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WINTER SCAVENGING OF UNGULATE CARRION BY BALD EAGLES, COMMON RAVENS, AND COYOTES IN NORTHERN ARIZONA

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ABSTRACT.—Ungulate carrion supports an unusual canine-corvid-eagle winter scavenging guild in northern Arizona. To evaluate the effect of location and habitat on carcass use and longevity, between December 1996 and April 2008 we recorded 870 observations of Bald Eagles (*Haliaeetus leucocephalus*), Common Ravens (*Corvus corax*) and coyotes (*Canis latrans*) scavenging 123 ungulate carcasses: 103 elk (*Cervus canadensis*), 12 mule deer (*Odocoileus hemionus*), seven pronghorn antelope (*Antilocapra americana*), and one domestic cow (*Bos taurus*). Our temporal metric for measuring carcass longevity and scavenger presence was carcass-day (CD), numbered consecutively from the first day a carcass was recorded until it was consumed. We observed 38 separate carcasses (individual placement), 39 carcasses as part of three-carcass arrays in habitat associated with open, edge, and forest cover types (simultaneous choice), 22 carcasses left along the roadway where killed (monitored in place), and 24 carcasses partially skinned and/or cut open (facilitated). Elk carcasses lasted a mean 11.9 d (range 3–41), with 60% consumed during the first wk. Deer and pronghorn lasted 5.5 d (range 3–12) and 3.0 d (range 2–4), respectively. Ravens normally arrived by CD 3, Bald Eagles by CD 4, and coyotes by CD 6. Bald Eagles relied on ravens for discovery and sentinel duties, whereas both species depended on coyotes for accessibility. Winter- and road-killed carrion, not canine predation, drove carcass availability. Bald Eagles and coyotes used natural carrion more than human-influenced (road-killed or cut-open) carcasses, whereas Common Ravens were uninhibited by the latter. Removing ungulate carcasses from highway rights-of-way and partially opening them will promote quicker carcass consumption and safer avian scavenging by reducing potential for collisions with passing vehicles. A better understanding of the use of road-killed, large ungulate carrion may facilitate managing this supplemental food source as potential mitigation for other anthropogenic threats to both Bald and Golden Eagles (*Aquila chrysaetos*), including wind-energy development.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *Common Raven*; Corvus corax; *coyote*; Canis latrans; *carrion*; *guild*; *winter scavenging*.

BÚSQUEDA INVERNAL DE CARROÑA DE UNGULADOS POR *HALIAEETUS LEUCOCEPHALUS*, *CORVUS CORAX* Y *CANIS LATRANS* EN EL NORTE DE ARIZONA

RESUMEN.—La carroña de los ungulados sustenta en invierno a un inusual gremio de carroñeros formado por canidos-córvidos-águilas en el norte de Arizona. Para evaluar el efecto de la ubicación y del hábitat en el uso y la longevidad de los cadáveres, entre diciembre de 1996 y abril de 2008 registramos 870 observaciones de consumo de carroña por parte de *Haliaeetus leucocephalus*, *Corvus corax* y *Canis latrans* sobre 123 cadáveres: 103 de *Cervus canadensis*, 12 de *Odocoileus hemionus*, siete de *Antilocapra americana* y uno de *Bos taurus*. Nuestra métrica temporal para medir la longevidad del cadáver y la presencia de carroñeros fue el cadáver-día (CD), numerado consecutivamente desde el primer día en que se registró el cadáver hasta que se consumió. Observamos 38 cadáveres separados (ubicaciones individuales), 39 cadáveres en formaciones de tres cadáveres en hábitats asociados con tipos de cobertura abierta, de borde y bosque (selección simultánea), 22 cadáveres abandonados a lo largo de la carretera donde murieron (monitoreados) y 24 cadáveres parcialmente desollados y/o abiertos (facilitados). Los cadáveres de alce duraron una media de 11.9 d (rango 3–41), con un 60% consumido durante la primera semana. El ciervo y el antílope duraron 5.5 d (rango 3–12) y 3.0 d (rango 2–4), respectivamente. Los cuervos normalmente llegaron el CD 3, las águilas el

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CD 4 y los coyotes el CD 6. Las águilas se apoyaron en los cuervos para las tareas de descubrimiento y de centinela, mientras que ambas especies dependieron de los coyotes para la accesibilidad. La carroña de invierno y de los atropellos en carretera, pero no la de la depredación de cánidos, determinó la disponibilidad de cadáveres. Las águilas y los coyotes usaron la carroña natural más que los cadáveres de origen antrópico (atropellos en carretera o abiertos), mientras que los cuervos fueron inhibidos por los coyotes. La eliminación de los cadáveres de ungulados de los derechos de paso de las autopistas y su apertura parcial promoverá un consumo más rápido y seguro de la carroña por parte de las aves, al reducir las posibilidades de colisión con los vehículos en tránsito. Un mejor entendimiento del uso de la carroña generada por el atropello de grandes ungulados puede facilitar el manejo de esta fuente adicional de alimento como una medida de mitigación potencial de otras amenazas antrópicas a *H. leucocephalus* y *Aquila chrysaetos*, incluyendo el desarrollo de la energía eólica.

[Traducción del equipo editorial]

Some raptors use carcasses extensively in winter but the dynamics of this use are poorly understood. Reliance on carrion as an alternative food source by facultative scavengers during prey shortages or stressful environmental conditions can have a substantial effect on their population dynamics and associated community structure (Selva et al. 2003, Wilmers et al. 2003b, Selva and Fortuna 2007). Natural carcass availability generally depends on location and cause of mortality (e.g., disease, parasites, malnutrition, exposure, or accidents; DeVault et al. 2003). Scavenger adaptations and abilities to locate and exploit carrion (such as visual and olfactory senses, foraging behavior, and ability to break into a carcass) also determine availability and subsequent accessibility of the carcass (Selva et al. 2005). Use of carrion by scavengers is a complex process involving environmental factors, facilitative interactions, and behavioral adaptations (Selva and Fortuna 2007). Strategies that enable scavengers to learn about foraging opportunities include traveling the landscape and visually locating food by chance, foraging where other scavengers are seen foraging, responding to vocalizations from other scavengers, and following conspecifics, who have previously located food, from nocturnal roosts (Stahler et al. 2002). Ravens (*Corvus* spp.) are extremely efficient at locating carcasses (Stahler et al. 2002, Selva et al. 2005; T. Grubb unpubl. data), in part because they and eagles (*Haliaeetus* spp.) both have large foraging radii plus a developed sociability through adjacent communal roosting (Grubb 1985, Wilmers et al. 2003b). Local enhancement (learning by observation, i.e. when a demonstrator's presence or interaction with objects at a location increases the likelihood of an observer visiting or interacting with objects at that location; Hoppitt and Laland 2013) is also an important aspect for these two genera in their utilization of spatially and temporally unpredictable carrion in open habitat (Stahler et al. 2002).

