



University of
Massachusetts
Amherst

Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California

Item Type	article;article
Authors	Fedriani, Jose M.;Fuller, Todd K.;Sauvajot, Raymond M.
DOI	https://doi.org/10.1111/j.1600-0587.2001.tb00205.x
Download date	2024-08-08 00:57:43
Link to Item	https://hdl.handle.net/20.500.14394/37366

Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California

Jose M. Fedriani, Todd K. Fuller and Raymond M. Sauvajot

Fedriani, J. M., Fuller, T. K. and Sauvajot, R. M. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. – *Ecography* 24: 325–331.

To evaluate whether the abundance of coyotes *Canis latrans* was influenced by the availability of anthropogenic foods in a humanized landscape, we compared three neighboring areas (hereafter referred to as NA, CA, and SA) under contrasting human pressures within the Santa Monica Mountains of California, USA. We quantified the use of anthropogenic foods by coyotes and assessed local densities within these three regions. Overall, 761 coyote feces were analyzed; identified food items were categorized into 11 food types (7 native and 4 anthropogenic). Though small mammals (lagomorphs and rodents) were the main prey of coyotes in all areas and seasons, log-linear modeling of multiway contingency tables indicates that consumption of anthropogenic foods by coyotes varied significantly throughout study areas. Thus, in the most humanized area (CA; 24% of this region is residential habitat), anthropogenic foods (trash, livestock, domestic fruit) comprised seasonally between 14 and 25% of total items in coyote diets, whereas in the least humanized area (NA; 2% residential) anthropogenic foods only comprised seasonally between 0 and 3% of items. Coyote density, estimated by foot-hold trapping surveys and by genotyping feces, was also highly variable between areas. The heavily human-impacted CA area had the highest coyote density (2.4–3.0 ind. km⁻²), whereas coyote density was significantly lower (0.3–0.4 ind. km⁻²) in the least humanized area (NA). In the third region (SA; 10% residential), with an intermediate level of human pressure, both importance of anthropogenic foods in coyote diet (4–6%) and coyote density (1.6–2.0 ind. km⁻²) were intermediate compared to the other regions. Our data suggest that subsidization by anthropogenic foods augments coyote densities and alters their diets in the Santa Monica Mountains, California. We include data from literature to show that anthropogenic foods are used by omnivorous mammals throughout the world. Surprisingly, however, the potential effects of allochthonous inputs on such species are not well-understood. Thus, further research on this phenomenon in humanized landscapes is needed.

J. M. Fedriani and T. K. Fuller, Dept of Natural Resources Conservation, Univ. of Massachusetts, Amherst MA 01003-4210, USA (present address of J.M.F. and correspondence: fedriani@ebd.csic.es, Unidad de Ecología Evolutiva, Estación Biológica de Doñana (CSIC), Avda María Luisa s/n, E-41013 Sevilla, Spain). – R. M. Sauvajot, U.S. National Park Service, 401 West Hilcrest Dr., Thousand Oaks, CA 91360, USA.

Consumer population size is generally considered to be a strong function of primary productivity (DeAngelis et al. 1996, Persson et al. 1996). Consequently, areas of high primary productivity are expected to support large populations of consumers, whereas few consumers

should occur in areas of low primary productivity (Odum and Biever 1984, Osenberg and Mittlebach 1996, Persson et al. 1996). Nevertheless, even local communities that appear discrete are open and connected in myriad ways to outside influences. For in-

Accepted 15 September 2000

Copyright © ECOGRAPHY 2001

ISSN 0906-7590

Printed in Ireland – all rights reserved

stance, transport of nutrients and prey can sustain communities of abundant consumers even in places with little primary productivity (e.g., deserts, snow fields; Polis and Hurd 1996, Polis et al. 1997). Besides, consumers can be more abundant than levels sustained by local productivity if they forage in many habitats, as is often the case among omnivore mammals (Rose and Polis 1998, Fedriani et al. 1999). Across-habitat transport of nutrients and active movement of consumers exert major effects (e.g., increase of primary and secondary productivity, enhance of predator abundance) on most kinds of aquatic and terrestrial native habitats (see Polis et al. 1997 for a review). Surprisingly, however, little is known about potential effects of such phenomena in humanized habitats (e.g., urban, suburban areas), where a large amount of heterogeneous foods such as trash and carcasses may be generated (Gill and Bonnett 1973). Such input can be incorporated into adjacent native habitats via assimilation by opportunistic consumers (Teagle 1967, Harris 1981a).

