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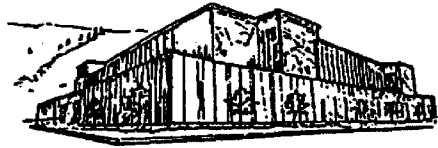
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FECAL PELLET DEPOSITION AND DISAPPEARANCE RATES FOR SNOWSHOE HARES NEAR SEELEY LAKE, MONTANA

by

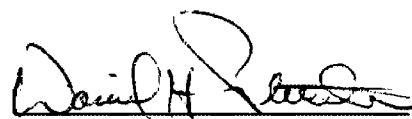
Pilar T. Rivera

B. S. The University of Arizona, 2000

presented in partial fulfillment of the requirements
for the degree of
Master of Science in Wildlife Biology

The University of Montana
2005

Approved by:



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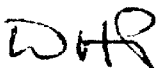
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Fecal Pellet Deposition and Disappearance Rates for Snowshoe Hares Near Seeley Lake, Montana (33 pp)Chairperson: Daniel H. Pletscher **Abstract:**

The snowshoe hare (*Lepus americanus*) has recently received increased attention because the Canada lynx (*Lynx canadensis*), its specialist predator, was listed as Threatened in the contiguous United States under the U.S. Endangered Species Act (USFWS 2000). Lynx require habitat that contains an adequate number of hares, and survival is unlikely if their diet is predominated by alternate prey species. Low hare densities adversely affect lynx density, lynx home range size, lynx reproductive success and body condition, and lynx mortality rates. Consequently, wildlife managers must be able to obtain reliably accurate estimates of hare density to develop lynx conservation plans such as reintroductions.

Counts of hare fecal pellets are a common and popular index of abundance because they are cheap, easy, quick, and therefore can cover extensive spatial and temporal scales. Furthermore, counts can be used to predict hare density, although the use of a single regression equation to characterize density is controversial because of the largely untested assumption of spatial generality concerning the hare-pellet relationship.

Differential pellet deposition and disappearance rates may be mechanisms causing the relatively low precision observed when the Krebs (1987, 2001) method developed in southwestern Yukon is applied to Montana, USA. I investigated these rates in the Seeley-Swan area of western Montana to evaluate whether deposition was comparable across forest types (diets), years, and seasons, and whether disappearance was comparable across pellet types and forest types. Mean daily pellet deposition (n=49 captive hares) was similar across 2 forest types (diets) and 2 years, but was significantly higher ($p < 0.01$) in summer than winter. Adult hares deposited 575 ± 108 (mean \pm 1 SD) pellets/day during the summer and 467 ± 82 pellets/day during the winter, regardless of forest type (diet) and year. Disappearance was similar between pellets produced in summer and winter, and across 4 forest types with approximately 14 pellets remaining per enclosure, out of an initial 20, after 16 months of weathering.

ACKNOWLEDGEMENTS

Living in Missoula, MT over the past few years, and working on my thesis project in particular, has powerfully altered my life in countless positive ways, some boldly obvious and others delicately quiet. I am amazed, although I should not be, by the number and weight of life lessons garnered from holding a snowshoe hare, feeling its breathing body apprehensively waiting from inside the dark of a pillowcase. First his pelage was brown and then magically white, only to become brown again, and gradually I learned the secrets, tricks, and truths he taught on changing colors; and on being born ready, surviving with instinct, judging when to wait and when to go, the ethics of keeping the wild in a cage, being the painful sacrifice of a meal in a trap, the hopeful promise of release in order to fight the good fight.

I am eternally grateful for the bridge that joined my Sonora desert home to the wonderland of the Rocky Mountains. Many helped with my initial crossing and/or subsequent growth, and I would like to first bow in overwhelming respect, admiration and gratitude to: Mr. James H. Haskell (USFS RMRS, retired), Mr. John B. Montoya (USFS R-3, retired), Dr. Daniel H. Pletscher (University of Montana), Dr. Leonard Ruggiero (USFS RMRS-Missoula FSL), and Mr. Randall A. Smith (USFS R-3 Coronado NF). Dan's dedication, guidance, and reassurance as my main mentor were invaluable, and I will never adequately voice to him my deep appreciation for everything he has done on my behalf. I hope Len realizes the significance of the indelible imprint his professionalism, commitment, and friendship has beneficially left. In addition to Dan, my academic committee consisted of Dr.'s Chris Guglielmo, Karen Hodges, and Kevin McKelvey. This group of exemplary scientists both intimidated and inspired me, and their involvement guaranteed the success of my research. It was an honor to benefit from their remarkable intellect. Funding came from the USFS Rocky Mountain Research Station, and I owe an enormous thank you to them for supporting me fully as both a student and employee. Their contributions made all the difference, and I could not have wished for a more rewarding experience than the one I have had, and continue to have, with the Forest Service. Huge hugs and kisses to my beautiful friends, all of which were faithful confidants and several of which were perfect laborers in the field, especially Colin Ruggiero, to whom I am thoroughly indebted. The most to my family, beginning with my mother, Nancy Rivera, and brother, Diego; they love unconditionally and indefinitely, and are beyond words and compare. They are my heart and I simply could not do without them...

And to complete the circle, maintain the cycle, I return to you. Back to your exquisite fur. Back to your tall and attentive ears, their skin tender, thin, and pink. Back to your strong legs and functional paws. Back to your tell-all eyes, tuft of a tail, impatient nose, two pairs of incisors. This world would be poorer, and certainly hungrier, were it not for you and your ways. Thank you.

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INTRODUCTION

The recent listing of the Canada lynx as threatened in the contiguous United States (USFWS 2000) has intensified interest in snowshoe hares because they are this felid's primary prey species (O'Donoghue et al. 1997; Aubry et al. 2000; Ruggiero et al. 2000). Ecological textbooks often present lynx-hare dynamics as a classic example of Lotka-Volterra predator-prey population dynamics. Declining/low hare numbers decrease lynx density, reduce lynx reproductive success and body condition, lead to higher lynx mortality (Ward and Krebs 1985; O'Donoghue et al. 1997), and cause lynx to exhibit behavioral adjustments (i.e., increasing home range size and daily travel distances, relinquishing territories to become nomadic) (Ward and Krebs 1985; O'Donoghue et al. 1998). Consequently, lynx require habitats where hares are abundant and cannot persist on diets composed primarily of alternate food sources (Murray et al. 1994; Kloor 1999; Ruggiero et al. 2000). Ruggiero et al. (2000:446) argued that lynx distribution is dictated by "...forests that support some minimum density of snowshoe hares (e.g., at least 0.5 hares/ha in northwestern Canada, but unknown further south)," and therefore, accurate and precise hare density estimates are critical when considering the management of lynx.

