Scat removal: a source of bias in feces-related studies

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Abstract Consumption of feces (coprophagy) may alter findings of dietary studies and population estimates based on fecal analyses, but its magnitude is poorly understood. We investigated seasonal incidence of scat removal on Fort Riley, Kansas, from January through December 2000. We placed feces from captive bobcats (*Lynx rufus*), captive coyotes (*Canis latrans*), and free-ranging coyotes randomly on tracking stations in forest and prairie landscapes to determine rates of scat removal by local wildlife. Rates of removal of feces from captive bobcats, captive coyotes, and free-ranging coyotes varied from 7% during spring to 50% during summer. We identified opossums (*Didelphis virginiana*) as the most common species present at stations where scat removal occurred. Feces may be an important seasonal source of food for opossums and may provide seasonal dietary supplements for other species. Other factors responsible for disturbance of feces included a woodrat (*Neotoma floridana*) caching coyote feces, removal of captive coyote feces by free-ranging coyotes accompanied by deposition of fresh feces, a bobcat burying a captive bobcat sample and depositing fresh feces, and rain storms. Dietary studies based on fecal analyses could be biased by scat removal, assuming that contents in feces are representative of the proportion of foods consumed.

Key words bobcat, *Canis latrans*, coprophagy, coyote, *Didelphis virginiana*, diet, feces, Kansas, *Lynx rufus*, opossum

Feces provide a low-cost, non-invasive basis for determining species presence in diet (Sperry 1941) and evaluating ecological relationships (Putman 1984). In many cases feces are the only materials readily available for study. Fecal surveys have been used to estimate relative densities of mesopredators in North America (Knowlton 1984, Stoddart 1984, Cavallini 1994). Molecular study of epithelial cells shed from intestinal linings and contained within fecal samples has been used to identify species and accurately identify individuals within a population (Kohn and Wayne 1997). Coe and Carr (1983) suggested a linear relationship between dry weight of feces and body size of the defecator. Relative accumulation of feces from specific species in particular areas has been considered an indicator of relative importance of those areas (Bever 1955, Riney 1957, Rogers et al. 1958, Loudon 1979).

In order for accurate inferences to be drawn from fecal data, however, they must provide representative samples of animal occurrence, behavior, diet, or other traits being studied. Our objectives were to determine whether scat removal or other disturbances influenced availability and distribution of feces from coyotes (*Canis latrans*) and bob-

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cats (*Lynx rufus*) in prairie and forest habitats, identify species that engaged in activity associated with scat removal, and review reasons why animals may remove feces.

Study area

We conducted the study on Fort Riley Military Reservation, a 40,273-ha United States Army training facility in the Flint Hills of Geary, Riley, and Clay counties, northeastern Kansas. Steep slopes, shallow limestone soils, and an ecotone of prairie and forest vegetation dominated by tall and mixed grasses interspersed with woody ravines and riparian areas characterized the Flint Hills (United States Army 1994). Major grasses included big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Scizachyrium scoparium*). Common trees included bur oak (*Q. macrocarpa*), chinquapin oak (*Quercus muhlenbergii*), American elm (*Ulmus americana*), red mulberry (*Morus rubra*), black walnut (*Juglans nigra*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), and honey locust (*Gleditsia triacanthos*) (United States Army 1994).

Common mammalian predators on Fort Riley included coyotes, bobcats, red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), opossums, mink (*Mustela vison*), badgers (*Taxidea taxus*), feral dogs, and feral cats.

Fort Riley, located at the confluence of the Smoky Hill and Republican rivers, received about 80 cm average annual precipitation.

Methods

We placed individual fecal samples collected from free-ranging coyotes, captive coyotes, and captive bobcats randomly on tracking stations located in forest and prairie at Fort Riley. We monitored the fate of these samples over time to determine rates of removal and to identify species possibly engaging in scat removal.

