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REVIEW

A review of the impacts of invasive wild pigs on native vertebrates

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Abstract

The wild pig (*Sus scrofa*) is a successful invasive species that has become well established outside of its native range in Eurasia. The invasive wild pig is the result of released or escaped domesticated livestock becoming feral, or Eurasian boar introduced for hunting purposes. The global spread of wild pigs has recently been exacerbated in some areas, such as the USA, by anthropogenically assisted dispersal. Once established in novel ecosystems, wild pigs have the potential to have significant negative impacts on the ecosystem, and the scientific literature is replete with examples. It is generally accepted that wild pigs negatively impact native fauna where they have become established, yet the degree to which they impact faunal communities has not been well described. This paper serves as a review of the information to date on the implications of wild pig invasions and impacts they have on terrestrial vertebrates in their invasive range. In addition, the review highlights our need for more research in this area, particularly regarding declining species.

Keywords *Sus scrofa* · Wild pig · Impacts · Vertebrates · Invasive

Introduction

Nonnative invasive species are those which are transplanted to a foreign ecosystem where they establish viable populations and disrupt that ecosystem. Invasive species often share common characteristics that make them successful invaders, such as: r-selected reproductive strategy, early sexual maturity, high fecundity, ability to exploit niches, and potential to outcompete native organisms (Sakai et al. 2001). Humans frequently will relocate fauna outside of its native range, and in doing so allow species to establish new populations. Globalization in the past millennia has exacerbated the introduction of invasive species around the world (Vitousek et al. 1997; Davis 2003). Anthropogenic introductions of invasive species often stem from agricultural endeavors and have led to established feral, domestic animals that escaped or were released, populations of goats (*Capra hircus*), burros (*Equus asinus*) and wild pigs (*Sus Scrofa*) (Vitousek et al. 1997). Introduced species may alter community dynamics in ways that are unfavorable to native species, and invasions often contribute to the decline and even extinction of local species through direct predation, competition, and habitat destruction (Davis 2003).

Wild boar are native to Europe and Asia, but wild pigs are an invasive exotic species introduced to the USA and other parts of the world as a result of globalization and fit the major characteristics of an invasive species (Comer and Mayer 2009; Mayer 2009). Wild pigs that have been introduced outside their native ranges are generally the result of released or escaped domestic pigs that have become feral, introduced Eurasian wild boar, or hybridization between these two morphs of the species *Sus scrofa*. Domestic pigs were selectively bred to produce large litters and maximize reproduction, and follow a more r-selected life history compared to their wild ancestors who already display a high reproductive output for an ungulate of their size (Taylor et al. 1998; Frauendorf et al. 2016). In addition to large litter sizes,

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female wild pigs can breed as young as 5 months old and can average 1.8 litters per year (Dzięciołowski et al. 1992). The high fecundity and early sexual maturity of female wild pigs can lower the propagule pressure needed to result in establishment of new populations due to their high intrinsic rate of increase (Crawley et al. 1986). In Europe, wild boar are ecosystem engineers that have helped shape natural communities (Sandom et al. 2013). Where wild pigs are invasive, though, the same characteristics that make them an ecosystem engineer make them an incredibly destructive invasive species.

Wild pigs cause damage to not only anthropogenic resources, but also native ecosystems. Where they are invasive, these systems did not evolve with wild pigs and tend to be very susceptible to perturbations caused by wild pig populations (Campbell and Long 2009; Sandom et al. 2013). Rubbing, wallowing, rooting and their voracious feeding habits are often the source of negative impacts to native ecosystems and accompanying flora and fauna (Tolleson et al. 1995; Sweitzer and Van Vuren 2002; Campbell and Long 2009). Wild pigs depredate seeds and seedlings which causes reduced regeneration, as Lipscomb (1989) found while studying the regeneration of long-leaf pine (*Pinus palustris*). In addition to their impacts on plant regeneration, Bratton (1975) found they can drastically reduce understory cover through feeding behaviors. Wild pigs will affect the medium that plants grow in as well. They will overturn soil and mix the soil horizons in a way that mimics tilling of a field causing leaching of key nutrients out of the soil to be accelerated (Ballari and Barrios-García 2014; Gray et al. 2020).

The impact that wild pigs have on native fauna extends beyond direct interactions and are often more profound than impacts on flora. The fauna that wild pigs impact cover a wide breadth of taxa from mammals to annelids (Henry and Conley 1972; Scott 1973; Barrett and Birmingham 1994; Taylor and Hellgren 1997; Baubet et al. 2003), and their impacts on these species can be both direct and indirect. Impacts on fauna can include depredation, disease transmission, competition, aggressive exclusion, and habitat degradation. While there are many documented cases of wild pigs impacting fauna in their nonnative range, a comprehensive review of these impacts has yet to be developed. As a result, description of the impacts of invasive wild pigs on faunal species are usually very general in nature. Due to the varying manner in which wild pigs impact fauna, a binary classification system (e.g., direct vs. indirect impacts) does not allow the variation to be captured effectively. A more appropriate way to describe their impacts may be as a continuum, with direct and indirect impacts at opposite ends of the continuum. The purpose of this paper is to serve as a comprehensive review that describes the impacts of wild pigs on fauna within their nonnative range, and these impacts are presented along a continuum from the most direct effects to the least.

Methods

We conducted all searches for this review in Google Scholar and JSTOR as they are comprehensive and navigable databases. The terms that we used in our searches began with more general searches and evolved into more specific searches based on the resources found in the general searches. We conducted searches using “sus scrofa” OR “wild pig” OR “wild boar” OR “wild hog” as nomenclature often used interchangeably. We repeated these searches with the inclusion of geographic ranges where wild pigs are considered a nonnative invasive species (e.g., North America, Australia, New Zealand, South America) and different clades and species of native vertebrates that may be impacted (e.g., mammals, birds, small mammals, reptile, amphibian). We then conducted searches using the previously mentioned words as well as types of impacts that wild pigs may have on other species (e.g., predation, nest predation, competition, exclusion, habitat destruction). We also used resources referenced in articles and book chapters found during the initial search that either provided additional or new original information. Our criteria for relevant information were resources that provided data supporting both direct and indirect impacts on native vertebrate species and resources that had a speculative hypothesis based on collected data and observations and noted them as such in this review. Also, in our criteria for relevant information, we included gray literature, such as thesis, dissertations, and technical manuals produced by government agencies that may further provide evidence of the impacts of invasive wild pigs on native vertebrate species.

Wild pig impacts on native large mammals

Invasive species are likely to compete with organisms with similar characteristics for occupied niches within an ecosystem (Colwell and Futuyma 1971). Being large mammals, wild pigs interact with and impact sympatric large mammals within their nonnative range. These interactions have the potential to affect behavior, habitat use, reproduction, diet and health of native fauna.

As omnivores, wild pigs not only consume large amounts of vegetation, but also consume other animals through direct predation or scavenging (Taylor and Hellgren 1997; Ballari and Barrios-García 2014). When examining the stomach contents of wilds pigs in the USA, Scott (1973) found the remains of white-tailed deer (*Odocoileus virginianus*) and Wilcox and Van Vuren (2009) found the remains of mule deer (*Odocoileus hemionus*). Whether the consumption of these animals was from predation or opportunistic scavenging of carrion could not be determined by analyzing the stomach contents (Scott 1973; Wilcox and Van Vuren 2009). Active predation of white-tailed deer fawns has been observed (Ditchkoff and Mayer 2009); however, no fawn survival studies have yet to document a single predatory event by wild pigs (Cook et al. 1971; McCoy et al. 2013; Linnell et al. 2018), suggesting that predation rates are very low. In Argentina, pampas deer (*Ozotoceros bezoarticus*) fawns undergo similar pressures to white-tailed deer fawns in North America. Pérez Carusi et al. (2017) and Pérez Carusi et al. (2009) discuss possible predation of pampas deer fawns by wild pigs. Pérez Carusi et al. (2017) even documented, in one instance, a mother pampas deer defending her fawn from a wild pig.

