Invasive Wild Pigs in North America
Ecology, Impacts, and Management

Wild Pig Spatial Ecology and Behavior

Publication details
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Published online on: 07 Jan 2019

Accessed on: 13 Jul 2021
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3.1 INTRODUCTION

The behaviors and spatial ecology of invasive wild pigs (Sus scrofa) in modern North America reflect the capacity for wildlife to evolutionarily adapt, develop complex behaviors honed from interactions with the environment, survive, and in some cases thrive in increasingly human-dominanted landscapes. Biologically, wild pigs reach sexual maturity at a young age, are capable of farrowing large litters, breed year-round (Comer and Mayer 2009), and have high survivability in the wild (see Chapter 4). Behaviorally, wild pigs exhibit substantial plasticity and can readily adjust life history strategies in response to their surroundings. For example, in urban landscapes wild pigs increase nocturnal activity to minimize their interactions with humans (Hanson and Karstad 1959, Podgórska et al. 2013). Furthermore, as dietary generalists (Senior et al. 2016) wild pigs can readily adapt to a variety of environments (Baskin and Danell 2003) and these attributes help make wild pigs successful invaders in novel environments.

The spatial ecology of wild pigs is highly varied across their North American range. Wild pigs are capable of traversing long distances in short amounts of time (Lapidge et al. 2004) and can move fluidly (and often undetected) through a variety of landscapes. Depending on geographic location, wild pigs can be found utilizing a diversity of vegetation types and features. The underlying motivations
associated with space use in wild pigs include interactions among available forage, cover, breeding condition, social structure, and their need to thermoregulate. Therefore, spatial and temporal patterns of landscape use for wild pigs illustrate highly variable and complex life-history strategies, making efforts to describe scalable principles (i.e., across space and time) on wild pig behaviors challenging.

In this chapter, we summarize information on the behaviors and spatial ecology of wild pigs in North America. Although our focus is on free-ranging pigs, we include relevant research on captive animals and from other wild pig populations worldwide, both native and non-native, to provide a thorough synthesis of the primary topics concerning behaviors and the spatial ecology of wild pigs. Consistent with other chapters in this book, we refer to pigs within and outside of their native ranges as wild boar and wild pigs, respectively.

### 3.2 BEHAVIORS

#### 3.2.1 Social Organization

Most of what is known about the social organization of wild pigs stems from research on native and invasive populations occurring outside of North America. Wild pigs are a highly social species with matrilineal group structure often consisting of multiple generations of females and their young, referred to as sounders (Spitz 1986, Kaminski et al. 2005). After birthing, daughters will primarily remain with their mother. However, in some instances, yearling females will leave to form sister groups and pursue reproductive opportunities (Kaminski et al. 2005). Genetic and spatial structure analyses of wild boar social groups confirmed that individuals closely associated in space were often inter-related (Poteaux et al. 2009). Yet social groups are flexible and their composition can fluctuate over time (Ilse and Hellgren 1995a). In fact, female groups maintain a fission-fusion society, where individuals form sub-groups that readily merge and separate, thereby exchanging individuals (Gabor et al. 1999), although the mechanisms regulating the fission-fusion process of social groups are poorly understood. Adult males are mostly solitary but younger males are sometimes observed in bachelor groups (Braza and Alvarez 1989, Fernández-Llario et al. 1996). Furthermore, structure of wild boar social groups apparently affects individual willingness to incur risk (Focardi et al. 2015). Adult males, yearlings, and piglets will enter potentially risky areas first, allowing for a foraging advantage, with adult and sub-adult females being more risk averse (Focardi et al. 2015). Additionally, larger social groups had longer effective foraging times than smaller groups (Focardi et al. 2015). In North America, the social organization of wild pigs is comparable to what has been observed in native populations, but anecdotal evidence suggests variability among regions (e.g., larger groups in areas of the southwest United States), but the mechanisms regulating group structure in North America remain poorly understood.

#### 3.2.2 Territoriality

Territoriality has been observed in several different contexts for wild pigs, however this remains a topic in need of further inquiry. Males are often solitary and grapple with other males for access to resources and mating opportunities (Graves 1984, Mayer 2009). For females, increased territoriality has been observed during the farrowing period, when a female will actively defend a nesting area from predators and conspecifics (Graves 1984, Fernández-Llario 2004). Territoriality has also been observed among female social groups, presumably to ensure access to resources. In Fort Benning, Georgia, individual females within a sounder exhibited extensive home range overlap whereas each respective sounder often occupied an exclusive area (Sparklin et al. 2009). However, the precise mechanisms influencing territoriality remain unclear, and variation in this behavior may correspond to geographic location, density, resource availability, and climate. We caution that results from Sparklin et al. (2009) were based on a limited sample, but their findings provide initial insights into territorial behavior among sounders. This phenomenon was also observed in Texas, where it was hypothesized that territoriality was necessary due to poor habitat quality, high population density, and limited access.
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3.2.3 Rooting

Wild boar are known to adjust foraging strategies to take advantage of seasonally available food resources (Sandom et al. 2013). One of the primary modes of foraging is through rooting, where individuals will upturn soil using their spade-like snouts in search of subterranean food. Rooting can vary in intensity, from sifting through surface leaf-litter to deeply excavating large areas (Figure 3.1). Wild pigs use their superior sense of smell and sensitivity of their snout to explore and understand the areas they occupy.

Where wild pigs choose to root can vary seasonally, again based on food availability (Baron 1982, Sandom et al. 2013). Wild pigs tend to root in saturated areas (e.g., swamps and lowlands), presumably because the soil structure is more pliable (Mitchell and Mayer 1997, Welander 2000). There seems to be a tendency to root in these areas during the summer or in geographic regions that feature a wet season, but rooting has also been noted during times of low mast production (Graves 1984). Across landscapes, rooting tends to occur at higher frequency during winter and spring, likely due to the decreased availability of aboveground food (Wilson 2004, Sandom et al. 2013). During these seasons, rooting will commonly occur along ridgelines and in areas where mast is plentiful (Stegeman 1938, Barrett 1982). During years of poor acorn crops, wild pigs will shift their activity to exploit alternative food sources. For example in the Great Smoky Mountains National Park, wild pigs were observed to shift their activity to beech (Fagus spp.) forests where intensive rooting was observed (Bratton et al. 1982). Wild pigs will also revisit previously disturbed areas rather than root a new site (Groot Bruinderink and Hazebroek 1996, Parkes et al. 2015), presumably related to the quantity and quality of forage at these locations. In a coastal dune system on St. Catherine’s Island, Georgia, wild pigs returned to previously rooted sites approximately every 5 years (Oldfield and Evans 2016).