Assessment of the effects of subsidization by anthropogenic foods on consumers could be particularly important in areas experiencing rapid development, such as the state of California (USA), with a growth rate of over 600 000 people annually and where over 300 000 ha are developed annually (Anon. 1991). To evaluate whether subsidization by allochthonous (anthropogenic) foods at the interface humanized and native habitats exerts similar effects to those found among adjacent native habitats (Polis et al. 1997), we chose three neighboring areas under contrasting human pressures within the Santa Monica Mountains of California. We relate variation in the use of anthropogenic foods by coyotes *Canis latrans* with local density. Coyotes in the Santa Monica Mountains are known to rely on rodents (Fedriani et al. 2000); however, their usage of anthropogenic foods is uncertain and the effect that such input could have on coyote populations is questionable. We hypothesize that human-derived foods would subsidize coyotes, resulting in an increase in density. The expectation, then, is that areas with greater human development interface will contain higher densities of coyotes than areas with less development interface.

Study areas and methods

The Santa Monica Mountains of California are located adjacent to Los Angeles metropolitan area, where human pressures are great and formerly continuous habitat has been encroached upon and fragmented by urbanization. The most represented habitats are chaparral, coastal sage scrub, oak forest, grasslands, and suburban/residential (Holland 1986, Sawyer and Keeler-Wolf 1995). The climate is typically Mediter-

anean with mild rainy winters and hot dry summers. Coyote persecution is not generally permitted and is minimal throughout the area. Fieldwork was conducted in three study areas (see Fedriani et al. 2000 for details): 1) North Area (hereafter NA; 14.4 km²) is a zone of very low human pressure, located in the northern portion of Cheeseboro and Palo Comado Canyons. It is characterized by brushy habitats (e.g., chaparral, coastal sage scrub) which occupy 80% of the area, whereas suburban/residential uses occupy only 2%. Human presence is essentially limited to recreational visitors (hikers, bikers). 2) Central Area (hereafter CA; 6.5 km²) is a zone of high human pressure, located in the southern portion of Cheeseboro and Palo Comado Canyons. Suburban/residential habitat occupies 24% of the area, and includes a large landfill (the Calabasas Landfill, 1.2 km²). Brushy habitats occupy 43% of the area. 3) South Area (hereafter SA; 12 km²) is a zone with an intermediate amount of human pressure and habitat composition compared with other areas, and is located in and around Malibu Creek State Park. Brush and suburban/residential habitats comprises 69% and 10% of the area, respectively.

The Ventura Freeway (US Highway 101) crosses the Santa Monica Mountains from east to west, separating SA from NA and CA. Coyotes in SA are generally isolated from the other two areas because this freeway acts as a substantial movement barrier (Fedriani et al. 2000, Sauvajot et al. 2000). Moreover, during three years of intensive foot-hold trapping (overall, 9734 traps-night) only one individual was captured in both NA and CA, suggesting a high degree of independence among all sites (Fedriani et al. 2000). The use by coyotes of native and anthropogenic foods was assessed through fecal analysis (overall, 761 samples). Feces were collected monthly from November 1997 to October 1998 in the three areas. Fecal analysis was made by standard methods (Reynolds and Aebischer 1991), and food items identified were categorized into 11 types: lagomorphs, rodents, native carnivores, domestic cat, deer, livestock, "other vertebrates", invertebrates, wild fruit, domestic fruit, and trash. The importance in the diet of each prey type was quantified by two methods (see Fedriani and Travaini 2000 for the rationale of using those two methods): 1) percentage of occurrence = number of occurrences of each prey type \times 100/total number of occurrences, and 2) dry weight of prey remains = dry weight of remains of each prey type \times 100/dry weight of total feces. According to patterns of precipitation (Russell 1926), we considered separately diets of dry (May–October) and wet (November–April) seasons. The Shannon diversity index (H') was used to estimate seasonal diet diversity (Brower and Zar 1984) for each area, using both percentages of occurrence and dry weight of prey remains. To evaluate variations in the occurrence of different prey types (P) between study areas (A), and seasons (S), we catego-

rized frequency data along multiple dimensions, yielding multiway contingency tables (Toft 1984). Log-linear modeling of such tables have proven a powerful tool in ecological research (Schoener and Adler 1991, Cerda et al. 1998). We added the constant 0.5 to each cell before modeling, a convenience when there are many table cells with small expected frequencies (Vepsalainen et al. 1988). In the models, interaction of any two (or more) variables is denoted by lack of a comma (PA). A higher-order interaction term in the model includes all the lower-order interactions and the main effects (PAS thus includes PA, PS, AS, P, A, and S). When goodness-of-fit $p > 0.05$, data were considered to fit the model in question. The best model was considered to be the most parsimonious acceptable ($p > 0.05$) one. To interpret this model, we examined the contribution of each cell of the contingency table to the maximum likelihood ratio χ^2 statistic (G^2). Analyses were performed with the program Statistica (Anon. 1994).

