations. These six habitat types were chosen to represent a range of environmental conditions which may be encountered within low elevation habitats in the boreal forest of northwestern Canada, and may affect the physical decay and disappearance of ungulate pellets. Within each of these six habitats we established five replicated pellet sampling plots in late spring (May 2008). Pellet sample plots were distributed a minimum of 150 m from each other. At each pellet sampling plot we placed an elk pellet-group, 5 m from the plot centre, in each of the four cardinal directions, to increase replication of our sampling units (pellet-groups). Therefore, for each habitat type, we deposited 20 elk pellet-groups, distributed among five replicates of each pellet sample plot. Our design called for the establishment of a total of 120 pellet-groups.

Pellets used in our experiments were freshly collected from elk temporarily held in captivity within the study area during March 2008, and would have represented a late-winter diet. Temporarily captive elk were held in situ and fed largely on natural forage, but were also provided with hay as supplemental feed. Pellets were kept frozen (–20°C) for 43–49 days before being deployed at our pellet sample plots in May 2008. Similar to other studies (Prugh and Krebs 2004, Hibert et al. 2010), we arbitrarily used a fix number of 30 pellets for each pellet-group, in order to allow for a standardized comparison among our experimental plots.

Pellet sample plots were revisited in September 2008, May 2009, September 2009, and September 2010, representing 4, 12, 16 and 28 months after deposition, respectively. Our revisit schedule allowed for examination of pellet decay and disappearance after the initial growing season after deposition, one year after deposition (including over the first winter), and for annual persistence after each growing season thereafter. However, we were unable to calculate pellet decay and disappearance rates at finer temporal scales (e.g. weekly or monthly), given our experimental design. No observations were made during winter due to snow cover. At each visit we counted and digitally photographed the number of visible pellets, in doing so we did not disturb vegetation or debris on and around the pellets, similar to the method used by Persson (2003) and Skarin (2008). The physical decay of pellets was assessed using a four-point scale, similar to the decay scale used by Hibert et al. (2010), with pellets scoring 4 having the greatest signs of aging and decomposition (Table 1). Pellet decay was classified by viewing the photographs of the pellet groups on a computer, and were all done by the same person to reduce observer bias.

Table 1. Criteria used for classifying the decay of elk *Cervus canadensis* pellets. Modified from Hibert et al. (2010).

	Criteria	
Decay class	Pellet colour shade	Pellet cracking
1	dark and wet, with a glossy patina	smooth surface
2	dark but dry on surface, without patina	light cracking thinner than a hair
3	dull	wider cracks (< 1 mm wide)
4	grey	deep cracks (≥ 1 mm wide)

Pellet disappearance rates may be measured a variety of different ways. For example, pellet-groups may be assigned a physical intactness score (Fairbanks 1979, Lehmkuhl et al. 1994), or the number of visible pellets (Persson 2003, Skarin 2008) or pellet-groups (Laing et al. 2003, Massei et al. 1998) can be counted. We used the last two metrics to assess pellet disappearance. We used the percent of the 30 pellets remaining visible in each pellet-group, during each revisit of our plots, as a measure of the number of individual pellets visible. To quantify the number of pellet-groups remaining visible we used the percent of the 20 pellet-groups that had a minimum number of pellets visible in each habitat type, during each plot revisit, as our metric. For this metric we established a minimum number of pellets in a pellet group, following Massei et al. (1998) and Hemami and Dolman (2005). Similar to Månsson et al. (2011), we considered pellet-groups that contained < 10 pellets to have functionally disappeared. We based this threshold on our observation that most pellet-groups containing < 10 pellets often were scattered and did not appear as a cohesive pellet-group, and they usually were difficult to detect in the field and in photographs. Counts of individual pellets remaining provided a measure of pellet disappearance for each pellet group in each replicate, while the percent of pellet groups remaining (based on a lower threshold of ≥ 10 pellets) provided a comparative measure of pellet group disappearance between habitats.

