

CARNIVORE USE OF AN AVOCADO ORCHARD IN SOUTHERN CALIFORNIA

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ABSTRACT

In southern California avocados are an important commercial fruit that often are planted near or immediately adjacent to wildlands. Among cultivated fruits, avocados are unusually high in both lipids and proteins. Fruits remain green on the tree and ripen only after they fall to the ground or are harvested. As a result, they offer a relatively constant, year-round food source in the form of unharvested, fallen fruit. In 2005 for 5.5 months, we camera-trapped medium and large mammals in 13.5 ha of a 55.5 ha commercial avocado orchard in southern California. We also monitored fruit fall and subsequent removal to quantify the amount of energy available to mammals and estimated how much of the ground fruit they consumed. Cameras captured 7 carnivores: black bear, *Ursus americanus*, domestic dog, coyote, *Canis latrans*, bobcat, *Lynx rufus*, gray fox, *Urocyon cinereoargenteus*, raccoon, *Procyon lotor*, and striped skunk, *Mephitis mephitis*; non-carnivores included western gray squirrel, *Sciurus griseus* and Virginia opossum, *Didelphia virginiana*. All but bobcats were photographed eating avocados. Black bears, gray foxes and striped skunks frequented the part of the orchard least affected by human activities. In contrast, coyotes and raccoons were more common where humans and domestic dogs were present. Mammals consumed all or nearly all marked avocados on the ground, usually within 50 days. We estimated that they consumed only a small portion (<2%) of the total fruit crop. Avocado orchards offer super-rich food patches that are readily accessible to an array of medium and large mammals.

INTRODUCTION

Fleshy fruits are a staple in the diet of a wide array of carnivorous mammals (order Carnivora) (Herrera 1989, Willson 1993, McCarty et al. 2002). In the last decades there has been an explosion of studies on the role of native fruits in the diets of mammals. Nearly all of the research on frugivory in carnivores has centered on four topics: 1) the role of native fruit in the diet of individual species and the physiological constraints

frugivory imposes on them (Welch et al. 1997, Rode and Robbins 2000), 2) seed dispersal of native plant species (Debussche and Insenmann 1989, Herrera 1989, Willson 1993) 3) the effects of passage through the gut on seed germination (Traveset and Willson 1997, Traveset 1998), and 4) the co-evolution of mammals and fruits (Herrera 1987).

Cultivated fruits have been mentioned as occurring in the diets of many carnivores, even in diets where agricultural areas were outside the main study areas (Padial et al. 2002, Schaumann and Heiken 2002). As diet studies continue to accumulate, they reveal that mammals thought to be primarily or entirely carnivorous often consume large amounts of fruit (e.g., Goszczynski et al. 2000) and the consumption of cultivated fruit increases where carnivores live in or near human-modified habitats (Bermejo and Guitian 2000, Fedriani et al. 2001). In these settings, cultivated fruits increase and sometimes even replace native fruits in their diets (Facure and Monteiro-Filho 1996, Bermejo and Guitian 2000, Goszczynski et al. 2000, Facure et al. 2003, Dell'Arte and Leonardi 2005).

Understanding the role of cultivated fruit in the ecology and conservation of carnivores and other mammals is important because human-dominated ecosystems, especially agricultural systems, now pervade temperate and tropical latitudes. As human populations continue to increase and the demand for food grows, agricultural expansion threatens to deplete some of the last remaining hotspots of biodiversity (Gorenflo and Brandon 2005) and particularly threatens large carnivores (Woodroffe 2000, Cardillo et al. 2004).

In this study we examine the use of a commercial avocado, *Persea americana* orchard in Ventura County, coastal southern California by medium and large-sized mammals. Among cultivated fruits, avocados are unusual because they are large (150 to 300 g) and calorie-rich (30 and 32 kJ/gram dry weight in this study; Slater et al. 1975). More importantly, mature fruits have high levels of both oils (70.2% of dry weight) and protein (6.0% of dry weight). Eaten fruit, scats containing avocado, and numerous sightings by orchard owners suggested to us that mammals utilized avocados on a regular basis. In addition, there are references from other regions of the Americas to jaguars, *Panthera onca*, van der Pijl 1982), crab-eating foxes, *Dusicyon thous* (Motta-Junior et al. 1994), black bears (Lyons 2005) and hooded skunks, *Mephitis m. macoura* (Ramirez-Pulido et al. 2005) consuming avocados.