The number of coyotes in CA was calculated by Kohn et al. (1999) through genotyping coyote feces. To estimate coyote densities in NA and SA, we used factors that indexed density of coyotes in CA with densities in the other two areas. Those factors were estimated by Fedriani et al. (2000) through foot-hold trapping surveys as: number of individuals captured/trapping effort (i.e. number of traps-night). Such indirect measures of density are common (e.g., Harris 1981b, Creel and Creel 1996) as direct measures of these nocturnal and highly mobile consumers are difficult to obtain. Though the techniques employed by Kohn et al. (1999) to estimate the population size in CA may have considered unsettled nomads individuals,

there is no reason to think that such issue affected in a contrasting manner across our three study sites; however, caution is needed in comparisons with studies that do not consider nomads individuals in their density estimates. Abundance of rabbits (*Sylvilagus bachmani* and *Sylvilagus audubonii*) was estimated by counting their pellets in fixed plots, set in brushy habitats within the three areas (overall, 62 plots), from May to October 1998. An index of rabbit abundance was calculated for each area as: number of pellets found in plots/number of plots. Though we did not measure availability of other prey, availability of rodents was assumed to be similar across areas since coyotes consistently rely on these prey in all three areas (Fedriani et al. 2000). Because farms, livestock, pets, garbage, and domestic fruit trees are abundant in suburban/residential areas within the Santa Monica Mountains (Shargo 1988, Sauvajot et al. 2000), we used percent of each area covered by suburban/residential as a surrogate variable of anthropogenic food availability.

Results

Coyote food spectrum and density

Table 1 summarizes the percentages of occurrence and dry weight of different prey types and the estimates of seasonal diet diversity of coyotes in our three study areas. Both indices of coyote diet illustrate the relative importance of native food items. Diet diversity was highest in CP, whereas in NP and SP were lower and similar (Table 1). Rodents were most commonly and consistently found in feces (37–47% occurrence); they

Table 1. Percentage of occurrence and percentage of dry weight of specific items from native and anthropogenic resources found in coyote feces, during both seasons (dry and wet), at the three study areas selected within the Santa Monica Mountains of California (NA, North Area; CA, Central Area; SA, South Area). Values of Shannon diversity (H') for each area, season, and diet estimation also are shown.

	Percentage of occurrence						Percentage of dry weight					
	NA Dry	Wet	CA Dry	Wet	SA Dry	Wet	NA Dry	Wet	CA Dry	Wet	SA Dry	Wet
Native items (Total)	(96)	(100)	(75)	(86)	(94)	(95)	(97)	(99)	(74)	(87)	(95)	(98)
Lagomorph	9	10	13	16	12	18	12	12	19	18	15	12
Rodents	40	37	39	42	47	45	58	47	45	52	57	46
Carnivores	tr*	1	tr	1	1	1	1	2	tr	1	2	2
Deer	6	4	3	2	5	5	7	9	4	3	9	3
Other vertebrates	15	7	8	5	9	3	9	2	3	2	3	1
Invertebrates	18	18	9	13	4	5	4	4	1	3	1	tr
Wild fruit	8	23	3	7	16	18	6	23	1	8	8	34
Anthropogenic items	(3)	(tr)	(25)	(14)	(6)	(4)	(3)	(1)	(26)	(13)	(5)	(2)
Domestic cat	tr	tr	tr	1	tr	0	tr	tr	tr	1	tr	0
Livestock	1	0	1	5	tr	1	1	0	1	5	tr	tr
Trash	0	tr	13	5	1	0	0	tr	13	2	tr	0
Domestic fruit	2	0	11	3	5	3	2	0	12	5	5	2
No. occurrences	261	288	238	178	219	148						
No. feces	141	145	137	113	121	104						
H'	1.71	1.63	1.84	1.82	1.67	1.59	1.42	1.46	1.52	1.58	1.42	1.30

*tr < 1.

