

# Factors Determining Coyote (*Canis latrans*) Diets

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## Abstract

Although studies have documented the potential for coyote (*Canis latrans*) food use to negatively affect wildlife populations and domesticated animals, they are often equivocal, possibly because most are of small spatial extent, and little is known of factors determining coyote diets. Our objectives were to quantify the diet and identify factors determining coyote food use, particularly game species and livestock, over a large spatial and temporal extent. Contents of gastrointestinal tracts were identified from 263 coyotes opportunistically obtained from hunters, trappers, and as road-kills throughout Florida, 2011-2015. We employed logistic regression in an information-theoretic framework to understand determinants of coyote food use. Coyotes were opportunistic and omnivorous foragers with a diverse diet of vegetation, insects, birds, reptiles, amphibians, and more than 25 species of mammals (including important game species and livestock). They commonly consumed 11 food items (Virginia opossum [*Didelphis virginiana*], non-mast vegetation, feral hog [*Sus scrofa*], northern raccoon [*Procyon lotor*], insects, rabbits (*Sylvilagus* spp.), skunks [*Mephitis mephitis* and *Spilogale putorius*], white-tailed deer (*Odocoileus virginianus*), mast, birds, and cows [*Bos taurus*]). Food use was determined by coyote age, sex, and body mass, season of the year, deer hunting and fawning seasons, livestock calving season, and coyote collection method and location/region. As coyotes expand their range and numbers, conservationists may find it useful to understand how this opportunistic and adaptable predator uses available food sources to reduce conflict across the landscape.

## Keywords

*Canis latrans*, Coyote, Determinants, Diet, Factors

## 1. Introduction

Historically found west of the Mississippi River, the coyote (*Canis latrans*) has

expanded its range throughout most of North America [1]. Increasing numbers of coyotes in areas such as the southeastern United States [2] [3] are a concern as they may feed on a variety of food items, including important game species, livestock, and pets [4] [5]. Coyotes have been implicated in the decline of numerous wildlife species, negatively affecting them through competition for resources (e.g., bobcats [*Lynx rufus*]; [6]), predation (e.g., white-tailed deer [*Odocoileus virginianus*; hereafter, deer]; [7]), and changes in community structure [8] [9] [10].

Although studies have documented the potential for coyote food use to negatively affect wildlife and domesticated animals, they are often equivocal, possibly because most are of small spatial extent, which can mask broader habitat and ecosystem effects [11]. In addition, beyond a limited knowledge of the influence of season and animal sex and age, we lack an understanding of determinants of coyote food use [11]. A better understanding of these determinants is needed to tailor management strategies and mitigate the negative effects of coyotes. Coyotes are often considered to be opportunistic and generalist predators [1] [5] [12]. Some studies have suggested coyotes focus primarily on a relatively few (3 - 5) food types in an area (e.g., large mammals such as deer, insects, rabbits, or small mammals; [13] [14] [15] [16] [17]) while others suggest a more diverse diet, with many food types commonly consumed (e.g., [18] [19]).

Our objectives were to quantify the diet and identify factors determining coyote food use, particularly game species and livestock, over a large spatial and temporal extent. We expected coyotes would be opportunistic and have a diverse diet, where one or few items did not dominate; exhibit age, sex, and size differences in diet, to reduce intraspecific competition for food, with older, more experienced animals consuming larger and more difficult to prey upon items, and coyote size positively related to prey size consumed; and have diets that vary with season and location, to take advantage of available food assemblages, such as deer and livestock calves. Finally, we wished to investigate if some combination of these factors might further affect coyote food use.

## 2. Materials and Methods

We opportunistically obtained coyote carcasses and gastrointestinal (GI) tracts from hunters, trappers, and as road-kills throughout Florida from December 2011 to February 2015. Road-kills were typically less than 2 days old at the time of collection. Coyote carcasses were sexed and weighed, and a canine from the lower jaw was removed, aged via cementum annuli, and used to assign coyote age class (Matson's Laboratory LLC, Milltown, MT; [20]; **Table 1**). We determined body mass classes arbitrarily (*i.e.*, dividing the range of values into three equal parts), and following Giuliano *et al.* (1989), an ocular kidney fat index was used to assess coyote condition (**Table 1**). Collection date, method, and location (**Table 1**) were documented for all animals. To examine the effects of season on coyote food use, we partitioned collection dates into three relevant season