In Ventura County, California avocados begin to develop in July and reach near full size in December-January. Soluble sugars account for much of the increase in fruit tissue during the early growth phase (Liu et al. 1999). As fruits near maximum size, oils replace sugars so that by December-January, oil content is near maximum. Fruits on the trees remain green and do not fully ripen to dark purple color until they fall to the ground. Until fruits are harvested they remain on the tree for much of the year, providing a constant supply of fallen fruit.

Based on orchard structure (continuous broadleaf evergreen canopy not unlike evergreen oak forests that were replaced), landscape position (often juxtaposed to native vegetation), high potential food value, and relatively low levels of human activity, it appeared likely that avocado orchards could serve as foraging habitat for medium and large-sized mammals. In addition, we suspected that proximity to human

habitation and disturbance might influence mammalian species composition and patterns of orchard use (Odell and Knight 2001, Maestas et al. 2003). Thus, the objectives of this research were 1) to determine the species composition of mid- and large-sized mammals using portions of a commercial avocado orchard 2) to estimate the amount of fruit they consumed and 3) to assess the possible effects of human activities and domestic dogs on mammalian composition in the orchard.

METHODS

Study area

The study area is a commercial avocado orchard nested within the 336-ha Rancho Dos Rios located on the foot slopes of Sulphur Mountain, 4 km southwest of Ojai in Ventura County, California (N 34.41°, W 119.27°). In this region urban and residential development is mainly confined to valleys and lower foothill elevations (150-250 m msl), while citrus and avocado orchards are common on lower mountain slopes below 500 m msl and to a lesser extent in the valleys. Undisturbed chaparral, coastal sage scrub, and coast live oak forests dominate the middle and higher elevations and ravines.

The total area in avocado orchard at the study site is 55.5 ha. We selected two sections of the orchard for study (Table 1 and Fig. 1). Trees were planted in 1972 are spaced 10 m apart. They now form a nearly continuous canopy of approximately 128 trees/ha. A system of 3-m wide trails accesses each orchard section (Fig. 1). Trails are approximately 30 m apart and are aligned with the contours. We chose these sections because both were adjacent to wildland areas but were as widely separated as possible (800 m) and within the same orchard.

An extensive area of native shrublands and grassland borders the orchard to the west (Fig. 1). Smaller remnants of grasslands, shrublands and oak woodlands surround the orchard. A 17-ha belt of forest (*Quercus agrifolia*-*Juglans californica*) and mixed chaparral runs east-west on steep slopes above the orchard (Fig. 1).

Section 7 is more affected by human disturbance than S3 because the orchard manager lives at the edge of the section (Fig. 1) and owns three medium-sized domestic dogs that freely roam most of the ranch, especially the orchard. Section 7 is bounded on the east by a moderately used paved road. In contrast, S3 is relatively free of human activity except for seasonal picking, operation and maintenance of the irrigation system, and infrequent scraping of unpaved roads that service the orchard.

Table 1. Site characteristics of S3 and S7. Values are means \pm 1 SE.

Section	Elevation (m)	Area (ha)	Slope angle	Orientation	Tree height (m)
S3	265-335	5.51	17.3° \pm 1.3°	north-northeast	7.9 m \pm 0.4
S7	210-270	8.04	15° \pm 1.4°	north-northwest	8.4 m \pm 1.7

