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## DESICCATION SENSITIVITY AND HEAT TOLERANCE OF *PRUNUS ILICIFOLIA* SEEDS DISPERSED BY AMERICAN BLACK BEARS (*URSUS AMERICANUS*)

Mark Borchert<sup>1</sup> and Claudia M. Tyler<sup>2</sup>

**ABSTRACT.**—Carnivore consumption of fruit is a principle means by which many fleshy-fruited plant species achieve long-distance seed dispersal. We examined carnivore dispersal of hollyleaf cherry (*Prunus ilicifolia*) seeds, specifically assessing the survival, desiccation sensitivity, and germination of seeds found in bear scats. Studies were conducted both in the laboratory and in 2 burn areas in Los Padres National Forest, California. Bear scats containing *P. ilicifolia* seeds were collected in burned and unburned chaparral. We counted seeds in each scat and noted whether endocarps had tooth punctures or rattled audibly when shaken. For comparative germination trials, we also collected fruits and seeds directly from mature shrubs. In the laboratory, following a cold-moist stratification period, seeds were assessed for germinability. In the field, we compared desiccation rates and germinability of seeds from bear scats and freshly collected seeds. We compared rates of moisture loss and germination for seeds subjected to several different conditions, including 25 °C (room temperature), 30 °C and 65 °C (in the lab), and placement on exposed soil in a burn area (in the field), where midday temperatures were approximately 45 °C but likely much higher by late afternoon.

*Prunus ilicifolia* seeds collected from bear scats were largely undamaged; the vast majority of these seeds germinated. In some cases, germination rate was higher for seeds from scats than for seeds from intact fruits. Several results indicate that desiccation is an important cause of reduced germinability. First, seeds that rattled audibly germinated poorly; and the louder the rattle, the lower the germination percentage. Second, seeds (both fresh and those from bear scats) placed in the field under protective screens had greatly reduced levels of germination (an 84% decline) after only 7 days. Third, seeds dried in the lab, even at relatively moderate temperatures, showed a decline in germination with seed moisture loss. The addition of high temperatures accelerated this decline in germination. We discuss the relevance of heat and desiccation sensitivity of seeds dispersed by bears to successful seed germination in burned and late-seral mesic and xeric chaparral.

*Key words:* seed dispersal, endozoochory, carnivore, chaparral, *Prunus ilicifolia*.

**RESUMEN.**—El consumo de fruta por carnívoros es uno de los principales medios por los que muchas especies de plantas de frutos carnosos logran dispersar sus semillas a través largas distancias. Examinamos la dispersión por carnívoros de las semillas del islay (*Prunus ilicifolia*), un arbusto del chaparral, evaluando concretamente la supervivencia, la sensibilidad a la desecación y la germinación de semillas encontradas en las heces de oso. Estos estudios se llevaron a cabo tanto en el laboratorio como en dos áreas quemadas en Los Padres National Forest, California. Se colectaron heces de oso que contenían semillas de *P. ilicifolia* en el chaparral quemado y en el no quemado. Contamos las semillas en cada bola fecal y notamos si los endocarpios tenían marcas de dientes y si vibraban audiblemente al agitarse. Para llevar a cabo pruebas comparativas de germinación, también colectamos frutos y semillas directamente de los arbustos maduros. En el laboratorio, después de un período de estratificación fría-húmeda, evaluamos la capacidad de germinación de las semillas. En el campo, comparamos las tasas de desecación y de germinación de semillas de las heces de oso con aquellas de semillas colectadas directamente de los arbustos. Se compararon las tasas de pérdida de humedad y germinación de las semillas sujetas a diversas condiciones, entre ellas 25 °C (temperatura ambiente), 30 °C y 65 °C en el laboratorio, y en el campo sobre suelo expuesto en un área quemada, donde la temperatura al mediodía era ~45 °C pero probablemente mucho más alta por la tarde.

En general, las semillas de *P. ilicifolia* colectadas en las heces de oso no estaban dañadas; la gran mayoría de estas semillas germinaron; en algunos casos la tasa de germinación fue más alta que la de frutos intactos. Varios resultados indicaron que la desecación es una causa importante de la reducción en la capacidad de germinación. Primero, las semillas que vibraban audiblemente germinaron poco, y cuanto más fuerte el sonido, menor la germinación. Segundo, las semillas (tanto las frescas como las colectadas de heces de oso) colocadas en el campo bajo una malla protectora exhibieron niveles de germinación muy reducidos (una disminución del 84%) después de sólo siete días. Tercero, la germinación de las semillas desecadas en el laboratorio, incluso a temperaturas relativamente moderadas, disminuyó con la pérdida de humedad de las semillas. Temperaturas más altas aceleraron esta disminución en la germinación. Discutimos la importancia de la sensibilidad al calor y a la desecación en las semillas dispersadas por los osos para la germinación exitosa en el chaparral méxico y árido, tanto en el chaparral recién quemado como en el que está en las etapas finales de sucesión.