3.2.4 Diet

Wild pigs are omnivorous and opportunistic (Stegeman 1938, Sweeney et al. 2003), a strategy that allows them to utilize a variety of food resources. In fact, the ability of this species to adapt and 

FIGURE 3.1 Forest floor rooting in the central Lower Peninsula of Michigan detailing (a) low-intensity and (b) high-intensity rooting events. (Photos by S. Gray. With permission.)
opportunistically exploit resources is one of the reasons why wild pigs are such successful invaders and are found in so many areas worldwide (Senior et al. 2016). Furthermore, the diet of wild pigs fluctuates by season and spatial location (Table 3.1). Throughout both their native and invasive ranges, wild pig diets principally rely upon plant matter (Schley and Roper 2003, Ballari and Barrios-García 2014). Wild pigs eat subterranean foods such as roots and bulbs (Giménez-Anaya et al. 2008, Schlichting et al. 2015), but consumption of these items is more common between fall and early summer when other food sources are scarce (Dardaillon 1987). When available, acorns appear to be a common food item (Sjarmidi et al. 1996, Elston and Hewitt 2010), as wild pigs will scour forest stands and ridgelines where hard mast is abundant (Stegeman 1938, Barrett 1982). A review of diets throughout the native range indicated that mast, such as acorns and similar energy-rich food items, were a staple in most wild boar diets (Schley and Roper 2003). Wild pig diets tend to be low in energy, high in fiber, and often seasonally deficient in protein (Baber and Coblentz 1987). To offset protein deficiency, wild pigs may rely heavily on animal matter (Wilcox and Van Vuren 2009).

**TABLE 3.1**
Percent Composition of Material by Volume in Wild Pig Diets in the United States

<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Percent Composition of Diet</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>South</td>
<td>Great Smoky Mountains National Park, NC/TN</td>
<td>84.6–99.3, 0.0–18.6, 0.7–10.8</td>
<td>Ackerman et al. (1978)</td>
</tr>
<tr>
<td>South</td>
<td>Davis Mountains, TX</td>
<td>97.5, 2.5</td>
<td>Adkins et al. (2006)</td>
</tr>
<tr>
<td>South</td>
<td>Horn Island, Gulf Islands National Seashore, MS</td>
<td>77.5, 18.8</td>
<td>Baron (1979)</td>
</tr>
<tr>
<td>West</td>
<td>Dye Creek Ranch, Tehama County, CA</td>
<td>98.4, 1.6</td>
<td>Barrett (1978)</td>
</tr>
<tr>
<td>West</td>
<td>Kipahulu Valley, Maui, HI</td>
<td>93.2, 6.8</td>
<td>Diong (1982)</td>
</tr>
<tr>
<td>South</td>
<td>Yturria Ranch, Willacy County, TX</td>
<td>95.2, 4.8</td>
<td>Everitt and Alaniz (1980)</td>
</tr>
<tr>
<td>West</td>
<td>Island of Hawaii, HI</td>
<td>93.0–96.0, 4.0–7.0</td>
<td>Giffin (1970)</td>
</tr>
<tr>
<td>West</td>
<td>Mendocino County, CA</td>
<td>71.5, 28.5</td>
<td>Grover (1983)</td>
</tr>
<tr>
<td>South</td>
<td>Tellico Wildlife Management Area, TN</td>
<td>89.4, 6.4, 4.2</td>
<td>Henry and Conley (1972)</td>
</tr>
<tr>
<td>South</td>
<td>Great Smoky Mountains National Park, NC and TN</td>
<td>98.0, 2.0</td>
<td>Howe et al. (1981)</td>
</tr>
<tr>
<td>West</td>
<td>Monterey, San Luis Obispo, and San Benito Counties, CA</td>
<td>80.9–94.2, 5.8–19.1</td>
<td>Pine and Gerdes (1973)</td>
</tr>
<tr>
<td>South</td>
<td>Great Smoky Mountains National Park, NC and TN</td>
<td>99.1, 0.3, 0.2</td>
<td>Scott and Pelton (1975)</td>
</tr>
<tr>
<td>South</td>
<td>Cottle, Dickens, Foard, King, and Motley Counties, TX</td>
<td>98.4, 1.7</td>
<td>Schlichting et al. (2015)</td>
</tr>
<tr>
<td>South</td>
<td>Aransas National Wildlife Refuge, TX</td>
<td>75.0–83.9, 1.7–14.6, 16.1–25.0</td>
<td>Springer (1975)</td>
</tr>
<tr>
<td>South</td>
<td>Chaparral Wildlife Management Area, TX</td>
<td>93.0, 6.7, 0.3</td>
<td>Taylor and Hellgren (1997)</td>
</tr>
<tr>
<td>South</td>
<td>Hobcaw Barony, SC</td>
<td>83.0–97.4, 0.8–11.7, 1.3–5.6</td>
<td>Wood and Roark (1980)</td>
</tr>
</tbody>
</table>

* Diets reported as percentages using point frame sampling techniques described in Chamrad and Box (1964).

Source: Adapted from Ditchkoff and Mayer (2009).
Compared to plant matter, animal matter makes up a considerably smaller proportion of wild pig diets (Table 3.1). However, the occurrence of animal matter in wild boar diets is common (Irizar et al. 2004, Giménez-Anaya et al. 2008). Wild pigs will consume invertebrates, birds, herptiles, small and large mammals, and carrion. In fact, wild pigs have been shown to be efficient members of the scavenging community (Turner et al. 2017). One of the most common animal components consumed by wild pigs is earthworms (Hanson and Karstad 1959, Challies 1975). Wild pigs appear to exploit animal food resources based on availability. For example, in Spain, wild boar consumed more birds frequently during the molting period when juvenile birds were both accessible and easily preyed upon (Giménez-Anaya et al. 2008). In the southeastern United States, wild pigs were observed targeting herpetofauna when they were vulnerable during the breeding season (Jolley et al. 2010). Overall, animal protein may play an important role in the growth and survival of wild pigs (Schley and Roper 2003), and an absence of these proteins could degrade body condition (Klaas 1992). We note that while wild pigs will also consume fungi, in most seasons this makes up a small proportion of the overall diet (Fournier-Chambrillon et al. 1995, Baubet et al. 2004), but we caution that the presence of fungi is difficult to assess via dietary studies (Schley and Roper 2003) unless using molecular methods. It is also worth noting that wild boar are notorious for their ability to locate truffles, which aids in truffle dispersal and survival (Piattoni et al. 2014). According to a review of wild pig diets in the native and invasive ranges, it appears that animal matter and fungi are consumed in greater quantities in the invasive range (Ballari and Barrios-García 2014).

In landscapes where agriculture is abundant, wild pigs may heavily use this resource. Their use of crop fields has been documented mainly during the summer and fall months (Sparklin et al. 2009, Schlichting et al. 2015), after fields have been recently planted or when crops are mature. For example, in the plains of Texas, crops were an abundant dietary item throughout the year with peak consumption occurring in the fall (>60% of the total diet; Schlichting et al. 2015). In an agroecosystem of Spain, wild boar primarily fed on crops, with ~77% of the diet by volume consisting of corn (Herrero et al. 2006). Taller crops such as cereal, wheat, and corn are favored during the late summer months as these crops provide both food and shelter (Labudzki et al. 2009). When crops are available, some wild pig populations will exclusively feed and reside in agricultural fields. In an assessment of damage caused by wild boar in the native range, frequently damaged crop types included oats, rye, and potatoes with a distinct preference for oats (Andrzejewski and Jezierski 1978), while other studies found high amounts of maize, wheat, barley, and alfalfa in wild pig diets (Herrero et al. 2006, Gentle et al. 2015). However, it is important to note that some of these dietary relationships may strictly be driven by the availability of crops in the landscape.