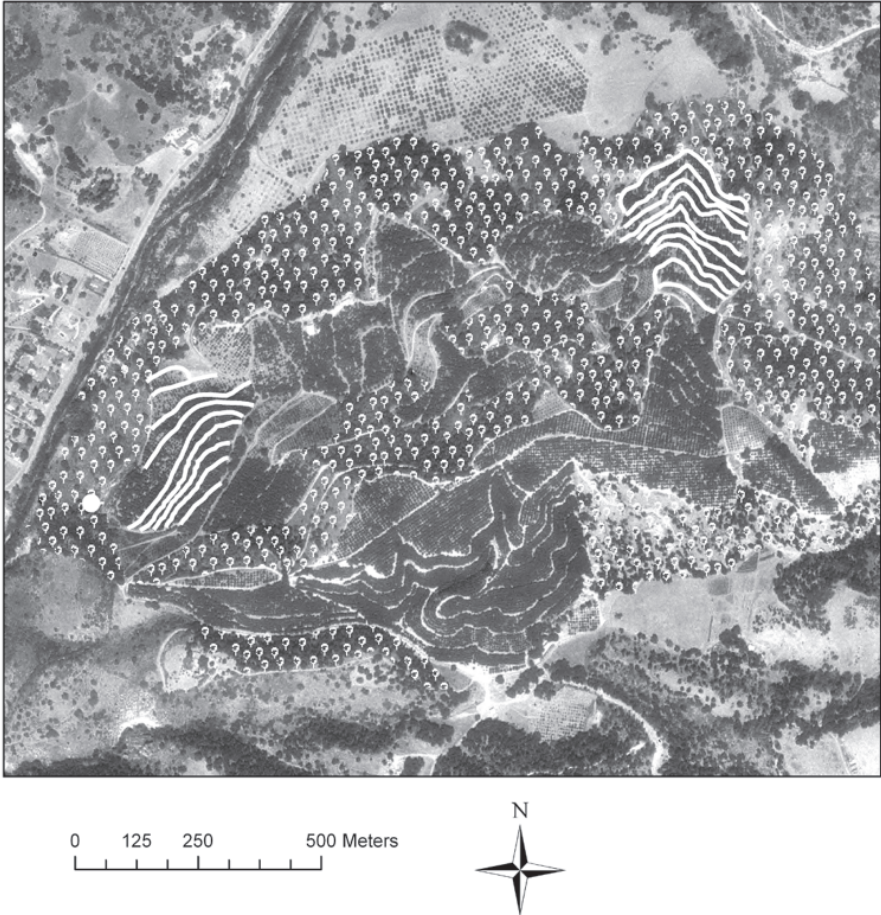


Fig. 1. Aerial view of study site showing the study transects (bold white lines) and areas of native shrublands and forests (stippled areas) immediately adjacent to the study orchard.

Fruit production

To compare fruit production in S3 versus S7, we analyzed the 11 most recent years of harvest records which we obtained from the orchard owner.

Fruit pulp dry weight

We weighed 20 green avocados (ten from each section) and measured the maximum width and length of each. After each fruit had ripened, we removed the pulp, dried it at 70°C for 24 hours, and reweighed it to obtain water content. In November and December we thoroughly mixed the dried pulp from 16 ripe avocados, 8 from each

section and sent them to Washington State Wildlife Habitat Laboratory (Washington State University, Pullman, WA, USA) for analysis of crude protein, crude fat, and total energy content.

Fruit fall estimates

Each week, we counted the number of fruits on the ground along 1380 m (0.414 ha) of contour trails in S7 and 1532 m (0.459 ha) of roads in S3. We tossed fruits at least 3 m off the trails after counting them so that they would not be recounted. We counted avocados in both sections for 11-12 weeks during the period January-April 2005 and for 8-9 weeks during November 2005-January 2006.

Camera trapping

We camera-trapped 14 stations in each section from 8 January to 1 April 2005 and again from 11 November to 25 December 2005. Every 2 weeks we moved cameras to a different station so that over the course of 6 months, we sampled all parts of each section. At each station we used a Trailmaster (TM1550, Goodson Associates, Lenexa KS 66215, USA) active infrared monitor and a 35-mm camera with receivers set to trigger the camera after an interruption of two infrared pulses (0.25 sec). Camera delay between exposures was at least 2 minutes; cameras operated 24 hours per day.