These avian scavenging advantages are evident in northern Arizona where, unlike in previously documented northern winter scavenging guilds in Yellowstone National Park, USA (Stahler et al. 2002, Wilmers et al. 2003a, 2003b), and in the Bialowieza Primeval Forest, Poland (Selva et al. 2003, Selva et al. 2005, Selva and Fortuna 2007), canine predation does not drive large ungulate carrion availability for the avian cohorts of this guild. Our long-term study of wintering Bald Eagles (*Haliaeetus leucocephalus*) in northern Arizona (Grubb and Kennedy 1982, Grubb 1996, Grubb and Lopez 2000) revealed their dependence on elk (*Cervus canadensis*) for food, in the form of hunter-abandoned gut piles in the late fall to road- and winter-killed carrion throughout the winter months (Wilmers et al. 2003b, Selva and Fortuna 2007). The close association between Bald Eagles and Common Ravens (*Corvus corax*) was also immediately apparent during our night-roosting observations (Grubb 1985, Wilmers et al. 2003b, Stromseng 2007) and at bait stations during eagle-trapping efforts (Grubb et al. 1989, 1994). However, it was not until we began manipulating and closely monitoring elk carcasses for the various trials detailed below, that the significant role of coyotes (*Canis latrans*) in this somewhat unusual, canine-corvid-eagle winter scavenging guild became evident.

Regardless of the specific scavenging dynamics, few data exist on the influence of specific location or microenvironment where an animal dies upon carcass availability or accessibility (DeVault et al. 2003); these authors suggested additional research was needed to elucidate the spatial and temporal trends in carcass availability to better understand the influence on scavenger behavior and ecology. We undertook the current experimental study as a first

step toward the broader research goal of modeling the effects of spatial and temporal variation in availability of large ungulate carrion on wintering Bald Eagle population and habitat use in northern Arizona. We here report only the results of that initial study in which we measured the influence of habitat associated with open, edge, and forest cover types, plus road rights-of-way, on winter ungulate carrion availability, accessibility, and longevity. Our field experimentation also enabled us to better document the function and dynamics of this previously undescribed canine-corvid-eagle winter scavenging guild.

METHODS

Study Area. Our study area was on the Colorado Plateau in northern Arizona, within Coconino and Yavapai Counties, on the Coconino National Forest (35°8′N, 111°40′W). Elevation ranged between 1524–2439 masl in gentle to steep mountainous terrain (Chronic 1983). Dominant vegetation was Rocky Mountain Montane Conifer Forest comprised of ponderosa pine (*Pinus ponderosa*) associations, with mixed conifer associations of Douglas- and white fir (*Pseudotsuga menziesii* and *Abies concolor*) at higher elevations, and Great Basin Conifer Woodland/pinyon-juniper associations (*P. edulis–Juniperus scopulorum*) at lower elevations (Brown and Lowe 1982). Winter weather varied greatly within and among years with occasional heavy snows (0.3–0.6 m) and cold temperatures (lows ≤ -18°C), interspersed with dry periods of mild temperatures (high ≥ 10°C) and general loss of snow cover (T. Grubb unpubl. data).

Carcass Collection and Distribution. Between December 1996 and April 2008, we collected road-killed elk carcasses and relocated them for our various scavenger trial scenarios. We patrolled local interstate highways two or three times per week for fresh road kills. We also coordinated with Arizona Department of Transportation (ADOT) and Arizona Department of Game and Fish (AZGF) to be notified of any fresh road kills. We picked up several mule deer (*Odocoileus hemionus*) opportunistically, and AZGF also provided seven pronghorn antelope (*Antilocapra americana*) that had died during translocation. We loaded most carcasses onto a utility trailer for transportation to trial sites. Because these sites were located away from roadways, we used all-terrain vehicles (ATVs) or snowmobiles to drag or trailer/sled carcasses to trial sites away from roads. In later years of the study, when instead of removing road kills, ADOT began leaving carcasses on site but pushed clear of the right-of-way, we adopted an additional protocol of monitoring some of those carcasses in place.

Estimates of Mass and Percent Remaining. We were only able to weigh a limited number of carcasses with a spring scale and automotive hoist but in doing so, we were soon able to reliably estimate mass within 10%, as verified by the hoist and scale. Percent remaining was a subjective metric, based on the remaining amount of edible tissues (Selva et al. 2005). Largely inedible skeleton, and to a lesser extent, hide were not considered part of the percent remaining (Wilmers et al. 2003a). We (TGG, RGL) worked together developing subjective but common standards and evaluation metrics, then tested ourselves in the field until we honed our ability to estimate percent remaining comparably. Intact carcasses rated $\geq$95% remaining were required for inclusion in our controlled experimental trials. Carcasses monitored in place were often discovered after partial consumption, but only those with $\geq$95% remaining were included in our analyses. Our basic temporal metric for measuring carcass longevity and scavenger presence was carcass d (CD), numbered consecutively from the first d the carcass was put out (CD 1) until it was gone (CD *n*). We typically checked each carcass once per d, i.e., one observation = one carcass check/d; however, more than one carcass was often checked on the same d when multiple trials or choices were underway. Nearly all of our carcass checks were in the morning, usually between dawn and approximately 1000 H; however, the generally unpredictable and highly variable geographic distribution of carcasses prevented consistently timed carcass visits and therefore also prevented structured temporal analyses any finer than by CD. During each carcass check, we recorded date, time, the percent of the carcass remaining, and the number of eagles, ravens, and coyotes on or near the carcass (Stahler et al. 2002). We also noted any tracks or avian excreta ("whitewash") present.