While predation leads to a fatality, wild pigs can exhibit nonfatal aggression, such as competitive exclusion, toward a variety of large mammals. In their native range, Ferretti et al. (2011) observed Eurasian wild boar displacing roe deer (*Capreolus capreolus*) where these species cooccurred. Similarly, in the nonnative range of the wild pig, Taylor and Hellgren (1997) reported observing white-tailed deer being excluded from feeding areas by wild pigs, and Tolleson et al. (1995) reported that deer will avoid feeding in areas utilized by wild pigs. Likewise, Keever (2014) reported that wild pigs negatively affect white-tailed deer density and attributed this to competitive exclusion from pulse resource areas.

Interspecific aggression is typically caused by niche overlap and competition for resources (Grether et al. 2017), and wild pigs consume mast, such as acorns (*Quercus spp.*) and fruits, in large quantities in their nonnative range (Barrett 1978; Tolleson et al. 1995; Elston and Hewitt 2010). Hard mast is considered a pulse resource that is limited spatially and temporally, and is therefore easily defensible, allowing pigs to potentially exclude deer and other large mammals as hypothesized by Keever (2014). This phenomenon was observed by Pérez Carusi et al. (2009), who used aerial surveys to study the spatial relationship between wild pigs and pampas deer in Samborombón Bay Wildlife Refuge in Argentina. They found a negative correlation in the space use of wild pigs and pampas deer, suggesting that wild pigs and pampas deer experience negative interspecific interactions. Galetti et al. (2015) found, while studying temporal partitioning between ungulates, that white-lipped peccaries (*Tayassu pecari*) shifted their temporal feeding habits around fruit trees when pigs were present to times of the day when pigs were least active. This temporal shift was likely a mechanism to reduce interspecific aggression at feeding areas. Similar interspecific aggression between white-tailed deer and wild pigs was observed by Taylor and Hellgren (1997) and speculated by Elston and Hewitt (2010) when comparing the rates of acorn consumption by wild pigs and white-tailed deer. While there is little investigation into the effects of this interaction, interference competition exhibited by wild pigs could limit the resources available to other species and consequentially the nutritional condition of deer in the population (Minot and Perrins 1986; Wentworth et al. 1992; Taylor et al. 1998). Ultimately, if wild pigs limit access to mast for native species like white-tailed deer, poorer body condition and reduced fecundity would likely become evident within the population (Verme 1969; Wentworth et al. 1992). Native species like white-tailed deer may show effects; however, there is little data that explore the effects of interference competition between deer and wild pigs in their invasive range.

In addition to aggressive exclusion of resources, wild pigs can affect species through inherent competition. Competition is common between species that utilize similar resources or have dietary overlap like wild pigs and white-tailed deer. Barrett (1978) found that within 2 weeks of acorns dropping from oaks, wild pigs shifted their diet to match seasonal availability of acorns which suggests they have preference for acorns. The strong dietary overlap and preference for acorns lead to direct competition between wild pigs and white-tailed deer, as Elston and Hewitt (2010) suggested based on the similar rates of mast intake by wild pigs and white-tailed deer. A similar interaction occurs with other mast-consuming species such as black bears (*Ursus americana*) and raccoons (*Procyon lotor*). However, as a generalist, wild pigs sustain growth from an abundant pulse resource, like acorns during a good mast year, by supplementing this growth with higher quantities of less desirable forage (Ostfeld and Keesing 2000). This response was demonstrated when Warren and Ford (1997) showed that fat reserves and reproductive performance of wild pigs were related to short-term increases in food intake based on availability.

Carrion is an important component of wild pig diets (Taylor and Hellgren 1997), and wild pigs consume greater amounts of carrion in their nonnative than their native range (Ballari and Barrios-García 2014). Ballari and Barrios-García (2014) found that the amount of animal matter consumed by wild pigs can be up to 33% of their diet in nonnative range compared to up to 16% in their native range. The increased consumption in the nonnative range likely stems from an increased need for protein to sustain a higher rate of reproduction (Comer and Mayer 2009; Wilcox and Van Vuren 2009; Ballari and Barrios-García 2014). When wild pigs opportunistically consume carrion, they compete with native scavengers. Some species in the myriad of scavengers that rely on carrion as a part of their diet are large mammals. DeVault and Rhodes (2002) found, using camera traps over small mammal carcasses, that pigs in the southeastern USA compete with native mammals such as the eastern coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), raccoon, striped skunk (*Mephitis mephitis*), and Virginia opossum (*Didelphis virginiana*) for carrion, and could potentially have negative impacts on these species.

While Colwell and Futuyma (1971) suggest that niche overlap does not always indicate competition, there is conflicting data regarding the degree to which wild pigs affect other ungulates in their invasive range (Ilse and Hellgren 1995; Desbiez et al. 2009; Galetti et al. 2015). While collared peccaries (*Pecari tajacu*) have seasonal dietary overlap with invasive wild pigs, the extent of competition is unknown. Ilse and Hellgren (1995) and Desbiez et al. (2009) both reported that dietary overlap between collared peccaries and wild pigs was greatest during times of resource abundance, suggesting that negative impacts of dietary overlap may be balanced by high resource abundance. While resource partitioning between wild pigs and collared peccaries in North America reduces competition, Ilse and Hellgren (1995) largely attributed the partitioning to the arid environment and slight differences in habitat requirements between these two species. Wild pigs tend to utilize areas with greater moisture while collared peccaries are able to use drier areas. With the lack of dietary overlap between these two species being attributed mainly to the difference in habitat use, areas like the Pantanal Mato-Grossense in Brazil, where there are more areas that experience both regular flooding and dry periods, there is a greater potential for resource competition. Sicuro and Oliveira (2002) observed wild pigs feeding in the same areas as collared peccaries and white-lipped peccaries, suggesting that competition between these species may be subject to habitat type and food availability.

Sicuro and Oliveira (2002) confirmed that the morphology, specifically the bite force that wild pigs could generate, gave wild pigs the potential to compete with both collared peccaries and white-lipped peccaries for food. However, Desbiez et al. (2009) conducted a dietary study of these three species and found less overlap than what would be expected from an invasive species of similar morphology and reported that niche partitioning was occurring. In a later study conducted by Galetti et al. (2015), high dietary overlap was found between wild pigs and white-lipped peccaries, but not collared peccaries. The ephemeral fluctuations in the environmental conditions of the Pantanal area sometimes limit food supply, and limited resource availability combined with dietary overlap would lead to increased competition between these species as Galetti et al. (2015) suggests. More research is needed on the interaction between peccary species and invasive wild pigs to clarify these conflicting results in North and South American landscapes.

As wild pigs expand their range (Snow et al. 2017), their potential as a vector of pathogens to native large mammals, like the white-tailed deer, also increases. Wild pigs and cervids can clinically contract and be carriers for a variety of the same diseases ranging from bacterial infections, such as bovine tuberculosis and brucellosis, to viral diseases, such as foot and mouth disease and avian influenza (Hermoso de Mendoza et al. 2006; Miller and Sweeney 2013; Miller et al. 2017). Epizootic diseases are much more difficult to eradicate from a population because of cross species transmission and subsequent reinfection of populations where they may have been extirpated. Hermoso de Mendoza et al. (2006) demonstrated this using data from native wild boar, red deer (*Cervus elaphus*), and domestic cattle (*Bos taurus*) that were tested for bovine tuberculosis in Europe. They found that spikes in bovine tuberculosis in cattle after periods of decline coincided with a greater prevalence in wild ungulate species during those years. They suggested the mechanism for transfer in the area was likely from game species to domestic cattle as they observed frequent reinfection of cattle herds in the area, while areas absent of game species did not experience the same levels of infection. The same could hold true for other diseases and areas where there is a wildlife–livestock interface. Corn and Yabsley's (2020) study contains an up-to-date table with a comprehensive description of diseases that wild pigs can carry and transfer to other species.