**Table 1.** Factors determining coyote (*Canis latrans*) food use in Florida, USA, 2011-2015.

Factors <sup>a</sup>	Food Group
Age <sup>b</sup>	Small mammals <sup>c</sup>
Sex <sup>d</sup>	Medium mammals <sup>e</sup>
Body mass (Mass) <sup>f</sup>	Large mammals <sup>g</sup>
Condition class (Condition) <sup>h</sup>	Birds
Calendar season (CSeason) <sup>i</sup>	Reptiles and Amphibians
Deer season (DSeason) <sup>j</sup>	Insects
Livestock season (LSeason) <sup>k</sup>	Vegetation (non-mast)
Collection method (Method) <sup>l</sup>	Mast (Fruits, seeds, and nuts)
Collection location (Location) <sup>m</sup>	Small game <sup>n</sup>
Age + Sex	Large game <sup>o</sup>
Age + Condition	White-tailed deer ( <i>Odocoileus virginianus</i> )
Sex + Condition	Livestock <sup>p</sup>
Sex + CSeason	
Sex + DSeason	
Sex + LSeason	
CSeason + Location	
DSeason + Location	
LSeason + Location	
DSeason + Method	
LSeason + Method	
DSeason + Method + Location	
LSeason + Method + Location	

<sup>a</sup>Predictor variables in *a priori*, single- and multiple-variable candidate models used to determine coyote food use. <sup>b</sup>Juveniles (J; <1 year old), young adult (YA; 1 year old), and adult (A; ≥2 years old). <sup>c</sup>*Blarina* sp., mole sp., cotton rat (*Sigmodon hispidus*), eastern woodrat (*Neotoma floridana*), Florida mouse (*Peromyscus floridanus*), marsh rice rat (*Oryzomys palustris*), and round-tailed muskrat (*Neofiber alleni*). <sup>d</sup>Male (M) and female (F). <sup>e</sup>Nine-banded armadillo (*Dasypus novemcinctus*), Virginia opossum (*Didelphis virginiana*), rabbits (*Sylvilagus spp.*), northern raccoon (*Procyon lotor*), skunks (striped [*Mephitis mephitis*] and spotted [*Spilogale putorius*]), squirrels (*Sciurus spp.*), weasels (*Mustela spp.*), and domestic cats (*Felis catus*). <sup>f</sup>Small (S; <11.34 kg), medium (M; 11.34 - 15.88 kg), and large (L; >15.88 kg). <sup>g</sup>Coyote (*Canis latrans*), domestic dog (*Canis lupus familiaris*), white-tailed deer (*Odocoileus virginianus*), feral hog (*Sus scrofa*), cow (*Bos taurus*), and horse (*Equus caballus*). <sup>h</sup>0 (no fat = poor condition), 1 (minimal fat = fair condition), 2 (some fat deposits = good condition), and 3 (large fat deposits = excellent condition). <sup>i</sup>Coyotes collected in winter (W; December, January, or February), spring (SP; March, April, or May), summer (SU; June, July, or August), or fall (F; September, October, or November). <sup>j</sup>Coyotes collected in the deer fawning (F; birthing period), hunting (H; general gun hunting period), or other (O; outside of birthing and general gun hunting periods) season, as determined by location and date of collection. <sup>k</sup>Coyotes collected during the livestock calving (C; October-February) or other (O; March-September) season. <sup>l</sup>Coyotes collected by hunting (H), trapping (T), or as road-kill (R). <sup>m</sup>Coyotes collected in north (N; Alachua, Bradford, Citrus, Clay, Duval, Flagler, Jefferson, Madison, Marion, Sumter, Taylor, and Union counties), central (C; Brevard, Desoto, Hardee, Highlands, Manatee, Okeechobee, Osceola, Pasco, and Polk counties), or south (S; Charlotte, Glades, and Palm Beach counties) Florida. <sup>n</sup>Nine-banded armadillo, Virginia opossum, rabbits, northern raccoon, skunks, and squirrels. <sup>o</sup>White-tailed deer and feral hog. <sup>p</sup>Cow and horse.

classifications: calendar, deer, and livestock (**Table 1**). Coyote use of deer may increase during the deer fawning season when adult females and fawns are particularly vulnerable to predation [7] [22], and during deer hunting seasons, as entrails from harvested animals may be left in the field and deer may be left wounded and easily killed. We used both the coyote's location and date of collection to determine the deer hunting and fawning seasons, using the Florida Fish and Wildlife Conservation Commission's Deer Management Plan, which contains fawning seasons by region, and deer management unit regulations as a guideline ([23]; **Table 1**). Similarly, coyote use of livestock may increase during the livestock calving season, as there are more calves available at that time. Calving seasons were determined by the University of Florida, Agricultural Extension Service (J.R. Selph, Florida Cooperative Extension Service, University of Florida, Arcadia, FL [personal communication, 2015]; **Table 1**).

