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Implications of predation by wild pigs on native vertebrates: a case study

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Following escape from a purposeful introduction on Hooper Bald in the Appalachian Mountains of North Carolina in 1912, European wild boars (*Sus scrofa*) have spread across the United States via invasions and translocations; they now occur in an estimated 44 of 50 states (for a complete review, see McCann et al. 2014). An early translocation from the North Carolina population brought wild pigs to California in 1925, where they were introduced into Monterey County by private landowners for sport hunting (Hoene 1994). From the Monterey County introduction and subsequent translocations, wild pigs spread throughout California, hybridizing with domestic pigs brought by 18th-century Spanish explorers and 19th-century immigrants to America. Vigorous hybrids now occur in 56 of 58 counties within California (Waithman et al. 1999, McCann 2012, McCann et al. 2014, CDFW 2015). Hereafter, I refer to these hybrids as wild pigs.

Wild pigs are omnivores but prefer vegetative matter, foraging heavily on the seasonal acorn mast crop in California rangelands and hardwood forests (Barrett 1982, Loggins et al. 2001, Sweitzer and Van Vuren 2002). Nonetheless, numerous wild pig diet investigations have listed vertebrate remains among stomach contents (reviewed by Ballari and Barrios-Garcia 2013). Wild pigs are known to scavenge dead vertebrates, and scavenging could explain the presence of vertebrate remains in some diet analyses, but Loggins et al. (2002) and Jolley et al. (2010) observed wild pigs actively hunting vertebrate prey. Furthermore, other investigators recently reported wild pigs as opportunistic predators of vertebrates. In California, Wilcox and Van Vuren (2009) found that 40.4% of collected pig stomachs contained vertebrate remains, including 167 individuals representing 20 species, of which 99% were mammals. In stomachs containing vertebrate prey, 61% held more than one vertebrate; one stomach contained 18 individuals of six different species (Wilcox and Van Vuren 2009). In the southeastern United States, Jolley et al. (2010) reported 64 individual reptiles and amphibians in 68 wild pig stomachs, with as many as five different species in a single stomach; one pig stomach contained 49 individual spadefoot toads (*Scaphiopus holbrookii*).

In a review of wild pig diets worldwide, Ballari and Barrios-Garcia (2013) concluded that wild pig populations in their native ranges generally consumed fewer vertebrate prey than those where wild pigs were introduced. Those authors theorized that the increased consumption of vertebrates where pigs are introduced is due to native vertebrates having evolved without pigs as predators. As members of the order Artiodactyla, wild pigs are hooved animals (ungulates), which generally are obligate herbivores. It follows that in landscapes where wild pigs are introduced, native small vertebrates would not have experienced selective pressures to avoid, escape from, or defend against ungulates. Without coevolved responses to ungulate predators, native small vertebrates are particularly vulnerable to the predatory behavior of introduced wild pigs, especially when the pigs forage in large sounders. Here I describe small vertebrates found in the stomach contents of a large wild boar after a single night of foraging within a reserve in the central Coast Range of California. Based on vertebrate prey items found among its stomach contents, and using wild pig population density estimates from studies within the reserve and from similar habitats nearby, I project the potential impacts to small vertebrates within the reserve area.

The 1300-hectare Blue Oak Ranch Reserve (BORR), one of 38 University of California Natural Reserves, is situated within the California Floristic Province between 550 and 915 meters elevation. This is an area of mixed oak woodland and grasslands, approximately 8 km east of the southern portion of San Francisco Bay in Santa Clara County, California. For a more complete site description of BORR, see Wilcox et al. (2004). On 22 September 2010, I killed a large (126 kg field-dressed) male wild pig on the reserve after it became a destructive nuisance. Immediately after dispatching the pig with a rifle, I removed the stomach and hand-sorted the contents, separating out vertebrate remains (Wilcox and Van Vuren 2009). In addition to a wide assortment of vegetable matter, including a large volume of the masticated rhizomes of cattail (*Typha latifolia*), the stomach contained 23 individual vertebrates comprising eight species (Table 1), including a gopher snake (*Pituophis catenifer*)

Table 1.—Vertebrate prey from the stomach contents of a single male wild pig (*Sus scrofa*) after one foraging event on the Blue Oak Ranch Reserve in Santa Clara County, California, and estimates of the numbers of each prey species that theoretically could be removed per foraging bout if predation rates were identical for individual wild pigs. N represents the number of individuals of each prey species found in the stomach contents described in this paper. The potential range of N (i.e., the theoretical number of prey of a particular taxon per foraging event) is the product of multiplying each prey species in the stomach by the range (lowest to highest) of pig densities estimated for Blue Oak Ranch Reserve and surrounding lands in Santa Clara County.