To photograph mammals as small as squirrels, we placed the transmitter and receiver 15 cm above the ground on 1-m T-posts and used 5-10 ripened avocados as bait. We located the transmitter and receiver on each side of the trail 3-3.5 m apart.

Fruit and seed removal

We monitored fruit losses in each section in two ways. First, we placed pin flags at stations spaced 15 m apart along contour trails. Section 7 had 110 stations and S3 had 104 stations. To assess ripeness, we placed fruits into four categories using skin color and pulp hardness: green and hard (least ripe), green-purple and hard (intermediate ripeness), purple and soft (most ripe), and purple-brown and shriveled (rotten). On 5 January 2005, we placed a single, numbered, unripe (green and hard) avocado across the trail (3 m) from each flag and recorded missing fruit each week until all had been eaten, disappeared or rotted.

The second method of monitoring removal involved following the fate of marked avocados that fell during high wind events. Beginning 8 January in S7 and 11 November in S3 we numbered one end of each fruit and placed it in the middle of the trail at the nearest flagged station (for ease of relocation). We also recorded the length and maximum width of each fruit to determine if fruit size varied between sections. To follow seed removal, we placed a single fresh seed next to every other station beginning 3 February and monitored them for displacement or in situ consumption over for the next 4 weeks.

Data Analyses

We used dates on the photos to record the number of days a camera actually took photos and marked a species present or absent for each camera day. If a species appeared more than once in a 24-hour period, we counted it as one capture. This was necessary because we could not identify individuals of most species. Because there were no differences in composition or capture frequencies within a section between the two periods, we pooled capture-days for each species. Sample sizes were 100 camera-days for S3 and 207 days for S7. The difference in camera-days was almost entirely due to disruption of cameras by black bears in S3 as well as to occasional camera malfunctions (moisture in cameras or heavy leaf fall during wind events that triggered the cameras).

We used Mann-Whitney U Test to compare capture frequencies of each species between the two sections and log-transformed avocados counted on trails and yearly total weights of harvested avocados. We used log-rank tests to compare fruit removal functions among transect and natural fruit fall trials.

RESULTS

Fruit Production

Based on 11 years of harvest records, mean annual fruit production was comparable between S3 ($6,500 \pm \text{SE} 0.21 \text{ kg/ha}$) and S7 ($5,566 \pm \text{SE} 0.15 \text{ kg/ha}$). Annual harvests were significantly correlated between the two sections ($r = 0.72$, $p < 0.01$) indicating similar inter-annual variability in production.

Fruit size, weight and caloric content

Fruit wet weight was highly correlated with fruit size ($R^2=0.91$) as was pulp dry weight ($R^2=0.78$). Mean pulp water content was $86.5\% \pm 5.4$ (SD). Dried avocados analyzed from November 2005 had 7.3% protein, 58.1% fat and gross energy of 30 KJ/g dry weight. By January 2006 protein had dropped to 6% while fat had increased to 70.2%; gross energy also increased to 32 KJ/g dry weight.

Fruit fall

The number of fallen fruits was similar between the two sections from January to April (Fig. 2). Much higher numbers were on the ground in S3 vs. S7 from November 2005 to January 2006. Most of the increase in S3 resulted from occasional high-wind events, although density-dependent thinning of fruit also was a factor. Similar wind-fall also occurred in S7; however, the ranch owner occasionally collected fallen fruit for market before our weekly counts.