We removed vegetation from circular tracking stations 1 m in diameter, smoothed the ground surface, and sifted a substrate of sand and soil onto the station to facilitate recognition of tracks from animals that visited the stations (Linhart and Knowlton 1975, Roughton and Sweeny 1982). We placed individual fecal samples, selected randomly, in the center of each station. For each feces type, we constructed 20 stations≥0.5 km apart and evenly distributed them in forest and prairie. We established 12 unbaited (e.g., no scats) control stations distributed evenly in forest and prairie and monitored fecal samples from free-ranging coyotes, captive coyotes, and captive bobcats through 2000. We monitored the stations during winter (4 January–19 March), spring (20 March–20 June), summer (21 June–21 September), and autumn (22 September–20 December).

We set stations on day 1 and read them during subsequent 24-hour periods to identify species, estimate numbers of visitors, and document occurrences of scat removal or other disturbances. We monitored stations until fecal samples were removed or degraded naturally from rainfall, desiccation, or wind action. We recorded tracks of visitors and identified species when possible. When all or part of feces remained, we smoothed the tracking surface and prepared for the next 24- hour period. Monitoring occurred ≥30 days each season.

We collected all fecal samples during the same season that they were placed on the stations for observation. We collected free-ranging coyote samples along segments of unimproved roads at Fort Riley within 24 hours of an initial removal of feces along collection routes to ensure fresh samples. Feces from sexually intact male and female captive coyotes fed a diet of PMI Adult Formula dog food (Purina Mills, St. Louis, Mo.), and sexually intact captive bobcats fed Feline Diet (Central Nebraska Packing, North Platte, Nebr.) were collected in zoos. We stored all samples in freezer bags, froze them, and then thawed each 24 hours prior to use.

We analyzed data separately for each season using a generalized linear model (McCullagh and Nelder 1983) with binomial error distribution and logit link (SAS Institute 2000) to determine relationships between forest or prairie and species of feces as they related to removal (coprophagy or some other disturbance). For statistical analysis, we considered stations as positive at the first detection of removal (due to causes other than weather), even if partial samples of feces remained on the station.

Results

Winter

We documented 140 visits to stations baited with feces during winter (Table 1), although only 4 of 60

fecal samples were removed: 2 from captive bobcats, 1 from a captive coyote, and 1 from a free-ranging coyote. Three of the samples taken from tracking stations were in forest, and opossum tracks were present at 2 of those stations. Tracks of coyotes, cottontail rabbits (*Sylvilagus floridanus*), deer (*Odocoileus virginianus*), and small rodents also were present at sites where feces were removed. Too few samples disappeared during winter to meaningfully assess relationships between habitat and feces type relative to removal.

Spring

We documented 125 visits to stations baited with feces during spring (Table 1). Nine of 58 samples placed for observation during spring were removed: 6 were from either captive or free-ranging coyotes. Removal was linked to an interaction between the species that deposited the sample and the area in which it was placed for observation ($P = 0.03$). Neither area ($P = 0.13$) nor feces type ($P = 0.17$) alone appeared to influence rates of removal during spring. Opossums were the most frequent visitors and were present at 33% of stations where scat removal occurred. Other species present included coyotes, raccoons, and bobcat. We documented 1 occurrence where a bobcat buried the study sample and defecated on the station. At 2 other stations where removal occurred, coyote tracks were present and the stations had been excavated and covered with fresh urine and feces.

Summer

We documented 176 visits to stations baited with feces during summer (Table 1). Thirty of 60 fecal samples (50%) were removed and appeared to have been consumed. Removal differed significantly between areas ($P = 0.01$); 67% of the samples taken from forest and 33% from prairie. Of those removed, 11 were from free-ranging coyotes, 10 were from captive coyotes, and 9 were from captive bobcats. While opossums were identified as the most frequent visitors to stations where feces were removed, others included coyotes, bobcats, deer, insects, rabbits, and various small rodents. Feces type did not appear to influence removal ($P = 0.71$), and there appeared to be no interaction between area and feces type ($P = 0.78$).