Table 2. Models used in the multidimensional contingency table (log-linear) analysis testing for seasonal and among areas differences in occurrence of different prey types (P) in feces of coyotes at Santa Monica Mountains. The variables considered are: study area (A), and season (S). In the models, interaction of any two (or more) variables is denoted by the lack of a comma (PA). A higher-order interaction term in the model includes all the lower-order interactions and main effects (PAS thus includes PA, PS, AS, P, A, and S). These “saturated models”, by definition, are significant. We did not model for some prey types (carnivores, cats) because of low values at contingency table cells. All models are significant (goodness-of-fit, $p > 0.05$).

Item	Model	DF	G ²	p
Native				
Lagomorphs	P, A	8	7.5	0.483
Rodents	PAS		saturated	
Deer	P, A	8	9.8	0.278
Other vertebrates	PA, PS	4	5.5	0.243
Invertebrates	PA	6	5.0	0.541
Wild fruit	PAS		saturated	
Anthropogenic				
Livestock	PA	6	8.5	0.201
Trash	PA, PS	4	3.2	0.529
Domestic fruit	PA, PS	4	2.8	0.589

comprised the major portion of coyote diet as indicated by percent of dry weight (45–58%). Lagomorphs, wild fruit and invertebrates were relatively common, although only lagomorphs and wild fruit comprised a significant portion of coyote diet (dry weight 12–19% and 1–23%, respectively).

Relative abundance of coyotes in the most humanized area (CA) was 7.9 higher than in NA (the least humanized area) and 1.5 times higher than in SA (the area of intermediate human pressure). Density of coyotes in CA was estimated at between 2.4 and 3.0 ind. km⁻², based on Kohn et al. (1999). Therefore, our estimate of density of coyotes in NA ranged from 0.3 to 0.4 ind. km⁻², and in our estimate in SA ranged from 1.6 to 2.0 ind. km⁻².

Variation of food items between sites

For each prey type, the most parsimonious model for its occurrence in coyote diets is shown in Table 2. Of the native prey items, lagomorphs and deer occur equally in feces between the three study sites as denoted by lack of interaction terms in the simplest models that were fitted to the food item data. However, for “other vertebrates” and invertebrates, the simplest model (interaction PA) indicated that the occurrence of these prey among the three areas was indeed variable. For example, there was a higher seasonal occurrence of invertebrates in NA (18%) vs CA (9–13%) and SA (4–5%; Table 1).

Anthropogenic food items (livestock, trash and domestic fruit) occurred more often in CA (overall 14–25%) than NA (0–3%) or SA (4–6%) (interaction PA

in Table 2) and were an important dietary component (13–26% of dry weight). Specifically, trash (5–13% occurrence) and domestic fruit (3–11%) were consumed more often in CA, the area of highest humanized habitat.

Seasonal variation of food items

Many food items were consumed differently between the wet and dry seasons. For instance, the group “other vertebrates” was consumed more frequently in the dry season in all three areas (interaction PS). Moreover, the simplest model that fitted the data for rodents and wild fruit included the higher-order interaction (PAS), indicating that their occurrence varied among areas, but dissimilarly so in different seasonal periods. Whereas during the dry season the highest consumption of wild fruit was in SA (16% vs 3% and 8%; Table 1), and during the wet season the highest consumption of wild fruit was in NA (23% vs 7% and 18%). Similar seasonal discrepancies occur with anthropogenic foods within CA. Trash and domestic fruit were both ingested more often during the dry season (11–13%) than wet (3–5%).

Local abundance of rabbits

Pellets counts in fixed plots resulted in average indexes of rabbit abundance of 17.6 (1 SD = ± 20.8, n = 20), 9.3 (1 SD = ± 14.8, n = 21), and 3.6 (1 SD = ± 7.9, n = 21) for CA, NA, and SA, respectively. These values were significantly different between study sites (GLM from Anon. 1990, F = 4.20, DF = 2, p = 0.020). These results suggest that there is no clear relationship across study areas between abundance of rabbits and level of humanized land use and coyote density.

Discussion

Suburban coyotes in the most urbanized area (CA) were subsidized by foods associated with human activities and, consequently, their diet diversity was increased. Intensive use of this area, and particularly of the Calabasas landfill, was corroborated by extensive data from radio-tracked coyotes, and by data of capture-recapture through photographic surveys (Fedriani et al. 2000, Sauvajot et al. 2000). Moreover, numerous tracks and sightings of coyotes at the landfill indicated that they routinely searched the area for trash and carrion (Fedriani unpubl.). In addition, the Calabasas landfill is partly surrounded by residential areas and density of domestic fruit trees (e.g., peaches and apricots, *Prunus* spp., in yards) may be as high as 32 trees ha⁻¹ (Shargo 1988); thus, coyotes had another abundant source of energy that likely is particularly important during the dry season (Table 1).