We removed gastrointestinal tracts from carcasses, rinsed contents with warm water, and separated materials using a 4-sieve kit (Hubbard #3076 Screen Four Sieve Kit). After air-drying for 24 hours, we sorted samples into components (e.g., hair, bone, plant material, insects, etc.). Items were identified micro- and macroscopically using attributes such as hair length, color, and scale patterns by comparison to reference collections [21] [24]. We separated deer fawns and adults based on hair characteristics following Wilkins *et al.* (1982). Dietary items were grouped for analyses, with some items appearing in multiple groups. Because we were particularly interested in factors determining coyote use of game species and livestock, we separately examined these groups (**Table 1**). We counted any type of item found within a coyote GI tract only once, regardless of how many of the individual food item were in the GI tract. All dietary items (e.g., Virginia opossum [*Didelphis virginiana*]) and food groupings (e.g., small mammals) were expressed as percent (%) occurrence (*i.e.*, number of coyotes with the food item or group/total number coyotes).

To understand determinants of coyote dietary habits, we employed logistic regression in an information-theoretic framework [25]. For each food group (*i.e.*, consumed or not consumed), we developed and evaluated the same set of 22 a priori, single- and multiple-variable candidate models (**Table 1**) based on the literature, prior knowledge and field experience, and study objectives. Individual models were limited to 3 predictor variables to reduce the likelihood of overfitting. We examined Akaike's Information Criterion with small-sample correction ( $AIC_c$ ) values,  $AIC_c$  differences ( $\Delta AIC_c$ ), Akaike weights ( $w_i$ ), and model goodness of fit ( $-2 \log$ -likelihood; when  $P \leq 0.10$ , models were considered to fit) for models with different combinations of predictor variables, and considered models with  $\Delta AIC_c < 2$  supported. Where multiple models were supported, we used model averaging to increase precision of inference and examine the relative contribution of each variable from all supported models [25]. When 85% confidence intervals (CI) for variables within supported models overlapped with zero, we considered them to have a weak effect on the dependent variable and be uninformative [26]. For brevity and clarity, we only present results of

supported models. All analyses were conducted using R software [27].

All research and animal welfare protocols were reviewed and approved: University of Florida Animal Research Permit (003-11WEC) and Florida Fish and Wildlife Conservation Commission Research Permit (SPGS-11-68).

### 3. Results

Coyotes ( $n = 263$ ) had a diverse diet, consuming vegetation, insects, mammals ( $\geq 25$  species), birds, amphibians, and reptiles, with 11 foods commonly consumed (occurring in  $>10\%$  of coyotes). Frequently used food items included Virginia opossum, feral hog (*Sus scrofa*), northern raccoon (*Procyon lotor*), rabbits (*Sylvilagus* spp.), skunks (striped skunk [*Mephitis mephitis*] and spotted skunk [*Spilogale putorius*]), deer (adults and fawns), insects, mast, and other vegetation (Table 2).

