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FEATURED ARTICLE

Hog Heaven? Challenges of Managing Introduced Wild Pigs in Natural Areas

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ABSTRACT: The geographic distribution and size of wild pig (*Sus scrofa*) populations has rapidly expanded in recent years globally, resulting in increased impacts on natural and anthropogenic environments. In this review, we discuss the impacts of wild pigs on native ecosystems in terms of habitat degradation, competition with and depredation of native species, and disease transmission, and highlight recent developments in population control techniques, including areas where further research is required. We also provide an overview of many of the behavioral and demographic characteristics that make it difficult to control wild pigs and additional factors affecting the success of pig management programs in natural areas. Finally, based upon our review of contemporary research and successfully conducted pig eradication campaigns, we provide recommendations for the development of effective wild pig management programs. Overall, we recommend (1) managers implement strategies to detect wild pigs prior to the establishment of stable, breeding populations, (2) management strategies be tailored to specific regional habitat and climatic characteristics, and (3) control be implemented within an adaptive management framework, when possible, to allow further refinement of management objectives and improved characterization of the effects of wild pigs on natural areas.

Index terms: adaptive management, control techniques, invasive species, population management, *Sus scrofa*

INTRODUCTION

Wild boar (*Sus scrofa* L.) are a large ungulate native to Eurasia, and the ancestor of domestic pigs (Guiffra et al. 2000). Wild boar and domestic pigs have been introduced into numerous locations throughout the globe as a source of food, and as a result *S. scrofa* is currently found on all continents except Antarctica and considered nonnative in Australia, North and South America, parts of Africa, and numerous islands (Massei and Genov 2004; Mayer and Brisbin 2008; Barrios-Garcia and Ballari 2012). Due to genetic mixing of wild boar with feral pigs (i.e., domestic pigs that have become feral), these animals are often referred to as wild pigs in their introduced range (Keiter et al. 2016) and, thus, we refer to them as such throughout this paper. In this paper, we discuss management of wild pigs in their introduced range, but draw upon research of wild boar, as the two are closely related.

In their introduced range, wild pig populations have historically become established due to free-ranging husbandry practices, stocking by management agencies for harvest, and escapees from captivity (Mayer and Brisbin 2008). As a result, the contemporary genetic composition of wild pig populations varies greatly across their range (McCann et al. 2014) and is determined by the manner in which the species was introduced (feralized domestic pigs vs. wild boar), although many populations have since undergone introgression by wild boar genetics (Mayer and Brisbin 2008). For example, wild pigs in the United States descend from both feral pigs and wild boar. Domestic pigs were introduced to the U.S. in the 1500s by Spanish colonists and often allowed to roam freely leading to breeding populations of feral pigs; beginning in 1890, wild boar were imported for hunting purposes, and subsequently interbred with feral pigs in many states (e.g., California, Texas, South Carolina; reviewed in Mayer and Brisbin 2008). Since the 1980s, wild pigs and wild boar have undergone substantive expansions in both population size and geographic range globally (Bevins et al. 2014; Massei et al. 2015). For example, in the U.S. the number of states with reported wild pig populations expanded from 17 to 38 between 1988 and 2011 (Bevins et al. 2014). This recent range expansion is thought to be due in large part to their intentional introduction to new areas by pig-hunting enthusiasts (Gipson et al. 1998; Spencer and Hampton 2005; Bevins et al. 2014), increases in availability of anthropogenic food sources (e.g., crops, edible garbage), increased access to preferred habitats, and reduced severity of winters (Melis et al. 2006; Massei et al. 2015; Vetter et al. 2015). Recent research on wild pigs in North America suggests warm temperatures, availability of water, and presence of agriculture might be strong drivers of their geographic distribution (Brook and van Beest 2014; McClure et al. 2015). Similarly, it is suspected that winter severity and vegetative productivity limit wild boar densities in their native range (Melis et al. 2006).

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With recent increases in their abundance and range, there have been concomitant increases in the impacts of wild pigs (Bevins et al. 2014). While economic impacts of introduced pigs can be extensive in agricultural ecosystems (e.g., estimated $1.5 billion/year in the United States alone; Pimental 2007), many effects of pigs occur in natural areas, where they can threaten native habitat, wildlife, and visiting humans. For this reason, wild pigs are frequently managed as an invasive or pest species. Despite intensive management efforts, it has proved to be extremely difficult to eradicate invasive wild pigs from many areas, or successfully control their populations, due to their high fecundity (Morrison et al. 2007) and compensatory reproduction, behavioral adaptation, and logistical constraints associated with different methods of control. Geographically consistent management strategies are further confounded by local conditions including ecosystem type, regulations and laws, and the landscape matrix surrounding the managed area.

