Journal of Mammalogy, 90(1):114–118, 2009

WILD PIGS AS PREDATORS IN OAK WOODLANDS OF CALIFORNIA

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Wild pigs (*Sus scrofa*) are considered opportunistic omnivores that consume primarily plant matter; vertebrates are thought to constitute only a minor component of their diets, primarily as carrion, but active predation on vertebrates has been suspected. We examined the stomach contents of 104 wild pigs collected during a 7-year period in oak woodlands of the Diablo Range, California, and found that 40.4% contained vertebrate prey comprising 20 species, including 11 mammals, and totaling 167 individuals. Most stomachs with vertebrate prey included multiple individuals ($\leq$18) of $>$1 species ($\leq$6). Predation occurred in both male and female pigs and was most frequent during summer and fall, probably in response to protein deficiency in the diet. Wild pigs are a conservation concern because of their rooting behavior and consumption of mast; our results extend their potential impact to include predation on vertebrates, especially small mammals.

Key words: diet, feral pigs, oak woodlands, predation, protein deficiency, *Sus scrofa*, wild pigs

Wild pigs (*Sus scrofa*), which include feral pigs, European wild boars, and their hybrids, are distributed across much of the southern United States and are a management concern because of damage to natural and agricultural systems caused by their foraging and rooting behavior (Long 2003; Sweeney et al. 2003; Sweitzer 1998). In California, wild pigs have expanded in range and numbers in recent years, particularly in oak woodlands (Waithman et al. 1999), where they compete with native animals for the acorn mast crop and reduce oak recruitment by consumption of acorns and by seedling disturbance during rooting (Barrett 1982; Sweitzer and Van Vuren 2002). Rooting also dislodges native plant species, allowing invasive plants a competitive advantage (Kotanen 1995), and reduces plant productivity, potentially affecting resource availability for a wide variety of vertebrates and invertebrates (Sweitzer and Van Vuren 2002).

Wild pigs cause damage through their foraging activities (Loggins et al. 2002), and the damage potential is exacerbated by the breadth of their diets. Wild pigs are opportunistic omnivores that show no particular forage preference except that of vegetation over animal matter. They graze on grasses and forbs and root for mast, tubers, and roots, with animals such as earthworms and small vertebrates probably consumed opportunistically while rooting (Sweeney et al. 2003; Sweitzer 1998). Vertebrates have been reported in diets of wild pigs in California (Baber and Coblentz 1987; Barrett 1978; Pine and Gerdes 1973) and elsewhere (Belden and Frankenberger 1990; Henry and Conley 1972; Schley and Roper 2003; Scott and Pelton 1975; Springer 1977), but most researchers concluded that vertebrate remains were either carrion or a minor part of the diet. Active predation by pigs on wild vertebrates has been strongly suspected (Taylor and Hellgren 1997; Wood and Brenneman 1977), but the evidence in support has been limited largely to observations of pigs actively searching for vertebrate prey (Scott and Pelton 1975) and documented predation by pigs on juvenile domestic sheep and goats (Choquenot et al. 1997; Littauer 1993; Pavlov and Hone 1982).

Recently, Loggins et al. (2002) reported evidence suggesting active predation by wild pigs in oak woodlands of the Diablo Range, in the central coastal region of California. Seven (13%) of 53 pig stomachs collected during 1 year contained rodents, especially California ground squirrels (*Spermophilus beecheyi*) that were unlikely to have been scavenged. Further, 1 pig with a recently dead squirrel in its stomach was shot as it was seemingly in the act of hunting squirrels (Loggins et al. 2002). However, the generality of these findings is uncertain; if active predation was occurring, it could have been limited to a small portion of the wild pig population for a relatively brief period.

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Table 1.—Occurrence of vertebrate prey in stomachs of wild pigs in oak woodlands of the Diablo Range, California, 2000–2006.

