



---

U.S. Department of Agriculture  
Animal and Plant Health Inspection Service  
Wildlife Services

U.S. Government Publication

---



Commentary

# Research Priorities for Managing Invasive Wild Pigs in North America

JAMES C. BEASLEY,<sup>1</sup> *Savannah River Ecology Laboratory, Warnell School of Forestry and Natural Resources, University of Georgia, PO Drawer E, Aiken, SC 29802, USA*

STEPHEN S. DITCHKOFF, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

JOHN J. MAYER, *Savannah River National Laboratory, SRNS LLC, Savannah River Site, Aiken, SC 29808, USA*

MARK D. SMITH, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

KURT C. VERCAUTEREN, *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521-2154, USA*

**ABSTRACT** With recent increases in distribution and numbers of feral pigs (*Sus scrofa*; invasive wild pigs) in North America, there has been a concurrent increase in the ecological and economic effects they have had on native and anthropogenic ecosystems. Despite the amplified interest in invasive wild pig research, there remains a significant knowledge gap regarding their basic biology and ecology, the scope of the damage they cause, and the efficacy of many control strategies. Such information is important to support the successful management of invasive wild pigs throughout North America and other areas. In 2016, members of the National Wild Pig Task Force met and developed a set of research priorities to aid in effective management of invasive wild pigs. These research priorities identify 4 topical areas where increased effort and science is most needed to manage invasive wild pigs: biology and ecology, economic and ecological damages, control strategies, and education and human dimensions, with particular emphasis on areas where specific data gaps remain within each topical area. Resolution of such knowledge deficits would advance the understanding of invasive wild pig ecology, enabling more efficient and effective management of this species. © 2018 The Wildlife Society.

**KEY WORDS** control, damage, ecological effects, feral pig, feral swine, invasive species, management, *Sus scrofa*, wild pig.

Since the late 1980s the geographic distribution of feral pig (*Sus scrofa*; invasive wild pig; Keiter et al. 2016) populations have expanded, resulting in increased ecological and economic effects (Barrios-Garcia and Ballari 2012, Keiter and Beasley 2017). For example, in the United States the number of states reporting invasive wild pig populations increased from 18 to 35 between 1982 and 2016 (Corn and Jordan 2017). Concurrently, the scale, frequency, and types of damage caused by invasive wild pigs have rapidly expanded, causing billions of dollars in losses annually in the United States (Pimental 2007). Given the extent of these effects, combined with potential disease risks, including introduction and dissemination of foreign animal diseases, invasive wild pigs have emerged as a priority of national concern for extensive and coordinated control (U.S. Department of Agriculture 2015). Although the number of researchers studying invasive wild pigs and breadth of peer-reviewed literature has increased concomitantly with expansion of invasive wild pig populations, there remains a

paucity of data on their basic biology and ecology, damage they cause, and efficacy of options to control them. Such data are essential to develop robust management strategies to reduce damages associated with this destructive invasive species, and thus there is an important need to establish research priority areas to guide invasive wild pig research and management efforts.

To address this growing ecological and economic issue, over the last several years there has been a surge in organized efforts throughout North America to better understand and disseminate information on issues associated with invasive wild pigs (e.g., >40 local- and state-level invasive wild pig working groups or task forces have been established). Of significance, in 2014 the U.S. Department of Agriculture (USDA) initiated a nationally coordinated damage management program, the National Feral Swine Damage Management Program, to address issues associated with invasive wild pigs (USDA 2015). This program has served as a catalyst for coordinating and implementing invasive wild pig management at a national scale. Establishment of an invasive species management program at a national scale is rare in the United States and exemplifies the extent of invasive wild pig issues.

Received: 1 July 2017; Accepted: 11 January 2018

<sup>1</sup>E-mail: [beasley@srel.uga.edu](mailto:beasley@srel.uga.edu)

Further, during 2016 the National Wild Pig Task Force (NWPTF) was established, representing a technical, scientific, and leadership alliance of conservation partners working to address issues associated with invasive wild pig populations in North America. On 4 March 2016 several members of this task force met to identify fundamental gaps in knowledge of the ecology and management of invasive wild pigs. The outcome of this meeting was a consensus set of research priorities within 4 topical areas: biology and ecology, economic and ecological effects, control strategies, and education and human dimensions. These priorities were reviewed by members of the NWPTF research sub-committee who provided additional input. In this paper we highlight research recommendations within these 4 topical areas that represent priority areas for invasive wild pig research. Further advancement of research within these areas will help fill important knowledge gaps in the understanding of the ecology and management of invasive wild pigs, ultimately aiding in reducing damages associated with this rapidly expanding and destructive invasive species.

## RESEARCH PRIORITIES

### Biology and Ecology

Effective management strategies for wildlife pest species depend on a solid understanding of the biology and ecology (e.g., behavior, diet, productivity patterns) of the species. For example, understanding of physiology is essential to develop safe and effective toxicants and contraceptives. Similarly, effective visual, auditory, and chemical deterrents can only be developed with an understanding of sensory function (Blackwell and Fernández-Juricic 2013). Invasive wild pigs are no different than any other species in this regard. Fortunately there are some aspects of invasive wild pig biology that we know more about than most free-ranging species. Physiologically, we understand pigs because of their value as a food commodity and their use as a surrogate in medical research for humans, although currently little field data exist for wild populations (especially in arid or cold environments). Similarly, the hormonal foundation, gestational requirements, fetal development, and many other aspects of reproduction have been discovered from domestic pigs (Comer and Mayer 2009).

