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Blake Eugene Mccann

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GENETIC RELATIONSHIPS OF WILD PIGS (*Sus scrofa*) IN THE UNITED STATES: GEOGRAPHIC ORIGINS AND GENOTYPIC DISTRIBUTION OF THE SPECIES WITH IMPLICATIONS FOR MANAGEMENT

by

Blake Eugene McCann
Bachelor of Science, Southern Illinois University Edwardsville, 1999
Master of Science, Southern Illinois University Carbondale, 2003

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This dissertation, submitted by Blake McCann in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done, and is hereby approved.

Chairperson

This dissertation is being submitted by the appointed advisory committee as having met all of the requirements of the Graduate School at the University of North Dakota and is hereby approved.

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Blake McCann
15 March 2012

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To Homer R. Johnson and Jock F. T. N. Woods

ABSTRACT

Wild pigs are a damaging invasive species with a long history in the United States. However, during the last 30 years wild pigs have drastically expanded their invasive range and are now present in 44 U.S. states. Though historic records provide insights regarding original introduction histories in areas where pigs are long-established, little is known regarding sources for new populations. To develop a better understanding of recent invasions, I utilized an array of molecular markers (mitochondrial DNA sequence, nuclear microsatellites, and nuclear single nucleotide polymorphisms) to evaluate both the evolutionary history of introduced pigs and gene flow between populations indicative of dispersal pathways.

Mitochondrial sequence provided a basal understanding of pig invasions (i.e., geographic origins and breed associations) through evaluation of U.S. pigs in context of published sequence from around the world. However, mitochondrial relationships must be considered cautiously, as introduction sources can be obscured due to shared ancestry between Eurasian wild boar and domestic pigs and the ubiquity of some haplotypes in national and global datasets.

With microsatellites and single nucleotide polymorphisms, I identified multiple genetic groupings that corresponded to geographic distributions and known introduction histories. Through individual and population genetic distance analyses, I found that dispersal patterns and sources for invasions of wild pigs can be identified using molecular techniques. I also identified an isolation by distance relationship at the national level and in California, which suggests that range expansion can be tracked in terms of gene flow across the landscape. However, my results did not resolve whether the association of genetic distance with geographic distance has resulted from diminishing rates of gene flow under a natural dispersal scenario or from genetic drift associated with anthropogenic dispersal; evidence of both pathways for pig invasion was apparent in my dataset. Further, landscape genetic analyses suggested some role for natural dispersal in range expansion in California.

My findings here suggest that ongoing research in the area of wild pig genetics would be productive. Additional samples from throughout the United States will be necessary to further resolve population genetic relationships and the role of anthropogenic and natural dispersal in range expansion.

CHAPTER I

PIG (*Sus scrofa* L.): NATURAL HISTORY, STATUS AS AN INVASIVE SPECIES, AND PERSPECTIVES ON MANAGMENT

Volumes have been written on the natural history of pigs and their association with humans (Towne and Wentworth 1950, Jonsson 1991, Rothschild and Ruvinsky 1998). Here, I provide a synopsis of the taxonomy of the species, impacts resulting from domestication and anthropogenic dispersal, and life-history traits of domestic and wild swine important for invading new environments. I then review the invasion history of pigs in the United States and explore their ecological and economic impacts. Next, I summarize management practices for introduced pigs and identify areas of management need that can be addressed with molecular research. Finally, I establish research objectives to be addressed in proceeding chapters of this dissertation.

Natural History and Human Impacts

Taxonomy

Pigs are classified as follows: Class Mammalia, Order Artiodactyla, Family Suidae, Genus *Sus*, Species *scrofa* L. There are five genera in Suidae, including *Phacochoerus* (warthogs), *Potamochoerus* (red river hog and bush pig), *Hylochoerus* (giant forest hog), *Babyrousa* (babirusa), and *Sus* (pigs) (Feldhamer et al. 2007; Figure 1.1). Within *Sus*, there are seven to ten recognized species, depending on the reference consulted: *S. barbatus* Muller (bearded pig), *S. ahoenobarbus* Huet (Palawan bearded pig), *S. verrucosus* Muller (Javan pig), *S. bucculentus* Heude (Vietnamese warty pig), *S. sylvanius* Hodgson (pygmy hog), *S. celebensis* Muller and Schlegel (Celebese/Sulawesi warty pig), *S. cebifrons* Heude (Visayan warty pig), *S. philippensis* Nehring (Philippine warty pig), *S. oliveri* Groves (Oliver's warty pig), and *S. scrofa* (Eurasian wild boar and domestic pigs) (Groves and Grubb 1993, Lucchini et al. 2005; Figure 1.1). Among *S. scrofa*, there are eighteen subspecies associated with four geographic regions in the Eastern Hemisphere: "Western races" in Europe to North Africa and the Middle East, "Indian races" in Sub-Himalayan regions from Iran to North India and Burma, "Eastern races" from Mongolia and Siberia to China and Japan, and "Indonesian races" on the Malay Peninsula throughout Java and off-shore Islands (Groves 1981, Mayer and Brisbin 1991, 2009; Groves and Grubb 1993, Oliver et al. 1993) (Figure 1.2). The number of accepted subspecies varies, depending on results of morphological versus molecular analyses (Groves 1981, Randi et al. 1989, Larson et al. 2005, Mayer and Brisbin 2009).

The native range of *S. scrofa* extends approximately from Northern Africa, throughout Europe, the Middle East, India, and most of East Asia, including the Malay Peninsula and some off-shore Islands, including Japan (Mayer and Brisbin 1991; Figure 1.2). Mitochondrial DNA evidence suggests divergence of *S. scrofa* in Southeast Asia between five and one million years ago (Randi et al. 1996, Mona et al. 2007), followed by a radiation of the species across Eurasia during the last 500 thousand years (Giuffra et al. 2000, Larson et al. 2005; 2010, Lucchini et al. 2005). Anthropogenic dispersal of the species began as early as 11,400 years ago (Vigne et al. 2009). Due to human movement, pigs are now found on many islands and all continents except Antarctica (Oliver and Brisbin 1993).

Domestication

Among *Sus*, only *S. scrofa* and *S. celebensis* have been domesticated (Groves 1981). Domestication of *S. celebensis* occurred on South Pacific islands, where resulting breeds have remained geographically isolated (Groves 1981, Larson et al. 2007). Domestication of *S. scrofa* has occurred in numerous locations throughout Europe and Asia and domestic forms have been distributed globally (Larson et al. 2005; 2010, Luetkemeier et al. 2009). The exact date of earliest domestication is uncertain, though archaeological and molecular evidence suggest humans began the process ≥9000 years ago (Giuffra et al. 2000, Larson et al. 2007, Vigne et al. 2009).

Numerous indigenous breeds of pig have been identified throughout the native range of *S. scrofa* (Hongo et al. 2002, Toro et al 2002, Yang et al. 2003, Ishiguro et al. 2008, Cho et al. 2009). However, all *S. scrofa* subspecies are capable of interbreeding, and domestic pigs from multiple geographic regions have been hybridized. A classic example is the crossing of Asian breeds with European breeds that began in the late 1700s, causing admixture of swine lineages previously separated by millennia of divergence (Darwin 1868, Jones 1998). From the 1800s onward consumer demand and government requirements have led to development of a vast array of new breeds through crossing and artificial selection (Jones 1998). Currently, there are more than 200 domestic breeds of pig, including as many as 100 local breeds in China (Jones 1998, Fang and Andersson 2006).

Life-history Traits

Phenotypic variation across wild *S. scrofa*, domestic breeds, and feral pigs is considerable, demonstrating the adaptability of this species in both wild and domestic environments (Groves 1981, Mayer and Brisbin 1991). Mayer and Brisbin (1991) describe four morphotypes for pigs; "domestic", "feral", "hybrid", and "Eurasian wild boar" (Figure 1.3). The term Eurasian wild boar (EWB) here refers to all wild *S. scrofa* (i.e., undomesticated pigs) and the term hybrid represents any level of crossing between domestic pigs and EWB or feral pigs and EWB (Mayer and Brisbin 1991; Figure 1.3).

Though it is possible to identify pigs to morphotype based on discriminant analysis of physical characters, it is important to note that morphology varies within each of the four categories (Mayer and Brisbin 1991). For instance, European and Asian domestic breeds differ in external body morphology and physiology, with some Asian breeds having drooping abdomens, concave backs, and slow maturation; these attributes are not typically observed among European breeds (Jones 1998). Thus, feral pig morphology varies depending on contributing breeds and hybrid pig phenotypes will depend in part on the degree of crossing between differing domestic lines and EWB (Mayer and Brisbin 1991). Eurasian wild boar are also divided by morphology into subspecies (Groves 1981, Mayer and Brisbin 2009). Therefore, introduced pigs will reflect a gradient of morphological characteristics depending on their origins and introduction histories (McCann et al. 2003).

Despite wide variation within categories, it is useful to view pigs in terms of the above listed morphotypes to evaluate phenotypic variation and other life-history traits that affect the capability of pigs to invade novel habitat. Because of hybridization, introduced pigs are commonly referred to simply as “pigs” or “wild pigs” unless specific references to wild or domestic origins are necessary for clarity of discussion.

Morphology. It is thought that swine body size is largely dependent on nutrition, though genetic sources of variation are obviated by differences in size between domestic breeds (Jones 1998). Generally speaking, domestic pigs achieve larger body dimensions and greater weights than feral pigs and EWB (Mayer and Brisbin 1991). This large size of domestic pigs is attributable to a combination of artificial selection for meat production and nutrition provided during domestic rearing (Jones 1998). Feral pigs are highly variable in body weight and external body measurements, which is logical considering their diverse origins and the multitude of environments that they have invaded (Mayer and Brisbin 1991). Feral pigs on islands are typically smaller than those in mainland locations (e.g., 22-24 kg versus 55-67 kg); due to varying annual forage availability or other environmental factors (Brisbin et al. 1977, Baber and Coblentz 1986). Feral pigs from some mainland locations may be extremely large, such as the famed 360 kg “Hogzilla” that was harvested in Georgia (Minor 2005). However, most wild-living pigs in the United States exhibit body size intermediate to these extreme examples. Adult wild pigs typically weigh between 31-225 kg, stand 67-71 cm at the shoulder, and are 0.9-1.7 meters in length (Mayer and Brisbin 1991).

Domestication has caused changes in skull morphology and soft tissue in a number of vertebrate species, including pigs (O'Regan and Kitchener 2005, Dinu 2009). Foraging requirements in different environments are thought to have selected for varying skull morphology observed across pig types (Mayer and Brisbin 1988; 1991). In comparison to EWB, the anterior portion of the crania has been shortened and the angle of the occipital wall has decreased for domestic pigs (Mayer and Brisbin 1991). Both elements of the skull are important for foraging in natural environments; these traits begin to revert to the wild form in feral populations that have been established for long periods of time (e.g., >200 years; Mayer and Brisbin 1991). Differences in stresses on the musculature of pigs may result in developmental changes in musculoskeletal arrangements in individuals (Dinu 2009). This rapid adaptability of pigs to novel environments is a hallmark of successful invasive species (Ehrlich 1984).

Pelage. Molecular studies have identified a gene, melanocortin receptor 1, which is important for determining pelage characteristics in pigs (Kijas et al. 1998, Koutsogiannouli et al. 2010). This marker has been used to estimate drift effects and identify artificial selection leading to various pelage colors and patterns in domestic swine (Fang et al. 2009, Mayer and Hochegger 2011). White is the most common color for domestic pigs while black is predominant for feral pigs, though a variety of colors and patterns are common to both types (Mayer and Brisbin 1991). Brisbin et al. (1977) suggest that selection against white coloration in wild environments explains disparities in color frequencies between domestic and feral types. In addition to pelage color, there is evidence that selection is resulting in the redevelopment of under-fur in feral pigs, which is absent in domestic breeds (Mayer and Brisbin 1991).

Other pelage traits appear to be altered or selected against during domestication. Eurasian wild boar and hybrids have longer and thicker dorsal guard hairs than domestic and feral pigs (Mayer and Brisbin 1991). Eurasian wild boar also exhibit “wild-grizzled” pelage, where hairs have a dark shaft and a light tip (Mayer and Brisbin 1991). This pelage type varies in body coverage from throughout the pelt to only in the margins of the face and flanks, depending on the individual (Mayer and Brisbin 1991). In hybrids, a combination of wild-grizzled pelage and a full range of domestic pelage patterns and colors may be observed (Mayer and Brisbin 1991). Pelage of young EWB (≤4 months) has longitudinal stripes that serve to camouflage piglets from predators; hybrid young may or may not exhibit this pattern (Mayer and Brisbin 1991). Importantly, wild-grizzled and striped pelage are observed almost exclusively in EWB and hybrids and may be used as an indicator of hybridization in introduced pig populations (Mayer and Brisbin 1991).

Behavior. Pigs are intelligent animals with highly adaptable and complex behavior schemes (Hafez and Signoret 1969, Singer et al. 1981, Gabor et al. 1999). In wild environments, pigs alter activity patterns depending on variation in temperature, food, water, and reproductive status (Kurz and Marchinton 1972, Gabor et al. 1999). Pigs are typically crepuscular, except when food sources are scarce or when seasonal foraging opportunities arise (Barrett 1978, Everitt and Alanis 1980, Singer et al. 1981). When conditions become unfavorable, pigs modulate movement patterns or occupy new locations (Singer et al. 1981). For example, hunting pressure can cause pigs to become nocturnal (Hanson and Karstad 1959). Further, studies have demonstrated the ability of pigs to respond to human activity and evade control and eradication efforts (Caley and Ottley 1995, Morrison et al. 2007).

Pigs are social and often travel in groups, and females are more gregarious than males (Kurz and Marchinton 1972). Females associate in maternal groupings with several generations composing the ranks (Barrett 1978, Cousse et al. 1994, Gabor et al. 1999). Group structure and territoriality defines resource partitioning within populations for female pigs (Gabor et al. 1999, Sparklin et al. 2009). Territoriality associated with breeding is observed for male pigs; though fighting among both sexes is common (Hanson and Karstat 1959, Barrett 1978, Sweeney et al. 2003). Males break maternal ties by 16 months of age and sometimes make long-distance exploratory movements in search of mating opportunities (Barrett 1978, Gabor et al. 1999). Otherwise, natural dispersal occurs through exploratory forays out of natal ranges as young pigs mature, and pig movements may be punctuated by pulse resource availability (Cousse et al. 1994, Bieber and Ruf 2009). Though patterns in habitat use are linked to resource availability, pig dispersal is not thought to be density dependent (Truve et al. 2004).

Home Range. Home range size and habitat use is highly variable for pigs, depending on environmental factors in invaded areas and demographics of pig populations (Kurz and Marchinton 1972, Boitani et al. 1994, Sweitzer et al. 2000, Sparklin et al. 2009). The spatial distribution of forage and water resources often define how pigs utilize the landscape (Wood and Brenneman 1980, Adkins and Haverson 2007). Generally speaking, home range size varies inversely with resource abundance and density (Singer et al. 1981). However, considerable variation in both home range size and habitat use have been described; differences observed throughout North America are at least in part attributable to varied ecology and geographic range of invaded areas (Singer et al. 1981, Baber and Coblentz 1986, Sweitzer et al. 2000). For example, arid conditions and low forage availability have been linked to large home ranges (e.g., >40 km^2) reported in parts of Texas (Adkins and Haverson 2007).

Home range size also varies for different types of pigs (i.e., feral, hybrid, EWB) throughout their native and introduced range (Sweitzer et al. 2000). In Europe, mean home range of EWB varies between 3.7-12.7 km^2 and may be as high as 24 km^2 (Boitani et al. 1994, Massei et al. 1997). In some parts of North America, mean home range of feral pigs is less than that of hybrid EWB, but there is much overlap in range size between individuals of both types (Sweitzer et al. 2000). For example, in South Carolina home range for feral pigs averaged ~4 km^2, whereas home range for hybrids in Tennessee and North Carolina averaged 3.64 km^2 (Kurz and Marchinton 1972, Singer et al. 1981).

Reproduction. Pigs are polyestrous and capable of producing numerous young per litter, exhibiting exceptionally high fecundity for a large mammalian species (Foccardi et al. 2008, Rutherford et al. 2011). Gestation period is 115-118 days and sex ratio in pigs is typically 1:1 (Hagen and Kephart 1980, Baber and Coblentz 1986). Considerable variation in reproductive capability between pig types has been observed in wild and domestic environments. Some breeds of domestic swine can bear more than 20 young (Rutherford et al. 2011). Eurasian wild boar typically produce 4-6 young per litter, though larger litters are attainable with high levels of environmental nutrition (Bieber and Ruf 2005, Focardi et al. 2008). In the U.S., mean wild pig litter size is between 5-8 piglets (Sweeney et al. 1979, Barrett 1978, Baber and Coblentz 1986, Taylor et al. 1998). Reproduction is biannual in wild pigs, with winter and summer parturition observed in the Northern Hemisphere (Sweeney et al. 1979, Baber and Coblentz 1986). Winter parturition is typically the most productive in wild pigs and is thought to be linked to hard mast availability and seasonal environmental factors (Barrett 1978, Baber and Coblentz 1986, Taylor et al. 1998).

Puberty occurs at 5-7 months for males and 10 months for females, though age of maturation may be reduced depending on nutrition (Sweeney et al. 1979). For instance, Barrett (1978) found that sows with high-quality forage reached puberty at 6-8 months. This early fertility and high rate of reproduction means that introduced pigs can recover from high rates of annual mortality, making it incredibly difficult to control population numbers through lethal removal techniques (Hone and Robards 1980).

Diet. Pigs are omnivorous; their diet is based on vegetation but also depends on animal sources of protein (Everitt and Alanis 1980, Howe et al. 1981, Loggins et al. 2002, Wilcox and Van Vuren 2009). In the United States, pigs generally feed on herbaceous understory foods during the spring and summer and depend heavily on mast during autumn and winter (Henry and Conely 1972, Howe et al. 1981, Singer et al. 1981). Pigs are opportunistic foragers that will capitalize on almost any type of available high-energy food source (Henry 1969). For instance, pigs will raid food stores of ground dwelling mammals, and in some instances pigs focus on small mammals as prey (Foccardi et al. 2002, Loggins et al. 2002, Grinde 2006, Wilcox and Van Vuren 2009). The ability to root deeply through the soil matrix and forest floor detritus allows pigs to access herbaceous foods and invertebrate prey items not available to other large vertebrate species, which may provide a nutritional advantage in competitive scenarios (Hanson and Karstad, 1959, Ilse and Hellgren 1995).

Physiology. Pigs do not have sweat glands, which may limit invasion in arid locations with few water sources (Mount 1968, Signoret et al. 1975, Gabor et al. 1997).

Renal morphology of pigs is less adapted to hot and dry climates than that of collared peccary (*Tayassu tejacu*), but morphological plasticity and adaptive behavioral schemes appear to contribute to survival of pigs in arid locations (Gabor et al. 1997). In warm climates or during warm seasons pigs will seek shelter during the peak of daytime temperatures in canyon bottoms, on northern slopes, or in dense cover, and are typically crepuscular (Kurz and Marchinton 1972, Baber and Coblentz 1986, Wilcox et al. 2004). With these morphological and behavioral adaptations, wild pigs have successfully invaded arid locations in the desert southwestern United States and Mediterranean climates of California (Figure 1.4). Further, the natural range of EWB in the Palearctic and Oceania explains the ability of wild pigs to proliferate in the temperate hardwood forests of the Midwest and northern tier states and subtropical portions of the southeastern United States (Figure 1.1, 1.4).

Overview of Natural History and Human Impacts on Pigs

Pigs have a rich natural history and a long association with humans that has resulted in a mixture of beneficial and detrimental outcomes for both species. Humans have drastically impacted the physical and molecular characteristics of pigs through domestication and hybridization; during the process pigs have achieved a global distribution that includes feral and hybrid populations. This association with humans has led to a variety of changes in the morphology, physiology, and reproductive biology of pigs that has contributed to phenotypic diversity of pigs invading new environments.

The life-history traits discussed previously explain why pigs are such capable invaders. Pigs are morphologically and physiologically adaptable, with an omnivorous diet and unique foraging behavior allowing them to capitalize on almost any kind of environmentally available energy source. Pigs are long-lived and have a reproductive strategy that more closely resembles small mammals (Focardi et al 2008). These are important considerations, given that longevity and reproductive rate are both correlated with invasiveness (Kolar and Lodge 2001). Further, the intelligence of pigs and the social structuring of populations contribute to difficulties in their eradication and control (Morrison et al. 2007). Finally, the association of nutrition with reproductive success and dispersal may promote natural range expansion in some locations (Bieber and Ruf 2005, Focardi et al. 2008).

Introductions to the United States

Hawaii

Hawaii was the first U.S. state to be invaded by pigs. Polynesian explorers released pigs on the archipelago ≥1000 years ago when Hawaii was first settled (Mayer and Brisbin 1991). The specific origin of the first pigs introduced to Hawaii is uncertain, but it is thought that introductions occurred as part of human migrations beginning in Oceania over 3000 years ago that radiated through Polynesian islands and eventually to remote island chains, including Hawaii (Allen et al. 2001). Pig populations on Hawaii were well-established by the time of European contact in the 1700s, after which various introductions of domestic stock occurred (Mayer and Brisbin 1991). Feral populations on Hawaii are now a mixture of indigenous breeds and European and Asian domestic breeds (Mayer and Brisbin 1991, Allen et al. 2001, Larson et al. 2005). It is unclear how ancient and recent introductions have contributed to feral pig distributions on the islands today and to what extent feral Polynesian pigs have been crossed with European and Asian domestic pigs.

North America

The first recorded introduction of pigs to the continental United States occurred during the DeSoto expedition from 1539-1542 (Towne and Wentworth 1950, Mayer and Brisbin 1991). DeSoto's men drove pigs along the way as a mobile provision while traversing parts of nine or ten present-day states in the Southeastern U.S. (Mayer and Brisbin 1991). During the expedition some animals escaped and established the first known feral pig populations in North America. From this time forward feral populations were commonly established in association with exploration and colonization, due to free-range livestock practices, escape, or release (Mayer and Brisbin 1991). Feral swine were historically located near Spanish, French, and English settlements in the southeastern U.S. (Towne and Wentworth 1950, Hanson and Karstad 1959, Mayer and Brisbin 1991). On the west coast, Spanish exploration and missionary settlements led to initial introductions of feral pigs to island and mainland locations (Pine and Gerdes 1973, Barrett and Pine 1980, Mayer and Brisbin 1991). From the colonial period onward, pigs were repeatedly introduced to many locations throughout North America, with some populations persisting and others perishing (Towne and Wentworth 1950).

By the late 1800s, established feral populations were present in at least thirteen U.S. states in the southern tier of North America, and pigs began to gain popularity as a game species (Mayer and Brisbin 1991). Interest in pig hunting led to at least three separate importations of EWB from Europe during 1890-1912 (Mayer and Brisbin 1991). These EWB bred freely with feral pigs wherever populations came into contact, and their descendants have subsequently been widely dispersed throughout the U.S. (Mayer and Brisbin 1991; 2009, Waithman et al. 1999). The crossing of EWB and feral pigs has led to the occurrence of hybrid animals with a range of intermediate phenotypic characteristics in many locations (Mayer and Brisbin 1991). During the 1900s translocation of pigs throughout the U.S. for hunting purposes became commonplace, and hybrid animals with EWB phenotypic characteristics were selected for establishment of new populations or improvement of existing herds (Barrett 1977, Mayer and Brisbin 1991, Waithman et al. 1999).

Anthropogenic dispersal is thought to be the leading cause of range expansion in the U.S. during the last 30 years (Gipson et al. 1998, Waithman et al. 1999). The geographic range of pigs has increased from seventeen to 44 U.S. states since 1980 and estimates of individual numbers are at all time highs (Mayer and Brisbin 1991; 2009, Gipson et al. 1998; Figure 1.4). Considering the adaptability of pigs as an invasive species and human assistance in their dispersal, range expansion will continue if left unchecked (Loggins 2007).

Ecological and Economic Impacts

Introduced pigs cause a wide array of damages (Tisdell 1982, Pimmental et al. 2000; 2007). The impacts of pigs can be considered broadly in terms of ecological damages and economic losses, though both categories are linked through intrinsic or monetary values of natural resources (Sweitzer and McCann 2007). Here, I will consider these two categories and discuss a third, disease transmission, which also has both ecological and economic implications.

Ecological Impacts. The impact of introduced pigs on natural systems is related primarily to their diet, behavioral attributes, and high population densities (Sweitzer and McCann 2007). Though there is a paucity of evidence for direct competition between pigs and other medium to large vertebrate species, pigs consume many forage types (e.g., mast) and occupy habitats important for survival of native large vertebrates (Hanson and Karstad 1959, Isle and Hellgren 1995). Empirical evidence for competition between pigs and small mammal species has been documented. Pigs are known to raid food stores of ground dwelling mammals and sometimes target small mammals as prey items (Focardi et al. 2000, Grinde 2006, Wilcox and VanVuren 2009). Stomach content analyses have demonstrated that a wide variety of vertebrates and invertebrates are preyed upon by pigs, and there is some indication that pigs prey opportunistically on ground nesting birds (Henry 1969, Henry and Conely 1972, Howe et al. 1981). In addition to competitive interactions, the mere presence of pigs can have cascading effects on ecosystems. For example, the presence of abundant feral pigs attracted golden eagles (*Aguila chrysaetos*) to Santa Cruz Island, California, resulting in increased predation of endemic island fox (*Urocyon littoralis*) (Roemer et al. 2001).

Foraging behavior of pigs, particularly rooting of the ground, is damaging on a systemic level. Rooting limits the tunneling of fossorial mammals and reduces the abundance of invertebrates in soils (Howe et al. 1981, Singer et al. 1984). Rooting also depletes herbaceous understory and woody root biomass and exposes soil for colonization by exotic plant species (Howe et al. 1981, Kotanen 1995, Cushman et al. 2004). In California, uprooting and trampling of Oak (*Quercus spp.*) seedlings by pigs has been linked to reduced regeneration of Oak forests and imperilment of Oak-savannah ecosystems (deNevers and Goatcher 1990, Sweitzer and Van Vuren 2002, Gomez et al. 2003). Loss of biomass, exposure of soil, and mixture of soil layers affect rates of nutrient loss through runoff (Singer et al. 1984). Furthermore, pigs are known to root and wallow in streams (Lewis 1966). Therefore, where pigs occur at high population densities, considerable changes in soil matrix composition and elevated levels of nutrients in watersheds may be expected (Singer et al. 1984, Grinde 2006).

Browsing, trampling, and soil compaction along foot trails is another effect of high densities of introduced ungulates (Coblentz 1978). High population densities of pigs also exacerbate ecological impacts of social behaviors such as tusking and rubbing of trees and physiologically-linked behaviors like wallowing in wetlands; where more pigs occur, greater mechanical damage to environment elements can be expected. Finally, as with most terrestrial vertebrate species, population density is linked to rates of disease in wild pigs (Saunders and Bryant 1988, Gresham et al. 2002).

Disease Transmission. Pigs host a number of important internal and external parasites. Notable internal parasites include: nematodes (e.g., *Trichenella spiralis* and *Ascaris suum*), tape worms (e.g., *Taenia solium* and *Spirometra spp.*), and flukes (e.g., *Fasciola hepatica* and *Echinococcus granulosus*) (Corwin and Stewart 1999, Gray et al. 1999). A variety of internal parasites have been reported for feral pigs throughout the U.S. (Hanson and Karstad 1959, Gipson et al. 1999, Gray et al. 1999). Though internal parasites rarely cause death in pigs, they can have more serious implications in other vertebrate species (e.g., Trichinosis in humans).

External parasites of pigs include: mange, lice, ticks, fleas, and mosquitoes. Mange (*Sarcoptes scabiei*) is one of the most damaging external parasites of livestock, causing reduced productivity domestic herds (Cargill and Davies 1999). Hog lice (*Haematopinus suis*) are species-specific and are thought to serve as a vector for some viruses (Cargill and Davies 1999). Otherwise, lice impose a physiological strain on heavily infested animals, similar to that observed for tick infestations. Hog lice have been reported for feral pigs throughout North America (Hanson and Karstat 1959, Gipson et al. 1999). Ticks, fleas, flies, and mosquitoes are not host-specific, but may play a role in disease transmission in domestic and wild environments.

Pigs are susceptible to a wide variety of viral and bacterial pathogens transmissible to humans, wildlife, and livestock. Among bacterial diseases, Leptospirosis (*Leptospira spp*.) and Brucellosis (*Brucella suis*) are two that are commonly associated with feral pigs in the United States (Clark et al. 1983, Corn et al. 1986, Van der Leek et al. 1993, Gipson et al. 1999). Both cause reproductive failure and urogenital disease in livestock, and both pose serious health risks when transmitted to humans (MacMillan

1999, Ellis 1999). Importantly, Leptospirosis survives outside of the body and may be transmitted through infected waters, such as streams and ponds (Mason et al. 1998).

Important viral diseases in swine are: pseudorabies (PRV), porcine parvovirus (PPV), and porcine reproductive and respiratory syndrome (PRRS). Pseudorabies causes respiratory, reproductive, and nervous system complications, often leading to death in pigs and other livestock (Kluge et al. 1999). In the U.S., PRV has been detected in feral swine samples from numerous locations (Corn et al. 1986, Pirtle et al. 1989, Van der Leek et al. 1993). Porcine parvovirus is associated only with fetal death and does not impact adult pigs (Mengeling 1999). However, PPV has been identified in feral pigs from several states and is a concern for pork growers (New et al. 1994, Gipson et al. 1999). Porcine reproductive and respiratory syndrome affects all ages of pigs, and PRRS generally manifests in respiratory complications, abortion and gestational shifts that affect the productivity of swine rearing operations (Benfield et al. 1999).

These and other trade-limiting pathogens less common among feral pigs in the U.S. (e.g., foot and mouth disease) have the potential to become established and perpetuated in feral populations while the livestock industry and government agencies invest vast sums to eradicate disease. In this manner, feral pigs may serve as a reservoir for disease and a vector for long-distance dispersal through anthropogenic movements. Spread of disease will be exacerbated by the continuing popularity of pigs as a game species and their ongoing range expansion in the U.S., increasing interactions with livestock and humans.

Economic Impacts. Pigs are responsible for a wide variety of economic damages as a nuisance species within their native range and as an exotic species (Tisdell 1982, Geisser et al. 2004). Economic losses to agriculture are typically incurred through damage to crops, injury or death of livestock, physical property damage (e.g., broken fences, undermining of watering impoundments), and rooting and wallowing of roads (Tisdell 1982, Pavlov and Hone 1982, Adams et al. 2005). Municipalities, private individuals, and enterprises typically experience damages from rooting of lawns and gardens, motor-vehicle collisions, and investment in control or eradication programs (Pimmentel et al. 2000, Sweitzer and McCann 2007).

Alternately, not all parties view introduced pigs as a pest. For instance, many state agencies have traditionally classified pigs as a game species to generate revenue, and private individuals benefit from recreational hunting opportunities (Miller 1993). For some landowners, leased hunting revenues outweigh the cost of damages incurred, resulting in a net economic gain from pig presence on their property (Miller 1993). As such, an industry has developed around paid hunting that provides economic support to a faction of U.S. citizens. However, on a national scale the presence of feral pigs is generally viewed as detrimental among resource managers, and public perception is starting to be swayed against pigs (West 2010).

In the U.S., pigs have been implicated in the loss of $800 million through damages and $500,000 through control and eradication efforts annually (Pimentel 2000; 2007). However, it is difficult to assess an economic value to damaged ecological resources, which suggests that the actual dollar amount could be much higher (Engeman et al. 2003; 2004). As pigs continue to increase their invasive range in the U.S., the monetary value assessed to their damage will increase over time (Mayer and Brisbin 2009). Furthermore, the amount spent on management will increase, though it varies depending on socio-political environments and differences in investment of private, state, and federal resources in pig control and eradication. For example, far more than $500,000 annually was spent in California alone during the period 2004-2006 (Sweitzer and McCann 2007, McCann and Garcelon 2008). A recent estimate of costs incurred from damage and control of introduced pigs is $1.5 billion annually (Pimentel et al. 2007).

The discussed ecological impacts of introduced pigs affect the intrinsic value of natural resources and reduce the aesthetic value of natural environments for human enjoyment. Though economics often drive management decisions, it is important to consider ecological perspectives regarding invasive species, especially considering current trends resulting in increasingly fragmented habitats for native species. Both ecological and economic considerations should be taken into account when developing management strategies for pigs; the success of management actions will be measured in terms of savings in both categories.

Management Strategies

A variety of effective techniques have been developed to control pig numbers and protect resources. For control or eradication, common practical approaches include trapping, snaring, poisoning, shooting, hunting with dogs, the “Judas” technique, and aerial gunning (Choquenot et al. 1990, McCann et al. 2004, Sweitzer and McCann 2007, West et al. 2010). Fencing has been employed as both a tool for eradication and for protection of resources as a non-lethal alternative to mitigate damages (Sweitzer and McCann 2007). Chemical sterilization has also been proposed as a non-lethal alternative to control pig populations (West et al. 2010). To assess the current state of pig management in the United States, it is important to understand the positive and negative attributes of tools available to managers. Here, I will review each of the above methodologies and consider their application in context of prior control and eradication efforts in the United States and elsewhere.

*Trapping.*Trap configurations vary widely, but there are three primary types; box, corral, and panelized corral (Barrett 1978, Sweitzer et al. 1997, McCann et al. 2004). Box traps are typically the smallest and are self-contained units that can be transported by vehicle or by hand (Stiver and DeLozier 2009). Corral traps vary in design, are constructed at field sites, and can be made to any size (West et al. 2010). Panelized corral traps are a hybrid design that incorporates pre-made panels for easy transport and construction at field sites (Sweitzer et al. 1997, McCann et al. 2004). Any variation of the above can be used effectively to trap pigs, provided that strong materials such as chain-link, welded-steel livestock panels, etc. are used. A trap floor or roof may be necessary to prevent escape; corral-style traps must be anchored to the ground (McCann and Garcelon 2008). Most traps employ a swinging or guillotine style door mechanism that is mechanically triggered by entrance or manipulation of a bait receptacle (Sweitzer et al. 1997, McCann et al. 2004).

Trapping is an integral part of most pig control or eradication programs because it efficiently removes a large number of pigs with minimal effort (McCann and Garcelon 2008, Morrison et al. 2007). A large trap line can be maintained with a few personnel and operated at all hours to encounter pigs in the removal area (Schuyler et al. 2000, McCann et al. 2004, McCann and Garcelon 2008). However, trap success inevitably depends on bait acceptance, which varies due to seasonal fluctuations in natural forage and the presence of alternate sources of nutrition (McIlroy et al. 1993, Saunders et al. 1993, Choquenot and Lukins 1996). Though a variety of bait types have been tested for attracting pigs, baits composed of grain crops are most widely used (West et al. 2010). Despite the typically successful deployment of these devices, trapping techniques are not successful in all locations (Coblentz and Baber 1987, Katahira et al. 1993, McCann et al. 2003). Further, not all animals in a population can be removed using traps alone (McCann and Garcelon 2008).

Snaring. Snares are typically constructed with steel cable and set with a large loop (>25cm) positioned above the ground along trails that are frequented by pigs (Katahira et al. 1993). Cable snares are anchored to trees or other solid substrate and are designed with a self-locking mechanism that closes around a pig's head and neck (Coblentz and Baber 1987, Katahira et al. 1993). A snare of this design will either kill pigs via strangulation or incapacitate them until they can be euthanized by gunshot or other means.