Analysis

Data were visually inspected for normality with box plots. We tested for differences in the physical decay of pellets within each sampling period using likelihood ratio chi-square tests. We used a repeated measures analysis of variance (RM-ANOVA) to assess the disappearance of pellets in relation to time and habitat type, and their interaction. We nested replicates within each sampling plot ($n = 5$ per habitat type) within our model to account for the sub-plot structure of our experimental design. Our analytical approach was similar to that of Prugh and Krebs (2004), who studied snowshoe hare *Lepus americanus* pellets with similar sampling intervals. SYSTAT (ver. 13.0) was used for statistical testing, and we used an α level of ≤ 0.05 to denote statistical significance.

Results

Pellet decay

The decay class of pellets differed significantly among habitat types for all revisits of our plots ($\chi^2_{20} \geq 38.420$; $p \geq 0.048$; Table 2). In wet conifer and dense aspen stands, pellets remained in relatively pristine condition throughout the 28-month study period (three plant growing seasons), showing little sign of aging or decomposition (decay classes 1 or 2). In sharp contrast, pellets became well-aged and began to decompose in grass meadow and grass slope habitats by the end of our study (decay class 3 or 4, Table 2). Pellets in open aspen and dry conifer habitats were intermediate, as they were beginning to age but showed no signs of decomposition (decay classes 2 or 3). Interestingly, while pellets progressively decayed over time, most pellet decay occurred in after the

Table 2. Mean (± SE) decay class of elk *Cervus canadensis* fecal pellets in six different habitat types, 0, 4, 12, 16 and 28 months after deposition, in southwestern Yukon, Canada. Decay classes vary from 1 to 4, with 4 having the greatest level of decay. Definitions of decay classes are in Table 1.

	Habitat type						Likelihood ratio test	
Months since deposition	Dense aspen	Open aspen	Wet conifer	Dry conifer	Grass meadow	Grass slope	χ^2	p
4 (Sept-2008)	1.3 ± 0.2	2.4 ± 0.3	1.1 ± 0.2	2.0 ± 0.1	3.3 ± 0.3	2.6 ± 0.2	38.420	0.008
12 (May-2009)	1.6 ± 0.3	2.6 ± 0.6	1.1 ± 0.1	2.1 ± 0.1	3.1 ± 0.3	2.7 ± 0.3	50.483	0.011
16 (Sept-2009)	1.8 ± 0.3	2.5 ± 0.5	1.2 ± 0.1	1.9 ± 0.2	3.3 ± 0.4	3.3 ± 0.3	43.982	0.048
28 (Sept-2010)	1.7 ± 0.2	2.5 ± 0.5	1.1 ± 0.1	2.2 ± 0.2	3.7 ± 0.3	3.9 ± 0.1	66.651	< 0.001

first growing season (the first four months since deposition). Decay class of pellets was not statistically different in the survey periods (i.e. 4–28 months since deposition, Table 2) in any of the habitat types ($\chi^2_{12} \geq 10.850$; $p \geq 0.195$).

Pellet disappearance

As can be expected, individual pellets disappeared over time ($F_4 = 78.935$, $p < 0.001$). The largest rate of pellet disappearance (up to 69%) was recorded after the first plant growing season (four months after deposition; Fig. 1). Little change in disappearance rates occurred between 4 and 12 months after deposition, as this was during the winter. The following pellet station checks (16 and 28 months after deposition) showed moderate decreases in pellet disappearance, with up to 26% and 24%, after the second and third plant growing seasons, respectively (Fig. 1). A similar pattern was seen when we considered the percent of pellet-groups that disappeared during the course of the study (Fig. 1).

