GERMINATION OF NATIVE AND EXOTIC PLANT SEEDS DISPERSED BY COYOTES (*CANIS LATRANS*) IN SOUTHERN CALIFORNIA

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ABSTRACT—Seeds collected from coyote scats in southern California were tested for germination. Eighteen of 38 plant species germinated. Native species that germinated included *Arctostaphylos glauca, Arctostaphylos* sp., *Heteromeles arbutifolia, Opuntia littoralis, Prosopis glandulosa, Prunus ilicifolia,* and *Washingtonia filifera.* Exotic species that germinated included *Annona cherimola, Cucumis* sp., *Ficus* sp., *Lycopersicon esculentum, Panicum miliaceum, Phoenix* sp., *Prunus* sp., and *Pyracantha* sp. Additional species thought to be exotic that germinated were *Fragaria* sp., *Vitis* sp., and an unidentified species. Compared to seeds directly off the plant, *O. littoralis* germinated significantly more frequently following passage through coyotes, whereas *H. arbutifolia* germinated significantly less often. Although coyotes are dispersing exotic plant seeds in viable condition, none of the seeds identified in this study were considered invasive.

RESUMEN—Se analizó la germinación en semillas colectadas de heces de coyote en el sur de California. Dieciocho de las 38 especies de plantas germinaron. Las especies nativas que germinaron incluyeron *Arctostaphylos glauca, Arctostaphylos* sp., *Heteromeles arbutifolia, Opuntia littoralis, Prosopis glandulosa, Prunus ilicifolia,* y *Washingtonia filifera.* Las especies exóticas que germinaron fueron *Annona cherimola, Cucumis* sp., *Ficus* sp., *Lycopersicon esculentum, Panicum miliaceum, Phoenix* sp., *Prunus* sp., y *Pyracantha* sp. Otras probables especies que se creyeron exóticas que germinaron fueron *Fragaria* sp., *Vitis* sp., y una especie no identificada. Comparadas con las semillas cosechadas directamente de la planta, *O. littoralis* germinó significativamente más frecuentemente después de pasar por los coyotes, mientras que *H. arbutifolia* germinó significativamente menos frecuentemente. Aunque los coyotes están dispersando semillas de plantas exóticas en condiciones viables, ninguna de las especies encontradas en este estudio fue considerada invasora.

Animals that disperse seeds capable of germination are considered ''legitimate'' seed dispersers (Fleming and Sosa, 1994). Numerous researchers have examined the germination potential of seeds dispersed by vertebrates (Traveset, 1998; Traveset and Verdu, 2002). In a review of mammalian frugivory in North America, the order Carnivora was conspicuous in numbers of frugivorous and potentially seed-dispersing taxa (Willson, 1993). Carnivores generally are highly mobile, wide-ranging, medium-bodied to large-bodied, with long digestion times; they have the capacity to carry many seeds long distances (Willson, 1993). Coyotes (*Canis latrans*) are widespread throughout North America and have an omnivorous diet, including 33 genera of native fleshy fruits (Willson, 1993). In southern California, coyotes are locally abundant and highly frugivorous (Ferrel et al., 1953; MacCracken, 1982; Bowyer et al., 1983) and thus have considerable potential to disperse seeds.

Few researchers have recognized coyotes as legitimate seed dispersers. In southern California, seeds of *Washingtonia filifera* and *Prunus ilicifolia* were shown to germinate from coyote scats (Bullock, 1980; Bullock 1981). In other locations, seeds germinating from coyote scats include those of *Prosopis glandulosa* in Texas (Meinzer et al., 1975), *Diospyros texana* in Texas (Everitt, 1984), *Opuntia rastrera* in Mexico (Mandujano et al., 1997), *Prosopis* in Texas (Kramp et al., 1998), *Diospyros virginiana, Prunus americana,* and *Asimina triloba* in Illinois (Cypher and Cypher, 1999), and *Neobuxbaumia tetetzo* in Mexico (Godínez-Alvarez et al., 2002).