Studies suggest that snares may be useful tools when used as part of a comprehensive program, but that snaring is not the most productive form of pig removal (Coblentz and Baber 1987, Kathira et al. 1993). Further, there are several drawbacks to the use of snares. For instance, damage frequently renders snares inoperable (Coblentz and Baber 1987). Further, the use of snares involves issues regarding humane treatment of animals, and native species may also be entrapped. Capture of non-target species is minimized in island ecosystems absent of native large vertebrates but is a serious concern where snares are employed in North America. Regardless, snaring remains a common pig removal technique in some parts of the continental Unites States (e.g., Texas; West et al. 2010).

Poisoning. Poisoning is generally viewed as unacceptable in the United States due to the possibility of negative effects on native species encountering poisoned baits or feeding on carcasses of poisoned pigs (West et al. 2010). However, in Australia toxicants are commonly used to control pig populations and have proven effective in many cases (Choquenot et al. 1990, Twigg et al. 2005). Poisoning, like trapping, depends on bait acceptance which may be limited in certain environments (Twigg et al. 2005). Recent work to produce pig-specific delivery systems for poisons may allow for the use of this tool in the U.S. in the future (West et al. 2010); although, it is uncertain whether poisoning would ever be deemed acceptable based on the perception of inhumane euthanasia of pigs, a charismatic mammalian species.

Shooting. Ground hunting methods employing stalking, still-hunting, stand hunting, and shooting from motor vehicles are flexible options for pig removal that are often used as focused elements of control or eradication projects (McCann et al. 2004). For example, the staff at Great Smoky Mountains National Park have used a combination of hunting techniques as a primary part of their pig control program for decades (Stiver and Delozier 2009). Further, ground hunting has been instrumental in a number of eradication projects in the U.S. and elsewhere (Coblentz and Baber 1987, Lombardo and Faulkner 2000, Schuyler et al. 2000).

A wide range of firearms, including rifles, shotguns, and pistols can be effective tools for dispatching free-ranging pigs. In most cases the selection of hunting tools (e.g., makes and models, calibers, sighting devices, etc.) will depend on the range of environments encountered at the removal site and personal preferences of removal staff (McCann et al. 2004, Sweitzer and McCann 2007). In some instances, suppressed firearms are desirable to minimize sound pollution and to avoid habituation of pigs to gunshots (Stiver and DeLozier 2009). In addition to the generalized techniques listed above, methodologies employing night-vision optics and baited sites can prove valuable for removing wary animals (McCann and Garcelon 2008).

The effect of hunting techniques on the managed population is an important consideration for pig removal by shooting. Pigs will adapt cryptic behavior in response to hunting pressure, impacting the overall success of removal efforts and leading to difficulty in completing eradications (Hanson and Karstad 1959, Morrison et al. 2007). Use of shooting also involves public perception, where ground-hunting techniques may be misconstrued as sport hunting in the media. In some instances public outcry against pig removal methodologies and destruction of animals has led to court injunctions or administrative decisions halting pig removal programs (Sweitzer and McCann 2007). A final concern is public safety, which necessitates the use of trained staff that exhibit professionalism during control events (McCann et al. 2004).

Dogging. A variety of dog breeds have been adapted for pig hunting, including those that are proficient at trailing scent (e.g., Plot hounds), those that are visual hunters (e.g., Catahoula breed), and “catch dogs”, those that are best known for physically subduing pigs (e.g., Staffordshire Terriers) (Caley and Ottley 1995, McCann et al. 2004). Typically, field personnel will release dogs on fresh sign and track them with radio-telemetry until the dogs have pigs at bay. Field personnel will then locate the dogs and dispatch pigs by gunshot or by knife, depending on accepted protocols (McCann et al. 2004).

In the U.S. and elsewhere, dogs have been used extensively for pig removal (Tisdell 1982, Hone and Stone 1989, Caley and Ottley 1995, Garcelon et al. 2005). Dogging accounted for 30% and 86% of pigs removed from island sites in California and Hawaii, respectively (Katahira et al. 1993, Schuyler et al. 2000). Dogs are also a valuable tool for locating residual pigs when populations are at low density, which may be difficult with other techniques (Caley and Ottley 1995, McCann et al. 2004, McCann and Garcelon 2008). A primary advantage of dogging over other removal techniques is that it does not rely on the ability of field personnel to locate pigs nor does it require pigs to come to specific locations. This is an important consideration in complex habitats where visual encounters with pigs limit ground hunting opportunities and large amounts of natural forage reduce the efficacy of baits (McCann et al. 2004).

Disadvantages of dogging include the physical effort of tracking dogs, medical care for resulting canine injuries, maintenance of kennels, and the random behavior of dogs in sensitive natural areas (McCann et al. 2004). Tracking dogs and handling bayed pigs can be strenuous and often results in the removal of only a minimal number of animals at each encounter (Caley and Ottley 1995). Dogs, even wearing protective devices (e.g., Kevlar vests and collars), can be injured during physical contact with pigs, incurring medical costs. Further, dogs must be trained to avoid non-target species, especially where wildlife of conservation concern is present (McCann et al. 2004).

The Judas Technique. The Judas technique capitalizes on the social nature of animals for targeted removal through tracking of individuals with radio-telemetry (Taylor and Katahira 1988). Animals are captured and fitted with a radio-telemety collar and then released back into the removal site. Field personnel then locate collared animals, observe them, and attempt to dispatch any non-collared animals associated with the Judas individual. Hence, the collared animal unwittingly betrays its associates.

The Judas technique was first developed for use in eradication of feral goats (*Capri hircus*) (Taylor and Katahira 1988, Keegan et al. 1994). More recently this technique has been adapted for use with pigs (McIlroy and Gifford 1997, Wilcox et al. 2004). Studies have yielded mixed results on the efficacy of this technique for use with pigs, but most indications are positive (McIlroy and Gifford 1997, Wilcox et al. 2004, McCann and Garcelon 2008). In addition to assisting in primary removal efforts, the Judas technique provides opportunities for managers to monitor populations, evaluate pig use of the landscape, and identify residual individuals for removal (McCann and Garcelon 2008). However, the potential of Judas animals to contribute to population numbers through reproduction should be considered (Campbell et al. 2005). For example, McCann and Garcelon (2008) reported considerable work effort to remove offspring of Judas pigs during the late stages of an eradication project in California and recommended sterilization of all animals prior to release for future work.

Aerial Gunning. During aerial gunning, a helicopter is used to locate pigs, after which marksmen positioned in open door wells dispatch them using rifles or shotguns (McCann et al. 2004, Morrison et al. 2007). The use of helicopters as an aerial platform for pig removal can be highly effective, especially where drastic decreases in population density in a short period of time are desired (Saunders and Bryant 1988, Saunders 1993). Aerial gunning is most effective in open terrain where animals can be flushed from cover so that entire sounders can be tracked and removed simultaneously (Saunders and Bryant 1988, Morrison et al. 2007). However, the efficacy of helicopter operations may be limited in areas with dense vegetation (West et al. 2010). Additionally, as pig populations decline the effectiveness of this technique diminishes and other techniques must be used to further reduce populations (Saunders 1993, Choquenot et al. 1999).

Shooting from helicopters is a high-profile technique that may have either negative or positive impacts on the political environment surrounding a control operation. One negative impact is public perception, as with ground hunting methods. Alternately, aerial gunning operations provide opportunities for consolidation of control operations across private and public lands and avoid ground operations that are often undesirable to private landowners (Saunders 1993). The cost of operating helicopters and trained personnel is a consideration that may also limit the use of this technique in some locations, depending on the scope and scale of the work (Saunders 1993).

Fencing. A variety of fence types have been employed to effectively restrict the movement of pigs (Hone and Atkinson 1983, Geisser and Reyer 2004, Lavelle et al. 2011). Tensioned fence with bracing structures, panelized steel mesh, or any number of fencing materials using tightly linked elements are viable options. Fencing for pigs typically includes a combination woven wire mesh to a height of ≥80cm and a ground anchoring system to prevent lifting; strands of barbed wire may or may not be strung along the top or bottom of the woven wire (Hone and Atkinson 1983, Katahira et al. 1993, Schuyler et al. 2000, McCann and Garcelon 2008). Though tensioned fence designs are most common, recent research suggests that panelized fences are most effective (Lavelle et al. 2011).

Fencing can be used for two primary purposes in pig control: 1) isolation of pigs for eradication, and 2) exclusion of pigs to protect sensitive habitats or property. The use of fence as a tool for eradication has proven effective in a number of locations and falls into two further subcategories, containment and subdivision. On small islands, pigs are already contained (i.e., there is no emigration or immigration) and a strategy of subdivision can be particularly useful for systematically eradicating pigs (Schuyler et al. 2000). On large islands and in mainland locations fencing is used to contain populations within a manageable area and subdivisions may or may not be employed (Katahira et al. 1993, McCann and Garcelon 2008). Once pigs are eradicated the role of the fence switches from containment to exclusion. Otherwise, exclusionary fences are typically erected on small scales where the absence of pigs within the exclosure can be confirmed visually. These exclosures may be used successfully to protect sensitive habitats (e.g., wetlands) or even to protect individual plants or properties (Didion and Lunsford 1993, Peart et al. 1994, Sweitzer and McCann 2007, Stiver and DeLozier 2009).

Primary concerns associated with fencing are the restriction of native wildlife movements and damages incurred from fallen trees, storm events, livestock, or humans that could undermine the integrity of the fence (McCann and Garcelon 2008). Fence integrity is an important consideration, especially for large eradication projects requiring considerable work effort and economic expense (McCann and Garcelon 2008). The cost of establishing fences is a separate consideration, ranging from hundreds of dollars for small sites, tens of thousands of dollars for county parks, to >$1 million for large eradication programs (Sweitzer and McCann 2007). In addition to installation costs, the expense of ongoing monitoring and repair and replacement of fences must be considered where exclosures will be continually challenged by pigs.

Sterilization. Chemo-sterilization is a non-lethal alternative commonly put forth as an option for pig control. However, there are a number of technical problems with sterilization approaches for reducing wildlife numbers (Miller et al. 1998, NPS 2006). For instance, many chemical sterilants are not permanent, requiring successive applications (Miller et al. 2004). Considering the reproductive potential of pigs, a handful of untreated animals could still result in increasing pig numbers in areas managed with chemical sterilization techniques. The continued presence of sterilized animals at disturbed locations is an additional negative consequence that may be unacceptable.

Overview of Techniques

Much has been learned during the course of pig control and eradication programs during the last 50 years. It is apparent that there is no standard formula for pig control or eradication that can be broadly applied and no single technique will drive populations to extinction. Given the adaptability of pigs, the range of landscapes that they invade, and the varying perspectives of private individuals and policy makers on pigs, managers must be flexible when developing removal strategies. Clearly, pig control is most effective when a combination of the above techniques is matched to the unique physical attributes of removal sites and socio-political environments dictating acceptable methodologies (McCann and Garcelon 2008).

Perspectives on the Current State of Wild Pig Management

Management of wild pigs in the United States has become an ever-increasing challenge because of rising population densities and range expansion (Gipson et al. 1998, Mayer and Brisbin 2009). Though control of populations can be effective at the local scale with intensive programs employing the techniques discussed above, much of the management of pigs in the United States occurs on private lands where efforts are often loosely organized. Therefore, it is important to consider pig management on a broader and more inclusive context, where the individuals involved may not be united in a strong front against invasive pigs. In fact, many private individuals are in favor of pig invasion, as evidenced by a long history of introductions and continuing trends of anthropogenic dispersal (Mayer and Brisbin 2009). Further, the view of pigs as a game species by some state agencies has likely contributed to the ongoing production of pigs and their continued range expansion (Waithman et al. 1999).

In a broader context, managers are losing ground in the battle to reduce pig population densities in long-established areas. At the state level, pig management has been attempted through hunting seasons but it is unclear whether hunter harvest is effective at reducing pig numbers beyond localized areas; at least 60% annual harvest is necessary for population declines to begin (Hone and Robards 1980, Waithman et al. 1999). States agencies also offer depredation permits and issue liberal regulations regarding the take of pigs. For example, in Texas the state has authorized aerial gunning by private individuals (Tompkins 2011). Though these regulatory methods offer effective tools for landowners to remove pigs, cooperation among adjoining property owners is not ensured; in many cases neighboring lands provide refuge from which pigs continually filter back into controlled areas (Adams et al. 2005). Another option for landowners is to enlist wildlife contractors to conduct pig removal, but these groups are costly and have a limited scope of control that can be affected on private lands. Therefore, a positive path forward for controlling pig numbers across private lands in historically affected areas is currently unclear.

A more productive area of management action may be to prevent the spread of pigs to new locations. To their credit, some states have taken aggressive steps to prevent the establishment of pigs within their jurisdiction. For instance, introduced pigs were eradicated from two locations in North Dakota during 2007-2009 (McCann unpublished data). Other states (e.g., Tennessee) have implemented regulations making hunting of pigs illegal in an effort to thwart additional introductions driven by sport hunting demand (TWRA 2011). The efficacy of regulatory approaches at preventing spread of pigs is still uncertain.

For significant gains in control of pigs to occur at the national level in the United States, public perception of pigs must change. Pigs have garnered much enthusiasm lately with reports of “giant” feral pigs on the internet, television programs documenting the actions of pig removal contractors, and news reports on controversies regarding changing legislation in various states. Though many media reports note ecological and economic damage, this information is often minimized by the charismatic nature of pigs and the sense of adventure surrounding pig hunting. Therefore, the net impact on public perception resulting from recent media exposure is unclear.

Management Needs

Very little is known regarding specific origins or types of pigs invading many parts of the U.S. Though recorded accounts provide insights for pig origins in locations where populations are long established, it is unclear if lineages from historic introductions persist or if they have been replaced by subsequent invasions. The clandestine nature of anthropogenic dispersal within both the historic and recent invasive range of pigs in North America has added to uncertainty regarding origins and types of pigs invading all areas (Mayer and Brisbin 2009).

Management efforts would benefit from a detailed understanding of: 1) the global origins for pigs introduced to North America, 2) the types of pigs invading new locations, 3) intracontinental origins for newly established populations, and 4) the role of natural landscapes and human assistance in dispersal of pigs. The study of global origins for introduced pigs would provide background necessary for elucidating putative domestic breeds and EWB lineages from which feral populations were established. Identification of pig types occurring throughout the U.S. would provide insights potentially useful for developing management strategies at the local or regional scale. For example, breed fecundity or hybridization with EWB may impinge on reproductive responses to management actions and overall invasiveness (Waithman et al. 1999). Determination of origins and human-mediated dispersal patterns for introduced pigs would benefit management by providing information useful for thwarting future introductions. Finally, an understanding of ecological and anthropogenic factors contributing to dispersal of pigs is desirable and would be valuable for generating population control strategies that incorporate human dimensions of wildlife management or those that seek to identify the geographic extent of populations for focused removal.

Given the absence of information on recent translocations, an imprecise record on domestic breeds contributing to feral populations, and unclear origins for introduced EWB, developing an understanding of biogeography for introduced pigs is unlikely based on written and oral accounts alone (Mayer and Brisbin 1991, Gipson et al. 1998). Further, oral accounts may be unreliable, depending on individual motives of those offering information to wildlife managers. Therefore, the most practical and objective approach to answering these management needs is the use of molecular techniques (Le Roux and Wieczorek 2008).

Molecular Techniques for Management

A variety of molecular markers have been identified for studies of phylogeny and population genetics in vertebrate species, including polymorphisms from both the mitochondrial and nuclear genomes (Avise 1994). Though gene regions in both genomes provide useful information on evolutionary relatedness of species, neutral markers (e.g., tandem repeats, synonymous nucleotide substitutions) are most appropriate for studies of gene flow and relatedness because they are not under selective pressure and are thought to evolve at a more constant rate (Lin et al. 1999). In the mitochondrial genome, the control region (D-loop) is widely used for phylogenetic and phylogeographic studies of vertebrate species, in part because of a faster rate of evolution than that observed for nuclear sequence (Brown et al. 1979). In the nuclear genome, microsatellite (MS) loci have a proven record in population genetic studies and provide considerable power for elucidating parentage, population structure, and phylogeogrpahy (Alexander et al. 1996, Putnova et al. 2003, Lutkemeier et al. 2009). More recently, single nucleotide polymorphisms (SNP) have been recognized as a valuable tool for nuclear DNA studies of population genetics and divergence where fine-scale resolution of relationships and genomic interpretation of phenotypic variation are desirable, especially where large numbers of loci (e.g., >50,000) can be evaluated (Rhorer et al. 2007, Gray et al. 2009).

Though a number of other neutral makers are useful for evolutionary and population genetics studies, mtDNA, microsatellites, and SNP are the most practical markers for molecular research on introduced pigs in the United States. This is because of the availability of primers and assays for laboratory work, and the wide use of these marker types in studies of wild and domestic pigs globally (Scandura et al. 2011). Respective contributions of these markers to molecular investigations of pigs and other vertebrate species should be considered.

Mitochondrial DNA. Sequence variation in mtDNA has been used to evaluate biogeographic and evolutionary relationships of a wide array of large vertebrate species, including domesticates such as horses and donkeys (*Equus spp.*) (Aranguren-Mendez et al. 2004, McGahern et al. 2006) and wild animals including bison (*Bison bison*), tigers (*Panthera tigris*), and deer (*Cervus spp.*) (Cracraft et al. 1998, Randi et al. 2001, Halbert et al. 2004). In pigs, mtDNA has proven useful for phylogeographic studies of EWB and domestic breeds (Larson et al. 2005, Scandura et al. 2008, Luetkemeier et al. 2010). Mitochondrial studies have elucidated centers of breed development in Asia and Europe and helped identify patterns of human-mediated dispersal between continents (Giuffra et al. 2000, Gongora et al. 2004, Fang and Andersson 2006, Luetkemeier 2010). Additionally, haplotyic relationships have aided in identification of hybridization events between domestic pigs and EWB (Fang et al. 2006, Scandura et al. 2008). Finally, the availability of a global dataset of published sequence makes mtDNA a particularly valuable genetic marker for analyses to identify putative origins for introduced pigs in the U.S. (Giuffra et al. 2000, Loggins 2007).

Though mtDNA has many positive attributes for evaluating the invasion history of introduced pigs, important limitations inherent to this maker must be considered. Mitochondrial DNA is a single haploid marker that is maternally inherited, which means that translocation of male pigs cannot be tracked beyond the dispersing individual. Further, it is debatable whether mtDNA lineages appropriately represent the evolutionary histories of organisms or simply the phylogeny of an organelle (Ballard and Whitlock 2004). Due to the recent availability of multi-locus nuclear DNA markers, the use of mtDNA alone to elucidate phylogeographic relationships has been scrutinized (Zink and Barrowclough 2008, Edwards and Bensch 2009). Additionally, there is evidence that mtDNA sequence is not truly under neutral selection (Ballard and Whitlock 2004). Regardless, a vast literature supports the use of mtDNA in identifying vicariance for vertebrate species, which suggests that mtDNA would be useful for evaluating global geographic origins and haplotypic variation of introduced pigs (Barrowclough and Zink 2009).

Microsatellites. Short tandem repeats in sequence, commonly referred to as microsatellites, have been a popular marker for molecular studies in humans and other vertebrate species since the mid 1990s (Rubenstein et al. 1995, Jaarola and Tegelstrom

1996, Paetkau et al. 1998, Xuebin et al. 2005). In pigs, numerous polymorphic MS markers have been identified that are useful for varying types of genetic research on domestic and wild forms (Alexander et al. 1996, Lowden et al. 2002). For example, analyses of MS have identified population structure and evolutionary relationships for domestic pigs, feral pigs, and EWB (Martinez et al. 2000, Hampton et al. 2004, Nikolov et al. 2009, Frantz et al. 2009). Microsatellites have also been used to elucidate hybridization events for EWB and to estimate rates of gene flow between European and Asian domestic breeds of pig (Fang et al. 2005, San Cristobal et al. 2002, Scandura et al. 2008).

The demonstrated utility of MS markers for analyses of pig genetics at global, continental, and local scales suggests that similar analysis at the national and regional level in the U.S. would be productive at identifying population structure and dispersal events. In Australia, research on variation in MS loci has identified animals that were translocated between geographic areas, suggesting that anthropogenic pathways of range expansion could be explored similarly in the U.S. (Spencer and Hampton 2005). Prior research using MS in the U.S. has contributed to a better understanding of local-scale population genetics and demographic relationships for wild pigs in Texas and California (Gabor et al. 1999, Heeg 2006, Acevedo-Delgado 2010).

Single Nucleotide Polymorphims. Whole-genome sequencing technologies have resulted in the development of SNP data for a number of vertebrate species, including humans and dogs (Salmela et al. 2008, Jones et al. 2008, Gray et al. 2009, McEvoy et al. 2011). Because of the economic importance of pigs, the swine genome has been sequenced and a large number of SNP have been identified (Rhorer et al. 2007, Kerstens et al. 2009, Archibald et al. 2010). Though SNP loci can only express three allelic states (heterozygous and two homozygous), the large number of loci available provide considerable molecular power for differentiating population structure and individual relationships in admixed populations (Turakulov and Easteal 2003, Rhorer et al. 2007, Haasl and Payseur 2010). In pigs, SNP are currently used to approach research questions that range from phylogeography and breed relationships to identification of the molecular basis for lameness and disease (Scandura et al. 2011, Xu et al. 2011). Therefore, SNP panels should be a powerful tool for evaluating molecular relatedness of introduced pigs to elucidate population structure and identify translocations among admixed populations.

Application of Molecular Techniques to Wild Pig Management

In the following chapters I will employ mtDNA, MS, and SNP markers to answer research questions focusing on current management needs. I will use mtDNA to identify putative global origins and types of pigs (e.g., domestic breeds and EWB) introduced to the United States and to develop hypotheses for pathways of dispersal (Chapters II, III). I will utilize MS and SNP data to evaluate population structure and evidence for anthropogenic dispersal at the national and regional scale (Chapter IV). I will then perform a landscape genetic analysis of wild pigs at the regional level in California to elucidate spatio-genetic relationships of pigs and identify landscape and anthropogenic factors important for dispersal and range expansion (Chapter V).

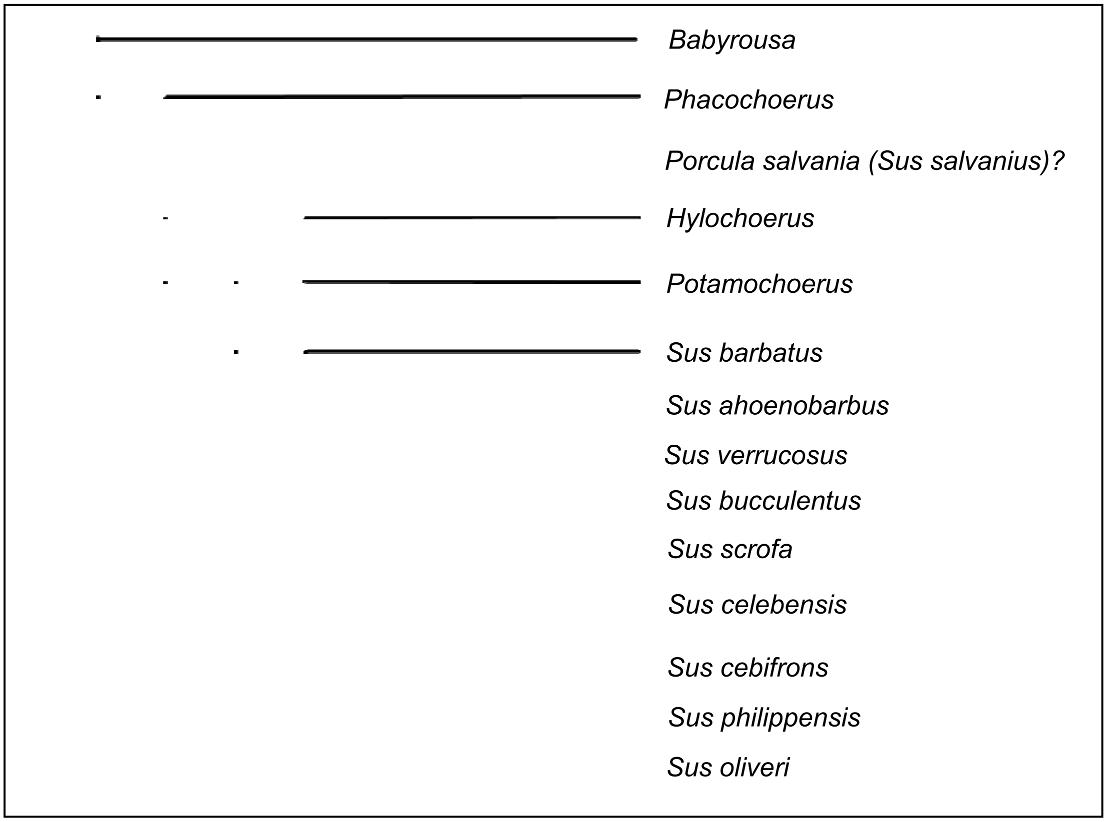

Figure 1.1. Cladogram of Suidae modified from synthesis of molecular and morphological findings available at (http://www.ultimateungulate.com/Cetartiodactyla/Suidae.html). Taxa are listed to genus level for the five genera and to the species level within *Sus*. The taxonomic position of *Sus salvanius* is currently unclear, and this group may represent an additional lineage.

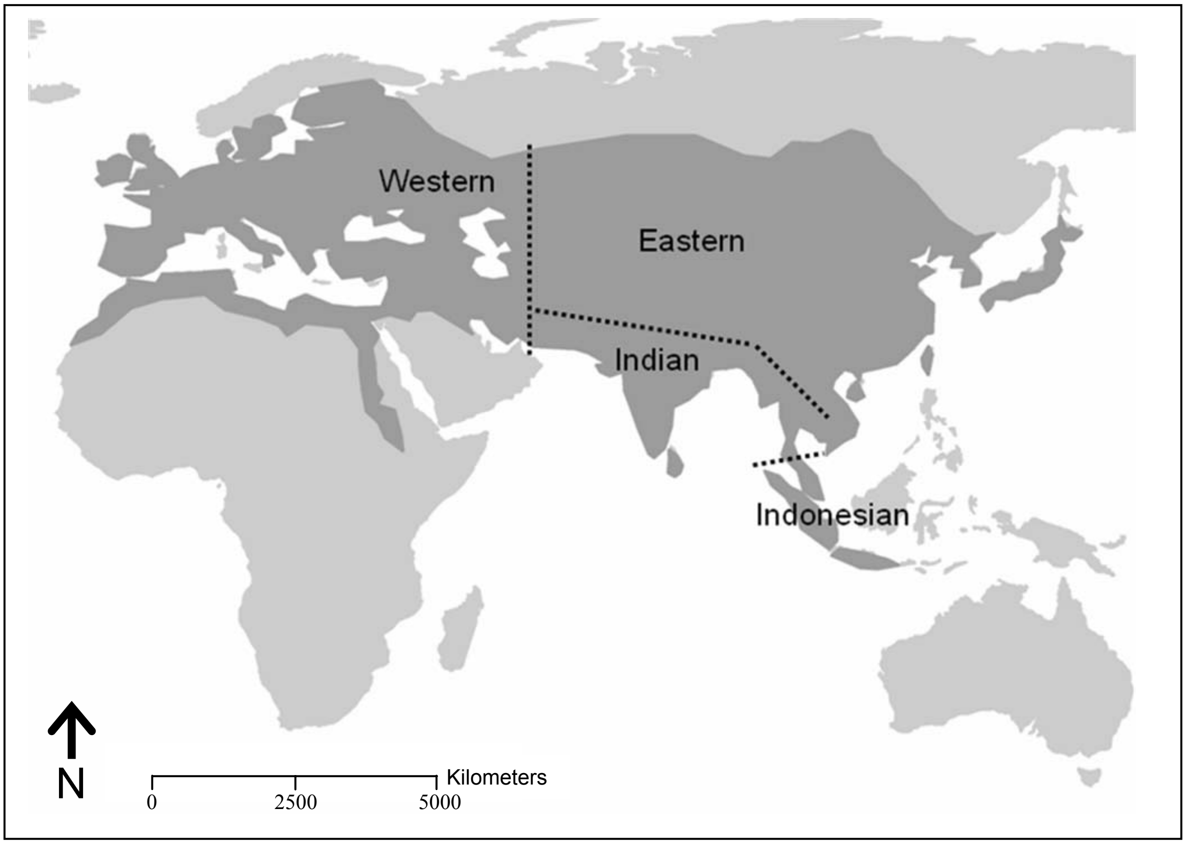

Figure 1.2. Approximate geographic extent of Eurasian wild boar range in the Eastern hemisphere (dark gray shading; modified from Mayer and Brisbin 1991). Note: populations are not contiguous across landscape within shaded region. Dotted lines approximate geographic divisions between four races of pigs described in Oliver et al. (1993).

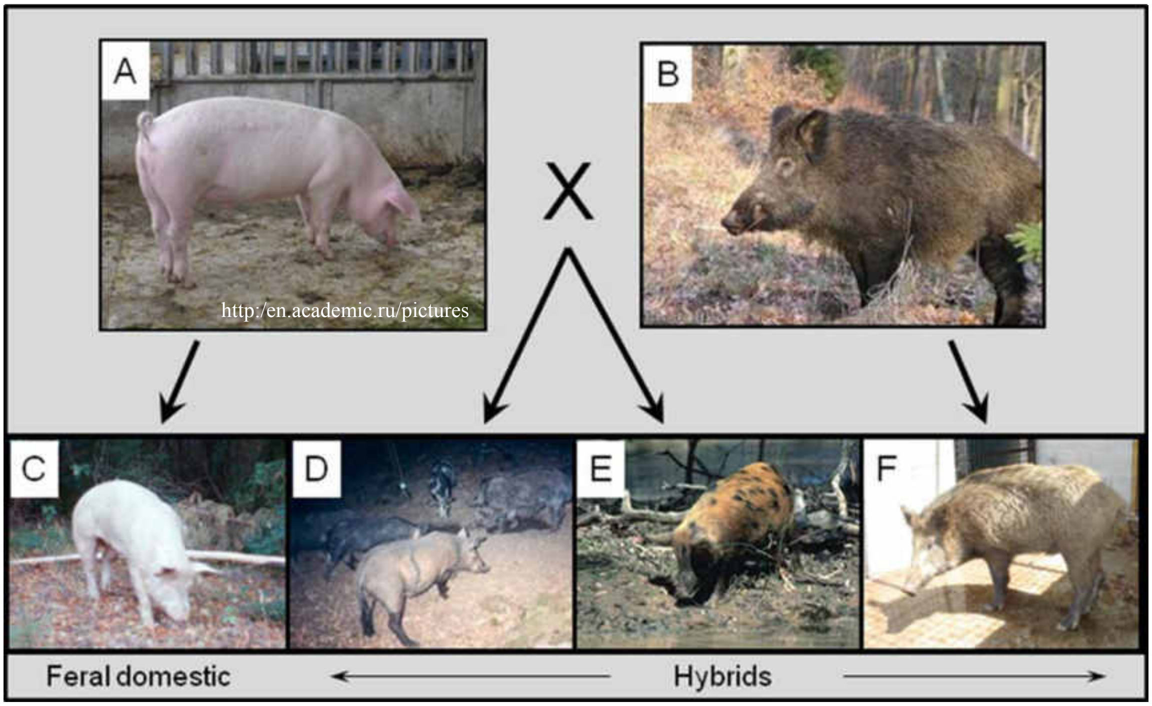

Figure 1.3. Typical external body dimensions for domestic pig (plate A) and Eurasian wild boar (plate B). Evidence for direct contributions of domestic lines (plate C) and Eurasian wild boar (plate F) to wild-living populations in California and Kentucky, respectively. Morphological evidence for crossing of feral domestic pigs and Eurasian wild boar in California (plates D and E). Internet sources for pictures at top are embedded; photograph credits for pictures at bottom are as follows: R. A. Sweitzer (plates C, D); J. Clark (plate E); and S. Dobey (plate F).

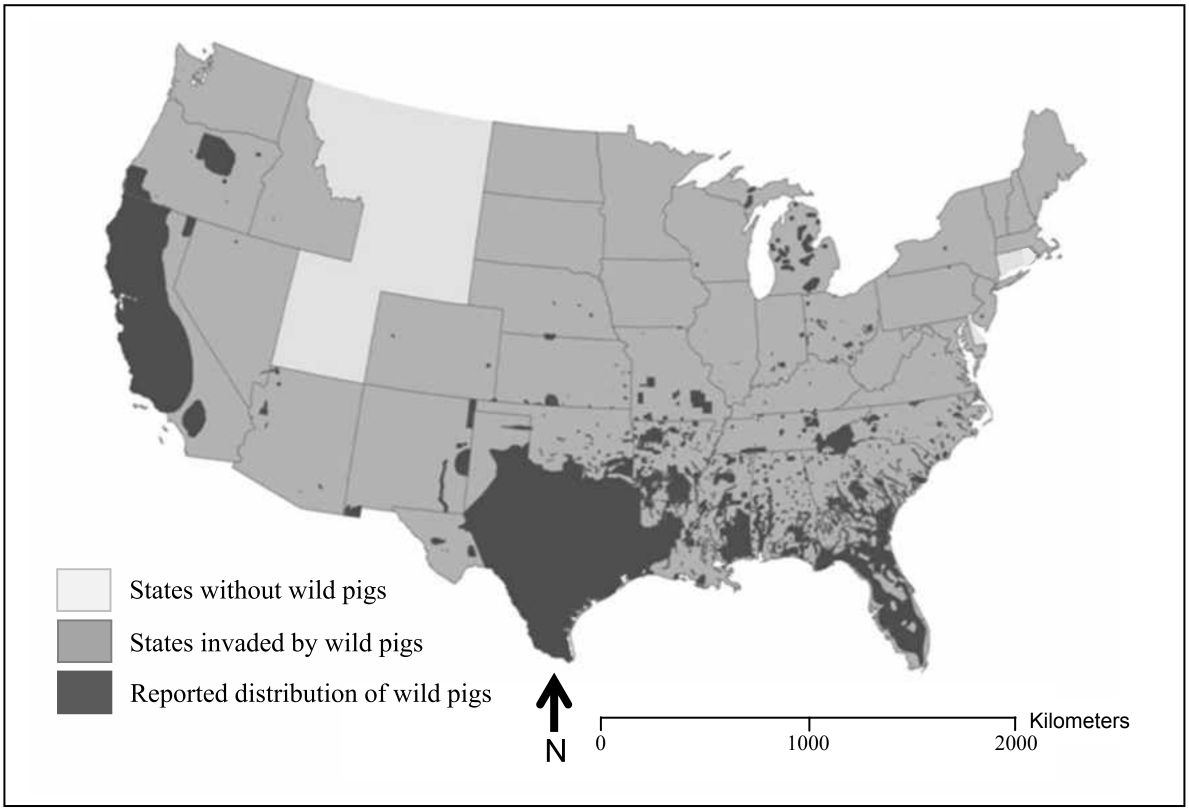

Figure 1.4. Distribution of wild pig populations in 42 continental U.S. states. States without pigs are light gray; states invaded by pigs are shaded; darker shaded polygons overlaying states indicate areas of established pig populations as denoted by state agencies and USDA Wildlife Services (SCWDS 2010 National Feral Swine Mapping System, Southeastern Cooperative Wildlife Disease Study, University of Georgia, http//:www.ferals winemap.org). Note: Alaska and Hawaii have pig populations but are not represented.

CHAPTER II

MITOCHONDRIAL DNA RELATIONSHIPS OF WILD PIGS IN THE UNITED STATES

Introduction

Invasive species present one of the greatest threats to native ecosystems globally. In the United States, tens of thousands of nonnative species have been introduced, posing serious risk to natural systems and accounting for >$100 billion in damages annually (Pimentel et al. 2005). Though not all nonnative species are invasive, some are particularly adept at colonizing new environments (Kolar and Lodge 2001). In some cases, close association with humans aids dispersal. This is especially true for pigs (*Sus scrofa*; Mayer and Brisbin 1991).