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Carnivore endozoochory is a principle means by which many fleshy-fruited plant species achieve long-distance seed dispersal (Corlett 1998, Jordano et al. 2007). As seed dispersers, carnivores are particularly effective because they can consume large numbers of a wide variety of fruits that pass mostly undamaged through their digestive systems (Herrera 1989, Willson 1993, Traveset 1998). Moreover, during the time it takes for fruits to process in the gut, carnivores move long distances (Hickey et al. 1999, Otani 2002, Graae et al. 2004, Alves-Costa and Eterovick 2007). Thus the seed rain of an individual plant can be expanded significantly (Hardesty et al. 2006).

Seed dispersal by carnivores involves a series of steps, beginning with fruit removal and ending with seed germination. At each step, viable seeds may suffer mortality. Seeds can die by mastication (Dungan et al. 2002, Stoner et al. 2007) or by exposure to scarification and gastric chemicals as they pass through the digestive system (Murray et al. 1994, Auger et al. 2002, Graae et al. 2004, Zhou et al. 2008a). Once seeds are voided by the animal, several factors determine whether seeds survive and arrive at sites where germination is likely. For example, other predators may consume seeds embedded in feces (LoGiudice and Ostfeld 2002) or carry them to locations, such as deep burrows or nests, where germination is unlikely. Toxic compounds in the manure can inhibit germination (Marambe and Ando 1993), and pathogens can infect the seeds of some *Prunus* species (Nakamura et al. 2006). On the other hand, manure in feces can also have positive effects on bear-dispersed seeds. For example, the animal material contained in some feces increased seed germination and seedling growth rates of 2 common Alaskan shrubs (Traveset et al. 2001).

Functional traits of the seed, specifically sensitivity to desiccation and tolerance of high temperatures, also can influence the number of viable seeds dispersed by carnivores. In general, these traits of animal-dispersed seeds have been overlooked as factors limiting postdispersal germination (Chambers and MacMahon 1994). Sensitivity of seeds to desiccation has been studied in detail, but primarily in relation to storage and conservation (Berjak and Pammenter 2001). Almost no attention has been given to the ecological effects of moisture loss on seeds dispersed by vertebrates. In California chaparral, for example, seed tolerances to high

temperatures have been studied extensively. However, these studies have centered on the role of heat in breaking dormancy of soil-stored seeds (e.g., Keeley 1987, Keeley 1991) but have not examined its potential role in limiting postdispersal seed germination.

The questions we addressed in this study were as follows: (1) Do *Prunus ilicifolia* (hollyleaf cherry) seeds survive consumption and digestion by black bears? (2) Is seed sensitivity to desiccation and high soil temperatures in burn areas different in seeds dispersed by carnivores than in seeds dispersed in other ways (e.g., gravity)? And (3) how do functional seed characteristics affect the likelihood of germination and recruitment?

## METHODS

### Study Areas

The Wolf burn study area is 300 m northwest of the Piedra Blanca Group Camp (34°33'N, 119°10'W), just north of Sespe Creek on the Ojai Ranger District of Los Padres National Forest in southern California. In June 2002, an 8100-ha wildfire burned the study site, which is situated on an old river terrace approximately 30 m above Sespe Creek at 940 m elevation. The area is flat and had been dominated by 70-year-old chamise (*Adenostoma fasciculatum*), with widely scattered chaparral whitethorn (*Ceanothus leucodermis*). The fire burned at high intensity through the entire area leaving only charred shrub bases. By 2005 (the year of this study), chamise resprout cover averaged 20%.

The Piru burn study area is 9 km north of Fillmore, California, in an area called Squaw Flat (34°29'N, 118°54'W) also on the Ojai Ranger District. The area has rugged, mountainous terrain. Eighty-eight-year-old chamise mixed with hoaryleaf ceanothus (*Ceanothus crassifolius*) dominated the area before it burned on 23 October 2003. A high-intensity fire swept 25,900 ha leaving little in the way of shrub skeletons or unburned islands.

### The Species

*Prunus ilicifolia* (hollyleaf cherry) is an evergreen shrub that ranges from 2 to 3 m in height. In September and October, it produces large (approximately 13 × 17-mm) scarlet drupes. The fruit, which is covered by a smooth skin (exocarp) and a thin (2–3-mm) layer of sweet pulp (mesocarp), is mostly a bony endocarp enclosing

the seed. Most fruits occur as singletons or in clusters of 2.