**Table 2.** Food items identified in gastrointestinal tracts of coyotes (*Canis latrans*) from Florida, USA, 2011-2015.

Food Item	% Occurrence ( $n = 263$ )
Virginia opossum ( <i>Didelphis virginiana</i> )	31.6
Vegetation (non-mast)	28.1
Feral hog ( <i>Sus scrofa</i> )	24.7
Northern Raccoon ( <i>Procyon lotor</i> )	22.1
Insects	17.5
Rabbits (eastern cottontail [ <i>Sylvilagus floridanus</i> ] and marsh [ <i>Sylvilagus palustris</i> ])	15.6
Skunks (striped [ <i>Mephitis mephitis</i> ] and spotted [ <i>Spilogale putorius</i> ])	15.6
White-tailed Deer ( <i>Odocoileus virginianus</i> )	14.8
Adult	11.8
Fawn	3.0
Mast (fruits, seeds, and nuts)	14.1
Birds	11.0
Cow ( <i>Bos taurus</i> )	10.3
Reptiles and amphibians	6.5
Rodents (cotton rat [ <i>Sigmodon hispidus</i> ], eastern woodrat [ <i>Neotoma floridana</i> ], Florida mouse [ <i>Peromyscus floridanus</i> ], marsh rice rat [ <i>Oryzomys palustris</i> ], and round-tailed muskrat [ <i>Neofiber alleni</i> ])	6.1
Squirrels (eastern gray [ <i>Sciurus carolinensis</i> ] and fox [ <i>Sciurus niger</i> ])	5.3
Nine-banded Armadillo ( <i>Dasypus novemcinctus</i> )	2.7
Weasels (long-tailed [ <i>Mustela frenata</i> ] and mink [ <i>Mustela vison</i> ])	2.3
Non-rodent small mammals ( <i>Blarina</i> sp. and mole sp.)	1.5
Canids (coyote [ <i>Canis latrans</i> ] and domestic dog [ <i>Canis lupus familiaris</i> ])	0.8
Domestic cat ( <i>Felis catus</i> )	0.4
Horse ( <i>Equus caballus</i> )	0.4

Young adult coyotes were less likely than adults to eat medium-sized mammals and small game, and juveniles were less likely than adults to eat birds. Age was not a factor determining use of any other food groups. Compared to females, male coyotes were less likely to consume small mammals and more likely to consume medium-sized mammals and small game. Use of any other food groups was not determined by sex. Small coyotes were less likely than larger animals to use large game, and mass was not a factor determining use of any other food groups. While animal condition appeared in 2 supported models predicting bird use by coyotes, it was an uninformative individual predictor variable, and condition was not a factor determining use of any other food groups (**Table 3** and **Table 4**).

Coyotes were less likely to ingest mast during the spring and winter than fall, and calendar season was not a factor determining use of any other food groups. Coyotes were more likely to eat small mammals, large mammals, deer, and livestock and less likely to consume reptiles and amphibians during the deer hunting season than during the deer fawning season. Outside of the deer hunting and fawning seasons, coyotes consumed more small mammals and mast and less deer than during the fawning season. While deer season appeared in 2 supported models predicting vegetation use by coyotes, it was an uninformative individual predictor variable, and use of any other food groups was not determined by deer season. Consumption of insects was more likely and small mammals, large mammals, large game, and livestock by coyotes was less likely outside of the livestock calving season than during the calving season. While livestock season appeared in 1 supported model predicting bird use and 1 supported model predicting mast ingestion, it was an uninformative individual predictor variable. Livestock season was not a factor determining use of any other food groups (**Table 3** and **Table 4**).

Trapped coyotes were more likely to consume large mammals, birds, vegetation, and livestock and less likely to eat reptiles and amphibians, insects, and mast than hunted coyotes. While collection method appeared in 1 supported model predicting large game use by coyotes, it was an uninformative individual predictor variable, and coyote collection method was not a factor determining use of any other food groups. Coyotes in northern and southern Florida were more likely to eat birds than coyotes in central Florida. In northern Florida, consumption of reptiles and amphibians and mast were more likely and livestock less likely than in central Florida. While collection location appeared in 2 supported models predicting small mammal use, 1 supported model of large mammal use, and 1 supported model of deer use, it was an uninformative individual predictor variable, and use of any other food groups was not determined by location of coyote collection (**Table 3** and **Table 4**).

#### 4. Discussion

Coyotes had a diverse diet, consuming vegetation, insects, mammals ( $\geq 25$  species), birds, amphibians, and reptiles. Similar to other studies (e.g., [13] [16] [18]

**Table 3.** Supported models<sup>a</sup> of factors determining coyote (*Canis latrans*) food use in Florida, USA, 2011-2015.

