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Does hunting affect the behavior of wild pigs?

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Abstract: Wild boar and feral swine (*Sus scrofa*) numbers are growing worldwide. In parallel, their severe ecological and economic impacts are also increasing and include vehicle collisions, damage to crops and amenities, reduction in plant and animal abundance and richness, and transmission of diseases, the latter causing billions of U.S. dollars in losses to the livestock industry each year. Recreational hunters are the main cause of mortality for this species, and hunting has traditionally been the main method to contain populations of wild pigs. Hunting might affect the behavior of the species, which potentially can lead to these animals moving to new areas or to an increase in disease transmission. This review summarized the evidence that recreational hunting influences the behavior of wild pigs. Twenty-nine studies reported the effect of recreational hunting on social, spatial, and temporal behavior. Although most found that recreational hunting caused changes in home range size, home range shifting, habitat use, and activity patterns, there was little agreement between studies on the size, direction, and duration of these effects. Several studies suggested that other factors, such as season and food availability, equally affect the behavior of this species. Very few studies provided details about the type and frequency of hunting, the number of hunters and dogs (*Canis lupus familiaris*), the number of animals harvested, or the presence of reserve areas where hunting was forbidden on neighboring sites. As wild pigs adapt to human disturbance, these factors should be investigated to minimize the effects of recreational hunting on the behavior of the species, particularly in the context of disease transmission.

Key words: disease transmission, home range size, hunt, population management, social behavior, spatial behavior, *Sus scrofa*, wild boar

Wild boar and feral swine (*Sus scrofa*) occur worldwide as native from Eurasia or introduced populations (Ballari et al. 2015, Snow et al. 2017, Keuling et al. 2018, Melletti and Meijaard 2018). Wild boar and feral swine belong to the same species *Sus scrofa*. Hereafter, we use the term "wild pig" for animals in their introduced ranges, where feral swine, wild boar, or hybrids may occur, as well as in their native Eurasian range. In the last decades, the number and range of wild pigs have increased dramatically worldwide, due to several factors that include the adaptability of the species to a variety of habitats, mild winters, reforestation, increased availability of crops, supplementary feeding, and introductions of both wild boar and feral swine in all continents apart from Antarctica (Bevins et al. 2014, Oja et al. 2014, Skewes and Jaksic 2015, Mayer 2018, Rutten et al. 2019, Vetter et al. 2020). This increase is also due to the fact that wild pigs have the highest reproductive rate among ungulates, with annual population growth rates that may exceed 2.0 (Bieber and Ruf 2005, Keuling et al. 2013, Frauendorf et al. 2016, Drimaj et al. 2020). In parallel, the number of recreational hunters, who have traditionally been the main cause of mortality for wild pigs (Keuling et al. 2013), is declining in many countries (Massei et al. 2015).

The economic and environmental impacts of the species on conservation and economic interests are substantial, and the World Conservation Union lists *Sus scrofa* among the 100 worst alien invasive species (Lowe et al. 2000). These impacts comprise vehicle collisions (Thurfjell et al. 2015); transmission of diseases to wildlife, livestock, and people (Ruiz-Fons et al. 2008, Ruiz-Fons 2015); damage to crops and amenities (Schley and Roper 2003, Gentle et al. 2015); predation on native species (Barrios-Garcia and Ballari 2012); changes in soil chemistry (Wirthner et al. 2012); and reduction in plant and animal abundance and richness (Welander 2000, Hone 2002, Massei and Genov 2004, Bueno et al. 2010, Barrios-Garcia and Ballari 2012). For instance, in 11 U.S. states,

wild pigs caused annual agricultural losses of $190 million USD for 6 crops (Anderson et al. 2016), and the combined annual costs of damage and control was estimated to be $ 1.5 billion USD in the United States (Pimentel et al. 2002) and $100 million AUD in Australia (Choquenot et al. 1996).