### 3.2.5 Wallowing

Wallowing, where an individual will cover its body in mud, is a common behavior exhibited by wild pigs. The primary function of this behavior is to reduce body temperature and protect against potentially harmful insects and parasites (Eisenberg and Lockhart 1972, Frädrich 1974, Díong 1982). Wallows can be naturally inundated shallow depressions or may be created via rooting (Figure 3.2). Wallows tend to be oval in shape and frequently occur along trails, streams, and areas of slow moving or standing water (Belden and Pelton 1976). Moreover, wild pigs seek wallows in areas that are cool, wet, and shaded (Stegeman 1938). These areas can often be identified by trampled and muddy vegetation near the wallowing site (Stegeman 1938). Wallows are used most frequently during the summer (Crouch 1983). However, in some instances wallows are used year-round, even in cold weather months, and may be visited repeatedly by individuals or groups (Stegeman 1938). In Spain, mature males primarily used wallows during the rutting period (October-February), which suggests wallowing might also serve a sexual function (Fernández-Llario 2005). The duration of wallowing is variable but individuals will often remain in wallows longer when temperatures are warm (Graves 1984). In fact, during times of the year when temperatures are high, wild pigs will spend the entire diurnal period wallowing before moving to shade in the early evening (Graves 1984).
Rubbing and tusking behaviors are performed as a method of self-grooming to remove mud, hair, and ectoparasites (Conley et al. 1972, Graves 1984). It has also been suggested that these behaviors might serve as a method for marking territory (Conley et al. 1972) but additional research is needed. Rubbing is often performed near wallows where an individual will remove excess mud using the base of a nearby tree. Rubbing is conducted on a variety of objects as long as they are sturdy and upright, but preference has been shown for smaller diameter (<15 cm) pines (Stegeman 1938). Wild pigs have also been observed rubbing against creosote-soaked poles (Campbell and Long 2009) and, in some cases, this behavior is vigorous enough to cause damage (Figure 3.3).

Similar in function to rubbing, tusking is when an individual will use its tusks to scrape a tree causing it to release sap or pitch, which is then rubbed against to serve as a deterrent to ticks and lice (Graves 1984). Tusking can vary from a single slash to prolonged and repeated tusking events (Graves 1984), which can result in tree mortality in extreme cases (Stegeman 1938). Of the few studies on tusking, preferred trees are pine and hemlock (Graves 1984), and access to pitch is considered to be one of the main drivers of this behavior (Stegeman 1938).
3.2.7 Bedding

Wild pigs will opportunistically bed in shallow depressions or construct beds for resting (Figure 3.4). Beds share similarities to farrowing nests and can be difficult to differentiate (Figure 3.4); however, resting beds tend to be smaller in size (Mayer et al. 2002), and are often less structurally complex (Frädrich 1974). Resting beds will often be rooted to expose mineral soil, and sometimes are lined with plant material, although this is more common in beds occupied during cold-weather months (Conley et al. 1972, Mayer et al. 2002). Beds are frequently placed along ridgelines and in areas with dense cover (Stegeman 1938, S. M. Gray, Applied Forest and Wildlife Ecology Laboratory, Michigan State University, personal observation). These areas are often heavily shaded and a single bed may be occupied by one or more individuals (Hanson and Karstad 1959). When resting, wild pigs will remain in close physical contact with others sharing the same bed (Hediger 1950, 1955). Many times a bed will be used more than once and some individuals will use the same bed repeatedly (Frädrich 1974, S. M. Gray, personal observation).

3.2.8 Scent Marking

Wild pigs have several glands located on their body that they use for scent marking. The most studied glands are the carpal glands that occur in a series along the posterior of the forefeet (Farnesi et al. 1999, Bacchetta et al. 2007). These glands are found in both males and females, and are often larger in mature individuals (Heise-Pavlov et al. 2005, Bacchetta et al. 2007). Carpal glands likely function as a means of intra-sounder communication and serve as a method for delineating territories and facilitating reproduction (Graves 1984, Bacchetta et al. 2007). Furthermore, it may be possible to utilize carpal gland secretions to affect wild pig behavior. In captive trials, study subjects were attracted to and investigated carpal gland secretions collected from unknown individuals.
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(B. S. Schmit, USDA/APHIS/WS/National Wildlife Research Center, personal communication). However, additional research on the function of carpal glands is necessary.

There are also several glands that occur on the upper lip of wild pigs that are concentrated around the tusks. Use of these glands primarily occurs when an individual is tusking and they are rubbed against a tree or associated object. Wild pigs also mark areas by generating saliva, which helps release the scent associated with these glands (Diong 1982). These submaxillary glands appear to serve a sexual function, as their removal hinders the ability of males to induce the mating stance in females and these individuals consequently had lower libido (Perry et al. 1980). The preputial gland is found in males near the distal end of the penis (Mayer 2009). Secretions from this gland emit a scent called “muskone” (Barrett 1978), a foul-smelling odor that is commonly associated with males (Mayer 2009). Marking via this gland occurs during urination and has also been observed during carpal marking (Mayer 2009). Excretions from the preputial gland are believed to play a role in mating and dominance, as dominant males have been found to scent mark more frequently with this gland than subordinate males after being in close proximity to multiple females (Mayer and Brisbin 1986). Preorbital glands are found below the eye. Overall, there is limited information on this gland and its associated function, however it may play a role in reproduction. Females will use these glands to mark objects, primarily trees, during the time leading up to estrus (Meynhardt 1982). Wild pigs have several other glands but the purpose of these glands in scent marking remains largely unknown (Groves and Giles 1989).

3.2.9 Vigilance

Wild pigs will exhibit vigilance behaviors to detect and escape from potential predators or sources of anthropogenic disturbance. Research on vigilance behavior has primarily been conducted on wild boar populations in their native range. When assessing vigilance behavior, Quenette and Desportes (1992) observed an oscillating pattern of long and short scanning events, rather than a random scanning pattern. The temporal pattern of this behavior varied by individual, and increasing the number of conspecifics lowered overall vigilance in individuals (Quenette and Desportes 1992). Similarly in Poland, Podgórski et al. (2016) noted that wild boar spent a small proportion of time exhibiting vigilance behaviors. The authors further noticed that vigilance varied seasonally, where wild boar were less vigilant during seasons featuring limited access to food resources (Podgórski et al. 2016). In both wild and captive studies, collective vigilance was found to decrease with increasing group size (Quenette and Gerard 1992, Podgórski et al. 2016). Additionally, Focardi et al. (2015) found the presence of conspecifics improved foraging efficiency in adult males since other individuals frequently resided near the periphery of the group and shared the burden of vigilance. Due to a lack of natural predators in North America, it can be argued that vigilance of wild pigs may substantially differ from what has been observed in the native range. Thus, further research is needed to better understand the role of vigilance in wild pigs inhabiting North America.