Trials and Definitions. We developed four types of experimental trials to evaluate elk carcass longevity and associated patterns of avian and canine scavenger use. The first was *individual* placement, where we placed a single carcass by itself, in habitats associated with open, edge, or forest cover, as described below. The second type was a simultaneous *choice* trial in which we placed three comparably sized carcasses about 0.4 km apart, one each in habitats associated

with open, edge, and forest cover. We conducted one anecdotal choice trial with an elk, deer, and pronghorn all placed in open cover. We also conducted two choice trials with three pronghorn carcasses in each. For some analyses, we combined individual and choice carcasses into a *natural* grouping, because all these carcasses were in settings away from anthropogenic influence. The third type of trial was *monitored* in place, in which we left carcasses where they lay along local interstate highways or paved US Forest Service roads, with daily observations commencing on the d they were reported or discovered. By definition, all monitored carcasses were along roadways. The last type of trial was *facilitated*, in which we cut the hide open to expose underlying soft tissue, usually along the neck, belly, fore, and/or hind quarters. In extreme examples of a facilitated trial (described below), we skinned entire elk and placed the carcasses where coyote discovery was unlikely. For some analyses, we combined monitored and facilitated trials into a *human-influenced* grouping, indicating the carcass was road-killed or cut open. For all our carcass placements, we defined cover types as *open* if $\geq$100 m from nearest, continuous forest stand; as *edge* if along forest/open interface, typically among scattered trees with $<$25% canopy cover; and as *forest* if within a continuous forest stand, with $>$30% canopy cover and $\geq$100 m from any edge.

Scavenging Metrics. We calculated *presence* as the percent of carcasses within each trial type visited by each scavenger (Selva et al. 2005). *Scavenging frequency* was the percent of total d a carcass was checked that a scavenger was seen on or near that carcass (Wilmers et al. 2003b). To calculate an average daily consumption or *carcass depletion rate* (Selva et al. 2003) for each type of ungulate carrion, we first calculated mean mass of all carcasses in each type for which we had actual or estimated mass (n = 77 for elk, nine for deer, seven for pronghorn antelope). We then took 68% of the mean mass as an approximation of edible biomass available to scavengers (Wilmers et al. 2003a). We only used intact carcasses that were entirely consumed to calculate average daily consumption rates (for all three scavengers combined) by dividing available biomass by the number of d required for carcass depletion ($<$5% remaining). Because coyotes were a vital third of this scavenging guild in their role as primary facilitator for avian accessibility to carrion, we have included them throughout our data summaries and analyses. However, coyote daytime data are included as only a relative indication of behavioral patterns for comparative purposes. They do not represent coyote scavenging activity or presence, which occurred mostly at night and was beyond the scope of our field capabilities.

Skinned Elk Trials. To experimentally eliminate primary scavenging by canines, and to gain insight into the potential extent of avian scavenging if given unfettered access (i.e., to a totally exposed, skinned carcass) without the typical corresponding loss of consumable tissue to canines, we conducted four trials in January–March 2005. For each trial we placed a skinned elk carcass (three adult cows and one yearling) within the median of Interstate Highway I-17, where the north and south bound lanes were separated by nearly 1 km (approximately 960 m), forming a natural barrier perimeter discouraging to most coyote traffic in the area. The relatively open cover of the pinyon-juniper vegetation association at this site was accessible to ravens and eagles. We placed the carcass for each trial in the open, midway between the highway lanes on a hillside, where it was visible from the northbound lane 400–500 m away. We monitored scavenging activity from the highway every d of each trial. We estimated 60% available biomass and a subsequent avian scavenging rate for these trials by combining percentages determined by Wilmers et al. (2003a): 8% hide and brain, 32% rumen and inedible bone. The total d and available biomass for each trial were: (1) trial one: 9 d, 127.9 kg; (2) trial two: 3 d, 129.3 kg; (3) trial three: 4 d, 81.6 kg; and (4) trial four: 7 d, 104.8 kg. We visually monitored for canine or any other mammal scavenging during the trials, and checked the soft ground near carcasses for tracks at the end of each trial.

Other Anecdotal Trials. Not included in our primary data analyses were one domestic cow (*Bos taurus,* 230 kg estimated mass) collected as an intact road kill, and three unsuccessful platform efforts intended to eliminate any canine influence on avian scavenging, but which failed to attract ravens or eagles. We conducted the skinned carcass, cow, and platform trials to explore alternatives for manipulating ungulate carcasses to supplement eagle winter forage. We placed the cow along the forest edge of a continuous grass-dominated meadow, typical of northern Arizona rangeland, where we could observe it from a vehicle on an adjacent roadway approximately 350 m away. For the platform experiments, we constructed a 2-m high, 2.4 $\times$ 2.4 m wooden platform in an open meadow and

Table 1. Length of time until the first appearance of Common Ravens, Bald Eagles, and coyotes on or near fresh elk carcasses, and the maximum number of scavengers occurring at a carcass. Type of placement includes all-data-except-facilitated, all data, individual, and simultaneous choice placements in natural forest settings, monitored along roadways, and facilitated by being partially skinned or opened, in northern Arizona, during winters 1996–2008. (Table includes all carcasses regardless of percent initially present, as long as monitoring began prior to any evidence of scavenging.)