Wild pigs have also colonized urban areas, where their impact includes extensive damage to private gardens, public parks, sport grounds and cemeteries, and transmission of diseases to humans and companion animals (e.g., Cahill et al. 2012, Stillfried et al. 2017, Castillo-Contreras et al. 2018).

This species hosts a large number of parasites as well as viral and bacterial diseases, which pose serious threats to human health and livestock (e.g., Ruiz-Fons 2015). The costs of diseases outbreaks such as foot-and-mouth disease (FMD) and African swine fever (ASF) are of particular concern. Foot-and-mouth disease is a highly contagious viral disease that affects even-toed ungulates and results in destruction of infected livestock, of livestock at infected sites, and destruction of livestock in areas that may have been exposed by direct or indirect contact (Ruiz-Fons et al. 2008). For instance, the FMD outbreak in the United Kingdom in 2001 resulted in a total cost estimated at $9–13 billion USD (Forman et al. 2009). African swine fever is also a viral disease, which causes devastating fatalities among wild pig populations and significant losses to the pig industry. For instance, the economic loss due to ASF outbreaks in the Russian Federation between 2008 and 2011 was estimated at approximately $240 billion USD (Callaway 2012).

In recent years, disease outbreaks have catalyzed discussions on options to reduce local densities of wild pigs, with hunting generally assumed to decrease the impacts of the species (e.g., Lange et al. 2018, Croft et al. 2019, Miguel et al. 2020). Disease persistence is often associated with population size, contact rate, and spatial behavior (Ruiz-Fons et al. 2008, Prentice et al. 2019, Miguel et al. 2020), which may in turn be affected by hunting. Several studies indicated that hunting may affect spatial, social, and temporal behavior of wildlife as well as population structure (age and sex; e.g., Pepin et al. 2017*b*, Prentice et al. 2019, Miguel et al. 2020). For group-living species such as the wild pig, hunting can also affect group composition and stability (Iacolina et al. 2009). In wild pigs, social groups may temporarily break, reform, or exchange individuals (Gabor et al. 1999, Poteaux et al. 2009), but group members usually form stable and long-lasting relationships, even under hunting conditions (Podgórski et al. 2014*a*). High removal pressure on 1 sex may lead also to changes in the mating systems. Poteaux et al. (2009) and Müller et al. (2018) suggest that high hunting pressure on males might shift from polygyny to promiscuity.

In other ungulate species such as the reindeer [*Rangifer tarandus*], hunting increases long-distance movements (Mysterud et al. 2020). Culling-induced social perturbation has been reported in European badgers [*Meles meles*], associated with increased prevalence of bovine tuberculosis in areas surrounding those where culling occurred (Riordan et al. 2011). In raccoons [*Procyon lotor*], culling led to immigration of dispersing males into depopulated areas, thus increasing disease transmission risks (Beasley et al. 2013).

The contribution of recreational hunting to controlling wildlife diseases is based on the assumptions that transmission is density dependent and that there is a population density threshold below which the disease cannot persist (Anderson et al. 1981, Carter et al. 2009). While many studies investigated the effects of recreational hunting on wild pig population dynamics (e.g., Keuling et al. 2013, Pepin et al. 2017*a*, González-Crespo et al. 2018, Croft et al. 2020), little attention has been paid to the effect of hunting on wild pig behavior. Massei et al. (2011) found little agreement among studies on the effect of recreational hunting on the behavior of wild pigs.

Studies on population control of wild pigs, particularly those on eradications, suggest that several methods should be used to reduce population size (McIlroy and Saillard 1989, Alexandrov et al. 2011, Pepin et al. 2017*a*, Croft et al. 2020). However, as hunting is still the most widespread method for reducing numbers of this species (McIlroy and Saillard 1989, Keuling et al. 2013, Massei et al. 2015), this review focused on studies based on this method.