In this article, we review some of the negative impacts of wild pigs in natural areas and recent developments in, and limitations of, control techniques to provide managers with information regarding effects of wild pigs and methods of mitigation and control. We also discuss specific challenges that wild pigs pose to managers due to their ecology and behavior, and additional factors affecting success of management programs in natural areas. It is our hope that this information can be used to help guide the development of management programs to allow more effective control of wild pigs in natural areas where they may pose a serious threat to native species and ecosystems.

Impacts of Wild Pigs on Natural Areas

The impacts of wild pigs on natural ecosystems can be broadly separated into three categories: (1) habitat degradation; (2) competition with and predation of native species; and (3) the spread of infectious diseases, all of which are well reviewed in Barrios-Garcia and Ballari (2012). These impacts are, however, likely to vary among ecosystems based upon their susceptibility to disturbance, necessitating further study across a range of ecosystem types. While the risks wild pigs pose to natural and anthropogenic ecosystems are well recognized, further development of methods to quantify the impacts of wild pigs on natural areas is necessary (e.g., Felix et al. 2014).

Habitat Degradation

Invasive wild pigs are considered “ecosystem engineers” as they can severely alter the composition of native habitats and resources available to other species (Boughton and Boughton 2014). Many of the negative impacts of wild pigs occur as a result of rooting, a behavior in which wild pigs push their noses through the soil in search of food items, effectively tilling areas where rooting occurs to a maximum recorded depth of 120 cm (Figure 1; Mayer 2009). Rooting can have a multitude of ecosystem-level effects including altering soil chemistry, arthropod communities, and vegetative composition (reviewed in Barrios-Garcia and Ballari 2012). It is believed that rooting by pigs may facilitate invasion by, and establishment of, nonnative plant species (Cushman et al. 2004; Fujinuma and Harrison 2012; Oldfield and Evans 2016), and there is evidence that rooting can promote positive-feedback relationships between wild pigs and certain native plant species in their introduced range (e.g., Carolina redroot (*Lachnanthes caroliniana* (Lam.) Dandy); Boughton and Boughton 2014; Bankovich et al. 2016).

Due to their lack of sweat glands, wild pigs thermoregulate behaviorally more than physiologically (Baber and Coblentz 1986) and are frequently associated with wetlands and riparian areas, which can act as thermal refugia (Choquenot and Ruscoe 2003). For this reason, their impacts on wetland areas may be particularly severe.

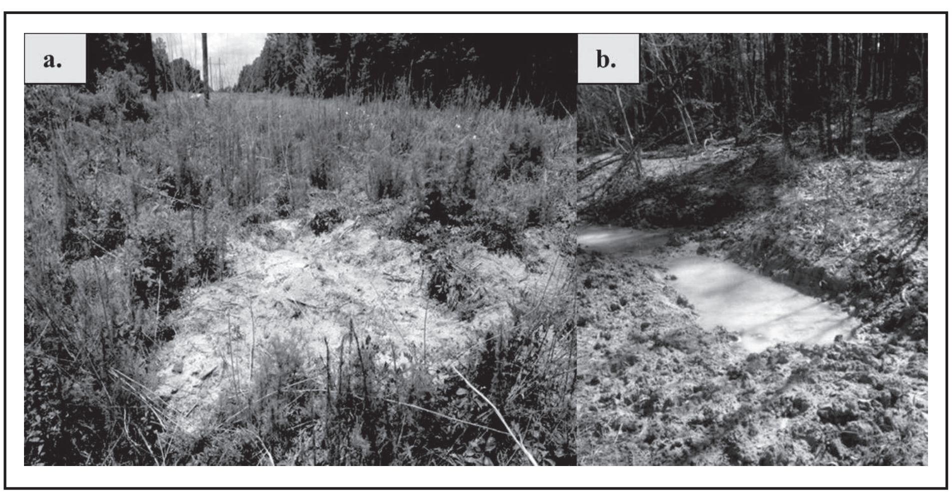

Figure 1. Wild pig (*Sus scrofa*) rooting (a) and wallow (b) at the Savannah River Site, South Carolina, USA, 2016.

For example, wallowing behavior and other habitat damage by wild pigs, can negatively affect salamander populations (Maerz et al. 2015) and degrade water quality, leading to declines in diversity and abundance of freshwater mussels and insects (Kaller and Kelso 2006). Similarly, wild pigs may cause anoxic conditions and high pH levels and destroy aquatic macrophytes in lagoons (Doupé et al. 2010).