It seems highly unlikely, considering the potential of coyotes as seed dispersers, that only these 10 taxa reported in the literature are dispersed by coyotes. I did not find that any confirmed exotic species had been tested for germination from coyote scats. Invasion by nonnatives is considered a major threat to native biodiversity (McKnight, 1993), and coyote diets include exotic species of plants (Ferrel et al., 1953). There is a need to determine whether coyotes disperse exotic and invasive species.

The purpose of this study was to examine which seeds dispersed by coyotes were able to germinate, further establishing the role of coyotes as legitimate seed dispersers. I considered seeds found in coyote scats from diverse ecosystems and climates, in natural and urban regions, to maximize the number of plant species. Native and exotic species were included to demonstrate the natural ecological role of seed dispersal by coyotes and their potential for spreading exotics.

METHODS—I collected seeds from coyote scats in an opportunistic manner along hiking trails in or near San Diego County, California from February 1998 through April 2001. The sampling locations included diverse natural areas, ranging from small urban canyons (e.g., Lopez Canyon) to large protected areas (e.g., Joshua Tree National Park), representing coastal sage scrub (e.g., Tecolote Canyon), chaparral (e.g., Sycamore Canyon), montane (e.g., Cuyamaca State Park), and desert (e.g., Anza-Borrego Desert State Park) plant communities (Fig. 1).

Seeds were removed from scats in the field and stored dry in paper coin envelopes. Some seeds were pretreated with hot and cold stratification, fire, or scarification to enhance germination or were washed in a 5% bleach solution to kill fungi or both (Tables 1, 2). Stratification involved storing seeds in moist soil at specified temperatures and lengths based on recommendations by Young and Young (1986). Fire pretreatments included burning seeds with leaves, placing seeds in a hot oven, adding ash to soil, or burning litter over planted seeds (Tables 1, 2).

I conducted germination trials from August 1999 to September 2002 by planting seeds in compartmentalized (3 cm × 4 cm × 6 cm) plastic growing trays containing Scott's Seed Starter potting soil (Scott's Miracle-Gro Company, Marysville, Ohio). Growing trays were stored in various locations outdoors and indoors (including the greenhouse of San Diego State University) according to the feasibility and timing of the trials, without regard to the species being tested. Trays were kept moist and checked regularly for germination. Heating pads were used in the later stages of a few indoor trials to raise the soil temperature above room temperature in an attempt to enhance germination during the winter months. Trials varied in length from 48 to 506 days, but were not discontinued until no germination had occurred for at least a month (mean per seed = 273 days; Tables 1, 2). A seed was considered germinated once it broke the soil surface. Seeds were checked for germination below the soil upon clearing out of trays (Silverstein, 2004).

I collected available seeds from plants in the field and treated them in an identical manner to compare germination rates of fresh seeds with those of seeds that had been ingested by coyotes (Table 3). I compared percentage of germination, cumulative over the length of the trial, using Fisher's exact test, which examines a 2-by-2 cross table for contingency, similar to the chi-square test but with more accuracy for small sample sizes and uneven comparisons. When both fresh and ingested seeds germinated, I compared rate of germination as the mean time, using a 2-tailed *t*-test that tested the hypothesis that no difference would exist between each sample. Only fresh and ingested seeds collected from the same location, pretreated identically, and tested in the same trials were considered for comparison. Pretreatments of compared seeds included *Xylococcus bicolor* with stratification (67% of seeds), fire (42%), wash (35%), including some with multiple treatments; *Arctostaphylos* with stratification (81%), fire (58%), or both; and *Citrus* with wash (50%).

I compared seeds of *Opuntia littoralis* from seedy (seeds > 50%) scats with those from furry (fur > 50%) scats from the same location, assuming that seedy scats pass through coyote more quickly due to the laxative effects of fruits (Murray et al., 1994), which could influence germination.