Fecal pellet counts per area are frequently used as relative metrics of hare abundance to compare population sizes, infer trends, assess activity levels, and describe habitat selection and use patterns to deduce habitat quality (Dolbeer and Clark 1975; Wolfe et al. 1982; O'Donoghue 1983; Pietz and Tester 1983; Litvaitis et al. 1985; Koehler 1990; Nams et al. 1996; Ferron et al. 1998). Counts are popular because they are a cheap, easy, and quick alternative to lengthy, laborious, and expensive capture-mark-

recapture (CMR) studies (Murray et al. 2002; Mills et al. 2005). Furthermore, the advantages of counts permit coverage of extensive spatial and temporal scales.

Most efforts to estimate density with counts have centered on the regression analysis work done by Krebs et al. (1987, 2001) in southwestern Yukon, which changed pellet counts from an index of relative abundance into estimates of density. Krebs et al. (1987) demonstrated that average pellet numbers on annually cleared plots were highly correlated to CMR population estimates ($r^2=0.88$). The authors deemed pellet counts a viable method for rapidly obtaining accurate and precise hare densities on an extensive scale. In a follow-up publication, Krebs et al. (2001) applied a log transformation to a new dataset and addressed temporal generality of the previously established hare-pellet relationship. Switching from a linear to a log-log regression reduced underestimation at densities >1.5 hares/ha and overestimation at densities ≤ 0.5 hares/ha, the latter being particularly helpful because concern regarding lynx is related to areas with lower densities of hares. The general pattern described in their earlier paper proved repeatable ($r^2=0.58$). Lastly, the authors recommended a careful examination of the relationship between pellet counts and hare density in boreal and montane forests of the western USA. Bartmann and Byrne (2001) and Murray et al. (2002) also suggested a cautionary interpretation of the spatial generality of the existing equation, and reiterated the importance of testing for site-specific relationships in peripheral hare habitat in the southern Rocky Mountains.

Mills et al. (2005) conducted a test of the Krebs et al. (1987, 2001) regressions in western Montana. The ln-transformed functional regression equation they developed for their Seeley Lake study area indicated the existence of a weak correlation between pellets

and hares ($r^2=0.27$); they also discovered the slope of the Yukon equation (Krebs et al. 2001) was included in the 95% confidence intervals of this locally-derived equation. Lack of geographic distinction led Mills et al. (2005) to conclude that the Yukon equation was appropriate for estimating hare density in Montana. The authors proposed using local pellet counts from 0.155 m^2 rectangular plots and the Krebs et al. (2001) equation to identify areas as having low, medium, or high hare densities. Mean counts of <0.6 pellets/plot (converting to roughly <0.3 hares/ha) meant hare densities below the threshold believed necessary to sustain lynx, and >1.6 pellets/plot (roughly >0.7 hares/ha) denoted high hare densities. Mills et al. (2005) advocated CMR studies when counts fall between 0.6 - 1.6 pellets/plot and where estimates may have crucial implications for lynx conservation.

Research significance and objectives

Mills et al. (2005) found their locally-derived equations and the Yukon equation all performed equally throughout the range of observed hare densities and poorly at low to moderate densities. They suggested using regression analysis to assign density levels, but encouraged conducting CMR when precise estimates are required in areas categorized as moderate. These moderate densities (0.3 - 0.7 hares/ha) were chosen because they contain the minimum density threshold (0.5 hares/ha) thought required by lynx to survive (Ruggiero et al. 2000) and are typical of southern hare habitat (K. McKelvey, pers. comm.). The Mills et al. (2005) Seeley Lake regression does not account for 73% of the variance between pellets and hares, and explaining and reducing this variance is essential for biologists to implement the desirable pellet-plot method in regions near the southern extent of lynx range (e.g., Colorado, Idaho, Montana,

Washington, and Wyoming).

The unexplained variation observed when correlating 2 variables is due to sampling and process variation. Partitioning total variation into these 2 components, evaluating their contributions, and understanding their causes is the first step towards improving a correlative relationship. Process variation, in this case, is explained by differential pellet production and decomposition (more broadly, disappearance) rates across plots where pellets are counted. The major assumption behind using pellets to answer density-related questions is that means and variation of both these rates are not substantially different in a predictable way between seasons, years, habitat types, or regions. The validity of this largely untested premise is questionable, and it may be lowering regression precision and/or introducing bias if incorrect. Different forest types conceivably supply hares with different diets, while identical diets can still lead to dietary differences because of individual hare preferences. Deposition could differ based on what and how much a hare eats, and disappearance may differ based on interactions between pellet composition, microclimate, roughness of forest floor, and litter fall. Season may also affect these rates; for example, a hare's summer diet consists of a variety of forbs, grasses, and shrubs, while in winter they consume predominately woody deciduous and coniferous browse (Keith 1990; Hodges 2000a, b). Murray et al. (2002) and Prugh and Krebs (2004) have called for attention to focus on possible differential disappearance rates between pellets deposited in summer and winter (Murray et al. 2002; Prugh and Krebs 2004). Geographic inconsistencies in the hare-pellet relationship may occur because hare habitat differs fundamentally across the range of snowshoe hares (Murray et al. 2002); the southern portion is characterized by an interspersed of

fragmented sub-boreal and montane forests in contrast to the extensive, uniform boreal forests of the north (Hodges 2000b). Deposition and disappearance rates may vary in response to bio-geographical and climatic diversity, and are potentially causing the relatively poor correlation seen by Mills et al. (2005).

I investigated fecal deposition and disappearance rates for snowshoe hare in the Seeley-Swan landscape of western Montana to quantify process variation by determining (i) whether deposition was comparable across forest types (diets), years, and seasons; and (ii) whether disappearance was comparable across pellet types (summer, winter) and forest types. With reference to objective (i): diets were formulated for forest types and each forest type represented a single, distinct, collective diet; summer and winter pellet types refer to pellets produced during these seasons. These objectives will (i) document fecal pellet deposition and disappearance rates for hares in western Montana; and (ii) reveal the extent to which these rates are responsible for the total variation observed by Mills et al. (2005), hopefully modifying regressions and leading to a better ability to predict hare density.

STUDY AREA

My study area was on the Lolo National Forest within the greater Seeley-Swan landscape in western Montana. Lindberg Lake bounded the study area to the north, Salmon Lake to the south, the Bob Marshall wilderness to the east, and the Mission Mountains to the west (Mills 2000). This area is near the town of Seeley Lake, located roughly 80 km northeast of Missoula.