The pellet disappearance rate differed among habitat types ($F_5 = 8.824$, $p < 0.001$). Overall, the greatest pellet disappearance rates were in dense aspen and wet conifer habitats, and the least in the two grassland (grass meadow, grass slope) habitats (Fig. 1). At the end of three plant growing seasons, the mean percentage of pellets that did not disappear was 14.0 ± 5.4% and 16.7 ± 6.1%, in dense aspen and wet conifer habitats, respectively. In contrast, > 75% of the pellets in the grass slope and grass meadow habitats remained 28 months after deposition (Fig. 1). When we considered the functional disappearance of pellet-groups, the pattern was similar (Fig. 1), except pellet-groups in grass slope habitats disappeared more than when considering that for individual pellets. Between 10% and 85% of the pellet-groups remained visible over the course of the study, with those in dry conifer and wet conifer having the least and greatest pellet disappearance rates, respectively (Fig. 1).

We found a significant interaction between time and habitat type in pellet disappearance ($F_{20} = 5.555$; $p < 0.001$). Substantial initial increases in pellet disappearance occurred in aspen-dominated habitats at the four-month interval (after the first plant growing season), whereas the initial disappearance of pellets and pellet-groups occurred more gradually in the other habitat types (Fig. 1). In the two aspen-dominated habitat types the number of visible pellets increased between these months, likely as a result of leaves settling and pellets that were concealed at four months in the fall, once again becoming visible in the spring, 12 months after deposition.

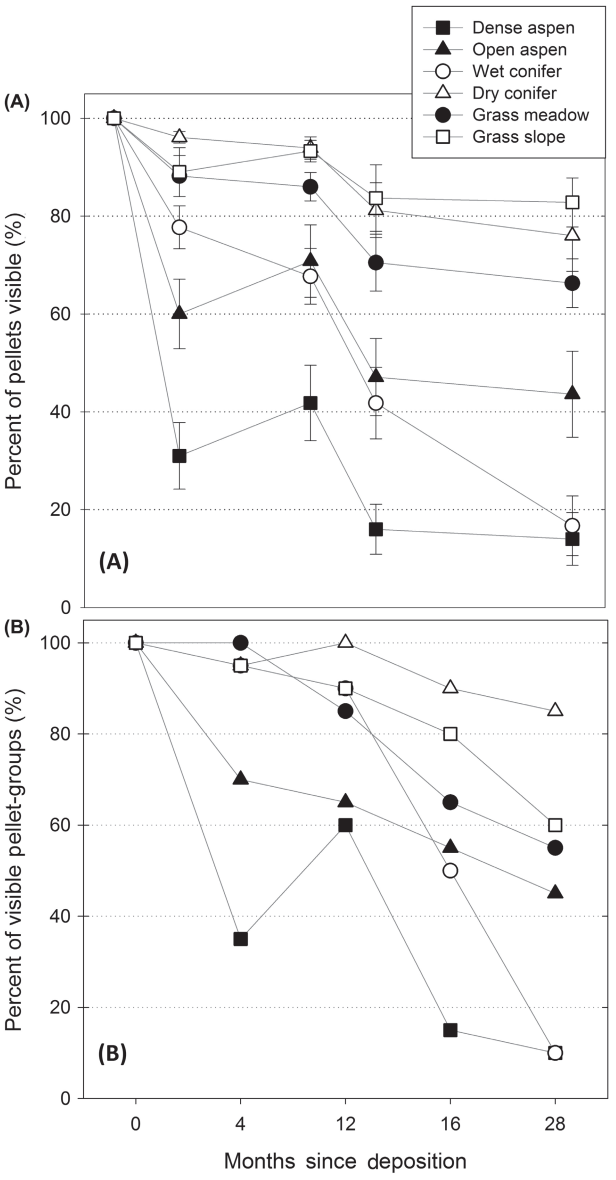

Figure 1. Mean (± SE) percent of individual elk *Cervus canadensis* fecal pellets (A) and percent of pellet-groups (B) remaining visible in six different habitat types, 0, 4, 12, 16 and 28 months after deposition, in southwestern Yukon, Canada. Twenty pellet groups were deposited in each of the six habitat types. Pellet groups were considered to have functionally disappeared when < 10 pellets remained. 0, 4, 12, 16 and 28 month plot visits corresponded to May 2008, September 2008, May 2009, September 2009 and September 2010, respectively.