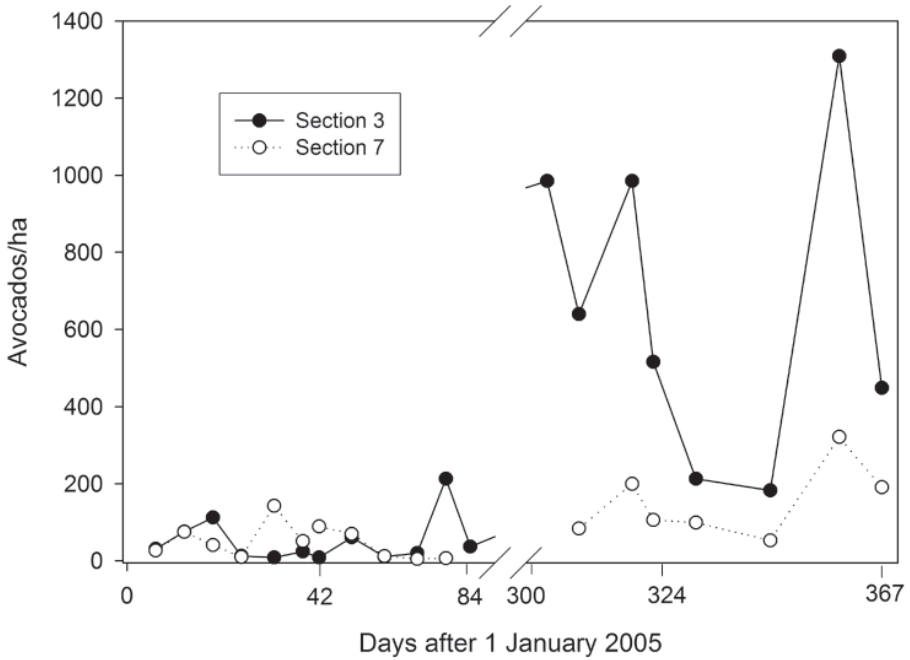


Fig. 2. Avocados/ha falling in the two sections during the study period.

Mammalian species composition and activity

Six native carnivores and one sciurid were detected at some time in the two sections (Fig. 3). Virginia opossums and domestic dogs were the only non-native species. Capture frequencies of gray foxes, black bears, and striped skunks were higher in S3 than S7; conversely, frequencies of domestic dogs, coyotes, and raccoons were higher in S7 than S3 (Fig. 3). Bobcats and western gray squirrels did not differ in captures between the two sections. Based on differences in pelage color, at least two adult bears and one cub used S3. Cameras captured two gray foxes in the same photo in S3 and two coyotes in a single photo in S7.

In S7, cameras detected gray foxes during the night with the highest activity (73%, N=45) between 2400 and 0400. Black bears also were nocturnal but activity was evenly distributed through the night (N=17). In S7 coyote activity was both diurnal and nocturnal (N=10) while raccoons were entirely nocturnal with a peak of activity between 2400 and 0400 (75%, N=16). Domestic dog movements (N=23) also were divided equally between day and night. The few captures of western gray squirrels and bobcats were diurnal in both sections.

Fruit removal rates

Avocado depletion curves for transects were not significantly different between the two sections (log-rank test $\chi^2=2.65$, $df=1$, $P=0.10$, Fig. 4) After 30 days, nearly 50%

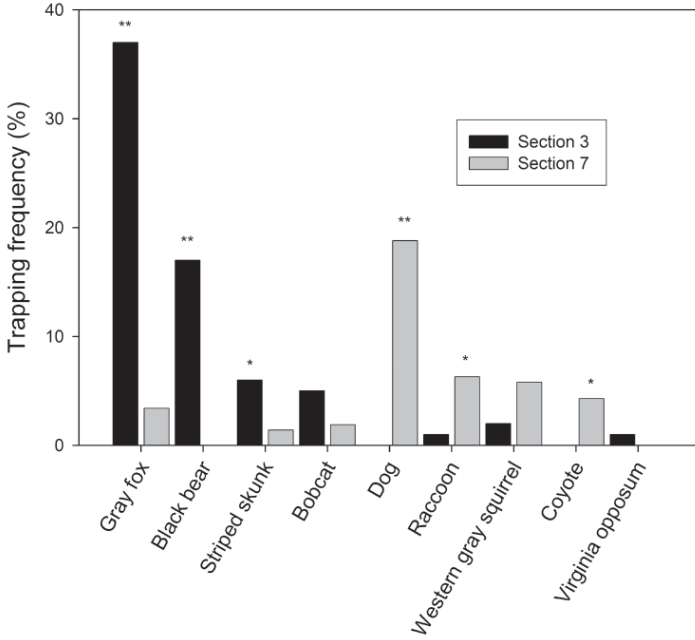


Fig. 3. Percent frequency of mammals in the two sections of the orchard. Bars with ** are significantly different at $P < 0.001$ between the 2 sections while those with * are significantly different at $P < 0.05$ using the Mann-Whitney U test.