3.3 Spatial Ecology

3.3.1 Home Range

Multiple studies on wild pig home ranges exist throughout North America (Table 3.2). Wild pigs exhibit notable variation in home range sizes among geographic regions, with these differences oftentimes attributed to biotic (e.g., vegetation types, pig densities, human activity, sex, age) and abiotic (e.g., distribution of water or roads, climate, weather, season) factors. Additionally, it is noteworthy that different methods used to calculate home ranges vary in strengths and weaknesses and thereby, will yield variable estimates (Kernohan et al. 2001). This makes comparisons of home ranges among studies that use different estimators difficult. A second issue is that studies of home ranges are often conducted over different time scales or at different times during the year,
## TABLE 3.2
List of Home Range Sizes Reported for Wild Pigs in the United States Organized by Study, Sex, Region, and Method

<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Female (n)</th>
<th>Male (n)</th>
<th>Method&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>South</td>
<td>Davis County, TX</td>
<td>28.3 (6)</td>
<td>35.0 (7)</td>
<td>95% MCP</td>
<td>Adkins and Harveson (2007)</td>
</tr>
<tr>
<td>South</td>
<td>Davis County, TX</td>
<td>43.4 (6)</td>
<td>58.7 (7)</td>
<td>95% AK</td>
<td>Adkins and Harveson (2007)</td>
</tr>
<tr>
<td>West</td>
<td>Santa Catalina Island, CA</td>
<td>1.5 (4)</td>
<td>2.4 (6)</td>
<td>95% utilization contour</td>
<td>Baber and Coblenz (1986)</td>
</tr>
<tr>
<td>West</td>
<td>Santa Catalina Island, CA</td>
<td>0.7 (4)</td>
<td>1.4 (6)</td>
<td>MCP</td>
<td>Baber and Coblenz (1986)</td>
</tr>
<tr>
<td>West</td>
<td>Dye Creek Ranch, CA</td>
<td>10.0–25.0</td>
<td>50.0+</td>
<td>–</td>
<td>Barrett (1978)</td>
</tr>
<tr>
<td>South</td>
<td>Kleberg and San Patricio Counties, TX</td>
<td>1.3–5.5 (4–7)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.3–5.5 (5–9)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>95% FK</td>
<td>Campbell et al. (2010)</td>
</tr>
<tr>
<td>South</td>
<td>San Patricio County, TX</td>
<td>0.7–1.4 (10)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>–</td>
<td>95% FK</td>
<td>Campbell et al. (2012)</td>
</tr>
<tr>
<td>South</td>
<td>Savannah River Plant, SC</td>
<td>7.9 (4)</td>
<td>14.0 (3)</td>
<td>MCP</td>
<td>Crouch (1983)</td>
</tr>
<tr>
<td>West</td>
<td>Kipahula Valley, Maui, HI</td>
<td>1.1 (4)</td>
<td>2.0 (5)</td>
<td>MCP</td>
<td>Diong (1982)</td>
</tr>
<tr>
<td>Central Southern MO</td>
<td></td>
<td>4.7 (7)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>3.8 (6)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>MKDE</td>
<td>Fischer et al. (2016)</td>
</tr>
<tr>
<td>South</td>
<td>Congaree National Park, SC</td>
<td>1.9 (9)</td>
<td>2.2 (7)</td>
<td>95% FK</td>
<td>Friebel and Jodice (2009)</td>
</tr>
<tr>
<td>South</td>
<td>Congaree National Park, SC</td>
<td>1.4 (9)</td>
<td>1.5 (7)</td>
<td>100% MCP</td>
<td>Friebel and Jodice (2009)</td>
</tr>
<tr>
<td>South</td>
<td>Lowndes County, AL</td>
<td>4.0 (6)</td>
<td>4.0 (5)</td>
<td>95% AK</td>
<td>Gaston et al. (2008)</td>
</tr>
<tr>
<td>North</td>
<td>Central Lower Peninsula, MI</td>
<td>1.3 (6)</td>
<td>3.0 (2)</td>
<td>BBMM</td>
<td>S. M. Gray, unpublished data</td>
</tr>
<tr>
<td>West</td>
<td>Dye Creek Ranch, CA</td>
<td>1.5 (3)</td>
<td>–</td>
<td>Modified MCP&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Grover (1983)</td>
</tr>
<tr>
<td>South</td>
<td>Grenada County, MS</td>
<td>3.8–15.1 (1–4)</td>
<td>2.1–8.1 (3–6)</td>
<td>MCP</td>
<td>Hayes et al. (2009)</td>
</tr>
<tr>
<td>South</td>
<td>Savannah River Plant, SC</td>
<td>5.7 (5)</td>
<td>13.6 (6)</td>
<td>MCP</td>
<td>Hughes (1985)</td>
</tr>
<tr>
<td>South</td>
<td>Savannah River Plant, SC</td>
<td>4.4 (1)</td>
<td>5.3 (4)</td>
<td>Modified MCP&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Kurz and Marchinton (1972)</td>
</tr>
<tr>
<td>South</td>
<td>Savannah River Plant, SC</td>
<td>2.5 (2)</td>
<td>4.0 (2)</td>
<td>MCP</td>
<td>J. J. Mayer, unpublished data</td>
</tr>
<tr>
<td>South</td>
<td>TXU Corporation’s Big Brown Mine, TX</td>
<td>6.5 (10)</td>
<td>15.8 (6)</td>
<td>MCP</td>
<td>Mersinger and Silvy (2007)</td>
</tr>
<tr>
<td>South</td>
<td>Kent County, TX</td>
<td>23.9 (11)</td>
<td>52.2 (3)</td>
<td>MCP</td>
<td>Schlichting et al. (2016)</td>
</tr>
<tr>
<td>South</td>
<td>Great Smoky Mountain National Park, NC/TN</td>
<td>2.7–3.5 (4)</td>
<td>3.8–3.9 (9)</td>
<td>MCP</td>
<td>Singer et al. (1981)</td>
</tr>
<tr>
<td>South</td>
<td>Fort Benning Military Reservation, AL/GA</td>
<td>–</td>
<td>2.0–3.7 (4–5)&lt;sup&gt;f&lt;/sup&gt;</td>
<td>95% K</td>
<td>Sparklin et al. (2009)</td>
</tr>
<tr>
<td>West</td>
<td>Santa Cruz Island, CA</td>
<td>1.0 (5)</td>
<td>1.4 (5)</td>
<td>–</td>
<td>Sterner (1990)</td>
</tr>
<tr>
<td>South</td>
<td>Hobcaw Barony, SC</td>
<td>1.8 (3)</td>
<td>2.3 (3)</td>
<td>MCP</td>
<td>Wood and Brenneman (1980)</td>
</tr>
<tr>
<td>South</td>
<td>Southern TX</td>
<td>4.6–17.2 (5–6)</td>
<td>7.7–19.4 (5–10)</td>
<td>95% K</td>
<td>Wyckoff et al. (2012)</td>
</tr>
</tbody>
</table>

<sup>a</sup> Abbreviations for commonly used methods to estimate home range: BBMM = Brownian Bridge Movement Models, MCP = Minimum Convex Polygon (100%), 95% MCP = 95% Minimum Convex Polygons, 95% AK = 95% Adaptive Kernel, 95% FK = 95% Fixed Kernel, 95% K = 95% Kernel, MKDE = Movement-based Kernel Density Estimator.