In forested ecosystems, the presence of wild pigs is frequently associated with reduced vegetative cover and decreased regeneration of certain tree species (see Campbell and Long 2009 for review). For example, Cole and Litton (2014) documented decreased vegetative cover, reduced diversity of ground-rooted plants, and lower abundance of plant species of conservation concern in areas of pig presence, when compared to areas where pigs had been removed. Similarly, Barrios-Garcia et al. (2014) found reduced plant biomass and altered plant community composition and structure in areas inhabited by invasive wild pigs. In contrast to Cole and Litton (2014), Brunet et al. (2016) found short-term increases in species richness following rooting by wild boar in their native range, although they suggest long-term losses might be expected.

Research in grassland ecosystems also suggests pigs may cause shifts in plant community composition (Bankovich et al. 2016) and the reduction in abundance or species richness of native species due to the speed at which invasive plants may colonize areas disturbed by pigs (Tierney and Cushman 2006). This is corroborated by the work of Oldfield and Evans (2016), which suggests wild pigs promoted the spread of yellow nutsedge (*Cyperus esculentus* L.), an invasive plant species, in an island ecosystem. Further investigation into whether wild pigs facilitate dispersal of plant species in general, and invasive species in particular, through ingestion and deposition of seeds in scat or entanglement in hair is necessary.

Competition with and Depredation of Native Species

The broad diet of this species also brings it into conflict with native species through active predation and competitive interactions. Wild pigs and wild boar exhibit a highly plastic diet (see Ballari and Barrios-Garcia 2014 for review), which greatly reduces the potential for food resource limitation and is an underlying factor contributing to their success throughout much of their nonnative range. The diet of wild pigs is dominated by vegetation (e.g., Adkins and Harveson 2006; Ditchkoff and Mayer 2009; Schlichting et al. 2015), but depredation of vertebrates is common, particularly in their introduced range (see Campbell and Long 2009 and Barrios-Garcia and Ballari 2012 for review). Pigs appear to commonly scavenge (Turner 2015), and likely hunt, other vertebrate species, particularly fossorial or semi-fossorial animals, which may be captured during rooting behavior (Wilcox and Van Vuren 2009). Wild pigs also have been observed actively depredating amphibians (Jolley et al. 2010), and are known to depredate nests of reptiles (Cruz et al. 2005) and ground-nesting birds (Rollins and Carroll 2001), a behavior that is thought to have led to the extinction or extirpation of a number of island species (Cruz et al. 2005).

In addition to direct depredation, pigs may compete with native wildlife species for high-value food resources, such as acorns (Sweitzer and Van Vuren 2002), which may adversely affect local populations. Wild pigs have been reported to exclude white-tailed deer (*Odocoileus virginianus* Zimmerman) from foraging on acorns (Taylor and Hellgren 1997) and bait piles (C. Crank and R. Boughton, University of Florida, unpub. data). Few studies have empirically compared dietary overlap between wild pigs and native species (but see Ilse and Hellgren 1995), and, thus, further investigation into this topic is necessary to assess potential impacts of competition on native wildlife. In particular, it seems likely that extensive use of hard mast by wild pigs (e.g., Schlichting et al. 2015) might lead to competition with native game species, such as squirrels (*Sciurus* spp. L.), wild turkey (*Meleagris gallopavo* L.), black bears (*Ursus americanus* Pallas), and deer (*Odocoileus* spp.).

Transmission of Infectious Diseases

Wild pigs and wild boar also can carry a number of diseases that can be transmitted to livestock, wildlife, and humans (see Ruiz-Fons et al. 2008 and Barrios-Garcia and Ballari 2012 for review). The greatest potential for interspecific transmission of these diseases in natural areas may occur where the environment favors aggregation of wild pigs and other species, such as localized water (Carrasco-Garcia et al. 2015; Payne et al. 2015) or food resources (Campbell et al. 2013a), although further study of intraspecific contact rates is necessary (Pepin et al. 2016). Similar patterns might be expected in prairies, deserts, or comparable ecosystems where water resources, thermal refugia, or highly preferred food resources are limited, constraining the distribution of wild pigs. Transmission of certain diseases carried by wild pigs to humans, such as brucellosis, may occur due to unsafe field dressing or preparation of harvested pigs (Centers for Disease Control 2012). Recent research has also highlighted the threat that this species may pose to humans through its involvement in vehicle collisions (Beasley et al. 2013; Sáenz-de-Santa-María and Tellería 2015; Thurfjell et al. 2015). These threats to human and environmental health emphasize the necessity of understanding the ecology of this species to better assess potential risks and develop effective management regimes.