Food Group <sup>b</sup>	Model <sup>c</sup>	$K^d$	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i^e$	Model Fit ( $P$ ) <sup>f</sup>
Small mammals	LSeason	2	141.367	0.000	0.200	0.041
	Sex + LSeason	4	142.016	0.649	0.144	0.054
	DSeason	3	142.845	1.479	0.095	0.093
	DSeason + Location	5	142.857	1.490	0.095	0.064
	LSeason + Location	4	142.227	1.860	0.079	0.093
Medium mammals	Age + Sex	6	306.947	0.000	0.375	0.015
Large mammals	LSeason + Method	4	356.832	0.000	0.324	0.001
	DSeason + Method	5	357.342	0.510	0.251	0.002
	DSeason + Method + Location	7	358.356	1.525	0.151	0.002
Birds	Condition	5	184.002	0.000	0.236	0.012
	Age + Condition	8	184.770	0.768	0.161	0.010
	LSeason + Method + Location	6	185.171	1.168	0.132	0.017
	Location	3	185.876	1.873	0.092	0.032
	Age	4	185.929	1.926	0.090	0.030
Reptiles and Amphibians	DSeason + Method + Location	7	123.593	0.000	0.895	≤0.001
Insects	LSeason + Method	4	227.884	0.000	0.375	≤0.001
	Method	3	228.435	0.551	0.285	≤0.001
Vegetation (non-mast)	DSeason	3	319.925	0.000	0.259	0.051
	DSeason + Method	5	320.801	0.876	0.167	0.056
	Method	3	321.121	1.196	0.143	0.093
Mast	DSeason + Method + Location	7	187.635	0.000	0.272	≤0.001
	CSeason + Location	6	188.236	0.601	0.201	≤0.001
	LSeason + Method + Location	6	188.434	0.799	0.182	≤0.001
	Method	3	188.785	1.150	0.153	≤0.001
Small game	Age + Sex	6	306.947	0.000	0.381	0.015
Large game	LSeason	2	352.496	0.000	0.349	0.033

## Continued

White-tailed deer	LSeason + Method	4	354.173	1.677	0.151	0.072
	Mass	4	354.448	1.952	0.132	0.082
	DSeason	3	214.285	0.000	0.403	≤0.001
	DSeason + Location	5	214.442	0.157	0.372	≤0.001
Livestock	LSeason + Method	4	179.609	0.000	0.281	0.002
	LSeason + Method + Location	6	180.733	1.125	0.160	0.003
	DSeason + Method + Location	7	181.066	1.458	0.136	0.003
	DSeason + Method	5	181.162	1.553	0.129	0.003

<sup>a</sup>Akaike's Information Criterion [AIC];  $\Delta AIC_c \leq 2$ . <sup>b</sup>Food groups defined in Table 1. <sup>c</sup>Model predictor variables described in Table 1. <sup>d</sup>Number of model parameters. <sup>e</sup>Akaike weight. <sup>f</sup>When  $P \leq 0.10$ , models were considered to fit.

**Table 4.** Model-averaged variable coefficients from supported models<sup>a</sup> of factors determining coyote (*Canis latrans*) food use in Florida, USA, 2011-2015.

Food Group <sup>b</sup>	Variable <sup>c</sup>	$\beta$	SE	85% CI	
				Lower	Upper
Small mammals	Sex (M)	-0.804	0.490	-1.509	-0.099
	DSeason (H)	1.675	1.085	0.114	3.237
	DSeason (O)	2.020	1.101	0.436	3.604
	LSeason (O)	-1.179	0.641	-2.102	-0.256
	Location (N)	0.513	0.581	-0.323	1.349
	Location (S)	-15.140	1131.103	-1643.398	1613.119
Medium mammals	Age (J)	0.231	0.406	-0.353	0.814
	Age (YA)	-0.723	0.418	-1.325	-0.122
	Sex (M)	0.597	0.295	0.172	1.022
Large mammals	DSeason (H)	1.059	0.366	0.533	1.585
	DSeason (O)	0.301	0.376	-0.240	0.843
	LSeason (O)	-0.752	0.270	-1.141	-0.363
	Method (R)	-0.474	0.751	-1.555	0.608
	Method (T)	0.721	0.308	0.278	1.165
	Location (N)	-0.455	0.320	-0.915	0.006
	Location (S)	0.603	0.653	-0.336	1.542
Birds	Age (J)	-1.052	0.540	-1.829	-0.274