However, invasive wild pig populations in the United States are primarily hybrids between free-ranging domestic pigs and wild boar (Keiter et al. 2016) and the influence of the natural environment on their physiology and reproductive parameters is poorly understood. Numerous studies (Comer and Mayer 2009) have reported basic reproductive parameters including litter size and breeding season dates for invasive wild pig populations, although substantial data gaps remain. Furthermore, it is almost universally accepted that animal density and natural perturbations in environmental conditions, both of which could influence food availability and body condition, should affect reproduction (Choquenot 1991). To date though, there have been few studies that have examined this aspect of reproduction in invasive wild pigs (Ditchkoff et al. 2012). Similarly, data are needed on the

influence of agricultural food resources and varying mast availability on reproductive ecology and population dynamics of invasive wild pigs.

Our understanding of population dynamics of invasive wild pigs also is incomplete, especially considering the historical focus of the wildlife management field on understanding basic population parameters (e.g., age- and sex-specific survival, cause-specific mortality). Recent efforts to examine movement patterns of invasive wild pigs have provided some survival rate data, yet few studies have thoroughly examined survival (Keiter et al. 2017*b*), data essential to population modeling and development of efficient control strategies. Similarly, there are few data on dispersal and population growth rates in invasive wild pigs, even though such data are fundamental to our understanding of rates of population expansion and development of appropriate control strategies.

On an even more basic level, biologists have a limited understanding of why density varies, by how much, and how density may influence dispersal or control strategies, although Lewis et al. (2017) investigated how biotic and abiotic factors influence invasive wild pig density across their global distribution. We also have an important need for accurate techniques to determine density. Numerous studies have used complex statistical techniques to assess density of invasive wild pigs (Hanson et al. 2008, Ebert et al. 2012), yet most are too quantitatively complex, too costly, and too time consuming to be effective in most situations. Development of simple, yet accurate tools to assess density would enable managers to more efficiently respond to needs for invasive wild pig control (Davis et al. 2017, Keiter et al. 2017*a*).

Control strategies for any species depend on an understanding of their spatial ecology and resource selection patterns. Such data also are essential to elucidate the potential for invasive wild pigs to invade and sustain populations outside their existing range. Spatial ecology and resource selection also will influence the area affected by control strategies, and the specific strategies that are selected (e.g., Judas pig method [where individuals are radio-tagged and used to lead managers to more invasive wild pigs], whole sounder removal). One aspect of their spatial ecology that is poorly understood is whether invasive wild pigs exhibit territoriality. Although some authors have reported evidence of territoriality among female social groups (Ilse and Hellgren 1995, Gabor et al. 1999, Sparklin et al. 2009) others have reported a lack of territoriality in females (Boitani et al. 1994). Such discrepancies reflect the behavioral plasticity of invasive wild pigs and suggest spatial ecology can vary across their range. Factors such as density of pigs and land-cover and land-use characteristics (e.g., agriculture, forest) may influence spatial dynamics of invasive wild pigs, but there is almost no information available regarding these relationships. Thus, holistic studies of invasive wild pig spatial ecology incorporating datasets from across the species' range would be beneficial (Kay et al. 2017). Unfortunately, without a solid understanding of how far pigs range, or the spatial strategies they use, it is almost impossible to develop effective control strategies, or predict for how long control efforts may be effective after their cessation.

Invasive wild pigs are social, large mammals and their social nature could be used to inform how we determine densities and implement control strategies. However, social dynamics is probably the least understood aspect of the species' ecology. In some areas control strategies for invasive wild pigs have begun to evolve from a strategy that focuses on maximizing number of individuals removed, to a more precision-based approach targeting social groups. Few studies, though, have examined social dynamics of invasive wild pig sounders (i.e., social units typically consisting of females and their associated young). For example, what is the relatedness of individuals in the group, and how might this influence stability of the sounder? How do sounders form and what factors (e.g., size) influence fragmentation of groups into multiple unique sounders or juvenile dispersal patterns? Additionally, interaction of mature males with sounders presumably occurs only for reproductive purposes but has not been studied.

### Damages

Management of damage from invasive species is difficult and often expensive to successfully implement, yet understanding and being able to quantify economic costs of damage provides a sound basis for 1) determining magnitude of damages; 2) identifying previously undiscovered damages; 3) fostering development of strategies to abate and prevent damage; 4) prioritizing the list of damages and determining level of funding needed to reduce, remediate or prevent these negative effects; and 5) informing policy development. For invasive wild pigs, this knowledge base exists for only the anthropogenic component of their environment. There have been some studies documenting invasive wild pig damage related to the agricultural industry (i.e., crops, livestock), the timber and forestry industry, vehicle collisions, developed property damage (e.g., lawns, fencing, landscaping), and disease (e.g., human food crops, potable water supplies; Mayer and Brisbin 2009, Barrios-Garcia and Ballari 2012, Bevins et al. 2014, Keiter and Beasley 2017). However, in many cases there are data gaps on timing, extent, and cost of such damages, and efficacy of abatement strategies.