RESULTS—Seeds from 38 species of plants were found in scats, confirming that coyotes in southern California are highly frugivorous (Tables 1, 2). Seeds of 18 of these species germinated following passage through coyote digestive tracts, and I compared the percentages of germination and rates of germination (mean days to germination; Table 1). The habitats of native species that germinated were desert (*Washingtonia filifera* and *Prosopis glandulosa*), montane (*Arctostaphylos glauca* and *Arctostaphylos* sp.), and chaparral-coastal sage scrub (*Opuntia littoralis, Heteromeles arbutifolia,* and *Prunus ilicifolia*). Exotic plant seeds that germinated came from *Annona cherimola, Cucumis, Ficus, Lycopersicon esculentum, Panicum miliaceum, Phoenix, Prunus,* and *Pyracantha.* Seeds

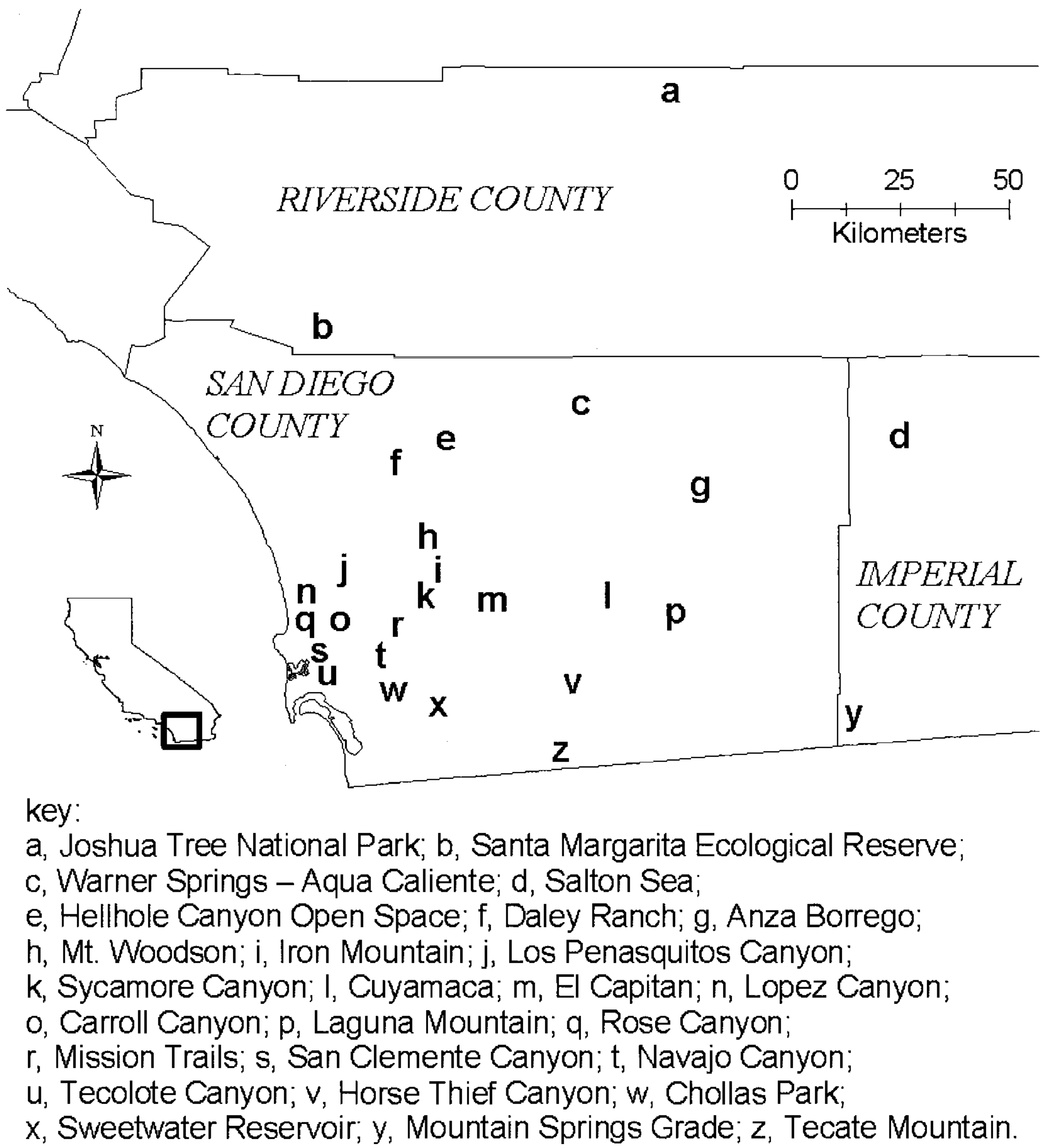

FIG. 1—Locations of seeds collected from coyote (*Canis latrans*) scats in southern California.

of 3 additional taxa (*Fragaria, Vitis,* and an unidentified species) of probable exotic status germinated. The seeds of 20 plant species did not germinate following passage through the digestive tracts of *C. latrans* (Table 2). Many of these 20 species were represented by small sample sizes, including 11 species for which fewer than 10 seeds were tested.

Compared to seeds collected directly from plants, the percentage of germination by *O. littoralis* was significantly higher after passage through coyotes, whereas germination by *H. arbutifolia* was significantly lower. Other comparisons of the percentages of germination were not significant (Table 3). The rate of germination could be compared only for *A. cherimola,* the only species of which both fresh and ingested seeds germinated. The mean numbers of days to germination for fresh and ingested cherimoya seeds were 77.1 ± 16.1 days