*Prunus ilicifolia* is a primary constituent of mesic chaparral which typically occupies north-facing slopes with low solar insolation (Keeley 1998). Other fleshy-fruited species that co-occur with *P. ilicifolia* in this setting include toyon (*Heteromeles arbutifolia*), coffeeberry (*Rhamnus californica*), redberry (*Rhamnus crocea*), and hollyleaf redberry (*Rhamnus ilicifolia*). Mesic chaparral occurs as distinct patches in the chaparral landscape, usually in a matrix of the more pervasive xeric chaparral. Along with scrub oak (*Quercus berberidifolia*) and mountain mahogany (*Cercocarpus betuloides*), mesic chaparral shrubs possess a suite of similar morphological, physiological, and life history characteristics: all are long lived, deep rooted, and relatively drought intolerant (Keeley 1998). Furthermore, they are "postfire obligate resprouters," because they resprout prolifically after fire but recruit few seedlings (Keeley 1992). Except for mountain mahogany, which is wind dispersed, fruits of the other mesic chaparral shrubs are thought to be animal dispersed (Keeley 1991).

#### Seed Collection and Germination

Between 20 August and 9 September 2004, we collected 10 fresh black bear feces laden with *P. ilicifolia* seeds in the Piru burn area along a 2-km section of dirt road. Seeds in bear feces formed small, separate piles. All pulp was missing, and bare seeds were mixed with dried exocarps. Although we could not locate the plant(s) producing fruits eaten by the bear(s), we suspect the fruits came from along the narrow streamside fringe of shrubs that survived the fire in the canyon above the road. We counted and weighed seeds in each scat and noted whether endocarps had tooth punctures (1-mm diameter) or an audible rattle when shaken.

In late October 2005, we collected 327 seeds in dried bear scats from beneath 2 heavily fruiting shrubs in unburned chaparral next to a paved road (Highway 33) at 1180 m elevation. We noted whether seeds had punctures and if they rattled audibly when shaken. In addition, we recorded the relative loudness of the rattle and sorted them into 4 categories: no rattle, faint, moderate, or loud.

For comparative germination trials, as well as laboratory and field trials, we collected fruits and seeds that had not passed through an animal gut. We picked ripened fruits directly

from 8 mature shrubs in late September 2004 and 15 shrubs in 2005 in unburned chaparral along a roadside (Highway 33 between Ojai and Rose Valley Road) at elevations between 790 and 850 m. For a portion of fruits collected, we removed the exocarps and mesocarps and washed them for 30 seconds with a 5% solution of bleach; these seeds we refer to as "cleaned." We also retained whole fruits (exocarp and mesocarp intact) for comparative germination tests. Both the freshly collected fruits and the cleaned seeds were stored in plastic bags at 8–10 °C.

We used the same germination protocol for all trials. We put seeds in plastic bags containing moist vermiculite and stored them in the dark for 30 days at 4 °C. After this cold-moist stratification, seeds were germinated for 26–95 days on a cycle of 12 hours of dark at 20 °C and 12 hours of light at 30 °C. We recorded seeds as having germinated when their radicle extended 3 mm from the endocarp or, in the case of whole fruits, from the pericarp.

We collected a total of 401 seeds from 15 fresh bear scats in the Piru burn. These we sorted into 3 groups: punctured seeds, intact seeds that rattled, and intact seeds without a rattle. For punctured seeds, we germinated 6 samples of 10 seeds per sample (total number of seeds = 60). For intact seeds that rattled, we germinated 15 samples of 10 seeds per sample (total number of seeds = 150); and for intact seeds without a rattle, we had 6 samples of 10 seeds per sample (total number of seeds = 60). The total number of seeds from the "bear burn" samples was 270.

Similarly, for seeds collected from bear scats in unburned chaparral along the roadside, we sorted seeds into 4 categories, based on the relative loudness of the rattle. Sample sizes were as follows: 6 samples of 10 seeds with no rattle, 3 samples of 10 seeds with a faint rattle, 3 samples of 10 seeds with a moderate rattle, and 5 samples of 10 seeds with a loud rattle. The total number of seeds from the "bear roadside" samples was 170.

For germination of freshly collected seed, we used 130 "cleaned" seeds and 110 whole fruits. In addition, to examine the effects of cold storage on seed viability and germinability we maintained a sample of "cleaned" seeds for 2 years (in plastic bags at 8–10 °C) and then germinated them after this period; for these samples, we used 50 "clean, stored" seeds.