Pigs were first domesticated ≥9000 years ago (Giuffra et al. 2000, Larson et al. 2007, Vigne et al. 2009) and domestication has occurred subsequently in multiple locations throughout Eurasia (Larson et al. 2005, 2010; Luetkemeier et al. 2010). Pigs have been repeatedly transported to new locations and released under free-range livestock conditions, often leading to establishment of new wild populations. With the advent of world travel and trade in the 16th century this situation was exacerbated. Though native to portions of Europe, Asia, and Africa, wild pigs can now be found on many islands and all continents except Antarctica (Oliver and Brisbin 1993).

Among U.S. states, Hawaii was the first to be impacted by introduced pigs. Polynesian settlers are thought to have released pigs on the islands ≥1000 years before present (Mayer and Brisbin 1991). However, introduction of European domestic stock in the 1700s and subsequent introduction of a variety of domestic breeds continuing to modern times has resulted in much interbreeding among feral island populations (Mayer and Brisbin 1991). It is unclear the extent to which these ancient and recent introductions have contributed to feral pig distributions on the islands today.

Domestic pigs were first brought to North America during explorations of the 1500s (Towne and Wentworth 1950, Mayer and Brisbin 1991). Because of free-range livestock practices, escape, or release, feral populations were commonly established around colonies (Mayer and Brisbin 1991). As the interior of the continent was settled, pigs were introduced to many locations, with some populations persisting and others perishing. By the late 1800s established feral populations were present in at least thirteen U.S. states in the southern tier of North America (Mayer and Brisbin 1991). At this time, there was an increased interest in pig hunting that prompted the importation and release of Eurasian wild boar (EWB). Eurasian wild boar bred freely with feral pigs wherever populations came into contact, leading to hybrid animals with a range of intermediate phenotypic characteristics (Mayer and Brisbin 1991). Since then trade and translocation of pigs throughout the U.S. for hunting purposes became commonplace and hybrid animals possessing wild boar phenotypic characters were highly sought after for establishment of new populations or improvement of existing herds (Mayer and Brisbin 1991, Waithman et al. 1999). A famous example is the 1912 introduction of EWB to a game preserve on Hooper Bald in Western North Carolina, after which the animals escaped and hybridized with feral pigs already present in the region (Mayer and Brisbin 1991). Hybrid pigs resulting from this introduction expanded their range to inhabit Great Smoky Mountains National Park (GRSM) by the 1950s, where they have been managed since. Pigs from this introduction have been translocated elsewhere in Tennessee and North Carolina and to six other U.S. states (Figure 2.1; Mayer and Brisbin 2009). The type of pigs colonizing areas is an important consideration for managers, as it may impact the course of establishment and the rate of range expansion (Waithman et al. 1999).

During the last 30 years, anthropogenic factors are thought to be the leading cause of range expansion in the U.S. (Gipson et al. 1998, Waithman et al. 1999). Since 1980, the invasive range of pigs has increased steadily from seventeen to 44 U.S. states (Mayer and Brisbin 1991; 2009, Gipson et al. 1998). Very little is known regarding the origins or types of pigs involved in this expansion. Though recorded accounts provide some insights, it is unclear if stock from historic introductions persist or if they have been replaced by subsequent invasions. The clandestine nature of recent anthropogenic dispersal has added to this uncertainty, and calls into question the continued accuracy of establishment and translocation records.

Molecular techniques provide the best opportunity for understanding origins and dispersal patterns of pigs in North America. Mitochondrial DNA (mtDNA) has been used successfully for phylogeographic studies of wild boar and domestic breeds throughout Eurasia (Larson et al. 2005, Scandura et al. 2008, Luetkemeier et al. 2010) and has helped identify putative geographic and breed origins for feral populations in New Zealand and Australia (Gongora et al. 2004). Further, mtDNA phylogenies have elucidated patterns of transcontinental human dispersal of pigs and associated breed development in Asia and

Europe (Giuffra et al. 2000, Fang and Andersson 2006, Luetkemeier 2010), and mtDNA has helped identify hybridization events between domestic pigs and EWB (Fang et al. 2006, Scandura et al. 2008). Finally, the vast amount of published sequence makes mtDNA a particularly valuable genetic marker for global analysis to identify putative origins for introduced pigs in the U.S. (Giuffra et al. 2000).

Though mtDNA presents many positive attributes for global phylogenetics, the history of U.S. wild pigs presents challenges for molecular investigation on a national scale. Genetic relationships may be confounded by human redistribution of the species, the short duration of inhabitation in North America, and the introduction of both domestic pigs and EWB to wild-living populations. All would preclude the effective use of divergence-based analyses for examining wild pig dispersal subsequent to introduction, as we cannot expect DNA variation to reflect geographic distribution (Spencer and Hampton 2005). Alternately, invasions can be tracked with mtDNA by linking haplotype occurrences between historic and newly invaded areas (Evans et al. 2003, Tooman et al. 2011). This method is a simple but effective tool for elucidating pathways of invasion. However, important limitations intrinsic to mtDNA and published sequence must be considered when assessing both global and national molecular genetic relationships for pigs. For instance, mtDNA is a single haploid marker that is prone to stochastic variation. Therefore, genetic drift, founder effect, and bottlenecks may limit mtDNA haplotypes shared between sampled locations. Also, published sequence may be incorrectly identified to species or breed and may contain nucleotide errors, impacting breed identification to haplotype and phylogenetic anlaysis, respectively (Wesche et al. 2004, Nilsson et al. 2006). Additionally, mtDNA pseudogenes (NUMTs) can possibly be amplified, leading to erroneous phylogenetic results (Parr et al. 2006, Goios et al. 2009). Though NUMTs have been identified for domestic cats and humans (Lopez et al. 1994, Bensasson et al. 2003), we could find no reference to rates of occurrence for NUMTs in pigs. To address the possibility of NUMTs biasing phylogenetic analysis we used recently compiled genomic data (Archibald et al. 2010) to search for duplication events (see methods). All of the above were considered while preparing these analyses and interpreting results.

Here, we explore phylogenetic relationships of a subsample of wild pigs across their invasive range in the U.S. in the context of published mtDNA sequence for domestic pigs and EWB. Our objectives are to: 1) Identify world geographic and breed associations for introduced pigs in the United States, 2) Determine if mtDNA relationships reflect recorded history of introduction and translocation, using the Hooper Bald EWB introduction as a case study, and 3) Develop hypotheses of undocumented anthropogenic dispersal pathways for range expansion during the last 30 years.

Study Area

We sampled pigs occurring on private and public lands from 61 counties in 30 U.S. states during the period July 2007 – May 2010. We included locations representative of both long-established and emerging occupation sites in North America (Figure 2.1). We also included published sequence of pigs reported from the U.S. and four other continents (Figure 2.2).

Methods

Sampling Techniques

We cooperated with USDA Wildlife Services, National Park Service, state agencies, and private organizations involved in sanctioned pig control, eradication, or research programs to obtain samples. When a pig was destroyed, field personnel collected blood or other somatic tissue (e.g., skeletal muscle, skin), recorded pelage characteristics, sex of each animal, date, and sample location. Blood samples were stored on FTA (Whatman Inc., Florham Park, NJ, USA) cards, allowed to air dry, and sent to the University of North Dakota (UND) where we stored them at room temperature. Other somatic tissues were frozen and shipped overnight to UND and stored at -20°C upon arrival. We obtained 81 samples for mtDNA analysis (Figure 2.1). All samples were collected secondarily from management actions authorized by state and federal agencies required to adhere to welfare protocols for handling of mammalian species. Therefore, this research was deemed exempt by the UND institutional animal care and use committee.

We established a global dataset by obtaining published mtDNA control region sequence (n=904) from National Center for Biotechnology Information (NCBI; http://www.ncbi.nlm. nih.gov/) representing wild, domestic, and feral pigs from around the world. Among these we included sequence representing 114 haplotypes of the control region identified by Scandura et al. (2008) and incorporated breed and geographic information referenced therein. We also searched NCBI for sequence from entries submitted after this publication and for samples from new geographic areas available as of July 2010. Accessions, geographic associations, and respective publications contributing to published sequence used in our analysis are provided in supplemental information (Appendix A).

Laboratory Methods

For total DNA extraction, we followed standard protocols for dried blood (Whatman Inc., Florham Park, NJ, USA) and tissue with the DNEasy blood and tissue kit (Qaigen, Santa Clarita, California, USA). We quantified genetic concentrations utilizing a ND-1000 spectrophotometer and software V3.1.0 (Nanodrop Technologies, Inc., Wilmington, DE, USA), and diluted with distilled H_20 as necessary for PCR. We amplified an approximately 550 base pair segment of the mtDNA control region using forward primer PigF (5' – ACTCTGGT CTTGTAAACC-3') and reverse primer PigR (5' – TAAGGGGAAAGACTGGGC-3'; Okumura et al. 1996, Loggins 2007). We conducted PCR with the Ex Taq kit (Takara biotechnology Co., Ltd) using standard procedures in an Eppendorf thermocycler (Eppendorf, Hamburg, Germany; Simmons and Scheffer 2004). We then checked product for presence and size of DNA fragments on a 2% agarose gel containing 0.1µg/ml of ethidium bromide, and visualized gels with an AutoChemi ultraviolet transilluminator and Labworks 4.6 computer software (UVP Bio-Imaging Systems, Cambridge, UK). We cleaned PCR products for sequencing using a Qiaquick PCR purification kit (Qiagen, Santa Clarita, CA, USA).

We performed sequencing reactions with a Big Dye Terminator Version 3.1 sequencing kit (Applied Biosystems, Foster City, CA, USA) and the forward and reverse primers described above. We used an ABI 3100 system (Applied Biosystems, Foster City, CA, USA) to visualize and record the sequence and BIOEDIT 5.0.6 (Hall 2001) for alignment and assembly of consensus sequences. Finally, we trimmed all sequences to minimize missing data in our matrix, resulting in a 401 base pair alignment of the control region for analysis. Sequences are available in online holdings at NCBI (JF701989-JF702002, JF702006, JF702009-JF702012, JF702017, JF702023-JF702037, JF702040, JF702046, JF702049, JF702054, JF702056-JF702078, JF702081, JF702087-JF702093, and JF702105-JF702115).

To avoid errors associated with NUMT contamination, we re-processed any samples where ambiguities were observed in chromatograms. Further, we conducted a Basic Local Alignment Search Tool (BLAST; Altschul et al. 1990) search using our mtDNA sequence to probe the pig genome (Sscrofa 10; http://www.ncbi.nlm.nih.gov /genome/guide/pig/) for NUMTs. We downloaded all BLAST results with >90% coverage and identity for our mtDNA matrix. We then compared the nuclear sequence with our mtDNA matrix to ensure that none matched mtDNA consensus sequences or polymorphic nucleotide positions defining haplotypes.

Phylogenetic Analyses

We used TCS 1.21 (Clement et al. 2000) with gaps set as a fifth character state to determine number of haplotypes and produce a haplotype network. To root trees we included sequences (n=13) from other *Sus* spp. published at NCBI (Appendix A). We constructed phylogenetic trees utilizing MRBAYES 3.1.2 (Ronquist and Huelsenbeck

2003) with 10,000,000 Markov Chain Monte Carlo generations using the GTR+I+G model as determined by jModeltest (Guindon and Gascuel 2003, Posada 2008). We examined uncorrected pairwise distances (p-dist.) in PAUP* (Swofford 2002). In global analysis of published and novel sequence, we established a world phylogeography dataset. With this reference we then linked mitochondrial haplotypes to broad-scale geographic origins (i.e., where a majority of published geographic collection sites and phylogenetic results agreed) and tracked global dispersal and national distribution in the U.S. We then examined domestic breed and EWB associations of mtDNA haplotypes observed in the U.S.

For the Hooper Bald introduction and translocation case study, we evaluated breed and geographic associations of pigs collected at GRSM (n=17) in light of introduction histories for Tennessee and North Carolina described in Mayer and Brisbin (1991). We then compared haplotypes from GRSM to those identified elsewhere in North Carolina (n=1) and in six other states (n=16) where animals were translocated to determine if molecular data corroborated records of dispersal referenced in Mayer and Brisbin (2009; Figure 2.1).

To develop dispersal hypotheses, we identified parsimonious molecular and geographic explanations for haplotype displacement between states occupied by wild pigs as of 1980 and those invaded subsequently by linking the closest occurrences of same haplotypes. We also incorporated information on the reputed Canadian (farmed EWB) origin for five animals collected from a game preserve in Michigan.

Results

We identified 148 haplotypes for our 401base pair mtDNA alignment, delineated by 38 transitions, one transversion, and 12 insertions/deletions. Fifteen haplotypes had both EWB and domestic breed associations (shared), 59 were reported only for domestic and feral pigs (domestic only), 63 were reported only for EWB, and eleven were of unknown (exclusive) breed associations (Appendix A).

Phylogenetic relationships

We note a phylogeographic split between Western (WEST) and Eastern (EAST) mtDNA lineages in Eurasia in the global analysis of published sequence (Figure 2.2). Within WEST our analysis returned a "mixed" polytomy (M1) consisting of a mixture of wild and domestic animals and two monophyletic groups representing EWB from Europe. In EAST we observed another mixed polytomy (M2) and monophyletic EWB, domestic, mixed, and feral (F1) assemblages associated with East Asian and South Pacific geography (Figure 2.2).

Mitochondrial DNA lineages from both WEST and EAST have been introduced to the U.S. Among the 81 U.S. wild pigs sampled, we identified fourteen mtDNA haplotypes, which were associated with M1 (n=11) and M2 (n=2) unresolved assemblages and F1 (n=1). One published sequence from Hawaii grouped in M2 (AY884613; Larson et al. 2005). This sequence constitutes a fifteenth U.S. haplotype (i.e., total adjusted U.S. sample, n=82; Table 2.1).

Network analysis of M1, M2, and F1 haplotypes (n=120) provided additional support for WEST and EAST division and revealed substructure within groups and additional insights on the importance of select haplotypes to the global distribution of pigs (Figure 2.3B). Many haplotypes found in the U.S. are shared between domestic pigs and EWB and are the most frequent and widely distributed globally (Figure 2.3). Geography for published sequence matching U.S. wild pigs included >30 countries (Figure 2.3A, Table 2.1). Haplotypes found in the U.S. were of shared (n=7), domestic only (n=4), or exclusive (n=4) types, and corresponded to >70 domestic breeds in 15 countries and EWB from 20 countries. In the U.S., pigs representing WEST (n = 69) were more common and more widely distributed than those of EAST (n=13; Figure 2.3C & D).

Case Study: Hooper Bald, GRSM

We identified six mtDNA haplotypes at GRSM, of both M1 and M2 groupings associated with >40 domestic breeds and with EWB from fourteen countries (Table 2.1). We found haplotype matches for all six states to which pigs were reportedly translocated, and elsewhere in North Carolina. Haplotype h17 was most common for GRSM (n=12) and was present in animals sampled from California (n=5) and Mississippi (n=1). Haplotype h19 was found in California (n=1), Florida (n=1), Georgia (n=2), and West Virginia (n=2), and h7 matched animals in South Carolina (n=1) and Eastern North Carolina (n=1). Haplotypes h145, h146, and h147 were found exclusively at GRSM.

Hypotheses of Undocumented Dispersal

Eight of the fifteen U.S. haplotypes were found in more than one state. Six were distributed between historic and recent pig ranges and two were found only in recently occupied states (Table 2.1). Informative geographic associations for single haplotypes ranged from two states (h20, h148) to seventeen states (h19), resulting in variation among haplotypes regarding their utility for tracking dispersal (Table 2.1). We can clearly hypothesize dispersal between Northern California and Nevada for h17 and from Virginia to Pennsylvania and New Jersey for h37 (Figure 2.4A). A link between Texas and Colorado for h19 is less clear based on geographic association and the common occurrence of this haplotype (Figure 2.4A, Table 2.1). The nature and polarity of relationships becomes more questionable with increased distance and haplotype frequency (e.g., for h17 and h37 in the Upper Midwest and h39 in Ohio and Michigan; Figure 2.4A). Because of these limitations it is not possible to elucidate the spread of M2 in the U.S. (Figure 2.4B). Both h2 and h7 were identified for pigs collected from Michigan that were reportedly EWB from Canada, presenting possible northern origins for these haplotypes (Figure 2.4B). Haplotype h2 was found only Michigan and Idaho, areas occupied subsequent to 1980, and h7 was equally distributed among historic and recently occupied states.

Discussion

Origins

The phylogeographic distribution of haplotypes in WEST and EAST in global analysis generally agrees with prior research that divides pig lineages into European and Asian clades (Alves et al. 2003, Gongora et al. 2004, Larson et al. 2005). It is well documented that domestic breeds have arisen in both world-geographic regions and that European and Asian cross-breeding has occurred during development of modern pig breeds (Kim et al. 2002, Fang and Andersson 2006, Larson et al. 2010). The starburst features associated with shared haplotypes in our network support rapid diversification and suggest independent domestication in multiple locations, as reported previously (Fang and Andersson 2006, Larson et al. 2010 Luetkemeier et al. 2010; Figure 2.3B). Molecular evidence for Asian and European mtDNA interchange is also obvious from the geographic distribution of M1 and M2 haplotypes (Figure 2.2). This distribution has direct bearing on wild pigs in the U.S., because a handful of select haplotypes were filtered through Europe and then distributed globally (Larson et al. 2005). Therefore, the occurrence of both WEST and EAST haplotypes in the U.S. is explained in simplest terms by European settlement. Similar mtDNA links to European settlement have been reported for feral pigs in New Zealand and Australia (Gongora et al. 2004). Unfortunately, it is not possible to comment on the specific number of colonization events in the U.S. due to the sharing of mtDNA haplotypes among common domestic breeds and between domestic pigs and EWB, all of which could have arrived via multiple separate introductions (Table 2.1).

Because of mitochondrial introgression between EAST and WEST, it is difficult to differentiate direct EAST (e.g., Chinese domestic breed) introductions to the U.S. from mtDNA transfer via European stock. However, some breeds of EAST origin (e.g., Vietnamese potbelly pigs) are popular in the U.S. Hence, it is likely that EAST mtDNA lineages have arrived in U.S. locations through both direct and indirect pathways. A clear example is the occurrence of three very different mtDNA haplotypes (p-dist. = 0.0305) among Hawaiian wild pigs. In Hawaii h13 and h19 probably represent domestic swine introduced after European settlement due to the association of these haplotypes with many modern domestic breeds of EAST and WEST origin (Table 2.1). Alternately, h84 likely represents the earliest introductions to Hawaii because of its exclusive occurrence among wild-living pigs on other South Pacific islands with human populations arising from Polynesian dispersal (Allen et al. 2001, Larson et al. 2005; Table 2.1).

The sharing of mtDNA haplotypes among domestic lines prevents assignment of specific breeds to wild pigs sampled from most locations in the U.S. Two notable exceptions are h20 from North Dakota and South Carolina and h103 in Mississippi. From these haplotype associations we can infer that Duroc, Large White, and Tamworth breeds are possible sources of introduction for North Dakota and South Carolina, and Landrace is a potential source for pigs in Mississippi (Table 2.1). Large White (also known as Yorkshire) and Landrace are breeds originally developed in Europe that have been propagated globally. The Duroc was developed in the U.S. from European stock and it is thought that Tamworth lines may have an ancestral tie to this breed, explaining the haplotypic relationship (Jones 1998). All of these breeds achieved popularity in the late 1800s or early 1900s and have continued to be developed since in the U.S. and elsewhere (Jones 1998). Specific association of these breeds with livestock rearing in respective states bears further investigation. For example, Durocs are reputedly hardy animals capable of surviving cold climates of northern latitudes, which may explain the association of this breed with pigs collected in North Dakota.

The combination of breed histories and molecular data provides interesting insights. However, it is important to note that breed associations for haplotypes were identified primarily with published sequence from Europe. Modern breeds propagated in the U.S. have direct ties to those in Europe, but mtDNA relationships between wild pigs and domestic pigs from the U.S. are not fully addressed with the current dataset. Comparison of mtDNA from domestic breeds currently reared in North America will be necessary to better understand intracontinental origins for these and other haplotypes among wild pigs.

Hooper Bald, GRSM

Elucidating the invasion history at GRSM at first appears intractable with mtDNA, but closer examination of written and oral accounts of introduction provides useful insights. For instance, the individual pig bearing h19 at GRSM was thought to be a recent introduction because of morphological and behavioral differences observed by park staff (W. H. Stiver, NPS, personal communication). Historic populations, therefore, are represented only by h7 and h17, and h19 is not relevant regarding translocations. With mtDNA data, we can then corroborate records of translocations to California and Mississippi (h17) and South Carolina and North Carolina (h7).

Given the EAST – WEST mtDNA interchange described above, both h7 and h17 could have arrived from feral stock introduced around English settlements in North Carolina beginning in the 1700s or from subsequent free range livestock practices and intentional release throughout the region (Mayer and Brisbin 1991). The origin of the EWB first introduced to Hooper Bald in the 1900s is unclear but the consensus view is that these animals were from Europe or Western Russia (Mayer and Brisbin 1991). Therefore, h17 is the most likely representative of EWB from Hooper Bald because of its WEST phylogeographic affiliation and its frequency at GRSM. The high occurrence of h17 among our California samples lends support to this assertion, as pigs from Hooper Bald arrived separately in GRSM and California via natural range expansion and human translocation, respectively (Mayer and Brisbin 1991). This relationship suggests that historical records of introduction are still relevant for understanding pathways of pig dispersal.

Insights on pig invasion can also be gleaned from evaluation of exclusive haplotypes (h145, h146, h147) occurring at GRSM. The presence of these unique haplotypes among U.S. pigs and the global dataset suggest three possibilities: 1) exclusive haplotypes represent historical breeds that have been replaced by modern domestic breeds, 2) these haplotypes represent divergence after introduction, or 3) these individuals are descended from EWB occurring in parts of Eurasia not previously sampled. Haplotype replacement has been identified for pig mtDNA in Eurasia and is indicated within our own dataset for parts of Hawaii (Larson et al. 2005; 2007).

Therefore, it is plausible that exclusive haplotypes in North America have originated from swine introduced during the colonial period and have persisted in the wild to present. Alternately, the close association of h145 and h147 with shared domestic and EWB haplotypes in network analysis suggests that they could have diverged from either domestic lines or EWB (Figure 2.3). It is currently unclear whether exclusive haplotypes diverged prior or subsequent to introduction or if they signify imported EWB such as that released at Hooper Bald. As described above, one possible source for the Hooper Bald EWB is Western Russia, which is not represented in published sequence (Figure 2.2). The same limitations apply for identifying origins of h148 (Kansas and Indiana; Table 2.1). Additional global sampling will be necessary to further resolve geographic origins for exclusive haplotypes and to clarify their role in pig invasion of the U.S.

Dispersal Hypotheses

Haplotype frequency and geographic distribution in North America were related directly to the utility of individual mtDNA haplotypes for tracking dispersal. For example, h19 is widely distributed in the U.S. and is also found in a variety of domestic breeds and EWB. The ubiquity of h19 could be explained by two hypotheses. It is possible that the distribution of h19 represents the human-assisted dispersal of wild-living pigs. Alternately, domestic animals having h19 may have been introduced to multiple locations as escaped livestock. Neither scenario is mutually exclusive. These considerations are a possibility for all haplotypes and cannot be resolved with mtDNA alone. In contrast, the association of h7 with a possible Canadian source provides new insights regarding wild pig range expansion to the Northeastern U.S., which might otherwise only be considered a south to north invasion. Despite its drawbacks, mtDNA provides information beyond written and oral accounts for determining sources of introductions.

Positive mtDNA associations provide additional information for managers. The link between Nevada and California (h17) is supported by our case study above for Hooper Bald EWB. A logical deduction would suggest a California source for wild pigs in Nevada because of geographic association. In contrast, similar reasoning would not arrive at a putative Michigan source for wild pigs in Idaho as indicated for h2 (Figure 2.4B). In fact, field personnel suspected California as a source for the Idaho introduction (McCann unpublished data). This demonstrates the utility of molecular evidence for identifying potential long-range, anthropogenic dispersal events necessary for rapid wild pig invasion of the upper Midwest (Gipson et al. 1998). In this manner, all mtDNA relationships (i.e. those presented in Figure 2.4 and those inferred from Table 2.1) can provide useful information for directing inquiries on intracontinental movement of wild pigs.

Summary and Future Directions

Clearly, mtDNA provides limited resolution of relationships for wild pigs in the U.S. Shared ancestry and inbreeding precludes definitive identification of unique mtDNA profiles for EWB or domestic lines in most instances. Stochastic variation also appears to have a role in mtDNA diversity among U.S. wild pigs, as demonstrated by exclusive haplotypes. Regardless, mtDNA sequence is the only widely used molecular marker at this time for global-scale analysis. While the accuracy of published sequence is a concern, it appears that this issue does not impact overarching phylogeographic results, such as the identification of EAST and WEST mtDNA lineages among published sequence and for samples obtained from the U.S.

Within the U.S., mtDNA corroborates written histories of introduction and translocation, and can yield useful hypotheses for undocumented dispersal events. More extensive sampling might produce further haplotype links corroborating written history, as in the case of Hooper Bald. Additionally, extensive range expansion documented for hybrid pigs in California provides a unique opportunity to explore the relationship between h17 and EWB further with a regional analysis (Pine and Gerdes 1973, Barrett 1977, Waithman et al. 1999). However, it is possible that mtDNA is at the limit of its utility to answer some questions. The nearly ubiquitous nature of h19 among U.S. wild pigs suggests that additional molecular markers are needed to resolve its distribution. Ongoing research utilizing multilocus nuclear DNA markers or genes linked to morphological traits (e.g., pelage) will be necessary to more effectively track dispersal and parse out specific domestic breed and EWB contributions to wild-living pigs in the U.S. (Hampton et al. 2004, Spencer and Hampton 2005, Koutsogiannouli et al. 2010, Scandura et al. 2011).

Management Implications

Mitochondrial DNA analysis has provided new insights on the origins and anthropogenic dispersal of wild pigs in the U.S. Molecular corroboration of historical accounts indicates that written and oral records of introduction are still relevant. The most powerful method for managers is likely the combination of written, oral, and molecular information in a total evidence approach. In this way mtDNA will contribute to the identification of potential sources for new introductions so that future translocations can be prevented. Additionally, disease surveillance could be improved with knowledge of long-range dispersal of pigs and associated pathogens. Finally, this work is instrumental in promoting and guiding future research exploring molecular genetic relationships for wild pigs in the U.S.

Table 2.1. Phylogeography and breed-specific details of 15 mitochondrial DNA haplotypes representative of 81 wild pigs collected from 30 U.S. states during the period July 2007-May 2010 and one published sequence for wild pigs from Hawaii. Samples from the United States are compared to published sequence from around the world (n=483) within haplotypes. Published sequences for global analysis were obtained from National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov/). Phylogeographic descriptors EAST and WEST correspond to a division of mtDNA lineages in Eurasia identified through MrBayes 3.1 analysis of a ~400 base pair region of the mtDNA control region (D-loop) under the GTR+I+G model and 10,000,000 Markov Chain Monte Carlo generations. Descriptors M1 and M2 represent unresolved assemblages in WEST and EAST phylogenies, and F1 represents a single EAST haplotype found only on Hawaii and South Pacific Islands. Geographic origin of sequence and type of pigs represented are denoted for each haplotype; GRSM = Great Smoky Mountains National Park; U.S. states are abbreviated.

Haplotype	Phylogeography	Phylogeny	No. domestic	No. wild	No. feral	No. other	No. U.S.	Total	US geography	World geography (No. wild animals reported "w#")	Breed associations
2[a]	EAST	M2	40	3	12	3	3	61	ID, MI	Australia, China, Europe, France, Germany, Japan (w3), Sweden, Taiwan, Thailand, UK	>20 Asian and European domestic breeds
7	EAST	M2	42	9	1	1	8	61	MI, NC, OH, PA, SC, TN	Belgium (w1), China (w3), East Asia, Europe, France, Italy (w2), Japan, Malaysia (w1), Mariana Islands, South Carolina USA, Russia (w1), Spain, Thailand (w1), UK, US - GRSM	~20 Asian and European domestic breeds
13[b]	EAST	M2	64	5	3	3	1	76	HI	China (w1), UK, Korea, Europe, Germany, Spain, Japan (w1), Hawaii, Australia, Thailand, Italy (w3)	~16 Asian and European domestic breeds
17	WEST	M1	25	12			22	59	AR, CA, MS, NC, ND, NV, TN,	Belgium (w1), Europe, Germany, Iberian Peninsula, Iceland, Italy, Macedonia (w1), Norway (w1), Spain (w9), UK, US - GRSM	12 European domestic breeds

Table 2.1 cont.

Haplotype	Phylogeography	Phylogeny	No. domestic	No. wild	No. feral	No. other	No. U.S.	Total	US geography	World geography (No. wild animals reported "w#")	Breed associations
19	WEST	M1	91	32		8	22	153	AL, AR, CA, CO, FL, GA, HI, KY, LA, MI, ND, OH, OK, TN, TX, WI, WV	Corsica (w3), Europe, Finland, France (w1), Germany (w2), Hungary, Holland (w1), Iberian Peninsula, Italy (w24), Portugal, Sweden (w1), UK, US - GRSM	>20 European domestic breeds
20	WEST	M1	10				3	13	ND, SC	Europe, UK	Duroc, Large White, Tamworth
37	WEST	M1	22	19		5	12	58	AZ, CA, KS, LA, ND, NJ, NE, NM, OK, PA, TX, VA	Austria (w1), Bulgaria (w1), Europe, Germany (w2), Hungary (w8), Iberian Peninsula, Indonesia, Italy, Korea, Morocco (w1), Poland (w5), Portugal, Spain (w1), UK	12 European domestic breeds, 1 Asian type "Korean Native"
38	WEST	M1	24	34		2	1	61	KY	Austria (w1), Corsica (w2),Denmark, Europe, France (w12), Germany (w1), Hungary, Iberian Peninsula, Italy (w18), Portugal, Sardinia, UK	Bisaro, Duroc, Gloucester Old Spot, Hampshire, Hungarian Mangalica, Iberian Red, Landrace,
39	WEST	M1	7				3	10	FL, MI, OH	Germany, Europe, Sweden	Angler sattleschwein, German Angler, Hampshire
84	EAST	F1			3		1	4	HI	Papua-New Guinea, US - Hawaii, Vanuatu	Feral animals only
103	WEST	M1	2				1	3	MS	Europe	Landrace

Table 2.1 cont.

Haplotype	Phylogeography	Phylogeny	No. domestic	No. wild	No. feral	No. other	No. U.S.	Total	US geography	World geography (No. wild animals reported "w#")	Breed associations
145	WEST	M1					1	1	NC	US - GRSM	Unique haplotype
146	WEST	M1					1	1	TN	US - GRSM	Unique haplotype
147	WEST	M1					1	1	TN	US - GRSM	Unique haplotype
148[a]	WEST	M1					2	2	IN, KS	US	Unique haplotype

[a] Found only in U.S. states occupied during the last 30 years

[b] United States haplotype reported only for published sequence for a feral pig from Hawaii (AY884613; Larson et al. 2005)

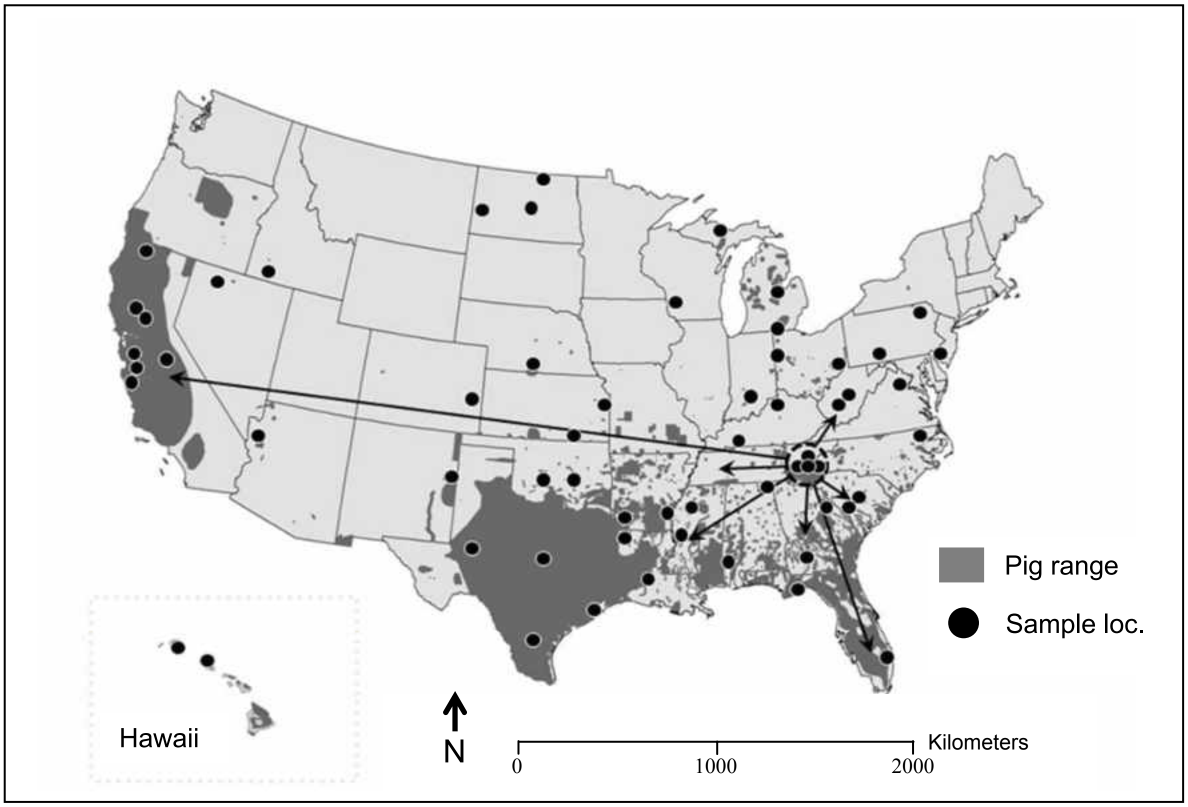

Figure 2.1. Distribution of 81 samples from wild pigs (*Sus scrofa*) collected during the period July 2007-May 2010. Dark regions of map indicate areas of established pig populations as denoted by state agencies and USDA Wildlife Services (SCWDS 2010 National Feral Swine Mapping System, Southeastern Cooperative Wildlife Disease Study, University of Georgia, http//:www.feralswinemap.org). Encircled area indicates Hooper Bald introduction site and subsequent hybrid pig range in GRSM, and arrows represent anthropogenic redistribution of animals to California, Florida, Georgia, Mississippi, South Carolina, and West Virginia (modified from Mayer and Brisbin 2009).