Scavenger	Type of Placement	Maximum Number of Scavengers	Length of Time Until First Appearance (d)			
			Mean	SD	Range	*n*
Common Raven	All data except facilitated	50	2.6	2.70	1–22	94
	All data	67	2.4	2.59	1–22	117
	Individual	40	2.9	2.26	1–14	34
	Choice	45	2.1	1.10	1–5	38
	Facilitated	67	1.8	2.02	1–10	23
	Monitored	50	3.0	4.64	1–22	22
Bald Eagle	All data except facilitated	17	3.6	4.09	1–31	81
	All data	18	3.5	3.89	1–31	98
	Individual	14	4.2	3.47	1–15	32
	Choice	17	2.6	1.66	1–8	36
	Facilitated	18	3.1	2.82	1–10	17
	Monitored	7	4.7	8.19	1–31	13
Coyote[a]	All data except facilitated	7	5.4	6.59	1–34	95
	All data	7	5.3	6.38	1–34	103
	Individual	7	5.7	6.43	1–34	35
	Choice	6	5.0	4.64	1–25	39
	Facilitated	4	3.5	2.39	1–9	8
	Monitored	1	5.9	9.59	1–32	21

[a] Coyote daytime data are included as a relative indication of behavioral patterns for comparative purposes, but they do not reflect actual scavenging activity or presence, which occurred mostly at night.

formerly high-use area for scavenging, where ADOT had disposed of carcasses in years past. We estimated 60% available biomass for trials one and two (skinned carcasses), and 68% for trial three (intact carcass), by using percentages of Wilmers et al. (2003a) mentioned above. Dates, total d, carcass species, and available biomass for each trial were: (1) trial one: December 2002, 15 d, cow elk, 115.7 kg; (2) trial two: January 2003, 5 d, yearling mule deer, 34.0 kg; (3) trial three: February–March 2003, 53 d, adult mule deer, 40.8 kg.

Statistical Analyses. We used generalized linear models to compare presence and scavenging frequency among the treatments. We modeled presence using a binomial error structure with differences among groups assessed via deviance ratios. We modeled scavenging frequency using a Gaussian (normal) error structure with differences assessed using *F*-statistics on residual variance (ANOVA). In comparisons that included simultaneous choice carcasses, we weighted observations to account for nonindependence of observations within the choice experiments ($w_{i,j} = 1/3$ for each carcass within a simultaneous choice experiment versus $w_{i,j} = 1$ for non-choice carcasses, where i = specific carcass and j = number of carcasses within trial). We modeled both experimental type and habitat as represented by cover type as categorical variables, with a Bonferroni-Holm adjustment for post-hoc comparisons among treatments.

Results

Observations and Trials. Between December 1996 and April 2008, we recorded 870 observations of wintering Bald Eagles, Common Ravens, and coyotes scavenging 123 ungulate carcasses: 103 elk, 12 mule deer, seven pronghorn antelope, and one domestic cow. We observed 38 separate carcasses (individual), 39 as part of three-carcass simultaneous trials (choice), 22 left in place along the roadway where killed (monitored), and 24 carcasses partially skinned or otherwise opened (facilitated).

First Appearance. Whereas all three scavenger species, especially Common Ravens, were sometimes present on the first CD, on average ravens arrived by CD 3, Bald Eagles by CD 4, and coyotes by CD 6 (Table 1). Based on mean values alone, Bald Eagles appeared soonest at choice carcasses, then facilitat-

Table 2. Mean carcass longevity (total d) and mean length of time (d) until the first appearance of Common Raven, Bald Eagle, and coyote on or near elk, mule deer, and pronghorn antelope carcasses placed as individual carcasses in habitats represented by open (≥100 m from nearest, continuous forest), edge (along forest/open interface), and forest (within continuous forest stand ≥100 m from any edge) cover types, or simultaneously in these three cover types for feeding choice trials, in northern Arizona during winters 1996–2008.

		Mean Length of Time (d) Until First Appearance			
Type of Placement	Cover Type	First Raven Mean (SD, *n*)	First Eagle Mean (SD, *n*)	First Coyote[a] Mean (SD, *n*)	Carcass Longevity Mean (SD, *n*)
Individual	Open	2.4 (1.08, 10)	2.3 (1.12, 9)	3.7 (2.50, 10)	11.1 (6.10, 10)
	Edge	3.1 (3.14, 15)	4.8 (4.17, 14)	6.0 (6.21, 15)	15.9 (14.64, 15)
	Forest	2.9 (1.45, 9)	5.2 (3.38, 9)	4.1 (2.96, 10)	11.7 (6.40, 10)
Choice	Open	1.6 (0.63, 15)	2.1 (1.06, 15)	3.2 (1.47, 15)	8.2 (5.03, 15)
	Edge	2.3 (1.07, 12)	3.6 (2.46, 11)	4.5 (3.20, 12)	10.2 (7.17, 12)
	Forest	2.6 (1.36, 11)	2.3 (0.68, 10)	3.4 (3.00, 12)	6.9 (3.73, 12)
Combined (both types)	Open	1.9 (0.91, 25)	2.2 (1.06, 24)	3.4 (1.92, 25)	9.4 (5.55, 25)
	Edge	2.4 (0.98, 27)	3.8 (2.76, 25)	5.3 (5.07, 27)	11.6 (8.04, 27)
	Forest	2.8 (1.37, 20)	3.7 (2.75, 19)	3.7 (2.93, 22)	9.1 (5.55, 22)

[a] Coyote daytime data are included as a relative indication of behavioral patterns for comparative purposes, but they do not reflect actual scavenging activity or presence, which occurred mostly at night.

ed, individual, and monitored ones; ravens and coyotes appeared soonest at facilitated carcasses, followed by choice, individual, and monitored carcasses, respectively. However, none of these trends were statistically significant. Maximum numbers of Common Ravens, Bald Eagles, and coyotes we observed visiting a carcass at any one time during daylight hours were 67, 18, and 7, respectively, with the largest number of avian scavengers occurring at facilitated carcasses. Eagles and ravens tended to linger longer at depleted carcasses than coyotes. All three scavenger species consistently appeared soonest at carcasses in open areas, regardless of whether individually placed or part of a three-carcass simultaneous trial (Table 2).