**Continued**

	Age (YA)	-0.346	0.547	-1.134	0.441
	Condition (1)	0.542	0.798	-0.607	1.691
	Condition (2)	-0.127	0.840	-1.337	1.082
	Condition (3)	-15.189	980.887	-1427.207	1396.828
	Method (R)	-15.799	1206.684	-1752.858	1721.261
	Method (T)	0.818	0.529	0.0565	1.579
	Location (N)	1.161	0.458	0.502	1.820
	Location (S)	1.961	0.937	0.612	3.310
	LSeason (O)	-0.176	0.431	-0.796	0.444
Reptiles and Amphibians					
	DSeason (H)	-2.740	0.895	-4.028	-1.452
	DSeason (O)	-0.289	0.557	-1.092	0.513
	Method (R)	-0.563	1.026	-2.040	0.914
	Method (T)	-1.943	0.597	-2.802	-1.085
	Location (N)	1.646	0.602	0.779	2.512
	Location (S)	-15.507	1096.569	-1594.053	1563.039
Insects					
	LSeason (O)	0.560	0.345	0.064	1.056
	Method (R)	0.262	0.691	-0.733	1.257
	Method (T)	-1.683	0.358	-2.198	-1.168
Vegetation (non-mast)					
	DSeason (H)	-0.393	0.403	-0.972	0.187
	DSeason (O)	0.351	0.352	-0.156	0.858
	Method (R)	-0.091	0.838	-1.297	1.115
	Method (T)	0.576	0.318	0.118	1.033
Mast					
	CSeason (SU)	-0.206	0.708	-1.225	0.814
	CSeason (SP)	-2.636	0.628	-3.541	-1.732
	CSeason (W)	-2.057	0.474	-2.739	-1.375
	DSeason (H)	0.218	0.574	-0.609	1.044
	DSeason (O)	0.869	0.562	0.060	1.678
	LSeason (O)	-0.089	0.414	-0.685	0.507
	Method (R)	0.036	0.731	-1.016	1.089
	Method (T)	-2.273	0.451	-2.922	-1.624
	Location (N)	1.161	0.458	0.502	1.820
	Location (S)	0.755	0.716	-0.276	1.785
Small game					
	Age (J)	0.231	0.406	-0.353	0.814

## Continued

	Age (YA)	-0.723	0.418	-1.325	-0.122
	Sex (M)	0.597	0.295	0.172	1.022
Large game					
	Mass (S)	-0.895	0.419	-1.498	-0.292
	Mass (M)	-0.318	0.321	-0.781	0.144
	LSeason (O)	-0.574	0.275	-0.970	-0.178
	Method (R)	-0.901	0.828	-2.094	0.291
	Method (T)	0.194	0.280	-0.210	0.597
White-tailed deer					
	DSeason (H)	0.814	0.439	0.182	1.445
	DSeason (O)	-0.864	0.550	-1.656	-0.072
	Location (N)	0.419	0.385	-0.136	0.973
	Location (S)	-15.335	1100.391	-1599.383	1568.712
Livestock					
	DSeason (H)	1.600	0.812	0.431	2.769
	DSeason (O)	0.859	0.879	-0.407	2.124
	LSeason (O)	-1.192	0.568	-2.009	-0.374
	Method (R)	1.076	1.261	-0.739	2.891
	Method (T)	1.516	0.661	0.565	2.467
	Location (N)	-0.972	0.576	-1.801	-0.143
	Location (S)	0.221	1.312	-1.667	2.110

<sup>a</sup>Akaike's Information Criterion [AIC];  $\Delta AIC_c \leq 2$ . <sup>b</sup>Food groups defined in **Table 1**. <sup>c</sup>Model predictor variables described in **Table 1**.

[19] [28] [29] [30] [31] [32]), we found coyotes often used mast, non-mast vegetation, insects, birds, medium-sized mammals (e.g., Virginia opossums, rabbits, skunks, and northern raccoons), and larger mammals (e.g., feral hogs, deer, and livestock). However, our results suggest that Florida coyotes had a broad diet, with many (11) food types commonly consumed, which contrasts studies that suggested relatively few (3 - 5) types were important food items to coyotes (e.g., [13] [14] [15] [16] [32]). Additionally, our findings are in partial contrast to several studies that noted a greater importance of deer, insects, small mammals, and mast in coyote diets (e.g., [13] [14] [15] [16] [17] [28] [32] [33]). These differences may be due to differences in food availability among regions, limited spatial and temporal extent of the contrasting studies, and examination of scats to determine diets in most studies. The latter will lead to differing diet composition as some items are digested fully and do not appear in scats as opposed to GI tracts, and may reflect the preference of a single or a few animals, rather than the habits of the entire population. In addition, our study is not subject to predator misidentification, a substantial problem with most scat-based studies, as they do

not genotype scats to species [34]. Furthermore, we established the importance of coyote age, sex, and body mass, season (*i.e.*, calendar, livestock calving, and deer fawning and hunting), coyote collection method (*i.e.*, hunted, trapped, or road-killed), and location (*i.e.*, region of Florida) as determinants of coyote food use, which may also explain differences relative to other studies that typically could not examine these factors.