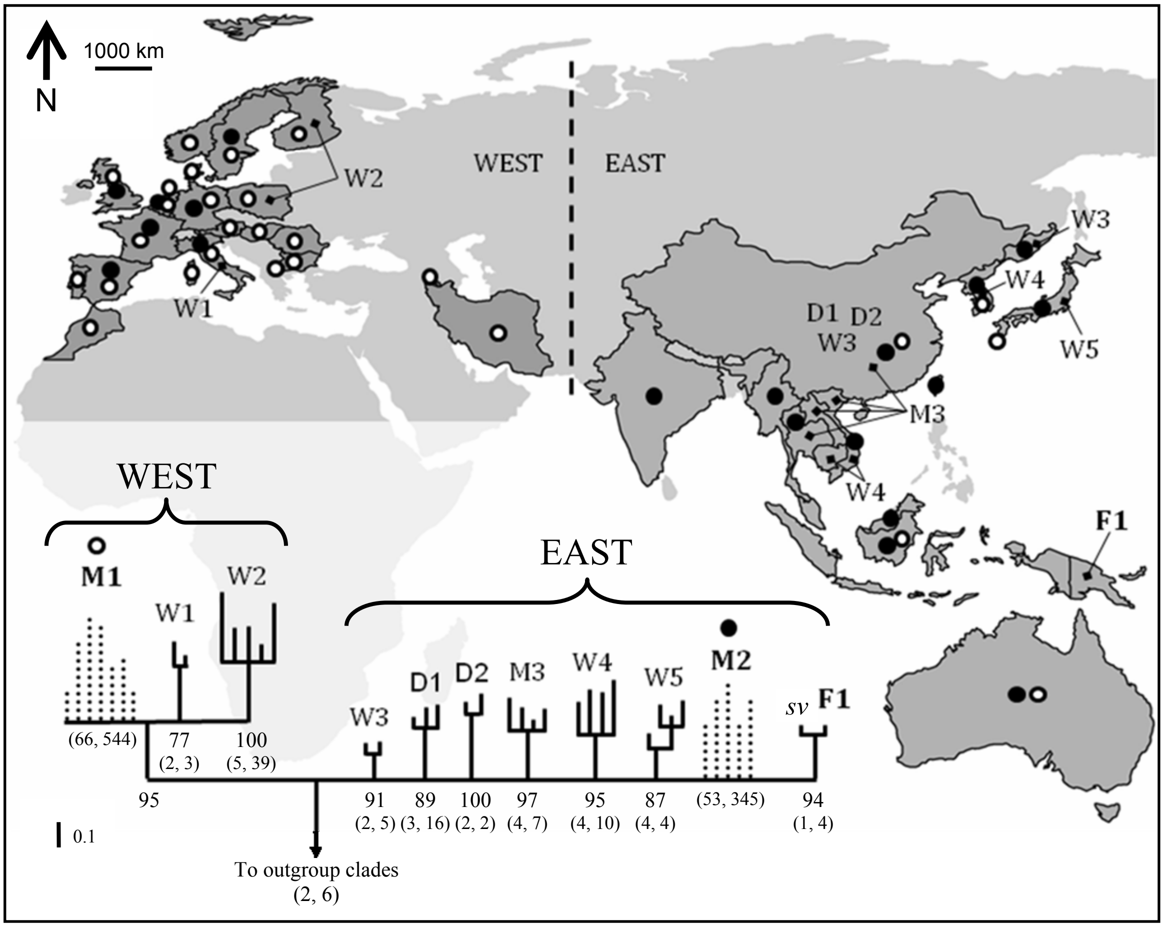

Figure 2.2. Rooted phylogram of 148 *Sus scrofa* haplotypes constructed using a GTR+I+G model with 10,000,000 generations in MRBAYES 3.1.2. Represented are: 81 individuals collected from 30 U.S. states during the period July 2007-May2010, 904 published sequences for *S. scrofa* from around the world, and 13 sequences from five other *Sus* spp. Shaded countries with black outlines indicate geographic locations referenced in published sequence (Iceland, South Carolina USA, Hawaii, and some Pacific islands are not shown). Dashed line on map represents division corresponding to the Western (WEST) and Eastern (EAST) phylogeographic split denoted in tree. Phylogenetic groupings are further described by pig type within EAST and WEST in tree and on map; W (Eurasian Wild Boar), D (domestic), M (mixed, shared between domestic pigs and Eurasian Wild Boar; M1=white dots, M2=black dots), F (feral), and *sv* (*Sus verrucosus*). Assemblages containing haplotypes found in the U.S. are in bold: M1 (h17, h19, h20, h37, h38, h103, h146, h147, h148), M2 (h2, h7, h13, h145), and F1 (h84). Dotted lines in tree indicate polytomies from unresolved phylogenetic assemblages M1 and M2; number of lines is proportional by an approximate factor of ten to the count of haplotyes in each branch. Numbers at nodes indicate mean posterior probabilities (≥75% shown) and numerals in parentheses indicate number of haplotypes and number of individual sequences, from left to right. Note: scale bar (bottom left) indicates genetic distance, dotted lines excluded.

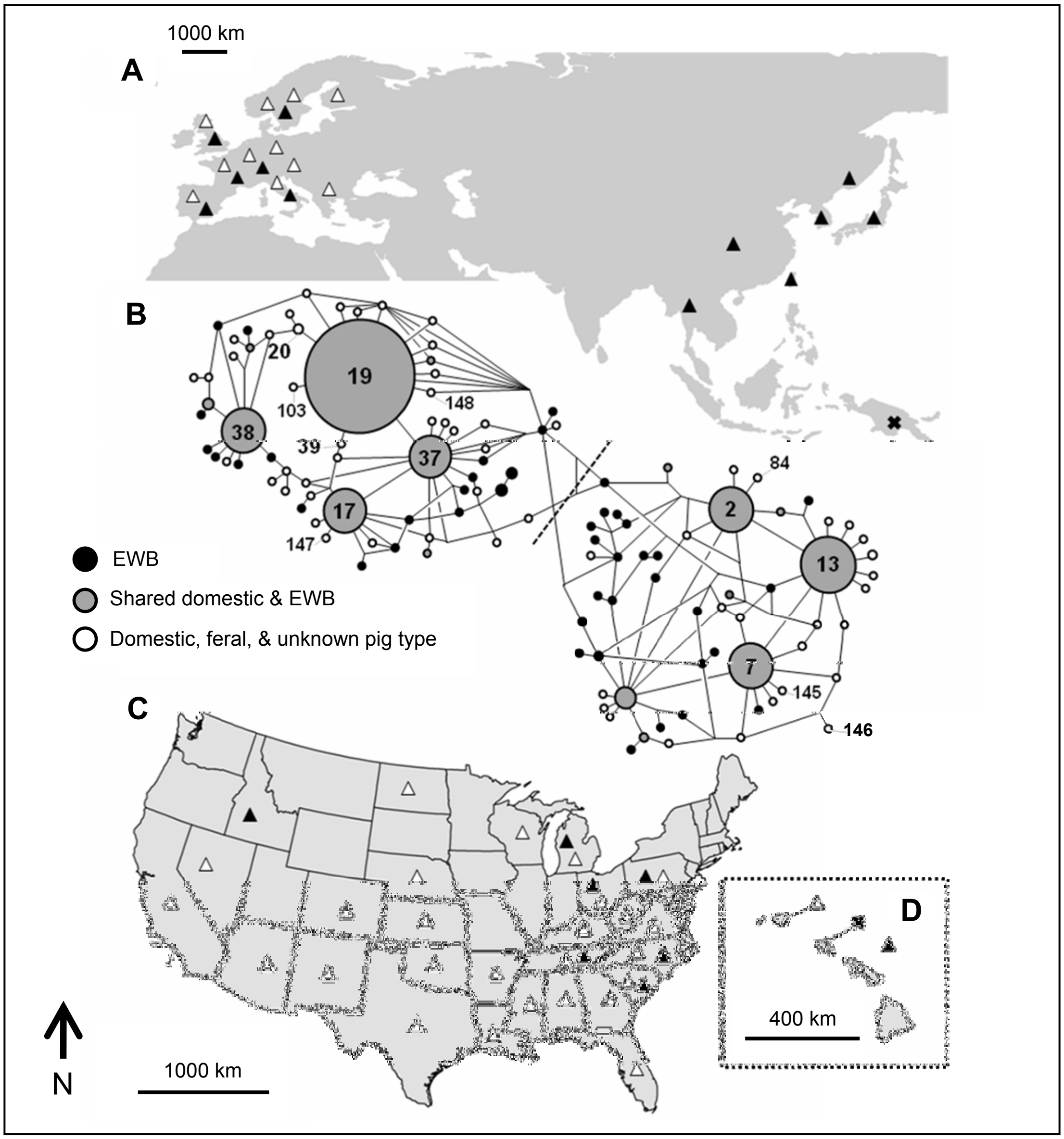

Figure 2.3. Haplotype network (panel B) constructed in TCS 1.21 with 120 *Sus scrofa* haplotypes representing M1, M2, and F1 haplotypes of wild and domestic pigs from the United States and around the world. Dashed line in network indicates phylogeographic split of WEST (above line) and EAST (below line), with the exception of h146 that grouped among M2 haplotypes in network analysis. Frequency of haplotypes in dataset is represented by relative size of nodes (smallest ≤ 10 individual sequences, largest=153 individual sequences). Pig types inferred from accessions are denoted by black (Eurasian Wild Boar; EWB), gray (shared between domestic and EWB), and white (domestic, feral, unknown, or exclusive U.S. haplotypes) color schemes. Haplotypes found in the U.S. are numbered within or next to nodes. Intermediate nodes, mutational steps, and genetic distance are not represented. World (panel A) and U.S. (panels C and D) distributions of haplotypes are presented as follows: M1 (white triangle), M2 (black triangle), and F1 (black x). Note: island location for EAST haplotype in Hawaii is unknown (panel D).

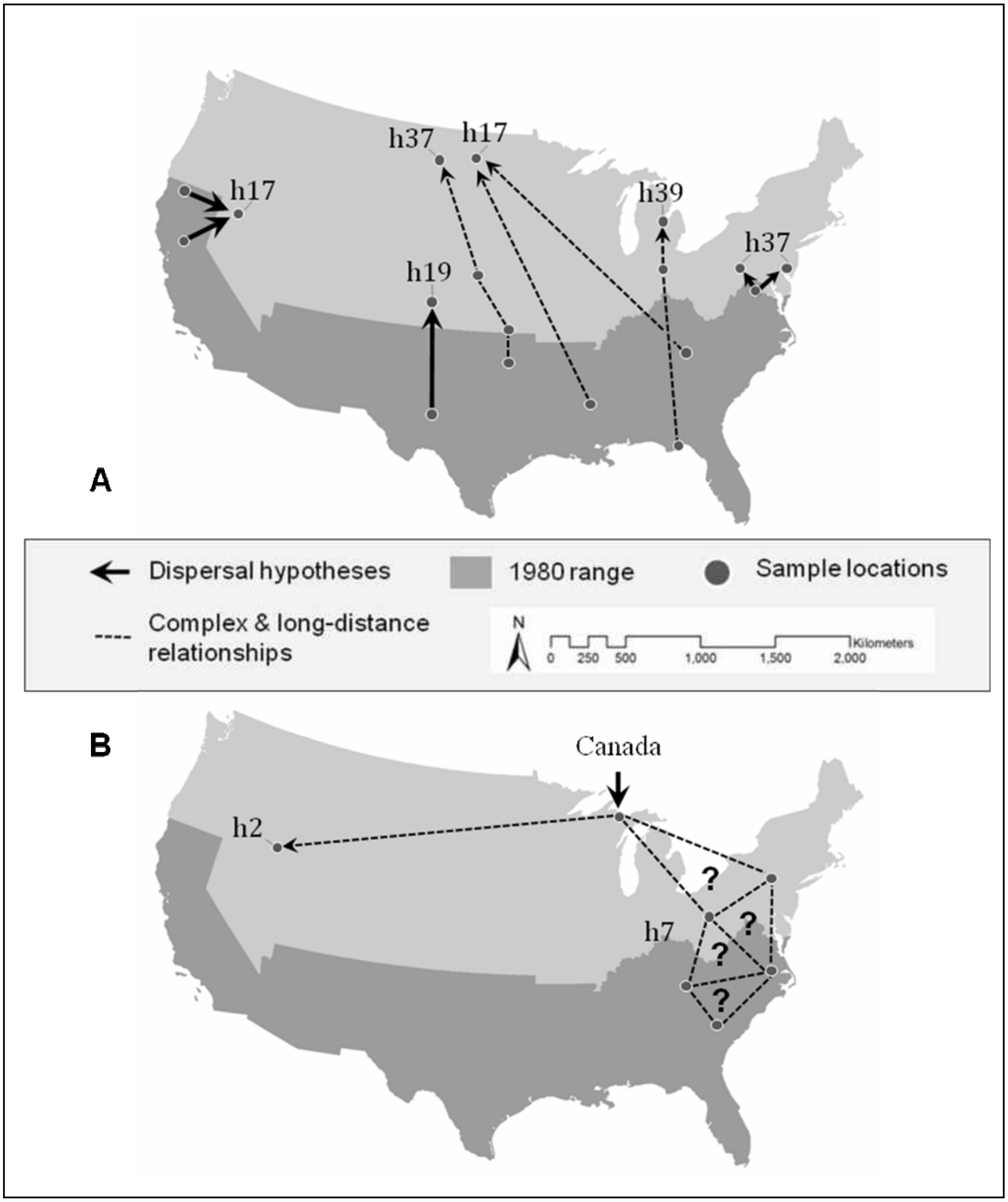

Figure 2.4. Hypotheses of dispersal for a subset of M1 (panel A) and M2 (panel B) mtDNA haplotypes in the United States. Closest geographic occurrence of same haplotypes interpreted to identify putative geographic dispersal pathways. Not all sample locations or haplotype relationships are presented. Arrow at top of map (panel B) indicates reported Canadian source for Eurasian Wild Boar hybrid pigs sampled in Michigan, from which M2 haplotype dispersal is considered to possibly originate.

CHAPTER III

MITOCHONDRIAL DNA PERSPECTIVES ON THE INTRODUCTION AND SPREAD OF WILD PIGS IN CALIFORNIA

Introduction

Pigs (*Sus scrofa*) were first introduced to North America during the 1500s (Towne and Wentworth 1950, Mayer and Brisbin 1991). Through human exploration and settlement feral domestic pigs became established due to free-range livestock practices, escape, and release (Mayer and Brisbin 1991). By the late 1800s feral populations were present in at least thirteen U.S. states (Mayer and Brisbin 1991). At this time increased interest in pig hunting led to importation and release of Eurasian Wild Boar (EWB) from throughout Europe and Eastern Russia, which hybridized with existing feral populations in many parts of the country because of anthropogenic dispersal (Mayer and Brisbin 1991). Enthusiasm over wild pigs as a game species has resulted in their occurrence in new locations during the twentieth century (Mayer and Brisbin 1991). Drastic range expansion during the last 30 years has resulted in spread of pigs from seventeen states in 1980 to 44 U.S. states currently (Mayer and Brisbin 2009; Gipson et al. 1998).

The story of wild pigs in California parallels the continental history outlined above. Domestic pigs were initially introduced to California by Spanish explorers and missionaries from the 1500s-1700s, followed by continual introductions including domestic swine and EWB (Mayer and Brisbin 1991). It is thought that pigs may have invaded both island and mainland locations in California during the early 1500s; however, the first recorded introduction in the region occurred on Santa Cruz Island in association with a Spanish penal colony in the 1580s (Mayer and Brisbin 1991). Spanish exploration and settlement are also likely sources for pigs on Santa Rosa Island, though the exact origin of this population is uncertain. Santa Cruz Island and Santa Rosa Island once sustained ranching ventures that may have also contributed domestic stock to feral pig populations; records indicate that pigs were taken from Santa Rosa Island to establish a population on Santa Catalina Island in the 1930s (Mayer and Brisbin 1991). Feral pigs once occurred on five Channel Islands but all have now been eradicated (Mayer and Brisbin 1991, Schuyler et al. 2002, Ramsey et al. 2009).

On the mainland, feral pigs were first recorded in coastal areas around Spanish missions during the 1700s (Barrett and Pine 1980, Pine and Gerdes 1973, Mayer and Brisbin 1991). Subsequent release of domestic swine from settlements and the livestock industry led to the establishment of feral populations in many mainland locations (Mayer and Brisbin 1991). King City in Monterey County was referred to as “Hog Town” during the 1880s, because pigs were driven to stockyards there for shipping and many animals escaped to populate the surrounding countryside (Pine and Gerdes 1973, Mayer and Brisbin 1991). Despite repeated introductions, feral pig populations remained localized in California until the middle of the twentieth century. Since then drastic range expansion has occurred, from nine counties in the 1960s to nearly the entire state (Waithman et al. 1999; Figure 3.1).

In 1925, EWB hybrids (n=12) from Hooper Bald, North Carolina, were released in Monterey County (Pine and Gerdes 1973, Mayer and Brisbin 1991). These EWB hybrids dispersed and bred with feral domestic pigs, whose progeny were later transferred to other counties in Central and Northern California (Mayer and Brisbin 1991). The anthropogenic dispersal of hybrid pigs is thought to explain recent range expansion in California based on the hypotheses that hybrids are more invasive than feral domestic pigs. Further, it is possible that humans preferentially select pigs with EWB characteristics for translocation (Barrett 1977, Waithman et al. 1999). These assertions have not been investigated beyond written and oral histories of introductions and invasion within California.

As in other parts of the United States, illegal translocation of wild pigs for hunting purposes is a leading cause of range expansion in California (Mayer and Brisbin 1991, Gipson et al. 1998, Waithman et al. 1999). It is unclear to what extent natural dispersal, anthropogenic dispersal, and the types of pigs introduced have shaped the current distribution of pigs in California. Considering the clandestine nature of recent introductions, molecular techniques provide the best opportunity for examining these factors (Spencer and Hampton 2005, Chapter II).

Mitochondrial DNA (mtDNA) has been used successfully for a number of phylogeographic studies of pigs. Previous work has evaluated the adaptive radiation of suids across Eurasia and identified centers of domestication (Giuffra et al. 2000, Larson et al. 2005, 2007; Luetkemeier et al. 2010). Prior studies of mtDNA have also aided in identifying ancient and historic anthropogenic dispersal of EWB and domestic swine (Fang and Andersson 2006, Scandura et al. 2008, Vigne et al. 2009). Published mtDNA sequence has become a valuable resource for global analysis of pig ancestry and is useful for elucidating origins and dispersal patterns of introduced pigs (Gongora et al. 2004, Chapter II). Though mtDNA and published sequence have intrinsic limitations regarding stochastic variation, sequence error, and nuclear pseudogenes (Wesche et al. 2004, Nilsson et al. 2006, Parr et al. 2006, Goios et al. 2009), these factors do not seem to impact overarching phylogenetic relationships of introduced pigs (Chapter II).

In an analysis of mtDNA from 81 wild pigs collected in 30 U.S. states (Chapter II), the greatest limitation to tracking dispersal was high frequency of occurrence for some mtDNA haplotypes. Results were also impacted by sparse nationwide sampling, which was thought to affect observed mtDNA variation. Despite these issues, translocations of EWB from Hooper Bald to California could still be corroborated (Chapter II). These data also suggested that regional analysis would yield greater insight regarding the role of EWB in recent range expansion within California. To address these issues and evaluate wild pig invasion of California from a molecular perspective, we have obtained mtDNA sequences for wild pigs from throughout the state and analyzed them in context of published sequence including U.S. wild pigs and a global dataset of EWB and domestic swine. Here, we seek to: 1) evaluate mtDNA variation in California wild pigs, 2) identify mtDNA haplotypes associated with historic and recent wild pig invasion in California, and 3) assess population-level genetic relationships among wild pigs in California and the U.S. to elucidate patterns of gene flow indicative of sources for new populations.

Study Area

We obtained tissue samples from 151 wild pigs in 23 California counties during the period 1996-2010, spanning recent and historic distribution of the species in the state (Figure 3.1). We obtained published sequence of wild and domestic swine from California, 29 other U.S. states, and four other continents (Chapter II; Figure 3.1).

Methods

We obtained wild pig tissue samples from throughout California by cooperating with USDA Wildlife Services, National Park Service, California Department of Fish and Game, and private organizations involved in sanctioned pig control or eradication programs. For each animal, field personnel collected blood or other somatic tissue (e.g., skeletal muscle, skin) recorded pelage characteristics, date, and geographic coordinates for each sample. Blood was transferred to FTA (Whatman Inc., Florham Park, NJ, USA) cards and mailed to the University of North Dakota (UND) for analysis. Other somatic tissue was frozen, shipped overnight to UND, and stored at -20°C. We also incorporated samples and representative sequences for wild pigs in California obtained during prior research at UND (Accessions: AY96871-AY968729, AY968731-AY968742, AY968744-AY968763, AY968765-AY968806, AY973042; Loggins 2007). In total our dataset included samples from 151 individual pigs in 23 California counties (Figure 3.1; Appendix A). Because animals were destroyed for sanctioned purposes, or research was deemed exempt from approval by the UND institutional animal care and use committee.

We processed sample specimens using standard protocols, as previously described for wild pigs (Chapter II.). We used forward primer PigF (5'-ACTCTGGTCTTGTAA ACC-3') and reverse primer PigR (5' –TAAGGGGAAAG ACTGGGC-3') to amplify and sequence an approximately 550 base pair segment of the mtDNA control region (Okumura et al. 1996, Loggins 2007). We manually aligned sequences and trimmed our matrix to 400 base pairs for phylogenetic analysis (Chapter II). We then submitted sequences to online holdings at NCBI Genbank (http://www.ncbi.nlm. nih.gov/). Accessions are as follows: JF702003-JF702008, JF702013-JF702016, JF702018-JF702022, JF702038-JF702039, JF702041-JF702048, JF702050-JF702053, JF702055, JF702079-JF702080, JF702082-JF702104, and JQ792040.

We aligned sequence for wild pigs from California with a 400 base pair matrix of 148 mtDNA haplotypes identified for *Sus scrofa* sampled from 30 U.S. states and published sequence for wild and domestic swine from around the world (Chapter II). We included sequence for five other species of *Sus* (n=13) in the alignment to serve as outgroups for phylogenetic analysis. A list of accessions, geographic sources, and publications for sequences is provided in our supplemental information (Appendix A). We evaluated the possibility of nuclear pseudogene bias with mtDNA of pigs as previously described; we found no evidence of pseudogenes in our dataset (Chapter II).

We collapsed sequences to haplotype using TCS 1.21 with gaps set as fifth character state (Clement et al. 2000). We used JMODELTEST to determine the most appropriate evolutionary model for phylogenetic analysis (GTR+I+G; Guindon and Gascuel 2003, Posada 2008). We then constructed phylogenies in MRBAYES 3.1.2 (Ronquist and Huelsenbeck 2003) with 10,000,000 Markov Chain Monte Carlo (MCMC) sampling generations and retained consensus tree structure with >75% posterior probabilities.

To determine if observed mtDNA variation increases with additional regional sampling in California, we compared the number of observed haplotypes for the 151 newly evaluated individual pigs to those previously identified for seven pigs from California (Chapter II; JF702006, JF702017, JF702037, JF702040, JF702046, JF702049, JF702081). We then combined all California samples, resulting in 158 individual specimens for analysis of mtDNA relationships within the region.

We identified mtDNA haplotypes associated with different stages of invasion by comparing their geographic distributions to written histories of introduction and range expansion (Barrett 1977, Pine and Gerdes 1973, Barett and Pine 1980, Mayer and Brisbin 1991, 2009; Waithman et al. 1999) and with the evidence for wild pig mtDNA relationships elsewhere in the U.S. (Chapter II). To facilitate interpretation of molecular data we grouped the 158 California wild pigs into four discrete clusters of geographic and management importance: 1) Santa Catalina Island (n=6), 2) Santa Cruz Island (n=11), 3) Historic mainland ("Historic"; n=77), and 4) Recent mainland ("Recent"; n=64). We divided mainland samples by historic and recent distributions of wild pigs within the state, and designated Historic as those samples obtained from nine coastal counties occupied by pigs as of the 1960s (Waithman et al. 1999); Recent includes animals from all other mainland locations in California (Figure 3.1).

We assessed gene flow indicative of invasion sources in California by analyzing population-level mtDNA sequence relationships in ARLEQUIN 3.5 (Excoffier et al. 2005). We compared five population groupings; the four California populations described above and an arbitrarily assigned population of wild pigs (n=74) sampled from 29 other U.S. states that we refer to as "29US" (Chapter II; Table 3.1).We performed a standard AMOVA on pair-wise differences with 1023 permutations to estimate significance. We conducted an exact test of population differentiation with 100,000 MCMC steps based on haplotype frequencies. We then calculated pair-wise F_{ST} and N_m among groups and evaluated statistical results in context of haplotype distributions in California and other U.S. states.

Results

We identified 151 haplotypes among all mtDNA sequences and nine for California pigs. Six haplotypes are new discoveries for California; three were exclusive (h149-h151), two (h84 and h13) have been identified for wild pigs in Hawaii but not previously in for wild pigs in North America, and one (h38) matched other U.S. wild pigs only in Kentucky. The remaining three haplotypes are common across the U.S. (h17, h19, h37) and have wide geographic distributions (Table 3.1).

Phylogenetic analyses revealed three major clades among the 151 mtDNA haplotypes that were associated with geography; Eastern Eurasia (EAST), Western Eurasia (WEST), and Island Southeast Asia (ISEA), as previously described (Larson et al. 2005, Chapter II; Figures 3.1, 3.2). Geography agreed with phylogeny for some groupings, though global distribution of many haplotypes associated with domestic breeds resulted in phylogeographic discordance (Figure 3.2). Most haplotypes observed in California were globally distributed and associated with unresolved assemblages in

WEST and EAST (M1 and M2, respectively) representing a mixture of domestic swine and EWB (Figure 3.2). One haplotype (h84) was placed in a monophyletic grouping (F1) for feral pigs and *S. verrucossus* observed only in ISEA and Pacific Islands, including Hawaii (Figure 3.2, Table 3.1).

In California, WEST mtDNA was more common than EAST (Table 3.1). Two WEST haplotypes in particular, h17 (n=59 individuals) and h19 (n=68 individuals), had wide distributions spanning both historic and recent pig range (Figure 3.3). Other WEST haplotypes involved in range expansion include h38 and h150 (Figure 3.3). We observed exclusive haplotypes primarily within historic range and on the Channel Islands. Geographic distribution of EAST haplotypes was more restricted; h84 was found only on Santa Catalina Island and h13 was observed only in two Recent locations (Figure 3.3).

Population-level mtDNA variation between the five population groupings was significant (AMOVA $_{4,\,228}$; $p<0.00000$). Exact tests of population differentiation were highly significant ($p<0.00000$) for all but Historic-Recent ($p=0.00197$, SE±0.0011) and Santa Catalina Island-Santa Cruz Island ($p=0.02991$, SE±0.0008). All population F_{ST} measures were significant except Recent and 29US, for which numbers of migrants were estimated as exceptionally high when compared to other populations within the state (Table 3.2). In California, h13, h37, h84, h149, and h151 were confined to single population groupings, and h150 was the only haplotype shared between island and mainland locations (Figure 3.3, Table 3.1). Haplotypes h17, h19, and h38 were shared by Historic, Recent, and 29US.

Discussion

Though we aim to understand relationships among pigs in California, it is important to frame these results in the context of global phylogeny. Our phylogeographic result of EAST, WEST, and ISEA groupings generally agrees with findings of other studies evaluating mtDNA control region sequence in pigs (Alves et al. 2003, Gongora et al. 2004, Larson et al. 2005). This finding provides confidence in the accuracy of our dendrogram in describing sequence relationships that we use to evaluate the invasion of wild pigs in California.

The unresolved nature of M1 and M2 haplotypes within respective WEST and EAST branches of the phylogeny likely represents an increased rate of nonsynonymous changes in the mtDNA genome resulting from domestication, as described for dogs (Bjornerfeldt et al. 2006). Representatives of these mixed groups (i.e., with domestic and EWB associations) have achieved the greatest geographic distributions through anthropogenic dispersal, and prevalence among introduced pigs in the U.S. and elsewhere (Chapter II; Table 3.1). As such, humans have impacted both the genetic composition and geographic distribution of pigs globally, resulting in a lack of phylogenetic resolution for some mtDNA lineages. Therefore, we should capitalize on discrete mtDNA variation (i.e., haplotypes) to track dispersal of wild pigs where possible (Chapter II).

Regional mtDNA Variation

Additional regional sampling detected greater mtDNA variation among wild pigs than observed with subsampling of California (Chapter II). Detection of more diversity here suggests that additional nationwide sampling would produce a higher-resolution picture of pig invasion through mtDNA relationships. However, the predominance of h17 and h19 among extant California populations indicates that ubiquitous mtDNA profiles would continue to limit the utility of mtDNA as a marker for defining origins and dispersal patterns of introduced pigs on both national and regional scales (Chapter II).

The low mtDNA diversity observed on Santa Catalina Island (two haplotypes) and Santa Cruz Island (one haplotype) represent genetic drift associated with isolation or bottlenecks from culling and mast failures (Baber and Coblentz 1986). Both populations endured periodic reduction efforts from the 1940s onward, prior to eventual eradication in the early 2000s (Mayer and Brisbin 1991, Schuyler et al. 2002, Ramsey et al. 2009). The low mtDNA variability detected on the islands is an important observation for management because it suggests that wild pig populations are resilient even when at low genetic diversity.

It is possible that additional mtDNA variation is present among wild pigs in areas that we did not sample, including one historically invaded county (Humbolt County; Figure 3.1). More samples would be necessary from all mainland locations to provide a definitive estimation of mtDNA variation among wild pigs in California. Additional sampling might also reveal new insights as to the distribution of common haplotypes h17 and h19, and could assist in developing a clearer picture regarding the role of exclusive haplotypes in wild pig invasion of mainland locations.

Haplotypes Associated with Recent and Historic Invasions

Historic Invasion. It is not possible to develop a definitive timeline of invasion based upon mtDNA lineages, but insights can be gained from assessment of molecular relationships in light of phylogeny and introduction histories. The WEST phylogeographic association of most haplotypes in California suggests that historic and recent introductions are equally likely, given the European influence on early settlement. However, common haplotypes (e.g., h37) are routinely associated with a variety of modern domestic breeds, which supports more recent introductions (Table 3.1). Following this logic, the lack of breed references for exclusive haplotypes suggests that they represent older introductions of swine with mitochondrial lineages that have been lost in modern breeds (Chapter II). This hypothesis is supported by the distribution of h149, h150, and h151 primarily within the historic range of pigs in mainland and island locations and the association of some haplotypes with specific introduction histories (Figure 3.3). For example, the sharing of h150 between Santa Catalina Island and Santa Cruz Island corroborates a common origin for populations on the Channel Islands resulting from introductions by the Spanish (Mayer and Brisbin 1991). Spanish settlement then might also explain the occurrence of h150 on the mainland, as there is no record of gene flow between island and mainland locations. Though drift has limited observed mtDNA variation on islands, isolation of the Channel Islands from the mainland appears to have prevented original lineages from being replaced by successive waves of introduced pigs.

Our identification of h84 on Santa Catalina Island is interesting, as this haplotype has been observed nowhere else except pacific islands, including Hawaii (Figure 3.2; Chapter II, Larson et al 2005). One possible pathway for introduction of h84 to California is the voyages of Captain Cook during the 1700s (Clarke and Dzieciolowski 1991, Loggins 2007). Cook transferred livestock between many island locations in the South Pacific and also visited the Oregon coast, though we could find no records of visits to mainland California or the Channel Islands. Due to the absence of this haplotype on Santa Cruz Island and the lack of samples for Santa Rosa Island (the source of pigs on Santa Catalina Island), the origin of h84 in California remains a mystery. Additional samples from Hawaii and archival samples obtained from the Channel Islands during the course of eradication programs would be useful for further exploring this unrecorded historic pathway of introduction.

Recent Invasion. Regardless of specific origins, h17 and h19 are the haplotypes most involved with recent range expansion in California (Figure 3.3). The ubiquity of h17 and h19 appear to represent a scenario where these animals have been recently propagated by humans (Figure 3.3). Haplotype h19 is distributed throughout North America and represents wild pigs in both historic and recently invaded portions of the continent (Chapter II). Likewise, the distribution of h19 in California indicates that historic populations are a source for new invasions within the region (Figure 3.3). The origin of h19 in U.S. wild pigs is unclear, as this haplotype is associated with a wide variety of wild and domestic swine populations globally (Chapter II). Alternately, h17 is linked to EWB introduced to Hooper Bald, North Carolina and then translocated to California (Chapter II). The geographic distribution of h17 in California mirrors recorded anthropogenic dispersal of EWB hybrids within the state to the north and east of the original introduction site in Monterey County (Figure 3.3; Mayer and Brisbin 1991). This finding supports the importance of EWB hybrids in range expansion, at least to some portions of California (Barrett 1977, Barrett and Pine 1980, Waithman et al. 1999).

The roles of h13, h38, and h150 in recent invasion are less clear. Haplotype h13 is the only EAST mtDNA lineage observed on the mainland, suggesting that it does not represent original introductions by Spanish explorers (Table 3.1). Further, h13 was found exclusively within recent range (Figure 3.3). These factors combined indicate that h13 was recently introduced to California, possibly from escape or through cross-breeding with domestic swine (Table 3.1). The low frequency of occurrence and limited distribution of h38 and h150 in California provide few clues as to the importance of these haplotypes for ongoing pig invasion (Table 3.1). However, recent anthropogenic dispersal appears to have resulted in the current distributions of h38 and h150, due to an apparent lack of population connectivity and barriers to gene flow between island and mainland locations (Figure 3.3).

Population Genetic Relationships for Wild Pigs in California

Sequence relationships between populations have helped elucidate subtle differences between populations. The close F_{ST} association of Recent and 29US samples is due to the sharing of h13 between these groups and the occurrence of other EAST mtDNA sequences (h2, n=3; h7, n=8) elsewhere in the U.S. that were not found in California (Table 3.1). When h2 and h7 sequences were removed from the analysis, the F_{ST} relationship between Historic and 29US was no longer significant, though comparison of the Historic and Recent groups was significant (results not shown). This relationship exemplifies potential problems with pair-wise mtDNA sequence analysis of introduced pigs, for which haplotype tracking techniques may be more appropriate (Chapter II). Significant exact tests of population differentiation based on haplotype frequencies revealed a similar pattern and support some level of relatedness for Recent and Historic and a common origin for wild pigs on the Channel Islands, through reduced significance values (Table 3.2).

Apparent gene flow between Recent and Historic in the form of common haplotypes (i.e., h17 and h19) indicates that pigs are dispersing at the regional level within California. It is often not possible to separate natural dispersal from anthropogenic dispersal based on molecular evidence alone. However, human movement is obvious in some cases (e.g., h38 in southern California; Figure 3.3). Wild pigs are known to disperse on their own within the state, possibly accounting for similar haplotypes observed in close proximity (Waithman et al. 1999). The sharing of h13 between Recent and 29US suggest that new introductions have also occurred; either from outside of the state or from modern domestic breeds (Table 3.1). Therefore, wild pig range expansion in California appears to be progressing on multiple fronts; through natural dispersal, anthropogenic dispersal (e.g., propagation of h17 in Northern California), and new introductions (e.g., h13). This finding, based on molecular evidence, supports current hypotheses on range expansion dynamics for pigs in California and elsewhere (Waithman et al. 1999, Gipson et al. 1998, Mayer and Brisbin 1991).

Summary and Conclusions

We have determined that observed mtDNA variation increases with additional sampling at the regional level but that common haplotypes limit the resolution of relationships in California just as they have for nationwide sampling (Chapter II). Despite this drawback mtDNA is a valuable marker for tracking wild pig invasion, as evidenced by mtDNA corroboration of written accounts of translocation and range expansion. Exclusive haplotypes provide unique insights to historic introductions (e.g., on the Channel Islands) and may serve as indicators of demographic expansion where they occur at low frequency due to haplotype replacement.