Presence and Scavenging Frequency. Common Ravens were the most ubiquitous among northern Arizona scavengers in terms of presence at carcasses and scavenging frequency (Table 3). They were also little affected by human-influenced carrion as opposed to carcasses in natural settings (presence: 95.8% vs. 98.7% respectively, $D = 0.96$, $P = 0.33$; scavenging frequency: 67.6% vs. 62.7%, $F_{1,121} = 1.13$, $P = 0.29$). Bald Eagle presence and scavenging rates were lower at human-influenced sites (93.3% vs. 62.5% presence for natural vs. human-influenced sites, $D = 19.11$, $P < 0.001$; scavenging frequency: 47.0% vs. 30.2%, $F_{1,111} = 18.13$, $P < 0.001$). Coyote patterns were not reliably testable, but appeared to decline similarly at human-influenced vs. natural sites. Scavenging frequency at facilitated vs. monitored-in-place carcasses did not differ statistically (ravens: 73.2% vs. 61.4%, eagles 35.2% vs. 21.3%, coyotes: 9.5% vs. 5.9%; $F_{1,107} = 2.09$, $P = 0.15$). The presence of nearby multiple carcasses during simultaneous trials had little effect on the scavenging frequency of all three species ($F_{1,222} = 0.044$, $P = 0.83$). Scavenging presence and frequency did not differ by cover type among scavengers ($t = -2.731$, $P = 0.239$), except for ravens scavenging more frequently in the open than within forest cover, and coyotes being present more often in the open and along edges than within forest cover ($z = -3.009$, -3.151, respectively, $P \leq 0.005$). However, mean values for all three scavengers suggested a possible pattern of declining use from open through edge to forest cover.

Carcass Longevity. Mean carcass longevity varied among ungulate species, and for elk placed as an individual or simultaneously for feeding choice trials in natural forest settings, monitored as road kills along roadways, or facilitated by being partially skinned or otherwise opened (Table 4). Monitored road kills lasted >3 wk on average, approximately 10 d longer than individual carcasses placed in more natural settings ($F_{1,107} = 2.98$, $P = 0.003$), whereas partially skinned or opened carcasses typically were consumed in 1 wk. All categories of elk carcasses lasted much longer than mule deer or pronghorn antelope (Table 4). Longevity ranges for elk indicated carcasses may persist 2–3 times longer

Table 3. Presence (percent total carcasses where scavenger recorded) and scavenging frequency (percent total d scavenger recorded on or near a carcass) for Bald Eagles, Common Ravens, and coyotes recorded during daytime observations of individual and simultaneous placement (natural), monitored in place along roadways and facilitated (human-influenced), large ungulate carcasses ($n = 123$) in northern Arizona, during winters, 1996–2008. Presence and scavenging frequencies are also presented for the three cover types recorded during individual and simultaneous choice placements: open, edge, forest ($n = 25$, 26, and 22, respectively).

	Presence (% Carcasses)			Scavenging Frequency (% Days)		
Carcass Type/Cover Type	Eagles	Ravens	Coyotes[a]	Eagles	Ravens	Coyotes[a]
Natural	93.3	98.7	85.3	47.0	62.7	26.1
Individual	94.7	100.0	78.9	44.7	64.9	24.9
Choice	92.3	97.4	89.7	50.4	60.9	27.4
Human-influenced	62.5	95.8	35.4	30.2	67.6	8.6
Monitored	54.5	95.4	40.9	21.3	61.4	5.9
Facilitated	66.7	95.8	29.2	35.2	73.2	9.5
Cover type						
Open	96.2	100.0	96.0	54.0	70.4	29.3
Edge	92.6	100.0	92.3	46.0	62.7	26.8
Forest	91.7	95.8	72.7	40.4	54.8	19.5

[a] Coyote daytime frequencies are included as a relative indication of behavioral patterns for comparative purposes, but they do not reflect actual scavenging activity or presence, which occurred mostly at night.

than the mean time, whereas deer and pronghorn ranges did not exceed their longevity means by more than 1 wk. Although trial longevity means (Table 4) differed, simultaneously placed elk carcasses were not consumed any more quickly than carcasses deployed individually (9.9 d vs. 13.2 d, respectively; $F_{1,61} = 2.37$, $P = 0.13$).

Consumption Rates. Elk carcasses were consumed by scavengers on average in about 12 d (Table 4), although elk carcasses often lasted nearly 3 wk, with 60% being consumed during the first week (Fig. 1a). Smaller mule deer and pronghorn antelope carcasses usually lasted <1 wk (Fig. 1b and Fig. 1c), being consumed on average in approximately 5 and 3 d, respectively. Both mule deer and pronghorn antelope carcasses were often consumed entirely in one night once discovered by coyotes, which also sometimes dragged the remains away. Average daily consumption rate (by all three scavenger species combined, and determined from percent remaining estimates) was 11.1 kg/d for elk, 6.9 kg/d for mule deer, and 6.6 kg/d for pronghorn. Mean daily consumption rate of elk for all three scavengers combined started off slowly (4.4 kg/d for CD 1–3),

Table 4. Carcass mass, available mass, and carcass longevity (total d by species and placement) for 95 and 102 ungulate carcasses, respectively, scavenged by Bald Eagles, Common Ravens, and coyotes in northern Arizona, during winters 1996–2008, and mean daily, scavenging consumption rates (kg/d). Longevity calculations were based on carcasses initially ≥95% intact. Elk carcasses were observed as individual and simultaneous choice placements in natural forest settings, monitored along roadways, and facilitated by being partially skinned or opened.

	Carcass Mass (kg)				Carcass Longevity (d)				Available	Consumption
Carcass Species	Mean	SD	Range	*n*	Mean	SD	Range	*n*	Mass (kg)[a]	Rate (kg/d)
Elk	194.7	38.5	102–295	80	11.9	8.2	3–41	88	132.4	11.1
Individual	196.9	29.0	125–227	29	13.2	6.9	5–34	30	133.9	10.1
Choice	186.4	44.3	102–273	31	9.9	5.2	4–30	30	126.8	12.8
Monitored	226.8	18.5	204–250	3	22.9	13.1	5–41	10	154.2	6.7
Facilitated	200.9	39.5	102–295	17	7.0	2.9	3–13	18	136.6	19.5
Deer	56.1	14.5	30–79	7	5.5	3.0	3–12	6	38.1	6.9
Pronghorn	29.2	7.3	2–39	7	3.0	0.9	2–4	7	19.9	6.6
Domestic cow	227.3	–	–	1	59.0	–	–	1	154.6	2.6

[a] 68% total biomass (Wilmers et al. 2003).