In wet conifer habitat, we observed a rapid increase in the disappearance of pellet and pellet-groups at the 16- and 28-month intervals (i.e. after the second and third plant growing seasons; Fig. 1).

Pellet disappearance was the greatest in aspen-dominated habitat, where dead, fallen leaves effectively covered pellets each fall. In wet conifer habitat, pellet disappearance was largely attributable to mosses growing over the pellets and concealing them. In dry conifer habitats pellets were often concealed by the growth of forbs. In grass-dominated habitats, physical decay and trampling and scattering by elk, semi-feral horses *Equus ferus caballus* and arctic ground squirrels *Urocitellus parryii* contributed to the disappearance of pellets.

Discussion

Our central finding that ungulate pellets may persist and remain visible for long periods of time is consistent with other studies conducted in regions characterized by seasonally persistent snow cover and freezing temperatures (Persson 2003, Theuerkauf et al. 2008). In high-latitude habitats in Sweden, for example, where the plant growing season is short, ungulate pellet-groups may persist and remain visible for several years (Persson 2003, Skarin 2008). Similarly, Prugh and Krebs (2004) reported that the median time snowshoe hare pellets remained visible in the environment in interior Alaska was six years. Many of our pellets did not disappear by the end of three plant growing seasons. Other studies (Massei et al. 1998, Hibert et al. 2010) showed how the physical decay of ungulate pellets in semi-arid regions may be slow, and they may persist for several years. Based on slow decay and disappearance rates of elk pellets in some habitats in our study area, we suspect that they would persist for several years beyond the conclusion of our 28-month study, similar to that reported by Prugh and Krebs (2004). Similar studies in regions with a more temperate climate and less seasonal extremes in temperature have also reported ungulate pellets persisting for several years (Massei et al. 1998, Theuerkauf et al. 2008, Hibert et al. 2010).

More importantly, however, pellets decayed at significantly different rates among habitat types, which are consistent with findings in other regions (Harestad and Bunnell 1987, Lehmkuhl et al. 1994, Massei et al. 1998, Skarin 2008). In more southern, moist coastal habitats, pellet decay is relatively rapid, with those in the wettest habitats completely decaying within a year (Wigley and Johnson 1981, Harestad and Bunnell 1987, Lehmkuhl et al. 1994). In contrast, we observed that pellets in the habitats that apparently had the greatest moisture (i.e. dense aspen and wet conifer) had decayed the least. Many of the pellet groups in these habitats were in excellent condition (i.e. decay class 1 or 2) after three plant growing seasons (28 months after deposition), and they looked like they were relatively newly deposited. In contrast, elk pellets in open habitats were in an advanced decay class after the first plant growing season (four months after deposition). Working in interior boreal forest of Alaska, Prugh and Krebs (2004) also reported that aging snowshoe hare pellets as 'new' versus 'old' based on physical appearance was inaccurate.

Factors responsible for pellet decay in our study were unknown; however we can surmise what the likely causes of decay were in each of the habitats. For relatively wet habitats in our study area, the moisture and protection from the sun afforded by being covered by aspen leaves or moss likely reduced desiccation, and in combination with the brief plant growing season, substantially reduced the rate of organic decomposition. Persson (2003) came to a similar conclusion on the likely mechanism for moose pellets not decaying rapidly in moist, high-latitude boreal forest in Europe. This is in contrast with studies done at lower latitudes, which consistently report more rapid decay of ungulate pellets in moist habitats (Harestad and Bunnell 1987, Lehmkuhl et al. 1994). Our wettest site (closed canopy spruce forest) had a forest-floor covered mostly by mosses; however, these sites were likely not as wet as some of the wet sites sampled in other studies, which may explain the discrepancy between our results and those from similar studies that found pellet decay the highest at the wettest sites (Harestad and Bunnell 1987, Skarin 2008).