Wild pigs can indirectly affect trophic cascades in their introduced range, such as with the decline of the island fox (*Urocyon littoralis*) that is endemic to the Channel Islands of California, USA. The island fox has one major predator on the island, the golden eagle (*Aquila chrysaetos).* Using hyperpredation models, Roemer et al. (2001) determined that wild pigs served as a supplemental food source for golden eagles, thereby allowing their populations to grow well beyond historic levels on the island. This increase in eagles resulted in greater predation pressure on island foxes and a subsequent decline in island fox densities. The resulting decline threatened to extirpate island foxes on Santa Cruz in a period of 6.7–11.5 years. With the suppression of the island fox population, the competing island spotted skunk (*Spilogale gracilis amphiala*) population experienced competitive release. In 2006, wild pigs were intensively eradicated from the island and subsequently island foxes increased from less than 100 individuals to an estimated 736 individuals with a 96.2 annual survival rate in 2011 (Parkes et al. 2010; Morrison 2011).

Wild pig impacts on native small mammals

Just as wild pigs can have adverse effects on large mammals, their behaviors can have negative implications for small mammals as well. Wild pigs can affect small mammals through predation, competition, and habitat destruction. While wild pigs compete for similar resources with many small mammals, the ways in which they compete differs from how they compete with large mammals.

Because the plant-based diet of wild pigs is sometimes seasonally low in protein (Ditchkoff and Mayer 2009), wild pigs supplement their diet with animal protein when they can (Baber and Coblentz 1987). Wilcox and Van Vuren (2009) demonstrated how wild pigs exhibit dietary plasticity to obtain protein via consumption of animal matter through predation and scavenging. Three dietary studies using the stomach contents of wild pigs in the USA (Scott 1973; Loggins et al. 2002; Wilcox and Van Vuren 2009) found that small mammals consumed by wild pigs are often fossorial or semi-fossorial. Some of these species are the Botta's pocket gophers (*Thomomys bottae*), broad-footed moles (*Scapanus latimanus*), California ground squirrels (*Spermophilus beecheyi*), California voles (*Microtus californicus*), and other voles (*Microtus spp.*). It is speculated that these species are likely opportunistically predated during rooting behavior. These studies also found that wild pigs will consume terrestrial and arboreal mammals opportunistically, including deer mice (*Peromyscus maniculatus*), piñon mice (*Peromyscus truei*), western harvest mice (*Reithrodontomys megalotis*), and various lagomorphs in North America (Scott 1973; Loggins et al. 2002; Wilcox and Van Vuren 2009). In Chile, Skewes et al. (2007) found the remains of three rodent species in the stomachs of wild pigs: the olive grass mouse (*Abrothrix olivacea*), the long-clawed mouse (*Geoxus valdivianus*), and the long-tailed mouse (*Oligoryzomis longicaudatus*). They reported animal matter to be 16.1% of the wild pig diet in their study and largely attributed that number to a recent increase in the populations of the aforementioned species at the time of the study along with the opportunistic feeding habits of wild pigs.

When hard mast is abundant, wild pigs will compete with other mast consumers like gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) (McShea and Schwede 1993). McShea and Schwede (1993) found that peak acorn consumption for squirrel species occurs after peak mast fall, suggesting they generally consume acorns that remain after larger mast consumers have fed. Loggins et al. (2002) demonstrated that wild pigs shift their diet to consume mainly acorns when the availability of acorns is greatest. Given wild pig's efficient feeding behaviors on acorns during the fall, as described by Elston and Hewitt (2010), increased mast consumption by wild pigs during peak feeding season would likely decrease the amount of acorns available to squirrels during their peak consumption period. Wild pigs also compete with other small mammals for seeds. In Argentina, Sanguinetti and Kitzberger (2010) found that wild pigs compete with numerous species of small mammal, such as the greater clawed mouse (*Chelemys macronyx*), long-haired mouse (*Abrotrix longipilis*), long-tailed mouse, and arboreal mouse (*Irenomys tarsalis*) for the seed of the monkey puzzle tree (*Araucaria araucana*). They reported that wild pigs consume 10–30% of the seed crop from the monkey puzzle tree. As a pulse resource, the competition for the seed mast produced by the monkey puzzle tree is similar to competition for and response in wild pigs to oak mast in North America, and likely will have greater impacts on native faunal species during a poor mast year (Ostfeld and Keesing 2000).

Wild pigs can continue to negatively impact the availability of mast resources to other species even after peak mast production. Squirrels will hoard and cache acorns to serve as a food source during later seasons. The raiding of cached resources, like acorns, could be extremely detrimental to squirrel populations that rely almost exclusively on these caches for survival during the winter. The importance of seed caches was demonstrated by Wauters et al. (1995) who found that Eurasian red squirrels (*Sciurus vulgaris*) who recovered more hoarded resources were more likely to survive and reproduce. Focardi et al. (2015) found wild boar in Europe will search for burrows of small mammals that are likely to cache acorns and focus their subterraneous foraging efforts in the immediate area of these burrows, suggesting that wild pigs selectively search for cached resources. They also found that the amount of rooting decreased with distance from small mammal dens, further documenting targeted searches. A similar interaction is likely to occur in their nonnative range where squirrels and pigs co-occur because of the importance of acorns and other mast for nonnative wild pigs (Barrett and Birmingham 1994; Loggins et al. 2002; Schuyler et al. 2002). Since the eastern chipmunk (*Tamias striatus*) is another caching species (Clarke and Kramer 1994), this effect is likely to be seen with them where they share habitat with pigs. When wild pigs pilfer caches of acorns, they not only steal resources from those that cached the acorns, but also compete with other fauna that pilfer caches. In California, USA, Schubert et al. (2018) used camera traps to study acorn cache pilferage and found wild pigs were among an assemblage of species pilfering cached acorns, including California deer mice (*Peromyscus californicus*), dusky-footed wood rats (*Neotoma fuscipes*), and Botta's pocket gophers.

Shelter is another resource that is essential to the survival of small mammals because of its importance for protecting small mammals from predation and harsh environmental conditions. As wild pigs root in search of food, they disturb leaf litter and debris on the forest floor, which serves as habitat for small mammals and their prey. Singer et al. (1984) found that the southern red-backed vole (*Myodes gapperi*) and the northern short-tailed shrew (*Blarina brevicauda)* were absent from historic areas following invasion of wild pigs. The intense rooting disturbance by wild pigs caused leaf litter to be reduced by up to 59%. They attributed the disappearance of these species to both the direct loss of habitat and, in the case of the northern short-tailed shrew, to loss of prey as a result of the habitat disturbance.

Wild pig impacts on native avian fauna

The extent of impacts that wild pigs have on fauna in their nonnative range extends beyond that of the mammalian community. Wild pigs adversely impact avian species, many of which are endemic and/or threatened (Cruz and Cruz 1987; Taylor 2000; Donlan et al. 2007; McClure et al. 2018). Wild pigs affect avian communities across their nonnative range by predation of adults, juveniles and nests, competition for food, and habitat destruction.