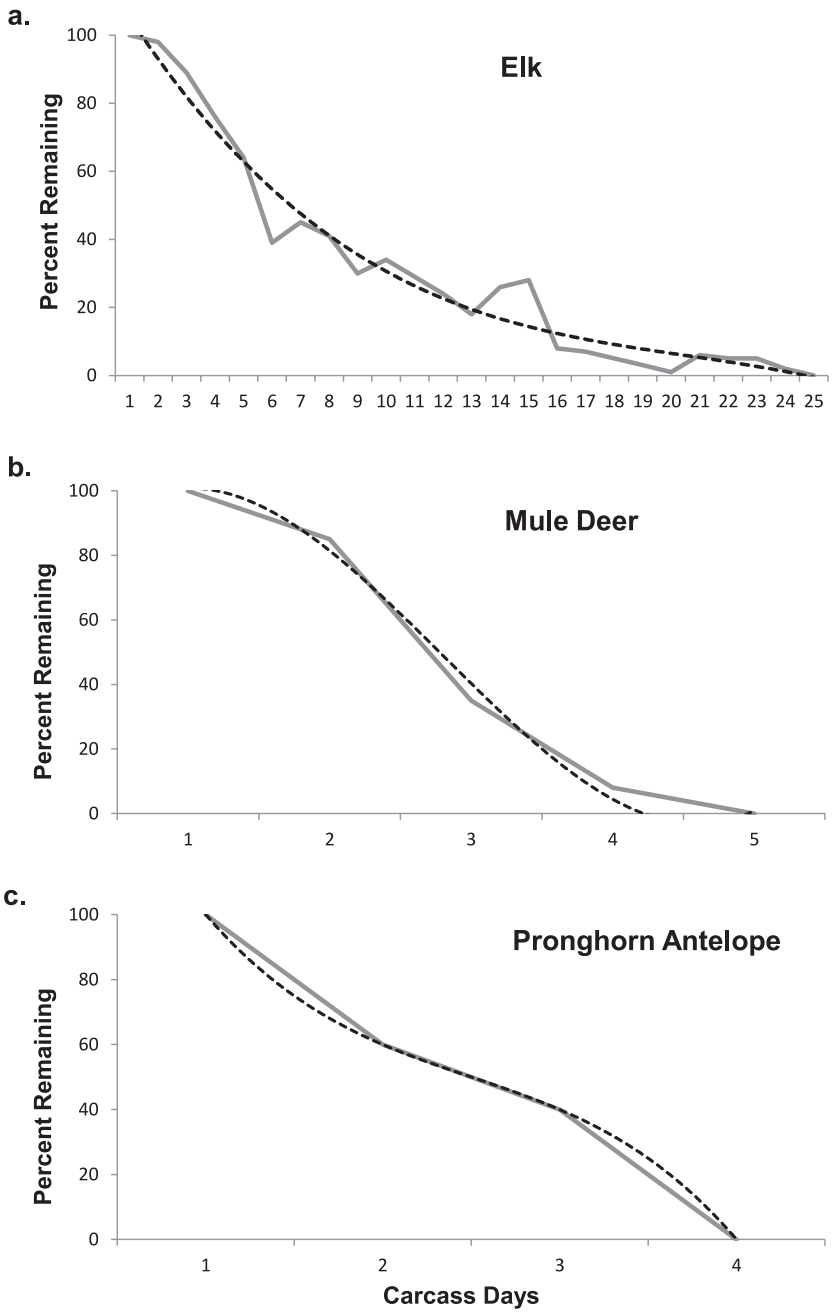

Figure 1. (a) Elk ($n=88$, $\bar{X}=11.9$ carcass d [CD]), (b) mule deer ($n=6$, $\bar{X}=5.5$ CD), and (c) pronghorn antelope ($n=7$, $\bar{X}=3.0$ CD) carcass longevity as measured by mean percent remaining (averaged across all carcasses for each species) and numbered in consecutive CD from initial placement or discovery until carcass depletion (<5% remaining) by scavenging Bald Eagles, Common Ravens, and coyotes in northern Arizona, during winters 1996–2008. Third order polynomial trend lines provide smoothed estimates of carcass depletion and evidence of strong, predictive relationships for carcass longevity.

peaked between CD 4–10 (11.4 kg/d), and was lowest after the bulk of the carcass had been consumed, between CD 11–25 (2.7 kg/d).

Skinned Elk Trials. Common Ravens were already present when we placed all four skinned elk trial carcasses, and were on or near the carcasses 23 (96%) of 24 total observation d. Bald Eagles were present at two initial placements, and were on or near the carcasses 18 (75%) of 24 total observation d. We found coyote tracks on CD 9 (last d) of trial one, although there was no evidence of prior canine presence nor use. We observed a bobcat (*Lynx rufus*) feeding on the carcass on CD 4 (of seven) during trial four. However, we found no evidence of any other scavengers except ravens and eagles during trials two and three, when both species were present every d. Numbers of ravens and eagles and average consumption rates for the four trials were: (1) trial one: 6–32 ravens, 2–12 eagles, 14.2 kg/d; (2) trial two: 9–40 ravens, 1–18 eagles, 43.1 kg/d; (3) trial three: 15–30 ravens, 8–12 eagles, 20.4 kg/d; and (4) trial four: 0–20 ravens, 1–14 eagles, 15.0 kg/d.

Other Anecdotal Trials. The domestic cow carcass lay essentially untouched for nearly 7 wk between 20 November 2003 and 15 January 2004, with only 1–2 Bald Eagles and 1–5 Common Ravens recorded on or near the carcass on 11 occasions. We saw 1–2 coyotes in the vicinity of the cow carcass three times. Between CDs 49–59, the cow was finally consumed, presumably by coyotes although we saw only four in the vicinity once during that period. We also observed 1–3 eagles and 2–10 ravens scavenging the cow carcass once it was exposed.