<sup>b</sup> Mean home ranges pooled across sex and study area.

<sup>c</sup> Mean home ranges of control population pooled by sex.

<sup>d</sup> Mean home ranges of control population.

<sup>e</sup> Modified version of minimum convex polygon using ⅛ of an individual’s range to test for outlying points (Harvey and Barbour 1965).

<sup>f</sup> Home range estimates for controls. Sample size corresponds to sounders rather than individuals. Use of individual and multiple animals per sounder in some home range estimates.

**Source:** Adapted from Mayer (2009).
introducing additional challenges in comparing home range estimates across studies since wild pigs may alter their movements depending on season (Kay et al. 2017). Telemetry studies are also further complicated by the difficulty in equipping and maintaining collars attached to wild pigs, as these animals grow rapidly and their behaviors (e.g., rubbing, wallowing) can hinder collar performance and lead to potential malfunction (see Chapter 9).

Home ranges for wild pigs in the United States have previously been summarized by Mayer (2009) and Schlichting et al. (2016), as well as in this chapter (Figure 3.5; Table 3.2). To date, individual radio telemetry studies have generally been based on <10 individuals (by sex) and used 95% minimum convex polygon (MCP) or kernel methods to estimate home range sizes (Table 3.2). One exception is Kay et al. (2017) that reanalyzed global positioning system (GPS) data from 226 wild pigs from 14 different studies across the southern United States to compare home range size estimators (MCP versus autocorrelated kernel density estimator (AKDE); Figure 3.5) and analyze determinants of home range size. AKDE is a novel kernel approach that accounts for temporal autocorrelation that is inherent in GPS data (Fleming et al. 2015). On average, wild pig monthly MCP home ranges in the southern United States are 3.4 km² (sd = 4.6 km²) with an overall home range size of 6.1 km² (sd = 7.8 km²; Kay et al. 2017). In comparison, average overall wild pig home ranges using AKDE were 12.4 km² (sd = 21.0 km²). Seasonal variations in home range sizes are well documented, with most differences attributed to changes in food (Calenge et al. 2002, Hayes et al. 2009) or water availability (Kay et al. 2017). For example, Singer et al. (1981) found a 3-fold increase in home range sizes of wild pigs during winters following a mast failure, compared to winters following good mast years. Similarly, in Mississippi, home ranges were larger during the dry season than in the wet season when food was more abundant (Hayes et al. 2009). Indeed, telemetry evidence suggests sounders will exclude other groups from core areas in environments with more dense wild pig populations (Sparklin et al. 2009), but this pattern may not be consistent for individual animals (Baber and Cobler 1986, Boitani et al. 1994). Generally, home range size tends to non-linearly decrease as density of conspecifics increases (Saunders and McLeod 1999), with apparent density-dependent effects occurring when wild pig densities were <9 pigs/km² (Figure 3.6; Table 3.3). However, exceptions to this pattern exist (e.g., agricultural landscapes of Belgium; Morelle and Lejeune 2014), likely related to variation in nutritional carrying capacity of the occupied areas.
Wild pig home range sizes also vary by sex. Generally, home ranges of males are 3.5–5 km² larger than females in North America (Kay et al. 2017), although most of this information stems from research in the southern United States. These trends have also been observed in the invasive populations of Australia (Caley 1997, Morini et al. 2014). Differences in home range sizes between sexes may be related to differences in body mass (Saunders and McLeod 1999), but behavior also plays a role. This pattern is especially true during the breeding season, when males will travel long distances to secure mating opportunities. However, it is worth noting that differences in home range sizes between sexes are not always evident (South Carolina: Wood and Brenneman 1980; Italy: Massei et al. 1997).

For wild pigs, younger individuals appear to use larger home ranges than adults, likely related to younger individuals exploring and establishing territories (Alabama: Gaston et al. 2008; Germany: Keuling et al. 2008a). This was particularly noticeable in females (New Zealand: McIlroy 1989) and in younger individuals during the hunting season (France: Calenge et al. 2002). Younger wild boar tend to flush more easily compared to adults, potentially contributing to larger home ranges for younger animals when subjected to hunting pressure (Maillard et al. 1996).

The shape of wild pig home ranges varies, but has generally been described as circular to elongate, depending on topography, human activity, and the distribution of food and other pigs, among other factors (Singer et al. 1981, McIlroy 1989). Wild pig home range shapes can vary by season, with summer home ranges being more circular than winter (Singer et al. 1981), but these patterns may differ depending on the analytical method being used. Furthermore, natural and anthropogenic features such as roads, rivers, and railways can also contribute to the overall shape of wild pig home ranges.

Wild boar home ranges typically consist of a high-use (core) area, which is used for resting, and peripheral areas that are primarily used for feeding (Boitani et al. 1994). Core areas are often small.
and provide dense cover, with some potential variation among sexes. For example, core areas of males were more heterogeneous and used less frequently compared to females in Italy (Boitani et al. 1994). Males tend to use portions of their home ranges more widely while female movements are more concentrated (Wood and Brenneman 1980, Boitani et al. 1992).

Most wild pig populations worldwide are subjected to population control and hunting, and researchers have documented the ways in which these events have impacted home ranges. In response to aerial gunning in Texas, Campbell et al. (2010) did not observe differences in home range sizes before and after control events. Similarly, researchers in Missouri found that wild pig home range centroids did not shift following pursuit by dogs, hunters, helicopters, or after trap-and-release events, although core home range area shrunk and diurnal movement distances increased.

### TABLE 3.3
Description of Density Calculation Methods, Reported Densities, Home Range Sizes by Sex, and Home Range Estimators Used in Published Research on Wild Pigs

<table>
<thead>
<tr>
<th>Calculation method</th>
<th>Avg. Pigs/km²</th>
<th>Male</th>
<th>Female</th>
<th>Estimator</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capture-recapture techniques, computed using program CAPTURE by dividing estimate of population size by area of use</td>
<td>28</td>
<td>1.4</td>
<td>0.7</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Calculated using removal methods, observation, comparison between communities, and program CAPTURE</td>
<td>28</td>
<td>1.6</td>
<td>0.9</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Unknown</td>
<td>37</td>
<td>2</td>
<td>1.1</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Unknown</td>
<td>15</td>
<td>2.3</td>
<td>1.8</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Unknown</td>
<td>2</td>
<td>10.7</td>
<td>4.9</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Combination of mark-recapture, observation, and the ratio method</td>
<td>3</td>
<td>33.5</td>
<td>24.1</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Unknown</td>
<td>2</td>
<td>35</td>
<td>11.1</td>
<td>MCP</td>
<td>Saunders and McLeod (1999)</td>
</tr>
<tr>
<td>Unknown</td>
<td>4.85</td>
<td>3.85</td>
<td>3.1</td>
<td>MCP</td>
<td>Singer et al. (1981)</td>
</tr>
<tr>
<td>Based on number of individuals captured/total area</td>
<td>0.65</td>
<td>35</td>
<td>28.3</td>
<td>95% MCP</td>
<td>Adkins and Harveson (2007)</td>
</tr>
<tr>
<td>Based on number of individuals captured/total area</td>
<td>0.65</td>
<td>58.7</td>
<td>43.4</td>
<td>95% AK</td>
<td>Adkins and Harveson (2007)</td>
</tr>
<tr>
<td>Unknown</td>
<td>6.5</td>
<td>3.4</td>
<td>3.4</td>
<td>95% AK</td>
<td>Campbell et al. (2010)</td>
</tr>
<tr>
<td>Program MARK abundance estimate/avg. effective sampling area</td>
<td>1.2</td>
<td>—</td>
<td>2.85</td>
<td>95% K</td>
<td>Sparklin et al. (2009)</td>
</tr>
</tbody>
</table>