The specific objectives of this review were: (1) to summarize the evidence that recreational hunting influences the behavior of wild pigs, (2)

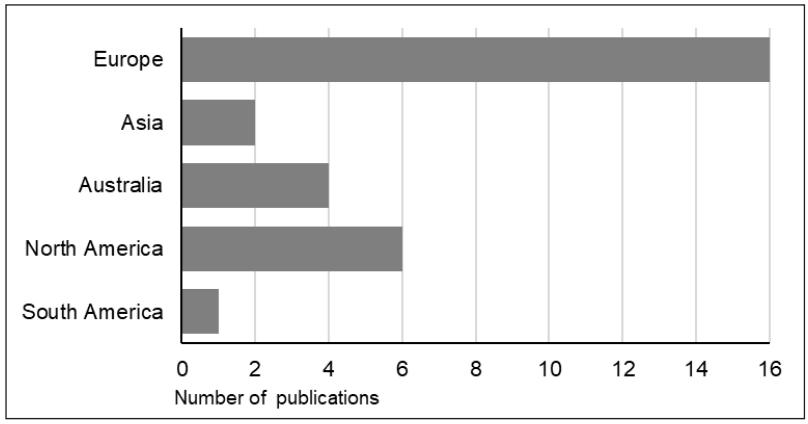

Figure 1. Number of studies reporting the effect of hunting on wild pigs (*Sus scrofa*), subdivided into continents (*N* = 29).

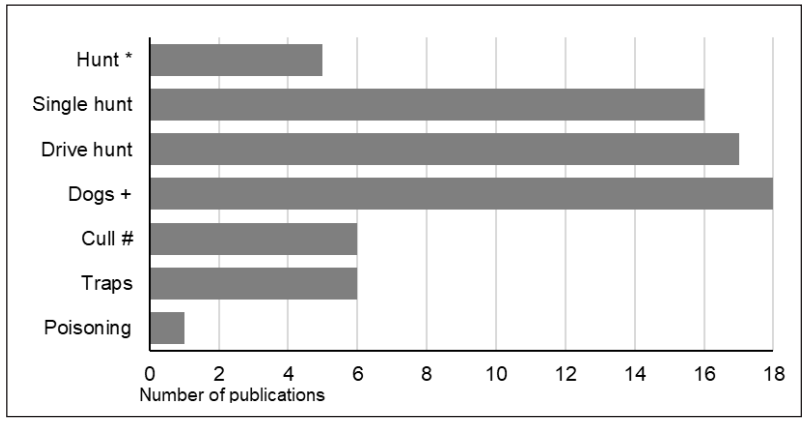

Figure 2. Number of wild pig (*Sus scrofa*) studies (*N* = 29) mentioning different types of hunting/culling. Combinations of different methods were possible. * Hunt = no further explanation given; + Dogs = might be combined with all other hunting/shooting methods; # Cull = shooting by professional hunters/game wardens/wildlife managers.

to examine the factors that might affect whether hunting influences the behavior of this species, and (3) to highlight knowledge gaps for future research.

Methods

We searched within our own databases (>1,700 titles with "*Sus scrofa*") and additionally in VetSearch (©2020 EBSCO Industries, Inc.; using search in PubMed, Web of Science, Cabi, AGRIS, Academic OneFile, BASE, Online Contents, Wiley, Science Direct, Springer Link, SciELO, DBIS, Zotero, etc.). The key words used were *Sus scrofa*, wild pig, wild swine, feral pig, feral swine, feral hog, or wild boar, each always in combination with all the following terms: cull*, hunt*, trap*, removal, behaviour/behavior, home range, movement, space use, habitat usage (e.g., "wild boar AND cull*," "feral pig AND home range," "*Sus scrofa* AND hunt*." Only papers that mentioned the effects of hunting in the title or in the abstract were included. To focus on recreational hunting (i.e., culling carried out by shooting), we did not include studies on trapping. The search included peer-reviewed studies as well as reports, book chapters, and theses.

