

RESEARCH NOTE

Summer diet of California's recolonizing gray wolves

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After an estimated 87-year absence (circa 1924–2011), gray wolves (*Canis lupus*) have begun to recolonize California (Grinnell et al. 1937; Kovacs et al. 2016). Prior to European colonization, gray wolves are thought to have subsisted on native prey including mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*; Grinnell et al. 1937). Due to concerns about the potential effects of gray wolves on both native ungulates and livestock, our objective was to assess the diet of California gray wolves (CDFW; Kovacs et al. 2016).

Gray wolves generally use prey species in accordance with their availability (Nowak et al. 2011; Meriggi et al. 2015). For example, native ungulates are more abundant in North America than in Europe and Asia, and gray wolves in North America rely primarily on native ungulates while gray wolves in Europe and Asia rely more on domestic animals (Torres et al. 2015; Newsome et al. 2016; Janeiro-Otero et al. 2020). As there are lower densities of native ungulates in California than other areas of North America where gray wolves exist (CDFW 2018; Furnas et al. 2018), gray wolves in California may use relatively more alternative prey such as beavers (*Castor canadensis*), rabbits (*Sylvilagus* spp. and *Lepus* spp.), and livestock. While it will require additional work to thoroughly describe the diet of wolves in California, our approach and analyses to date offer a framework for future study and helping wildlife managers better understand aspects (e.g., diet composition and scavenging behavior) of wolf diet in California.

The Lassen pack, located east of Lassen Peak and Lake Almanor, roams over parts of Lassen and Plumas Counties and was first documented in 2016. The pack has produced litters each year from 2017–2020. We used abandoned den and rendezvous sites of the Lassen pack to collect adult-sized wolf scats to determine the diet of the pack. We also collected adult sized wolf scats opportunistically along dirt roads, game trails, and feeding sites. Because the Lassen pack has mostly distinct summer and winter ranges, we assumed scats collected opportunistically in the summer home range were deposited during summer months. Scats were collected in 2017 (May–October), 2018 (June–October), and 2019 (April–July); the majority (89%) of overall scats represent scats deposited April–July for all years.

A subset (47%) of collected scats were genetically verified (Frantzen et al. 1998; Adams et al. 2007) as originating from *Canis lupus*; others were identified as adult wolf based on size (≥ 29 mm diameter for adult scat; Weaver and Fritts 1979) or by location at a den/rendezvous site. All scats >29 mm were genetically verified as wolf scats, supporting our use of scat diameter alone to identify adult wolf scat (e.g., Dellinger et al. 2011b).

Scats were individually washed to separate hair and bone fragments. Those contents were identified by comparing them to reference materials (e.g., CDFW collections; Moore et al. 1974) and assigned to one of three categories: black-tailed deer (*Odocoileus hemionus columbianus*), cattle (*Bos taurus*), and small mammals (e.g., raccoon [*Procyon lotor*], rabbit, beaver, and ground squirrel [*Spermophilus* spp.]). We used two metrics to rank and determine overall and annual (i.e., each summer during the three years of data collection) percent contribution of food items in scats. One metric was percent frequency of occurrence (PFO; Ciucci et al. 1996; Steenweg et al. 2015), where the frequency with which each food item occurs in individual scats is expressed as a percentage of the total number of occurrences of all food items. The second metric was biomass ingested (BI; Weaver 1993; Dellinger et al. 2011a), which is an estimate of prey biomass consumed per collectable scat produced. Each method is recognized as having biases and using both may provide a better description of diet than using only one method (Ciucci et al. 1996; Dellinger et al. 2011a). PFO can over represent smaller prey items in the diet (Klare et al. 2011) but, unlike BI, PFO does not rely on assumptions of live weight of each species consumed. Items that were $<1\%$ of a scat were ignored (Gable et al. 2017). For BI we set live weight of each species as: black-tailed deer – 45 kg (average weight of a black-tailed deer across all sex and age classes per Walmo 1981 when weighted by age and sex demographic ratios per Furnas et al. 2018), cattle – 272 kg, small mammals – 8 kg (Jameson, Jr. and Peeters 2004). Live weight for cattle was derived from average estimated live weight of calves, yearlings, and cows present in the Lassen packs home range (CDFW unpublished data). Average live weight for small mammals was determined by considering frequency of each small mammal species (beaver, raccoon, rabbit, and ground squirrel) in the diet as well as typical live weight of each (Jameson, Jr. and Peters 2004).

We collected 92 adult scats from the Lassen pack (13, 45, and 34 scats in summer and fall 2017, 2018, and 2019, respectively). PFO for black-tailed deer, cattle, and small mammals for scats pooled across years was 51%, 32%, and 17%, respectively. BI for scats pooled across years indicated black-tailed deer, cattle, and small mammals made up 29%, 59%, and 12%, respectively, of the Lassen pack diet (Table 1). The divergent estimates for these two primary items are expected based on the differences in how the two metrics are derived, and since neither is definitively correct, these results demonstrate the value of using multiple metrics to assess diet. Though the two metrics indicate differential, and almost opposite, contribution of black-tailed deer and cattle to the Lassen pack diet during summer, together both indicate black-tailed deer and cattle are key food sources. We did not find any vegetation, fruit, or anthropogenic material in scats. Although elk comprise an important part of the diet of many packs in the western United States (Newsome et al. 2016), they are uncommon transients in the Lassen pack territory (CDFW, unpublished data) and were not detected in scats. However, population growth and expansion of the elk population in northern California could change prevalence of elk in the Lassen pack diet (CDFW 2018).