On CDs 1–2 of platform trial one, we observed an unrecorded number of ravens (<10) on or near the carcass. A mountain lion (*Puma concolor*) claimed the carcass on CD 3, and remained attending the carcass, either feeding or resting underneath in the shade of the platform, 5 d more during which it consumed about 50% of the available biomass. Although ravens perched or flew in the area every d, they never returned to the remaining platform carcass again, even after the mountain lion departed. We terminated the trial after an additional 7 d (15 d total for trial). We observed no avian scavengers during platform trial two. For trial three, we added an unskinned, male mule deer to the same platform. Although we recorded 20 ravens in the area on CD 10, and 3 eagles on CD 14, neither species approached the platform nor were recorded again during the remainder of the trial, which lasted 53 d until we removed both intact carcasses and the platform on 31 March 2003.

Coyote/Bald Eagle Confrontation. Intraspecific squabbles, especially among eagles and ravens, were common throughout our study. Interspecific interactions usually involved eagles supplanting ravens, and both species being flushed or kept at bay by scavenging coyotes, with no direct contact. However, on 4 February 1994, several Bald Eagles were fighting among themselves near a female mule deer and fawn carcass in a small forest opening, when a coyote rushed in and caused the eagles to flush. As the coyote began to feed, a large adult female Bald Eagle flew at the coyote. The coyote bolted several meters away, as the eagle landed atop the carcass. After the eagle began to feed, the coyote rushed in again, causing the eagle to flush and land a few meters away. After only a few more seconds, the eagle flew at the coyote, which lunged upward snapping with open jaws at the attacking eagle. The eagle backed away with wings widespread and talons out-thrust, just out of reach of the coyote's lunges. The two sparred back and forth in this fashion for nearly 1 min, coming close but never making contact. Ultimately they separated with the coyote standing a few meters off to one side of the carcasses, and the eagle a similar distance away on the opposite side. After a few more minutes, both walked slowly and hesitantly toward the carcasses and began to warily feed on separate pieces <2 m apart. Once the two antagonists started feeding separately, other eagles resumed fighting with the adult female, and a second coyote came in to feed when the first coyote eventually walked off.

Discussion

Consumption Rates and Carcass Longevity. Wilmers et al. (2003a) described four scavenging stages (plus a fifth inedible category) for elk consumption by Bald Eagles, Common Ravens, coyotes, and three other facultative scavengers in Yellowstone National Park, USA. Wilmers et al.'s (2003a) Stage 1–3 organs and entrails (14%), major muscle (31%), and minor muscle (15%), respectively, were consumed during the first wk in northern Arizona, when on average about 60% of elk carcasses were consumed. Remaining biomass after that consisted of a little remaining Stage 3 minor muscle, and Stage 4 brain and hide (8%) with remnants of attached soft tissue, and any broken bones with exposed marrow, which eagles and ravens often pecked. The sheer bulk of Wilmers et al.'s (2003a) Stage 4 hide, along with inedible

bone, explains the nearly 2-wk lingering attention to Arizona elk carcasses, primarily by avian scavengers, beyond the 12-d consumption mean. Smaller mule deer and pronghorn antelope carcasses typically lasted no more than 1 d beyond their mean longevities (5.5 and 3.0 d, respectively). Later activity at all carcasses became predominantly avian after Wilmers et al.'s (2003a) Stage 3 muscle was consumed, presumably because insufficient biomass remained to be energetically worthwhile for coyotes.

Selva et al. (2003) found European bison (*Bison bonasus*) carcasses lasted an average of 106 d and were consumed by 13 species of avian and mammalian scavengers at an average rate of 3 kg/d with a peak consumption of 6.8 kg/d during the first 2 wk. Their maximum consumption rate was 68 kg/d, for all scavengers. Our overall estimate for elk carcass consumption in Arizona was 11.1 kg/d (Table 4), and our highest rate recorded was during the avian trial when 43 kg/d were consumed by eagles and ravens alone. Consumption rate in our trials peaked during the first wk at 11.4 kg/d. The difference in consumption rates may be attributable to different species of ungulate carrion and the European bison scavenging guild's reliance on wolves (*Canis lupis*) to facilitate both availability and accessibility. The longest carcass longevity and the resulting lowest consumption rate at monitored carcasses (22.9 d and 6.7 kg/d, Table 4) were likely attributable to the disturbance imposed by passing traffic. In Washington State, Bald Eagles fed less often at disturbed sites, ate less, and seldom returned to feed the same day after leaving carcasses in response to human activity (Skagen et al. 1991).

Cover Type Influence on Scavenging Rates. Although trends were not statistically significant, all three scavengers tended to appear sooner at carcasses placed in open areas, perhaps in part due to better visibility, availability, and visual security (Grubb and Kennedy 1982). In Poland, nearly all of 13 recorded scavengers were observed significantly more often at bison carcasses located in clearings compared to those in forests (Selva et al. 2003). Ravens scavenged bison carcasses 82.8% in the open and 48.9% in forest. In our study, Common Raven scavenging rates of 70.4% for open areas and 54.8% for forest cover were relatively comparable (Table 3), and were the only scavenging rates that differed among cover types for the three scavengers. Arizona Bald Eagles still scavenged in forest although much less than in the open (40.4% vs. 54.0%, respectively), whereas White-tailed Sea Eagles (*Haliaeetus albicilla*) in Poland did not frequent carcasses in forests at all and scavenged only 24.5% in the open (Selva et al. 2003). In addition to likely differences in species' behavior, northern Arizona forests may be more open than forests in Poland, permitting easier access by avian scavengers. The differences among open and forest edge for coyote presence are likely an artifact of observer bias favoring spotting coyotes in more open cover types.

Variability Among Carcasses and Trials. Given the large size of our data set, we did not expect the inherent variability within many of our analytical metrics nor the lack of strong differences in statistical comparisons. However, because none of our focal species are obligate scavengers, this lack of verifiable patterns or detectable differences may simply be explained by the fact that facultative scavenging is a highly flexible strategy for resource acquisition (Wilson and Wolkovich 2011). The unpredictability of naturally occurring, large ungulate carcasses in winter in northern Arizona, driven by highly variable weather patterns that fluctuate dramatically within and among years (Grubb and Kennedy 1982, Grubb and Lopez 2000), is consistent with this explanation. In addition, this region is on the southern periphery of Bald Eagle winter range, resulting in few, widely scattered eagles, and highly nomadic patterns of roosting and foraging (Grubb et al. 1989). The largely open and uniform nature of ponderosa pine forest and pinon-juniper associations in our study area (Brown and Lowe 1982, Reynolds et al. 2013) may generally facilitate avian searching, while reducing the effects of differential discovery by ravens and eagles.