Invasive wild pig damage to natural areas is much less understood and studied, and likewise economic assessments of this damage are limited (Engeman et al. 2003). There is a basic level of understanding that invasive wild pigs affect native organisms; nonetheless, details are lacking, including standardized metrics to quantify effects. Broad categories of such effects include depredation of native flora, predation of native fauna, competition with or displacement of native wildlife, transmission of diseases and pathogens to native flora and fauna, alteration of habitats, and potential spread of invasive plants. However, with some exceptions (Singer et al. 1984, Cushman et al. 2004, Wilcox and Van Vuren 2009), details associated with these categories are anecdotal or observational at best. There has been considerable research on diets of invasive wild pigs (Ditchkoff and Mayer 2009) because of the widespread availability of carcasses from control efforts, and new molecular techniques are greatly expanding our knowledge base. However, other factors, such

as competition, have been largely inferred (e.g., dietary overlap) rather than being explicitly proven. Depredation of native flora, predation of native fauna, and competition with other wildlife should to be better characterized so the affected species, frequency of occurrence, geographic distribution, seasonality, and breadth of influence of these damages on ecosystems can be better understood. Invasive wild pigs carry and transmit a variety of diseases to native wildlife, livestock, and humans. Aside from anecdotal cases or assumed relationships, however, the full effect of invasive wild pigs on native wildlife and humans is unknown. Pseudorabies virus, which can be fatal in non-suid hosts, is of concern with respect to native wildlife, especially protected species (e.g., the Florida panther [*Puma concolor coryi*]; Glass et al. 1994) that prey on invasive wild pigs, although interactions of pseudorabies with many wildlife species are unknown. The full spectrum of transmission of floral pathogens (e.g., root rot fungus [*Phytophthora cinnamom*], Kliejunas and Ko 1976; southern pine [*Leptographium terebrantis*] decline, Eckhardt et al. 2016) is also poorly understood. Furthermore, although invasive wild pigs carry numerous diseases transmissible to livestock, research on disease transmission between invasive wild pigs and livestock has been limited.

Invasive wild pigs also have the capability of physically altering terrestrial and aquatic habitats through foraging. There is documentation of microhabitat destruction for small mammals and microfauna (Singer et al. 1984, Mohr et al. 2005); however, the full effect of this damage is not known. Other damage to the natural environment includes alterations to abiotic chemical and physical components that affect living organisms and ecosystem function. Most environmental damage likely occurs through foraging and rooting activities of invasive wild pigs. This includes negative alterations to soil (e.g., texture, porosity, pH, nutrient leeching, cycling), water (e.g., quality, pH, contamination, sedimentation, silting), and topographic resources (e.g., erosion, slumping, drainage channel diversion). However, aside from a few studies (Singer et al. 1984, Groot Bruinderink and Hazebroek 1996), the understanding of these effects on ecosystems is limited and in many cases anecdotal. Further characterization of the frequency and location(s) of such damage are needed. In addition, potential for increased environmental damage due to invasive wild pig rooting associated with natural disturbances (e.g., flooding) should to be considered.

### Control

At present, the only viable control options available to manage invasive wild pigs include lethal removal, exclusion or fencing, and supplemental or diversionary feeding. Lethal control measures are typically the most efficient methods to manage invasive wild pig populations, and trapping is one of the most common techniques (Williams et al. 2011). However, further research is needed to increase trapping efficiency and effectiveness. Specific needs include determining strategies to reduce pre-baiting time, best times of year to trap, optimal trap spacing and number of traps

required, and improvements in trap design. Similarly, research to improve materials, techniques, and strategies for selectively snaring invasive wild pigs, and efforts to disseminate this information among managers would improve control efforts. Drop nets, rocket nets, and cannon nets can also be effective for capturing pigs (Gaskamp 2012), but to date little research has been published regarding these methods specifically for invasive wild pigs.

A variety of baits and attractants have been used for trapping pigs, but there is need for improvement. Bait consumption by non-target species is often an issue, so developing means to attract invasive wild pigs but no other species is desirable (Campbell and Long 2008). Further, ascertaining seasonal or regional bait and attractant preferences of pigs could increase trapping success. Such information is critically needed because baiting regulations curtail the trapping of invasive wild pigs during white-tailed deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*) hunting seasons in many states, which in some cases last several months.

Shooting in various recreational and professional forms, including over bait, hunting with dogs, night shooting using infrared or thermal technologies, and from fixed-wing or rotary aircraft are common and effective control techniques (West et al. 2009, Massei et al. 2011). However, recreational hunting alone has proven ineffective at controlling populations in many circumstances (Campbell and Long 2009). The role of aerial shooting in invasive wild pig management programs has increased substantially in recent years, therefore requiring decision support tools to maximize efficacy and guide selection of appropriate shooting techniques. Further, evaluation of the cost effectiveness of using aircraft to remove invasive wild pigs compared to alternative methods and under varying density scenarios would be useful to inform management plans. Additional research to assess the response of remaining individuals after conspecifics are culled is also needed.