---

a Method found in Baber and Coblentz (1986).
b Method found in Coblentz and Baber (1987).
c Method found in Caley (1993).
d Value found in Singer et al. (1981).
e Method found in Ilse and Hellgren (1995b).
f Method and value found in Hanson (2006).
suggesting some fluctuations in space use in response to harassment (Fischer et al. 2016). However, individual pig response to hunting pressure can be mixed. After drive hunts in Germany, some individuals increased while others reduced the size of their resting ranges (Sodeikat and Pohlmeyer 2007). Although it is generally accepted that wild boar avoid human activity, they will move into human-dominated areas to exploit anthropogenic food sources and agriculture when other forage is scarce (Bieber and Ruf 2005, Cahill et al. 2012).

3.3.2 HABITAT USE AND SELECTION

Habitat use is broadly concerned with the distribution of individuals throughout landscapes (Hutto 1985). Habitat selection is the behavioral response exhibited by individuals where a particular area is selected in favor of other areas (Hutto 1985, Block and Brennan 1993). In wild pigs, habitat use and selection can widely vary since this species is a generalist and has the ability to thrive in a diversity of environments. As such, wild pigs primarily use habitats in relation to their availability in the landscape (Ilse and Hellgren 1995b, Gabor et al. 2001), but seasonal differences exist (Baber and Coblentz 1986, Keuling et al. 2009). However, trends in resource selection by wild pigs will become clearer as research is conducted using GPS data and robust analytical techniques at multiple spatial and temporal scales.

As with most animals, the primary determinants of wild pig distributions are the availability of water, food, and cover (McIlroy 1989). Wild pigs will respond to fluctuations in these components by spatially adjusting their habitat selection to capitalize upon seasonally available resources (Germany: Keuling et al. 2009b; Texas: Campbell and Long 2010). In many cases, wild pigs select areas that satisfy all of these life history requirements. In the Sierra Foothills of California, wild pigs selected oak thickets as both ample cover and acorns for food were available (Barrett 1982). In central Alabama, wild pigs selected wetlands during the summer months as these areas provided food, water, and cover, as well as quality areas for farrowing (Gaston et al. 2008). In Tennessee, wild pigs used oak-pine slopes during the winter because these areas offered thermoregulatory cover and acorns (Singer et al. 1981). During the summer months, however, individuals moved extensively between multiple forested habitats to meet food, cover, and thermoregulatory requirements (Singer et al. 1981). In South Carolina, changes in monthly habitat use were mainly related to food availability (Kurz and Marchinton 1972). Wild pigs on Santa Cruz Island, California, moved from canyon bottom to ridgelines due to weather and food availability (Van Vuren 1984). In an area of their native range in Eurasia, wild boar selected European beech (Fagus sylvatica) and hornbeam (Carpinus betulus) forests during the winter since these habitats offered forage and cover (Fonseca 2007). These habitat selection patterns also hold true in agricultural areas, where wild boar will utilize wheat, cereal, and corn during the summer months when these crops are mature and provide both food and shelter (Labudzki et al. 2009).

Wild pigs have an affinity for water and associated vegetation types (e.g., riparian areas, marshes, swamps). Overall, wild pigs are poor thermoregulators and require access to water to cool down during periods of high temperatures. This affinity for water is especially pronounced in arid areas where open water can be scarce. For example, in east and south Texas, open water and saturated soils were important habitat components affecting the distribution of wild pigs (Mersinger and Silvy 2007, Cooper and Sieckenius 2016). Wild pigs in the southeast United States also selected habitats closely associated with water, which can be exacerbated by drought conditions (Friebel and Jodice 2009). In response to high temperatures on Santa Catalina Island, California wild pigs selected canyon bottoms that offered a cool environment and increased access to water (Baber and Coblentz 1986), patterns that were attributed to a physiological need for water. The influence of water on spatial distribution of wild pigs is most pronounced during drier seasons. For example, in southern Sweden wild boar preferred areas with abundant water in all seasons except during springtime when water was generally present throughout the landscape (Thurfjell et al. 2009).

Because wild pigs seek areas with adequate food, cover, and water, selection of areas associated with water like wet scrub-shrub, bottomland forest, and emergent marsh, is likely related to the
dense vegetation and productivity of these areas. Wild pigs used the margins of fresh and brackish marshes in all seasons of the year in coastal South Carolina, as these areas featured an abundance of roots and tubers (Wood and Brenneman 1980). Other studies have also observed intense rooting in wetter habitats that feature a rich herbaceous understory (Bratton et al. 1982). In the central Lower Peninsula of Michigan, wild pigs will often bed in areas that provide thick vegetative cover during the daytime, such as cattail marshes where extensive rooting has been observed along the edges of these habitats (S. M. Gray, personal observation). In east Texas, wild pigs selected riparian corridors that had dense vegetation, thus serving as visual cover and aiding in thermoregulation (Mersinger and Silvy 2007). Preference for riparian habitat has also been supported by research on vehicle collisions with wild pigs, where collisions occurred more frequently when in proximity to streams and associated bottomland vegetation (Beasley et al. 2014). Selection for riparian habitats has also been observed in wild pigs outside of North America, most notably in Australia (Caley 1997, Dexter 1998).

Scale is an important consideration in habitat use and selection studies, as this will ultimately influence inferences (Johnson 1980). For example, in the Chihuahuan Desert of Texas, population level habitat selection (second-order; sensu Johnson 1980) indicated selection for open-canopied evergreen woodlands by wild pigs (Adkins and Harveson 2007). However, individual-level selection was consistent with generalist behaviors that showed minimal preference for any particular habitat type (Adkins and Harveson 2007). Given this study occurred in a desert ecosystem, these findings highlight the importance of the scale of analysis and that wild pigs may display stronger selection in harsher climates. Overall, additional research is needed to better understand how wild pigs in North America select resources across multiple scales.