Wild pigs are proficient nest predators (Ballari and Barrios-García 2014), and there is particular concern for how nest predation affects endemic and threatened ground nesting, colony shorebirds (Taylor 2000). Ground nest predation of the dark-rumped petrel (*Pterodroma phaeopygia*), which is a colony species that nests in rocky caves or creates burrows in the highlands of the Galápagos Islands, was likely a cause of population declines in the Galápagos Islands before predator control was initiated, and wild pigs were among the predators observed feeding on nests (Cruz and Cruz 1987). On the islands of New Zealand, nest predation by wild pigs in shore bird colonies is listed as one of the greatest threats to the Gibson's albatross (*Diomedea gibsoni*) in the *Action Plan for Seabird Conservation in New Zealand* (Taylor 2000). In addition to nest predation, wild pigs will destroy nesting sites/habitat of some shore birds. In New Zealand, Cuthbert (2002) documented local extinction of Hutton's shearwater (*Puffinus huttoni*) colonies and attributed this to the presence of wild pigs. Cuthbert (2002) reported that the six colonies that were extirpated had wild pigs present, and the two colonies not extirpated did not have wild pigs present. He suggested that both predation and breeding ground destruction contributed to the decline of Hutton's shearwater. Taylor (2000) also discussed the threats of nest destruction by wild pigs to shore birds. He mentioned that wild pigs will destroy the cavities and burrows that some shore birds nest in, such as the Chatham Island taiko (*Pterodroma magenta*), Buller's shearwater (*Ardenna bulleri*), and the white-chinned petrel (*Procellaria aequinoctialis*).

Ground nest predation is detrimental to ground nesting shorebirds and upland avian species alike. In Australia, wild pigs have been observed feeding on the nests of cassowaries (*Casuarius casuarius*) and megapodes (*Megapodiidae*), although the extent and effect of this predation is not well studied (Crome and Moore 1990; Pavlov et al. 1992). For ground nesters that are exposed to anthropogenic mortality risks such as hunting, the impacts may be even greater. While Henry (1969) found that only 2.6% of dummy turkey nests in the Appalachian Mountains of the USA were predated by wild pigs, Lewis et al. (2019) have shown through analysis of historical data that the range and total numbers of wild pigs in North America have largely increased since then. This suggests that predation of ground nests by wild pigs may be greater than previously thought. The northern bobwhite (*Colinus virginianus*) is a game species in the southeastern USA that cryptically nests on the ground in well-drained grassy areas (Klimstra and Roseberry 1975). Tolleson et al. (1993) conducted two experiments of similar design to determine the effect that wild pigs had on northern bobwhite. The first of the experiments found that wild pigs depredated 28% of artificial bobwhite nests and the second found only 8% depredation by pigs, with many of the nest depredations being classified as the result of unknown predators. Tolleson et al. (1993) suggested that despite the experiments producing different results, it is likely that wild pigs play an important role in the predation of northern bobwhite nests, and others have suggested that nest predation may exacerbate population declines by affecting recruitment (Stegeman 1938; Rollins and Carroll 2001). The wild turkey (*Meleagris gallopavo*) is another ground nesting species that experiences wild pig nest predation (Dreibelbis et al. 2008; Perot 2011) and typically nest in areas with dense and diverse herbaceous understory to help conceal their nests from predators (Badyaev 1995). Like the northern bobwhite, the wild turkey is a game species that is subjected to hunting pressure and could be experiencing similar population-level impacts. In the USA, Sanders et al. (2020a, b) found that wild pigs predated simulated turkey nests at proportions that were statistically similar to common native nest predators. They also suggested that nest depredation by wild pigs is additive due to the greater rate of nest depredation observed in their study when compared to nest depredation studies where wild pigs were not nest predators. Sanders et al. (2020a, b) found no response in the spatial use of wild pigs in response to an abundance of ground nests; however, they suggest that wild pigs will opportunistically predate nests when they find them. They suggest that the nest predation pressure from wild pigs is relative to the density of both wild pigs and wild turkey nests in an area that both occur rather than a response to wild turkey nests as a pulse resource. These studies used artificial nests to control nest density in their study areas, which has limitations when mimicking natural nests. In addition to nest predation, wild pigs will predate adult birds. Scott (1973) found the remains of a Northern cardinal (*Cardinalis cardinalis*) in the stomach of a wild pig in the USA and Ditchkoff and Mayer (2009) reported an observation in which a wild turkey was preyed upon by three wild pigs while visiting a bait site. In South America, Skewes et al. (2007) found the remains of the black-throated huet-huet (*Pteroptochos tarnii*) and chucao tapaculo (*Scelorchilus rubecula*) while analyzing stomach contents from 20 pigs at two separate locations in Chile, Ballari et al. (2015b) found the remains of birds in the orders *Columbiformes* and *Passeriformes* in Argentina, and Coblentz and Baber (1987) found the remains of Galápagos finches (*Geospiza spp.*) in the stomachs of wild pigs on Isla Santiago.

The effect of wild pig predation on avian species can be exacerbated on island communities. This is partially due to the high densities that wild pigs can reach on islands and partially due to the inherent nature of islands containing a minimum assemblage of terrestrial predators (Sweitzer, Rick 1998; Banks et al. 2008). Banks et al. (2008) speculated, using the "predator archetype" theory of Cox and Lima (2006) that the natural lack of terrestrial predators on island ecosystems leads to an unfamiliarity of prey to the predation habits of an invasive terrestrial predator and would not be well adapted to escape when presented with a threat of predation. The impact of wild pigs is particularly concerning for endemic island species like the Galápagos rail (*Lateralius spilonota*), where predation has substantially reduced population size. Donlan et al. (2007) found that once pigs were removed, Galápagos rail population began to rebound toward historic numbers, suggesting that wild pigs greatly contributed to their decline. The dark-rumped petrel is a shoreline nester of the Galápagos Islands that is subjected to predation by wild pigs. Cruz and Cruz (1987) observed wild pigs seeking out and consuming both adult and immature birds. On Australia's Lord Howe Island, the introduction of wild pigs resulted in the decline of the Lord Howe Island woodhen (*Gallirallus sylvestris*), which Miller and Mullette (1985) reported as becoming spatially confined to two mountain summits as wild pigs occupied the high-quality bottomlands of the island. The summits were inaccessible to wild pigs, but were of lower quality for nesting purposes. A reintroduction program in 1980 included the near complete removal of pigs. The reintroduction was successful and the Lord Howe Island woodhen population expanded and increased beyond its previously confined range, demonstrating that wild pigs were the most limiting factor to the population's size and distribution. Taylor (2000) lists wild pig predation of juveniles and adults as a major concern for species conservation for the yellow-eyed penguin (*Megadyptes antipodes*), Gibson's Albatross (*Diomedea gibsoni*), white-chinned petrel, Chatham Island taiko (*Pterodroma magentae*), Chatham petrel (*Pterodroma axillaris*) and Buller's Shearwater. Challies (1975) found the remains of Auckland Island prions (*Pachyptila desolata*) and yellow-eyed penguins in the stomachs of wild pigs shot on Auckland Island. He mentioned that, although indiscernible from a myriad of predators, it is likely that predation from wild pigs added to the decline of mollyhawk and albatross (*Diomedea* spp.) nesting on Auckland Island. Many species that wild pigs predate on New Zealand's coastal islands are endemic and threatened in the wild (Challies 1975; Taylor 2000).

Avian species that are somewhat dependent on seasonal mast are impacted by wild pigs through competition. Wild turkeys utilize annual mast production in a similar manner to white-tailed deer (Barnett and Barnett 2008). As wild pigs consume large amounts of mast, they compete with wild turkeys for what could be a vital resource (Scott 1973; Elston and Hewitt 2010). Following the idea proposed by Henry and Conley (1972) that wild pigs may have an elevated impact on native wildlife during poor mast years, competition between wild pigs and wild turkey could be exacerbated during poor mast producing years and lead to population declines in wild turkey if outcompeted by wild pigs. (Barnett and Barnett 2008) speculate that hunting mortality may serve to exacerbate these impacts during poor mast years.

Competition with native birds is not limited to mast resources. DeVault and Rhodes (2002) conducted a study to identify scavengers of small mammal carcasses and found that both wild pigs and red-tailed hawks (*Buteo jamaicensis*) seek out and consume carcasses. A similar food searching behavior and dietary overlap displayed by these two species suggests a niche overlap as scavengers in forests. As a top predator in many ecosystems, red-tailed hawks need large amounts of meat to support their populations (Fitch et al. 1946). Given the niche overlap between red-tailed hawks and wild pigs as scavengers of small mammal carcasses, there is potential for competition between these two species.