The Judas pig method takes advantage of the social dynamics of pigs and has been used to reduce search time and define areas to concentrate trapping and shooting (Campbell and Long 2009, West et al. 2009). Areas deficient in research include if particular sex-age class combinations are better than others and effects of time of year. Managers would also benefit from information on how far pigs will travel in search of conspecifics, and how long it takes them to locate new groups of pigs.

Toxicants also are being explored as a tool to control invasive wild pigs. A warfarin-based toxicant for invasive wild pigs is now registered for use in the United States (Environmental Protection Agency Registration No. 72500-26) and development of other toxicants is underway (Snow et al. 2016). An ideal toxicant would be safe for users and non-target species but highly effective against invasive wild pigs, and produce rapid and humane mortality. One major challenge will be creating delivery systems and strategies specific to invasive wild pigs (Campbell and Long 2009, West et al. 2009). There have been multiple efforts to develop pig-specific delivery systems with promising results

(Long et al. 2010, Campbell et al. 2013, Lavelle et al. 2018), but continued research is needed (Campbell et al. 2012). One important aspect of bait delivery research is designing a system that is bear (*Ursus* spp.)-proof because use of toxicants could be substantially limited if they could not be used in areas where bears are present.

Though lethal techniques are generally more effective at controlling invasive wild pig populations, non-lethal strategies can be effective in some situations, especially to minimize damage at specific sites and times. Exclusionary wire mesh and electric fencing have been used to inhibit invasive wild pig movement (Massei et al. 2011). However, additional research to determine efficacy of specific fence designs relative to parameters such as the level of motivation to breach and cost is warranted. Most research has yet to identify effective chemical repellents or visual and acoustic frightening devices to which invasive wild pigs do not become habituated (Massei et al. 2011, Schlageter and Haag-Wackernagel 2011, 2012a, b), although some successes have been reported (Santilli et al. 2003, Wegorek and Giebel 2008, Dakpa et al. 2009). Bait diversion to direct pigs away from valuable resources such as agricultural crops has been used with varying success but is a short-term solution (Campbell and Long 2009, Mayer and Brisbin 2009). Development of strategies to exploit the natural attributes of pigs to protect resources is a research area with great potential, although challenging because of the keen senses and intellect of pigs.

Means to inhibit reproduction could complement lethal strategies. There are no registered contraceptives available for use in wild pigs in the United States, but advancements with immunocontraceptive vaccine injections have short-term success in making individuals infertile (Killian et al. 2006, Massei et al. 2007). Research to develop oral contraceptives, phage display, and cytotoxins that target oocytes is also being conducted (Samoylova et al. 2012; D. C. Eckery, USDA Animal Plant Health Inspection Service, personal communication). Oral contraceptives could potentially be administered on a broad scale, but pig-specific delivery methods will be required to ensure they are not consumed by non-target species. A contraceptive that requires only a single dose and eliminates reproductive potential for the life of the individual is also desirable. Though surgical sterilization is effective and may be useful in some research settings, its applicability for aiding in large-scale suppression of pig populations is unproven.

Monitoring invasive wild pig populations and the effects of control efforts must be an integral component of management (Engeman et al. 2013). Population and damage indices should be conducted pre- and post-control to quantify success (Campbell and Long 2009). Development of these indices should focus on percentage population reduction, percentage reduction in damage, and financial savings or resources protected rather than solely number of pigs killed.

Practical means to detect invasive wild pigs in areas following eradication efforts or in previously uninhabited areas are currently limited. Recent advancements in detection techniques include use of environmental DNA (eDNA) to

detect presence of pigs in water sources (Williams et al. 2016) and the method is being used operationally by USDA Wildlife Services (K. E. Williams, USDA Animal Plant Health Inspection Service, personal communication). Additionally, efforts to employ trained dogs to detect presence of invasive wild pigs based on scat are underway (M. A. Pepper, USDA Animal Plant Health Inspection Service, personal communication). Efforts are ongoing to improve these methods and they may be most valuable in determining the presence of invasive wild pigs in areas where populations are low or thought to have been eliminated. Similarly, the increased availability and affordability of thermal cameras and unmanned aerial vehicles has facilitated application of these technologies in pig management. These and additional detection tools and strategies will play an important role in areas where eradication efforts have occurred to determine if all pigs were eradicated from an area.

Successful application of the control methods described above is contingent upon numerous factors, including population size, population growth rate, and site characteristics. Thus, researchers need to develop strategies to economically and cost-effectively optimize integrated invasive wild pig management through modeling, the goal being to determine when to implement specific types of control, in what combination, with what level of funding and personnel, and within which time frames. Given the extent to which invasive wild pig control is implemented, there is a unique opportunity for researchers to more closely work with managers to develop adaptive management models in response to control. Models are particularly needed to elucidate behavioral and population responses of pigs to various control efforts, and risks and potential spread of infectious diseases within pig populations and among invasive wild pigs and other wildlife, livestock, and even humans. There has been extensive work on these topics for other ungulates, and these models could be adapted to invasive wild pigs. However, such efforts are limited by availability of data needed for model parameterization, reaffirming the importance of improved ecological data for this species. Our general treatise of the current state of lethal and non-lethal strategies to address wild pigs demonstrates that, though much work has been done and many tools are available, opportunity exists to improve existing tools and develop new ones. Furthermore, better preventative measures will be critical to aid control efforts. Specifically, improvements in legislation are needed in many states to curtail establishment of wild populations in new areas.