The study sites for my fecal deposition and disappearance experiments were a subset of those sites used by Mills (2000). His 550 x 300 m grids were a random

selection from a GIS database of USFS lands within this area that were (i) between 1,300-2,000 m elevations; (ii) located within 0.5 km of an accessible road; and (iii) of a relatively homogenous forest type ≥ 20 ha. GIS coverages provided by the Lolo National Forest included forest type and elevation based on USFS R-1 forest inventory data. Using the Mills (2000) grids ensured that the study sites for my research were representative of hare habitat around Seeley Lake, and that my findings would be applicable to Mills et al. (2005).

METHODS

Pellet deposition experiment

Hare characteristics (i.e., age, weight, sex), diet, season, and effects of captivity were identified as factors that could potentially influence deposition. Deposition is affected by diet digestibility (Arnold and Reynolds 1943; Cochran and Stains 1961), and seasonality dictates the availability of food plants. Season may further influence deposition because hares increase consumption in response to decreasing temperature (Pease et al. 1979; Sinclair et al. 1982), and energy requirements may vary between seasons due to breeding status (Eaton 1995).

Trapping hares and holding them in captivity

Wild hares were captured on grids within 2 western larch (*Larix occidentalis*) and 2 Douglas-fir (*Pseudotsuga menziesii*) forest stands (Mills 2000). Tomahawk single door, collapsible 50 x 17.5 x 17.5 cm traps were baited with apple slices and alfalfa cubes. Adult male hares with a body mass ≥ 900 g and adult females $\geq 1,000$ g were brought into captivity because these weights represented conservative minimums for healthy, well-nourished adult hares (K. Hodges, pers. comm.). Females were excluded

from summer trials to avoid interfering with pregnancy and/or nursing, but both sexes were used in winter trials. Injuries sustained from time in traps precluded otherwise qualifying hares from captivity.

Hares were weighed upon capture, and those suitable for captivity were caged individually in 150 x 70 x 60 cm hutches constructed of wood and wire mesh; all others were released. A piece of wood with a small square entrance/exit opening at the bottom divided the hutch into $2/3^{\text{rd}}$ and $1/3^{\text{rd}}$ sections. The back $1/3^{\text{rd}}$ of the hutch had sides of solid wood that created a hiding chamber for hare concealment and protective shelter. Clear plastic drop cloths covered the wire tops of the hutches to keep precipitation out, and a sheet of porous, synthetic weed-block fabric underneath the hutches enabled collection of feces and plants. Large yogurt containers were wired into hutch corners for holding water or snow, and salt rings were attached to the sides of the hutches. Hutches were spaced >3 m apart on level ground under tree cover. Hares were placed in hutches quickly and with minimal transport because hutches were only 50-100 m from the trapping grids. Hares were exposed to the ambient weather (except precipitation), light, and noise conditions of the forest.

Feeding trials with captive hares

Feeding trials were conducted during summer and winter months to reflect dietary and physiological changes. Summer trials occurred from July-October 2002 and June-September 2003, and winter trials from December-March of 2002-03 and 2003-04. Hares were kept in hutches for only 4 days (Appendix 1), and human contact and proximity were minimized. The effects of captivity are unknown (Eaton 1995), and stress of captivity, most prominently a severe restriction on activity and subjection to

human presence, may adversely affect the acquisition of accurate deposition rates.

A “buffet plate” experimental diet for captive hares was selected over a single-species experimental diet to match the diverse diet of free-ranging hares and because hares cannot be maintained on pure diets of even high-quality forage (Rodgers and Sinclair 1997). Seasonal experimental diets were formulated for the 4 forest types (western larch, Douglas-fir, lodgepole pine [*Pinus contorta*], subalpine fir [*Abies lasiocarpa*]) represented by Mills (2000) based on plant species compositions and relative abundances from his vegetation sampling data (Table 1). All species were known to be eaten by hares in the western U.S. (Rockies, Cascades, and Intermountain West), except western larch (Hodges 2000b). Western larch was included because it is so widespread within hare habitat (K. Hodges, pers. comm.). None of the 4 forest types provided obvious dietary extremes and 2 of the types were inaccessible in winter, so I used experimental diets from only western larch and Douglas-fir for my feeding trials. The experimental summer diet consisted of 7 species: western larch, Douglas-fir, lodgepole pine, common snowberry (*Symphoricarpos albus*), serviceberry (*Amelanchier alnifolia*), mountain huckleberry (*Vaccinium membranaceum*), and a mixed grass category, while the experimental winter diet consisted of 4 species: western larch, Douglas-fir, lodgepole pine, and velvety buckbrush (*Ceanothus velutinus*). Diets were fed ad libitum; each hare was provided with approximately 1,150 g/day of total fresh, wild, native plant biomass in the summer and approximately 1,050 g/day in the winter (Holter et al. 1974; Pease et al. 1979; Corn and West 1990). Hares ate about 31% of the vegetation offered in summer, and 22% in winter. Offering unconstrained amounts of food was deemed reasonable because individuals likely differ in their preferences, and all

hares had the same opportunity to consume preferred foods (K. Hodges, pers. comm.).

Table 1. Relative decreasing abundances of documented snowshoe hare food plants according to forest type, and the seasonal experimental diets for each, Seeley Lake, MT (Mills 2000).

Forest type*	Sapling tree species	Shrub species	Summer diet	Winter diet
<i>Larix occidentalis</i>	<i>Pseudotsuga menziesii</i>	<i>Ceanothus velutinus</i>	<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>
	<i>Larix occidentalis</i> **	<i>Symphoricarpos albus</i>	<i>Larix occidentalis</i>	<i>Larix occidentalis</i>
	<i>Pinus contortus</i>	<i>Amelanchier alnifolia</i>	<i>Pinus contortus</i>	<i>Pinus contortus</i>
		<i>Vaccinium membranaceum</i>	<i>Symphoricarpos albus</i>	<i>Ceanothus velutinus</i>
		<i>Salix</i> spp.	<i>Amelanchier alnifolia</i>	
		<i>Rubus</i> spp.	<i>Vaccinium membranaceum</i>	
		<i>Rosa</i> spp.	Grass category	
		<i>Juniperus scopulorum</i>		
		<i>Mahonia repens</i>		
		<i>Arctostaphylos uva-ursi</i>		
<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>	<i>Vaccinium membranaceum</i>	<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>
	<i>Larix occidentalis</i>	<i>Symphoricarpos albus</i>	<i>Larix occidentalis</i>	<i>Larix occidentalis</i>
	<i>Pinus contortus</i>	<i>Amelanchier alnifolia</i>	<i>Pinus contortus</i>	<i>Pinus contortus</i>
		<i>Ceanothus velutinus</i>	<i>Vaccinium membranaceum</i>	<i>Ceanothus velutinus</i>
		<i>Juniperus scopulorum</i>	<i>Symphoricarpos albus</i>	
		<i>Salix</i> spp.	<i>Amelanchier alnifolia</i>	
		<i>Rosa</i> spp.	Grass category	
		<i>Rubus</i> spp.		
		<i>Mahonia repens</i>		

Table 1. Continued.