Species	% of stomachs	Total individuals
Mammals		
Microtus californicus	34	109
Thomomys bottae	13	26
Peromyscus maniculatus	6	6
Scapanus latimanus	4	4
Spermophilus beecheyi	3	3
Neotoma fuscipes	2	2
Peromyscus truei	2	2
Odocoileus hemionus	2	2
Sorex trowbridgii	2	2
Sylvilagus bachmani	1	1
Reithrodontomys megalotis	1	1
Birds		
Callipepla californica	1	1
Phalaenoptilus nuttallii	1	1
Melanerpes formicivorus	1	1
Thryomanes bewickii	1	1
Pipilo crissalis	1	1
Reptiles		
Contia tenuis	1	1
Coluber constrictor	1	1
Crotalus viridis	1	1
Amphibians		
Pseudacris regilla	1	1

Our goal was to evaluate the generality of these preliminary results by sampling a larger number of wild pigs at the same location over a longer time frame. We focused exclusively on vertebrate prey in pig diets to describe the frequency and diversity of vertebrates consumed, and to determine if vertebrate consumption varied according to season, sex, or physical condition of individual pigs.

Materials and Methods

We studied diets of wild pigs over a 7-year period (January 2000–December 2006) by examining whole stomach contents from wild pigs taken by rifle on the 1,400-ha Blue Oak Ranch Reserve and adjacent 500-ha Rancho Cañada de Pala (37°24.5′N, 121°44.2′W) in the Diablo Range, Santa Clara County, California. Wild pigs have been present in Santa Clara County since at least 1965, and have achieved very high densities there (Waithman et al. 1999), and they have been present in the study area since at least the early 1980s. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Almost all precipitation falls during October through May. Vegetation consisted of oak woodland, oak savannah, and annual grasslands with pockets of coastal sage scrub and chaparral and strips of riparian forest (Wilcox et al. 2004). All wild pigs were collected with a valid California hunting license and wild pig tags, following guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Whole stomachs were immediately removed from shot pigs. The contents were emptied onto a flat surface where they were carefully searched visually, and then by palpation, for vertebrate remains. Small mammals were located among the stomach contents by searching visually for dark areas caused by concentrations of hair sloughed from the animal being digested. Wild pigs do not possess shearing cheek teeth, so vertebrates they consume are crushed and swallowed whole. During this study we learned that freshly killed animals quickly change in appearance due to the digestive process. Hydrochloric acid and digestive enzymes in pig stomachs break down collagen and hair follicles of mammal skins (Rowan et al. 1997), which leads to sloughing of hair and the texture and appearance of a tanned skin after hair has sloughed. The crushed carcasses are texturally different from the masticated plant matter surrounding them, which allowed us to feel through stomach contents to find palpable vertebrate remains in addition to using visual searches. Vertebrate remains were separated, bagged, and stored frozen before being thawed for identification. Most remains were subsequently discarded, but the contents of 9 stomachs from 2004 and 2005 were preserved and accessioned into the collection of the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley (MVZ-218997–219005). Mammals were identified on the basis of external features such as pelage; length of the ears, feet, and tail; and presence of cheek pouches; as well as internal features such as the skull and teeth. Birds were identified using feathers, and reptiles and amphibians were identified using external features such as skin and scales. We classified carrion as animal remains infested with fly maggots or exhibiting evidence of putrefaction, such as discolored skin or the odor of bacterial decomposition. We also assumed that a wild pig could not kill an adult black-tailed deer (*Odocoileus hemionus*), so this species was considered carrion as well. We used the MVZ collections to identify all vertebrate remains to the species level.

For each wild pig we recorded season and sex, and for all but 1 pig we determined physical condition. Seasons were classified as winter (December–February), spring (March–May), summer (June–August), and fall (September–November). We assessed physical condition based on the depth of rump fat between the skin and biceps femoris muscle by making a 7.5-cm incision 15 cm below the tail on the posteriormost point of the upper thigh and measuring the fat layer at its thickest point.

Results

Of 104 wild pigs collected, stomachs of 42 (40.4%) contained vertebrate remains totaling 167 individual prey animals (Table 1). We identified prey representing 20 species that included 11 mammals, 5 birds, 3 snakes, and 1 frog. California voles (*Microtus californicus*) were the dominant prey species, totaling 109 individuals and occurring in more than one-third of all stomachs. Botta's pocket gophers (*Thomomys bottae*) also were common prey, with 26 individuals in 13% of stomachs. The remaining 18 prey species were recorded as single occurrences in 1–6% of stomachs.