Our estimates of coyote density in NA (0.3–0.4 ind. km⁻²) coincided with typical estimates of coyote density (0.2–0.4 ind. km⁻²; Knowlton 1972, Andelt 1985, Windberg 1995), whereas density in SA (1.6–2.0 ind. km⁻²) was similar to reports for particularly favorable environments (2 ind. km⁻²; Knowlton 1972, Windberg 1995). Interestingly, our coyote density estimate in CA (2.4–3.0 ind. km⁻²; Kohn et al. 1999) nearly reached the highest value reported in the literature (3.2–4.6 ind. km⁻²; McClure et al. 1996); this density was attained in suburban Arizona where coyotes were also subsidized by anthropogenic foods (occurrence in 35% of scats; McClure et al. 1995). The notion that subsidization by allochthonous foods results in higher coyote densities is supported by the trend in coyote density and human development in our three study areas. In the most human-impacted area (CA), where 14–25% of items consumed were of anthropogenic origin, coyote density was approximately eight times higher than in the most natural area (NA). Factors such as contrasting availability of native prey or level of human coyote persecution also could account for local variation in Santa Monica Mountains coyote densities. However, coyotes intensively preyed on rodents in all areas and through the year, suggesting locally consistent availability of those prey with no seasonal limitation (Fedriani et al. 2000). In addition, the higher abundance of

rabbits in CA did not increase their consumption by coyotes in this area. Finally, coyote persecution was generally not permitted and is very uncommon in all three areas.

The use of anthropogenic foods by omnivorous mammals occurs worldwide, including among a wide range of both consumers and resources (Table 3). Mustelids and canids of variable body size arise as typical consumers of human-derived food, though this picture could be skewed by unequal research efforts. While mustelids primarily feed on trash, fruit and grain, canids often also include livestock in their diets (Table 3). For some populations of consumers, anthropogenic foods are, apparently, of major nutritive importance. For example, domestic fruit comprised 76% of biomass ingested by Eurasian badgers *Meles meles* in arid Spain (Rodriguez and Delibes 1992), grain occurred in 63% of feces of raccoon dogs *Nyctereutes procyonoides* in Finland (Kauhala et al. 1998), and trash occurred in 31–53% of feces of coyotes in Alberta (Todd 1985; Table 3). These omnivorous mammal populations are likely subsidized by such allochthonous input, as is probable for coyotes in the Santa Monica Mountains. Indeed, subsidized red foxes *Vulpes vulpes* in English cities (Harris 1981a, Saunders et al. 1993) obtained higher densities (1.0–3.6 families km⁻²) than in typical native habitats (0.1–1.0 families km⁻²; see Trehwella

Table 3. Predator species, location, percentages of different anthropogenic foods in feces or stomachs, and references reporting the use of such allochthonous input from humanized habitats. Range of percentages indicates variation among studies or seasons. Note that percentages represent different diet estimates (e.g., frequency of occurrence, percent of dry weight of prey remains). (URSS, former Soviet Union.)

	Locations	%Trash	%Fruit	%Grain	%Poultry	%Stock	References
Eurasian badger <i>Meles meles</i>	URSS	8–25	30–76	5–33			a, b, c, d
Eastern skunk <i>Mephitis mephitis</i>	USA	11–18		11–47			e
Spotted skunk <i>Spilogale intermedia</i>	USA			1–29	1–6	1	f
Dingo <i>Canis familiaris dingo</i>	Australia				8–10		g
Coyote <i>Canis latrans</i>	USA	4–53		4	3–9	4–40	h, i, j
Wolves <i>Canis lupus</i>	Europe URSS	2–6	36	7	18	2–96	k, l, m
Red fox <i>Vulpes vulpes</i>	Europe Pakistan	3–64	5–12		5–23	1–50	n, o, p, q
Gray fox <i>Urocyon cinereoargenteus</i>	USA	19*	9–18	38	3–7	1	p, r, s
Raccoon dog <i>Nyctereutes procyonoides</i>	Europe			63			t
Black bear <i>Ursus americanus</i>	USA			8–13		5–13	u
Brown hyena <i>Hyaena brunnea</i>	South Africa	36				6	v

* value representing total percentage of anthropogenic items in feces; References: a, Roper and Mickevicius 1995; b, Harris 1985; c, Lucherini and Crema 1995; d, Rodriguez and Delibes 1992; e, Hamilton 1936; f, Crabb 1941; g, Marsack and Campbell 1990; h, Todd 1985; i, Andrews and Boggess 1978; j, MacCracken 1982; k, Papageorgiou et al. 1994; l, Meriggi et al. 1996; m, Bibikov et al. 1985; n, Saunders et al. 1993; o, Pandolfi et al. 1988; p, Hockman and Chapman 1983; q, Blumstein and Robertson 1995; r, Harrison 1997; s, Errington 1935; t, Kauhala et al. 1998; u, Holcroft and Herrero 1991; v, Maddock 1993.

et al. 1988 review). Similar inputs and effects may also occur at the interface among native habitats (Rose and Polis 1998).