Wild Pig Ecology and Behavior

Wild pigs have a number of ecological and behavioral characteristics that predispose them to being successful invaders. These characteristics also likely influence outcomes of management and control programs for this species. Knowledge of basic wild pig ecology will allow managers to better take advantage of the characteristics of this animal and, therefore, more effectively manage populations.

In terms of social structure, female wild pigs often travel with related females and their offspring in groups, known as sounders, while adult males exhibit more solitary behavior (Gabor et al. 1999). This results in differing movement and behavioral strategies that can complicate management or monitoring of this species. These differing strategies may bias capture rates of wild pigs in live-traps; studies have suggested that females and juveniles are often more frequently captured than adult males (e.g., Choquenot et al. 1993; Williams et al. 2011). There is some evidence of territoriality among wild pig sounders (Sparklin et al. 2009), although additional studies quantifying home range use and potential territoriality in wild pigs are needed. Rates of recolonization by wild pigs following removal of a sounder are unknown and research into this topic will allow increased inference about efficacy of eradication programs. Further research is also necessary to assess independence of animals within and among sounders, as this topic could have implications in the efficacy of management programs, use of population monitoring methods, and spread of infectious diseases.

Wild pigs have an exceptionally high reproductive rate among large mammals, increasing the difficulty in controlling invasive populations. Wild pigs can reproduce at weights of ~25 kg, often before attaining one year of age (Dzieciolowski et al. 1992), and similar patterns have been observed in wild boar (Servanty et al. 2009). Moreover, the average number of piglets produced in a single litter can vary from 4.8 to 7.5 (Ditchkoff et al. 2012). Under favorable conditions (e.g., high food resources, moderate climate), wild pigs are able to reproduce twice in a single year or up to three times in 14–16 months (Dzieciolowski et al. 1992), further increasing the potential growth of populations, although few studies have extensively monitored the reproductive ecology of wild pigs in their introduced range. Such reproductive rates are elevated in comparison with those of wild boar due to the presence of domestic pig genetics in many wild pig populations (Fulgione et al. 2016). Timing of reproduction in pigs seems to be dependent on regional conditions: certain populations exhibit birth pulses (e.g., Baber and Coblentz 1986; Canu et al. 2015) while others exhibit year-round reproduction (Dzieciolowski et al. 1992; Ditchkoff et al. 2012).

In the native range of *S. scrofa*, a population under higher hunting pressure was found to reproduce at earlier ages and produce greater numbers of piglets per litter than a population under lower harvest pressure, indicating compensatory responses to harvest are likely (Servanty et al. 2011). Similarly, it has been suggested that greater rates of reproduction and immigration might compensate for increased harvest of wild pigs in the southeastern United States (Hanson et al. 2009). Genetic data provide further evidence of immigration and quick recovery in wild pig populations, as multiple studies have failed to find evidence of genetic impacts on pig populations, such as bottlenecks, following intensive culling efforts (Cowled et al. 2006; Delgado-Acevedo et al. 2013). There is also evidence that in areas of high hunting pressure, the birth date of wild boar may shift to allow earlier reproduction by subadults (Gamelon et al. 2011). Population growth of this species seems to be driven, in part, by pulsed resources (e.g., tree mast), which can allow increased reproduction and survival (Baber and Coblentz 1986; Bieber and Ruf 2005; Ditchkoff et al. 2012; Vetter et al. 2015). This may require flexibility in wild pig management programs to account for differing habitat conditions that drive population growth. For example, in an expected mast year and following seasons, managers might plan to devote greater resources to controlling pigs to deal with increased populations.

In the United States, the greatest cause of mortality reported in wild pigs is harvest by humans (Gabor et al. 1999; Hayes et al. 2009), although vehicle collisions are likely increasing as a cause of death (Beasley et al. 2013). Once a wild pig or boar reaches adult size, few animals are able to prey upon it, and those that can are often uncommon (Barrios-Garcia and Ballari 2012; Ballari et al. 2015). In the United States, the geographic range of many apex predators capable of depredating adult pigs (e.g., grizzly bears (*Ursus arctos* L.), gray wolves (*Canis lupus* L.), mountain lions (*Puma concolor* L.)) only slightly overlaps the geographic range of wild pigs; although wild pigs represent a common diet item of the endangered Florida panther (*Puma concolor coryi*; Maehr et al. 1990). The work of Melis et al. (2006) goes further in suggesting that across Europe, wolves, a primary predator of wild boar, have little effect in regulating wild boar density despite significant range overlap. Most studies of wild boar and wild pigs suggest survival of this species is higher for adults than juveniles, and often higher for females than males (Toïgo et al. 2008; Hanson et al. 2009). In general, known-fate studies of juvenile survival of this species are lacking, despite the suggestion that these age classes greatly contribute to population trajectory (Bieber and Ruf 2005; Servanty et al. 2009; Mellish et al. 2014). Knowing this, managers might target juveniles for control when trying to reduce population growth. In particular, in years of favorable habitat conditions, such as mast years, targeting juveniles will likely have the greatest effect on population growth, while targeting adult females will be more effective in years of unfavorable conditions (Bieber and Ruf 2005).