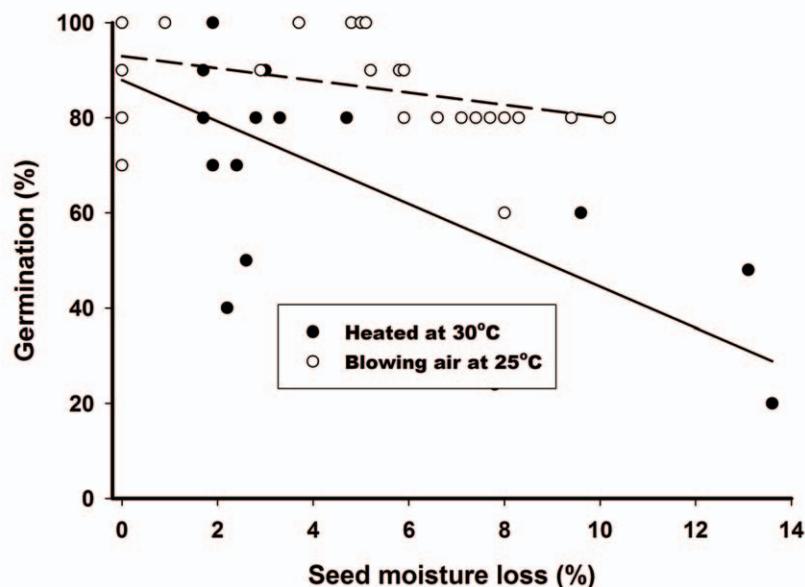


Fig. 1. Cumulative percent germination of *Prunus ilicifolia* seeds after 55 days in relation to moisture loss. Seeds were either dried at room temperature (25 °C) in blowing air (open circles, solid line) or heated at 30 °C with a commercial heating pad (solid circles, dashed line). Slopes of the 2 treatment regressions are significantly different (general regression models;  $F = 30.9$ ,  $df = 1$ ,  $P < 0.0001$ ). Percentages were arcsine square-root transformed for the analysis.

#### Seed Desiccation and Heat Tolerance Trials in the Laboratory

We placed 10 weighed, cleaned seeds in each of 20 plastic petri dishes (1.4 × 19 cm in diameter) and exposed them to moving air at 25 °C (room temperature). We periodically reweighed the samples over a 72-hour period to obtain target water-loss values between 1% and 10% of fresh weight, and we germinated samples when they reached the target moisture loss. Similar trials were carried out using a commercial heating pad, but without blowing air. We dried 16 samples of 10 seeds each by heating them at a constant 30 °C until we obtained moisture losses ranging from 3% to 13%.

#### Seed Desiccation and Germination Trials in the Piru Burn

On 7 September 2004, we selected 5 sites spaced 300–500 m apart in the Piru burn area for seed desiccation and germination studies. Elevations of the sites were between 740 and 768 m, slopes ranged from 17° to 20°, and aspects were between N and NE. For these studies, we compared desiccation and germination of 2 groups of seeds: those without rattles from bear scats (collected from the burn area)

and those from freshly collected fruits, which had all pulp removed (i.e., “cleaned”). Prior to the field trial, we determined percent germination for each group, as described above. On 10 September 2004, we recorded the weights of all seeds used for these trials and placed 10 intact seeds from each group in seed enclosures, one per site. Seed enclosures were 30 × 30-cm wire mesh (127 × 127-mm) screen placed over the seeds and secured to the soil with 20-cm metal stakes. Seven days later, we collected and reweighed the seeds. We counted the number in each group that rattled (caused by the drying cotyledons) and then determined germinability of 5 randomly selected seeds from each group. We returned the remaining seeds (5 per group) to the protective screens; and in early April 2005, we counted the number of germinated seeds and seedlings at each site.

#### Seed Desiccation and Heat Tolerance Trials in the Wolf Burn

In August 2005, we placed 10 exclosures 10 m apart on exposed soil between 3-year chamise resprouts. Exclosures were 29 × 29 × 21 cm, made of 127 × 127-mm wire mesh and staked into bare soil between resprouting shrubs. In each exclosure, we placed 3 groups of 10 cleaned