Physical characteristics of coyotes (*i.e.*, age, sex, and body mass) were important factors determining food use. The lower consumption by young adults of medium-sized mammals and small game and juveniles of birds compared with adults, the reduced use by males of small mammals and greater use of medium-sized mammals and small game compared with females, and the lower consumption by small coyotes of large game compared to larger (*i.e.*, medium and large) animals suggest that coyotes may be partitioning resources to reduce intraspecific competition [17] [35]. Additionally, foraging ability may differ depending on the age, sex, and size of coyotes, which may lead to differential effects on important prey (e.g., rabbits, deer, etc.) depending on coyote population structure. The lower consumption of birds and medium-sized mammals and small game such as armadillos, Virginia opossums, rabbits, squirrels, skunks, weasels, and northern raccoons, may reflect the inexperience of younger animals at finding and capturing prey [36]. Further, the greater use of large game species (*i.e.*, deer and hogs) by larger than smaller coyotes likely reflects smaller individuals not being able to physically handle such large prey and exclusion by dominant (*i.e.*, larger) individuals of deer and hog kills or carcasses. In contrast with other studies, we did not find that coyote age and sex were important in determining the use of other food groups. For example, Metzger *et al.* (2017) noted an overall difference in diet between males and females, and Albers (2012) noted juveniles using less mast and more deer than adults.

Seasonal variations (*i.e.*, calendar, deer, and livestock) were the more important type of factors determining coyote food use. Coyotes were less likely to consume mast during spring and winter than fall, which likely reflects its greater availability during the fall masting season [37] [38]. Although not noted in this study, Whitaker *et al.* (2015) suggested greater use of deer in fall and winter and hogs in spring and summer than other seasons, but statistical tests were not performed.

Similar to calendar season effects, availability likely increased use of large mammals, deer, and livestock and decreased use of reptiles and amphibians by coyotes during the deer hunting season compared to the fawning season, and led to greater mast and reduced deer use outside of both the deer hunting and fawning seasons. Deer hunting season was generally during fall-early winter and provided less than ideal conditions for most reptiles and amphibians to be active (*i.e.*, dryer and cooler; [38]). However, a large portion of the deer season outside of both hunting and fawning seasons included parts of spring and fall masting periods [37] [38]. The increased use of large mammals (comprised primarily of deer, hog, and cow), deer, and livestock in the deer hunting compared with deer

fawning season may often reflect coyote scavenging habits, availability of livestock calves, hunting of deer and hogs, and landowner control programs of coyotes and hogs. During the deer hunting season, which overlaps with much of the livestock calving season, agricultural land managers kill many feral hogs and leave their carcasses in pastures while monitoring calving operations and use hog as bait while conducting coyote control programs leading up to and during the livestock calving season (J.R. Selph, Florida Cooperative Extension Service, University of Florida, Arcadia, FL, personal communication, 2015). Further, during much of this period, livestock are calving and deer are physically stressed with the conclusion of the breeding season, and hunters are harvesting (and wounding) deer and hogs during the hunting season [23]. Coyotes may be taking advantage of these easily obtained food sources by scavenging the remains of hogs used as bait, hogs and deer left in the field, and opportunistically depredating livestock calves and weak or wounded deer and hogs [33]. The greater use of deer by coyotes during the hunting season (26 % occurrence) than other seasons supports this conclusion [11].