Given that black-tailed deer and cattle made up most of the overall and annual summer diet of the Lassen pack, we attempted to discern if the pack was utilizing these food

Table 1. Overall and annual diet composition of the Lassen wolf pack in California, 2017-2019, according to adult scat analyzed using two diet metrics (percent frequency of occurrence and estimated biomass ingested). Amounts of each prey item contributing to diet composition are represented as percentages of total diet composition.

	Percent Frequency of Occurrence			Biomass Ingested (estimated)		
	Deer	Cattle	Small Mammals	Deer	Cattle	Small Mammals
2017	51	41	8	26	67	7
2018	55	31	14	31	58	11
2019	47	30	23	27	56	17
Combined Years	51	32	17	29	59	12

items in proportion to their availability (Meriggi et al. 1996, 2015; Milanese et al. 2012). We estimated availability of each food item in terms of both the number of individuals and the amount of biomass present within the pack's summer range. We first estimated the summer range (April–September) as ~284 km² using a 95% adaptive local convex hull (a-LoCoH; Getz et al. 2007) derived from 1,920 satellite-collar locations from one radio-collared member of the pack. Based on an estimate of 5.2 deer per km² for a study area that overlapped significantly with the Lassen pack's summer range (Furnas et al. 2018), we estimated ~1,477 black-tailed deer available to the pack. That estimate included both sexes and all age classes of deer with a fawn:doe:buck ratio of 0.67:1.0:0.37. Based on a weighted average of 20 kg for fawns (average for the entire summer), 54 kg for does, and 65 kg for bucks (Walmo 1981), we estimated deer biomass to be 233 kg/km² or 66,172 kg within the summer range.

We used United States Forest Service (USFS) and private lands stocking data to estimate cattle numbers and biomass in the summer territory. For USFS allotments, we determined how many cow-calf pairs were turned out in 2017, 2018, and 2019. We then calculated area of each allotment within the pack's home range, multiplied the clipped area of each allotment by the average annual cattle density for that allotment and summed the results across all allotments within the range, which provided an estimate of ~644 cow-calf pairs on federal allotments within the Lassen pack's summer range during the study period. We then queried livestock producers with range cattle on private lands within the territory to determine the number of cow-calf pairs on those lands that did not also range onto USFS allotments (660 pairs). We summed those "private-only" cattle with the cattle on USFS allotments to derive an estimate of 1,304 cow-calf pairs, or 2,608 individual cattle, within the estimated summer range. This total number is approximately 9.18 cattle/km². Using an average weight of 272 kg for all cattle available, and multiplying by the density of available cattle in the study area, we estimated 2,498 kg/km² of cattle biomass available to the Lassen pack during summer. This equated to an overall biomass of 709,432 kg of cattle within the Lassen summer range.

We then compared the overall number of scats containing each item as estimated from PFO to the estimated number of individuals available ((Meriggi et al. 1996; Milanese et al. 2012). We also compared the overall estimates for BI for both species to the derived biomass of each species available (Meriggi et al. 2015). A food item was deemed used more than expected if the 95% confidence intervals for proportion of that item in the diet were greater than the proportion of that item available (Manly et al. 2002). Conversely, a food item was deemed used less than expected if the 95% confidence intervals for proportion of that item in the diet were less than the proportion of that item available (Manly et al. 2002).

Based on the proportion of individuals available (36% and 64% deer and cattle, respectively, or 1,477 deer and 2,608 cattle) and proportion of scat composed of black-tailed deer (51%) and cattle (32%) as determined from overall PFO, we determined that in the summer the Lassen pack was utilizing black-tailed deer more than expected based on availability and cattle less than expected (Table 2). Based on the proportion of biomass available (9% and 91% deer and cattle, respectively, or 66,172 kg deer and 709,432 kg cattle) and proportion of diet composed of black-tailed deer (29%) and cattle (59%) as determined from overall BI, we also determined the Lassen pack was using black-tailed deer more than expected and cattle less than expected in summer. Although both the raw PFO and BI metrics for deer and cattle varied, our estimates of deer and cattle utilization relative to availability were consistent for both metrics. Janiero-Otero et al. (2020) also found that across their biogeographic range, wolves generally used wild prey more than livestock when the relative abundance of each was taken into account.