Results

The search delivered 424 publications, of which 29 mentioned the effects of recreational hunting on the behavior of wild pigs (Table 1, supplemental file). Studies on the effect of hunting on the behavior of this species were conducted in all continents (excluding Antarctica), with the exception of Africa, where this species is relatively poorly studied (compare Melletti

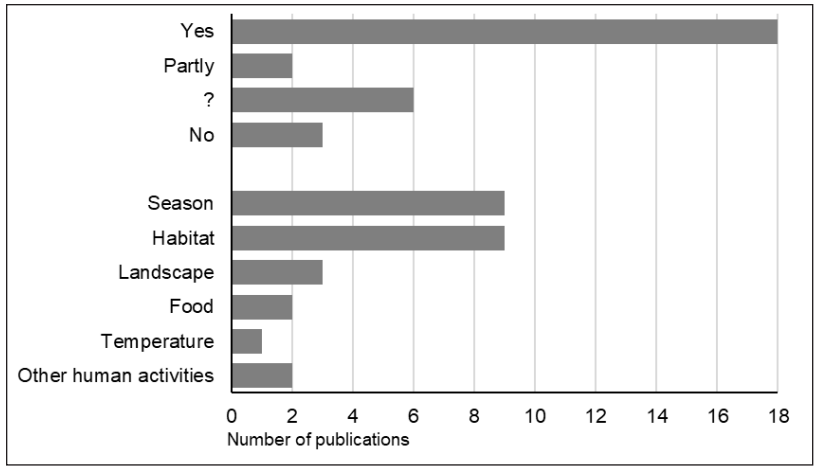

Figure 3. Number of studies reporting the effects of hunting (top) and other factors (underpart) on behavior of wild pigs (*Sus scrofa*). Yes = effect of culling/hunting proven; Partly = effect only in some cases; ? = effect of hunting inconclusive; No = no effect of hunting activity found.

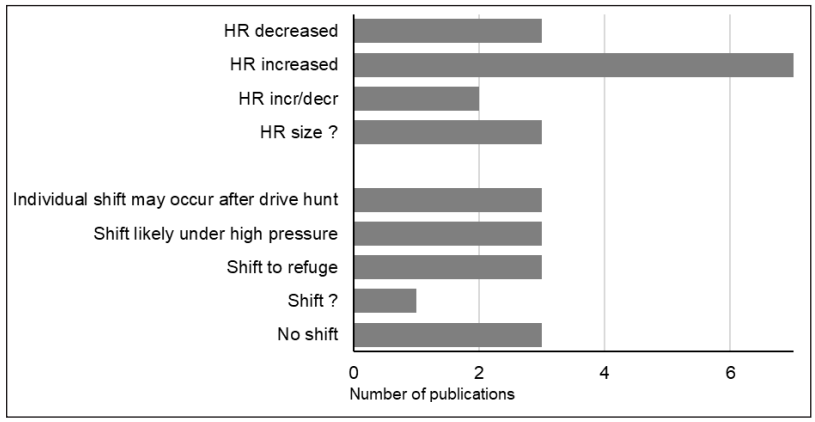

Figure 4. Number of wild pig (*Sus scrofa*) studies reporting alterations of home ranges in mean size (HR) and location (shift) in relation to hunting; ? = effect of culling questionable; incr/decr = home range decreased for some animals and increased for others.

and Meijaard 2018). Most of the studies were conducted in the traditional wild boar hunting regions in Europe. Invasive wild pigs were investigated much less (Figure 1). Eighteen publications (62%) focused on wild boar in their native range, 6 publications (21%) on wild pigs in the United States, 4 publications (14%) on wild pigs in Australia, and 1 publication (3%) on introduced wild pigs in Brazil. Most studies reported different hunting methods; dogs (*Canis lupus familiaris*) were usually employed for hunting wild pigs (Figure 2). Shooting by both recreational and professional hunters was by far the most widespread method to reduce wild pig numbers. Other culling methods like trapping, helicopter shooting, or poisoning were mentioned only rarely to complement hunting (Figure 2).