Wild pig impacts on native herpetofauna

Wild pigs in their nonnative range negatively impact native herpetofauna in a variety of ways. Wild pigs will cause top-down impacts such as adult predation and nest predation and destruction, to bottom-up affects including habitat degradation that could affect both adult survival and recruitment of young.

Wild pigs can severely impact marine turtles during the nesting phase similar to how they affect ground nesting birds. Before the hatching of marine turtle nests, the eggs are vulnerable to predators that can access them below the sand. Whytlaw et al. (2013) reported that, in Australia, up to 36% of total nests in one study were predated by wild pigs while studying nest depredation of flatback turtles (*Natator depressus*), olive ridley turtles (*Lepidochelys olivacea*), and hawksbill turtles (*Eretemochelys imbricata*). Wild pig predation of marine turtle nests at such a level is likely to have a profound effect on recruitment rates. The issue of wild pig predation on marine turtle nests is not just localized to Australia. In Florida, USA, the loss of loggerhead turtle (*Caretta caretta*) nests to wild pigs has sparked concerns on how to properly mitigate the predation. Engeman et al. (2014) found that wild pigs predated 100% of the nests that were being monitored within 50 days of the first predation event on Florida's Keewaydin Island in the USA. This suggests that once wild pigs identified the presence of nests, this resource was sought out and used to exhaustion. On land, wild pigs are a serious conservation concern for tortoises as well. On the Galápagos Islands, wild pigs are nest and hatchling predators of the Galápagos giant tortoise (*Chelonoidis spp.*), an endemic and endangered species on the Ecuadorian archipelago (Coblentz and Baber 1987; MacFarland et al. 1974). In addition to being an obstacle to turtle and tortoise conservation, wild pigs also affect large, freshwater reptiles as well. Wild pigs are known to predate caiman (*Caiman crocodilus yacar*) nests in Brazil and alligator (*Alligator mississippiensis*) nests in the USA (Elsey et al. 2012; Campos and Mourão 2015). Campos and Mourão (2015) conducted a camera survey over caiman nests to identify predators in forested wetlands and found that, although not a large proportion, wild pigs were among a myriad of predators observed on camera depredating caiman nests. In another study, Campos (1993) observed wild pig sign at a number of nests that had been predated, although direct predation was not documented. In Louisiana, Elsey et al. (2012) used a questionnaire sent to alligator farmers to understand nest predation by wild pigs and found that 51.4% of the respondents reported they had observed an impact. Wild pig predation of alligator nests seems to be increasing and could negatively impact alligator populations in the southeastern United States, and in areas where alligator harvest is legal, could have an even more profound effect (Elsey et al. 2012). These effects are dependent on whether wild pig nest depredation of alligators is additive or compensatory.

Like many other taxa, wild pigs will opportunistically predate a variety of herpetofauna including freshwater turtles. Turtle hatchlings are vulnerable to a myriad of predators, including wild pigs. Fordham et al. (2006) found that wild pigs caused 96% of the deaths of individual northern snake-necked turtles (*Chelodina oblonga*) that were monitored during the study and estimated up to 73% mortality in the population of the area. Fordham et al. (2008) modeled pig predation rates in relation to population persistence and hunting pressure and suggested that pig predation of the northern snake-necked turtle at the rates documented were likely to cause localized extinction within 50 years. Wild pigs will also predate terrestrial reptiles and amphibians. Specifically, wild pigs in North America have been found to consume green anoles (*Anolis carolinensis*), eastern fence lizards (*Sceloporus undulates*), red salamanders (*Pseudotriton ruber*), red-backed salamanders (*Plethodon cinereus*), eastern spadefoot toads (*Scaphiopus holbrookii*), wood frogs (*Lithobates sylvaticus*), various *Hyla* species, red-bellied snakes (*Storeria occipitomaculata*), and various other snake species (*Serpentes*) (Scott 1973; Jolley et al. 2010). In South America, some iguanian species (*Liolaemus spp.*), Darwin's frog (*Rhinoderma darwinii*), lava lizards (*Microlophus jacobii*), and the Galápagos snake (*Pseudalsophis dorsalis*) have been found in the stomachs of wild pigs (Coblentz and Baber 1987; Skewes et al. 2007). In Australia, stomachs of wild pigs contained the remains of the eastern bearded dragon (*Pogona barbata*), barking marsh frog (*Lymnodynastes fletcheri*), green tree frog (*Litoria caerulea*), spotted marsh frog (*Lymnodynastes tasmaniensis*), and the De Vis banded snake (*Denisonia devisi*). None of these species are listed as endangered in Australia, and the implications of their consumption by wild pigs is not well understood (Wishart et al. 2015).

Wild pig behavior can damage the habitat for herepetofauna as well (Doupé et al. 2009; Elsey et al. 2012). In Australia, Doupé et al. (2009) compared wetlands where wild pigs were excluded to areas where they were present and found that rooting and wallowing in lagoons caused the uprooting of macrophytes and created areas of open water and bare ground. Subsequently, turbidity, anoxia, and eutrophication increased to levels where the lagoons were unsuitable habitat for the long-necked turtle (*Chelodina longicollis*). As rooting and wallowing in wetlands are common behavior of wild pigs throughout their nonnative range, it is likely a threat to other species that rely on a dense macrophyte community to survive (Engeman et al. 2007; Bracke 2011). Similar concerns were expressed with the endangered Houston toad (*Bufo houstonensis*), which inhabits the wetlands of the Lost Pines in Texas. Brown et al. (2012) found increased nitrate and ammonium loading in wetlands due to wild pig rooting and wallowing, and suggested this could be toxic to the Houston toad. Additionally, they found increased total suspended solids (TSS) and lower pH with wild pig activity. They speculated that lower pH and increased TSS could affect the ability of Houston toad tadpoles to maintain homeostasis. Increased TSS lowers available oxygen in the water and a reduced pH affects osmoregulation within the tadpoles. Additionally, wild pig wallowing along wetlands where the Houston toad inhabits creates ephemeral pools (Bracke 2011). Brown et al. (2012) suggested that these structural changes could be detrimental if the Houston toad utilizes these pools for reproductive habitat and they dry up.

In addition to wetlands, rooting behaviors can destroy other amphibian habitats (Engeman et al. 2007). Means and Travis (2007) conducted abundance sampling 25 years apart on Eglin Air Force Base, located in Florida, USA, and observed the disappearance of the southern dusky salamander (*Desmognathus auriculatus*) from all of the sites and a 68% decrease in abundance of the spotted dusky salamander (*Desmognathus conanti*). While they did not directly study the cause of these declines, they observed wild pig rooting in 62% of seep heads necessary for reproduction of these species. They believe the main cause for the decline to be pathogens, but their observations led them to believe that wild pigs are an additive cause. A similar study conducted by Maerz et al. (2015) found that poor detection of the southern dusky salamander occurred in areas where wild pig damage was present, and there was an absence of wild pig damage at sites with an abundance of southern dusky salamanders. The reticulated flatwood salamander (*Ambystoma bishopi*) and the frosted flatwood salamander (*Ambystoma cingulatum*) inhabit the ecologically important littoral zones of wetlands surrounded by upland areas (Shulse et al. 2012; Jones et al. 2018). The littoral zone provides the most suitable habitat for the flatwoods salamanders and is an area that is often used by wild pigs for rooting and wallowing (Bracke 2011). Jones et al. (2018) suggested that rooting of wetland areas inhabited by these salamanders removes ground cover that is essential for their eggs. They found that wild pigs damaged 55% of historic wetland breeding sites during their study.