### **Education and Human Dimensions**

Although invasive wild pigs have been established in North America since the 1500s, there is a need for human dimension studies that address the knowledge, attitudes, and control efforts of stakeholder groups involved in their management. Landowners experiencing damage caused by invasive wild pigs agree they are a nuisance species that should be controlled (Adams et al. 2005, Harper et al. 2016); however, they may have misconceptions regarding the most

cost- and time-effective methods to reduce or eradicate local populations. For example, despite evidence hunting is ineffective at controlling invasive wild pigs in many instances (Campbell and Long 2009), some landowners, hunters, and other members of the public still view recreational hunting as an effective means for population control. Invasive wild pigs may be effectively controlled at local levels, but in most instances, county or statewide reduction of their populations will require the active cooperation and participation of private landowners, especially within the patchwork of private ownerships in the eastern United States. State wildlife and extension agencies conduct informational seminars on invasive wild pig management to help landowners reduce pig damage on their properties, yet it is unclear how effective these programs are in reducing populations at local scales or beyond. Measuring effectiveness of educational programs (e.g., adoption of best management practices) specifically targeted to stakeholder groups will be increasingly important, especially as emerging technologies such as toxicants and contraceptives become available.

Illegal (in most states) live capture, transport, and release of invasive wild pigs is the most frequently cited cause for the rapid expansion of invasive wild pigs in North America. The primary motivation behind these translocations is to facilitate increased recreational hunting opportunities (Tabak et al. 2017); however, the extent to which this illegal activity occurs is largely unknown. Using expected utility models, Caudell et al. (2016) reported current fines in most states are unlikely to serve as an effective deterrent for illegally moving invasive wild pigs, and states should consider creative fine structures and loss of hunting privileges for convictions. This largely overlooked aspect of invasive wild pig management has profound implications; an understanding of the factors influencing participation in illegal movement of invasive wild pigs will be useful to guide development and enforcement of laws to curtail this activity.

Although the negative financial and ecological effects of invasive wild pigs are well documented (Engeman et al. 2003, Pimental 2007, Barrios-Garcis and Ballari 2012, Bevins et al. 2014, Keiter and Beasley 2017), almost no studies have measured positive economic benefits from invasive wild pigs (e.g., hunting license sales, firearms and ammunition, guiding and outfitting services, non-resident travel expenses, trespass or lease fees, commercial sale of invasive wild pigs for meat). Likewise, no studies have examined characteristics such as motivations, willingness to pay, or attitudes of those who pursue wild pigs for recreational hunting. Even less understood is the influence of media (e.g., television, Youtube) in sensationalizing invasive wild pig hunting and shaping knowledge and understanding of their management and fueling the demand for recreational hunting. Although positive economic incentives for invasive wild pigs may increase their spread or incentivize landowners to maintain populations (Zivin et al. 2000), these stakeholder groups will play an important role in the decision-making process for managing this species. Furthermore, state transport and

harvest regulations currently do little to curb interest in harvest of invasive wild pigs, although several states are taking positive steps in this direction. Most states in the United States allow public pig hunting and several states allow live transport and sale of invasive wild pigs. Although such activities remove individuals from the population, due to their high reproductive capacity the number of invasive wild pigs removed through recreational hunting alone is typically insufficient to substantially suppress populations (Campbell and Long 2009). Thus, until promotion of opportunities to harvest pigs is curtailed at the state level, there will remain few incentives for many stakeholders to support aggressive invasive wild pig control programs. However, a few states have taken progressive action toward this goal by banning all invasive wild pig hunting on public lands (e.g., KS, MO, NE, NY, TN).

## CONCLUSIONS

The rapid increase in size and distribution of invasive wild pig populations throughout their introduced range, coupled with the multitude of stakeholders and natural systems affected by this species, necessitates integrative and adaptive management strategies rooted in sound ecological research. Despite growing awareness of the negative influences invasive wild pigs have on native and anthropogenic ecosystems, there remains a paucity of empirical data for many key aspects of the species' ecology needed to direct and evaluate management. Lack of sufficient knowledge of invasive wild pig ecology reflects the rapid expansion of pig populations that has greatly outpaced research on the species. Nonetheless, such data are essential to development of effective management that moves beyond simply culling pigs, to strategies effective at sustaining population reduction and reductions in damage. Indeed, one primary limitation of most pig management is that efficacy of control is often unknown or based on limited data because estimates of population size and damage are rarely quantified before and after population reduction. Such limitations stem from a lack of basic tools and techniques needed to conduct standardized assessments of population size and damage that are easy to implement in the field by managers but also yield precise estimates of the parameters of interest.