Forest type*	Sapling tree species	Shrub species	Summer diet	Winter diet
<i>Pinus contorta</i>	<i>Pseudotsuga menziesii</i>	<i>Vaccinium membranaceum</i>	<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>
	<i>Pinus contortus</i>	<i>Salix</i> spp. <i>Amelanchier alnifolia</i>	<i>Pinus contortus</i>	<i>Pinus contortus</i>
	<i>Larix occidentalis</i>	<i>Rosa</i> spp. <i>Symphoricarpos albus</i> <i>Ceanothus velutinus</i> <i>Juniperus scopulorum</i> <i>Mahonia repens</i> <i>Rubus</i> spp.	<i>Larix occidentalis</i> <i>Vaccinium membranaceum</i> <i>Salix</i> spp. <i>Amelanchier alnifolia</i> Grass category	<i>Larix occidentalis</i> <i>Ceanothus velutinus</i>
<i>Abies lasiocarpa</i>	<i>Pseudotsuga menziesii</i>	<i>Vaccinium membranaceum</i>	<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>
	<i>Pinus contortus</i>	<i>Salix</i> spp. <i>Symphoricarpos albus</i> <i>Rubus</i> spp.	<i>Pinus contortus</i> <i>Vaccinium membranaceum</i> <i>Salix</i> spp. <i>Symphoricarpos albus</i> Grass category	<i>Pinus contortus</i>

*Note: The 2 bolded types were used for feeding trials.

**Note: Western larch is not a documented food plant (Hodges 2000b); it was included as a test species due to widespread abundance.

Hares were given a single apple slice on the first day of captivity to compensate for a time lag between placement in a hutch and provision of experimental diets a few hours later, along with water or snow. Browse was cut from ≥ 3 individual plants growing where hares were captured. Each food species was weighed and provided to hares the day it was clipped in summer; in winter, food was clipped the previous day (because weather prohibited taking the moisture-sensitive laboratory balance into the field), weighed back at camp, and stored in paper bags outside in the snow.

Hares were weighed and moved into newly prepared hutches each day. Loss of

body mass was an indicator of stress and malnutrition; hares that lost $\geq 10\%$ of their initial weight were released and excluded from analysis (Pease et al. 1979; Sinclair et al. 1982; Rodgers and Sinclair 1997). Monel 1005-3 tags were inserted in the right ears of captive hares to avoid using them twice in the same season.

All fecal pellets and pellet fragments, and remaining plants and plant fragments were gathered daily and stored frozen prior to oven-drying at 60-75° C. Dry weights of initial plant quantities provided to hares were obtained by drying control samples of all plant species that corresponded to each feeding trial. Dry weights were used to calculate average amounts (g) consumed and average apparent digestibility of diets. Apparent digestibility refers to the fraction of dry matter of ingested food the body absorbs through the intestine, and is approximated by: $D = (\text{food intake [g]} - \text{fecal output [g]}) / \text{food intake (g)}$. The term apparent is used because feces contain endogenous materials along with undigested food. The first day was not excluded from deposition analyses because hares were given plants growing from the same forest grid where they were trapped, resulting in no dietary change associated with captivity.

Pellet disappearance experiment

I identified the season during which pellets are produced, pellet size, study site characteristics (i.e., microclimate), and weather as factors that could potentially influence disappearance. Pellet disappearance occurs due to decomposition, consumption, removal through animal activity, burial in soil or under litter, and transport out of the area by wind, rain, or snowmelt. Additions into an area can occur via defecation on the site or transport by animal activity, wind, rain, or melting snow.

The persistence of summer and winter pellets was monitored because pellet

degradation rates have varied according to diet (Taylor and Williams 1956; Cochran and Stains 1961; Flinders and Crawford 1977). Summer pellets generally have a high herbaceous component, whereas winter pellets consist of mostly fibrous, woody material and pine needles (Keith 1990; Hodges 2000a, b). The possible impact of the size or weight of pellets was believed negligible (Simonetti 1989; K. Hodges, pers. comm.). Because the disappearance of lagomorph pellets differs substantially between habitats and microhabitats (Taylor and Williams 1956; Cochran and Stains 1961; Angerbjorn 1983; Simonetti 1989; Eaton 1995; Forsy and Humphrey 1997), I selected a representative sample of forest types, and their respective microclimates, in the Seeley Lake area.

To examine disappearance rates, I built enclosures from July-August 2002 at 5 randomly selected locations within each of 12 grids (4 Douglas-fir, 3 western larch, 2 lodgepole pine, 3 subalpine fir), for a total of 60 enclosures; these were designed to preclude hare defecation and pellet transport. They were open-topped, circular structures roughly 1 m in diameter x 1.5 m high constructed of 5 x 10 cm, 14-gauge utility fabric that was secured to the ground with tent stakes. Strips of aluminum flashing 5-7.5 cm high divided each enclosure in half and were wrapped around their bases. Enclosures permitted the presence of leaf litter and did not prohibit small animal entry, but were hare-proof due to height and mesh size. They prohibited large animal disturbance such as trampling of pellets by ungulates, but otherwise imposed minimal interference while guaranteeing reliable location and identification of pellets during monitoring.

Fresh pellets of known age and season, collected from under traps containing recently captured adult hares, were used for the experiment. Summer pellets were

gathered from western larch and Douglas-fir forest types from July-September 2002, bagged separately, and stored frozen until placement inside enclosures October 2-10, 2002. The same process was followed for winter pellets; they were gathered from December 2002-February 2003 and placed in the field February 17-21, 2003. This schedule of pellet placement into enclosures mimicked the natural production of pellets by hares in the wild; summer and winter pellets are never deposited at the same time. Forty pellets (20 summer, 20 winter) were set in each of the 60 enclosures after clearing preexisting pellets, with enclosures in lodgepole pine and Douglas-fir forests receiving pellets originating from Douglas-fir forest, and those in larch and subalpine fir forests receiving pellets from larch forest. These combinations were based on similarity of average elevations (lodgepole pine [1,356 m], Douglas-fir [1,409 m], larch [1,493 m], subalpine fir [1,665 m]). Summer pellets were randomly assigned to enclosure halves, unless there was a slight slope to the ground, and then summer pellets were scattered on the uphill side so snowmelt would not transport winter pellets to the summer side. Winter pellets were later scattered on the other half.

All pellets were counted once a month during June-September 2003, and again in June of 2004. Study sites were visited as close together in time as possible, with counts usually taking 3-5 days. Enclosures were systematically examined; searches were not time-constrained, but observers did not dig into the forest floor or disturb the pine needle layer. Large debris, such as small branches or whole leaves, was carefully lifted and then replaced. Toothpicks were placed next to intact, identifiable pellets to ensure efficient, thorough counting while preventing double-counting. Toothpicks were removed after each count.