Despite numerous studies documenting the use of anthropogenic foods by omnivorous mammals (Table 3), very limited research on the potential effects of allochthonous inputs prevents us from making more decided statements on human-derived subsidies. Humanized habitats likely deviate from native ones in a variety of ways. For instance, whereas perimeter-to-area ratios of habitat patches and consumer mobility are major factors governing input, productivity and dynamics among juxtaposed native habitats (Andrén and Anglestam 1988, Polis and Hurd 1996, Polis et al. 1997), at the ecotone between humanized and native habitats such regulating factors include elimination of foods and routines of production. Further, by applying recent food webs concepts (Polis et al. 1997), subsidized coyotes in the Santa Monica Mountains may be expected to depress populations of native prey, such as lagomorphs and rodents. However, our data indicated that rabbits were more abundant in CA, the area with highest coyote density and the most humanized landscape. Rose and Polis (1998) suggest that subsidized coyotes in Baja California (Mexico) did not depress most native prey (omnivorous rodents) because prey were also subsidized by allochthonous input. However, rabbits in Santa Monica are not subsidized by human-derived foods since they are strictly vegetarian, although habitat changes associated with human development (e.g., increased water availability, ornamental landscaping, etc.) may benefit herbivorous species, including rabbits. Further work is needed to evaluate alternative hypotheses, such as the occurrence of indirect positive effects of coyotes on rabbit populations by controlling intermediate predators that also kill rabbits (gray foxes *Urocyon cinereoargenteus*, bobcats *Lynx rufus*; Fedriani et al. 2000). On the other hand, a dense rabbit population in CA, in spite of a dense coyote population, could also be related to the availability of alternative human-delivered food, leading coyotes not to prey so often on rabbits.

Subsidization by allochthonous foods occurs often among juxtaposed habitats (Polis et al. 1997), and thus it is important to understand how human-derived subsidies can affect consumer populations, resource availability, and food web and community dynamics. In addition to the purely theoretical value of a comprehensive understanding of this phenomenon, additional research can assist wildlife managers in understanding and controlling nuisance species such as some omnivorous mammals (e.g., red foxes, coyotes, etc. under some circumstances). Additional knowledge of the ecological effects of human-derived subsidies will also aid conservation efforts, including reserve design and sensitive species protection in and around humanized landscapes (Ehrenfeld and Toth 1997).

Acknowledgements – This paper is dedicated to the memories of Gary A. Polis and Michael D. Rose; their altruistic and enthusiastic attentions to issues in this paper and spatial subsidy in general have and will continue to inspire us all. We are thankful to Sharon Kim, Kristin Searcy, Sandy Ng, Veronica Farias, Jacki Duhon, and all others who helped with the field work; Robert K. Wayne for administrative and scientific support; and Sarah Low and Dan Stimson who provided lab assistance. The manuscript was significantly improved by Xim Cerdá, Gary A. Polis, Michael D. Rose and Alberto Meriggi. This study was supported by National Park Service (USA) and by a grant from Southwest Parks and Monuments Association. The senior author (J. M. F.) was supported by Ministerio de Educacion y Ciencia of Spain. We thank the Dept of Natural Resources Conservation (Univ. of Massachusetts) for logistic support.