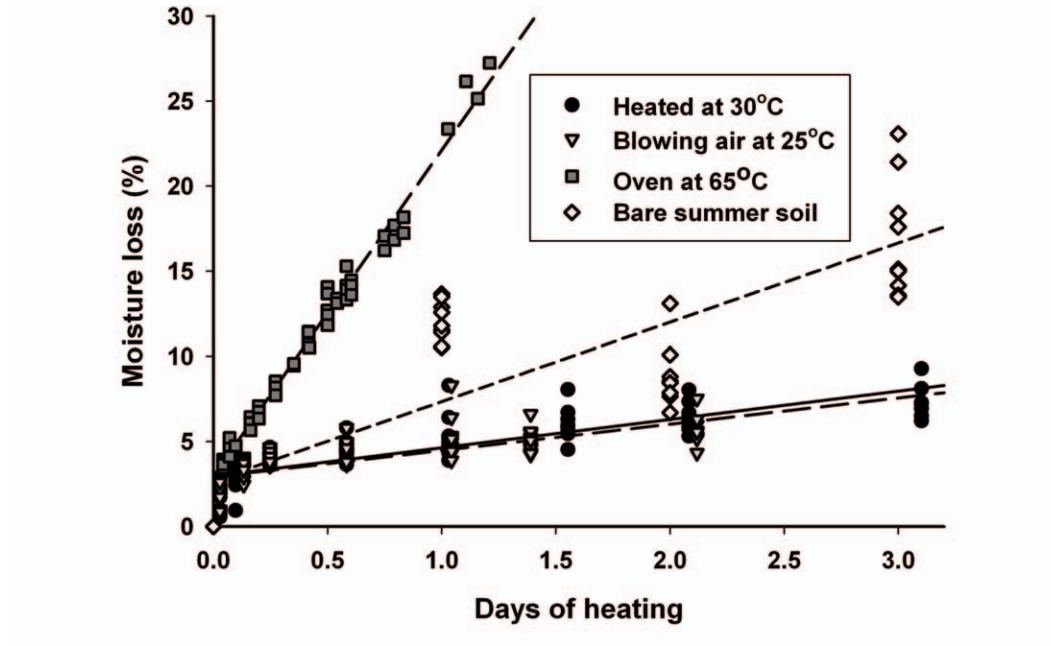


Fig. 2. Moisture loss of *Prunus ilicifolia* seeds under 3 treatments: dried at room temperature (25 °C) in blowing air, heated at 30 °C, oven-heated at 65 °C, and placed on the bare summer soil in enclosures. Slope regressions of samples dried at 25 °C and 30 °C are not significantly different (general regression models;  $F = 0.06$ ,  $df = 1$ ,  $P = 0.81$ ). The oven treatment at 65 °C is significantly different from the combined 25 °C and 30 °C treatments ( $F = 410.3$ ,  $df = 1$ ,  $P < 0.001$ ) and the soil treatment ( $F = 4.67$ ,  $df = 1$ ,  $P = 0.04$ ). The soil treatment is significantly different from the combined 25 °C and 30 °C treatments ( $F = 8.31$ ,  $df = 1$ ,  $P = 0.004$ ).

seeds; each group was weighed prior to placement in the field. Twenty-four, 48, and 72 hours after initiation, we retrieved one group of 10 seeds from each enclosure. We measured surface soil temperatures with a mercury thermometer (range 0–205 °C) near midday (11:00) on each visit. Before conducting germination trials on the seeds recovered from the field, we reweighed each sample to obtain its moisture loss.

## RESULTS

### Germination after Desiccation and Heating in the Laboratory

In the laboratory, seeds dried at 25 °C and those heated at 30 °C lost water at the same rate (Fig. 1)—approximately 5% moisture loss after 2 days—and were not significantly different from each other based on general regression models ( $F = 0.06$ ,  $df = 1$ ,  $P = 0.81$ ). For both treatments, germination was negatively related to seed moisture loss (Fig. 1); the rate of decrease differed significantly between the 2 treatments ( $F = 30.9$ ,  $df = 1$ ,  $P < 0.0001$ ),

with the heat treatment causing a steeper decline in germination. Seeds heated in the oven at 65 °C dried rapidly (Fig. 2); however, none of the oven-heated seeds germinated, regardless of moisture loss.

### Germination of Protected Seeds in the Piru and Wolf Burns

For seeds left in the field for 7 days under protective screens in the Piru burn, bear seed germination dropped from 100% (SD = 0.0) to 16.0% (SD = 26.1;  $t = -5.47$ ,  $df = 6$ ,  $P = 0.001$ ), and germination of fresh, clean seeds fell from 76.0% (SD = 16.8) to 12.0% (SD = 17.9;  $t = -4.61$ ,  $df = 8$ ,  $P = 0.002$ ). By spring 2005, only 3 of the 50 seeds under the screens had rooted in the soil, and, of these, 1 produced a seedling. None of the remaining 46 seeds germinated.