RESULTS

Pellet deposition experiment

Forty-nine feeding trials were completed (37 M, 10 F, 2?) and 9 were interrupted (6 resulted in hares being released, 3 resulted in hare deaths). Almost 4 times more males than females provided data, in large part because females were exempt from summer trials. The numbers of captives were divided fairly equally between forest types (diets), (Table 2). The overall average weight change for the 49 completed trials was -1.4% of initial hare body mass. Twenty-five hares lost weight, 12 gained weight, and 12 were released at their original weights. Weight change was similar between males and females ($t=1.11$, $df=45$, $p=0.28$), between summer and winter ($t=1.04$, $df=47$, $p=0.30$), and between Douglas-fir and western larch forest types (diets) ($t=0.20$, $df=47$, $p=0.56$).

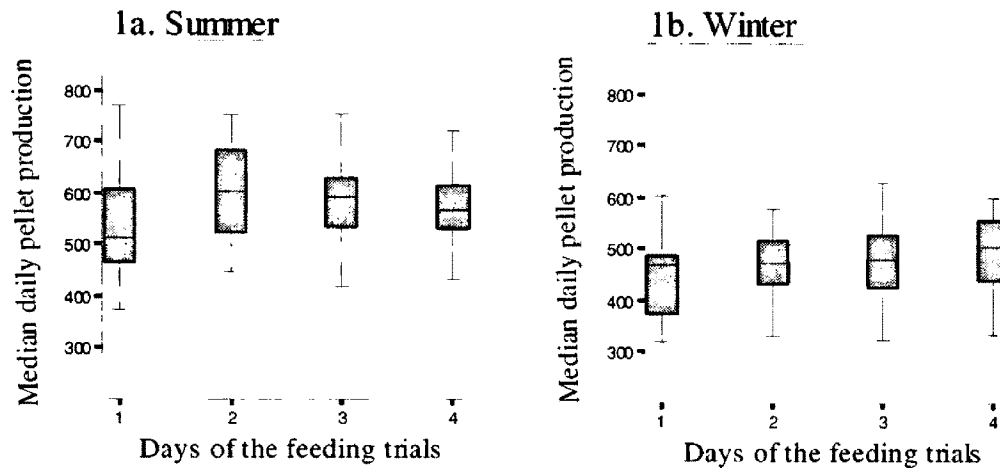
Table 2. Numbers of hares that completed feeding trials according to season, sex, and forest type (diet), Seeley Lake, MT, 2002-04.

Season	Sex			Forest type		Total
	M	F	Unknown	Larch	Douglas-fir	
Summer 02	4	0	0	0	4	4
Winter 02-03	5	2	1	3M, 1?	2M, 2F	8
Summer 03	14	0	0	7	7	14
Winter 03-04	14	8	1	6M, 4F, 1?	8M, 4F	23
Total	37	10	2	22	27	49

Pellet deposition data

Median daily pellet production was similar between all days of the feeding trials (Figures 1a, b).

Figures 1a, b. Median daily pellet production was similar for all days of the feeding trials, within a season, Seeley Lake, MT, 2002-04.



Mean daily deposition differed seasonally, but was not affected by body mass, sex, forest type (diet), or year (Table 3). I found no correlation ($r^2 < 0.01$, $F = 0.00$, $df = 48$, $p = 0.99$) between production and body mass via linear regression analysis. Production was (i) similar ($t = -0.39$, $df = 112$, $p = 0.70$) between males (465 ± 77 [mean \pm 1 SD] pellets/day) and females (472 ± 97 pellets/day) in winter; (ii) similar ($t = 0.21$, $df = 191$, $p = 0.84$) between Douglas-fir (509 ± 116 pellets/day) and western larch (505 ± 94 pellets/day) forest types (diets); and (iii) similar ($t = -1.10$, $df = 191$, $p = 0.28$) between Year 1 (summer 2002-winter 03) (492 ± 109 pellets/day) and Year 2 (summer 2003-winter 04) (512 ± 105 pellets/day). Data were pooled within seasons and deposition was significantly higher ($t = 7.29$, $df = 117.60$, $p < 0.01$) in summer than in winter. Mean (\pm 1 SD) deposition of adult captive hares feeding on either Douglas-fir or western larch experimental diets was 576 ± 108 pellets/day in summer, and 467 ± 82 pellets/day in winter, regardless of year.

Table 3. A univariate ANOVA model of pellet production with body mass, sex, forest type (diet), year, and season, Seeley Lake, MT, 2002-04.

Factor	F	df	p-value
Body mass (a covariate)	2.96	1	0.09
Sex	0.09	1	0.76
Forest type (diet)	0.51	1	0.45
Year	0.23	1	0.63
Season	52.29	1	<0.01
Error	-	179	-

Dietary consumption and digestibility data

Mean daily consumption (dry weight in g) of experimental diets differed seasonally, but was not affected by forest type (diet) (Table 4). Consumption was similar ($t=0.61$, $df=45$, $p=0.87$) between Douglas-fir (126 ± 51 [mean \pm 1 SD] g/day) and western larch (124 ± 40 g/day) forest types (diets). Consumption was significantly higher ($t=5.00$, $df=19.78$, $p<0.01$) in summer than in winter. Hares tended to eat 167 ± 47 (mean \pm 1 SD) g/day dry matter in summer and 103 ± 26 g/day in winter, regardless of forest type (diet).

Table 4. A univariate ANOVA model of diet consumption with forest type (diet), year, and season, Seeley Lake, MT, 2002-2004.

Factor	F	df	p-value
Forest type (diet)	<0.01	1	0.97
Season	34.72	1	<0.01
Error	-	44	-

Mean daily consumption (dry weight in g) of summer food plants was similar (independent samples t-tests for each plant yielded $p\geq 0.28$) between forest types (diets), but consumption of some winter food plants differed between forest types (diets). In winter, hares feeding on the 'Douglas-fir' experimental diet ate significantly less ($t=-2.29$, $df=27$, $p=0.03$) Douglas-fir, and significantly more ($t=2.20$, $df=27$, $p=0.04$) lodgepole pine and ($t=2.67$, $df=16.38$, $p=0.02$) buckbrush, but similar ($t=-1.06$, $df=27$,

$p=0.30$) amounts of western larch as hares feeding on the 'western larch' experimental diet (Table 5). Western larch served as a food species for every captive hare, but the mean daily amount eaten was significantly ($t=6.74$, $df=16.02$, $p<0.01$) higher in summer (26 ± 10 [mean ± 1 SD] g/day) than winter (8 ± 5 g/day).