TABLE 1—Plant species that germinated from seeds found in coyote (*Canis latrans*) scats in southern California. See Fig. 1 for key to locations. Locations marked with an asterisk (*) indicate a seed from scats at these locations germinated. Pretreatment codes: WASH = seeds washed for 30 sec with a 5% bleach solution prior to planting; SRFFIRE = layer of leaf litter burned on surface after planting seeds; OVEN = seeds placed in oven at 500°F for 15 min prior to planting; ASH = charred wood ash added to soil prior to planting; BURN = seeds burned with leaves prior to planting; SCAR = edge of seed filed to expose dark interior. Number and letter combinations indicate the number of days stratified under the following temperatures: H = 80°F, W = 65°F, L = 50°F, C = 40°F; for example 35W120C-4 (46) indicates stratification for 35 days at 65°F, followed by 120 days at 40°F, and 4% germination of 46 seeds tested. Some seeds received a combination of fire, stratification, and/or wash pretreatments.

Scientific name	Family	% germinated (number of seeds tested)	Locations and numbers of scats	Pretreatments and % germinated (number of seeds)	Mean duration of trial (days)	Mean days to germination
Annona cherimola	Annonaceae	27.1 (70)	b-1, f-1*, u-1, x-1	none	335	85
Arctostaphylos glauca	Ericaceae	1.6 (124)	c-2, g-2*, h-1, v-1, z-1	multiple[1]	267	48
Arctostaphylos	Ericaceae	0.2 (1,991)	h-1, 1-8*, p-1, r-1, z-8	multiple[2]	297	150
Cucumis	Cucurbitaceae	33.9 (59)	a-1, u-4*	none	161	30
Ficus	Moraceae	4.4 (450)	q-1, u-4*	none	274	48
Fragaria	Rosaceae	13.8 (80)	j-1*	none	364	45
Heteromeles arbutifolia	Rosaceae	6.8 (176)	j-5*, r-2, u-7	90C-0 (87), WASH-0 (68)	234	0
Lycopersicon esculentum	Solanaceae	40 (10)	j-1*	none	414	28
Opuntia littoralis	Cactaceae	2 (662)	k-5*, r-14*, u-1	SCAR-1 (150), WASH-0 (100)	190	54
Panicum miliaceum	Poaceae	3.2 (62)	a-1*, k-1, u-3	none	139	9
Phoenix	Arecaceae	46.7 (60)	g-12*, u-3*	WASH-17 (12)	354	95
Prosopis glandulosa	Fabaceae	14.3 (77)	g-8*	none	316	36
Prunus ilicifolia	Rosaceae	14.3 (91)	r-5*	WASH-25 (12)	275	70
Prunus	Rosaceae	3.6 (56)	g-3, q-3*, u-13*	35W120C-4 (46), WASH-4 (48)	204	130
Pyracantha	Rosaceae	0.4 (237)	a-5*, s-1	90C-0 (130), WASH-0 (123)	306	20
Vitis	Vitaceae	10.7 (290)	h-1, n-1, o-1, u-11*, w-1*	123C-18 (139), 90C-4 (139), WASH-4 (134)	183	17
Washingtonia filifera	Arecaceae	75.8 (244)	d-2*, g-19*	WASH-32 (25)	354	71
Unidentified seed		0.6 (155)	h-1*	WASH-0 (55)	104	58