In our study, pellets in open habitats (e.g. non-forested habitats) were in much more advanced stages of decomposition (i.e. decay classes 3 and 4) by the end of our study. Several factors may contribute to the increased decay of pellets in open habitats. Desiccation from solar exposure likely was the primary reason for pellets decaying relatively quickly in open habitats, as pellets in these habitats were more exposed to the elements (i.e. sun, wind and rain). Tasparis et al. (2009) similarly reported physical decay being the highest in open habitats, compared to forests, in the arid Mediterranean, and attributed this to solar exposure. Lehmkuhl et al. (1994) suggested that pellets in open habitats may also experience more freeze-thaw cycles than those in more sheltered habitats, and that this may contribute to faster decay rates. In addition, pellets in open areas may be more easily found by some animals that may break pellets apart while looking for insects or seeds within them (Hendricks and Hendricks 2001). Elk in our study area, along with semi-feral horses and arctic ground squirrels, preferred open habitats (Strong et al. 2013) and sometimes occupied them in relatively high densities, contributing to the physical decay of pellets through trampling. Finally, Hemami and Dolman (2005) reported a positive correlation between rainfall and pellet disappearance, and suggested that pellets in open areas were susceptible to the mechanical effect of rain eroding pellets. Our study, along with that of other recent studies (Hemami and Dolman 2005, Tasparis et al. 2009), demonstrate that ungulate pellets decay more readily in open habitats than forested habitats, likely due to exposure to the elements.

Habitat had a large impact on the disappearance of individual pellets and pellet-groups. We observed high variability in the percentage of pellet-groups that functionally disappeared among our plots, ranging from 15% to 90% disappearance in dry conifer and dense aspen habitats, respectively. While we found that pellets decayed the least in moist habitats (wet conifer and dense aspen), the disappearance of individual pellets and pellet-groups was among the greatest in those habitats, with 90% of the pellet groups functionally disappearing in those habitats. Our finding that pellet disappearance was greatest in wet habitats is consistent with similar studies (Harestad and Bunnell 1987, Persson 2003, Jenkins and Manly 2008). Moisture is an important factor in pellet disappearance, with pellets in moist environments generally

disappearing faster than those in drier environments (Wigley and Johnson 1981, Harestad and Bunnell 1987, Massei et al. 1998, Plumptre and Harris 1995). However, in most studies disappearance was related to physical decay. In our study, disappearance of pellets and pellet-groups in wet conifer and dense aspen (our wettest habitats) was mostly attributable to concealment by vegetation (moss) and fallen leaves. Other studies have also found that pellets generally disappear faster in wetter or more vegetated habitats. For example, the amount of leaf litter may affect pellet disappearance by visual concealment (Persson 2003, Skarin 2008) and by trapping moisture, which promotes invertebrate activity and organic decomposition (Fairbanks 1979, Harestad and Bunnell 1987, Lehmkuhl et al. 1994).

While the disappearance rate of individual pellets and pellet-groups in wet conifer and dense aspen was similar at the end of our study, we observed a marked difference in how quickly pellets disappeared in these habitats, with those in dense aspen rapidly disappearing after the first plant growing season (four months since deposition), and those in wet conifer disappearing at a much slower rate over three plant growing seasons. The observed difference was likely due to the different mechanisms responsible for pellet disappearance in the two habitats. Most of the pellet disappearance in dense aspen habitat occurred at the end of the first plant growing season (i.e. within the first four months) and was attributable to fallen leaves covering pellets. In contrast, pellet disappearance was low in wet conifer habitats until 12 months after deposition, at which time most pellets began to disappear, with large decreases between subsequent plant growing seasons (i.e. between 12–16 and 16–28 month revisits). This is likely because it took >12 months before the combined actions of pellets settling into the ground vegetation and that vegetation growing over and concealing pellets were of a large enough effect for pellets to disappear in wet conifer habitats. Similarly, disappearance of pellets in open aspen habitats occurred most rapidly in the first four months, after the first leaf fall after pellet deposition. These observations demonstrate the rapid impact that leaf fall may have on pellet disappearance.