Table 5. Mean (± 1 SD) daily consumption of winter food plant species by hares feeding on 'Douglas-fir' and 'larch' experimental diets in winter, Seeley Lake, MT, 2002-04.

Winter food plants	Mean daily consumption in winter (dry weight in g)	
	'Douglas-fir' experimental diet	'Larch' experimental diet
Douglas-fir	34 \pm 12	46 \pm 15
Lodgepole pine	52 \pm 13	39 \pm 17
Buckbrush	18 \pm 11	9 \pm 4
Western larch	7 \pm 4	9 \pm 5

Mean daily digestibility (%) of diets differed seasonally, but was not affected by forest type (diet) (Table 6). Diet digestibility was similar ($t=-0.53$, $df=45$, $p=0.60$) between Douglas-fir (57 ± 11 [mean ± 1 SD] %) and western larch ($59\pm 12\%$) forest types (diets). The summer diet was significantly ($t=4.28$, $df=45$, $p<0.01$) more digestible than the winter diet. Of the 167 g/day dry matter eaten in the summer, 110 g/day was digestible, and of the 103 g/day dry matter eaten in winter, 55 g/day was digestible, regardless of forest type (diet) (Table 7). Hares ate 62% more in summer and this diet was 23% more digestible than the winter diet (Table 7).

Table 6. A univariate ANOVA model of diet digestibility with forest type (diet), year, and season, Seeley Lake, MT, 2002-04.

Factor	F	df	p-value
Forest type	0.67	1	0.42
Season	18.45	1	<0.01
Error	-	44	-

Table 7. Mean (± 1 SD) daily diet consumption and digestibility according to season, Seeley Lake, MT, 2002-04.

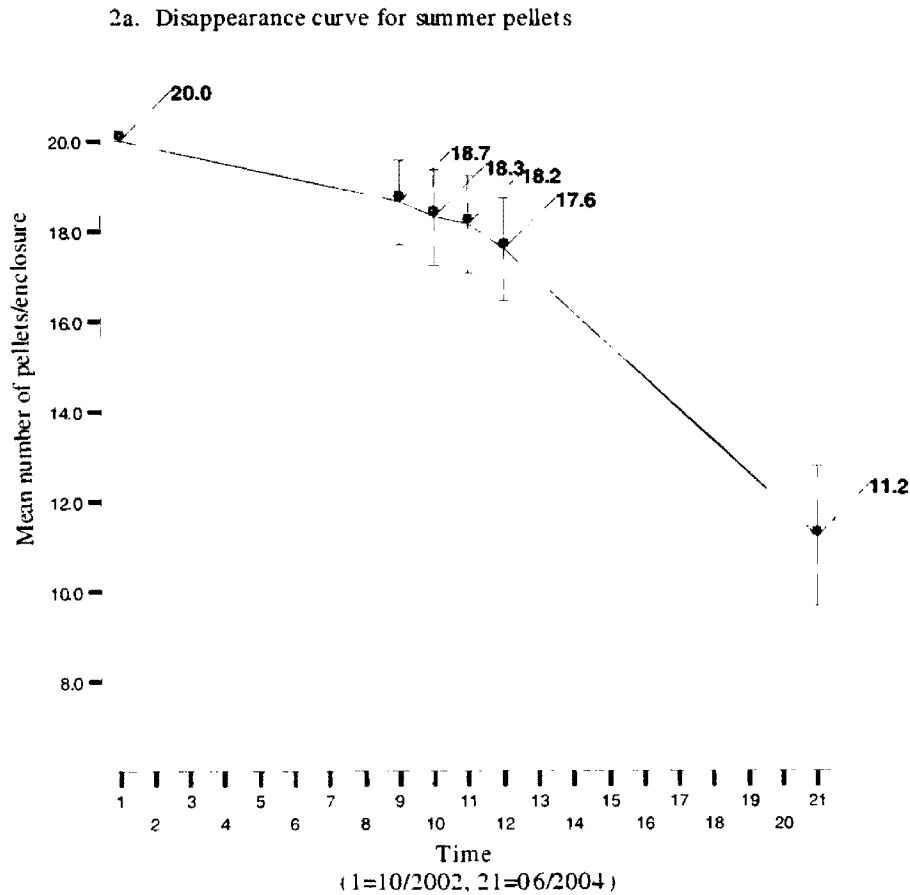
Season	Mean daily diet consumption (dry weight in g)	Mean daily diet digestibility (%)
Summer	167 \pm 47	66 \pm 9
Winter	103 \pm 26	54 \pm 10

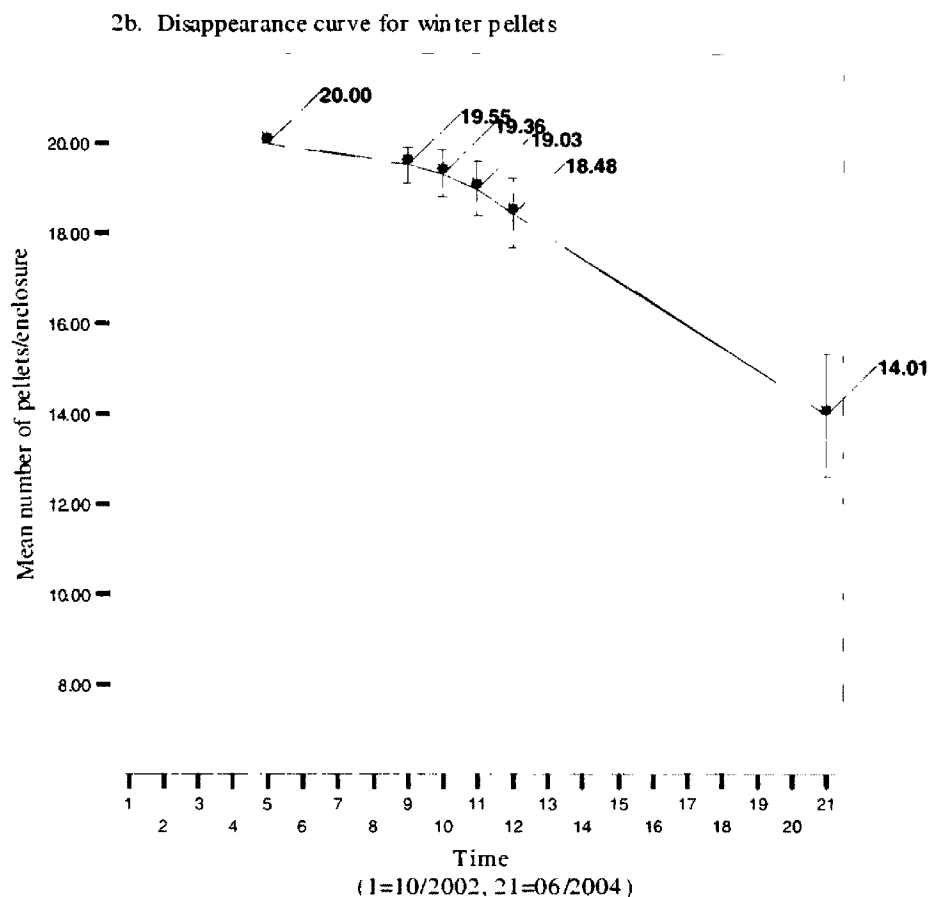
Pellet disappearance experiment

Disappearance was similar between forest types ($F=0.77$, $df=3$, $p=0.55$, Error [$df=7$]), with a mean (± 1 SD) number of pellets remaining per enclosure of 26 \pm 5, out of an initial 40.