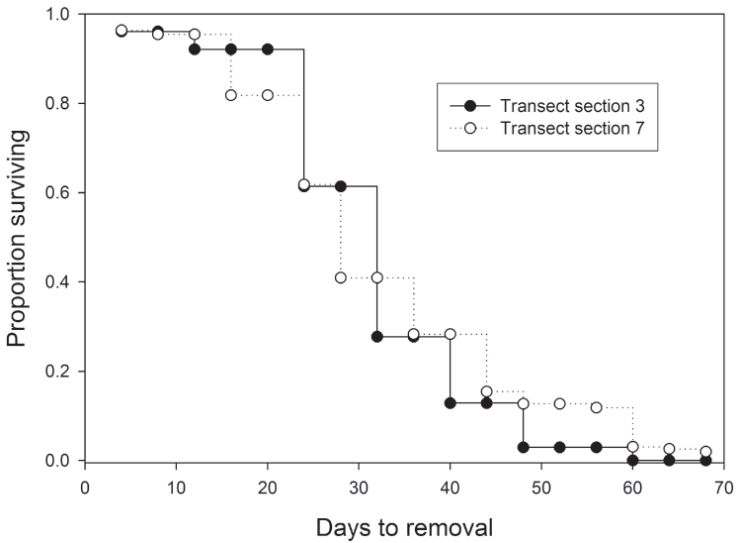


Fig. 4. Removal of green avocados placed along transects in the two sections.

of the fruit had been removed from trails in both sections; 10% percent of the fruit was still present after 48 days. Removal rates for fallen green fruit also were not significantly different between the two sections (log-rank test $\chi^2=3.31$, $df=1$, $P=0.07$, Fig. 5) Fifty percent of the fruit was removed from S7 by day 8, whereas it took 26 days for 50% removal in S3. In contrast to green fruit, intermediate and fully ripened fruit disappeared within 20 days (Fig. 5). The removal rate of ripened fruit in S7 was significantly different from green fruit in both S3 (log-rank test $\chi^2=60.00$, $df=1$, $P=0.0001$) and S7 (log-rank test $\chi^2=28.30$, $df=1$, $P=0.0001$), indicating that mammals removed ripened fruit faster than green fruit. Regardless of section or ripeness of fruit on the ground, mammals utilized all, or nearly all, of the avocados falling on the trails, usually within 50 days of falling to the ground. The opposite was true for seed removal. After 4 weeks only 6/103 (5.8%) of the seeds sown in transects had been removed.

DISCUSSION

Avocado consumption by carnivores

Avocado orchards present an unusually rich, spatially concentrated food source, and the two sections together attracted all of the common carnivores in the region. Missing from the trapping were the rarer carnivores such as mountain lion, *Felis concolor*, ringtail, *Bassariscus astutus*, and American badger, *Taxidea taxus*. Nor did we detect the usually ubiquitous domestic and feral cats. However, because we monitored only 17% of the 55-ha orchard, we may have missed these species. The absence of cats is perhaps not surprising since both coyotes (Crooks and Soule 1999) and bobcats (Harrison 1998) prey on them. Also, the orchard was far from urban and residential sources of domestic cats (although Caro et al. [2000] found cats in a variety of agricultural habitats, including orchards, well away from urban areas).

Except for bobcats, all species were photographed eating avocados. Bobcats are primarily flesh-eaters (Fedriani et al. 2000) although they sometimes take small amounts of fruit (Litvaitis 1981; Neale and Sacks 2001). The fact that jaguars eat avocados (van der Pijl 1982) raises the possibility that mountain lions may consume some avocados. Mountain lions have been observed in neighboring orchards and badgers occasionally are present on the ranch but have not been observed in the orchard.