Our findings regarding deer use are similar to those of Swingen *et al.* (2015), who found the greatest deer use in winter, but in contrast to Hidalgo-Milhart *et al.* (2001), Schrecengost *et al.* (2008), and Wooding *et al.* (1984), who noted greater deer use by coyotes during the deer fawning season. Although we documented adult and juvenile deer in coyote GI tracts, other items (e.g., medium-sized mammals, feral hogs, insects, and vegetation) were found more often [14] [39] [40]. The relative amount of deer consumed by coyotes in Florida was less than in other studies (e.g., [13] [14] [15] [18] [28] [32]). Florida is a large state with a diversity of ecosystems [41] that offer a variety of food from which coyotes can choose, possibly explaining differences with other studies. Additionally, in more northerly portions of coyote range, deer are easily preyed on in deep snow [42] [43] [44] [45] and other foods important to Florida coyotes (e.g., hogs and Virginia opossums) may be less abundant [46], partially explaining why deer are relatively less important to coyotes in Florida. Huebschman *et al.* (1997), Schrecengost *et al.* (2008), and Thornton *et al.* (2004) found deer fawns to be an important component of coyote diets, and recent studies have found coyotes to be important predators of deer fawns (e.g., [7] [22] [47] [48] [49] [50]). Our data partly support this conclusion, finding deer use to be greater in the deer fawning season compared with outside of both the deer hunting and fawning seasons, as fawns may be easy prey for coyotes [7]. However, deer fawns were generally, infrequently consumed in Florida, which is similar to that of Swingen *et al.* (2015).

Coyotes may be using deer and other food items more evenly through time as the fawning seasons in Florida can occur during 3 calendar seasons (e.g., spring, summer, and into fall; [51]), and food availability during each season may be dominated by other food items (e.g., mast in fall). Additionally, fawn remains may be digested at different rates than other prey items [52] [53], leading to a loss of evidence, and may be a reason why deer generally do not appear to be

important in coyote diets. Gier (1968), and to some extent Albers (2012) and Litvaitis and Shaw (1980), suggested that livestock were more important to coyote diets, particularly in winter when calves are most vulnerable and heifers are physically stressed and most likely to abort or abandon a calf, providing inexperienced animals with an easy meal [54]. The deer hunting season, when livestock use was high, includes much of the early winter period. Similar to deer hunting season, and to some extent deer fawning season, during the livestock calving season, coyotes consumed more large mammals, large game, and livestock than during the non-calving season, likely for the reasons described above for deer seasons.

Method and location of coyote collection also affected what coyotes consumed. Land managers consistently kill hogs, use their remains as bait to trap coyotes, and place traps and bait for coyotes around livestock carcasses to increase capture success. In addition, remains of harvested birds and poultry are often used as bait for coyotes. A portion of coyote consumption of hogs, livestock, and birds may be due to baited traps, as seen by the greater use of large mammals (including hogs), livestock, and birds by trapped than hunted coyotes. Further, the greater ingestion of vegetation by trapped than hunted coyotes often reflects trapped animals biting at anything within reach, while in a trap.

When compared to other regions of the Southeast, Florida may contain a greater variety of ecosystems and climatic conditions, explaining some of the observed differences in coyote food use [41]. North Florida exhibits more seasonality and is more forested compared with the remainder of the state [41] [55], contributing to increased mast production, and explaining the greater use of mast by coyotes in this region compared to the central region. In addition, the majority of the state's large-scale agricultural production, including livestock, occurs outside of north Florida [56], explaining why coyotes use livestock less in the north region. A superficial comparison of coyote food habits among the many studies with local extents suggests regional differences in coyote diets, and Metzger *et al.* (2017) noted regional differences in coyote diets in their larger scale Pennsylvania study.

As hypothesized, coyotes were opportunistic and omnivorous foragers with a diverse diet of vegetation, insects, birds, reptiles, amphibians, and more than 25 species of mammals (including important game species and livestock), with 11 food items commonly consumed (Virginia opossum, non-mast vegetation, feral hog, northern raccoons, insects, rabbits, skunks, deer, mast, birds, and cows). Food use was determined by coyote age, sex, and body mass, season of the year, deer hunting and fawning seasons, livestock calving season, collection method, and location/region, and suggests that coyotes are opportunistic, generalist predators that forage on the most available foods.

White-tailed deer is often the most utilized food of endangered red wolves (*Canis rufus*), with feral hogs also consumed but to a much lesser extent. Where red wolves and coyotes coexist, they often have very similar diets. However, red wolves rely more heavily on both deer and hogs [35]. To increase the availability

of these important food sources for red wolves, targeting for removal coyotes during the deer-hunting season may be a viable strategy. For deer managers and livestock producers, targeting for removal coyotes during the deer hunting and livestock calving seasons may relieve pressure on deer and calves, particularly in areas with little other seasonal coyote foods. As coyotes expand their range and numbers, conservationists may find it useful to understand how this opportunistic and adaptable predator uses available food sources to reduce conflict across the landscape.

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