References

- Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. – Wildl. Monogr. 94.
- Andrén, H. and Anglestam, P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. – *Ecology* 69: 544–547.
- Andrews, R. D. and Boggess, E. K. 1978. Ecology of coyotes in Iowa. – In: Bekoff, M. (ed.), *Coyotes: biology, behavior, and management*. Academic Press, pp. 249–265.
- Anon. 1990. SAS/STAT user's guide, ver. 6. – SAS Inst., Cary, NC.
- Anon. 1991. California 2000: biological ghettos, major issues in land conservation. – Assembly Office of Research, Rep. No. 389A, Sacramento, California.
- Anon. 1994. Statistica for the Macintosh. – StatSoft, Tulsa.
- Bibikov, D. I., Kudaktin, A. N. and Ryabov, L. S. 1985. Synanthropic wolves: distribution, ecology. – *Zool. Zh.* 64: 429–441.
- Blumstein, D. T. and Robertson, M. 1995. Summer diets of Tibetan red foxes in Khunjerab National Park, Pakistan. – *Z. Säugetierkd.* 60: 243–245.
- Brower, J. E. and Zar, J. H. 1984. Field and laboratory methods for general biology, 2nd ed. – Brown, Dubuque, IA, USA.
- Cerda, X., Retana, J. and Cros, S. 1998. Prey size reverses the outcome of interference interactions of scavengers ants. – *Oikos* 82: 99–110.
- Crabb, W. D. 1941. Food habits of the prairie spotted skunk in southeastern Iowa. – *J. Mammal.* 14: 349–364.
- Creel, S. and Creel, N. H. 1996. Limitation of African wild dogs by competition with larger carnivores. – *Conserv. Biol.* 10: 526–538.
- DeAngelis, D. L., Persson, L. and Rosemond, A. D. 1996. Interaction of productivity and consumption. – In: Polis, G. A. and Winemiller, K. (eds), *Foods webs: integration of patterns and dynamics*. Chapman and Hall, pp. 109–112.
- Ehrenfeld, J. G. and Toth, L. A. 1997. Restoration ecology and the ecosystem perspective. – *Rest. Ecol.* 5: 307–317.
- Errington, P. L. 1935. Food habits of mid-west foxes. – *J. Mammal.* 16: 192–200.
- Fedriani, J. M. and Travaini, A. 2000. Predator trophic guild assignment: the importance of the method of diet quantification. – *Rev. Ecol. (Terre. et. Vie)* 55: 129–139.
- Fedriani, J. M., Palomares, F. and Delibes, M. 1999. Niche relations among three sympatric Mediterranean carnivores. – *Oecologia* 121: 138–148.
- Fedriani, J. M. et al. 2000. Competition and intraguild predation among three sympatric carnivores. – *Oecologia* 125: 258–270.
- Gill, D. A. and Bonnett, P. 1973. Nature in the urban landscape: a study of city ecosystems. – York Press, Baltimore, MD.