Gray foxes were far more active in S3 than S7 (Fig. 3). We suspect that this difference may be due to greater activity and interference by dogs and coyotes in S7. In the nearby Santa Monica Mountains, coyotes are a significant cause of mortality among gray foxes (Fedriani et al. 2000) and foxes avoid areas where domestic dogs are abundant (Harrison 1993, Caro et al. 2000). Although both were active at night, dogs and black bears appeared to avoid each other. Dogs likely harassed bears and at least one dog was badly mauled by a bear. Black bears are normally diurnal but they were detected at night in this study. Others have documented that bears switch from diurnal to nocturnal where humans are active during the day (Beckmann and Berger 2003, Lyons 2005).

In this study, mammals consumed all or most of the fruit on the trails and (like humans) chose ripened over newly fallen, green avocados (Fig. 5). Mammals consumed

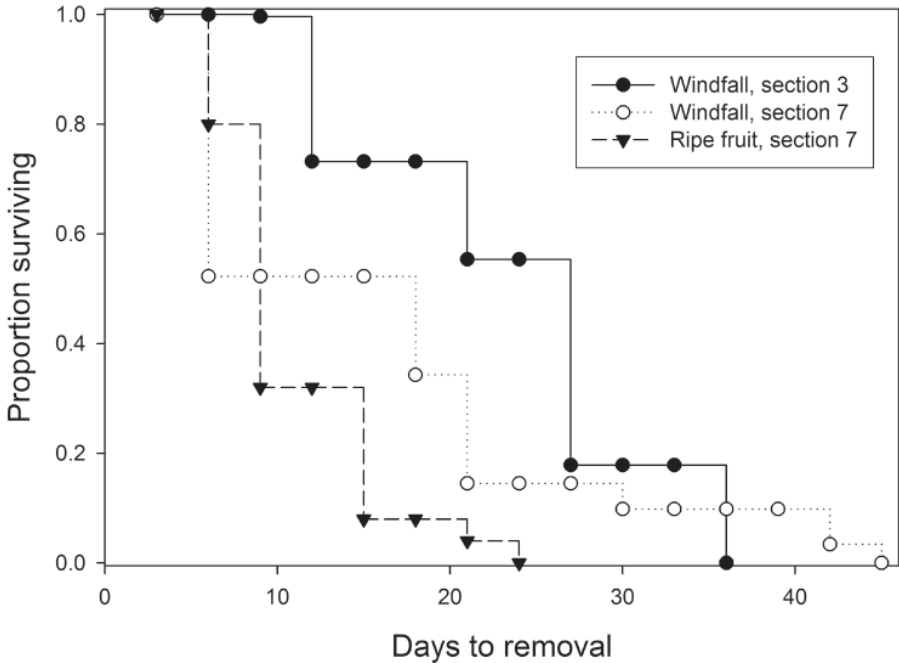


Fig. 5. Removal of naturally-fallen, green avocados in both sections and removal of ripe avocados in S3.

fruit placed in the transects (Fig. 4) slower than those placed in the center of the trails (Fig. 5). We suggest that removal rate of transect fruit likely reflected the consumption of isolated avocados in the orchard whereas those taken from the center of trails were more akin to losses from concentrations of fruit beneath individual or small groups of trees. In sharp contrast to the fruit pulp, mammals showed little interest in avocado seeds which are bitter and distasteful.

There was no indication that any of the species harvested avocados from the trees in the study area and, in general, they appeared to consume only a small percentage of the annual crop. We calculate that the average percent of harvested avocados in 2005 eaten by mammals in the 7 months of this study was 0.68% (range of 0.06-0.98%). Thus, we think it unlikely that >2% of the annual harvest is ever eaten by mammals. Of course, this may be an overestimate of the actual consumption because we confined our observations to trails and did not monitor avocados in the non-trailed portions of the sections. Nevertheless, we frequently observed eaten and partially eaten fruit away from the trails and there was no obvious accumulation of fruit on the ground as one would expect in the absence of consumption. Moreover, trails were not areas of unusual accumulations of avocados. Tree canopies covered the trails as they did in the rest of the orchard.