Over the course of the experiment, beginning in October 2002 and ending with the last pellet count in June 2004, summer pellets spent 20 months in the field and winter pellets spent 16 months. They experienced different total amounts of exposure in the field because of their separate, dissimilar “start” dates; pellet types are naturally deposited during different months and undergo differential weathering between any time interval. At the last count, 11 \pm 3 (mean \pm 1 SD) summer pellets and 14 \pm 3 winter pellets remained per enclosure, out of an initial 20. Disappearance was similar between pellet types, with approximately 14 pellets remaining per enclosure after 16 months (Figures 2a, b).

Figures 2a, b. Ninety-five percent confidence intervals of mean numbers of pellets remaining per enclosure, out of an initial 20, across 4 forest types at six points in time (dates of counts). Summer pellets were placed inside enclosures in October 2002 (Time 1) and winter pellets were placed inside enclosures in February 2003 (Time 5), Seeley Lake, MT, 2002-04.





DISCUSSION

Pellet deposition experiment

I tested the effects of adult hare sex and size, forest type (diet), season, and year on the deposition rate of hare fecal pellets.

'Adult hare' variable

The age, weight, and sex of mature captive lagomorphs do not appear to affect deposition rates (Arnold and Reynolds 1943; Cochran and Stains 1961). Although an identified difference in deposition between adults of different sexes and weights might have been interesting biologically, it would not have reduced variation around pellet-to-hare regressions because sex ratios close to 50:50 exist across hare habitat (K. Hodges, pers. comm.) and adults of all sizes are likely distributed randomly. Pellet plots across an

area being sampled likely receive the same relative contributions of pellets from all adults.

'Forest type (diet)' variable

The plant species lists and experimental diets for all 4 forest types were remarkably similar (Table 1). Experimental diets were a subset of the vegetation consumed by wild, free-ranging hares and were based on relative abundance because (i) availability is often linked to use; and (ii) for logistical reasons. While the “real-world” diets of hares might expose dissimilarity between types, my restricted use of a limited number of abundant plants resulted in essentially 1 experimental diet, for each season, representative of both western larch and Douglas-fir. Identical food plants can still lead to different diets because of selection by hares. It seems western larch and Douglas-fir types denoted diet treatments because hares ate differently from the common diet offered in winter, although they did not in summer. Two possible explanations for this are (i) hares would have eaten differently in summer from a common diet that included more herbaceous plants and shrubs (also preventing the potentially artificially-high consumption of less preferred tree species); or (ii) hares had similar summer-diet preferences, but not winter ones.

Forest type is relevant to regressions because different types might serve as different diets, and if similar numbers of hares produce more or less pellets across a landscape where pellet counts occur (and are compiled to produce an average), then stratification of types would decrease variation and increase precision around regressions. My finding of similar deposition rates between forest types (diets), within seasons, is good news for researchers and managers using pellet-hare relationships because hares

utilized a common winter diet differently and still defecated comparably. This likely means stratification of forest types, at least western larch and Douglas-fir types, is unnecessary. Arguably, feeding trials involving lodgepole pine and subalpine fir forests would yield similar deposition results because of the similarity in all experimental diets. None of the observed variation around the Mills et al. (2005) regressions was likely created by differential deposition rates on pellet plots between forest types (diets).

'Season' variable

Captive hares probably produced different numbers of pellets in summer and winter because seasonality controlled food availability and digestibility. Production may have been dictated by overall diet digestibility (a measure of quality) rather than the specific species comprising the diet, and hares may have consumed more in summer because this diet was more easily digestible, breeding status caused greater energy demands, or both (these factors would be consistent across any region, habitat, or year). Defecation rates are higher in lagomorphs fed abundant, high-quality food (Cochran and Stains 1961). Greater consumption of summer foods apparently prevailed over the lower digestibility of winter foods for dictating the direction of the seasonal influence on numbers of pellets produced. Captive hares did not eat an expected 20% more dry mass in winter to get an equal amount of digestible dry matter intake as in summer, and actually ate 38% less food. If diet and fecal energy contents and metabolic rates were similar in both seasonal experiments, then hares were surviving and maintaining mass in winter on half the metabolizable energy intake as in summer. Hares likely reduced their energetic demands, and thus the quantity of food needed, in winter by lowering metabolism. The greater bilby (*Macrotis lagotis*) has a higher field metabolic rate (FMR)

in summer than in winter (Gibson and Hume 2000), and juvenile scalloped hammerhead sharks (*Sphyrna lewini*) exhibit temperature-dependent changes in metabolic rates, having higher rates in warmer summer months (Lowe 2002).

Because captive hares produced different amounts of pellets depending on season, it is likely that only regressions developed in areas with similar seasonal patterns should be used interchangeably and/or compared (otherwise biased with respect to one another). Inappropriately "borrowed" regressions may yield biased density estimates. It is also important to know annual pellet accumulations cannot be broken down equitably into monthly rates because months are disproportionately weighted.

'Year' variable

The 'year' variable accounts for annual fluctuations in weather and resultant cumulative affects on this system. I found no significant annual difference ($p=0.28$) for pellet deposition rates over 2 consecutive years; sample size, however, was only 2 years.

Previous data on deposition

Four earlier studies provided data on fecal deposition rates of snowshoe hares, but most dealt with low numbers of captives, all derived their data from hares fed artificial diets, some used only a single day of deposition data per hare, and none recorded rates during summer and winter (Adams 1959; Bookhout 1965; Eaton 1995; Hodges 1998). Adams (1959) found an average of 225 pellets/hare/day for 2 penned hares fed commercial food, apples, canned milk, and 3 natural forage species over a 6-day period in Montana, but thought deposition of free-ranging hares was between this number and the 480 pellets/hare/day determined through field studies. Bookhout (1965) reported an average of 466 pellets/hare/day for 18 confined hares in Michigan. Eaton (1995)

observed an average of 360 pellets/hare/day for 7 captive hares fed commercial food, held indoors and outdoors, over 5-16 days (first 2 days excluded from analyses) during the winter in Nova Scotia, with 543 pellets/hare/day for 2 kept outdoors. Hodges (1998) obtained an average of 579 pellets/hare/day for 7 captive hares fed commercial food, willow, birch, and spruce, held indoors, for 2 days (first day excluded from analyses) during January-February in the Yukon. My results during winter were slightly lower but most similar to Eaton (1995) and Hodges (1998).