All the preceding explanations should also be considered in the longer-term context of climate change. Over the last 40 years, winters have generally become milder with less frequent and abundant snowfall (Garfin et al. 2013). Bald Eagle winter activity in northern Arizona has gradually shifted approximately 50 km north in latitude and 600 m up in elevation, numbers have declined, alternative winter prey sources of fish and waterfowl have declined or disappeared, and local elk wintering and migration patterns have shifted northward and upward, resulting in fewer highway crossings and resultant road kills in recent years (T. Grubb unpubl. data). In a non-predator-driven scavenging system such as this one in northern Arizona, the availability of winter-killed, large ungulate carrion will also likely continue to decline with milder winters (Wilmers and Getz 2005), potentially forcing local Bald Eagles,

Common Ravens, and coyotes to cultivate alternative winter foraging habits. However, at present, given the nomadic, opportunistic nature of all three scavengers, our results suggest even in this ever-changing, southwestern US environment, current scavenging guild dynamics are little affected by where elk mortality occurs.

Canine–Avian Scavenging Partitioning. Eagles and ravens commonly occur in winter scavenging guilds where wolves are the primary canine predator (Selva et al. 2003, Wilmers et al. 2003b). In such systems, ravens have often learned to follow wolves rather than ungulates, even to the point of neophobia, an avoidance of non-depredated, ungulate carcasses (Stahler et al. 2002). Any potential avian-canine competition is most often mediated by temporal partitioning (Stromseng 2007, Killengreen et al. 2011, Kendall 2014) and to a lesser extent resource allocation (Olson et al. 2016). Avian scavengers are most active in early mornings through the daylight hours, when they can search efficiently, carcass availability is highest (because most ungulate mortality occurs at night; Kendall 2013), and they can scavenge accessible portions of carcasses uncontested (T. Grubb unpubl. data). Canines typically hunt, forage, and scavenge at night (Stromseng 2007, Killengreen et al. 2011, Kendall 2014); coyotes are largely crepuscular and nocturnal (Andelt and Gipson 1979; Holzman et al. 1992). However, when coyotes, eagles, and ravens overlap at a carcass during daytime, the avian scavengers will usually be supplanted to peripheral, less desirable pieces (such as bones or bits of hide) or bumped off the carcass entirely (T. Grubb unpubl. data). The potential cost of direct confrontation for a bird far outweighs the slight energetic gain of trying to forage beside a canine predator, whereas for the coyote it is not worth the energetic cost of unsuccessfully chasing innumerable corvids or quick-flying eagles off the carcass (Stromseng 2007). Thus, we speculate that the coyote-eagle confrontation we recorded is probably uncommon and almost certainly attributable to the individual temperaments of the two antagonists, and was potentially exacerbated by a particularly severe winter in 1994.

Other Anecdotal Trials. Corvid neophobia for non-depredated, large ungulate carcasses may have influenced the lack of scavenging activity and the resultant longevity of our one cow carcass. Depressed social facilitation (among ravens; Marzluff and Heinrich 1991) and local enhancement (for ravens, eagles, and coyotes; Turner 1964) may have resulted from this initial carcass avoidance by ravens (Stahler et al. 2002). In Poland, 13 scavenger species, including five birds and six mammals, used undisturbed, dead ungulates less frequently than hunter or predator kills (Selva et al 2005). Unusual human presence (Skagen et al. 1991) in the form of anthropogenic structures may have had a detrimental effect on the outcome of our three platform trials. In Kenya, five experimental carcasses placed near areas of high human settlement density received no visits from seven avian scavengers, other than one occasionally flying overhead (Kendall 2013). The mountain lion's use of our first platform carcass may be analogous to mountain lions usurping kills of other predators (Koehler and Hornocker 1991); in addition, that lion remaining at the platform carcass for several d is consistent with typical mountain lion caching behavior (Mattson et al. 2007). The only other scavengers recorded during our study were one bobcat (*Lynx rufus*) and three Turkey Vultures (*Cathartes aura*), all occurring at the end of May.

Management Implications. Understanding patterns of large ungulate carrion use by Bald Eagles and their associated scavenging guild cohorts may help to identify much-needed, mitigation measures for other anthropogenic threats to both Bald and Golden Eagles (*Aquila chrysaetos*), such as wind-energy development (US Fish and Wildlife Service 2013, 2016). Both road kill removal (to reduce vehicle strikes) and prey habitat improvement (to increase eagle productivity) have been identified as compensatory mitigation strategies for Golden Eagles threatened by wind energy facilities (Allison et al. 2017). Our results indicate the following considerations may improve the effectiveness of both strategies. (1) Entirely removing ungulate carcasses from highway rights-of-way not only reduces the likelihood of collisions with vehicles, but increases avian scavenging efficiency. (2) Relocating carcasses as early in the day as possible, in the open, away from highway activity and any other anthropogenic influences or structures further increases the likelihood and efficiency of avian scavenging. (3) Larger ungulate carcasses such as elk last longer and provide more available biomass than smaller carcasses such as mule deer or pronghorn antelope. In addition, carcasses of larger species cannot be moved or as quickly consumed once discovered by canine scavengers. (4) Carcasses of domestic or exotic species, such as the cow in our study, may not be as attractive to avian scavengers as those of

indigenous ungulates. (5) Partially opening an ungulate carcass to improve accessibility both encourages avian scavenging and expedites carcass consumption and removal from the landscape. (6) Fully skinning a carcass encourages more rapid avian consumption, independent of canine discovery of the carcass (Kane and Kendall 2017). Items 2–6 should encourage both Bald Eagle and Golden Eagle scavenging, especially during winter months, and therefore supplement the concept of increasing prey availability through habitat improvement alone. In northern Arizona, management and protection of Bald Eagle wintering habitat should be flexible and adaptable, as the most suitable habitat in any year is largely dependent on elk concentrations and movements, which are influenced by seasonal weather conditions and winter severity (Grubb and Lopez 2000).

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