[1] 90H75C-0 (45), 60H60C-0 (58), SRFFIRE-29 (7), WASH-0 (92).

[2] 64W60C-0 (100), 90H75C-0 (230), 60H60C-0 (507), 90C-0 (375), BURN-0 (599), ASH-0.8 (120), SRFFIRE-0.6 (320), OVEN-0 (21), OVEN/ASH-0 (22), WASH-0.3 (767).

TABLE 2—Plant species that did not germinate from seeds found in coyote (*Canis latrans*) scats in southern California. See Fig. 1 for key to locations. See Table 1 for pretreatment codes.

Scientific name	Family	Number of seeds tested	Location and number of scats	Pretreatments and number of seeds	Mean duration of trial (days)
Citrus	Rutaceae	52	g-4	WASH-12	349
Helianthus	Asteraceae	1	a-1	none	86
Juniperus californica	Cupressaceae	75	g-2, y-3	75H90C-44, SRFFIRE-12, WASH-44	239
Malus	Rosaceae	5	a-1, m-1, q-1, t-1, x-1	none	150
Olea europaea	Oleaceae	51	m-1, k-1, u-2	60C-26, 28L-11, WASH-42	308
Prunus persica	Rosaceae	8	g-1, k-1, u-3	60C-7, WASH-3	290
Sorghum bicolor	Poaceae	24	a-1, u-1	none	134
Syagrus romanzoffiana	Arecaceae	28	m-1, q-1, t-1	WASH-5	326
Triticum aestivum	Poaceae	1	u-1	none	231
Xylococcus bicolor	Ericaceae	2,073	e-5, i-2, k-2, m-1, v-1, r-20	multiple[1]	294
Yucca	Agavaceae	10	a-1	none	214
Unidentified seeds		68	k-1, r-3, t-1, u-4, x-3	none	179

[1] 92W60C-98, 90H75C-259, 60H60C-529, 90C-290, BURN-504, ASH-158, SRFFIRE-324, OVEN-20, OVEN/ASH-22, WASH-922.

and 84.5 ± 8.4 days, respectively. Fresh seeds began germinating 6 days earlier than ingested seeds. The difference in germination rate was not significant (2-tailed *t*-test, $P = 0.11$). For *O. littoralis,* 4.0% ($n = 272$) of seeds from seedy scats germinated and 0.5% ($n = 210$) of seeds from furry scats germinated; seeds from seedy scats germinated significantly more often than those from furry scats (Fisher's exact test, $P < 0.01$).