3.3.3 Activity and Movement

Over most of their range, wild pigs are generally considered to be nocturnal (Keuling et al. 2008b, Campbell and Long 2010). This is broadly considered to represent a shift in behavior due to human interactions, where anthropogenic disturbance has caused wild pigs to adopt a predominately nocturnal activity pattern (Stegeman 1938, Keuling et al. 2008b). Indeed, in areas farther from human settlements wild boar have shown increased daytime activity (Podgórski et al. 2013). Similar to other aspects of wild pig spatial ecology, activity patterns are influenced by changes in food, cover, and temperature (Van Vuren 1984, Campbell and Long 2010). In landscapes with thick vegetative cover, wild pigs will be more active during the daytime (Stegeman 1938). During warm summer days, wild pigs will bed during the day and become more active at night. This pattern has also been observed in captive wild pigs (Blasetti et al. 1988). Conversely, during colder winter days, wild pigs increase activity during the afternoon (Kurz and Marchinton 1972, Van Vuren 1984). Seasonally, wild pigs also alter their activity in response to temperature (Van Vuren 1984, Blasetti et al. 1988, Campbell and Long 2010). For example, in North America wild pigs reduced daily movements in relation to temperature extremes while monthly and overall movement decreased in conjunction with rising mean temperatures (Kay et al. 2017).

Compared to other aspects of wild pig spatial ecology, research on the movement ecology of this species is limited (Morelle et al. 2014). Wild pig movement has predominantly been described as general wandering over short distances, particularly in landscapes with suitable food, cover, and minimal human disturbance. However, wild pigs are also capable of large-scale movements where individuals traverse long distances over short periods of time. For example, genetic studies in Australia indicated that wild pigs moved >100 km over several days to breed (Lapidge et al. 2004). Similarly, experimentally translocated sows in South Carolina made extensive movements post-release in an apparent attempt to locate their previous home range, with average daily movement rates and home range sizes that were significantly larger than those of non-translocated pigs (J. C. Beasley, unpublished manuscript). In this scenario, the magnitude of difference between groups was moderated by the quality of the surrounding resources they were introduced to, with wild pigs introduced into predominantly pine habitats exhibiting more extensive movements than those introduced into bottomland hardwood habitats (J. C. Beasley, unpublished manuscript). These extensive
movements were maintained for ~20–30 days prior to establishment of stable home ranges, at which point most individuals appeared to have assimilated within new sounders (J. C. Beasley, unpublished manuscript). The potential for large-scale movements in wild pigs has also been observed in populations that migrate. For example, some individual wild boar were recorded moving distances >250 km during the migration period in Poland (Andrzejewski and Jezierski 1978).

Movement metrics such as maximum distance or average hourly distance moved in a day or longer can also be informative for understanding wild pig spatial ecology and guiding management. In general, wild pigs are fairly sedentary in their movements during a given day (average = 0.35 km, maximum = 0.8 km) or month (average = 0.42 km, maximum = 2.1 km; Kay et al. 2017). Average hourly movement and maximum movement distances are affected by weather, season, geographic region, sex/age, and distance to water sources (Kay et al. 2017). In general, wild pigs in drier ecoregions (e.g., Southern Texas Plains and Ozark Highlands) have above average movement rates across all scales, while wild pigs in mesic ecoregions (e.g., Mississippi Alluvial Plain and Southern Coastal Plain) have below-average movement rates. Interestingly, the shape of the relationship between some of these factors and movement changes depending on the temporal scale of the analysis (i.e., daily, monthly, or overall time). For example, the maximum distance moved by males can be up to 1.3 km farther than females at the monthly scale, whereas at the daily scale sub-adult males show similar maximum daily movement rates to sub-adult females.

Some studies on wild pig movements have focused on responses to management and control activities. The responses of wild pigs to control activities are variable and ultimately depend on control method and repeated exposure. In general, wild boar reduce their activity after being subjected to hunting pressure (Sodeikat and Pohlmeyer 2007, van Doormaal et al. 2015). However, this can change with repeated hunting events (Fischer et al. 2016). If cover is dense, wild pigs may remain stationary when encountered by hunters. But individuals will flush from their hiding location, often in a random direction, once they feel imminently threatened (Marini et al. 2008). Also, flight distances tend to be small (<300 m), with many recorded distances being <25 m (Marini et al. 2008). After fleeing, individuals selected vegetation that offered abundant cover and forage; they also reduced their overall movement (Thurfjell et al. 2013). During drive hunts wild boar tended to flee, while individuals often hid and remained stationary in response to still hunting (Thurfjell et al. 2013). Furthermore, in response to drive hunts, wild boar used larger resting ranges, were reluctant...
to return to the same resting sites, and individuals subjected to the greatest amount of hunting pressure displayed the most erratic movements (Scillitani et al. 2009). The influence of other hunting techniques, such as aerial gunning, has elicited various responses by wild pigs. During aerial gunning in Texas, movement of wild pigs increased and ≥50% of individuals displayed movements outside of their documented home ranges but returned to their initial home range soon after aerial gunning ceased (Campbell et al. 2010). Other aerial removal events also reported minimal impact on movements of surviving wild pigs (Saunders and Bryant 1988, Dexter 1996), but individual responses can vary.

3.3.4 Natal Dispersal

Natal dispersal (hereafter dispersal) refers to the movement of individuals between their natal range and the location of first breeding (Howard 1960). Individually, dispersal has important implications for reproduction and survival (Réale et al. 2000, Cote et al. 2009), while contributing to gene flow among populations (Bowler and Benton 2005, Clobert et al. 2009). In wild boar, dispersal occurs most often in males but has also been observed in females (Keuling et al. 2009a, Prévot and Licoppe 2013). As males mature, they often become solitary and disperse from social groups in search of mating opportunities. Dispersal in females is less common, but is likely triggered by the same process. In general, dispersal distances are primarily greater in males than in females (males = 3.80–4.90 km, females = 1.60–2.49 km; Keuling et al. 2009a, Prévot and Licoppe 2013). It is worth noting that information pertaining to dispersal in wild pigs in North America is limited and merits additional study.

The age when most dispersal events occur varies by sex and location. In general, the maximum dispersal rate coincides with the age at which individuals reach sexual maturity (Trué and Lemel 2003). Variation in the timing of dispersal has been noted in North America. In the southeastern United States, dispersal was observed in individuals between 5 and 10 months of age (Crouch 1983, Hughes 1985). In Texas dispersal appears to occur later, where researchers reported a peak in male dispersal at 16 months of age, when individuals reached 40–50 kg (Gabor et al. 1999). In Sweden, dispersal in males began at ~10 months of age, peaked at 13 months, and declined at 16 months (Trué and Lemel 2003). For females, dispersal occurred when individuals were between 7 and 11 months of age (Trué and Lemel 2003). When dispersal occurs, female siblings may disperse together, thus lowering individual fitness costs (Kaminski et al. 2005). This phenomenon has also been observed in males, where dispersing individuals will form bachelor groups (Gabor et al. 1999). In some instances, younger males and females have been observed in a single group, and are believed to be siblings that have dispersed together (S. M. Gray, personal observation; J. C. Beasley, personal observation). Kaminski et al. (2005) noted that decisions by females to remain or leave the natal group was primarily determined by apparent fitness costs and benefits. For example, individuals born to younger mothers can be nutritionally deficient compared to young from more experienced mothers, making it more beneficial to remain in the group longer (Kaminski et al. 2005). Conversely, the ratio of mothers to daughters within a sounder may influence the likelihood of dispersal. In social groups where female yearlings outnumbered the adults, the probability of dispersal was high (Kaminski et al. 2005).