- Hamilton, W. J. 1936. Seasonal food of skunks in New York. – *J. Mammal.* 17: 240–246.
- Harris, S. 1981a. The food of suburban foxes (*Vulpes vulpes*), with special reference to London. – *Mammal. Rev.* 11: 151–168.
- Harris, S. 1981b. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. – *J. Appl. Ecol.* 18: 455–465.
- Harris, S. 1985. Ecology of urban badgers *Meles meles*: distribution in Britain and habitat selection, persecution, food and damage in the city of Bristol. – *Biol. Conserv.* 28: 349–375.
- Harrison, R. L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. – *J. Wildl. Manage.* 61: 112–122.
- Hockman, J. G. and Chapman, J. A. 1983. Comparative feeding habits of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in Maryland. – *Am. Midl. Nat.* 110: 276–285.
- Holcroft, A. C. and Herrero, S. 1991. Black bear, *Ursus americanus*, food habits in southwestern Alberta. – *Can. Field-Nat.* 105: 335–345.
- Holland, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. – The Resources Agency, Nongame Heritage Program, California Dept of Fish and Game, Sacramento, CA.
- Kauhala, K., Laukkanen, P. and Rege, I. 1998. Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. – *Ecography* 21: 457–463.
- Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanisms with some management implications. – *J. Wildl. Manage.* 36: 369–382.
- Kohn, M. H. et al. 1999. Estimating population size by genotyping faeces. – *Proc. R. Soc. Lond. B* 266: 657–663.
- Lucherini, M. and Crema, G. 1995. Seasonal variation in the food habits of badgers in an alpine valley. – *Hystrix* 7: 165–171.
- MacCracken, J. G. 1982. Coyote foods in a southern California suburb. – *Wildl. Soc. Bull.* 10: 280–281.
- Maddock, A. H. 1993. Analysis of brown hyaena (*Hyaena brunnea*) scats from the central karoo, South Africa. – *J. Zool.* 231: 679–683.
- Marsack, P. and Campbell, G. 1990. Feeding behaviour and diet of dingoes in the Nullarbor Region, western Australia. – *Aust. Wildl. Res.* 17: 349–357.
- McClure, M. F., Smith, N. S. and Shaw, W. W. 1995. Diets of coyotes near the boundary of Saguaro National Monument and Tucson, Arizona. – *Southwest. Nat.* 40: 101–104.
- McClure, M. F., Smith, N. S. and Shaw, W. W. 1996. Densities of coyotes at the interface of Saguaro National monument and Tucson, Arizona. – *Southwest. Nat.* 41: 83–86.
- Meriggi, A. et al. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. – *Ecography* 19: 287–295.
- Odum, E. P. and Biever, L. J. 1984. Resource quality, mutualism, and partitioning in food chains. – *Am. Nat.* 124: 360–376.
- Osenberg, C. W. and Mittlebach, G. G. 1996. The relative importance of resource limitation and predator limitation in food chains. – In: Polis, G. A. and Winemiller, K. (eds), *Foods webs: integration of patterns and dynamics*. Chapman and Hall, pp. 134–148.
- Pandolfi, M., Santolini, R. and Bonacoscia, M. 1988. Analisi stagionale dell'alimentazione della volpe (*Vulpes vulpes* L.), con riferimento a zone di ripopolamento e cattura e zone di caccia Libera. – *Suppl. Ric. Biol. Selvaggina.* 14: 425–440.
- Papageorgiou, N. et al. 1994. Status and diet of wolves in Greece. – *Acta. Theriol.* 39: 411–416.
- Persson, L. et al. 1996. Productivity and consumer regulation-concepts, patterns and mechanisms. – In: Polis, G. A. and Winemiller, K. (eds), *Foods webs: integration of patterns and dynamics*. Chapman and Hall, pp. 396–434.
- Polis, G. A. and Hurd, S. D. 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. – In: Polis, G. A. and Winemiller, K. (eds), *Foods webs: integration of patterns and dynamics*. Chapman and Hall, pp. 275–285.
- Polis, G. A., Anderson, W. B. and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Annu. Rev. Ecol. Syst.* 28: 289–316.
- Reynolds, J. C. and Aebischer, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. – *Mammal. Rev.* 12: 97–122.
- Rodriguez, A. and Delibes, M. 1992. Food habits of badgers (*Meles meles*) in an arid habitat. – *J. Zool.* 227: 347–350.
- Roper, T. J. and Mickevicius, E. 1995. Badger *Meles meles* diet: a review of the literature from the former Soviet Union. – *Mammal. Rev.* 25: 117–129.
- Rose, M. D. and Polis, G. A. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. – *Ecology* 79: 998–1007.
- Russell, E. J. 1926. *Climates of California*. – Univ. Calif. Publ. Geogr. 2: 73–84.
- Saunders, G. et al. 1993. Urban foxes (*Vulpes vulpes*): food acquisition, time and energy budgeting of a generalized predator. – *Symp. Zool. Soc. Lond.* 65: 215–234.
- Sauvajot, R. M. et al. 2000. Distribution and status of carnivores in the Santa Monica Mountains, California: preliminary results from radio telemetry and remote camera surveys. – In: Keeley, J. E., Keeley, M. B. and Fotheringham, C. J. (eds), *2nd interface between ecology and land development in California*, US. Geological Survey Open-File, Rep. 00-62, pp. 113–123.
- Sawyer, J. O. and Keeler-Wolf, T. 1995. *A manual of California vegetation*. – California Native Plant Society, Sacramento, CA.
- Schoener, T. W. and Adler, T. W. 1991. Greater resolution of distributional complementarities by controlling for habitat affinities: a study with Bahamian lizards and birds. – *Am. Nat.* 137: 669–692.
- Shargo, E. S. 1988. Home range, movements, and activity patterns of coyotes (*Canis latrans*) in Los Angeles suburbs. – Ph.D. thesis, Univ. of California, Los Angeles.
- Teagle, W. G. 1967. The fox in the London suburbs. – *Lond. Nat.* 46: 44–68.
- Todd, A. W. 1985. Demographic and dietary comparison of forest and farmland coyote, *Canis latrans*, populations in Alberta. – *Can. Field-Nat.* 99: 163–171.
- Toft, C. A. 1984. Resource shifts in bee flies (Bombyliidae): interactions among species determine choice of resources. – *Oikos* 43: 104–112.
- Trewhella, W. J., Harris, S. and McAllister, F. E. 1988. Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. – *J. Appl. Ecol.* 25: 423–434.
- Vepsäläinen, K., Savolainen, R. and Penttinen, A. 1988. Casual reasoning in modeling multiway contingency tables. – *Oikos* 53: 281–285.
- Windberg, L. A. 1995. Demography of a high-density coyote population. – *Can. J. Zool.* 73: 942–954.