Pellet disappearance experiment

'Forest type' variable

Distinct vegetative communities with specific microclimatic and soil conditions distinguish different forest types, and thus pellets might disappear at varying rates in plots across a landscape. Prugh and Krebs (2004) recommended that fecal disappearance be measured when counts from different habitats are compared. I found that stratification of forest types near Seeley Lake was unwarranted because pellet disappearance was similar across 4 forest types. None of the variation seen by Mills et al. (2005) was likely linked to this variable. Forest type may not have affected pellet disappearance because microclimates/soils did not differ substantially between forest types or differed substantially within types, and/or weather (i.e., precipitation, temperature) was more influential and was expressed uniformly across the 4 forest types.

'Pellet type' variable

My expectation that summer pellets would disappear more rapidly than winter pellets because of their seemingly lower durability, based on composition, and subjection to more months of warmer, wetter weather was not supported by 16 months of data.

Approximately $\geq 80\%$ (≥ 16 pellets/enclosure, out of an initial 20) of both pellet types persisted after 12 months of exposure, and approximately 70% (14 pellets/enclosure, out of an initial 20) of both types persisted after 16 months of exposure. In all probability, this variable did not contribute to variation surrounding the Mills et al. (2005) regressions.

Because seasonal patterns of a region will influence how many pellets are produced monthly and the length and type of weathering experienced by pellets during a year, regressions should only be applied to and compared with areas of similar seasons to avoid possibly introducing bias.

Previous data on disappearance

Decomposition rates of snowshoe hare pellets are extremely variable and support doing local studies. It may take 10 years or more before pellets begin to disintegrate at Kluane Lake, Yukon Territory (Krebs et al. 1987). Eaton (1995) found pellet degradation differed significantly between 6 habitats in Nova Scotia, and predicted the number of days to 90% disappearance ranged from 162 to 3474. Malloy (2000) reported the disappearance of 3 pellets, out of 40, during a 12-month period in Montana, with no further evidence of decomposition until 16 months of exposure. Murray et al. (2002) recovered 75% of pellets per plot after 1 year in northern Idaho, and found similar degradation rates between recent clear-cuts and mature forest, while Prugh and Krebs (2004) observed significantly different rates of pellet decay between 3 habitat types in the central Alaska Range.

CONCLUSIONS

I found that process variation does not seem to be a large component of the total

variation associated with the Mills et al. (2005) regression equations. Application of the pellet-plot method in the Seeley Lake area, and probably western Montana, does not need to involve stratification of forest types to reduce variation because pellets were produced and disappeared similarly across all forest types. Here, the relationship between hares and pellets is season specific, but this seasonal difference in deposition should affect all pellet plots being sampled equally. Other issues, such as sampling variation, are likely hampering the apparently very strong relationship between hares and pellets from precisely estimating hare numbers regardless of their density.

My data should be used prudently because they were gathered from captive hares and come from only a 2-year period.

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Appendix 1. Keeping hares in captivity.

Three captive hares died between September-December 2002 and all had lost <10% of their body weight at their last weighing the day prior to death. Two of the 3 carcasses were frozen, and John Weyhrich, Director of Laboratory Animal Resources (LAR) and Institutional Animal Care and Use Committee (IACUC) Protocol Review Manager, performed necropsies on January 13, 2002. He found no identifiable causes of death. The necropsies were incomplete because the hares had been dead and frozen for over 3 weeks, but showed that neither had skeletal injuries, obstructed throats, gastrointestinal tract damage (found fully formed feces in both), or macroscopic parasites, and both had healthy lungs and material in their stomachs. The adrenal glands in one were slightly swollen. There was little body fat on both (bone marrow was not inspected), but snowshoes typically do not store much body fat and can survive only 4-6 days on their small fat reserves without eating (Whittaker and Thomas 1983).

My original feeding trial was 7 days long, supplied commercial rabbit chow along with vegetation for the first 3 days, omitted chow from the remaining 4 days, and excluded the first of the last 4 days from analysis to allow for the passage of chow through the gut. This design gave 4 days of data. Previous researchers reported keeping hares in captivity for 2-21 days, and most experiments relied on the inclusion of commercial rabbit food in their feeding trials, or during pretrial or recovery periods (Adams 1959; Pease et al. 1979; Gingerich 1984; Corn and West 1990; Eaton 1995; Rodgers and Sinclair 1997; Hodges 1998).

After the necropsies, I shortened feeding trials to 4 days because I speculated blood stress hormones might have caused physiological problems even if little weight

loss occurred and reducing time in captivity would be most beneficial in addressing the deaths (K. Hodges, pers. comm.). Four days in captivity also appeared to be the maximum hares could withstand; deaths of captives were reported by Bookhout (1965) at between 2-4 days, and all 13 of the hares used in one of Pease et al.'s (1979) feeding experiments were dead by the 4th day. The weight minimums and acceptable weight loss limit that had been set were suitable and were not changed (K. Hodges, pers. comm.; C. Guglielmo, pers. comm.). The assumption that chow would pass out in a single day proved questionable because 1 of the necropsied hares had retained chow in its system 2 days after access to it. The shortened trial still had 4 data days, and guaranteed no contamination of the deposition rate by artificial food. Finally, salt licks were subsequently provided.

All cages the dead hares had occupied were thoroughly disinfected with a mild bleach solution and the porous cloths beneath them, along with water containers, were discarded.

After changing the feeding trials, in addition to the absence of more deaths, a larger proportion of hares that began trials finished them, average weight loss during captivity decreased, average weight gain increased, and a higher number of hares did not lose or gain weight (Table A1).

Table A1. Comparative numbers of captive hare deaths, releases, and mean weight changes before and after modifying feeding trials, Seeley Lake, MT, 2002-04.

Before changes (September-December 2002)	After changes (January 2002-March 2004)
3 deaths	0 deaths
5 released	1 released
4 of 12 trials completed	45 of 46 trials completed
Average % weight loss: 7.3 (3*)	Average % weight loss: 4.3 (22)
Average % weight gain: 3.3 (1)	Average % weight gain: 6.7 (11)
0 remained neutral	12 remained neutral

*Note: Numbers in parentheses refer to numbers of hares.

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