Eighteen studies (62%) found that hunting affects the spatial behavior of wild pigs, 3 studies (10%) found that this is not the case, and 8 studies (28%) were inconclusive, only assuming an effect or reporting marginal effects (Table 1, supplemental file). Nineteen studies (66%) suggested that several other factors, such as season or habitat, influenced spatial behavior in addition to or instead of hunting (Figure 3).

The most frequently mentioned behavioral changes were alterations in home range size (14 publications, 48%) and shift of home range (13 publications, 45%; Figure 4; compare also Table 1 [supplemental file] for different effects). A

shift of home range is defined by the distance between centers of temporary home ranges larger than half the range span (as in Keuling et al. 2008*a*).

Changes in activity patterns were also described in 9 studies (31%; Table 1, supplemental file). Reduced diurnal activity due to hunting was reported in 6 studies, but 5 interpreted this behavior also as a possible adaptation to warm climate or a general adaptation to human disturbance in recent centuries. Three studies reported that animals did decrease total activity in general; 1 study found that wild pigs switched to increased diurnal activity, and another study stated explicitly that the changes in activity patterns were not due to hunting but to other seasonal factors.

Ten (36%) studies mentioned changes in habitat use due to recreational hunting, with animals seeking dense vegetation or moving to less accessible habitats; 3 of these studies actually mentioned a refuge effect, where animals moved to areas where hunting was not occurring.

Discussion

The relatively small number of studies that mentioned the potential effects of recreational hunting on wild pig behavior confirmed the topic has received little attention. Of these studies, 62% found that recreational hunting affected size or location of home range, movements, and activity patterns of wild pigs. Only half of the studies were specifically aimed at testing the effects of hunting on this the spatial behavior of this species, while the others simply mentioned the topic as an additional finding. Few provided indications about the type and frequency of hunting, the size of the area where hunting occurred, or the effort of hunting, etc. Some reported the number of wild pigs culled, but only a few provided estimates of local population densities. Hunting pressure was rarely quantified and where mentioned was described as "high" or "low."

Overall, the results from these studies are mixed and often contradictory. For example, in France, hunting with dogs caused an increase in home range size of wild pigs (Calenge et al. 2002). In Germany, the mean home range of 6 wild pig groups out of the 9 groups monitored increased from 183 ha (before the hunt) to 299 ha after a drive hunt (i.e., a hunt based on a group of beaters with dogs driving the wild pigs toward the hunters waiting inside the driven area), and 3 groups also moved up to 6 km outside their previous range (Sodeikat and Pohlmeyer 2002). Once the hunt was over, wild pigs returned to their original area within 4–6 weeks (Sodeikat and Pohlmeyer 2002). Conversely, 2 other studies in Germany and Australia (McIlroy and Saillard 1989, Keuling et al. 2008*b*) found that hunting did not affect spatial behavior of wild pigs considerably. Another study carried out in the Namadgi National Park, Australia, reported that although on 19 occasions hunters with dogs walked within 100 m from wild pigs that were equipped with radio-transmitters, they found and killed only 1 of these pigs (McIlroy and Saillard 1989). Wild pigs that were active when the hunt started became stationary when the hunters moved closer, and most animals did not leave their home range. In single instances, wild pigs shifted home ranges up to 20 km directly after hunts (Sodeikat and Pohlmeyer 2002, Scillitani et al. 2010, Keuling et al. 2016), but similar shifts also occurred in areas without hunting (Gabor et al. 1999, Jerina et al. 2014; O. Keuling, personal observation).

The different results found in these studies are likely due to differences in method and frequency of hunting (e.g., from high seats, driven hunt, or stalk hunts), presence of dogs, time of the year, number of hunters, density of wild pigs, and availability and size of refuge areas next to those where culling occurred. With few exceptions, studies focused on the short-term effect of hunting on animal behavior and investigated size or location (shift) of home range, movements, and activity patterns before, during, and a few weeks after the end of the hunting season. Many studies (Table 1, supplemental file) also found that hunting caused a shift in habitat use, which was also observed by Rosell et al. (2004) in a natural reserve increasingly used by wild pigs where hunting occurred in the neighboring areas.