In general, wild pigs are recognized for their intelligence and adaptability, making their control more difficult. Following hunting pressure, wild pigs and wild boar often become nocturnal (West et al. 2009; Tolon et al. 2009) requiring additional effort to continue hunting campaigns. There also is evidence that wild boar shift their home ranges toward areas with lower hunting pressure in addition to shifting temporal activity patterns (Tolon et al. 2009). It is widely thought that an individual pig may become trap-wary, or educated, when it escapes capture in a trap, however little published data currently exists to support or refute this supposition, necessitating future evaluation. Anecdotal evidence suggests that in certain cases, adult wild pigs captured in traps may be recaptured in traps at a later date, although short-term avoidance is often noted (Figure 2; Beasley et al., University of Georgia, unpub. data, Boughton et al., University of Florida, unpub. data).

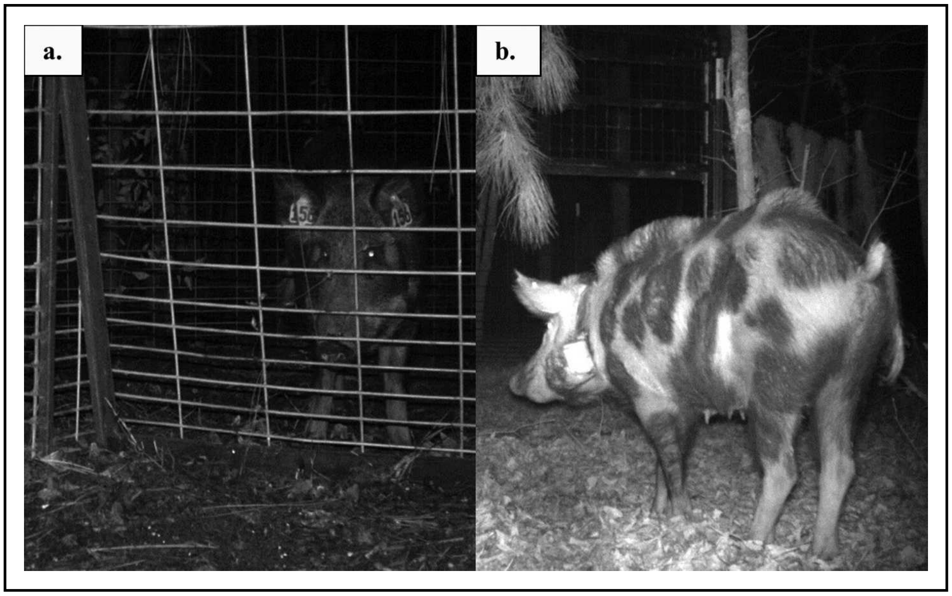

Figure 2. Ear-tagged wild pig recaptured in a corral trap (a) and a collared wild pig entering a trap (b) at the Savannah River Site, South Carolina, USA, 2015–2016.

Developments in Wild Pig Population Control Techniques

Methods of controlling wild pigs have been extensively reviewed in Campbell and Long (2009), West et al. (2009), and Massei et al. (2011). For this reason, we only briefly review methods, touch on new developments, and mention a handful of topics we believe merit further investigation. Without control, wild pig populations are likely to increase in areas of favorable conditions (e.g., Levy et al. 2015), causing greater harm to native ecosystems. Overall, we support the recommendation of Bengsen et al. (2014) that, when feasible, managers design control programs in a manner that generates valid data to establish causal relationships between pig density and the effects of pigs on ecosystems as well as the honing of management protocols (e.g., Krull et al. 2016). Use of this adaptive management approach in control programs will improve the ability of managers to set population management goals to achieve specific conservation or damage mitigation outcomes, such as reduction of negative impacts below a targeted threshold. The management techniques discussed below will likely be most effective in conjunction with one another, due to the ability of wild pigs to adapt to control methods, and, therefore, multiple control techniques should be implemented when possible (McCann and Garcelon 2008; Massei et al. 2011).