The mtDNA haplotypes most associated with recent range expansion in California are h17 and h19 (Figure 3.3). Collectively, these two haplotypes are reported from 20 U.S. states, making them two of the most commonly propagated maternal lineages at regional and national scales (Table 3.1). Both h17 and h19 are associated with a wide variety of domestic breeds and EWB globally, and h17 is linked to selective translocation of hybrid EWB in North America. Additional work to resolve the specific origins and distribution of these haplotypes would be valuable for understanding their pivotal role in wild pigs range expansion throughout North America.

Haplotype distributions and population-genetic relationships in California indicate that human translocation during the last century has altered wild pig populations, making them more capable of invading through natural dispersal, human selection, or both (Waithman et al. 1999). Our identification of new mtDNA lineages (e.g., h13) among wild pigs in California indicates that public interest in pig hunting is still shaping the molecular profile of populations. California state officials suspect recent importation and release of wild pigs from elsewhere in North America, and our findings generally support this statement (B. Gonzales pers. comm.). Considering the pervasive spread of wild pigs already in progress, additional introductions will be detrimental to management.

Though we have gained valuable insights from this analysis, our interpretation here was limited by the evaluation of a single haploid marker. The use of additional randomly-assorting genetic markers (e.g., microsatellites and single nucleotide polymorphisms) would be helpful for clarifying population-level genetic relationships and resolving patterns of gene flow between historic and recently invaded locations (Hampton et al. 2004, Spencer and Hampton 2005, Scandura et al. 2011). Considering the geographic and management significance attributable to haplotype distributions described above, ongoing research into the molecular genetics of wild pigs in California is warranted and would provide additional tools to managers interested in tracking range expansion.

Management Implications

This research has provided new insights on the utility of mtDNA for resolving wild pig relationships at the regional level in the U.S. Our findings also yield broad-scale world geographic relationships for introduced pigs in California. Sampling of historic and recent distributions of pigs in the state has provided information on temporal aspects of the invasion. Evaluation of island and mainland populations has helped elucidate effects of geographic isolation, stochastic variation, and management on mtDNA diversity of wild pigs. These findings will be instrumental in guiding future work on wild pig genetics in California and elsewhere in the U.S.

TABLE 3.1. Phylogeography and breed-specific details of 18 mitochondrial DNA haplotypes representative of 158 wild pigs from California and 74 wild pigs from 29 other U.S. states collected during the period 1996- 2010. Haplotypes observed in the U.S. but not in California are shaded (Chapter II). Samples from the United States are compared to published sequence from around the world (n=483) within haplotypes. Published sequences for global analysis were obtained from National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov/). Phylogeographic descriptors EAST and WEST correspond to a division of mtDNA lineages in Eurasia identified through MrBayes 3.1 analysis of a ~400 base pair region of the mtDNA control region (D-loop) under the GTR+I+G model and 10,000,000 Markov Chain Monte Carlo generations. Descriptors M1 and M2 represent unresolved assemblages in WEST and EAST phylogenies, and F1 represents a single EAST haplotype found only on Santa Catalina Island, Hawaii, and South Pacific Islands. Geographic origin of sequence and type of pigs represented are denoted for each haplotype; U.S. states are abbreviated.

Haoplotype	California population	Phylogeography	Phylogeny	Dom.	EWB	Feral	Other	US wild pigs in other states	Wild pigs in CA	Total	US Geography (States abbreviated)	World Geography for published sequence (No. wild animals reported"w#")	Breed information for haplotype
2	29US	EAST	M2	40	3	12	3	3		61	ID, MI	Australia, China, Europe, France, Germany, Japan (w3), Sweden, Taiwan, Thailand, UK	>20 Asian and European domestic breeds
7	29US	EAST	M2	42	9	1	1	8		61	MI, NC, OH, PA, SC, TN	Belgium (w1), China (w3), East Asia, Europe, France, Italy (w2), Japan, Malaysia (w1), Mariana Islands, South Carolina USA, Russia (w1), Spain, Thailand (w1), UK, US	~20 Asian and European domestic breeds
13[a]	Recent, 29US	EAST	M2	65	5	4	2	1	8	85	CA, HI	China (w1), UK, Korea, Europe, Germany, Spain, Japan (w1), Hawaii, Australia, Thailand, Italy (w3)	~16 Asian and European domestic breeds

Table 3.1 cont.

Haoplotype	California population	Phylogeography	Phylogeny	Dom.	EWB	Feral	Other	US wild pigs in other states	Wild pigs in CA	Total	US Geography (States abbreviated)	World Geography for published sequence (No. wild animals reported"w#")	Breed information for haplotype
17	Historic, Recent, 29US	WEST	M1	25	12			17	59	113	AR, CA, MS, NC, ND, NV, TN	Belgium (w1), Europe, Germany, Iberian Peninsula, Iceland, Italy, Macedonia (w1), Norway (w1), Spain (w9), UK, US	12 European domestic breeds
19	Historic, Recent, 29US	WEST	M1	91	32	8		21	68	220	AL, AR, CA, CO, FL, GA, HI, KY, LA, MI, ND, OH, OK, TN, TX, WI, WV	Corsica (w3), Europe, Finland, France (w1), Germany (w2), Hungary, Holland (w1), Iberian Peninsula, Italy (w24), Portugal, Sweden (w1), UK, US	>20 European domestic breeds
20	29US	WEST	M1	10				3		13	ND, SC	Europe, UK	Duroc, Large White, Tamworth
37	Historic, 29US	WEST	M1	22	19		5	11	1	58	AZ, CA, KS, LA, ND, NJ, NE, NM, OK, PA, TX, VA	Austria (w1), Bulgaria (w1), Europe, Germany (w2), Hungary (w8), Iberian Peninsula, Indonesia, Italy, Korea, Morocco (w1), Poland (w5), Portugal, Spain (w1), UK	12 European domestic breeds, 1 Asian type "Korean Native"

Table 3.1 cont.

Haoplotype	Haoplotype	Haoplotype	Haoplotype	Haop lotyp e	Haoplo type	Haop lotyp e	Hao ploty pe	Haoplotype	Haoplot ype	Haoplotyp e	Haoplotype	Haoplotype	Haoplotype
38	Historic, Recent, 29US	WEST	M1	24	34	2		1	2	63	CA, KY	Austria (w1), Corsica (w2),Denmark, Europe, France (w12), Germany (w1), Hungary, Iberian Peninsula, Italy (w18), Portugal, Sardinia, UK	Bisaro, Duroc, Gloucester Old Spot, Hampshire, Hungarian Mangalica, Iberian Red, Landrace
39	29US	WEST	M1	7				3		10	FL, MI, OH	Germany, Europe, Sweden	Angler sattleschwein, German Angler, Hampshire
84	SCAT, 29US	EAST	F1			3		1	3	7	CA, HI	Papua-New Guinea, US - Hawaii, Vanuatu	Feral animals only
103	29US	WEST	M1	2				1		3	MS	Europe	Landrace
145	29US	WEST	M1					1		1	NC	US	UNK
146	29US	WEST	M1					1		1	TN	US	UNK
147	29US	WEST	M1					1		1	TN	US	UNK
148	29US	WEST	M1					2		2	IN, KS	US	UNK
149	Historic	WEST	M1						1	1	CA		Unique haplotype
150	SCAT, SCI, Recent	WEST	M1						15	15	CA		Unique haplotype
151	Historic	WEST	M1						1	1	CA		Unique haplotype

[a] Found only in California counties occupied since 1960s; previously only reported for wild pigs in Hawaii and for "Ossabaw Island pig" breed from South Carolina (Larson et al. 2005; AY884613)

Table 3.2. Population genetic measures of F_{ST} (bottom half matrix) and N_m (top half matrix) for five populations assigned by geography and history of invasion: wild pigs from 29 U.S. states (29US; n=74), historic mainland (Historic; pigs from mainland sites within nine counties of historical occurrence in California; n=77), SCI (Santa Cruz Island California; n=11), SCAT (Santa Catalina Island; n=6), and recent mainland (Recent; pigs from mainland California sites other than the nine historical counties of occurrence; n=64). Analysis were performed in Arlequin 3.5.1.2. Significance of *F* statistics between populations is denoted in the lower half matrix as follows: *p<0.05, **p<0.01, ***p<0.0000.

	29US	Historic	SCI	SCAT	Recent
29US	0	4.72864	2.03882	1.71671	98.47133
Historic	0.09563***	0	1.01018	0.33321	8.44260
SCI	0.19695*	0.33109***	0	0.44595	2.65806
SCAT	0.22556*	0.60009***	0.52857*	0	1.07818
Recent	0.00505	0.05591***	0.15833*	0.31682***	0

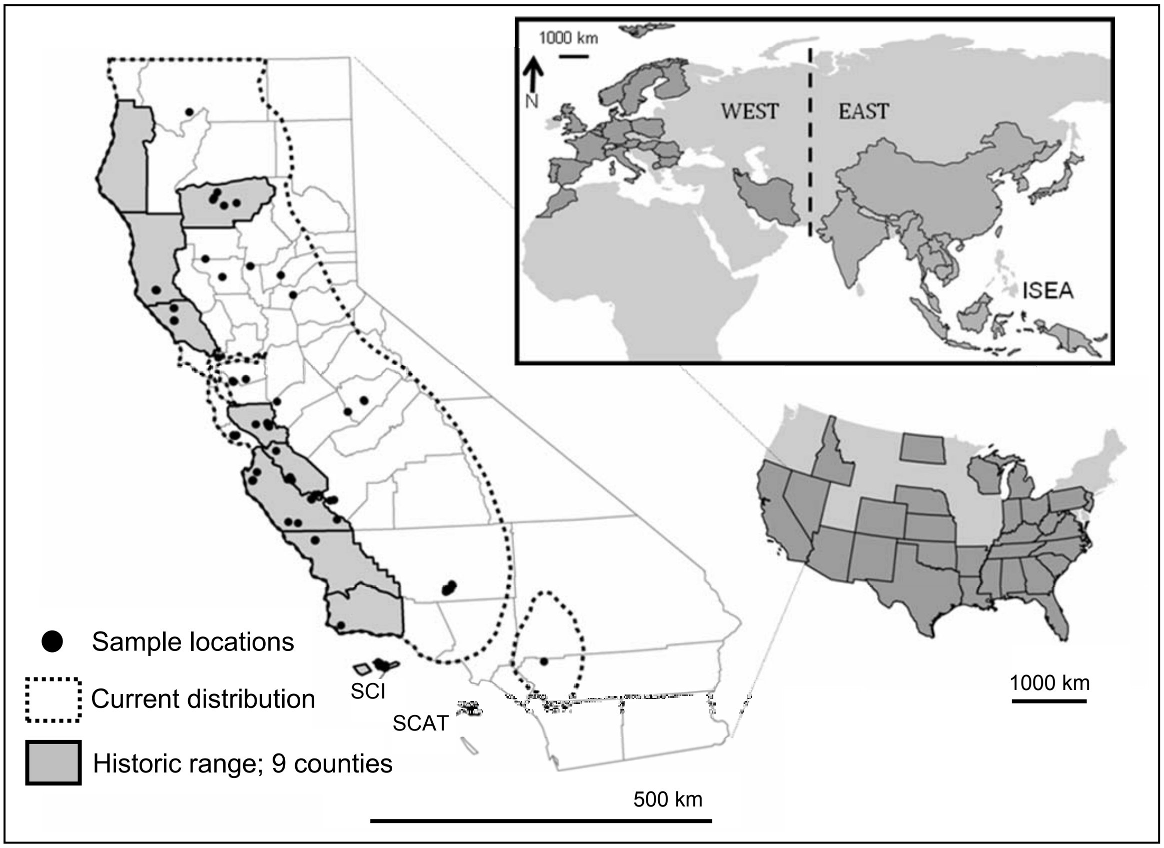

Figure 3.1. Distribution of 158 wild pig samples from 23 counties in California USA collected during the period 1996-2010, spanning historic and current invasive range of the species (SCWDS 2010 National Feral Swine Mapping System, Southeastern Cooperative Wildlife Disease Study, University of Georgia, http//:www.feralswine map.org). World geographic location of samples reported among published sequence (n=904) is represented by country (shaded) in inset, including Western Eurasian (WEST) and Eastern Eurasian (EAST) phylogeographic split adapted from (Chapter II), and Island Southeast Asia (ISEA) phylogeography denoted for some wild *S. scrofa* and other *S. spp* (n=5). Note: Australia, Hawaii, Iceland, and some Pacific Islands are not shown. United States geography for other published wild pig samples included.

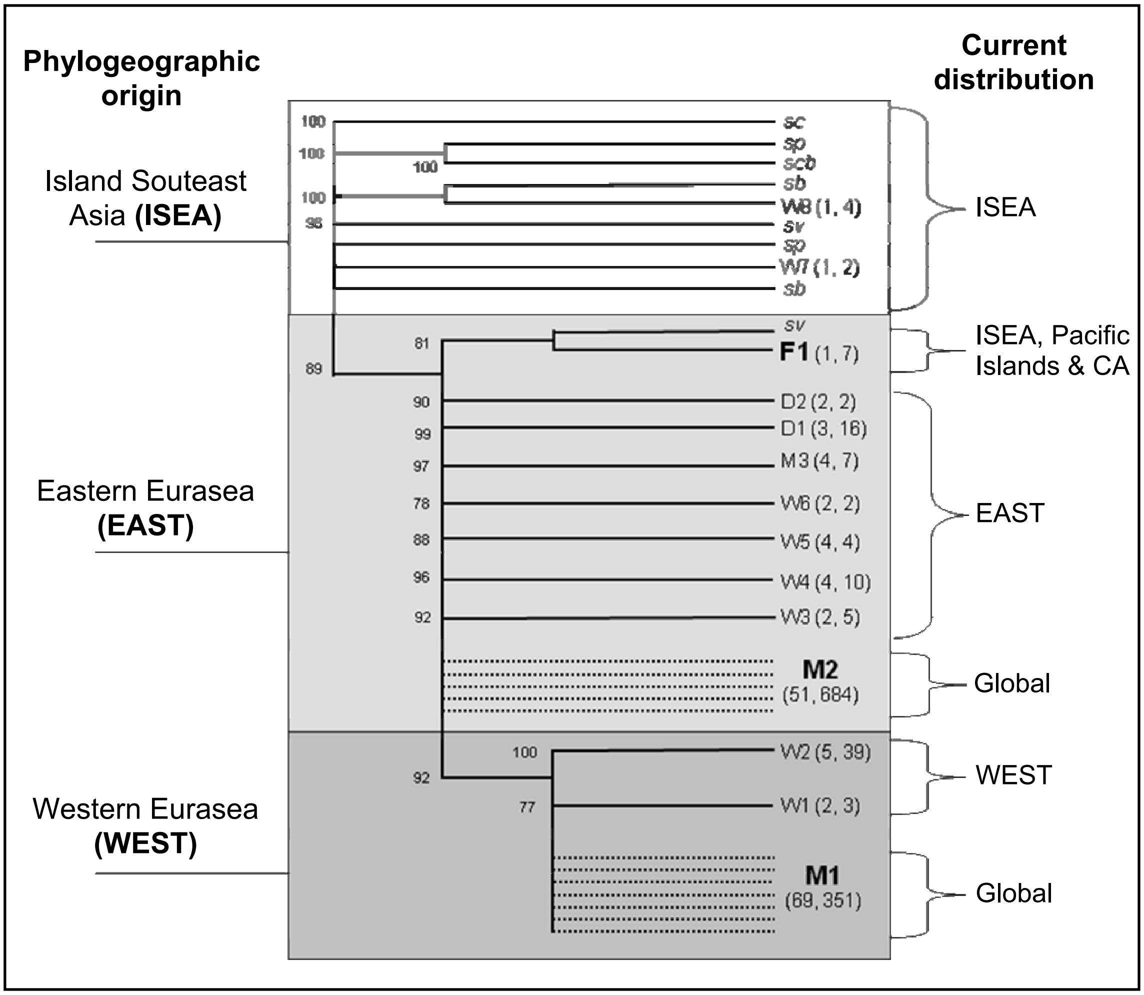

Figure 3.2. Cladogram of 151 *Sus scrofa* mtDNA haplotypes constructed using a GTR+I+G model with 10,000,0000 generations in MRBAYES 3.1.2. Represented are: 158 individuals from 23 California counties; 74 individuals from 29 other U.S. states; 904 published sequences for *Sus scrofa* from around the world; and 13 sequences from five other *Sus* spp. Shaded regions of tree denote overarching phylogeographic associations of mtDNA matching descriptions at left. Current distribution of haplotypes is denoted by bracketed descriptions at right. Phylogenetic assemblages in tree are described by pig type within EAST and WEST in tree; W (Eurasian Wild Boar), D (domestic), M (mixed, shared between domestic pigs and Eurasian Wild Boar), and F (feral). Other *Sus. spp.* are abbreviated; *sb* (*S. barbatus*), *sc* (*S. celibensis*), *scb* (*S. cebifrons*), *sp* (*S. philippensis*), and *sv* (*Sus verrucosus*). Groups containing haplotypes found in California are in bold: M1 (h17, h19, h37, h38, h149, h150, h151), M2 (h13), and F1 (h84). Dotted lines in tree indicate polytomies from unresolved phylogenetic assemblages M1 and M2; number of lines is proportional by an approximate factor of ten to the count of haplotypes in each branch. Numbers at nodes indicate mean posterior probabilities (≥75% shown) and numerals in parentheses indicate number of haplotypes and number of individual sequences, from left to right.

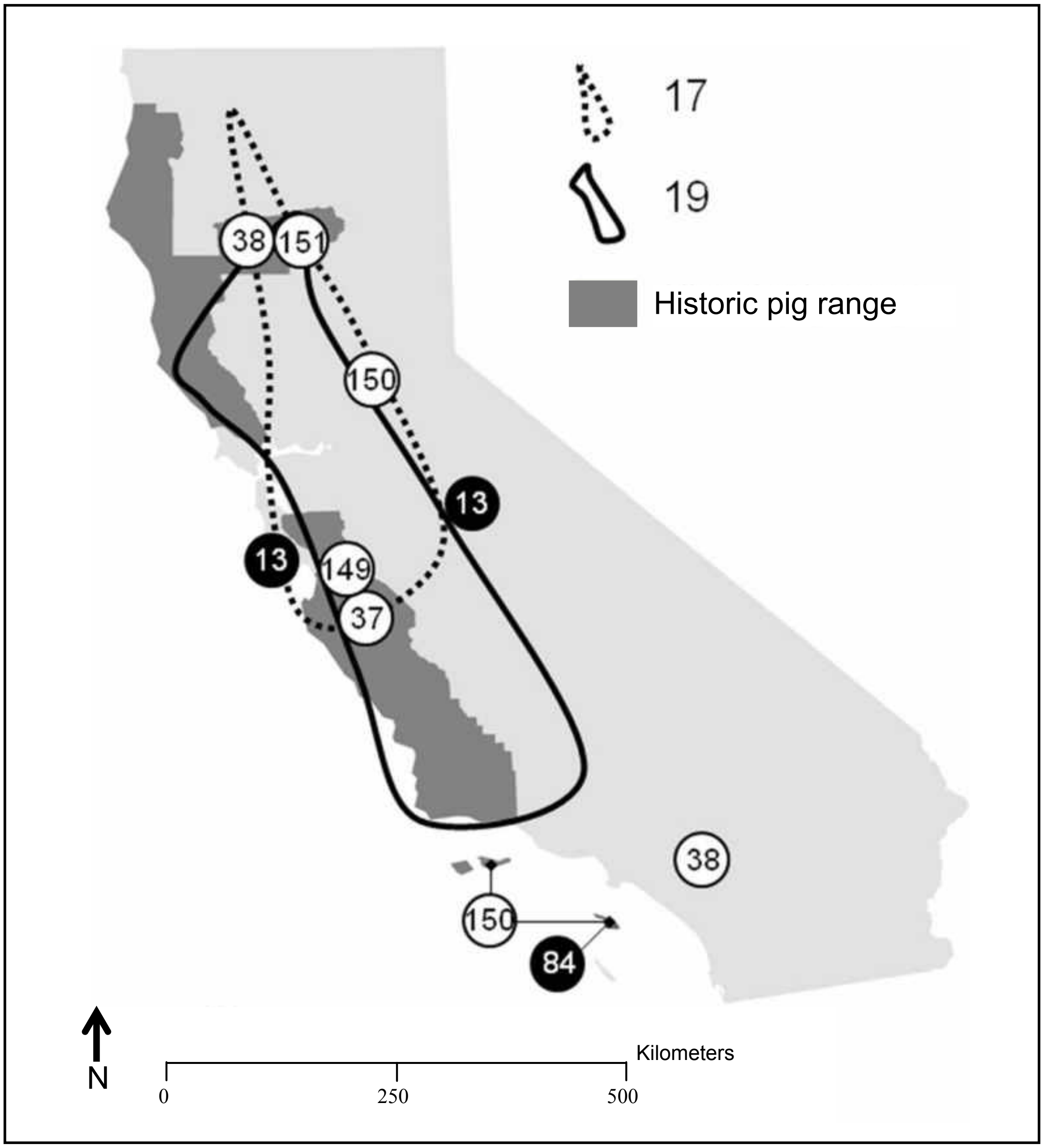

Figure 3.3. Distributions of mtDNA haplotypes representing 158 wild pigs sampled in mainland and island locations from 23 counties in California USA, collected during the period 1996-2010. Haplotypes with limited occurrence are presented by numbers in dots corresponding to phylogeography: WEST haplotypes (white circles) h37 (n=1), h38 (n=2), h149 (n=1), h150 (n=15), h151 (n=1); and EAST haplotypes (black circles) h13 (n=8) and h84 (n=3). Common WEST haplotypes h17 (n=59) and h19 (n=68) are described by minimum shapes with dotted and solid outlines, respectively. Historic pig range (shaded area) is described by county for mainland locations.

CHAPTER IV

IDENTIFICATION OF MOLECULAR POPULATION STRUCTURE FOR WILD PIGS IN THE UNITED STATES

Introduction

Management of wild pigs (*Sus scrofa*) in the United States has become an ever-increasing challenge because of rising population densities and range expansion (Mayer and Brisbin 2009). Pigs were first introduced to North America during the 1500s, and through subsequent escape and release of domestic stock (Towne and Wentworth 1950). Wild populations expanded their range in some locations but remained regionally distributed until the 1900s (Mayer and Brisbin 1991). Beginning in the 1880s, Eurasian Wild Boar (EWB) were introduced and have since interbred with feral pigs in many locations (Mayer and Brisbin 1991). It is thought that the introduction of EWB and enthusiasm about wild pigs as a game animal has contributed to range expansion at regional and national levels (Gipson et al. 1998, Waithman et al. 1999).

It has been theorized that EWB and hybrids (i.e., EWB crossed with feral pigs) are more invasive than feral pigs because of phenotypic characteristics that provide a survival advantage in new environments (Waithman et al. 1999). Domestication has caused morphological changes to pigs, including alterations of cranial morphology important for foraging and loss of striped pelage in piglets that provides concealment from predators (Mayer and Brisbin 1991, O'Reagan and Kitchener 2005). Phenotypic characteristics of EWB are also those preferred by sportsmen for hunting trophies (Mayer and Brisbin 1991). This artificial selection has led to multiple cases of EWB introduction and long-distance translocation of EWB and hybrids from established populations within North America (Mayer and Brisbin 1991, Gipson 1998, Waithman et al. 1999).

At least six separate introductions of EWB have occurred in North America (Mayer and Brisbin 1991). Two famous cases are the Corbin's Park introduction in New Hampshire during the 1880s and the Hooper Bald introduction in North Carolina during the early 1900s (Mayer and Brisbin 1991). Corbin's Park is a fenced game preserve where the first recorded introduction of EWB took place. Periodic escapes of EWB from the preserve occurred from the 1890s throughout the 1900s, establishing a free-ranging population in the region that has persisted to present day (Mayer and Brisbin 1991). The introduction at Hooper Bald also resulted in escape of EWB, which interbred with feral pigs already living in the region and eventually dispersed to populate Great Smoky Mountains National Park (GRSM; Mayer and Brisbin 1991). In the 1920s, EWB from Hooper Bald were translocated to California, where their hybrid progeny have been propagated throughout the state (Pine and Gerdes 1973, Barrett 1977, Waithman et al. 1999). Hybrid EWB from GRSM and the Hooper Bald area have also been translocated to new locations, including parts of Florida, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and West Virginia (Mayer and Brisbin 1991; 2009). Other introductions of EWB have occurred in New York, Texas, and Washington, with some populations persisting and others perishing (Mayer and Brisbin 1991). Given the recorded history of introduction and translocation, EWB have clearly played an important role in wild pig invasion of North America. However, it is currently unclear to what extent EWB have contributed to the various regional and local populations found throughout the U.S. today.

Anthropogenic dispersal of wild pigs is the leading cause of range expansion and has led to the invasion of 44 U.S. states (Mayer and Brisbin 2009). Though written accounts of translocation provide insights on the historic dispersal of pigs between geographic locations, recent anthropogenic dispersal is poorly described due to the clandestine nature of introductions (Mayer and Brisbin 2009). Previous analyses have demonstrated the ability of molecular techniques to elucidate pathways of anthropogenic dispersal for wild pigs in the United States using mitochondrial DNA (mtDNA; Chapters II, III). Mitochondrial DNA is an effective marker for evaluating the evolutionary history of pig species, centers of domestication, and phylogeography of pigs in their native range (Larson et al. 2005; 2010, Luetkemeier et al. 2009, Scandura et al. 2008). However, mtDNA is of limited utility for assessing wild pig relatedness in the U.S. due to common ancestry for EWB and domestic breeds, the ubiquitous nature of some maternal lineages, and the fact that it is a single molecular marker (Chapter II).

Multi-locus, nuclear genetic markers are the next logical step to understand range expansion of wild pigs in North America. Microsatellite (MS) markers have been used to elucidate hybridization events for EWB and rates of genetic interchange between European and Asian domestic breeds (Fang et al. 2005, SanCristobal et al. 2002, Scandura et al. 2008). Microsatellite analysis has also helped identify population structure for EWB in Europe (Nikolov et al. 2009, Frantz et al. 2009). In Australia, MS have been used to determine population structure for introduced pigs and to identify animals that were translocated between locations (Hampton et al. 2004, Spencer and Hampton 2005). In the U.S., MS analysis of wild pigs has contributed to a better understanding of local-scale population genetics and demographic relationships for wild pigs in Texas (Gabor et al. 1999, Acevedo-Delgado 2010). The utility of MS for determining genetic relatedness of pigs at global, continental, and local scales suggests that similar analysis at the national and regional level in the U.S. would be informative.

Whole-genome sequencing technologies have resulted in the identification of Single Nucleotide Polymorphisms (SNP) for a number of vertebrate species. In humans, SNP have been used to elucidate high-resolution molecular relationships that are informative for understanding our evolutionary history and global distribution (Salmela et al. 2008, McEvoy et al. 2011). In dogs, analyses of SNP have elucidated origins of domestication and genomic associations for breed traits (Jones et al. 2008, Gray et al. 2009). Because of the economic importance of pigs, the swine genome has been sequenced and a large number of SNP have been identified (Rhorer et al. 2007, Kerstens et al. 2009, Archibald et al. 2010). In pigs, SNP are being used to approach research questions ranging from phylogeography to identification of the molecular basis for lameness and disease among breeds (Scandura et al. 2011, Xu et al. 2011). Though SNP loci can only express three genotypic states (heterozygous and two homozygous), the large number of loci available and a genome-wide distribution provide considerable molecular signal for differentiating population genetic relationships (Turakulov and Easteal 2003). As such, SNP panels will be a powerful tool for evaluating molecular relatedness of introduced pigs.

In the U.S., it is uncertain whether or not population structure for wild pigs is detectable at the national scale due to the reported admixture of EWB and feral pigs and ongoing anthropogenic dispersal. Analyses of mtDNA suggest molecular variation indicative of regional and local population relationships, as well as genetic signal corroborating reported translocations and dispersal (Chapters II, III). In this study, we follow up on previous mtDNA analyses using combined molecular data from MS and SNP markers to identify population structure for wild pigs at national and regional scales. Our objectives are to: 1) Identify molecular population structure for wild pigs in the United States, 2) Elucidate gene flow indicating pathways of range expansion using California as a case study, and 3) Identify molecular links to EWB among wild pigs in North America.

Study Area

We collected tissue samples from 159 wild pigs occurring in recent and historic pig range from 31 U.S. states during the period 1996-2010, including seventeen samples from GRSM in Tennessee and North Carolina and four samples from the region surrounding Corbin's Park in New Hampshire (Chapters II, III; Figure 4.1). We obtained ten EWB samples from Southwestern Iran, which we used for comparison to U.S. wild pigs.

Methods

We obtained wild pig samples in the U.S. through cooperation with federal and state agencies and private organizations conducting control and eradication projects. We acquired EWB samples from Iran through cooperation with faculty at University of Azad University, Tehran, Iran. We included Iranian EWB in our sampling scheme for two reasons: 1) to provide an out-group of individuals that was expected to be molecularly dissimilar from U.S. populations (i.e., to serve as a control in analyses), and 2) to serve as a reference for identifying EWB lineages among U.S. wild pigs. When a pig was destroyed, field personnel collected blood or skeletal muscle along with the geographic location and biological information (Chapter II). Blood was stored on FTA cards (Whatman Inc., Florham Park, NJ, USA) and shipped to the University of North Dakota (UND) where we archived samples at room temperature. Skeletal muscle was shipped overnight to UND and stored at -20°C. Muscle tissue samples from Iran were preserved in 100% alcohol prior to shipment to UND. Since all samples were collected secondary to euthanasia of pigs for sanctioned research and management purposes, this work was deemed exempt from approval by the UND institutional animal care and use committee.

Laboratory Techniques

All wild pig tissue samples were processed for molecular data at an external laboratory (GeneSeek, Lincoln, Nebraska, USA). Genomic DNA was extracted with proprietary protocols of the external laboratory. Samples were genotyped for 96 SNP loci from the

Porcine SNP60 bead chip (Illumina Inc., USA; Ramos et al. 2009) using primers developed through USDA program MARC (Appendix B). Amplification proceeded with a single-base extension PCR, and nucleotide polymorphisms were scored using the MassARRAY® iPLEX Gold® assay (Sequenom, Inc., San Diego, California, USA). Samples were genotyped for fourteen microsatellite loci identified by the International Society for Animal Genetics for diversity studies of pigs and from USDA program MARC (Appendix B) with multiplex PCR followed by fragment length scoring on a LI-COR 4200 (LI-COR Biosciences, Lincoln, Nebraska, USA). Nuclear SNP and MS data were output in spreadsheet format and sent to UND.

Molecular Analyses

*Population structure.*We organized SNP and MS data in a total evidence matrix. Through visual inspection, we removed loci that were monomorphic and those that amplified for <40% of samples. We selected the 40% threshold because of the limits of Bayesian clustering programs to overcome issues with missing data (Pritchard et al. 2000). This resulted in selection of 103 loci (89 SNP and 14 MS) for analysis (Appendix B).

The pig genome is composed of 18-19 paired chromosomes and is approximately 2.7 billion bases in total length (Schmitz et al. 1992, Fang et al. 2006). For our 103 SNP and MS loci, the average number of loci per chromosome is five (Appendix B). To detect problems with physical linkage and deviation from Hardy-Weinberg equillibrium, we tested our matrix for linkage disequilibrium, heterozygote deficiency, and heterozygote excess using Hardy-Weinberg exact tests in GENEPOP (v4.0, 4.1; Rousset 2008). We performed Bonferroni adjustment of significance values to correct for family-wise error (Rice 1989). We also focused the same analysis on a subset of sixteen individual pigs collected from a single geographic region (GRSM) previously identified as a unique population based upon introduction history and molecular data (Mayer and Brisbin 1991, Chapter II). We compared full-matrix and subset statistical results to check for a Wahlund effect.

It has been demonstrated previously that continuous patterns of isolation by distance (IBD) can affect identification of population structure with Bayesian clustering approaches (Frantz et al. 2009). To test for IBD in our dataset, we calculated pair-wise individual F_{ST} for all wild pig genotypes in GENEPOP. We then identified sample locations from geographic coordinates provided by field personnel (n=101), from estimates based on written descriptions (n=24; Loggins 2007), and through approximation by county of collection (n=34). For approximated locations, we used ARCGIS 10 (Environmental Systems Research Institute, Redlands, California USA) to plot points at the manually estimated center of the county where they were collected. We used PASSAGE (v2; Rosenberg and Anderson 2011) for exploratory analyses and editing of geographic and genetic databases. We then compared geographic distance for wild pigs collected in North America (n=157) to pair-wise F_{ST} distances with a Mantel test in GENEPOP.

To avoid possible biases and error associated with any one analysis program, we used a series of software packages to elucidate molecular signal indicative of population structure (Frantz et al. 2009). We used the Bayesian clustering programs STRUCTURE (v2.3.3; Pritchard et al. 2000) and BAPS (v5.3; Corander et al. 2006; 2008), which use different criteria to delineate population membership based on individual multi-locus genotypes. We then performed Principal Components Analysis (PCA) and Multi-dimensional Scaling (MDS) to group molecular data in the absence of population-genetic assumptions.

In program STRUCTURE, we estimated *K*, the number of populations, with ten independent runs of *K* = 1 – 12 with 100,000 Markov Chain Monte Carlo (MCMC) iterations and a burn-in period of 10,000 MCMC iterations. We used the default settings with the admixture ancestry model and correlated allele frequencies among populations. We averaged the ten log-likelihood scores for each value of *K* and calculated the standard deviation. Next, we inferred the most likely number of clusters by calculating ΔK after Evanno et al. (2005). We then performed a "nested" analysis of our dataset, sequentially reanalyzing identified populations to detect substructure, as demonstrated for simulated molecular data by Evanno et al. (2005). In BAPS, we performed a population mixture analysis with default settings that ran five times each for *K* = 2 – 15. We accepted the most likely value of *K* as determined by the program. We then created a Neighbor Joining (NJ) tree using Kullback-Leibler divergence for Bayesian probabilities. We selected the NJ algorithm because it does not assume a constant rate of evolution. This is an important consideration when assessing molecular relationships for different types of loci and for evaluating phylogenetic relationships in species such as pigs that have undergone millennia of artificial selection during domestication and natural selection after release (Rubinsztein et al. 1995, Giuffra et al. 2000, Larson et al. 2007, Haasl and Payseur 2010).

Missing data is problematic for PCA. To overcome this issue, we used program PHASE (v2.1; Stephens et al. 2001, Stephens and Scheet 2005) to estimate missing genotypes for individuals from observed allele patterns in the total dataset. We recoded our combined matrix in a binary format; we coded each SNP locus in two columns (major allele = 1; minor allele = 0), we coded each MS locus with number of columns = number of alleles (allele presence = 1, allele absence = 0) as demonstrated previously for PCA (Patterson et al. 2006). We performed PCA in program STATISTICA (Statsoft Inc., Tulsa, Oklahoma, USA) and generated scatterplots to visualize presumptive groups. We imported pair-wise individual F_{ST} values for all wild pigs to STATISTICA and performed MDS analysis. We generated MDS scatterplots for comparison to PCA results.

We identified consensus populations by comparing the results of Bayesian clustering techniques. When one program identified more structure than the other, we collapsed subpopulations to larger groupings amenable to the results of both analyses. Where possible, we manually assigned individuals with ambiguous genetic relationships (i.e., those that differed in overarching group affiliations between analyses; n=8) to the most logical group based on geographic associations. We then overlaid PCA and MDS scatterplots with Bayesian consensus populations to visually assess the strength of molecular signal differentiating groups, using the Iranian EWB as an outgroup. Finally, we calculated F_{ST} and *Nm* for consensus populations and performed an exact test of population differentiation in GENEPOP to provide additional measures of group relatedness for evaluating our assignments.