Although there have been substantive advancements in our understanding of invasive wild pig ecology and management over the last few decades, the research priorities described herein highlight many key areas where further research is needed to more efficiently and effectively manage this economically important species. Ultimately, successful management of pig populations at a national scale will require careful integration of research and management, and assimilation of these activities into educational efforts to inform stakeholders of the importance of invasive wild pig management. Failure to integrate all 3 of these components into pig management programs will limit the broader effects of research on the species, and potentially slow the pace of public support for management of a species for which there is a tradition of hunting.

## ACKNOWLEDGMENTS

We thank the NWPTF for their support hosting the 4 March 2016 meeting that ultimately resulted in this paper, as well as all NWPTF research subcommittee members who provided input for this manuscript: A. N. Anderson, S. E. Backs, J. L. Corn, R. W. DeYoung, P. T. Hall, S. B. Hartley, L. A. Humberg, J. C. Kilgo, J. M. LaCour, R. S. Miller, K. M. Pepin, L. D. Staples, M. A. Tabak, and K. M. Tolson. Publication of this manuscript has been approved by the Steering Committee of the NWPTF. Further, we acknowledge all workshop participants and members of the research subcommittee of the NWPTF for their critical input in this manuscript and input from the associate editor and 2 anonymous reviewers; this manuscript was greatly improved from their insight and participation. Contributions were partially supported through funding by the U.S. Department of Energy under Award Number DE-EM0004391 to the University of Georgia Research Foundation (J. C. Beasley) and Contract DE-AC09-08SR22470 to Savannah River Nuclear Solutions LLC (J. J. Mayer).

## LITERATURE CITED

- Adams, C. E., B. J. Higginbotham, D. Rollins, R. B. Taylor, R. Skiles, M. Mapston, and S. Turman. 2005. Regional perspectives and opportunities for feral hog management in Texas. *Wildlife Society Bulletin* 33:1312–1320.
- Barrios-Garcia, M. N., and S. A. Ballari. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions* 14:2283–2300.
- Bevins, S. N., K. Pedersen, M. W. Lutman, T. Gidlewski, and T. J. Deliberto. 2014. Consequences associated with the recent range expansions of nonnative feral swine. *BioScience* 64:291–299.
- Blackwell, B. F., and E. Fernández-Juricic. 2013. Behavior and physiology in the development and application of visual deterrents at airports. Pages 11–22 in T. L. Devault, B. F. Blackwell, and J. L. Belant, editors. *Wildlife in airport environments: preventing animal-aircraft collisions through science-based management*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Boitani, L., L. Mattei, D. Nonis, and F. Corsi. 1994. Spatial and activity patterns of wild boar in Tuscany, Italy. *Journal of Mammalogy* 75: 600–612.
- Campbell, T. A., M. J. Bodenchuk, J. D. Eisemann, S. J. Lapidge, L. Staples, and P. Morrow. 2012. Preliminary assessment of the HogHopper™ for excluding non-target wildlife. *Proceedings of the Vertebrate Pest Conference* 25:333–336.
- Campbell, T. A., J. A. Foster, M. J. Bodenchuk, J. D. Eisemann, L. Staples, and S. J. Lapidge. 2013. Effectiveness and target-specificity of a novel design of food dispenser to deliver a toxin to wild pigs in the United States. *International Journal of Pest Management* 59:197–204.
- Campbell, T. A., and D. B. Long. 2008. Mammalian visitation to candidate wild pig attractants. *Journal of Wildlife Management* 72:305–309.
- Campbell, T. A., and D. B. Long. 2009. Feral swine damage and damage management in forested ecosystems. *Forest Ecology and Management* 257:2319–2326.
- Caudell, J. N., E. Dowell, and K. Welch. 2016. Economic utility for the anthropogenic spread of wild hogs. *Human-Wildlife Interactions* 10: 230–239.
- Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* 72: 805–813.
- Comer, C. E., and J. J. Mayer. 2009. Wild pig reproductive biology. Pages 51–75 in J. J. Mayer and I. L. Brisbin Jr., editors. *Wild pigs: biology, damage, control techniques, and management*. SRNL-RP-2009-00869. Savannah River National Laboratory, Aiken, South Carolina, USA.
- Corn, J. L., and T. R. Jordan. 2017. Development of the National Feral Swine Map, 1982–2016. *Wildlife Society Bulletin* 41:758–763.