In open aspen and the two grassland habitats, 40%–55% of the pellet-groups functionally disappeared. This we attribute largely to trampling and scattering by animals (e.g. elk, horses, ground squirrels, birds, insects), as these habitats were frequented by these species. Advanced desiccation and decay of pellets in these habitats likely further facilitated them becoming undistinguishable from fine woody debris and other matter on the ground by trampling. Only 15% of the pellet groups functionally disappeared in dry conifer stands. Reasons for the low rate of pellet-group disappearance in this habitat may be a result of a lack of understory vegetation to conceal pellets and relatively low use of these habitats by ungulates and other wildlife that might otherwise trample, break apart or scatter pellets. The difference in pellet disappearance among habitat types is consistent with other studies that found ungulate pellets persisting longer in dry sites than wet areas (Lehmkuhl et al.1994, Jenkins and Manly 2008); however, further study is needed to identify the mechanisms responsible for pellet disappearance in the habitats we studied.

Our study had several potential limitations. Specifically, our use of frozen pellets from elk held temporarily captive in situ may not have accurately portrayed the decay and disappearance rate of unfrozen pellets from elk with a completely natural diet. Diet composition and the influence of freezing of pellets may have had an impact on the decomposition of pellets. While this is potentially a confounding factor, we do not believe that it poses an issue with the interpretation of our results because all pellets used in our study came from the same source and were treated similarly before deployment in our experimental plots. Moreover, elk in this population annually have access to hay as forage, through depredation of agricultural fields in winter. So, pellets obtained from free-ranging elk likely would have also been from individuals that also fed on hay to an unknown degree. Further, pellets in our study area would have frozen during the spring and over winter in our study area, so the effect of us keeping pellets frozen prior to deposition would have likely been trivial. Koike et al. (2013) demonstrated that pellets deposited during winter by congeneric sika deer *Cervus nippon* did not begin to decay or disappear until the following spring. Thus, contrasts in pellet decay and disappearance between habitat types and over time, in our study area, remain valid despite these considerations. Regardless, an assessment of decay and decomposition between pellets from elk with diets with and without supplement forage, and those frozen and not frozen, would be helpful in understanding the impact of these differences.

In conclusion, the wide range in pellet decay and disappearance among habitat types after the first plant growing season (four months since deposition) points to several considerations when using pellets for monitoring populations of elk (and other ungulates) in our study area. Most notably, because aging of pellets is unreliable across a range of habitat types found in our study area, even over short time periods (four months), caution is required when utilizing field protocols that require subjectively aging pellets. FSC methods might potentially be applicable if constrained to habitat types with similar disappearance rates (e.g. grassy meadows and grassy slopes); but, further studies are needed to determine specific pellet decay and disappearance rates over shorter time intervals (e.g. weekly or monthly during the plant growing season) than provided by our study. FAR methods are likely more suitable in boreal ecosystems with a variety of open and closed canopy, and mesic and xeric, habitats, as they do not require correcting for differential decay or disappearance rates among habitat types, as required for FSC methods. FAR methods, however, are generally less favored because they are often perceived as being more labor-intensive and less cost-effective, even though they may produce more precise density estimates than FSC methods (Campbell et al. 2004). Our study was not designed to test whether FSC or FAR methods are most appropriate for elk in our study area; however, our results suggest that FAR may result in less bias for this particular application. Until such time that a more fulsome assessment is made of pellet decay rates in our study area, we recommend FAR-based methods be used there, in order to avoid biases associated with differential pellet decay and disappearance rates between habitats. Plots should be cleared in the spring and checked before leaves fall off the tress to avoid concealment of pellets by vegetation. These are important considerations when designing ungulate monitoring programs that utilize pellet counts.

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