Avocados as a food resource

Although carnivores may eat fruit throughout the year, fruit production and consumption in temperate climates is strongly seasonal. Carnivores exploit both native and cultivated fruits when they are most available, usually in late summer and autumn (Goszczyński 1976, Doncaster et al. 1990, Serafini and Lovari 1993, Lucherini et al. 1995, Genovesi et al. 1996).

In contrast to this highly seasonal production of most native and cultivated temperate fruits, commercial avocados offer a year-around food supply for local mammals. Unlike many other cultivated fruits, avocados are not utilized by birds, thus reducing competition for fallen fruits. The number of avocados on the ground can vary locally on weekly, monthly, and inter-annual time scales depending on crop size, timing of picking, and wind events. For example, in response to fluctuations in the avocado market, the ranch owner picked S7 in April 2005 but delayed entry into S3 until July to obtain a higher price. Even after harvest, fruit overlooked by pickers continued to fall. This low but steady supply of residual fruit was the main reason for the unusually large size of avocados in S7 in the second period (Table 2). Several other cultivated fruits also have extended periods of fruit fall. In Italy, olives ripened in spring but Eurasian badgers did not exploit them until months later in mid-winter (Pigozzi 1992). In Portugal, badgers waited until the next summer to dig up buried olives (Rosalino et al. 2005). Coyotes in western Washington ate apples well into the winter. Apples ripen later than other fruits and decompose slowly in low winter temperatures (Quinn 1997).

Only a few studies have quantified the energetic input of allochthonous food (Rose and Polis 1998, Fedriani et al. 2001). For this study, we calculated the number of black bears (weighing 143Kg each) that hypothetically could be supported by the highest and lowest weekly avocado falls. Using the field metabolic rate $FMR=4.82M_b^{0.734}$ where

Table 2. Weekly avocado fall and fruit energy content for the two periods in each section. Except for N and KJ/g dry weight, values are means \pm 1 SE.

	Avocados falling#/ section/week	No. of weeks	Avocado wet weight (g)	No. of avocados	KJ/g dry pulp weight	KJ/section/ week
Jan-Apr 2005						
S3	346.0 \pm 16.2	12	157.9 \pm 1.7	29	32	254,204 \pm 20,229
S7	187.7 \pm 16.8	11	152.5 \pm 1.7	32	32	132,354 \pm 20,137
Nov 2005-Jan 2006						
S3	2,932.4 \pm 12.3	9	124.6 \pm 2.7	30	30	1,510,356 \pm 17,104
S7	781.8 \pm 15.4	8	195.7 \pm 2.5	30	30	683,929 \pm 33,684

M_b is body mass in grams (Nagy 2005) and assuming a digestive efficiency of 80% (because of the avocado's high protein content), we estimate the highest weekly fall (S3, period 2) could support 5.9 bears/ha/week and the lowest (S7, period 1) 0.5 bears/ha/week. These density estimates give some idea of just how calorie-rich avocado orchards can be for mammals.

CONCLUSIONS

In southern California avocado orchards occupy the interface between lower montane wildlands, many of which are in public ownership, and heavily developed foothills and coastal plains. Although individual orchards are small in extent, they are food-rich patches that are typically adjacent to shrublands, oak forests and riparian areas that are habitat for native mammals. Furthermore, their structural similarity to oak forests, albeit with a much more open understory, may make them hospitable to forest-associated species such as black bear, gray fox, and western gray squirrel. Our study area may be especially attractive to native carnivores given its relatively large size and extensive interface with native shrublands and oak forests.

We need more research on orchards of different sizes and spatial context (e.g., more or less isolated from natural habitats, more or less surrounded by urban and other agricultural development) to better understand how avocado cultivation affects mammals and other fauna in the region. Given the decline of many carnivores and the rise in avocado cultivation in sub-tropical and Mediterranean-climate regions – notably Mexico, Chile, Spain, South Africa, Israel, and Australia – such research has broad relevance.

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