Common name	Scientific name	N	Potential range[a] of N
California vole	*Microtus californicus*	15	495–660
California mouse	*Peromyscus californicus*	2	66–176
Deer mouse	*Peromyscus maniculatus*	1	33–44
Western harvest mouse	*Reithrodontomys megalotis*	1	33–44
Bottae's pocket gopher	*Thomomys bottae*	1	33–44
Beechey ground squirrel	*Spermophilus beecheyi*	1	33–44
California quail	*Callipepla californica*	1	33–44
Pacific gopher snake	*Pituophis c. catenifer*	1	33–44

[a]Low density estimate (3.3/km^2) from Wilcox et al. (2004); high density estimate (4.0/km^2) from Sweitzer et al. (2007). A multiplier of 11 was determined from the approximate 1100 hectares of pig habitat on Blue Oak Ranch Reserve. Santa Clara County, California.

approximately 90 centimeters long. This vertebrate count exceeded the maximum quantity of any individual stomach reported by Wilcox and Van Vuren (2009), but reflected similar species composition: primarily small mammals, the majority of which were California voles (*Microtus californicus*). Because the gastric emptying rate for pigs is four to five hours (Ramonet et al. 2001), the vertebrate content of this boar's stomach likely represented a single night of foraging. The vertebrate prey of the BORR wild pig, combined with previous investigations in which multiple vertebrate species have been discovered among wild pig stomach contents (Scott and Pelton 1975, Skewes 2007, Wilcox and Van Vuren 2009, Jolley et al. 2010), suggest that predation of small vertebrates by wild pigs is not purely opportunistic, but should be considered facultative predation (*sensu* Callahan 1993).

To understand the potential implications of this predation event, I used the prey species count from the wild pig stomach contents described above to estimate the predation potential if every wild pig on BORR consumed the same number of vertebrates in a single night of foraging (Table 1), based on estimates of wild pig densities from prior investigations conducted on BORR and nearby within Santa Clara County. This boar was killed at a time of year when wild pigs (males and females) are thought to prey on vertebrates more heavily than in other seasons (Wilcox and Van Vuren, 2009); this prey consumption estimate, therefore, may represent an upper limit. In this example, and that of Wilcox and Van Vuren (2009), the largest numbers and diversity of vertebrate prey are attributed to large solo boars; however, female wild pigs showed a high capacity for predation of small vertebrates as well, with voles forming the largest component (Wilcox and Van Vuren 2009). Females, along with juveniles of both genders, normally form the largest sounders and, thus, have the potential to be involved in large-scale predation events. Prey numbers projected in Table 1 are unlikely to be sustainable for long before local prey populations would be exhausted, or the costs of hunting unprofitably would force pigs to relocate to areas with higher prey abundance.

California voles exhibit periodic population irruptions (Lidicker and Ostfeld 1991), providing a concentrated surplus for predators. Predation on the surplus from these periodic irruptions may explain the large number of individual voles found in some wild pig stomachs (Wilcox and Van Vuren 2009). Similarly, eastern spadefoot toads are explosive breeders (Wells 1977), briefly gathering at suitable breeding sites in large numbers. Breeding-site aggregations may account for the 49 individual eastern spadefoot toads from one stomach (representing one foraging event) reported by Jolley et al. (2010). However, the diversity of prey species in the BORR wild pig, and other pig stomachs, indicates wide-ranging foraging by wild pigs through varied habitats (Wilcox and Van Vuren 2009). This does not indicate that wild pigs key on a single species or event but, instead, merely that they are opportunistic predators. The contents of the BORR pig's stomach represented one foraging event during a season when wild pigs are hypothesized to experience a protein deficiency from an acorn-heavy diet (Barrett 1978, Belden and Frankenberger 1990, Loggins et al. 2002, Wilcox and Van Vuren 2009). Acquiring a high-protein meal coincident with a peak acorn drop makes hunting small vertebrates highly profitable, because protein is required to convert the high-starch acorn diets to stored fat for metabolic reserves (Barrett 1978).

The ability to switch opportunistically to a local, seasonally abundant, vertebrate prey confers on wild pigs the role of generalist predator (Closs et al. 1999). As an introduced species, occupying a novel and unique role as an ungulate predator, wild pigs may realize an advantage over native carnivores that also prey on small vertebrates (Barrios-Garcia and Ballari 2012). Thus, in large numbers, wild pigs may have significant local impacts on small vertebrates, resulting in measurable impacts on local food-web dynamics (Thompson et al. 2007), and compete with mesocarnivores dependent upon small vertebrates.

Landscapes are shaped by the evolutionary interplay of predator and prey (Hairston et al. 1960). Predation leaves detectable marks on a landscape by limiting herbivores and releasing some plant species to grow (Eisenburg 2010, Ripple and Beschta 2012). Brown et al. (1999) described fear of predation as an even stronger pressure than predation itself, because it directly affects foraging behavior of herbivores balancing their own metabolic needs with the potential to be eaten. But this "ecology of fear" is based on selective pressures relating to prey recognizing potential predators, and no such relationship has coevolved between introduced wild pigs and native small vertebrates. Some researchers have speculated that the wild pig in California is filling a niche that became available when grizzly bears (*Ursus arctos*) were extirpated from the state (Work 1993, Sweitzer and Van Vuren 2002, Grinde 2006). Native small vertebrates coevolved with grizzly bears and were likely to become prey incidentally or intentionally while grizzly bears grubbed rangelands for food (Mattson 2004a, 2004b). Wild pigs grub for food in a manner similar to grizzly bears, but no coevolution occurred in California between small vertebrates and ungulates such as wild pigs.

To better understand the role of wild pigs as novel predators, I suggest future investigators focus research on (1) dietary impacts on mesocarnivores such as bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and raccoon (*Procyon lotor*); (2) the degree to which wild pigs fill the niche formerly occupied by grizzly bears based on the behavioral differences between the two predators and the evolved responses of small vertebrate prey; and (3) the indirect impacts of introduced wild pigs on small vertebrate populations, particularly those affected by the reduction of voles. Doing so will be challenging if wild pigs are taking on the role of mesocarnivores in terrestrial food webs, and investigations should begin where wild pig densities are highest and landscape changes are easiest to detect (Sweitzer and Van Vuren 2007).

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