Gene flow in California. We identified potential paths of gene flow by plotting a network of individual F_{ST} values representing the closest matching genotypes for a subset of individual wild pigs (n = 52) collected throughout California and one location in Nevada. We hypothesized polarity of gene flow based on historic occurrence of pigs in nine California counties and dispersal subsequent to the 1960s (Waithman et al. 1999, Mayer and Brisbin 1991).

Identification of EWB Lineages. We used consensus population membership to identify U.S. wild pigs closely related to Iranian EWB. We then compared molecular groupings with known histories of introduction and translocation for EWB in North America. Finally, we compared relationships in our NJ dendrogram to identify putative links for EWB lineages among inferred populations.

Results

Molecular Population Structure

Overall heterozygote deficiencies and linkage disequilibrium were significant across the 169 wild pig genotypes (Table 4.1). Microsatellite loci were disproportionately prone to heterozygote deficiencies (12 of 14 loci) and contributed most to linkage disequilibrium; 28 pair-wise associations among MS loci and 22 pair-wise associations with SNP loci. For our subset of GRSM pigs, heterozygote deficiency and linkage disequilibrium were not significant after Bonferroni correction, though one locus was significant for heterozygote excess (Table 4.1). Comparison of full dataset and the single population subset results suggest that population structure is causing a Wahlund effect.

Isolation by distance for U.S. wild pigs was significant ($p<0.0000$). Genetic distance was positively correlated with geographic distance ($r = 0.1576$). The strongest relationships were between animals sampled in close proximity (e.g., 50-100 kilometers; Figure 4.2). Genetic variation was otherwise spread evenly across geographic extents (Figure 4.2).

Program BAPS identified eleven molecular clusters, with three consisting of individual pigs (Figure 4.3). Program STRUCTURE identified only two well-supported clusters based on ΔK from analysis of all 169 genotypes, but nested analyses elucidated a total of twelve subclusters (Figure 4.3, Appendix C). We accepted the eight BAPS clusters having multiple members as consensus populations due to their general agreement with nested STRUCTURE results and geographic associations for some groupings (Pops. 1-8; Figure 4.3). We considered the three BAPS clusters with single individual memberships as unresolved due to their ambiguous molecular profiles and geographic locations distantly separated from most wild pig populations in North America; Hawaii (Pops. 9, 10) and North Dakota (Pop. 11; Figure 4.3).

In PCA, the first four factors explained 13.1% of variation in the molecular data. Factor plots revealed that consensus populations generally corresponded to PCA results (Figure 4.4, panel A). We observed complete separation on multiple planes for populations 3, 6, and 8 (Figure 4.4, panel A). Populations 1, 2, and 4 were closely associated with population 7 and could not be confirmed based on this analysis (Figure 4.4, panel A). Populations 5 and 7 had the largest point distributions and overlapped peripherally on all factor planes (Figure 4.4, panel A). Output from MDS matched closely the point distributions of PCA (results not shown). Local and regional geographic boundaries generally matched molecular groupings, with the exception of population 7 that included wild pigs from 29 U.S. states (Figure 4.4, panel B).

Genetic distance between populations provided additional support for consensus groupings, with population 6 showing the greatest average distance from all others (Table 4.2). Populations 7 and 5 were most similar, and population 7 had the lowest F_{ST} values across all comparisons (Table 4.2). The greatest genetic distance was between populations 4 and 2 (Table 4.2). Populations restricted to islands (e.g., 1 and 2) and those having localized geographic distributions on the mainland (e.g., 3 and 8) also showed high F_{ST} values across comparisons (Table 4.2). Exact tests of population differentiation were significant ($p < 0.0000$) for all pair-wise comparisons.

Gene Flow in California

Pair-wise individual F_{ST} values within population 5 revealed multiple relationships between historic and recent range for wild pigs in California and Nevada (Figure 4.5). Molecular data suggest that long-range dispersal is originating from counties within the historical range of wild pigs in California, primarily from locations in Monterey and San Benito Counties (Figure 4.5). Pigs sampled from Humboldt County Nevada were also closely related to this west-central California source (Figure 4.5). We also observed strong genetic relationships for some animals sampled in close geographic proximity in both recent and historic range.

Identification of EWB Lineages

Populations 4, 6, and 8 all represent EWB or hybrid pigs based on geography and introduction histories. Population 4 includes three wild pigs collected in close vicinity to Corbin's Park in New Hampshire. Population 6 is composed of the ten EWB from Iran and one wild pig from New Hampshire (Appendix C). Population 8 is composed entirely of animals sampled from GRSM. Phylogenetic relationships support a link between wild pigs from New Hampshire and EWB from Iran (Figure 4.6). The structure of our Neighbor-Joining tree also suggests a relationship between the GRSM population and California populations, as well as an association of these groups with consensus population 7 (Figure 4.6).

Discussion

Molecular Population Structure

The general agreement of Bayesian clustering, PCA, and MDS results suggest that the molecular signal differentiating our population groupings is robust. Strong F_{ST} values and significant results for the differentiation of consensus populations provide additional support for this finding (Table 4.2). However, it is important to consider the biological significance of inferred populations (Frantz et al. 2009). In North America, geographic boundaries and known natural history of introduced animals are useful measures for evaluating population structure of wild pigs.

Biological Significance of Consensus Populations. Inferred molecular population structure segregating known EWB and hybrid pigs (i.e., Pops. 4, 6, and 8) provides confidence in the accuracy of all consensus groupings. Geographic relationships are also apparent for these EWB groupings and three other consensus populations (Figure 4.4, panel B). The local distribution of populations 1, 2, 3, 4, and 8 suggests that each represents introduction of unique lineages of swine (e.g., EWB) or divergence due to isolation or management practices. Pigs from population 3 were all collected at Sutter Buttes, which is a volcanic mountain range occurring in California's Central Valley that is a mainland island of habitat among agricultural plains. In this case, there appears to be limited gene flow between Sutter Buttes and other parts of California due to geographic isolation after introduction. Populations 1 and 2 from the Channel Islands of California exemplify the isolation and divergence scenario. These populations are thought to be closely related based upon introduction history and mtDNA associations (Mayer and Brisbin 1991, Chapter III). Despite high population F_{ST} measures, phylogenetic relationships based on nuclear DNA support a common origin for pigs from the Channel Islands (Table 4.2, Figure 4.6). It is possible that drift caused by isolation and bottlenecks resulting from varying forage availability and management practices have caused these populations to diverge (Baber and Coblentz 1986, Shuyler et al. 2000, Ramsey et al. 2009). Similar impacts of management may be working to shape population structure at GRSM, where heterozygote excess suggests a recent population bottleneck (Cornuet and Luikart 1996).

Management can also positively affect the distribution and frequency of alleles in wild pig populations. The classification of pigs as a game species in California has contributed to demand for hunting stock that has been met by private individuals engaging in the clandestine translocation of EWB hybrid pigs throughout the state (Barrett 1977, Waithman et al. 1999). The geographic distribution of population 5 appears to be directly linked to this private effort to expand wild pig range in California (see "Gene Flow in California" below). Similar trends regarding the selective redistribution of certain types of wild pigs have been observed throughout North America (Mayer and Brisbin 1991, Gipson et al. 1998). Based on a wide geographic distribution and variable genetic makeup, it is possible that population 7 represents a type of pig (e.g., a common breed) that has been selected for trade and translocation. However, phylogenetic relationships suggest that population 7 more likely represents an ancestry common to domestic breeds and EWB that has filtered into wild-living populations from a variety of sources (Figure 4.6). Mitochondrial DNA relationships previously identified for pigs in this dataset support this finding (Chapters II, III). The wide distribution of population 7 and its close genetic relatedness to all other populations prevent the development of specific biological explanations for this molecular grouping.

Spatial Relationships of Molecular Data. The weak IBD relationship that we detected for wild pigs in North America indicates a lack of genetic equilibrium across geographic scales (Hutchison and Templeton 1999). Other studies of introduced pigs have detected no IBD, though statistics were calculated for animals sampled in a much smaller geographic area (Spencer and Hampton 2005, Acevedo-Delgado 2010). Generally speaking, a lack of IBD suggests a recent invasion with recurrent gene flow where animals have not yet diverged. In our case, there is a positive relationship and there appears to be effective gene flow at shorter distances with genetic drift or other factors impacting long-range relationships (Hutchison and Templeton 1999).

Gene flow characteristic of natural dispersal or regional translocation with post-introduction isolation is occurring where populations are separated by ≤100 kilometers (Figure 4.2). Local and regional population structure of this type may have provided molecular signal necessary for identifying population 5 in California and Nevada. Drift and the multiple invasions of pigs throughout North America are likely influencing genetic distance observed at larger geographic extents (Figure 4.2; Chapter II). Given the unique genetic profiles and wide spatial separation for some populations (e.g., Pops. 1 and 8), large F_{ST} values observed at long-distances are easily explained (Figure 4.2). Close genetic relatedness of individuals that are separated by great distances is likely due to recent translocation. Considering that population 7 exhibits the full range of genetic relatedness and is distributed across all geographic scales, this molecular grouping appears to be the one most associated with national-scale range expansion. However, a lack of biological or geographic significance for this admixed grouping provides few insights for interpretation of origins.

Gene Flow in California

Molecular relationships from pair-wise F_{ST} evaluations corroborate written accounts of historic introductions of pigs to coastal counties and subsequent dispersal inland. Our results also agree with the history of EWB hybrid pig introduction to Monterey County California followed by eastward and northward translocations within the state (Figure

4.5; Mayer and Brisbin 1991, Waithman et al. 1999). Patterns of gene flow identified here match previous findings using mtDNA to identify pathways for invasion of California by wild pigs (Chapters II, III).

The close genetic relatedness of geographically distant samples provides empirical evidence for anthropogenic dispersal. The apparent source for many movements in the region is the area surrounding the initial EWB introduction site in west-central California (Figure 4.5). Multiple genetic links (i.e., closest pair-wise F_{ST} associations) to this origin provide evidence for the selection of EWB hybrid pigs for establishment of new populations, supporting a prominent role for EWB hybrids in recent range expansion. Molecular evidence suggests that pigs sampled from Humboldt County, Nevada are also descendants of this EWB introduction (Figure 4.5).

Similar genetic relationships observed for animals in close proximity throughout the state could represent population structure or natural dispersal after introduction (Figure 4.5). It is unclear from the current analysis what role natural movements have played in the range expansion of pigs in California. However, natural dispersal of feral domestic pigs and EWB hybrids has been reported throughout the state (Pine and Gerdes 1973, Mayer and Brisbin 1991, Waithman et al. 1999). Additional analyses using landscape genetic techniques to correlate molecular signal with landscape features will be necessary to further elucidate dispersal pathways for wild pigs in California (Acevedo-Delgado 2010).

Identification of EWB Lineages

The association of pigs from New Hampshire and Iran is a direct link to EWB among U.S. wild pigs (Figure 4.6). The grouping of one individual from New Hampshire with Iranian EWB is particularly interesting. It is possible that this animal (BM0444; Appendix C) is directly descended from original EWB first introduced to Corbin's Park. The other animals collected from New Hampshire (Pop. 4) might represent more admixed hybrid EWB resulting from recorded instances of out-breeding at the preserve (Mayer and Brisbin 1991).

The consistent membership of population 8 in all analyses indicates that GRSM pigs represent a unique population, different from the Corbin's Park animals. This finding corroborates the recorded history of EWB introduction to the region and previous findings based upon molecular data (Mayer and Brisbin 1991, Chapter II). A basal relationship of population 7 with GRSM may reflect the wide redistribution of Hooper Bald pigs throughout the U.S. after their first introduction (Figure 4.6; Mayer and Brisbin 2009). Alternately, GRSM pigs may be affiliated with population 7 through other separate EWB introductions reportedly originating from Northern Europe or Western Russia (Mayer and Brisbin 1991). As an interesting side note, one animal (BM0007; Appendix C) sampled from GRSM grouped in population 7. This finding supports previous findings regarding the recent introduction of this pig to the park based on mtDNA (Chapter II).

The exact role of EWB in range expansion at the national scale cannot be determined from our current dataset. Clearly, EWB have influenced the course of invasion in some parts of the country and it is logical that patterns observed in one region could be repeated elsewhere. The inclusion of samples representing EWB from throughout Eurasia will be necessary to further resolve the relatedness of EWB and wild pigs in the United States.

Overview of Molecular Findings and Future Directions

Isolation by distance has been shown to impact the accuracy of Bayesian clustering techniques. Frantz et al. (2009) reported inflated numbers of inferred populations for simulated data using both STRUCTURE and BAPS, where an IBD cline was present and allele frequencies deviated from Hardy-Weinberg proportions. The analysis of GRSM pigs above suggests that the 103 nuclear loci in our analysis are not closely linked and that Bayesian clustering results can be trusted. Further, an IBD cline representing a single invasion of pigs is highly improbable at the national scale in the U.S. because of the diverse origins of pigs and the discontinuous nature of invaded areas (Figure 4.1, Mayer and Brisbin 1991). Given the known links to EWB for several populations and the apparent human impacts on the distribution of others, we can identify biological or anthropogenic factors contributing to the membership of most consensus populations (i.e., biological and artificial significance). These observations of corroborating molecular signal, natural history, introduction histories, and management records provide confidence in the validity of our results.

It appears that shared lineages and repeated admixture events underlie a lack of resolution for some groupings. Historic introductions of EWB from Europe and a predominant European influence on domestic breeds in the United States suggest that wild pigs in North America share some level of European molecular ancestry regardless of specific wild or domestic origins (Jones 1998). Considering the sparse nature of our sampling scheme in most parts of the U.S., we may not have captured enough regional variation necessary to separate domestic breeds from EWB. Additionally, we know from recorded histories of introduction that a variety of domestic breeds have likely contributed to wild populations over time and that pigs in many areas are admixed due to anthropogenic dispersal (Mayer and Brisbin 1991, Gipson et al. 1998, Waithman et al. 1999). Both factors are probably responsible for the wide genetic variation observed in population 7 and to a lesser extent population 5 (Figure 4.4, panel A). It seems, however, that a more extensive sampling regime has helped return structure in the case of population 5 from California and Nevada.

Increased sampling will be necessary to further elucidate population structure for wild pigs in the United States at all geographic scales. For example, Delgado-Acevedo (2010) used thirteen MS markers to identify ten to twelve molecular populations for feral pigs in southern Texas. This finding combined with our results regarding wild pigs in California indicate that much additional regional population structure remains to be discovered in the U.S., and that a clearer national perspective could be gained with ongoing research that sampled pigs throughout their invasive range. We might also discover new links to EWB verifying written accounts of introduction with subsequent dispersal or genetic associations revealing undocumented releases. Additional samples representing EWB from Europe and a cross-section of common domestic breeds propagated in the U.S. would be useful for comparison. All of the above are important considerations for developing a better understanding of range expansion and biological aspects of managed populations.

Summary and Conclusions

We have used a series of statistical approaches to evaluate molecular population structure based on MS and SNP markers obtained for a subsample of wild pigs in the United States. The clear genetic relationships identified here suggest that this line of research is informative. Our identification of unique populations associated with EWB introductions and geography indicates that wild pigs in the U.S. are not simply a homogeneous conglomerate of admixed individuals. Some populations reveal more admixture than others, especially those in newly-invaded areas. However, the current dataset does not allow us to effectively evaluate population structure at the regional level in most states due to a lack of samples. Additional sampling throughout the U.S. will be necessary to further resolve population structure and gene flow.

In California, our results corroborate the written history of wild pig invasion. The observed utility of molecular data is important for management to effectively to track the dispersal of wild pigs in the absence of written accounts. Our analysis also indicates an active role of EWB hybrid pigs in recent range expansion in California and Nevada. The selective advantage of EWB (whether natural or artificial) will be an important consideration for range expansion at the national level. Additional research into the role that EWB have played in the invasion of other states will be necessary.

Given the ongoing threat of this invasive species to ecological and economic resources in the United States, it is important to invest in research that will aid management. Molecular techniques provide insights not otherwise available to managers that can be directly applied to the problem. Considering the affordability of molecular supplies and the availability of open-source analysis software, molecular tools are becoming a practical part of wildlife management. With continued efforts we can gain valuable insights useful for preventing further spread of wild pigs in the United States.

Management Implications

The identification of population structure for wild pigs in the U.S. is an important finding because it suggests that molecular techniques can be harnessed to augment management practices in several key areas. For example, Spencer and Hampton (2005) used Bayesian clustering techniques and assignment tests to detect translocations of introduced pigs in southwestern Australia. In our analysis, we have confirmed a new introduction to GRSM and a California source for wild pigs in Nevada (Figure 4.5). Information on translocations could be used to thwart future introductions and could provide insights regarding long-range dispersal of trade-limiting livestock diseases.

On a local scale, the geographic extent occupied by breeding populations could be determined (Hampton et al. 2004). This is important because control of wild pigs in mainland locations is often hampered by reinvasion (Hampton et al. 2004). An understanding of the geographic extent of a breeding population (e.g., a watershed) would allow managers to more efficiently allocate resources to improve returns on management investments (Hampton et al. 2004). Demographic relationships important for developing efficient control or removal programs could also be gleaned from genetic data (Gabor et al. 1999).

Genomic resources could also be applied to wild pig management (Scandura et al. 2011). New technologies such as the Porcine SNP60 beadchip (Illumina, Inc. USA; Ramos et al. 2009), allow for genome-wide searches of molecular variation useful for differentiating population structure and breed associations of swine at high resolution. Considering the important role of EWB in range expansion throughout California, an understanding of the types of pigs invading new areas will be important nationally. High-throughput tools are also being applied to molecular epidemiology and could provide insights as to rates of disease susceptibility observed among U.S. wild pig populations (Acevedo-Whitehouse et al. 2005, Xu et al. 2011).

Table 4.1. Hardy-Weinberg Exact tests of heterozygote deficiency (HD), heterozygote excess (HE), and linkage disequilibrium (LD) for single nucleotide polymorphism and microsatellite data from wild pigs collected in 31 U.S. states and Iran. Presented are total matrix (all individuals; US) and subset (16 individuals from Great Smoky Mountains National Park; GRSM) results of global analysis. * denotes significance at alpha = 0.05. At right are summarized Bonferroni corrections (Bc) of results.

Analysis	Dataset	Global tests		Single locus and pairwise tests (No. loci significant)	
		p-value	SE ±	before Bc	after Bc
HD	US	0.0000*	0.0000	87	58
	GRSM	0.9978	0.0004	5	0
HE	US	1.0000	0.0000	0	0
	GRSM	0.0017*	0.0002	1	1
LD	US			974	61
	GRSM			73	0

Table 4.2. Geographic distribution, number of individuals, F_{ST}, and *Nm* for eight consensus populations representing 166 wild pigs collected from 30 U.S. states and Iran; two samples from Hawaii and one from North Dakota not presented. Statistics were calculated from 89 single nucleotide polymorphism and fourteen microsatellit loci using GENEPOP 4.0, 4.1; F_{st} (lower half matrix), *Nm* (upper half matrix). States are abreviated and acronyms are used for three locations; SCAT (Santa Catalina Island, California), SCI (Santa Cruz Island, California), GRSM (Great Smoky Mountains National Park). Lowest and Highest F_{ST} values are shaded.

Geography	No. ind.	Consensus pops.	1	2	3	4	5	6	7	8	Mean F_{ST}
SCAT	3	1	0	0.1699	0.1670	0.2016	0.1987	0.1137	0.2577	0.1292	0.3085
SCI	3	2	0.3539	0	0.1513	0.1437	0.1731	0.1299	0.2501	0.1532	0.3348
Sutter, Co. CA	8	3	0.3396	0.3528	0	0.1496	0.3938	0.1161	0.4937	0.1830	0.3015
NH	3	4	0.3382	**0.4739**	0.3476	0	0.1892	0.0990	0.2480	0.1652	0.3300
CA, NV	52	5	0.25	0.2765	0.203	0.2467	0	0.2232	1.8765	0.7417	0.2176
Iran, NH	11	6	0.402	0.4131	0.4131	0.4508	0.296	0	0.3017	0.1298	0.3636
US mixed; 29 states	70	7	0.1313	0.1385	0.1354	0.1299	**0.07811**	0.2171	0	0.9077	0.1405
GRSM	16	8	0.3443	0.3349	0.3193	0.3227	0.1728	0.3531	0.1531	0	0.2857

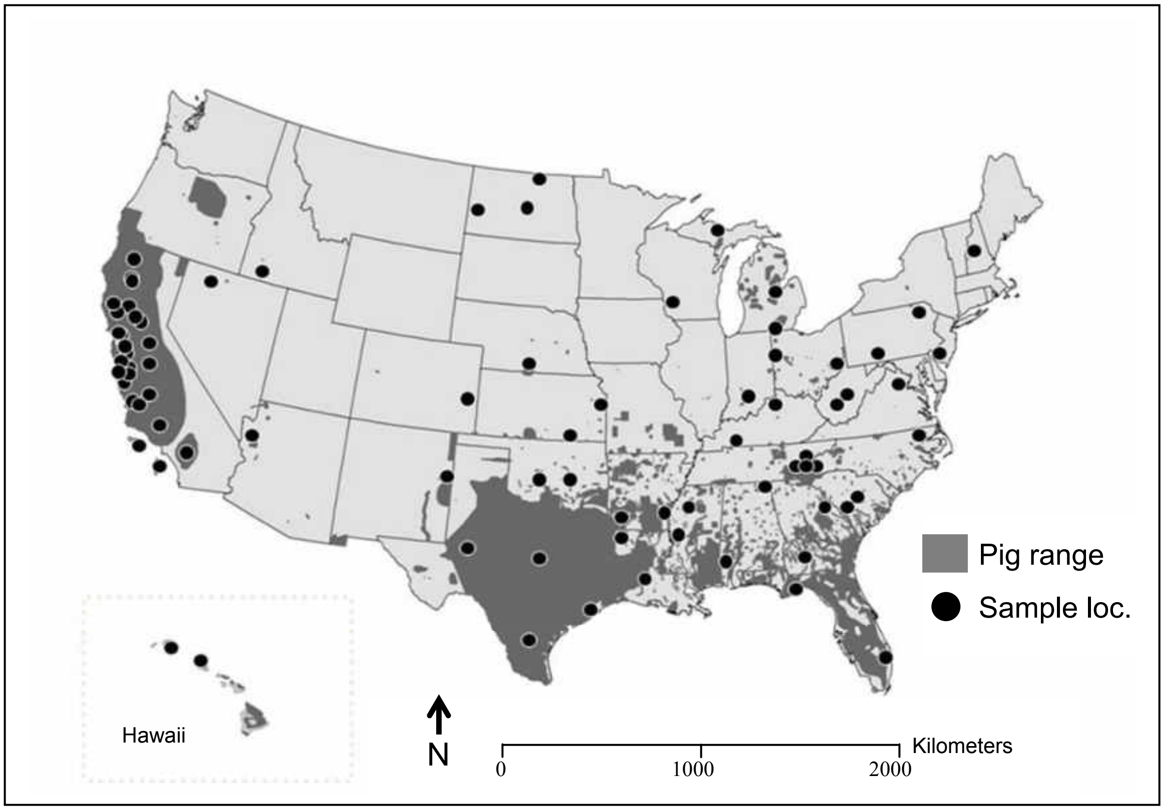

Figure 4.1. Distribution of 159 wild pig samples collected from 76 counties in 31 U.S. states during the period 1996-2010. Shaded area on map indicates approximate distribution of wild pigs in the United States as described by state agencies and USDA Wildlife Services (SCWDS 2010 National Feral Swine Mapping System, Southeastern Cooperative Wildlife Disease Study, University of Georgia, http//:www.feralswine map.org).

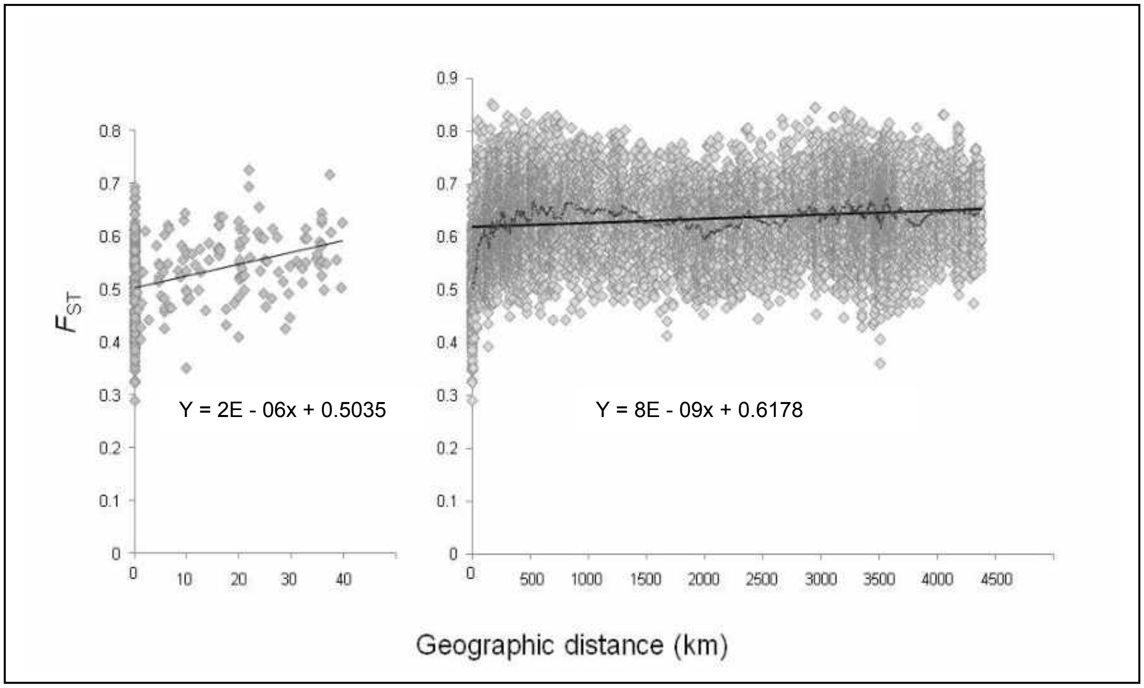

Figure 4.2. Genetic distance (pairwise F_{ST}) plotted against geographic distance (kilometers) for single nucleotide polymorphism and microsatellite loci from 157 wild pigs collected from 30 U.S. states in North America during the period 1996-2010. A trend line and equation describing slope are provided for full (page right) and local (≤40 km; page left) geographic extents. Dotted line in scatter plot of full dataset represents mean spatio-genetic relationship averaged over every 200 observations.

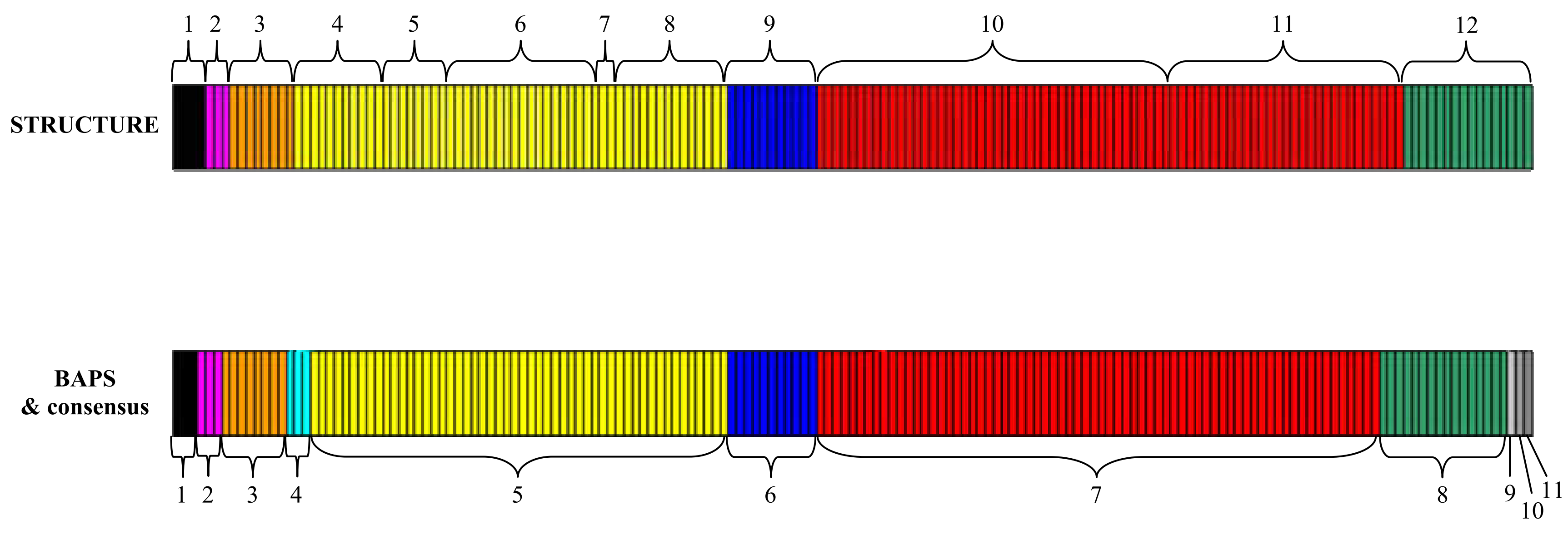

Figure 4.3. Composite barplots from nested STRUCTURE analysis (top) and BAPS analysis (bottom) of single nucleotide polymorphism and microsatellite loci for 169 wild pigs from 31 U.S. states and Iran collected during the period 1996-2010. Brackets denote theoretical molecular populations from each analysis. Colored bars denote areas of general agreement between Bayesian clustering methods, and colored lines indicate differences in population groupings for individual pigs between STRUCTURE and BAPS. Populations from BAPS were ultimately accepted as consensus (bottom) based upon geographic associations, PCA results, and F_{ST} relationships. Note: probabilities of assignment and degrees of admixture estimated by Bayesian clustering programs are not presented.

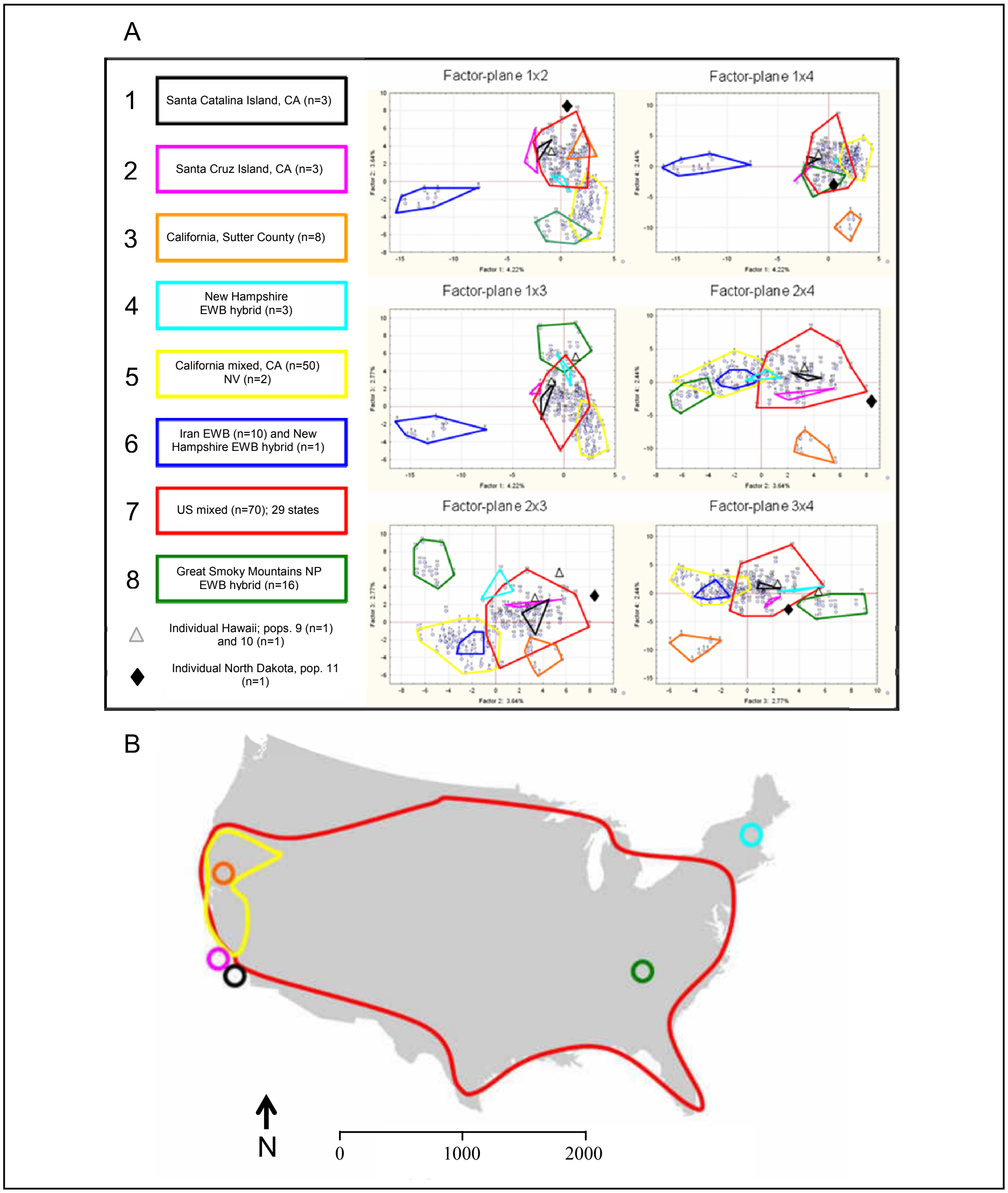

Figure 4.4. Factor plots from PCA analysis (panel A) single nucleotide polymorphism and microsatellite loci for 169 wild pigs collected in 31 U.S. states and Iran during the period 1996-2010. Polygons represent point distributions of eight consensus populations; geographic descriptions and number of individuals associated with molecular populations are provided in colored rectangles (top, page left). Three individuals that were not assigned to consensus populations are represented by symbols. Note: not all groups or individuals are depicted on each plane; numbers by points do not correspond to consensus populations. Approximated geographic distribution of consensus populations in North America is provided (panel B); populations are identified by color.