Relatively few studies addressed the effects of recreational hunting on social behavior, social structure, and contact rates of wild pigs, which were altered indirectly by changes in spatial behavior or population structure (e.g., Poteaux et al. 2009; Podgórski et al. 2014*b*, 2018). Others hypothesized that hunting affects group size and composition, which in turn might influence

spatial behavior and contact rates. For instance, hunting might lead to reorganization of non-kin group members (Gabor et al. 1999, Iacolina et al. 2009). In wild pigs, group members usually form stable and long-lasting relationships (Podgórski et al. 2014*a*). These groups are normally guided by adult sows, but if all the social group's adults are culled, the juveniles may move up to 50 km together (Genov and Ferrari 1998, Moennig et al. 1999), thus increasing the risk of spreading diseases. Addressing whether hunting affects contact rate would be particularly relevant for diseases as contact rate is often assumed to be constant when modeling disease transmission during management.

Home range size, movements, and activity patterns of wild pigs are also influenced by other factors, which include supplementary feeding, population density, season, climate, and availability of natural food (Massei et al. 1997, Keuling et al. 2009, Keuling 2010, Prévot 2010, Ježek et al. 2013, Morelle et al. 2015, Bisi et al. 2018). Indeed, a number of studies (Table 1, supplemental file) suggested that many of these factors, in addition to hunting, might have affected the spatial behavior of this species.

Several studies (Dexter 1996, Keuling 2009, Tolon et al. 2009) stated that the impact of hunting on wild pig behavior might depend on the level of human disturbance that animals have experienced. This highly adaptable species seems to respond to human disturbance by adopting behaviors that minimize interference (Russo et al. 1997, Keuling 2009, Tolon et al. 2009, Podgórski et al. 2013, Thurfjell et al. 2015, Stillfried et al. 2017, Johann et al. 2020*a*). For instance, where hunting pressure is constant and high, animals may respond by hiding or laying still until the hunters have moved away. Conversely, inexperienced animals, or animals in areas where hunting is a less predictable event, might expand their movements further in response to culling and thus increase their impact on neighboring areas. This is particularly relevant to disease transmission, as demonstrated in other wildlife species.

Conclusion

The review highlighted numerous knowledge gaps that should be addressed to establish in which contexts and how recreational hunting may affect spatial and social behavior of wild pigs. Without this knowledge, the trade-off between employing hunters to limit disease transmission and the risk of the geographic spread of the disease remains unknown. The incorporation of social and spatial behavior into disease ecology appears urgent, as unintended behavioral effects must be known to prevent any population control resulting in adverse effects (Mysterud et al. 2020). Behavioral changes might also increase the economic and environmental impact of wild pigs if animals move to new areas and expand their range, particularly if the species is occurring as isolated populations or as non-native wildlife.

Future studies should focus on quantifying spatial behavior before, during, and after hunting, on assessing the separate effects of factors such as season and food availability, on wild pig spatial and social behavior, and on addressing how different types and frequency of hunting affect spatial and social behavior, including contact patterns. Information on hunting effort (expressed as number of hunters, time spent hunting, frequency of hunting events, dogs, beaters), type of hunting method, duration of hunting season, size of area, animal density, and day and/or night hunting are needed.

The long-term (at least in months) effects of hunting on animal spatial and social behavior should also be investigated. In addition, the landscape context, with details on the size and location of hunting grounds versus location of reserves where hunting is not allowed, should be taken into account. In some instances, like in the recent outbreaks of ASF that led to significant depopulation of wild pigs from large areas, the above data could be collected with relatively little additional effort (Morelle et al. 2020).

The original question "Does hunting affect the behavior of wild pigs?" should be re-framed to take into account factors that might affect changes in social and spatial behavior. Understanding these factors will help to optimize interventions to minimize wild pig–human conflicts.

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Supplemental materials

Table 1 can be viewed as a supplemental file download at https://digitalcommons.usu.edu/hwi/vol15/iss1/11.

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