Seeds placed on the open summer soil in the Wolf burn dried rapidly, reaching up to 20% seed moisture loss after only 72 hours (Fig. 2); none of these seeds germinated. Soil temperatures in the field, measured at the midday visits, ranged from 43 to 46 °C but were almost always higher later in the afternoon.

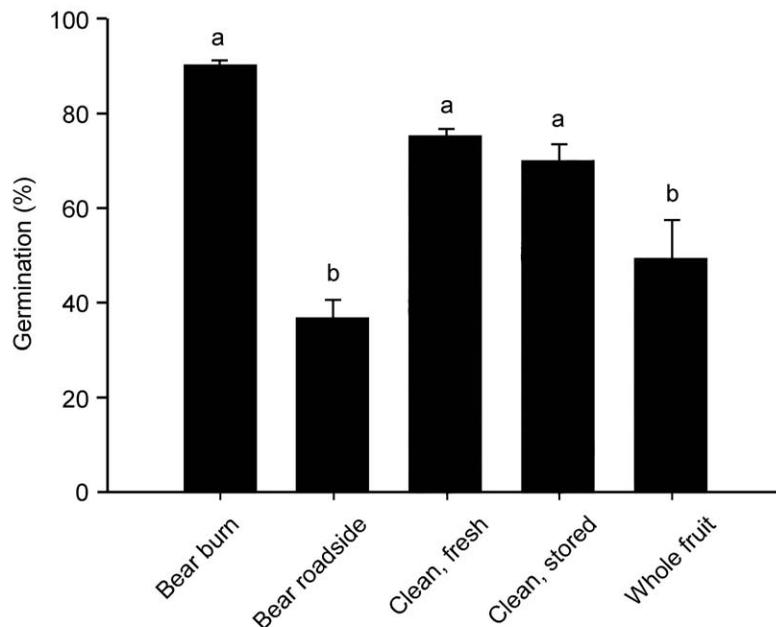


Fig. 3. Average cumulative percent germination of *Prunus ilicifolia* seeds after 60–65 days. Whisker bars indicate one standard error. “Bear burn” seeds were collected from fresh bear scats in the Piru burn. “Bear roadside” seeds were collected from dried bear scat (of unknown age) under unburned shrubs along Hwy. 33. “Clean, fresh” seeds were ripe, depulped seeds from roadside shrubs. “Clean, stored” seeds were depulped seeds from roadside shrubs stored for 2 years at 10 °C. “Whole fruits” were seeds from fruits with skin and pulp present. Bars with different letters are significantly different at  $P < 0.05$  (one-way ANOVA and Tukey’s honestly significant difference test for unequal sample sizes). Percentages were arcsine square-root transformed for the analysis.

#### Number and Relative Germination of Seeds in Bear Feces

The number of seeds in bear feces collected from the Piru burn area ranged from 6 to 125 per pile ( $\bar{x} = 36.1$ ,  $SD = 31.9$ ,  $n = 15$ ). Of the 401 seeds in these feces, the majority (61.8%) were undamaged (lacking both tooth punctures and rattles), 27.5% had pierced endocarps and rattled, and 10.7% rattled but were not punctured. Percent germination of seeds in fresh bear scats in the burn was very high overall and was comparable to that of cleaned fresh seeds and cleaned stored seeds (Fig. 3). Seeds from bear scats varied in their germination depending on whether they were damaged or desiccated (as indicated by a rattle); unpunctured seeds without rattles germinated rapidly and completely (Fig. 3), while those that either rattled or had punctures and rattled germinated poorly: 7.3% ( $SD = 11.6$ ) and 1.7% ( $SD = 4.1$ ), respectively (not shown in Fig. 3).

Seeds that had the skin and pulp removed—both “cleaned” seeds and those from bear scat in

the burn area—germinated significantly better than those within whole fruits ( $t = 3.82$ ,  $df = 23$ ,  $P = <0.001$  and  $t = 2.70$ ,  $df = 11$ ,  $P = 0.02$ , respectively; Fig. 3). Roadside bear seeds were significantly lower in germination than those collected in the burn ( $t = 9.37$ ,  $df = 7$ ,  $P < 0.0001$ ; Fig. 3). We also found that percent germination of seeds from bear scats collected under roadside shrubs was negatively correlated with the loudness of the cotyledon rattle ( $r = -0.86$ ,  $P < 0.001$ ), indicating that germinability decreased as the cotyledons dried.