Conclusion

Our understanding of how wild pigs impact native wildlife is improving but is still far from complete. While there are some ways in which wild pigs positively impact native species, such as serving as a prey source for large predators (Shoop and Ruckdeschel 1990; Caudill et al. 2019), the majority of the scientific literature indicates that invasive wild pigs are a threat to native species. Unfortunately, much of the information regarding these threats is surface level or anecdotal. There is a lack of research depicting the degree to which these impacts occur. For example, we know that wild pigs predate sea turtle nests (Engeman et al. 2014) but we do not have a firm grasp of the degree to which they impact populations. Additionally, much of the research that has been done on interspecific impacts of wild pigs outside of their native range is regional and largely focused on the USA. Areas such as Argentina (Ballari et al. 2015a) and Australia (Bengsen et al. 2017, 2014) are lacking in scientific research that quantify the degree to which wild pigs may be affecting native vertebrate populations and rely heavily on anecdotal evidence or isolated observations. These impacts, particularly to threatened and endangered species, likely have economic effects that trickle down to humans. To date, very few studies have attempted to describe these impacts in economic terms, and future studies in these areas would be more impactful if they could. As described by Ditchkoff et al. (2020), this information is necessary for educating the public, informing lawmakers, and improving resources available to mitigate the impacts of invasive wild pigs.

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References

Baber DW, Coblentz BE (1987) Diet, Nutrition, and conception in feral pigs on Santa Catalina Island. J Wildl Manage 51:306–317

Badyaev A (1995) Nesting habitat and nesting success of eastern wild turkeys in the Arkansas Ozark Highlands. Condor 97:221–232

Ballari SA, Barrios-García MN (2014) A review of wild boar Sus scrofa diet and factors affecting food selection in native and introduced ranges. Mamm Rev 44:124–134. https://doi.org/10.1111/mam.12015

Ballari SA, Cuevas MF, Cirignoli S, Valenzuela AEJ (2015a) Invasive wild boar in Argentina: using protected areas as a research platform to determine distribution, impacts and management. Biol Invasions 17:1595–1602. https://doi.org/10.1007/s10530-014-0818-7

Ballari SA, Cuevas MF, Ojeda RA, Navarro JL (2015b) Diet of wild boar (Sus scrofa) in a protected area of Argentina: the importance of baiting. Mammal Res 60:81–87. https://doi.org/10.1007/s13364-014-0202-0

Banks PB, Nordström M, Ahola M et al (2008) Impacts of alien mink predation on island vertebrate communities of the Baltic Sea archipelago: Review of a long-term experimental study. Boreal Environ Res 13:3–16

Barnett SW, Barnett VS (2008) The wild turkey in Alabama. Alabama Department of Conservation and Natural Resources, Montgomery

Barrett RH (1978) The feral hog at Dye Creek Ranch, California. Hilgardia 46:283–355. https://doi.org/10.3733/hilg.v46n09p283

Barrett RH, Birmingham GH (1994) Wild pigs. In: Hygnstrom SE, Timm RM, Larson GE (eds) The Handbook: Prevention and control of wildlife, 2nd edn. University of Nebraska-Lincoln, Lincoln, NE, pp 65–70

Baubet E, Ropert-Coudert Y, Brandt S (2003) Seasonal and annual variations in earthworm consumption by wild boar (Sus scrofa scrofa L.). Wildl Res 30:179–186. https://doi.org/10.1071/wr00113

Bengsen AJ, Gentle MN, Mitchell JL et al (2014) Impacts and management of wild pigs Sus scrofa in Australia. Mamm Rev 44:135–147. https://doi.org/10.1111/mam.12011

Bengsen AJ, West P, Krull CR (2017) Feral pigs in Australia and New zealand: Range, trend, management, and impacts of an invasive species. In: Melletti M, Meijaard E (eds) Ecology, conservation and management of wild pigs and peccaries. Cambridge University Press, Cambridge, pp 325–338

Bracke MBM (2011) Review of wallowing in pigs: Description of the behaviour and its motivational basis. Appl Anim Behav Sci 132:1–13. https://doi.org/10.1016/j.applanim.2011.01.002

Bratton SP (1975) The effect of the European wild boar, Sus scrofa, on gray beech forest in the Great Smoky Mountains. Ecology 56:1356–1366

Brown DJ, Jones MC, Bell J, Forstner MRJ (2012) Feral hog damage to endangered Houston toad (Bufo houstonensis) habitat in the Lost Pines of Texas. Texas J Sci 64:73–88

Campbell TA, Long DB (2009) Feral swine damage and damage management in forested ecosystems. For Ecol Manage 257:2319–2326. https://doi.org/10.1016/j.foreco.2009.03.036

Campos Z (1993) Effect of habitat on survival of eggs and sex ratio of hatchlings of Caiman crocodilus yacare in the Pantanal, Brazil. J Herpetol 27:127–132

Campos Z, Mourão G (2015) Camera traps capture images of predators of Caiman crocodilus yacare eggs (Reptilia: Crocodylia) in Brazil's Pantanal wetlands. J Nat Hist 49:977–982. https://doi.org/10.1080/00222933.2014.930757

Caudill G, Onorato DP, Cunningham MW et al (2019) Temporal trends in Florida panther food habits. Human-Wildlife Interact 13:87–97

Challies CN (1975) Feral pigs (Sus scrofa) on Auckland Island: Status, and effects on vegetation and nesting sea birds. New Zeal J Zool 2:479–490. https://doi.org/10.1080/03014223.1975.9517889

Clarke MF, Kramer DL (1994) Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, Tamias striatus. Anim Behav 48:299–308

Coblentz B, Baber D (1987) Biology and control of feral pigs on Isla Santiago, Galapagos, Ecuador. J Appl Ecol 24:403–418

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576. https://doi.org/10.2307/1934144

Comer C, Mayer J (2009) Biology of wild pigs: Wild pig reproductive biology. In: Mayer J, Brisbin I (eds) Wild pigs: Biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, pp 51–69

Cook RS, White M, Trainer DO, Glazener WC (1971) Mortality of young white-tailed deer fawns in South Texas. J Wildl Manage 35:407–419

Corn JL, Yabsley MJ (2020) Diseases and parasites that impact wild pigs and species they contact. In: Vercauteren KC, Beasley JC, Ditchkoff SS et al (eds) Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, pp 83–126

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674–680. https://doi.org/10.1016/j.tree.2006.07.011

Crawley AMJ, Kornberg H, Lawton JH et al (1986) The population biology of invaders. Philos Trans R Soc Lond B Biol Sci 314:711–731

Crome FHJ, Moore LA (1990) Cassowaries in north-eastern queensland: Report of a survey and a review and assessment of their status and conservation and management needs. Wildl Res 17:369–385. https://doi.org/10.1071/WR9900369

Cruz JB, Cruz F (1987) Conservation of the dark-rumped petrel Pterodroma phaeopygia of the Galápagos. Biol Conserv 42:303–311

Cuthbert R (2002) The role of introduced mammals and inverse density-dependent predation in the conservation of Hutton's shearwater. Biol Conserv 108:69–78. https://doi.org/10.1016/S0006-3207(02)00091-5

Davis MA (2003) Biotic globalization : Does competition from introduced species threaten biodiversity? Bioscience 53:481–489

Desbiez ALJ, Santos SA, Keuroghlian A, Bodmer RE (2009) Niche partitioning among white-lipped peccaries (Tayassu pecari), collared peccaries (Pecari tajacu), and feral pigs (Sus scrofa). J Mammal 90:119–128. https://doi.org/10.1644/08-MAMM-A-038.1

DeVault TL, Rhodes OE (2002) Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. Acta Theriol (warsz) 47:185–192. https://doi.org/10.1007/BF03192458

Ditchkoff SS, Beasley JC, Mayer JJ et al (2020) The future of wild pigs in North America. In: VerCauteren KC, Beasley JC, Ditchkoff SS et al (eds) Invasive wild pigs in North America. CRC Press, Boca Raton, pp 465–469

Ditchkoff SS, Mayer JJ (2009) Wild pig food habits. In: Mayer JJ, Brisbin IL (eds) Wild pigs: Biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina

Donlan CJ, Campbell K, Cabrera W et al (2007) Recovery of the Galápagos rail (Laterallus spilonotus) following the removal of invasive mammals. Biol Conserv 138:520–524. https://doi.org/10.1016/j.biocon.2007.05.013

Doupé ROG, Schaffer J, Knott MJ, Dicky PW (2009) A description of freshwater turtle habitat destruction by feral pigs in tropical North-Eastern Australia. Herpetol Conserv Biol 4:331–339

Dreibelbis JZ, Melton KB, Aguirre R et al (2008) Predation of Rio Grande wild turkey nests on the Edwards Plateau. Wilson J Ornithol 120:906–910. https://doi.org/10.2193/2005-751

Dzięciołowski RM, Clarke CMH, Frampton CM (1992) Reproductive characteristics of feral pigs in New Zealand. Acta Theriol (warsz) 37:259–270. https://doi.org/10.4098/at.arch.92-24

Elsey RM, Mouton EC, Kinler N (2012) Effects of feral swine (Sus scrofa) on alligator (Alligator mississippiensis) nests in Louisiana. Southeast Nat 11:205–218. https://doi.org/10.1656/058.011.0204

Elston JJ, Hewitt DG (2010) Intake of mast by wildlife in Texas and the potential for competition with wild boars. Southwest Nat 55:57–66. https://doi.org/10.1894/tal-03.1

Engeman RM, Stevens A, Allen J et al (2007) Feral swine management for conservation of an imperiled wetland habitat: Florida's vanishing seepage slopes. Biol Conserv 134:440–446. https://doi.org/10.1016/j.biocon.2006.08.033

Engeman RM, Addison D, Griffin JC (2014) Defending against disparate marine turtle nest predators: Nesting success benefits from eradicating invasive feral swine and caging nests from raccoons. Oryx 50:289–295. https://doi.org/10.1017/S0030605314000805

Ferretti F, Sforzi A, Lovari S (2011) Behavioural interference between ungulate species: Roe are not on velvet with fallow deer. Behav Ecol Sociobiol 65:875–887. https://doi.org/10.1007/s00265-010-1088-8

Fitch HS, Swenson F, Tillotson D (1946) Behavior and food habits of the red-tailed hawk. Condor 48:205–237

Focardi S, Morimando F, Capriotti S et al (2015) Cooperation improves the access of wild boars (Sus scrofa) to food sources. Behav Processes 121:80–86. https://doi.org/10.1016/j.beproc.2015.10.019

Fordham D, Georges A, Corey B, Brook BW (2006) Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia. Biol Conserv 133:379–388. https://doi.org/10.1016/j.biocon.2006.07.001

Fordham DA, Georges A, Brook BW (2008) Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: Managing a tropical freshwater turtle for sustainability and conservation. J Appl Ecol 45:52–62. https://doi.org/10.1111/j.1365-2664.2007.01414.x

Frauendorf M, Gethöffer F, Siebert U, Keuling O (2016) The influence of environmental and physiological factors on the litter size of wild boar (Sus scrofa) in an agriculture dominated area in Germany. Sci Total Environ 541:877–882

Galetti M, Camargo H, Siqueira T et al (2015) Diet overlap and foraging activity between feral pigs and native peccaries in the Pantanal. PLoS ONE. https://doi.org/10.1371/journal.pone.0141459

Gray SM, Roloff GJ, Kramer DB et al (2020) Effects of wild pig disturbance on forest vegetation and soils. J Wildl Manage 84:739–748. https://doi.org/10.1002/jwmg.21845

Grether GF, Pieman KS, Tobias JA, Robinson BW (2017) Causes and consequences of behavioral interference between species. Trends Ecol Evol 32:760–772

Henry VG (1969) Predation on dummy nests of ground-nesting birds in the Southern Appalachians. J Wildl Manage 33:169–172

Henry VG, Conley RH (1972) Fall foods of European wild hogs in the Southern Appalachians. J Wildl Manage 36:854–860

Hermoso de Mendoza J, Parra A, Tato A et al (2006) Bovine tuberculosis in wild boar (Sus scrofa), red deer (Cervus elaphus) and cattle (Bos taurus) in a Mediterranean ecosystem (1992–2004). Prev Vet Med 74:239–247. https://doi.org/10.1016/j.prevetmed.2005.10.005

Ilse LM, Hellgren EC (1995) Resource partitioning in sympatric populations of collared peccaries and feral hogs in Southern Texas. J Mammal 76:784–799

Jolley DB, Ditchkoff SS, Sparklin BD et al (2010) Estimate of herpetofauna depredation by a population of wild pigs. J Mammal 91:519–524. https://doi.org/10.1644/09-mamm-a-129.1

Jones KC, Gorman TA, Rincon BK et al (2018) Feral swine Sus scrofa: A new threat to the remaining breeding wetlands of the vulnerable reticulated flatwoods salamander Ambystoma bishopi. Oryx 52:669–676. https://doi.org/10.1017/S0030605316001253

Keever AC (2014) Use of N-mixture models for estimating white-tailed deer populations and impacts of predator removal and interspecific competition. Auburn University

Klimstra WD, Roseberry JL (1975) Nesting ecology of the bobwhite in Southern Illinois. Wildl Soc Bull 3–37

Lewis JS, Corn JL, Mayer JJ et al (2019) Historical, current, and potential population size estimates of invasive wild pigs (Sus scrofa) in the United States. Biol Invasions. https://doi.org/10.1007/s10530-019-01983-1

Linnell JDC, Aanes R, Andersen R (2018) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biol 7:209–223. https://doi.org/10.2981/wlb.1995.0026

Lipscomb DJ (1989) Impacts of feral hogs on longleaf pine regeneration. South J Appl for 13:177–181

Loggins RE, Wilcox JT, Van Vuren DH, Sweitzer RA (2002) Seasonal diets of wild pigs in oak woodlands of the central coast region of California. Calif Fish Game 88:28–34

MacFarland CG, Villa J, Toro B (1974) The Galápagos giant tortoises (Geochelone elephantopus) part 1: Status of surviving populations. Biol Conserv 6:118–133

Maerz JC, Barrett RK, Cecala KK, Devore JL (2015) Detecting enigmatic declines of a once common salamander in the Coastal Plain of Georgia. Southeast Nat 14:771–784. https://doi.org/10.1656/058.014.0419

Mayer JJ (2009) Biology of wild pigs: Wild pig behavior. In: Mayer JJ, Brisbin IL (eds) Wild pigs: Biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, pp 77–104

McClure ML, Burdett CL, Farnsworth ML et al (2018) A globally-distributed alien invasive species poses risks to United States imperiled species. Sci Rep 8:1–9. https://doi.org/10.1038/s41598-018-23657-z

McCoy JC, Ditchkoff SS, Raglin JB et al (2013) Factors influencing survival of white-tailed deer fawns in coastal South Carolina. J Fish Wildl Manag 4:280–289. https://doi.org/10.3996/032013-jfwm-026

McShea WJ, Schwede G (1993) Variable acorn crops: Responses of white-tailed deer and other mast consumers. J Mammal 74:999–1006

Means DB, Travis J (2007) Declines in ravine-inhabiting dusky salamanders of the Southeastern US Coastal Plain. Southeast Nat 6:83–96

Miller B, Mullette KJ (1985) Rehabilitation of an endangered Australian bird : The Lord Howe Island woodhen Tricholimnas sylvestris. Biol Conserv 34:55–95

Miller RS, Sweeney SJ (2013) Mycobacterium bovis (bovine tuberculosis) infection in North American wildlife: Current status and opportunities for mitigation of risks of further infection in wildlife populations. Epidemiol Infect 141:1357–1370