We identified vertebrate carrion in the stomachs of 6 pigs (6%). Three stomachs were collected concurrently from 1

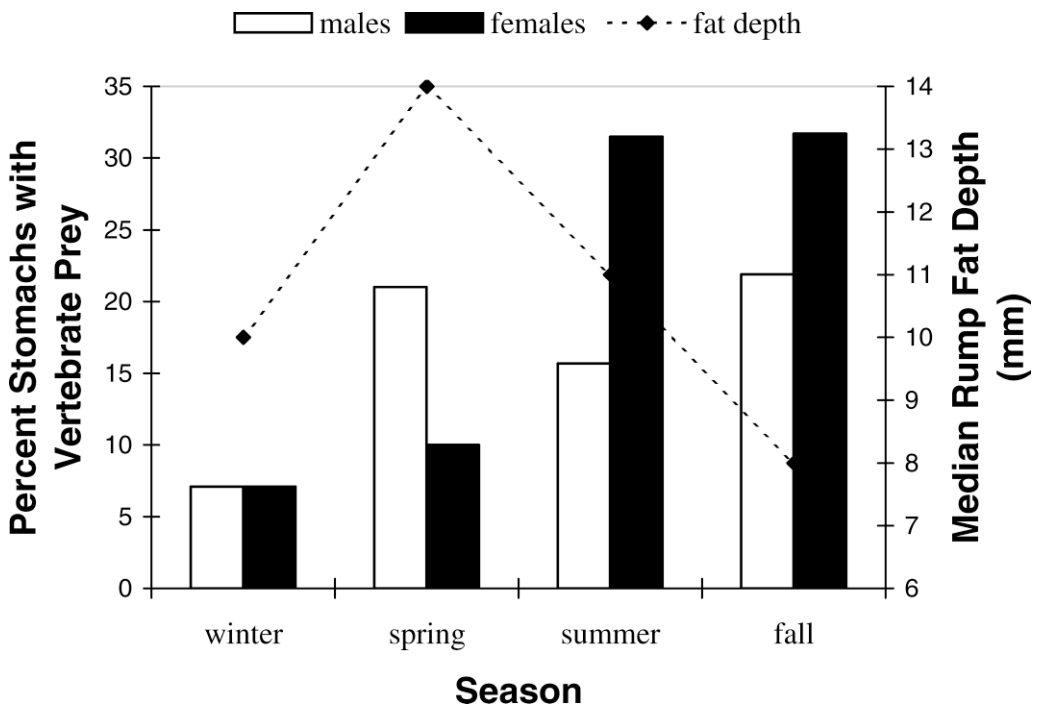

Fig. 1.—Seasonal variation in frequency of occurrence of vertebrate prey (sexes separate) and rump fat depth (sexes combined) of wild pigs in oak woodlands of the Diablo Range, California, 2000–2006.

group of pigs, and all 3 stomachs contained the putrefied skin and flesh of an adult black-tailed deer. The remaining 3 stomachs contained the remains of a brush rabbit (*Sylvilagus bachmani*) infested with maggots, a dehydrated section of the skin of a deer fawn (MVZ-218997) accompanied by the distinctive odor of bacterial action, a common poorwill (*Phalaenoptilus nuttallii*) infested with maggots, and unidentified carrion (MVZ-218999).

Of those stomachs containing vertebrate prey, most (61%, $n = 44$) included multiple prey individuals (range = 2–18), and in almost all stomachs with multiple prey individuals (85%, $n = 27$), >1 prey species was represented (range = 2–6). One male wild pig, which was radiotracked as part of a concurrent study (Wilcox et al. 2004), foraged in oak woodland, grassland, and riparian habitats for 11 h before being shot at dawn. Its stomach contained 7 voles, 2 gophers, 1 dusky-footed woodrat (*Neotoma fuscipes*), 1 deer mouse (*Peromyscus maniculatus*), 1 piñon mouse (*Peromyscus truei*), and 1 western harvest mouse (*Reithrodontomys megalotis*). The stomach of a female wild pig held 13 voles, 4 gophers, and 1 broad-footed mole (*Scapanus latimanus*). Consumption of vertebrate prey did not appear to be randomly distributed among wild pigs. On 7 occasions we shot multiple wild pigs (range = 2–6) concurrently from the same group, and in all but 1 of these events all pigs killed had vertebrate prey in their stomachs. In 1 case, the stomachs of 6 pigs collected from a group of 11 contained a combined total of 66 individual vertebrate prey, of which 49 were voles (MVZ-218999–219004).