Live-Trapping

Use of trapping and euthanasia as a method to mitigate negative impacts of pigs is widely practiced, and has been reviewed in Choquenot et al. (1993) and West et al. (2009). Trapping can effectively reduce the abundance of local populations of pigs, but may be infeasible as an effective control method at broader spatial scales due to cost of implementation (Massei et al. 2011; Bengsen et al. 2014). Recent research into pig trapping has focused on comparisons of the efficacy of different trap and gate types. This research suggests corral traps generally result in higher capture rates of pigs compared to box traps (Williams et al. 2011), that gate width does not affect corral trap success (Metcalf et al. 2014), that gate style (continuous-catch, or root, gate versus side-swing gate) does not influence capture of adult pigs, but may influence juvenile captures (Long and Campbell 2012), and that continuous-catch gates are not likely to catch more pigs than single-catch gates (Smith et al. 2014).

Recently, corral traps that incorporate a camera system and allow remote activation of the gate (e.g., via cellphone) have become commercially available and are now used in some management programs (Figure 3). These traps may be advantageous as managers can avoid capture of non-target species and forestall capture of pigs until they know the entire social group, or sounder, is present in the trap; this will avoid educating uncaptured members of the group, which might cause them to become trap-shy (Gaskamp 2012). The remote operation of these traps may also be advantageous in that they fulfill animal care requirements for trap checks without requiring expenditures of funding to check traps in person. However, cost-effectiveness and overall efficacy of remotely operated traps in wild pig control has yet to be fully evaluated. It has also been suggested that drop-nets and traps mounted above bait piles may be an effective alternative to conventional trapping methods, as pigs may acclimate to them more quickly or disregard their presence (Gaskamp 2012). Success of trapping may vary seasonally as a function of the amount of food resources present on the landscape and it is recommended that traps be pre-baited prior to the trapping period to increase overall success (West et al. 2009). Effectiveness of live-trapping is also likely to vary based upon habitat conditions that favor, or do not favor, aggregation of wild pigs (discussed below).

Figure 3. Examples of remotely activated corral traps and captured wild pigs in a remotely operated trap at the Savannah River Site, South Carolina, USA, 2015–2016.

Ground-Based Hunting

Hunting may be a situationally effective technique to assist in population control of wild pigs in that it can be selective, allowing problem animals and those likely to have the greatest impact on the population trajectory to be targeted; however, hunting alone has proven to be ineffective at controlling pig populations in many situations (Campbell and Long 2009; Massei et al. 2015). Hunting is likely most effective when performed at night using appropriate equipment, such as infrared or thermal scopes, due to the tendency of wild pigs to become more nocturnal following hunting pressure (West et al. 2009). In certain areas (e.g., Alabama, USA) it is also legal to hunt pigs using dogs, although regulations on the use of dogs to capture pigs vary. Ground-shooting and hunting with dogs can be used to remove animals that may be educated or trap shy, and it is possible that high shooting pressure and hunting with dogs could deter pigs from damaging specific areas of conservation concern (Caley 2010). This hypothesis has not been extensively tested (but see Tolon et al. 2009); if true, it could provide managers with an important technique to protect areas considered especially valuable or sensitive to disturbance. In addition, Judas animals can be employed to improve the success of control efforts (e.g., McCann and Garcelon 2008). Judas pigs are animals that are live-captured, radiomarked, and released, in the hopes they will lead the manager to other individuals that can be lethally removed, due to the social nature of pigs (Campbell and Long 2009). Use of Judas animals by management agencies is becoming more common, particularly in areas where wild pigs have been recently introduced and are found at low population densities. Ground-based hunting methods, including the Judas technique, are further reviewed in Campbell and Long (2009), West et al. (2009), and Massei et al. (2011).

Aerial Gunning

The technique of shooting wild pigs from helicopters is also well reviewed in Massei et al. (2011) and Campbell and Long (2009). Overall, aerial gunning can be effective at quickly removing large numbers of pigs, making it a good option for control of disease outbreaks and high density populations, and is widely practiced in areas of sparse vegetation (Massei et al. 2011). Little research has been performed on the efficacy of aerial shooting in controlling wild pigs, although research by Campbell et al. (2010) supports earlier work suggesting wild pigs do not expand core areas or home ranges following aerial gunning, although they may modify their behavior during periods of shooting.