Other mechanisms also influence dispersal in wild pigs. In terms of density, research in Sweden determined that the density of conspecifics was negatively correlated with wild boar dispersal (Trué et al. 2004). In southwest Australia, researchers reported that heavier animals often dispersed farthest to access breeding opportunities and that dispersal events (3–11 km) occurring over short periods of time were also observed in sows (Hampton et al. 2004). Furthermore, landscape features can affect the spatial configuration of dispersal in wild pigs. For instance, in France, animals dispersed towards natural areas rather than agriculture, often following the edges of open water (Dardaillon and Beugnon 1987). The dispersal process for wild pigs differs from some other large ungulates. The presence of rivers, roads, and railways was less influential on dispersal events in wild boar than in red deer (Cervus elaphus) in Belgium (Prévot and Licoppe 2013).
3.4 APPLICATIONS AND MANAGEMENT

Wild pigs are often described as intelligent animals, capable of exploiting a variety of habitats and resources. Given their expansive range, both in North America and abroad, there is need to understand the intricacies of the spatial ecology and behavior of wild pigs in these locations, as they are often quite different. To date, many methods have been developed to better manage this species using information gathered from behavioral and spatial ecology research. One of the most notable advances is the use of GPS telemetry devices to obtain detailed spatiotemporal information on wild pigs. A technique that explicitly uses this information is called the Judas pig approach. This technique exploits the social tendencies of wild pigs, and uses GPS/telemetry information from a tagged animal to locate other individuals in the landscape. This has been an effective method during removal efforts conducted in Australia (McIlroy and Gifford 1997) as well as in the United States, most notably California (Wilcox et al. 2004, Macdonald and Walker 2008). However, the Judas pig method is most effective when used in concert with other control methods or when wild pig populations persist at low levels. Thus, the Judas pig technique is especially useful in newly colonized areas that often have populations at low-densities (McIlroy and Gifford 1997), or when surviving individuals flee into previously unoccupied areas making them difficult to relocate. Similarly, despite the role of illegal translocations in the rapid spread of wild pig populations across North America (see Chapter 2), there is limited information available on the movement behavior of translocated pigs. Such data are essential to the development of management strategies in the event of a known release. For example, within a few weeks translocated sows often moved several kilometers from the release site in South Carolina, although the distance moved decreased with increasing habitat quality at the release site (J. C. Beasley, unpublished manuscript), suggesting localized management around suspected release locations is likely to be ineffective. Similarly, detailed spatial and temporal information can provide further insight into population connectivity and potential source-sink dynamics in response to management activities. Understanding how individuals move among populations and refill gaps in the landscape could be crucial in informing cost-effective and efficient control strategies at the landscape scale.

Another important application in understanding spatial behavior is for optimizing deployment of management tools such as traps or toxicants. Knowledge of factors driving the spatial ecology of pigs can inform how, when, and where to deploy traps or pharmaceutical baits in a manner that pigs are most likely to visit the attractant quickly and frequently. Similarly, for deployment of any toxicant, an understanding of group dynamics (i.e., dominance, interactions) during feeding is critical. Lastly, it is important to understand contact behavior among wild pigs to assess disease risk, and to test how management could affect disease risk through behavioral and spatial changes in how pigs come in contact with others in the area (see Pepin et al. 2016). Because wild pigs can be vectors of several potentially harmful zoonoses, there is a need to know which control methods can be carried out to limit this potential for disease spread (Pepin and VerCauteren 2016). Currently, dispersal of wild pigs in North America is poorly understood and remains a topic in need of further inquiry. Dispersal has important implications for managers as this can lead to disease spread and can further hinder removal efforts. In North America, wild pigs are believed to regularly disperse, especially juveniles/sub-adults when a new litter is born. However, much is left to be learned as to the ultimate function and consequences of this behavior from an ecological and management standpoint. Similarly, social structure and territoriality of wild pigs have important implications for managers, yet few studies have investigated these topics in North America. Additional research exploring group composition and social interactions within sounders as well as territorial interactions among sounders may inform and improve management efforts.

3.5 RESEARCH NEEDS

As pointed out throughout this chapter, there are several areas where research is lacking on the spatial ecology and behavior of wild pigs in North America. First, in terms of behavior, there remain many opportunities to explore wild pig communication and the function of several glands used in
scent-marking. Research to date is limited and a holistic understanding of the strategies used by wild pigs may aid in the development of an effective attractant to be used in management and control. Second, the majority of home range studies on wild pigs have estimated home ranges using MCP methods. Only recently have studies begun employing more informative estimators and appropriately accounted for the temporal autocorrelation that is inherent in GPS data, especially when collected frequently (i.e., hourly). The use of statistically rigorous estimators could provide less biased and more detailed estimates of home range. For example, AKDE has the advantage of incorporating an underlying movement process that predicts space mechanistically from the observed locations, thus learning from patterns in the data to estimate the overall home range (Fleming et al. 2015). However, care must be taken when applying these methods because adjustments must be made when natal dispersal or long-distance translocations are included in the dataset (i.e., movement that is non-stationary). A study by Kay et al. (2017) determined that MCP methods are an accurate metric for calculating home range size in most circumstances due to the limited movements exhibited by wild pigs. However, process-based models will be important for understanding other characteristics of home range and movement (e.g., behavior; see Hanks et al. 2015). Third, research on the movement of wild pigs in North America is limited. In fact, the movement ecology of this species is considerably understudied in comparison to other ungulates (Morelle et al. 2014). Most research on wild pig movement has occurred in the native and international invasive ranges, making the application of inferences to populations in North America limited. Recent advances in state-space (Patterson et al. 2008) and other behaviorally based models have increased the potential and applicability for movement studies on wild pigs. Fourth, most research on wild pigs has occurred in areas where animals are fairly common and often occur at high densities (e.g., Texas, Georgia, South Carolina). Continued range expansion and translocation of wild pigs into areas of northern United States and Canada merit additional research. These areas feature newly established populations and are currently at low densities in areas that are ecologically distinct based on climate and vegetation in comparison to the southern United States. These smaller populations are important for providing insight into how the spatial ecology and behavior of wild pigs differ during invasion as well as in new climates and habitat conditions. It is also important to understand how these populations respond to management activities as populations are removed and groups are potentially fractured. Additionally, spatial research on wild pigs in urban and residential areas is nonexistent in North America (see Chapter 19). Interactions between humans and wild pigs will likely increase moving forward; therefore, understanding how animals use and move within human-dominated landscapes can inform control and management efforts in these areas.

ACKNOWLEDGMENTS

We thank B.K. Strickland and S.S. Ditchkoff for thoughtful reviews, edits, and suggestions. Contributions from S.M.G., G.J.R., and R.A.M. were supported by Michigan State University and the Michigan Department of Natural Resources. Contributions from J.C.B. were partially funded by the US Department of Energy under award # DE-EM0004391 to the University of Georgia Research Foundation. Contributions from K.M.P. were supported by the USDA. Mention of commercial products or companies does not reflect an endorsement by the US Government.

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