#### DISCUSSION

##### Seed Desiccation Sensitivity and Heat Tolerance

Both our field and laboratory trials showed that the viability of *P. ilicifolia* seeds is sensitive to moisture loss and high temperatures. At room temperature (approximately 25 °C), seeds lost moisture slowly (Fig. 1) and after 2 months of drying, germination remained high (approximately 75%, Fig. 2). However, results from a

previous study (Keeley 1997) suggest that slow moisture loss would continue over time, with concomitant loss in germination. For example, cleaned *P. ilicifolia* seeds kept in paper bags at room temperature lost viability gradually over 12 months, dropping from 65% to 10% germination (Keeley 1997).

Exposure to temperatures above approximately 25 °C resulted in increased desiccation rates and reduced germination. In this study, seeds heated at 30 °C lost moisture at the same rate as those dried at 25 °C in moving air (Fig. 1). Nevertheless, the germination of heated seeds dropped significantly faster (Fig. 2), suggesting that the 5 °C increase may have killed some seeds. For seeds placed in the Piru burn area under protective screens, both intact seeds from bear scats and seeds that had been cleaned suffered sharp declines in germination after one week. Lastly, seeds placed on the hot summer soils in the Wolf burn and those placed in the oven at 65 °C died rapidly and failed to germinate, even at the lowest levels of water loss. Keeley (1987) noted that several fleshy-fruited chaparral species lost viability rapidly when heated at or above 70 °C. In addition to the high oven and soil temperatures, rapid drying rate in the oven and on the soil surface may have accelerated the loss in viability. Several studies have shown that the germination rate of desiccation-sensitive seeds decreases faster when they are dried rapidly (Berjak and Pammenter 2001, Konstantinidou et al. 2008).

#### Survival and Germinability of Seeds Dispersed by Bears

In other carnivore studies, mastication damage to fleshy-fruits has been low (<1%; Herrera 1989) or nonexistent (Koike et al. 2008). Although our sample size of scats containing *P. ilicifolia* seeds was small compared to other studies, the results suggest that damage due to mastication can be high in some cases, at least for bears. Seed damage was relatively high in scats collected from the burn area; 27.5% of *P. ilicifolia* seeds in these feces were punctured, and punctured seeds had a very low level of germination (1.7%). While piercing the endocarp probably did not kill the embryos, it likely reduced viability by accelerating cotyledon water loss.

Desiccation was a more significant source of mortality than mastication for seeds dispersed by bears. Approximately 40% of seeds extracted

from bear scats in the burn area rattled, indicating that the cotyledons had dried; fewer than 8% of these seeds germinated, in stark contrast to the very high levels of germination of undesiccated (nonrattling) seeds from scats. In addition, even for the unpunctured seeds from feces collected under shrubs, desiccation reduced their viability, as demonstrated by the negative correlation between rattle loudness and percent germination. For reasons that are unclear, undamaged seeds without rattles from roadside samples had lower levels of germination than bear seeds from the burn (Fig. 3). We suspect that seeds beneath the unburned shrubs dried more slowly than fully exposed seeds in the burn area. As a result, there was a wider range of seeds in various stages of desiccation.

In spite of seed losses due to mastication and desiccation, our study indicates that black bears are legitimate dispersers of *P. ilicifolia*. We found high numbers of seeds in bear scats, and the majority were undamaged, with germination ranging from approximately 40% ("bear roadside") to nearly 100% ("bear burn"; Fig. 3). The high level of germination observed for undamaged, undesiccated seeds from bear scats in the burn (Fig. 3) and the lack of a difference in germination between these and seeds that were manually cleaned, indicate that gut passage did not reduce germination. In fact, compared to whole fruits, pulp removal during digestion appears to have enhanced the germination of *P. ilicifolia* seeds—a result consistent with other studies showing positive effects of carnivore fruit consumption on germination (Traveset 1998).

#### Implications for Seedling Establishment

The heat and desiccation sensitivities of *P. ilicifolia* seeds have important implications for germination success in the field because microclimates vary widely among chaparral habitats. In 50-year-old xeric chaparral dominated by chamise, late summer and early fall soil temperatures often approach the maximum air temperatures above the canopy. For example, mean monthly soil temperatures in August and September range from 18 °C to 22 °C, but it is not uncommon for soil temperatures to reach or exceed 32 °C for several days in a row (Johnson-Maynard et al. 2004). In this microclimate of relatively high temperature and low humidity, *P. ilicifolia* seeds in feces likely desiccate quickly. By comparison, soil temperatures in

late-seral mesic scrub oak chaparral remain  $<23^{\circ}\text{C}$ , even when above-canopy air temperatures exceed  $32^{\circ}\text{C}$  (Johnson-Maynard et al. 2004). In this microclimate, seeds likely lose moisture more slowly and remain viable longer—much like seeds dried at room temperature in this and Keeley's (1997) study. In part, the desiccation sensitivity of *P. ilicifolia* explains why this shrub regenerates best in late-seral ( $>60$  years), mesic chaparral (Hanes and Jones 1967, Keeley 1987, Keeley 1991, Keeley 1992).