Toxicant and Contraceptive Use

Oral toxicants can be effective in reducing or suppressing wild pig populations and have been applied in Australia, New Zealand, and on a number of islands (e.g., Hone 1983, Cruz et al. 2005). Toxicants may be effective in removing individuals that are trap-shy, and aerial distribution of treated baits can allow application of this technique over a broad spatial area in a relatively cost-effective manner, assuming acceptable levels of non-target effects (Hone 1983; Massei et al. 2011). In some countries, such as the United States, there is not yet a toxicant approved for use in wild pigs (Campbell et al. 2013b), ruling out this technique until further development occurs. As part of the development of an acceptable toxicant in the U.S. and to decrease potential bycatch of non-target species, recent research has focused on toxicant type (Cowled et al. 2008), species-specific attractants, and bait matrices (Campbell and Long 2007; Campbell and Long 2008; Lapidge et al. 2012; Snow et al. 2016), and species-specific bait delivery systems (Ballasteros et al. 2009; Campbell et al. 2013b; Ferretti et al. 2014).

Contraceptives are often considered a humane management technique and might be applied in areas where lethal control is infeasible due to laws and regulations or in conjunction with lethal removal programs (Massei et al. 2011). Little research has been published on use of either oral or injectable contraceptives as a technique for reducing wild pig populations (see Massei et al. 2011 for review), although numerous studies have evaluated the utility of contraceptives to control deer populations (e.g., Seagle and Close 1996; Rudolph et al. 2000). Use of an injectable immunocontraceptive vaccine has been evaluated in wild boar (Quy et al. 2014), with the conclusion that it might be appropriate for use in managing populations, although development of an oral-delivery mechanism would improve the utility of this tool. Work by Delgado-Acevedo et al. (2010) suggests female wild pigs mate with multiple males, and therefore, contraceptive treatments targeting males may be less effective than those targeting females. However, neither toxicant nor contraceptive use is likely to fully suppress wild pig populations and these techniques will need to be used in conjunction with other management techniques for greatest efficacy.

Factors Affecting Management of Wild Pigs in Natural Areas

The difficulties in managing wild pig populations will often be area specific and affected by a variety of factors, including the probability of detecting pigs, implementation of laws and regulations regarding public interaction with pigs, proximity to established pig populations, habitat composition of the natural area, and composition of the surrounding landscape matrix. Unfortunately, the multitude of these factors means there is no "silver bullet" when it comes to managing wild pigs. Below we discuss how these factors can influence wild pig management programs and provide recommendations based upon successful eradication programs that might facilitate control of this invasive species.

Due to high reproductive rates, it is likely that once wild pigs are fully established in an area (i.e., have stable home ranges and are actively reproducing), they will be extremely difficult to eradicate. For this reason, it is important for managers to detect the presence of pigs as soon as possible following their introduction. Pig-free locations near existing pig populations are likely at greatest risk of colonization simply due to spatial proximity. In these locations, campaigns to educate the public about pig sign and request that they contact the managing organization if pig presence is suspected may increase the probability of detecting pigs prior to establishment of stable breeding populations. Campbell and Long (2009), Mayer (2009), and West et al. (2009) provide valuable descriptions and photographs of pig sign that might be incorporated in education programs. New techniques to assess the presence of wild pigs following eradication efforts, which may also bolster early detection efforts, are under development; these include environmental DNA (eDNA) testing (Williams 2016) and use of dogs trained to scent invasive wild pigs (C.R. Hicks and J.G. Martin, USDA Animal and Plant Health Inspection Service, Wildlife Services, pers. comm.).

The recent geographic expansion of wild pigs is thought to be due partially to intentional, and often illegal, introductions to new areas for hunting purposes (Gipson et al. 1998; Spencer and Hampton 2005; Bevins et al. 2014), meaning managers of natural areas in locations far from existing wild pig populations should still be aware of the risk of wild pig invasion and consider informal monitoring for pig sign. Managers of public land should be particularly aware of the possibility of illegal introductions of wild pigs, as these lands may be targeted due to public hunting access. To combat the problem of intentional translocations, in Australia and the United States, many states have created laws making it illegal to possess, transport, or release wild pigs and created phone hotlines to allow reports of illegal releases (e.g., Kentucky Department of Fish and Wildlife Resources 2014). Unfortunately, due to the secretive nature of these illegal actions, gathering data on the efficacy of such laws in preventing translocations is extremely difficult, despite their importance. Managers also should think carefully before incorporating public hunting into control programs for wild pigs as when managing agencies encourage hunting to control populations, pig-hunting gains popularity, and may lead to increased human movement of animals to establish new huntable populations (Bevins et al. 2014). For this reason, in the successful eradication campaign conducted in New York State, all hunting of pigs was outlawed to prevent this possible outcome and to minimize potential disturbance to trapping efforts (New York State Department of Environmental Conservation 2014). In general, public outreach emphasizing the numerous negative impacts of wild pigs is important to effectively manage this invasive species, particularly where colonization is recent. In Ohio, where presence of wild pigs is relatively novel, members of the general public have been reported visiting natural areas simply to find wild pig sign, and are unlikely to understand the dangers of wild pig establishment (C.R. Hicks and J.G. Martin, pers. comm.).