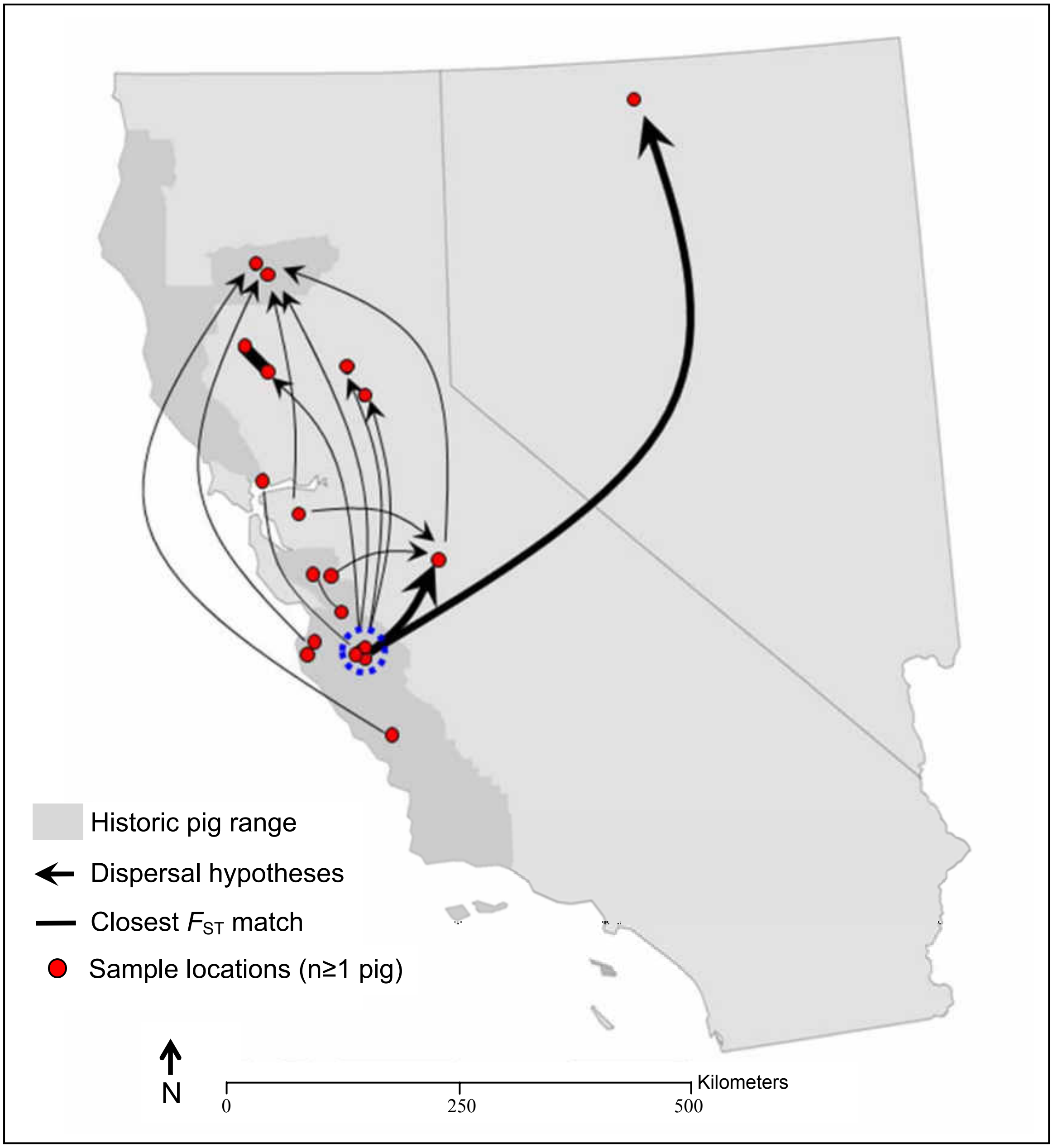

Figure 4.5. Closest pair-wise individual F_{ST} associations for 52 pigs from molecular population 5 “California mixed”. Lines indicate closest F_{ST} match between locations within California and Nevada; weight of lines is proportional to number of linkages. Arrows indicate the hypothesized direction of human translocation based upon historic coastal range of wild pigs in California (i.e. pigs are assumed to have moved from coastal areas to inland locations). Dotted blue circle surrounds locations in Monterey and San Benito Counties serving as a source for dispersal of pigs to Northern California and Nevada. Genetic links between locations in close proximity (i.e., separated by <10 km) representing local population structure or natural dispersal were apparent in the data but are not presented. Shaded area represents historic range of pigs in nine counties prior to the 1960s.

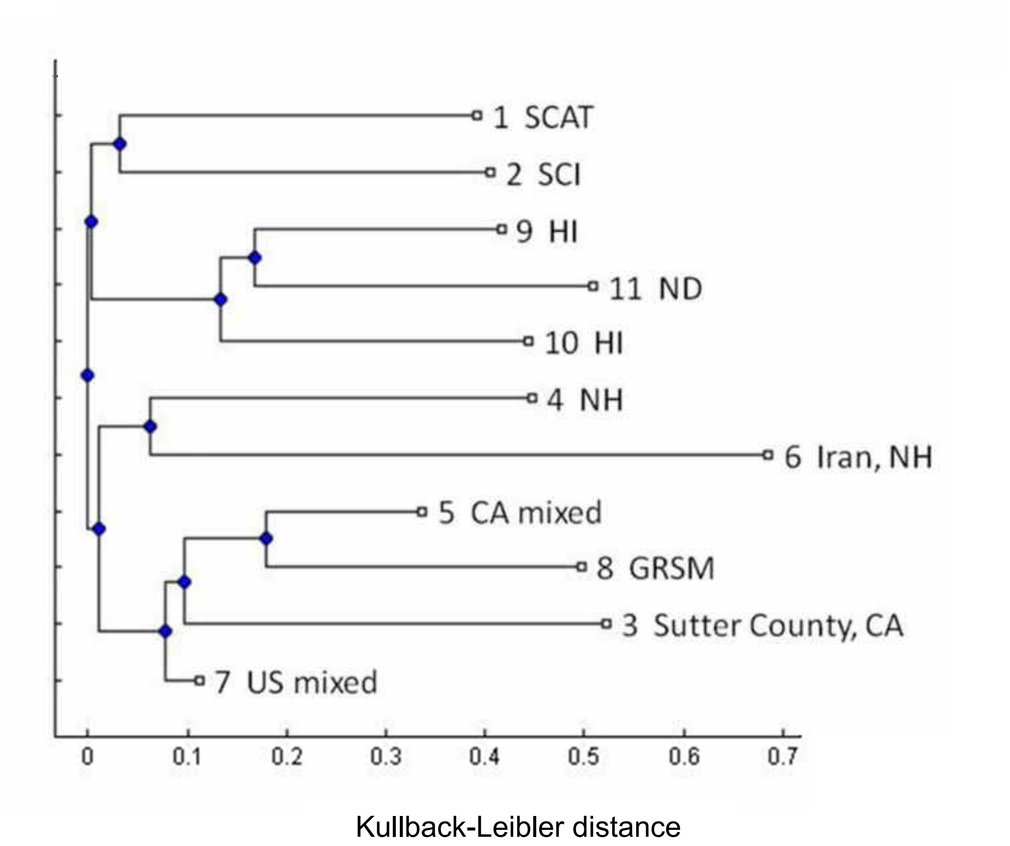

Figure 4.6. Phylogenetic relatedness of eleven molecular populations identified by program BAPS, based on single nucleotide polymorphism and microsatellite loci for 169 wild pigs collected in 31 U.S. states and Iran during the period 1996-2010. Dendrogram was created in BAPS using Kullback-Leibler distance to describe structure.

CHAPTER V

BROAD-SCALE LANDSCAPE GENETICS OF WILD PIGS IN CALIFORNIA

Introduction

Pigs (*Sus scrofa*) are large ungulates native to portions of Eurasia and North Africa that have been introduced by humans to many islands and all continents except Antarctica (Oliver and Brisbin 1993). Pigs were first introduced to North America during European explorations in the 1500s (Towne and Wentworth 1950, Mayer and Brisbin 1991). As the continent was populated, feral domestic pigs often became established due to free-range livestock practices, escape, and release (Mayer and Brisbin 1991). Intentional introductions of Eurasian wild boar (EWB) that began in the late 1800s have resulted in hybridization of feral domestic pigs and EWB in many locations throughout the U.S., including California (Mayer and Brisbin 1991). Because of hybridization, introduced pigs are commonly referred to simply as “pigs” or “wild pigs” unless specific references to wild or domestic origins are necessary for clarity of discussion.

In California, the first pig introductions are attributed to Spanish exploration as early as the 1500s and Missionary settlements in the 1700s (Pine and Gerdes 1973, Barrett and Pine 1980, Mayer and Brisbin 1991). From the period of first introductions to the middle of the 20th century, pig populations remained localized primarily in coastal counties where they were introduced. However, drastic range expansion from the 1960s onward has occurred; from nine counties to portions of 56 counties currently (Waithman et al. 1999, SCWDS 2010). It is thought that the introduction of EWB hybrids during the 1920s and increasing popularity of pigs as a game species are responsible for the spread of pigs in California (Wiathman et al. 1999). Because of these interacting factors, EWB hybrids are hypothesized to be more capable invaders than feral domestic pigs and animals possessing EWB phenotypic traits are preferentially selected by sportsmen for translocation to establish new populations for hunting (Barrett 1977, Waithman et al. 1999).

Prior molecular analyses of California wild pigs support a prominent role for EWB hybrids in range expansion (Chapters III, IV). Research at the national level has identified an isolation by distance (IBD) relationship that appears to be driven by local-scale (i.e., <100 km) relatedness among pigs, potentially representing natural dispersal (Chapter IV). However, the roles of natural and anthropogenic dispersal in range expansion of pigs in some portions of North America remain debatable, and very little is known about landscape factors contributing to the genetic diversity of wild pigs.

Landscape genetic studies of native large vertebrate species at localized extents (e.g., within 400km^2) have proven effective at identifying important geographic features for gene flow (Cushman et al. 2006, Perez-Espona et al. 2008). However, it appears that local scale studies of introduced pigs present considerable challenges for these approaches. Using microsatellite loci, Acevedo-Delgado (2010) evaluated landscape genetics of pigs in south Texas and found population structure but was unable to attribute allelic variation to geographic features. In California, Heeg (2006) used microsatellite markers to evaluate the role of landscape barriers in describing genetic variation of wild pigs from three counties. Though Heeg (2006) identified the San Benito River as a putative barrier to movement for pigs in this region of California, analyses of IBD revealed a negative correlation of genetic distance with geographic distance, and specific causes for geographic structuring of populations could not be determined. Both of the studies focused on localized geographic ranges, which may have confounded their assessment of gene flow in relation to larger landscape variables important for dispersal (Heeg 2006). The inability to assign biological significance to spatio-genetic relationships in these studies could be attributed to variations in home range size, behavioral aspects of wild pig ecology related to population density, or serial introductions of new molecular lineages over time (Mayer and Brisbin 1991, Gabor and Hellgren 1998, Heeg 2006). All of the above could be preventing establishment of allelic equilibrium necessary for detection of meaningful IBD patterns at the isolated local scales measured in these studies (Hutchison and Templeton 1999).

Despite these reported challenges, IBD patterns detected at the national scale in the continental U.S. suggest a spatial relationship that may provide meaningful insights to pig invasion if assessed at appropriate geographic extents (Chapter IV). At the national scale, landscape genetic approaches would be computationally challenging and generally inappropriate because of known long-range translocations that are intractable in terms of ecological aspects of invasion (Chapter IV). Here, we suggest that broad-scale analyses at the regional level (e.g., encompassing a large state) would be feasible and potentially informative. At the regional level, GIS computations are achievable and larger geographic features (e.g., vegetative communities, river systems) can be evaluated in terms of their effect on gene flow, potentially minimizing the impact of fine-scale details about variable home range size and population structure in analyses. Further, the role of regional anthropogenic dispersal through vehicle travel on roads could be assessed in concert with landscape effects. Finally, distance metrics based on estimated pig density could be developed to evaluate dispersal pathways associated with demographic aspects of existing pig populations. Data for these ecological and anthropogenic factors are available for California.

In this study, we utilized a subset of the genetic data analyzed in Chapter IV for spatio-genetic analyses of wild pigs in California. Our objective was to estimate geographic patterns of genetic variation of wild pigs in California and to test specific hypotheses about genetic structure; IBD and landscape effects. We then evaluated range expansion for wild pigs in California in context of IBD and landscape genetic findings.

Study Area

We obtained tissue samples from 71 wild pigs in 23 California counties during the period 1996-2008 (Chapters II, III, and IV). The study area spanned the central coast region where pigs were historically introduced, and portions of the Sierra foothills and Northern and Southern California that have been recently invaded by pigs (Waithman et al. 1999; Figure 5.1).

Methods

We used nuclear SNP and MS genotypes for 71 pigs collected from 23 California counties that were previously identified in Chapter IV to assess spatio-genetic relationships of wild pigs in California based on individual genetic variation. Latitude and longitude of the 71 samples were either obtained from collection records provided by United States Department of Agriculture (USDA; n=51) or were estimated from hunter harvest information (n=20) describing distance and direction from known geographic references (Loggins 2007). Geographic coordinates provided by USDA were randomly offset from true locations by a distance ranging from 100-1000 meters to protect the privacy of landowners, resulting in an assumed minimum error of 1000 meters. We identified 34 unique locations for the 71 individual pigs, which we imported to ARCGIS 10 (Environmental Systems Research Institute, Redlands, California USA) and converted to Universal Transverse Mercator (UTM) coordinates in Zone 16 North (Figure 5.1). Though randomization and estimation procedures resulted in local error of point locations, the typical home-range of wild pigs in California varies between 1-15.5 km^2, and may exceed 50 km^2 for some animals (Barrett 1978, Sweitzer et al. 2000). This suggests that geographic coordinates were accurate to the level of individual home-range, which is appropriate for the broad geographic scale at which landscape effects on genetics of wild pigs were assessed. Further, most landscape genetic analyses focus on population level estimates of genetic variation (Balkenhol et al. 2009). By evaluating individual genetic variation we may avoid biases associated with subpopulation structure potentially affecting test results and interpretation of statistical relationships, as samples in our dataset represent three previously identified molecular populations (Chapter IV, Cushman and Landguth 2010).

GIS Data Acquisition and Editing

We identified four landscape connectivity variables potentially important for wild pig dispersal in California: 1) “Habitat”; vegetative, ecological, and anthropogenic land cover, 2) “Pig density”; the estimated number of pigs occurring within specified locations, 3) “Streams”; major and minor waterways, and 4) “Roads”; local and primary vehicle routes. Our rationale for selecting these variables is based on aspects of the ecology of wild pigs and anthropogenic factors linked to range expansion. We selected habitat as a plausible connectivity metric for introduced pigs because land cover has been identified as an important factor for gene flow of a number of vertebrate species in North America and elsewhere (Balkenhol et al. 2009, Storfer et al. 2010). Pig density is an important factor because population increases have been linked to range expansion in the coastal region of California (Waithman et al. 1999, Sweitzer et al. 2000). Stream corridors are thought to be important to dispersal because population structure for pigs often reflects watershed geographic features (Hampton et al. 2004, Heeg 2006). Road distance between sample locations was included because anthropogenic dispersal is a leading factor in the spread of pigs throughout the U.S. (Mayer and Brisbin 1991, Gipson et al. 1998, Waithman et al. 1999). We obtained GIS data for California representing these variables through online geospatial data repositories and edited each in ARCGIS 10 as described below.

Habitat. We obtained land cover data representing habitat from California Department of Forestry and Fire Protection (Table 5.1). This was a raster dataset (100 meter resolution) with 55 land cover classes ranging from oak woodlands to barren and urban. We evaluated the quality of land cover classes for pig occupation and movement based on the ecology of wild pigs in California described in the literature (Barrett 1982, Mayer and Laudenslayer 1988, Sweitzer et al. 2000, Loggins 2007, Sweitzer and McCann 2007). We systematically assessed habitat quality and barriers to movement as high, medium, or low and arrived at consensus values for each land cover class (Appendix D, Figure 5.2). We then grouped quality assessments and reclassified the land cover raster to eleven ranks (1=high quality and low barrier; 11=low quality and high barrier; Appendix D)

Pig density. We obtained a 1:24,000 scale quadrangle grid for the U.S. developed by the United States Geological Survey (Table 5.1). We clipped the quadrangle coverage with an outline of California and created a new file that included only quadrangles having extents within California. We estimated density of wild pigs for each 7.5 minute quadrangle throughout California during 1992-2006 using hunter harvest information provided by California Department of Game and Fish (Loggins 2007, Sweitzer and McCann 2007). We converted the shapefile to raster with cumulative hunter harvest per 7.5º quadrangle as the value field and accepted the default output cell size (3800 m), based on the feature extent divided by 250. We then reclassified this pig density raster into ten ranks where landscape resistance was inversely correlated with pig density (1=high density, 10=zero pigs harvested; Appendix E, Figure 5.2). We chose this ranking scheme because locations with high pig densities could be considered optimal areas for pigs to occur and because high density reflected in hunter harvest represents a dynamic scenario where population densities are regulated by hunting (Waithman et al. 1999). For example, hunter harvest would eliminate individuals from the landscape, freeing resources for other animals to occupy, and hunting pressure may initiate dispersal (Caley and Ottley 1995).

Streams. We obtained hydrologic data for California from Cal-Atlas Geospatial Clearinghouse (Table 5.1). This was a vector dataset produced by the United States Bureau of Reclamation describing most stream courses occurring within California. To prepare a raster dataset describing stream and non-stream areas, we overlaid the stream vector with a polygon describing the boundaries of California. We then converted both the stream vector and California polygon to separate raster datasets, each with 100 meter resolution. We merged the rasters, specifying that overlapping cells retain stream values. Finally, we reclassified the merged raster to two rankings for preferential selection of stream courses for travel by pigs (1=stream, 2=other; Figure 5.2).

Roads. We downloaded two road vector files from Cal-Atlas Geospatial Clearinghouse, one for major roads (e.g., highways, interstate) and another for local roads (e.g., city streets, dirt roads; Table 5.1). To connect rural collection sites to major roads, we selected all local roads within a 25 km radius of sample locations and created a new vector shapefile. We then merged the 25 km local roads file with the major roads shapefile, resulting in a new coverage with vectors in close proximity to all sample locations (Figure 5.2).

GIS Analyses

We performed path analysis in Spatial Analyst Tools on habitat, pig density, and streams cost raster data sets. In path analysis, the least accumulative cost pathway between any two locations is determined using an algorithm to calculate the cost of all possible combinations of cell values in the cost raster surface linking the locations (Chang 2008). Since path analysis uses an exhaustive search it can be computationally inefficient depending on the raster resolution and the geographic extent of the study area (Chang 2008). Because of the 100 m resolution of habitat and streams rasters, we manually created a minimum convex polygon (MCP) shapefile extending 100km beyond our sample distribution in each cardinal direction. We then clipped the habitat and stream rasters with the MCP polygon, which allowed for identification of putative routes beyond the extent of the sample distribution to still be evaluated in path analysis while allowing calculations to complete in a manageable time frame.

We performed path analyses on individual collection sites, which generated a cost distance raster and cost backlink raster specific to unique locations. We used these distance and backlink rasters to calculate the least cost path between individual locations and all other sites. We then extracted path distance cell values for sample locations and appended data in a spreadsheet, sequentially processing all 34 unique locations. Working in this manner, we created distance matrices (i.e., pairwise cost distance) representing metrics of connectivity based on Habitat, Pig Density, and Watersheds for all 71 wild pigs sampled.

We performed a network analysis on the roads data using Network Analyst Tools. Network analysis is similar to the path analysis described above, except that routes are restricted to a system of linear features defined in a vector dataset (Chang 2008). In network analysis, the algorithm evaluates routes between locations based on geographic factors (e.g., line distance or topographic distance along vectors) or temporal impedances (e.g., speed limits, number of turns, road surface) important for delineating rates of vehicle travel between locations (Chang 2008).

To accomplish a network analysis, we created a geodatabase containing the merged California roads shapefile and built a network dataset specifying line length as the distance measure for evaluating connections. We initiated a “New Closest Facility” analysis and loaded the 71 pig coordinates as “Incidents”. We then sequentially loaded individual sample locations as the “Facility” and solved the network for all 71 locations. We exported “Route” shapefiles and extracted distances to a spreadsheet to produce a pair-wise distance matrix for sample locations.

Statistical Analyses

We calculated pair-wise genetic distance (F_{ST}) for the 71 wild pig genotypes using program GENEPOP (v4.0, 4.1; Rousset 2008). In preparation for spatio-genetic analyses, we determined pair-wise geographic Euclidean distance between the 71 California locations using program PASSAGE (v2; Rosenberg and Anderson 2011). We then tested the relationship of genetic data with Euclidean distance and landscape connectivity metrics using a variety of statistical techniques, including: Mantel tests, partial Mantel tests, multiple regression of distance matrices (MRM), and correlogram analyses.

Mantel tests are used to calculate correlation coefficients and estimate significance of the relationship between two square data matrices where observations are not independent (Mantel 1967). In Mantel tests, significance is estimated through random permutation of data, followed by an asymptotic approximation of the t-test. In ecological studies, Mantel tests are widely used to identify statistical relationships in distance-based data (Legendre and Troussellier 1988, Legendre 1993, Balkenhol et al. 2009). Partial Mantel tests are an extension of the standard Mantel approach where multiple matrices can be evaluated. Partial Mantel tests provide the ability to hold the variance of one or more distance matrices constant while analyzing the correlation and significance relationship of two other matrices (Smouse et al. 1986). Where geographic distance is held constant (i.e., the effect of spatial distribution is removed) partial Mantel tests are particularly valuable for identifying factors contributing to biological variation in spatial datasets (Cushman et al. 2006, Balkenhol et al. 2009).

Though partial Mantel tests allow us to remove the variance of competing predictor variables from analyses, they do not allow for assessment of the combined effect of variables typically afforded by multiple regression. The MRM method will permit determination of the combined effect of explanatory matrices (i.e., our landscape metrics) on the response matrix (pair-wise genetic distance) and evaluation of the significance of multiple models (Lichstein 2007). Finally, correlogram analysis is commonly used to identifying autocorrelation in spatial datasets (Cliff and Ord 1973). For distance matrices, Mantel correlograms can be used to determine the significance of correlations within pre-defined distance classes (Sokal et al. 1987). In our analysis, this was useful for determining the range of detectable gene flow and for identifying spatial ranges at which our explanatory variables differ.

Isolation by Distance

We tested for IBD with Mantel tests of pair-wise F_{ST} on Euclidean distance using programs PASSAGE and GENEPOP (v3.1d, Raymond and Rousset 1995). For both software applications we used the default settings of Spearman Rank Correlation and permutation tests with 999 iterations. In GENEPOP, we prepared two semi-matrices for the Mantel test, using untransformed genetic and geographic distances. We then used output from the GENEPOP analyses to prepare a regression equation and to plot the point distribution. Next, we performed a series of analyses of F_{ST} on Euclidean distance, arbitrarily selecting ten distance values defined by the following minima (km): 0, 1, 25, 50, 100, 150, 200, 300, 400, and 600. We selected these break points to determine if IBD was driven by local relationships or persisted across the range of spatial distances sampled, though we were limited in this regard due to a small number of samples pairs having distances between 1 and 25 kilometers. Using program PASSAGE, we then tested for spatial autocorrelation using the distance classes defined above, where in this case each class was the range of values between minima.

Tests of Landscape Effects

We tested each landscape metric against genetic distance in programs PASSAGE and GENEPOP using the procedures and analysis settings for standard Mantel tests described above. We then used PASSAGE to perform partial Mantel tests of genetic distance on each landscape distance metric while holding Euclidean distance constant, and vice versa. We evaluated test results under the assumptions that individual landscape metrics would be valuable for describing gene flow: 1) if the Mantel relationship was significant with Euclidean distance held constant, and 2) if the relationship between F_{ST} and Euclidean distance was not significant when the landscape metric was held constant (Cushman et al. 2006; 2010). We then performed a series of Partial Mantel tests on each variable meeting the above expectations, with the individual and combined variance of other significant variables and Euclidean distance held constant to identify relationships potentially masked by collinearity among explanatory variables.

We performed MRM of Euclidean distance of landscape metrics using the ecodist-package (Goslee and Urban 2007) in program R (R Development Core Team 2011). For this analysis we used Spearman Rank Correlation with 999 permutations for significance testing. Because permutation tests are used in MRM to determine significance, model selection using information theoretic approaches was not possible. Therefore, we performed backwards selection to determine the most parsimonious regression model, starting with the full model and sequentially removing the single variable with the highest p-value. We then evaluated all subsets to identify other parsimonious models with equivalent significance.

We performed a series of correlogram analyses of genetic distance on Euclidean distance and landscape distance metrics using ten distance classes having an equal number of pair-wise comparisons to evaluate variation between metrics across distances. Finally, we tested all possible combinations of Euclidean distance and landscape metrics to assess collinearity between predictor variables based on Mantel r values.

Results

Analysis of Isolation by Distance

Tests of IBD were significant at all minimum distances evaluated (Table 5.2, 5.3; Figure 5.3). The strongest IBD relationship was observed for the full dataset, with correlations weakening as minimum distance increased to 200 km (Table 5.3). From 200 km minimum value onward correlations modulated, suggesting considerable variance at the largest spatial extents (Table 5.3). Based on correllogram analyses evaluating variation within defined distance classes, correlation among individuals was strongest for samples in close proximity and dissolved at separation distances of 200-300 kilometers (Figure 5.4).

Analyses of Landscape Metrics

Individual Mantel tests were significant for F_{ST} on all landscape distance metrics (Table 5.2). Habitat had the highest correlation with genetic distance, followed by pig density, roads, streams, and Euclidean distance (Table 5.2). Partial Mantel analyses identified one variable as a candidate for exclusion from consideration regarding gene flow. When Euclidean distance was held constant, habitat, pig density, and roads were significantly related to genetic distance, whereas streams was not (Table 5.4). When each landscape metric was held constant, the relationship between Euclidean distance and genetic distance was not significant (Table 5.4).

In the full regression model, Streams had the highest p-value and was removed during the first round of backwards selection. After Streams was removed, all variables were significant ($p=0.001$) and the model could not be reduced further. Therefore, the most parsimonious regression model included habitat, pig density, roads, and Euclidean distance. Analyses of all subsets revealed no other four-variable models having high significance values for all variables. Three separate three-variable models had high levels of significance across variables and included combinations of all five distance metrics, though none included both Euclidean distance and Streams in the same model.

All distance metrics were correlated ($r \geq 0.90$), indicating collinearity in the dataset (Table 5.5). Comparative autocorrelation analyses provided a view of correlation structure between variables across spatial ranges and indicated that the greatest variation between metrics occurred from 50-200 kilometers (Figure 5.5). Notably, Streams and Euclidean distance were closely matched in this distance class and shared the highest correlation overall (Table 5.5; Figure 5.5). Collinearity among significant variables was also apparent from results of partial Mantel tests, and pig density was the only variable that retained significance when Euclidean distance and other landscape metrics were held constant (Table 5.6).

Discussion

Patterns of IBD in this regional analysis are similar to that described at the national scale in North America (Chapter IV). This result is not unexpected, as the California dataset comprised nearly half of the samples in that analysis. However, additional insights can be gained from our regional analysis. Through focused interpretation of genetic relationships at the regional scale, we can attribute ecological and anthropogenic causes for spatio-genetic relationships, not attainable for the national dataset.

Isolation by Distance

The significance of IBD tests across the range of spatial distances measured indicates that the overall relationship between genetic and geographic distances is not simply driven by high correlations at the local scale (Table 5.3). Though correlations at larger geographic distances decrease, a general trend of increasing divergence with increasing geographic distance implies a progressive invasion of California by pigs (Figure 5.3, 5.4). Based on recorded introduction histories, this trend in IBD could be explained by at least three dispersal scenarios: 1) pigs dispersed naturally to occupy locations where they were sampled, 2) pigs were aided in local dispersal by humans in a series of successive steps across the landscape, and 3) pigs were translocated great distances to establish new populations (Mayer and Brisbin 1991, Waithman et al. 1999).

Based on spatial autocorrelation results we can infer that there is a strong case for natural range expansion up to and including 150-200 km (Figure 5.4). However, evidence for both natural and anthropogenic dispersal is apparent from our results. For instance, natural dispersal is supported by the relatively strong IBD relationship for locations separated by less than 50 kilometers (Table 5.3, Figure 5.3). Considering that home range size for pigs in California ranges between 1-15.5 km^2 (Sweitzer et al. 2000) and male pigs are known to disperse farther (e.g., up to 50 km) for mating opportunities (Barrett 1978, Gabor et al. 1999), natural range expansion from introduction sites could explain this relationship. Alternately, the wide range of F_{ST} values across spatial scales supports a stepping stone scenario of human-mediated dispersal including new introductions of stock differing genetically from historic populations (Chapter III; Figure 5.3). Finally, long-range anthropogenic dispersal best explains lower F_{ST} values (<0.5) individually observed for some larger geographic distances (e.g., 400-600 km) in IBD plots (Figure 5.3). Therefore, all three dispersal scenarios presented above are plausible based on the data.

The wide variation in genetic distance (F_{ST} ranging from 0.28-0.70) for animals sampled from same locations alludes to the diverse introduction history for pigs in California and the admixture of populations over time (Barrett 1978, Pine and Gerdes 1973, Mayer and Brisbin 1991). Considering that there is a broad baseline for genetic distance at local scales, it is interesting that an IBD pattern was still detectible as distances increased (Table. 5.3). We can infer from this pattern that range expansion has not simply issued forth from a single historic interbreeding population at allelic equilibrium. Instead, it appears that admixed populations have dispersed across a range of distances. This spatial pattern generally agrees with historic accounts and prior molecular research findings linking EWB hybrids in California to range expansion (Waithman et al. 1999, Chapters III, IV). That is, where hybrids were introduced, they have interbred with local feral populations and animals have been translocated from historically occupied areas repeatedly in a series of steps across the landscape. Therefore, we could hypothesize that IBD in California is driven by EWB hybrid introductions, during which populations were established with relatively few individuals, leading to genetic drift and divergence.

Though these findings provide interesting insights, it is not possible to determine directly what role natural and anthropogenic dispersal have played in pig invasion based on spatial autocorrelation and IBD patterns alone. This is due in part to the stochastic nature of allelic variation for non-native species and the fact that pigs have been introduced to California from diverse geographic origins and from a variety of domestic and wild lineages (Chapters III, IV).

Landscape Effects on Genetic Variation of Pigs

Our analyses demonstrate that landscape cost distances explain a greater amount of observed genetic variation than IBD. The significance of habitat, pig density, and roads distance measures across analyses provides confidence that these variables are positively associated with pig movements. However, careful consideration of the role of each variable in range expansion for pigs in California will be necessary to understand factors responsible for this relationship and potential biases associated with our distance metrics and landscape genetic analyses in general. The non-significant result of streams should also be considered.

Habitat. The importance of landscape factors for gene flow is generally supported by research on a variety of vertebrate species (Storfer et al. 2010). For instance, Cushman et al. (2006) determined that forest connectivity was important for gene flow in black bear (*Ursus americana*). Further, connectivity of acceptable habitat is a primary concern for species survival in human-altered landscapes that has been identified through many landscape ecological studies (Belisle 2005, Fahrig 2007, Schwartz et al. 2009). Considering that Oak-savannah habitats are preferred by pigs and that Oak-savannahs are a prominent feature connecting many parts of the California landscape in our study area (Figure 5.2, Appendix D), it is not surprising that pig dispersal is linked to our Habitat variable that coded for low resistance of movement through these areas (Mayer and Laudenslayer 1988). However, the significance of the Habitat variable in our analysis only provides general information that land cover is important to gene flow. Because we ranked and grouped 55 land cover types into eleven categories, it was not possible for us to separate the individual or interactive role of specific cover types. Though, our findings here satisfy the broad objective of this study, we infer that additional information could be gleaned by a more in-depth analysis on the relationship of individual land cover types with genetic distance (Cushman et al. 2006).

In addition to vegetative cover, elevation and other barriers to movement are also typically assessed in landscape genetic studies (Storfer et al. 2010). For instance, Perez-Espona et al. (2008) determined that sea lochs and mountain slopes were important barriers to movement for red deer (*Cervus elaphus*) in Scotland. In our analysis we did not include elevation because all locations sampled were east of the Sierra Nevada and we could find no evidence that elevation gradients affect broad-scale pig movements in California. We also did not perform isolated analyses of other barriers to movement; including urban areas, desert, and alpine regions. Instead, we assigned these features high resistance values in our habitat variable, which served as a composite estimate of the impedance of land cover (Appendix D). Among these, urban areas and human population densities may be an important consideration for future research (Murtskhvaladze et al. 2010). However, due to anthropogenic dispersal, it is unclear whether human population densities in California impedes or promotes gene flow in pigs.

Pig density. Our identification of population density as an important factor for gene flow indicates that dispersal may be density dependent for introduced pigs in California. Dispersal is negatively correlated with population density in Eurasian wild boar in their native range (Truve et al. 2004). However, socio-genetic relationships for feral pigs are related to population density and home range size is linked to resource availability (Gabor et al. 1999, Adkins and Harveson 2007). For example, increases in wild pig population densities in the coastal region of California have been attributed to rainfall and forage availability (Sweitzer et al. 2000). Therefore, seasonal environmental fluctuations in California may be promoting range expansion, where dispersal is punctuated by population increases during years of abundant forage and water resources, followed by redistribution of animals during years of drought and mast failure (Baber and Coblentz 1986, Bieber and Ruf 2005, Adkins and Harveson 2007). Hunting may also facilitate pig movement by establishing a scenario where animals are harvested or pressured out of areas and new animals filter into available habitat (Caley and Ottely

1995, Sweitzer et al. 2000). The link between sport hunting and translocation of pigs also suggests that areas frequented by hunters are likely collection and introduction sites (Barrett 1977, Waithman et al. 1999).

Given the above factors, some manner of natural or human-mediated dispersal linked to population density is logical. However, several potential biases in our estimation of pig densities through harvest should be considered. For instance, areas not open to hunting (e.g., state and county parks) were not represented, and numbers of animals harvested per quadrangle fluctuated annually during the measured period. Additionally, estimates of wild pig population densities at the quadrangle level do not provide a high-resolution metric for scaling with our landscape variables (e.g., land cover measured at 100 meter resolution). Another consideration is the correlation of pig density with landscape features, as higher densities can be expected in ecologically optimal areas, which presents a clear link to our habitat variable. Though the exact relationship between population density and dispersal for introduced pigs is unclear, our results suggest that high-density areas could be viewed as corridors for dispersal.

Roads. The spread of invasive species by roads, either intentional or accidental, is well documented (Soule 1990, Kolar and Lodge 2001, Minchin et al. 2003, USDA 2010). Though most landscape genetic studies consider roads as barriers to movement, our analysis provides some evidence that roads serve as corridors for anthropogenic dispersal of wild pigs. Our findings fit the known practice of translocating pigs that has contributed to the range expansion of pigs throughout the U.S. (Mayer and Brisbin 1991, Gipson et al. 1998, Waithman et al. 1999). It is logical that greater distances by road would equate to a greater cost to humans translocating animals (measured in vehicle mileage, time, and gasoline), potentially establishing an IBD relationship for pigs that are introduced in a step-wise manner. However, it is unclear in what way the cost of anthropogenic dispersal scales with the physical cost of natural dispersal for pigs. Regardless, the relationship between road distance and genetic distance loosely supports the hypothesis of human selection for EWB hybrids outlined in our discussion of IBD above, where hybrid pigs would be dispersed by roads. Further investigation into the relationship of road distance with genetic distance for introduced pigs will be necessary to provide a clearer understanding of the role of roads as dispersal corridors.

Streams. Watersheds have been identified as important geographic features for defining population structure in introduced pigs (Hampton et al. 2004, Heeg 2006). As such, it is surprising that streams was not a consistently significant variable in our analysis. The high correlation of streams with Euclidean distance explains this result and suggests that the simple coding of a binary surface for low and high impedance based on water courses may not capture the complexity of pig movements related to streams and associated habitat. Heeg (2006) noted the potential importance of north to south stream courses for gene flow and postulated that seasonal variation in water presence may affect pig use of these corridors in California. Though we cannot support gene flow via streams here, we suggest that additional analyses incorporating seasonal aspects of water availability and stratified values representing the size of watersheds are necessary to further evaluate the role of this landscape feature in range expansion for wild pigs in California.

Overview of Landscape Genetics Analyses

Mantel tests and MRM comprise the majority of statistical options for evaluating distance-based measures in landscape genetic analyses (Balkenhol et al. 2009). Since these procedures calculate matrix correlations and permute data to estimate significance, both approaches provide relatively low power for identifying important relationships when compared to multiple regression and Canonical Variate analyses of point-estimated data in landscape ecological studies (Legendre et al. 2005, 2008). Additionally, because of collinearity among variables we must assume that habitat, pig density, and roads, though significant individually and in combination, may be somewhat interchangeable for explaining genetic distance. Our inability to reduce MRM models beyond four significant variables exemplifies this issue. We also cannot discount the potential collinearity of our variables with some other unmeasured landscape feature that is important to gene flow.