- Cushman, J. H., T. A. Tierney, and J. M. Hinds. 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. *Ecological Applications* 14:1746–1756.
- Dakpa, P., U. Penjore, and T. Dorji. 2009. Design, fabrication and performance evaluation of wild pig repellent device. *Journal of Renewable Natural Resources* 5:116–126.
- Davis, A. J., B. Leland, M. Bodenchuk, K. VerCauteren, and K. M. Pepin. 2017. Estimating population density for disease risk assessment: the importance of understanding the area of influence of traps using wild pigs as an example. *Preventive Veterinary Medicine* 141:33–37.
- Ditchkoff, S. S., D. B. Jolley, B. D. Sparklin, L. B. Hanson, M. S. Mitchell, and J. B. Grand. 2012. Reproduction in a population of wild pigs (*Sus scrofa*) subjected to lethal control. *Journal of Wildlife Management* 76:1235–1240.
- Ditchkoff, S. S., and J. J. Mayer. 2009. Wild pig food habits. Pages 105–143 in J. J. Mayer and I. L. Brisbin Jr., editors. *Wild pigs: biology, damage, control techniques, and management*. SRNL-RP-2009-00869. Savannah River National Laboratory, Aiken, South Carolina, USA.
- Ebert, C., F. Knauer, B. Spielberger, B. Thiele, and U. Hohmann. 2012. Estimating wild boar *Sus scrofa* population size using faecal DNA and capture-recapture modelling. *Wildlife Biology* 18:142–152.
- Eckhardt, L. G., R. D. Menard, and S. S. Ditchkoff. 2016. Wild pigs: inciting factor in southern pine decline? Pages 91–94 in C. J. Schweitzer, W. K. Clatterbuck, and C. M. Oswalt, editors. *Proceedings of the 18th biennial southern silvicultural conference*. e—General Technical Report SRS–212. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Engeman, R., G. Massei, M. Sage, and M. Gentle. 2013. Monitoring wild pig populations: a review of methods. *Environmental Science and Pollution Research* 20:8077–8091.
- Engeman, R. M., H. T. Smith, S. A. Shwiff, B. Constantin, J. Woolard, M. Nelson, and D. Griffin. 2003. Prevalance and economic value of feral swine damage to native habitat in three Florida state parks. *Environmental Conservation* 30:319–324.
- Gabor, T. M., E. C. Hellgren, R. A. Van Den Bussche, and N. J. Silvy. 1999. Demography, sociospatial behavior and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. *Journal of the Zoological Society of London* 247:311–322.
- Gaskamp, J. A. 2012. Use of drop-nets for wild pig damage and disease abatement. Thesis, Texas A&M University, College Station, USA.
- Glass, C. M., R. G. McLean, J. B. Katz, D. S. Maehr, C. B. Cropp, L. J. Kirk, A. J. McKeiman, and J. F. Evermann. 1994. Isolation of pseudorabies (Aujeszky's disease) virus from a Florida panther. *Journal of Wildlife Diseases* 30:180–184.
- Groot Bruinderink, G. W. T. A., and E. Hazebroek. 1996. Wild boar (*Sus scrofa*) rooting and forest regeneration on podzolic soils in the Netherlands. *Forest Ecology and Management* 88:71–80.
- Hanson, L. B., J. B. Grand, M. S. Mitchell, D. B. Jolley, B. D. Sparklin, and S. S. Ditchkoff. 2008. Change-in-ratio density estimator for feral pigs is less biased than closed mark-recapture estimates. *Wildlife Research* 35:695–699.
- Harper, E. E., C. A. Miller, J. J. Vaske, M. T. Mengak, and S. Bruno. 2016. Stakeholder attitudes and beliefs toward wild pigs in Georgia and Illinois. *Wildlife Society Bulletin* 40:269–273.
- Ilse, L. M., and E. C. Hellgren. 1995. Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern Texas. *Journal of Mammalogy* 76:784–799.
- Kay, S. L., J. W. Fisher, A. J. Monaghan, J. C. Beasley, R. Boughton, T. A. Campbell, S. M. Cooper, S. S. Ditchkoff, S. B. Hartley, J. C. Kilgo, S. M. Wisely, A. C. Wyckoff, K. C. VerCauteren, and K. M. Pepin. 2017. Quantifying drivers of wild pig movements across multiple spatial and temporal scales. *Movement Ecology* 5:14.
- Keiter, D. A., and J. C. Beasley. 2017. Hog heaven? Challenges of managing introduced wild pigs in natural areas. *Natural Areas Journal* 37:6–16.
- Keiter, D. A., A. J. Davis, O. E. Rhodes Jr., F. L. Cunningham, J. C. Kilgo, K. M. Pepin, J. C. Beasley. 2017a. Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. *Scientific Reports* 7:9446. <https://doi.org/10.1038/s41598-017-09746-5>
- Keiter, D. A., J. C. Kilgo, M. A. Vukovich, F. L. Cunningham, and J. C. Beasley. 2017b. Development of known-fate survival monitoring techniques for juvenile wild pigs (*Sus scrofa*). *Wildlife Research* 44(2): 165–173.
- Keiter, D. A., J. J. Mayer, and J. C. Beasley. 2016. What's in a "common" name? A call for consistent terminology for referring to non-native *Sus scrofa*. *Wildlife Society Bulletin* 40:384–387.
- Killian, G., L. Miller, J. Rhyhan, and H. Doten. 2006. Immunocontraception of Florida feral swine with a single-dose GnRH vaccine. *American Journal of Reproductive Immunology* 55:378–384.
- Kliejunas, J. T., and W. H. Ko. 1976. Dispersal of *Phytophthora cinnamomi* on the island of Hawaii. *Phytopathology* 66:457–460.
- Lavelle, M. J., N. P. Snow, J. M. Halseth, J. C. Kinsey, J. A. Foster, and K. C. VerCauteren. 2018. Development and evaluation of a bait station for selectively dispensing bait to invasive wild pigs. *Wildlife Society Bulletin* 42:102–110.
- Lewis, J. S., M. L. Farnsworth, C. L. Burdett, D. M. Theobald, M. Gray, and R. S. Miller. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. *Scientific Reports* 7:44152. <https://doi.org/10.1038/srep44152>
- Long, D. B., T. A. Campbell, and G. Massei. 2010. Evaluation of wild pig-specific feeder systems. *Rangelands* 32:8–13.
- Massei, G., D. Cowan, J. Coats, F. Gladwell, J. Lane, and L. Miller. 2007. Effect of the GnRH vaccine GonaCon on the fertility, physiology, and behaviour of wild boar. *Wildlife Research* 35:540–547.
- Massei, G., S. Roy, and R. Bunting. 2011. Too many hogs? A review of methods to mitigate impact by wild boar and feral hogs. *Human-Wildlife Interactions* 5:79–99.
- Mayer, J. J., and I. L. Brisbin Jr., editors. 2009. *Wild pigs: biology, damage, control techniques and management*. SRNL-RP-2009-00869. Savannah River National Laboratory, Aiken, South Carolina, USA.
- Mohr, D., L. W. Cohnstaedt, and W. Topp. 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biology and Biochemistry* 37:693–700.
- Pimental, D. 2007. Environmental and economic costs of vertebrate species invasions into the United States. Pages 2–8 in G. W. Witmer, W. C. Pitt, and K. A. Fagerston, editors. *Managing vertebrate invasive species: proceedings of an international symposium*. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, USA.
- Samoylova, T. I., A. M. Cochran, A. M. Samoylov, B. Schemera, A. H. Breitenicher, S. S. Ditchkoff, V. A. Petrenko, and N. R. Cox. 2012. Phage display allows identification of zona pellucida-binding peptides with species-specific properties: novel approach for development of contraceptive vaccines for wildlife. *Journal of Biotechnology* 162:311–318.
- Santilli, F., L. Galardi, and M. Bagliacca. 2003. Corn appetibility reduction in wild boar (*Sus scrofa* L.) in relationship to the use of commercial repellents. *European Vertebrate Pest Management Conference* 4: 213–218.
- Schlageter, A., and D. Haag-Wackernagel. 2011. Effectiveness of solar blinkers as a means of crop protection from wild boar damage. *Crop Protection* 30:1216–1222.
- Schlageter, A., and D. Haag-Wackernagel. 2012a. Evaluation of an odor repellent for protecting crops from wild boar damage. *Journal of Pest Science* 85:209–215.
- Schlageter, A., and D. Haag-Wackernagel. 2012b. A gustatory repellent for protection of agricultural land from wild boar damage: an investigation on effectiveness. *Journal of Agricultural Science* 4:61–68.
- Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. The effects of wild pig rooting in a deciduous forest. *Journal of Wildlife Management* 48:464–473.
- Snow, N. P., J. M. Halseth, M. J. Lavelle, T. E. Hanson, C. R. Blass, J. A. Foster, S. T. Humphrys, L. D. Staples, D. G. Hewitt, and K. C. VerCauteren. 2016. Bait preference of free-ranging wild pig for delivery of a novel toxicant. *PloS ONE* 11:e0146712.
- Sparklin, B. D., M. S. Mitchell, L. B. Hanson, D. B. Jolley, and S. S. Ditchkoff. 2009. Territoriality of feral pigs in a highly persecuted population on Fort Benning, Georgia. *Journal of Wildlife Management* 73:497–502.
- Tabak, M. A., A. J. Piaggio, R. S. Miller, R. A. Sweitzer, and H. B. Ernest. 2017. Anthropogenic factors predict movement of an invasive species. *Ecosphere* 8:e01844.