Success of wild pig management programs will depend largely upon the landscape matrix surrounding the natural area. One potential obstacle in control of wild pigs is the high probability of recolonization from surrounding areas, as immigration may effectively compensate for the effects of intense harvest, and, thus, reduce efficacy of control (Hanson et al. 2009). Therefore, control will be most effective when the possibility of recolonization is lowered, either through natural circumstances, such as in the successful eradication on Santiago Island (Galapagos archipelago; Cruz et al. 2005), or intentional implementation via use of pig-proof fencing (Morrison et al. 2007; McCann and Garcelon 2008; Parkes et al. 2010; Lavelle et al. 2011). In the successful eradication campaigns on Santa Cruz Island and at Pinnacles National Monument, California, pig-proof fences were installed and maintained to prevent recolonization of focal management areas by wild pigs, although at high cost (McCann and Garcelon 2008; Parkes et al. 2010). Cooperation with stakeholders surrounding the focal area will also be necessary to effectively control wild pig populations. If the area managed is surrounded by private land where wild pigs are not controlled, it might simply act as a vacuum, constantly attracting new pigs to replace removed individuals, whereas if pressure is applied across the landscape, local reductions may be more permanent (e.g., Engeman et al. 2014). In addition, if private lands surrounding the focal area engage in baiting of wildlife for hunting purposes, efficacy of trapping in the focal area can be reduced due to the overabundance of food resources on the landscape. Wild pig presence is often associated with agricultural lands (Brook and van Beest 2014; Allwin et al. 2015) and the damages they cause to crops and their potential to transmit infectious diseases to livestock should motivate owners of agricultural lands to support management programs and/or implement control on their property.

Management of wild pigs should be tailored to local habitat and climatic conditions for most effective implementation. In landscapes such as prairies and deserts where water sources are limited, control at these sources will likely be most effective, particularly during warmer temperatures. Similarly, trapping in the southeastern United States is often most effective in riparian areas where pig activity is often concentrated. This likely also applies regarding food resources in areas of marginal habitat and during seasons of food limitation, although the high plasticity of wild pig diets is likely to decrease the magnitude of this effect. In areas where water resources do not seem to limit pig populations, wooded ridges may act as movement corridors for multiple sounders of pigs (C.R. Hicks and J.G. Martin, pers. comm.). In open habitat types, such as marshes, prairies, and deserts, aerial shooting can be an effective method to quickly reduce high densities of wild pigs, while in areas dominated by dense vegetative cover, trapping may be more effective. Due to differences in habitat use across geographic regions, effective scouting, such as through the use of baited trail cameras, can be invaluable in informing the spatial focus of control efforts. In northern regions, wild pigs and wild boar typically exhibit more pronounced birth-pulses reflecting availability of food resources (Servanty et al. 2009) than in more southern latitudes (Ditchkoff et al. 2012), and implementation of population control prior to birth pulses may result in greater effectiveness.

CONCLUSIONS

Wild pig populations can have severe impacts on anthropogenic and natural areas, and their already broad geographic distribution is rapidly increasing throughout the globe. Management of this species is therefore necessary in many areas to reduce or mitigate impacts and decrease risks posed to wildlife, livestock, and human health. Unfortunately, a wide variety of demographic and behavioral characteristics make control of this invasive species extremely difficult. Therefore, flexible management programs should be implemented to take advantage of local habitat and climatic conditions in controlling this species and substantive effort should be put into detecting and controlling wild pigs before populations are fully established. Additionally, control of pigs will likely be most effective when managers implement multiple control techniques, and do so in an adaptive management framework to allow refinement of management strategies to meet specific goals. Effective management of this invasive species also will require the support of scientific research, and we have highlighted a number of areas of wild pig ecology and management requiring further study. Public outreach to emphasize the negative effects of wild pigs and collaboration with private landowners is also essential to prevent intentional translocations and more effectively implement control of wild pig populations. Furthermore, regardless of the method of control used, cooperation among agencies and organizations responsible for management of pigs is vital to the success of control programs. With cooperation between researchers, managers, and public stakeholders, we can begin to better understand this species and through its management, help conserve the natural areas it threatens.

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