Miller RS, Sweeney SJ, Slootmaker C et al (2017) Cross-species transmission potential between wild pigs, livestock, poultry, wildlife, and humans: implications for disease risk management in North America. Sci Rep 7:1–14. https://doi.org/10.1038/s41598-017-07336-z

Minot EO, Perrins CM (1986) Interspecific interference competition–nest sites for blue and great tits. J Anim Ecol 55:331–350

Morrison SA (2011) Trophic considerations in eradicating multiple pests. In: Veitch C, Clout M, Towns D (eds) Island invasives: eradication and management. IUCN, Gland, Switzerland, pp 208–212

Ostfeld R, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol Evol 15:269–288. https://doi.org/10.1201/b19209-16

Parkes JP, Ramsey DSL, Macdonald N et al (2010) Rapid eradication of feral pigs (Sus scrofa) from Santa Cruz Island, California. Biol Conserv 143:634–641. https://doi.org/10.1016/j.biocon.2009.11.028

Pavlov PM, Crome FHJ, Moore LA (1992) Feral pigs, rainforest conservation and exotic disease in North Queensland. Wildl Res 19:179–193. https://doi.org/10.1071/WR9920179

Pérez Carusi LC, Beade MS, Miñarro F et al (2009) Relaciones espaciales y numéricas entre venados de las Pampas (Ozotoceros bezoarticus celer) y chanchos cimarrones (Sus scrofa) en el refugio de vida silvestre Bahía Samborombón, Argentina. Ecol Austral 19:63–71

Pérez Carusi LC, Beade MS, Bilenca DN (2017) Spatial segregation among pampas deer and exotic ungulates: A comparative analysis at site and landscape scales. J Mammal 98:761–769. https://doi.org/10.1093/jmammal/gyx007

Perot M (2011) Coping with feral hogs. Louisiana Dep Wildl Fish Wildl Div - Priv Lands

Roemer GW, Coonan TJ, Garcelon DK et al (2001) Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Anim Conserv 4:307–318. https://doi.org/10.1017/s1367943001001366

Rollins D, Carroll JP (2001) Impacts of predation on northern bobwhite and scaled quail. Wildl Soc Bull 29:39–51

Sakai AK, Allendorf FW, Holt JS et al (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Sanders HN, Hewitt DG, Perotto-Baldivieso HL et al (2020a) Invasive wild pigs as primary nest predators for wild turkeys. Sci Rep 10:1–9. https://doi.org/10.1038/s41598-020-59543-w

Sanders HN, Hewitt DG, Perotto-Baldivieso HL et al (2020b) Opportunistic predation of wild turkey nests by wild pigs. J Wildl Manage 84:293–300. https://doi.org/10.1002/jwmg.21797

Sandom CJ, Hughes J, Macdonald DW (2013) Rewilding the Scottish highlands: Do wild boar, sus scrofa, use a suitable foraging strategy to be effective ecosystem engineers? Restor Ecol 21:336–343. https://doi.org/10.1111/j.1526-100X.2012.00903.x

Sanguinetti J, Kitzberger T (2010) Factors controlling seed predation by rodents and non-native *Sus scrofa* in *Araucaria araucana* forests: potential effects on seedling establishment. Biol Invasions 12:689–706. https://doi.org/10.1007/s10530-009-9474-8

Schubert SC, Pesendorfer MB, Koenig WD (2018) Context-dependent post-dispersal predation of acorns in a California oak community. Acta Oecologica 92:52–58

Schuyler PT, Garelon DK, Escover S (2002) Eradication of feral pigs (Sus scrofa) on Santa Catalina Island, California, USA. In: Veitch

CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, Gland, Switzerland and Cambridge, UK, pp 274–286

Scott CD (1973) Seasonal food habits of European wild hogs (Sus scrofa) in the Great Smoky Mountains National Park. University of Tennessee - Knoxville

Shoop R, Ruckdeschel CA (1990) Alligators as predators on terrestrial mammals. Am Midl Nat 124:407–412

Shulse D, Semlitsch D, Trauth KM, Gardner E (2012) Testing wetland features to increase amphibian reproductive success and species richness for mitigation and restoration. Ecol Appl 22:1675–1688

Sicuro FL, Oliveira LFB (2002) Coexistence of peccaries and feral hogs in the Brazilian Pantanal wetland: An Ecomorphological View. J Mammal 83:207–217. https://doi.org/10.1644/1545-1542(2002)083%3c0207:copafh%3e2.0.co;2

Singer FJ, Swank WT, Clebsch EEC (1984) The Richness, abundance and biomass of the arthropod communities on trees. J Wildl Manage 48:464–473. https://doi.org/10.4271/2002-01-2197

Skewes Ó, Rodríguez R, Jaksic FM (2007) Ecología trófica del jabalí europeo (Sus scrofa) silvestre en Chile. Rev Chil Hist Nat 80:295–307

Snow NP, Jarzyna MA, VerCauteren KC (2017) Interpreting and predicting the spread of invasive wild pigs. J Appl Ecol 54:2022–2032. https://doi.org/10.1111/1365-2664.12866

Stegeman LC (1938) The European wild boar in the Cherokee National Forest. Tennessee J Mammal 19:279. https://doi.org/10.2307/1374565

Sweitzer RA (1998) Conservation implications of feral pigs in island and mainland ecosystems, and a case study of feral pig expansion in California. Proc Vertebr Pest Conf 18:26–34. https://doi.org/10.5070/v418110136

Sweitzer R, Van Vuren D (2002) Rooting and foraging effects of wild pigs on tree regeneration and acorn survival in California's oak woodland ecosystems. USDA for Serv Gen Tech Rep 184:219–231

Taylor RB, Hellgren EC (1997) Diet of feral hogs in the Western South Texas plains. Southwest Nat 42:33–39

Taylor RB, Hellgren EC, Gabor TM, Ilse LM (1998) Reproduction of feral pigs in Southern Texas. J Mammal 79:1325–1331. https://doi.org/10.2307/1383024

Taylor GA (2000) Action plan for seabird conservation in New Zealand. Threat Species Occas Publ Arch 233–435

Tolleson DR, Pinchak WE, Rollins D, Hunt LJ (1995) Feral hogs in the rolling plains of Texas: Perspectives, problems, and potential. Gt Plains Wildl Damage Control Work 454:124–128. https://doi.org/10.1111/j.1468-3083.2007.02165.x

Tolleson DR, Rollins D, Pinchak WE, et al (1993) Impact of feral hogs on ground nesting gamebirds. Feral swine a Compend Resour Manag 76–83

Verme LJ (1969) Reproductive patterns of white-tailed deer related to nutritional plane. J Wildl Manage 33:881–887

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science (80-) 277:494–499. https://doi.org/10.1126/science.277.5325.494

Warren RJ, Ford CR (1997) Diets, nutrition, and reproduction of feral hogs on Cumberland Island, Georgia. Proc Fifty-First Annu Conf - Southeast Assoc Fish Wildl Agencies 51:285–296

Wauters LA, Suhonen J, Dhondt AA (1995) Fitness consequences of hoarding behaviour in the Eurasian red squirrel. Proc Biol Sci 262:277–281

Wentworth JM, Johnson AS, Hale PE, Kammermeyer KE (1992) Relationships of acorn abundance and deer herd characteristics in the Southern Appalachians. South J Appl for 16:5–8

Whytlaw PA, Edwards W, Congdon BC (2013) Marine turtle nest depredation by feral pigs (Sus scrofa) on the Western Cape York Peninsula, Australia: implications for management. Wildl Res 40:377. https://doi.org/10.1071/wr12198

Wilcox JT, Van Vuren DH (2009) Wild pigs as predators in oak woodlands of California. J Mammal 90:114–118. https://doi.org/10.1644/08-mamm-a-017.1

Wishart J, Lapidge S, Braysher M et al (2015) Observations on effects of feral pig (Sus scrofa) age and sex on diet. Wildl Res 42:470–474. https://doi.org/10.1071/WR15044