After fire, summer and fall soil temperatures in chaparral increase markedly, regardless of the prefire microhabitat (Christensen and Muller 1975, Auld and Bradstock 1996). Christensen and Muller (1975) monitored air and soil temperatures in August and September one year after a chaparral wildfire. They found that while air temperatures ranged from  $32^{\circ}\text{C}$  to  $40^{\circ}\text{C}$ , burned soil temperatures were much higher, ranging from  $60^{\circ}\text{C}$  to  $78^{\circ}\text{C}$ . Our results show that seeds deposited on the burned soils of both xeric and mesic chaparral lost viability within hours or, at most, a few days. This vulnerability to high temperature and associated water loss partly explains why the chance of successful establishment in burned areas is low even if seeds arrive there in considerable numbers via animal dispersal.

In addition to the effects of habitat on seed survival, within-habitat microsites influence the survival of desiccation-sensitive seeds. The postfeeding movements of carnivores determine the array of depositional sites available to seeds (Martínez et al. 2008). In general, carnivores deposit seeds in exposed microsites that are inhospitable to the germination of desiccation-sensitive seeds (Bustamante et al. 1992). For example, coatis (*Nasua nasua*) defecate on soil, trunks, stones, and paved ground (Alves-Costa and Eterovick 2007). The maned wolf (*Chrysocyon brachyurus*) voids seeds onto steep road banks, gravel mounds, rock outcrops, and mine tailings (Santos et al. 2003). Gray foxes (*Urocyon cinereoargenteus*) deposit scats on open roads or tops of rocks (Wilson and Thomas 1999); and ferret-badgers (*Melogale moschata*) void seeds on rock outcrops, gravel mounds, and rocky soils (Zhou et al. 2008b). In this study, bears commonly voided feces along roads and into the burn area.

The functional seed traits of *P. ilicifolia* appear to be adaptive in mesic chaparral where

conditions are conducive to the survival of desiccation-sensitive seeds. Outside this setting, however, seed desiccation potentially creates a significant bottleneck to recruitment, particularly for seeds dispersed into xeric chaparral, into recently burned areas, or onto exposed microsites. Thus, it seems likely that only a small number of viable seeds successfully move between patches of mesic chaparral or into relatively mesic microhabitats within xeric chaparral.

One way desiccation-sensitive seeds can avoid or reduce moisture loss and heat-kill, even within xeric habitats, is through their rapid removal and burial by secondary dispersers. Numerous rodent species remove seeds from feces and scatter hoard them in microsites where the effects of drying and heat on viability are greatly reduced (Vander Wall and Longland 2004, Vander Wall et al. 2005). In the Wolf burn, Pacific kangaroo rats (*Dipodomys agilis*) removed *P. ilicifolia* seeds from artificial bear scats (Borchert unpublished data). Nevertheless, even though this rodent both scatter hoards and larder hoards seeds, we know little about the fate of *P. ilicifolia* seeds after removal (Vander Wall et al. 2005). Even if rodents buried seeds, high soil temperatures in early postfire chaparral may kill all *P. ilicifolia* seeds. On the other hand, in later years, the chance for recruitment likely increases since shade of resprouting shrubs that recover rapidly may make the soil environment progressively less hostile to the survival of recalcitrant species.

In summary, as previous researchers have reported for coyote and gray fox (Bullock 1981, Wilson and Thomas 1999, Silverstein 2005), we found black bears to be legitimate dispersers of *P. ilicifolia* seeds. Moreover, the germinability of the seeds that passed through the gut and were deposited in bear scats was greater than that of seeds from fresh fruit (Fig. 3). We also found that, consistent with previous laboratory studies (Keeley 1987, 1997), *P. ilicifolia* seeds are highly sensitive to desiccation and heating; so seeds deposited in bear scats in exposed sites, such as recently burned and early seral chaparral, likely have a low probability of germination unless carried to a hospitable microsite by secondary dispersers. Nevertheless, because black bears often travel great distances, our findings suggest that they are important dispersers of germinable seed for this shrub species, particularly among the widely scattered

islands of mesic chaparral. Our findings also suggest that research is needed on the complex interactions among seed characteristics, the feces in which they are embedded, and the microsite characteristics where they are deposited. For species like *P. ilicifolia*, which possesses heat-intolerant and/or desiccation-sensitive seeds, this stage of the life cycle could greatly influence the likelihood of seedling recruitment.

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