We identified vertebrate prey in pig stomachs during every year of the study (frequency of occurrence, 14–91%; $n = 6$–23), except during 2000 when only 3 pigs were collected. Frequency of predation was lowest in winter and spring and highest in summer and fall, with the summer–fall peak in predation rate more pronounced in females than in males (Fig. 1). Rump fat depth (mm) of pigs with vertebrate prey in their stomachs (median = 8, range = 0–34, $n = 43$) was significantly less (Mann–Whitney U-test, $P = 0.027$) than that of pigs without vertebrate prey (median = 11, range = 2–31, $n = 59$). Rump fat was thickest during spring when predation frequency was low to moderate, then declined during summer and fall as predation frequency increased (Fig. 1).

Discussion

Our results confirm that wild pigs in oak woodlands of the Diablo Range are consuming substantial numbers of vertebrates, and that this phenomenon is common among pigs and persistent over time. The prevalence of multiple vertebrates per stomach indicates that this is not an occasional event, especially considering the rapid rate of gastric emptying in pigs (4–5 h—Ramonet et al. 2001). Our definition of carrion likely was conservative because some animals considered prey may have been consumed as recently dead carrion, particularly birds that do not forage or nest on the ground. Nonetheless, the large number and remarkable diversity of vertebrates contained in pig stomachs suggest that most of these animals were taken as live prey. Many of the vertebrate prey we identified are fossorial or semifossorial species, hence they may have been captured opportunistically by pigs during rooting or grazing. However, some are semi–arboreal or highly agile, suggesting that pigs may engage in active hunting (Loggins et al. 2002).

Frequency of predation was highest during summer and fall, consistent with the earlier findings of Loggins et al. (2002). Summer and fall in California's Mediterranean climate are

times of poor body condition for wild pigs (Baber and Coblentz 1987), and also the times when dietary protein is lowest (Baber and Coblentz 1987; Barrett 1978).

Acorns provide an abundant source of energy during fall, but they are deficient in protein so pigs may need to supplement an acorn diet with animal matter (Barrett 1978; Belden and Frankenberger 1990; Loggins et al. 2002). Hence, predation by wild pigs might reflect the generalized response of a malnourished animal seeking any available food, or it may be the more specialized response of seeking a particular food for a balanced diet. We found that pigs in poorer physical condition were more likely to prey on vertebrates, and predation frequency increased during summer and fall as physical condition declined, indicating that nutrition plays a role. However, rump fat in ungulates is the last to be deposited and the 1st to be mobilized (Harder and Kirkpatrick 1996; Kistner et al. 1980), hence the presence of measurable quantities in most of our pigs indicates they were not malnourished, whether they preyed on vertebrates or not. Thus, we suspect that protein deficiency was an important factor influencing predation on vertebrates, particularly for females facing the physiological cost of reproduction.

Wild pigs are a conservation concern because of the physical impact of rooting, the effect of mast consumption on tree regeneration, and competition with native species (Sweitzer 1998). Results of our study extend the potential impact of wild pigs to include predation on a wide variety of vertebrates, especially small mammals. The potential for predation may be especially pronounced in those environments, such as the Mediterranean climate of California, in which wild pigs face prolonged periods of protein deficiency. Considering the rapid rate of gastric emptying in pigs, the 40% frequency of occurrence of predation that we report could translate into a significant impact on native small mammals. In California, 11 small burrowing mammals are designated as federally threatened or endangered (CNDDB 2007), and more than one-half of them live within geographic areas currently occupied by expanding populations of wild pigs (Waithman et al. 1999). Conservation concerns for these small mammals could grow as wild pigs increase their range and numbers throughout the state.

Acknowledgments

We thank O. Pollack for his insight; R. Klinger, B. Lockshaw, and M. van Hattem for help in the field; C. Conroy and the staff at the Museum of Vertebrate Zoology; The Nature Conservancy; and the former owners of the Blue Oak Ranch. This paper is dedicated to the memories of R. Van Vuren, B. (Halverson) Van Vuren, and V. (Van Vuren) Wilcox.

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Submitted 14 January 2008. Accepted 10 June 2008.

Associate Editor was Martin A. Main.