- U.S. Department of Agriculture [USDA]. 2015. Final environmental impact statement—feral swine damage management: a national approach. APHIS-2013-0031-0100. U.S. Department of Agriculture, Washington, D.C., USA.
- Wegorek, P., and J. Giebel. 2008. The effectiveness of selected active substances in keeping away wild boar (*Sus scrofa* L.) from feeding on maize crops. *Progress in Plant Protection* 48:1002–1006.
- West, B. C., A. L. Cooper, and J. B. Armstrong. 2009. Managing wild pigs: a technical guide. *Human-Wildlife Interactions Monograph* 1:1–55.
- Wilcox, J. T., and D. H. Van Vuren. 2009. Wild pigs as predators in oak woodlands of California. *Journal of Mammalogy* 90:114–118.
- Williams, B. L., R. W. Holtfreter, S. S. Ditchkoff, and J. B. Grand. 2011. Trap style influences wild pig behavior and trapping success. *Journal of Wildlife Management* 75:432–436.
- Williams, K. E., K. P. Huyvaert and A. J. Piaggio. 2016. No filters, no fridges: a method for preservation of water samples for cDNA analysis. *BMC Research Notes* 9:298.
- Zivin, J., B. M. Hueth, and D. Zilberman. 2000. Managing a multiple-use resource: the case of feral pig management in California rangeland. *Journal of Environmental Economics and Management* 39:189–204.

*Associate Editor: Bruce Leopold.*