Autumn

We documented 271 visits to stations baited with feces during autumn (Table 1). The disappearance of feces varied significantly among areas ($P = 0.01$) and occurred nearly 3 times more often in forests than in prairies. Although feces type alone appeared not to influence removal ($P = 0.34$), 15 of 19 fecal samples taken were from captive coyotes and free-ranging coyotes combined. No interaction effect between area and feces type was apparent ($P = 0.77$). Several species, including small rodents, opossums, coyotes, whitetail deer, cottontail rabbits, and bobcats, visited stations during nights when feces were removed, but tracks of opossums were identified most frequently and were present at 37% of the stations where removal of feces occurred. We documented 1 occurrence of a bobcat burying the feces from a captive bobcat in the tracking station and defecating on the station and 1 occurrence of a woodrat removing coyote feces and caching it at a nearby den.

Visits to control stations rarely occurred in

Table 1. Species recorded at stations baited with coyote and bobcat feces at Fort Riley, Kansas, 2000.

	No. stations visited							
	Winter		Spring		Summer		Autumn	
Visitor	Forest	Prairie	Forest	Prairie	Forest	Prairie	Forest	Prairie
Small bird[a]	4	1	1	3	3	7	15	1
Bobcat	7	2	8	2	6	2	2	3
Coyote	18	10	7	18	3	24	19	24
Deer	30	8	18	9	11	12	27	8
Dog	0	0	0	0	0	0	2	2
Elk[b]	0	2	2	0	0	1	0	0
Fox	0	1	0	0	0	0	1	0
Insect	0	0	0	0	9	8	0	0
Opossum	13	0	4	2	43	8	34	2
Pheasant[b]	0	0	1	1	0	0	0	3
Rabbit	13	5	7	2	4	4	33	15
Raccoon	6	1	13	0	1	0	21	1
Skunk	2	1	0	0	2	1	3	2
Small rodent[c]	6	8	6	2	14	10	35	16
Turkey[b]	1	1	3	6	3	0	1	1

[a] All birds smaller than pheasant.

[b] Elk (*Cervus elaphus*); pheasant (*Phasianus colchicus*); turkey (*Meleagris gallopavo*).

[c] All rodent tracks classified as "small rodent."

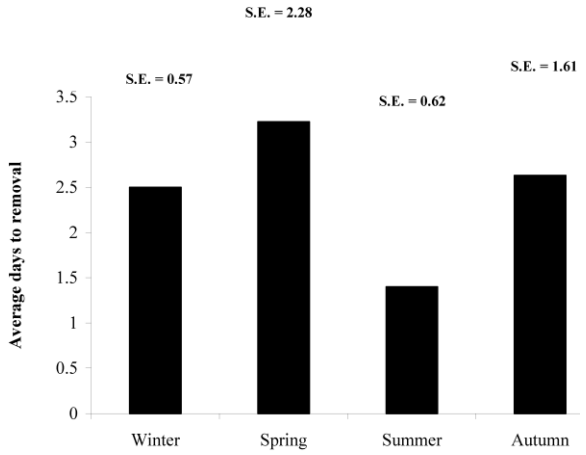

Figure 1. Average days to removal of feces collected from captive bobcats, captive coyotes, and free-ranging coyotes, placed at track stations in Fort Riley, Kansas, 2000.

any season. We recorded a single visit by a deer during spring, 1 rabbit during summer, and 1 rabbit during autumn. While it is possible that visits by rabbits could be attributed to dusting behavior, it is likely that the visit by the deer was incidental. In contrast, baited stations were visited frequently and feces were consumed or removed soon after stations were baited (Figure 1).

Scat removal occurred at varying levels on a seasonal basis (Figure 2), but positive identification of the scat-removing species was possible only when tracks of a single species were present at a station where it occurred. Where tracks of multiple species were recorded, we noted each species that was present during the 24-hour period in which feces were removed, but could not attribute scat removal to a particular species. Other reasons for disappearance of feces were speculative, but we believe territorial marking was a factor.

Although the majority of feces removed throughout this study appeared to be the result of coprophagy, other factors influenced removal. In addition to caching by woodrats and territorial behavior displayed by coyotes and bobcats (i.e., removal of study sample and deposition of fresh feces), feces removal was facilitated on ≥1 occasion by heavy rains during spring.