DISCUSSION—Seeds of 18 species germinated following passage through the digestive systems of coyotes, suggesting that the coyote might disperse seeds of numerous plant species in southern California. Seeds of an additional 20 species did not germinate, but negative results do not necessarily indicate that these seeds were incapable of germination from scats. The variability of natural conditions is difficult to recreate in the laboratory, and factors that influence germination often are unknown. Seeds of *O. littoralis* dispersed by coyotes germinated significantly more often than seeds collected directly from plants. However, seeds of *O. littoralis* from fruit-based scats germinated significantly more often than those from meat-based scats, suggesting that an optimal level of scarification in coyote stomachs was achieved by the laxative quality of fruits.

Seeds of the native fan palm (*Washingtonia filifera*) germinated most successfully of all seeds from coyote scats. Native fan palm occurs in isolated groves in the Colorado Desert. The common occurrence of these seeds in scats and the high germination rate following dispersal suggest that coyotes might play a significant role in the dispersal of this species. Similarly, with increasing fragmentation of natural landscapes, coyotes might play an important role in connecting isolated populations of fruit-bearing species, providing a dispersal vector to maintain genetic diversity and reestablish colonies following local extinctions. Their importance in long-distance seed dispersal is worthy of consideration in conservation plans.

The only seeds of *Arctostaphylos* sp. and *A. glauca* to germinate from scats were those pretreated by burning leaves on seed trays and adding charred ashes. Seeds of *Arctostaphylos* have been found in 29% of coyote scats in Cuyamaca State Park (Bowyer et al., 1983) and 25% of coyote scats in the western Sierra Ma-

TABLE 3—Germination comparison between seeds collected from coyote (*Canis latrans*) scats and seeds collected directly from plants in southern California.

Taxon	Scat-derived % germinated (number of seeds)	Plant-derived % germinated (number of seeds)	Fisher's *P*-value
Xylococcus bicolor	0.0 (1,158)	0.0 (856)	
Opuntia littoralis	9.1 (88)	0.0 (72)	<0.01
Arctostaphylos	0.0 (285)	0.0 (360)	
Heteromeles arbutifolia	0.0 (16)	81.3 (16)	<0.001
Pyracantha	8.3 (12)	0.0 (12)	>0.45
Citrus	0.0 (24)	12.5 (24)	>0.10
Annona cherimola	31.7 (60)	50.0 (18)	>0.05

dre, Mexico (Delibes et al., 1989). Seed dispersers and fire might complement the natural reproduction of this genus, with coyotes spreading the seeds and fires providing the ideal conditions for germination. This study provides evidence that the seeds can withstand both the gastric acids of coyotes and the heat and ashes from burning. The wildfires in southern California in October 2003 burned through 27% of the sampling locations for this study. How seed dispersal by coyotes in burned areas affects regeneration and recolonization of plants would be an interesting topic for further study.

Comparisons between seeds from scat and seeds from plants have been widely used in seed dispersal research, but they were not emphasized in this project. Many uncontrolled variables, such as variability in seeds, plants, or time in the gut, can influence the outcome of such comparisons. For example, seeds of *Solanum lycocarpum* dispersed by the maned wolf (*Chrysocyon brachyurus*) enhanced germination significantly in 4 experiments, significantly inhibited germination in 4 other experiments, and showed no significant difference in yet another 4 experiments, although the experiments were considered to be identical (Motta-Junior and Martins, 2002).

This study revealed that coyotes could play a role in introducing exotic species into natural areas. Eight confirmed exotic species and 3 probable exotics germinated from coyote scats. These species are garden and agricultural plants rather than invasive weeds. Their dispersal by coyotes does not seem to be a conservation threat. However, the abundance and viability of exotic seeds in coyote diets suggest that coyotes have the potential to be a dispersal vector for invasive species. Coyotes also have been shown to reduce the numbers of mesopredators, such as opossum (*Didelphis virginiana*) and raccoons (*Procyon lotor*) (Crooks and Soule, 1999). Given that mesopredators also eat fruits and likely disperse exotic seeds into natural areas, coyotes might limit other agents of seed dispersal. I suggest that, in southern California, coyotes are legitimate dispersers that have a significant impact upon the dispersal of seeds.

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