Table 2. Estimation of utilization by adult members of Lassen pack for two primary prey items, black-tailed deer and cattle, using number of individuals and biomass (kg) available, respectively. Derivations of numbers of individuals and biomass available are detailed within the text. Proportions of each prey item used were calculated from the overall percentages displayed in Table 1. Use of a prey item more than expected is indicated if the 95% confidence interval for the corresponding proportion of that prey item in the diet is above the proportion available. Use of a prey item less than expected is indicated if the 95% confidence interval for the corresponding proportion of that prey item in the diet is below the proportion available.

	Percent Frequency of Occurrence		Biomass Ingested (estimated)	
	Deer	Cattle	Deer	Cattle
Available (# and biomass)	1,477	2,608	66,172	709,432
Proportion Available	0.36	0.64	0.09	0.91
Proportion Used (95% CI)	0.51(0.39-0.63)	0.32(0.21-0.43)	0.29(0.20-0.39)	0.59(0.48-0.69)
Use Ratios	1.41	0.50	3.41	0.64
Use compared to expected	More	Less	More	Less

Because our data is only derived from a single California wolf pack, our results should be viewed as preliminary. The tendencies of the individual wolves in the pack or the physiography of the pack's territory may influence wolf diet composition. For example, the Lassen pack's den sites and most of their rendezvous sites have been close to large meadow complexes where grazing cattle are aggregated from May through October each year. Scats collected from those sites might be expected to contain an increased frequency of cattle remains than scats collected in other parts of the pack's summer range. Additional study limitations were the lack of systematic scat collection throughout the study period, despite a food base that varies temporally over the period (e.g., birth of deer fawns peaking in early to mid-June, turnout of cattle in mid-June, etc.). Scats were collected opportunistically and not in any temporally (e.g., every week) or spatially (e.g., routes) standardized way. Additionally, we pooled samples collected at den and rendezvous sites with samples from roads, trails, and feeding sites. While some studies have found no differences in the contents of scats collected at different locations (Gable et al. 2017), others have found differences in contents of wolf scats collected along roads and those collected at den and rendezvous

sites (Steenweg et al. 2015). It should be noted that contents of scats collected at feeding sites did not always match the species fed upon at the same site. Nonetheless, collection of 10–20 adult wolf scats per month from homesites or opportunistically can provide a general understanding of the annual diet of a given wolf pack (Dellinger et al. 2011a; Gable et al. 2017). We are currently employing spatially and temporally standardized scat collection methods (i.e., regularly surveyed routes bisecting the pack's summer range) and accounting for where scats are collected (i.e., homesite, road, or feeding site) to help address these limitations in the future.

We acknowledge that quantifying available number and biomass of black-tailed deer and cattle on the landscape is an imprecise exercise. Our estimate of black-tailed deer live weights was taken from the literature and may be greater than the typical live weights of deer living in the Lassen pack home range (CDFW, unpublished data). Our estimates of black-tailed deer biomass available on the landscape groups yearlings with adult deer which also likely contributes to overestimating deer biomass on the landscape. Further, estimating cattle live weight was difficult due to variation in calving cycles between local livestock operations. For example, calves born in the fall of a previous year would weigh more than calves born in spring of the following year. However, using lower black-tailed deer live weights and accounting for larger calves born in the fall would only increase the already large difference in estimated biomass of black-tailed deer and cattle available.

Our analysis does not indicate the proportion of the pack's diet that is scavenged versus killed. Although the Lassen pack sometimes kills and consumes cattle, pack members also regularly visit the carcasses of cattle that have died of natural (i.e., non-depredation) causes (CDFW, unpublished data). Petroelje et al. (2019) found that most cattle in the diet of wolves in Michigan, USA were from scavenging. When possible, future dietary studies in California should therefore use techniques that allow estimation of the proportion of killed vs. scavenged food items (e.g., satellite collars with many fixes per day, camera-collars, etc.). Further, understanding the role of smaller native animals in Californian gray wolf diets will also be important. Small native prey like beavers, lagomorphs, microtine rodents, birds, fish and, on occasion, other carnivores, can supplement wolf diets during ungulate shortages (Newsome et al. 2016)

Our assessment of diet was limited to samples gathered from the Lassen pack's summer range. The winter diet of the pack may differ from its summer diet, as it shifts its range to lower elevations in the winter (Morehouse and Boyce 2011). Deer and cattle are both present on the pack's winter range, but relative to summer range, cattle are fewer in number, confined to smaller pastures, and closer to human dwellings. Given that livestock depredation has thus far been less common in winter than summer (CDFW, unpublished data), it is possible that the Lassen pack may consume less cattle in winter relative to summer. To address this potential difference, we intend to expand upon our current efforts and study diet year-round.

Several recent assessments suggest potentially suitable gray wolf habitat is widespread in northern California and the Sierra Nevada where the potential for wolf-livestock conflict is high in many areas due to the extensive presence of livestock (Kovacs et al. 2016; Nickel and Walther 2019). Though our initial work suggests that wolves in California use native ungulates as, or more than expected based on availability, cattle depredations are likely to continue to occur given the abundance of cattle on the landscape (Janeiro-Otero et al. 2020). However, as this study demonstrates the importance of deer in the Lassen pack's diet, increases in deer populations may potentially reduce livestock predation.

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