Discussion

Determining rates of disturbance and disappearance of feces from known species on Fort Riley was readily accomplished, but determining the precise method of removal or which species may have engaged in scat removal presented a challenge. When partial fecal samples remained on the tracking station, closer examination often revealed tooth marks and small fragments of feces verifying that consumption likely occurred. Motion-sensitive photography or video systems would have provided positive species identification and more conclusive evidence of coprophagy, but significant levels of military and civilian activity at the study site and the associated threat of theft and vandalism precluded use of expensive equipment.

Several hypotheses about the importance of the consumption of feces to mammals have been presented (Barnes et al. 1965, Hintz 1969, Ebino et al. 1993, Crowell-Davis et al. 1995, Marinier and Alexander 1995), but the phenomenon of coprophagy among mammalian carnivores has not been adequately studied. Intraspecific coprophagy among carnivores may be important in mate selection and territory defense (Rich and Hurst 1998). Removing scent markers by consuming competitors' feces may suggest that a resident carnivore has the ability to defend its territory and therefore be indicative of that individual's fitness as a potential mate. It also has been suggested that coprophagy results from

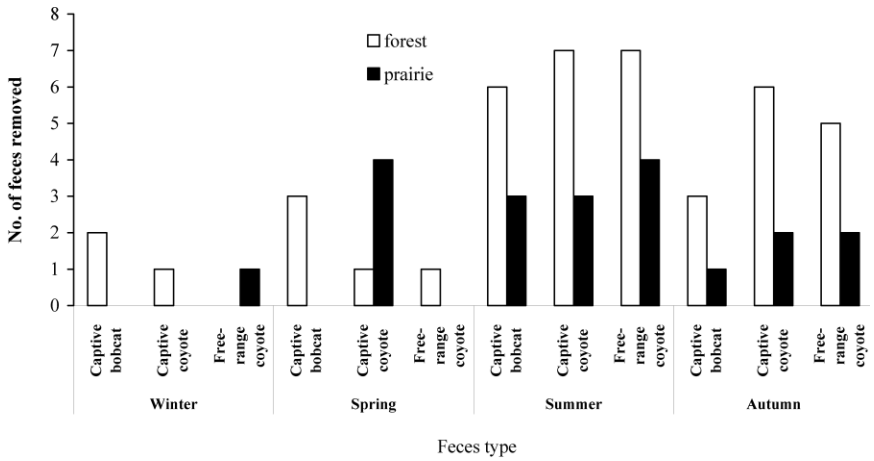

Figure 2. Removal of feces collected from captive bobcats, captive coyotes, and free-ranging coyotes, placed at track stations in Fort Riley, Kansas, 2000.

nutritional imbalances where coprophagous species experience nutritional gains from eating feces that are not available through other avenues (Chilcotte and Hume 1985, Flurer and Zucker 1988, Ebino et al. 1989). According to Giovannetti (1982), coprophagy is practiced by most animals and there is an inverse relationship between adequacy of diet, in terms of nutrients normally synthesized by the microflora of intestinal tracts, and the extent to which coprophagy is practiced.

We examined possible biases caused by scat removal upon carnivore dietary studies by comparing published results of coyote diets in Kansas. Gier (1957) reported on the diet of coyotes based on analysis of 1,190 coyote stomachs collected from 1948 through 1957. He reported that 57% of stomachs contained remains of lagomorphs, 38% contained remains of ungulates (mostly livestock), and 36% contained remains of rodents. In contrast, a second study of coyote diets based on food remains in 1,389 coyote feces collected in north-central Kansas during 1990 and 1991 (Brillhart and Kaufman 1995) found that 86% of coyote feces contained rodents while only 20% contained lagomorphs and approximately 6% contained ungulates.

It is possible that differences in diets reflected by these studies were influenced by changes in availability of rodents, rabbits, and ungulates during the time interval between the 2 studies, differential digestion of prey items, differential decomposition of scats with different food residues, or analysis techniques (i.e., stomachs vs. feces). We feel that selective removal of feces by coprophagous animals could explain some of the differences in the results of these investigations. In the study based on feces, opossums and other coprophagous animals could have removed a disproportionate number of feces that contained partially digested rabbit and ungulate tissue before they were collected by the research team, giving the false impression that rodents were more important than lagomorphs or ungulates in the coyote diets.

Retention time and level of digestion in carnivore digestive tracts vary according to prey size, and the relationship between prey size and digestibility may be a factor influencing protein content in feces. Meriwether and Johnson (1980) suggested that tissue from larger prey might be less completely digested than tissue from smaller prey. Given the tendency of coyotes and other carnivores to rapidly consume large quantities of tissue, it is likely that portions pass through the digestive tract without being completely digested. Johnson and Alred (1982) hypothesized that large pieces of food may contain portions that are more protected from the activity of digestive enzymes than those of smaller prey. Possible increase of protein concentrations in carnivore feces stemming from less complete digestion of larger prey, such as deer and lagomorphs compared to rodents, may have resulted in increased coprophagy. Further, carnivores may not consume as much hair and bone from large prey items and thus increase protein concentrations in feces as a result of minimal dilution by indigestible materials.

During late spring and early summer, there is an increase in availability of fruits and insects in Kansas. Our data suggest that opossums were the major consumers of feces during summer and possibly were attracted to high concentrations of protein-rich insects located on the feces. Sandidge (1953) reported that insects composed 86.7% of opossum diets in Kansas. Fifty percent of all feces we placed on stations during summer were removed, and opossums were present at half of those stations.

Eastern woodrats (*Neotoma floridana*) were another species whose tracks were often present at stations when scat removal occurred. Similar to opossums, woodrat activity occurred in forests, coinciding with the majority of coprophagous activity. Woodrats also may have been combating seasonal nutritional deficiencies by consuming carnivore feces. An alternate possibility is that woodrats took feces from tracking stations and cached them rather than consuming them (Poole 1940, LoGiudice 2000). While we were able to document one occurrence of caching by woodrats in our study, Horne et al. (1998) found owl pellets and a dropping from a dog among materials cached by woodrats in dens they examined on Fort Riley.

One concern regarding coprophagy, or even the transfer, by mouth, of feces from site to site, is the possibility of parasite and disease transmission. Many parasitic organisms rely on ingestion by an intermediate host to complete life cycles (Noble et al. 1989). This may be done through ingestion of feces often laden with eggs from parasitic organisms. When animals ingest feces infected with eggs or larvae of a parasitic organism, infection may be rapid and widespread (LoGiudice 2000). *Baylisascaris procyonis,* a common intestinal roundworm of raccoons, has been implicated in the

decline and extirpation of the Allegheny woodrat (*Neotoma magister*) from portions of its range in the northeastern United States (Balcom and Yahner 1996, LoGiudice 2000). Adult roundworms rarely caused overt pathology in raccoons, but the larvae were highly pathogenic when ingested by an intermediate host such as the woodrat. Woodrats forage in mammal latrines, and their habit of collecting feces and storing them in caches may put this species at increased risk of parasite mortality (Poole 1940, Whitaker and Hamilton 1998).

Conclusions

Coprophagy and other behaviors that lead to the selective removal of feces may impact results of some types of studies based on fecal analyses. For example, contents of feces often serve as the basis for dietary studies, and fecal counts may be used to document species presence and to estimate relative abundance. Fecal removal rates like those we encountered in northeastern Kansas (≤50%) could impact dietary studies based on fecal analyses if contents in feces are assumed to be representative of the proportion of foods consumed. Similarly, studies of wildlife populations based on the presence of feces could be biased by selective removal of feces via coprophagy, caching, or territorial behavior.

While coprophagy may play a role in nutrient gain by some mammals, it also may provide an avenue for parasite transmission. More physiological and behavioral studies of coprophagy are needed to understand why animals engage in this activity.

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