In our analysis, partial Mantel tests were useful for identifying habitat, pig density, and roads as important landscape variables. Further, by holding Euclidean distance and landscape metrics constant, we were able to determine that population densities explain genetic variation beyond that described by any other variables (Table 5.6). From this we infer that range expansion might be slowed if population densities are controlled (Bieber and Ruf 2005). However, as noted above, sport hunting as a means of population control may have unintended consequences that promote dispersal.

Summary and Future Directions

Here we have identified several key factors important to the movement of pigs in California, bringing us a step closer to understanding the dynamics of range expansion. To further elucidate landscape genetic patterns, it will be necessary to dissolve landscape metrics into a higher resolution set of predictor variables. As discussed above, each of the 55 land cover types in our Habitat variable could be isolated as individual factors and subjected to examination with partial Mantel tests to determine which specific habitat features are driving statistical relationships (Cushman et al. 2006). Barriers to gene flow (e.g., extreme slopes, urban areas, human population density) could also be identified and incorporated using path analysis techniques. Network analyses of road connectivity could be augmented in future studies using topographic distances between locations and information on impedances, such as speed limits and turns. Despite the non-significant result of streams in our analysis, ongoing research should consider the use metrics that capture aspects of watersheds not measured here.

Additional samples in intermediate locations would be valuable for future work on landscape genetics of pigs in California. Considering that multiple molecular populations have been identified within the state, it may be useful to employ Bayesian clustering techniques to isolate populations to reduce variation in the data attributable to separate introductions and radiations of pigs and spurious correlations associated with subpopulation structure (Cushman et al. 2010, Chapter IV). A final consideration is the inclusion of additional samples from throughout the state for a higher resolution study of regional and local genetic relationships. Contrary to the findings of prior research in

California, our analysis demonstrates that significant patterns of IBD are present in introduced pig populations (Heeg 2006). Though prior research in California and Texas suggests that fine-scale landscape genetics of introduced pigs may be somewhat intractable, too few studies have been attempted to rule out the utility of such approaches (Heeg 2006, Acevedo-Delgado 2010). Ongoing research could provide valuable information on landscape ecology of pigs and yield additional insights useful for management.

Management Implications

Our findings generally support both anthropogenic and natural pathways of range expansion for pigs in California, as implicated by studies of introduction histories and wild pigs as a game species within the state (Mayer and Brisbin 1991, Waithman et al. 1999). Though this analysis has not defined a new paradigm for pig dispersal, our work has identified the spatial extent at which natural range expansion may be occurring and the importance of wild pig population density for dispersal. The data also support the recent dispersal of an admixed population, which matches the history and suspected role of EWB in range expansion throughout California. Here, we have provided empirical evidence that contributes to our understanding of wild pig invasion of California, which is ultimately important to management.

Table 5.1. Sources and titles of Geospatial data used to quantify metrics for landscape genetics analysis of 71 wild pigs sampled throughout California during 1996-2010.

Landscape metric	Source	Title
Habitat	California Department of Forestry and Fire Protection (frap.cdf.ca.gov)	Multi-source Land Cover Data (v02_1)
Pig density	Geo community (www.geocomm.com): USGS	24k Quad grid
Roads	Cal-Atlas Geospatial Clearinhouse (atlas.ca.gov): U.S. Department of Commerce, U.S. Census Bureau, Geography Division	TIGER/Line shapefile, 2007, California Local Roads and Major Roads
Streams	Cal-Atlas Geospatial Clearinhouse (atlas.ca.gov): U.S. Bureau of Reclamation, Mid-Pacific Region, MPGIS Service Center	hydro24ca-selected hydrologic features 1:24,000-scale for California

Table 5.2. Mantel tests of Euclidean distance and four landscape metrics on genetic distance (pair-wise F_{ST}) based on nuclear genotypes for 71 pigs collected from 23 California counties during 1996-2010. Significance, regression parameters, correlation, and variance explained are provided as determined through analyses in programs GENEPOP and PASSAGE.

Variable measured against F_{ST}	p	a	b	r	R^2
Euclidean distance	≤0.001	0.5731	1.40E-07	0.309	0.095
Habitat	≤0.001	0.5674	8.00E-08	0.349	0.122
Pig density	≤0.001	0.5704	2.00E-08	0.344	0.119
Roads	≤0.001	0.5695	1.30E-07	0.332	0.110
Streams	≤0.001	0.5710	1.00E-07	0.313	0.098

Table 5.3. Mantel tests of pair-wise F_{ST} on Euclidean distance at progressively higher spatial scales for 71 wild pigs sampled throughout California during 1996-2010. Minimum distance listed is the lower limit of pair-wise Euclidean distances between samples selected for analyses in program GENEPOP.

Minimum distance (m)	r	R^2	a	b	p-value
0	0.31	0.10	0.5731	1.40E-07	<0.00000
1000	0.20	0.04	0.5919	9.00E-08	<0.00000
10000	0.18	0.03	0.5940	8.00E-08	<0.00000
25000	0.18	0.03	0.5943	8.00E-08	<0.00000
50000	0.19	0.03	0.5926	8.00E-08	<0.00000
100000	0.18	0.03	0.5918	9.00E-08	<0.00000
150000	0.14	0.02	0.5992	7.00E-08	<0.00000
200000	0.16	0.02	0.5940	8.00E-08	<0.00000
300000	0.24	0.06	0.5727	1.30E-07	<0.00000
400000	0.20	0.04	0.5703	1.30E-07	<0.00000
600000	0.23	0.05	0.5138	2.00E-07	<0.00000

Table 5.4. Partial Mantel variable selection with landscape metrics analyzed against genetic distance (Gen) while Euclidean distance is held constant, and Euclidean distance analyzed on genetic distance with landscape metrics held constant. Metrics are abbreviated as follows: Euclidean distance (Euc), Habitat (Hab), Pig density (Pden), Roads (Road), and Streams (Strm). For each Partial Mantel test, the variables being tested are separated by a hyphen and the matrix being held constant is separated from these by a period. Bold print indicates where results meet test expectations of significance for genetic distance on the landscape metric with Euclidean distance held constant or a non-significant result of genetic distance on Euclidean distance with the landscape metric held constant; * denotes significance at alpha ≤0.05.

Variables	Test expectations	Two tailed p-values
Habitat	Hab-Gen.Euc	**0.025***
	Euc-Gen.Hab	**0.655**
Pig density	Pden-Gen.Euc	**0.012***
	Euc-Gen.Pden	**0.209**
Roads	Road-Gen.Euc	**0.027***
	Euc-Gen.Road	**0.455**
Streams	Strm-Gen.Euc	0.455
	Euc-Gen.Strm	**0.868**

Table 5.5. Mantel correlation (lower semi-matrix) and two-tailed p-value (upper semi-matrix) for comparisons of all distance measures between 71 sampling locations where pigs were collected in California during 1996-2010. Variables are abbreviated as follows: Habitat (Hab), Pig density (Pden), Roads (Road), Streams (Strm), and Euclidean distance (Euc).

	Hab	Pden	Road	Strm	Euc	Mean r
Hab	-	0.001	0.001	0.001	0.001	0.925
Pden	0.908	-	0.001	0.001	0.001	0.954
Road	0.937	0.956	-	0.001	0.001	0.963
Strm	0.933	0.957	0.976	-	0.001	0.964
Euc	0.924	0.965	0.985	0.991	-	0.966

Table 5.6. Partial Mantel results for significant variables with other significant variables and Euclidean distance held constant. Genetic distance is abbreviated (Gen). Geographic and landscape distance metrics are abbreviated as follows: Euclidean distance (Euc), Habitat (Hab), Pig density (Pden), Roads (Road), and Streams (Strm). For each Partial Mantel test, the variables being tested are separated by a hyphen and the matrices being held constant are separated from these by a period. Note: * denotes significance at alpha=0.05.

Variable	Test	Two-tailed p-value
Habitat	Hab-Gen.Pden	0.198
	Hab-Gen.Road	0.117
	Hab-Gen.Pden, Road	0.144
	Hab-Gen.Pden, Euc	0.057
	Hab-Gen.Road, Euc	0.093
	Hab-Gen.Pden, Road, Euc	0.163
Pig density	Pden-Gen.Hab	0.362
	Pden-Gen.Road	0.191
	Pden-Gen.Hab, Road	0.253
	Pden-Gen.Hab, Euc	0.041*
	Pden-Gen.Road, Euc	0.043*
	Pden-Gen.Hab, Raod, Euc	0.031*
Roads	Road-Gen.Hab	0.833
	Road-Gen.Pden	0.910
	Road-Gen.Hab, Pden	0.503
	Road-Gen.Hab, Euc	0.126
	Road-Gen.Pden, Euc	0.074
	Road-Gen.Hab, Pden, Euc	0.192

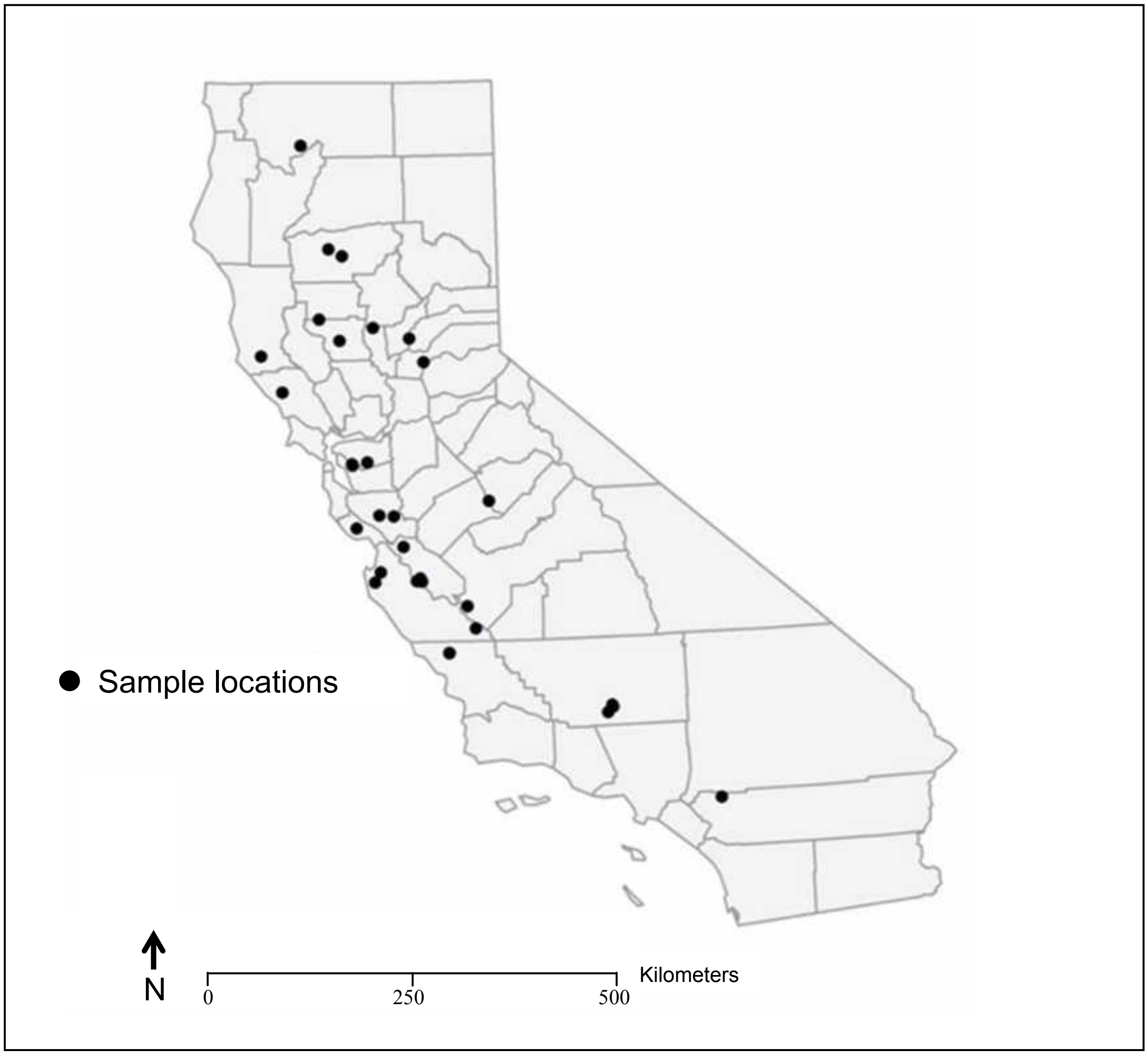

Figure 5.1. Distribution of 71 wild pig samples from 23 counties in California, USA. Samples were obtained during 1996-2010.

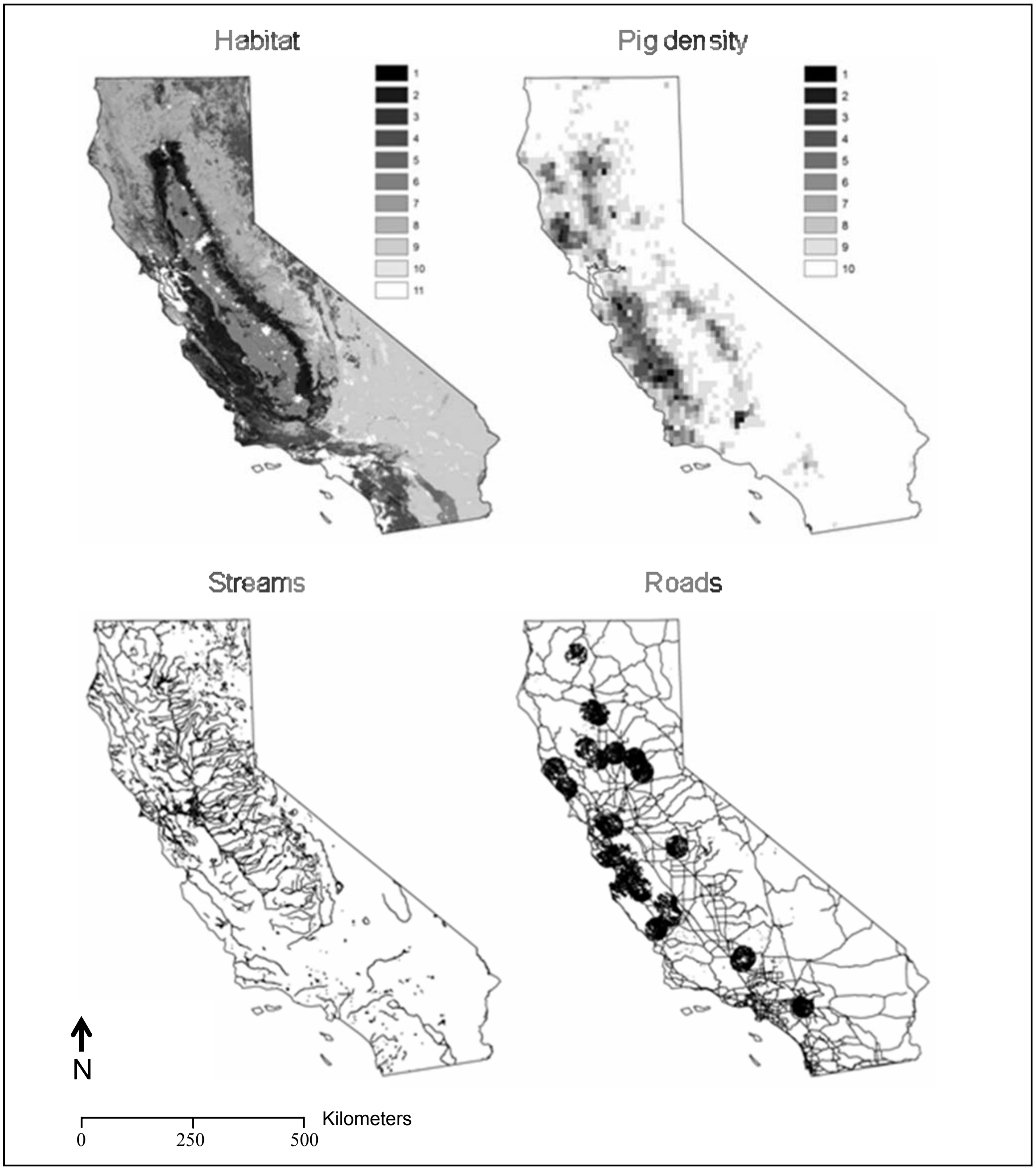

Figure 5.2. Landscape metric coverages developed for Habitat (top left), Pig density (top right), Streams (bottom left), and Roads (bottom right). Scaled values for Habitat and Pig density correspond to rankings for each variable described in Appendix D.

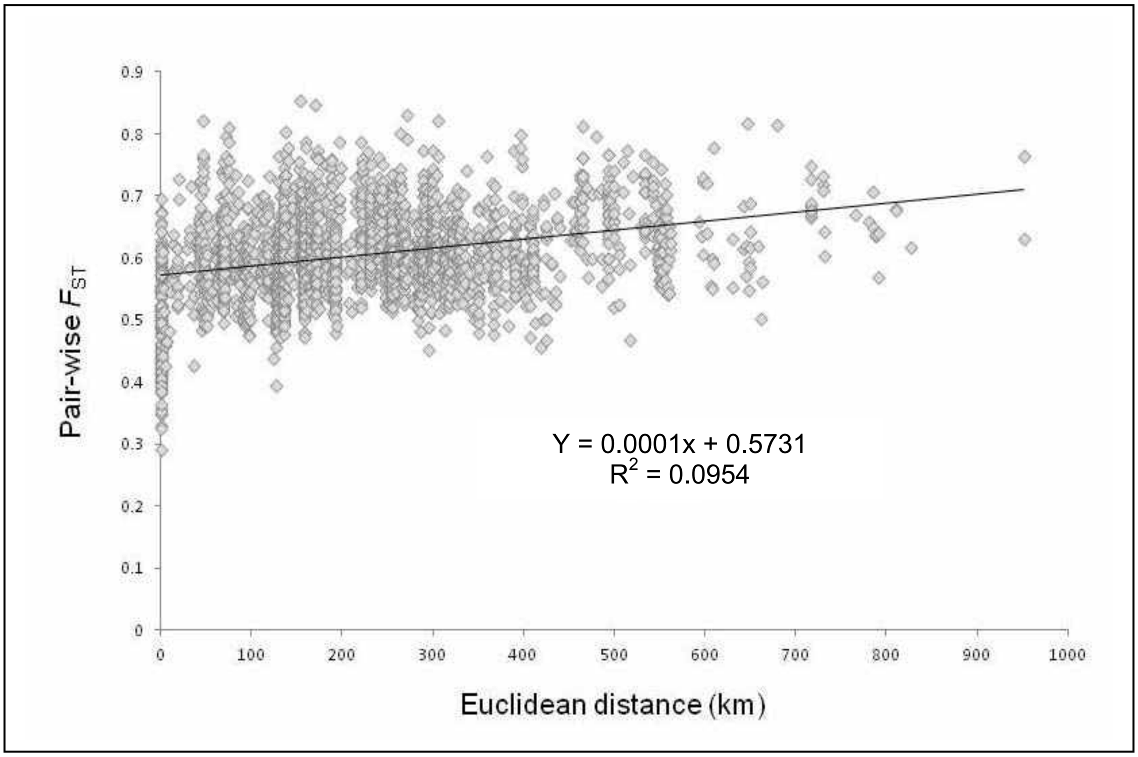

Figure 5.3. Scatterplots of F_{ST} on Euclidean distance. Slope of lines and R^2 value is provided; regression equation determined through GENEPOP analysis is presented for the full dataset.

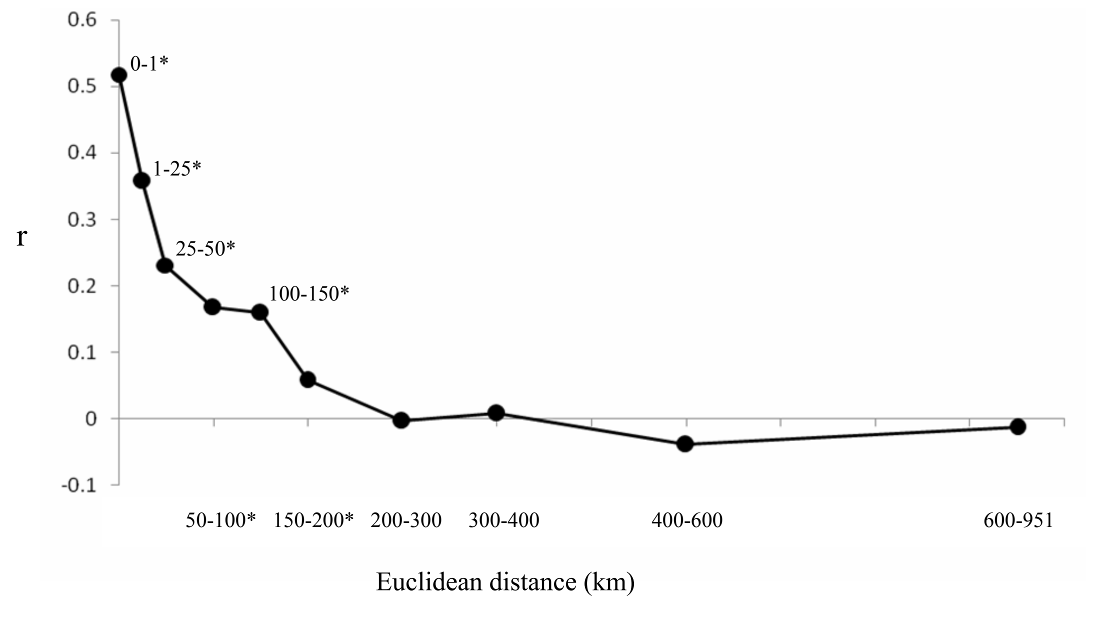

Figure 5.4. Mantel correlegram of pair-wise F_{ST} on Euclidean distance for ten distance classes. Mantel r is presented on the y-axis; Euclidean distance ranges are listed on the x-axis and by points on graph. Note: *denotes significant relationships detected for respective distance classes.

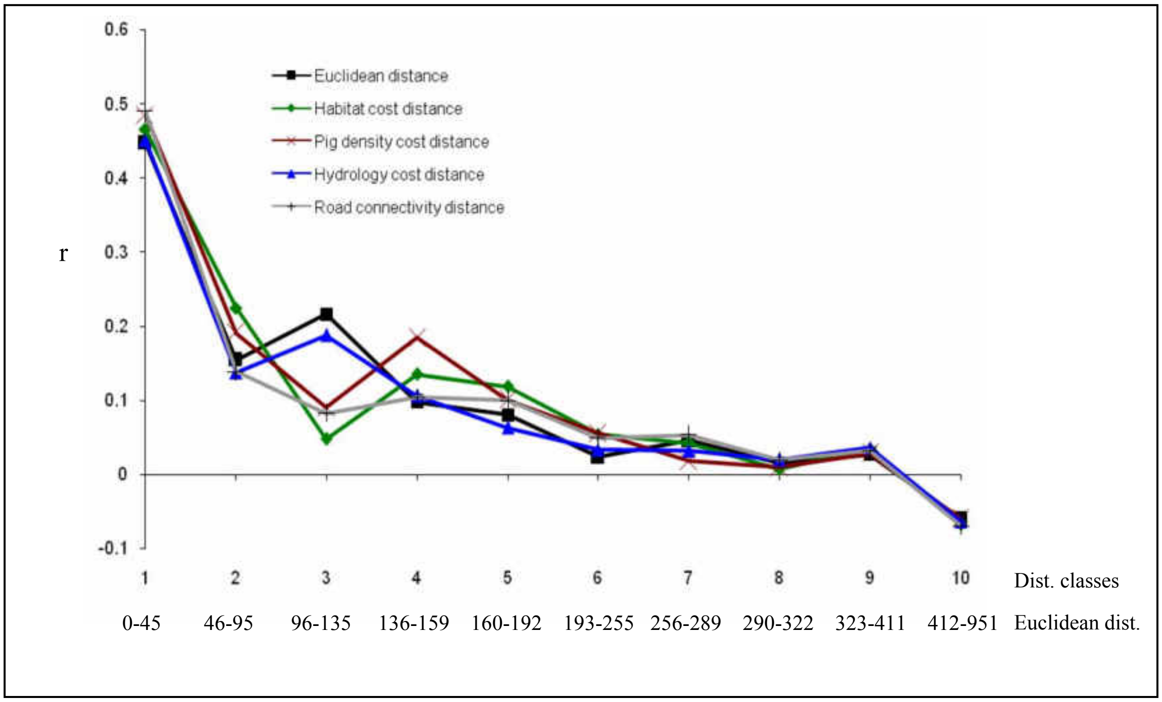

Figure 5.5. Mantel correlograms of pair-wise F_{ST} on all distance metrics across equal comparison distance classes. Range of Euclidean distances for each class is provided at bottom for reference.

CHAPTER VI

EPILOGUE

Summary of Research Findings

mtDNA

Origins

Due to the availability of published sequence from around the world, evolutionary relationships based on mitochondrial sequence have provided a basal understanding of pig invasions. Mitochondrial DNA was useful for identifying putative origins for introduced pigs (Chapters II, III); I determined that there are individuals with both European and Asian origins present in the U.S. The presence of these individuals supports the known hybridization of Asian and European pig lineages that led to the development of many common domestic breeds. Release of these breeds likely contributed to feral populations in the U.S. (Mayer and Brisbin 1991, Jones 1998, Fang and Andersson 2006, Chapter II). Among the lineages present in the U.S., I identified some specific breed relationships for introduction sites in North America and links to ancient sources for pigs in Hawaii (Chapters II, III). However, mitochondrial haplotype relationships should be considered cautiously, as introduction sources can be obscured due to shared ancestry between Eurasian wild boar and domestic pigs and the ubiquity of some haplotypes in national and global datasets. Though mitochondrial sequence relationships provided interesting insights regarding phylogeography and invasion histories, it is apparent that mtDNA has limited applicability for management of wild pigs.

Nuclear DNA

Population Structure

Microsatellite and single nucleotide polymorphism loci were useful for identifying genetic relationships at the national, regional, and local levels (Chapters IV, V). I found agreement of inferred groupings based on these data with known geographic boundaries and introduction histories (Chapter IV). Because of the identification of these populations, it is possible to further examine gene flow between these units, facilitating ongoing research in pig genetics and management. In particular, utilization of individual genetic distance measures for pigs in California suggests that dispersal patterns and sources for invasions can be identified (Chapter IV).

Despite the overall success of this approach, I was unable to assign origins to some groupings. Unresolved clusters of individuals (i.e., where no geographic or biological significance could be assigned to statistical groupings) could represent recent invasions at the national scale emanating from a single admixed source (Chapter IV).

However, the lack of resolution for our largest group of individuals is more likely a result of sparse sampling for most states (e.g., 1-6 pigs). A more intensive sampling scheme in California identified increased population structure at local and regional levels; I hypothesize that additional samples throughout the U.S. would likely yield additional population structure (Chapter IV). Despite some unresolved relationships, multi-locus nuclear genetic markers have clearly provided useful signal for management of pigs. My findings here have helped refine research questions for ongoing work on wild pig genetics, specifically in identification of invasive genotypes and in tracking of disease transmission.

Spatio-genetic Relationships

The presence of an isolation by distance (IBD) relationship at the national level and in California suggests that range expansion can be tracked in terms of gene flow across the landscape (Chapters IV, V). However, it is uncertain whether the association of genetic distance with geographic distance has resulted from diminishing rates of gene flow under a natural dispersal scenario or from genetic drift associated with step-wise anthropogenic dispersal. Under a natural dispersal scenario, individuals roam from establishment sites over a given period of time. Subsequent mutation causes allelic variation that increases with space over time, resulting in genetic distances for individuals or populations that scale with geographic distances (Hutchison et al. 1999). Under a step-wise human dispersal scenario, a few animals are translocated to establish a new population, which diverges from the source population through stochastic loss of alleles. The translocated population then serves as a source for additional relocations; a series of steps and divergence follows (Chapter V).

The short duration of pigs in North America (<500 years) casts doubt on the possibility of a naturally occurring IBD cline due to the slow mutation rate of nuclear DNA (Mayer and Brisbin 1991, Chapter IV). However, significant relationships identified for landscape variables with genetic distance support some role for natural dispersal in range expansion of pigs in California (Chapter V). Alternately, the known practice of translocating pigs fits a step-wise anthropogenic dispersal scenario potentially linked to high pig densities (Mayer and Brisbin 1991, Gipson et al. 1998, Waithman et al. 1999, Chapter V). Further, the similarity of some genotypes distantly separated confirms the role of long-distance anthropogenic dispersal in range expansion (Chapters IV, V). Therefore, I hypothesize that both natural and anthropogenic dispersal contribute to the spread of pigs in the United States. I conclude that additional research in the area of spatio-genetic relationships will be necessary to resolve questions regarding natural versus anthropogenic dispersal patterns for introduced pigs (Chapter V).

Implications for Management of Wild Pigs in the United States

Dissemination of my research findings will be important for researchers and managers in several key ways. Through peer-reviewed publications, I will make my findings widely available to resource managers and other scientists interested in pursuing molecular techniques for management of wild pigs. The methodologies and analyses described here will serve as a good starting point for ongoing work. Chapter II is in revision with *The*

Journal of Wildlife Management; I intend to submit the following chapters to other management-oriented forums.

I have been working with collaborators in numerous states to provide regional interpretations of my dataset to identify putative sources for introduced pigs. I envision that this work will be ongoing and that my dataset will expand through regional analyses, ultimately providing a baseline of wild pig population genetics that will serve as an increasingly powerful management tool for resource specialists. As I develop a more detailed picture of genetic variation among wild pigs throughout North America, I will be able to provide more definitive results regarding gene flow and patterns of anthropogenic dispersal.

My current research findings have led to additional collaborations with USDA Wildlife Services to further evaluate wild pig population genetics at the national scale and to elucidate the molecular basis for disease prevalence among populations and for individual pigs. This molecular epidemiology work, in combination with expansive population genetic analyses at the national level, will help track the spread of swine-borne diseases important to wildlife and the livestock industry.

Reflection on Program of Study and Research

The opportunity to pursue molecular techniques for wildlife management has broadened my perspective as a resource manager and scientist. Prior to arriving on campus at the University of North Dakota (UND), my experience with genetics was limited to a single course in my undergraduate program of study. However, with the aid of curricula focused on molecular techniques and with the specialized assistance of the faculty at UND, I have developed expertise in genetics and the analysis of molecular data. This educational experience enabled my undertaking of this ambitious research project on the genetic relationships of wild pigs in the U. S., never attempted at the regional or national scale.

My research at UND has launched me into a new career path and has greatly impacted the scope and context of my future work in wildlife management and science. My doctoral program at UND has provided the opportunity for collaborations with private organizations, state agencies, and federal agencies throughout the U.S. My collaborations with other wildlife professionals have been particularly rewarding on a personal level, and have spawned partnerships leading to ongoing research in the area of wild pig genetics and genomics. I see the research described in this dissertation as a starting point for the rest of my career, and I consider the skills that I have developed during my program of study to be vital components of my tool kit going forward as a biologist.

APPENDICES

Appendix A

Novel and Published Sequence Information

Supplemental table 1. Description of 151 *Sus scrofa* haplotypes (n=1136 sequences) and other *Sus* spp. (n=13 sequences) with phylogeographic references from Bayesian analyses of a ~400 base pair region of the mtDNA control region (D-loop) under the GTR+I+G model and 10,000,000 Markov Chain Monte Carlo generations. Phylogeographic descriptors WEST and EAST are denoted along with unresolved assemblages M1 and M2, and wild (W1-W6), domestic (D1, D2), and feral (F1) monophyletic clades and those haplotypes from outgroup clades. Geographic origin and "type" of pig are denoted as described by supplemental information Table S2 of Scandura et al. (2008; haplotype designations from this study are noted) and as inferred from records under accessions at NCBI GenBank.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AB015085	1	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h003
AJ314543	1	EAST	M2	M2	Wild	Japan	Randi et al. 2002	h003
AY232883	2	EAST	M2	M2	Domestic Large White	Europe	Alves et al. 2002	h004
AY232887	2	EAST	M2	M2	Domestic Pietrain	Europe	Alves et al. 2002	h058
DQ152876	2	EAST	M2	M2	Domestic Xiangxi	China	Fang and Andersson 2006	h004
DQ152884	2	EAST	M2	M2	Domestic Shanggao	China	“ “	h004
DQ152894	2	EAST	M2	M2	Domestic Xiangxi	China	“ “	h004
DQ152898	2	EAST	M2	M2	Domestic TiaMeslan	China	“ “	h004
DQ379146	2	EAST	M2	M2	Domestic Tongcheng	China	“ “	h004
DQ379147	2	EAST	M2	M2	Domestic Tongcheng	China	“ “	h004
DQ379148	2	EAST	M2	M2	Domestic Jinhua	China	“ “	h004
DQ379149	2	EAST	M2	M2	Domestic Jinhua	China	“ “	h004
DQ379150	2	EAST	M2	M2	Domestic Jiangquhai	China	“ “	h004
DQ379151	2	EAST	M2	M2	Domestic LargeWhite	Europe	“ “	h004
DQ379205	2	EAST	M2	M2	Domestic British Saddleback	United Kingdom	“ “	h004

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379206	2	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h004
DQ379207	2	EAST	M2	M2	Domestic Landrace	Europe	“ “	h004
DQ379208	2	EAST	M2	M2	Domestic Landrace	Europe	“ “	h004
DQ379209	2	EAST	M2	M2	Domestic Large White	Europe	“ “	h004
DQ379210	2	EAST	M2	M2	Domestic Leicoma	United Kingdom	“ “	h004
DQ379211	2	EAST	M2	M2	Domestic Leicoma	United Kingdom	“ “	h004
DQ379212	2	EAST	M2	M2	Domestic Large White	Europe	“ “	h004
DQ379213	2	EAST	M2	M2	Domestic Large White	Europe	“ “	h004
DQ379214	2	EAST	M2	M2	Domestic Large White	Europe	“ “	h004
DQ379225	2	EAST	M2	M2	Domestic AnglerSattelschwein	Germany	“ “	h004
DQ379226	2	EAST	M2	M2	Domestic TiaMeslan	China	“ “	h004
DQ379227	2	EAST	M2	M2	Domestic Laconie	France	“ “	h004
DQ379228	2	EAST	M2	M2	Domestic Laconie	France	“ “	h004
AF136566	2	EAST	M2	M2	Domestic Large White	Sweden	Giuffra et al. 2000	h004
AF276921	2	EAST	M2	M2	Feral Western-feral	Australia	Kim et al. 2002	h004
AF276924	2	EAST	M2	M2	Domestic Wanan	China	Kim et al. 2002	h004
AF276926	2	EAST	M2	M2	Domestic Wannanhua	China	Kim et al. 2002	h004
AF276927	2	EAST	M2	M2	Domestic Yanxin	China	Kim et al. 2002	h004
AF276930	2	EAST	M2	M2	Domestic Jinghua	China	Kim et al. 2002	h004
AF276931	2	EAST	M2	M2	Domestic Putian	China	Kim et al. 2002	h004
AF276932	2	EAST	M2	M2	Domestic Wanhua	China	Kim et al. 2002	h004
AF276936	2	EAST	M2	M2	Domestic Berkshire	United Kingdom	Kim et al. 2002	h004
AY884634	2	EAST	M2	M2	Wild	Japan	Larson et al. 2005	h004
AY884757	2	EAST	M2	M2	Domestic British Old Spot, Large White	United Kingdom	Larson et al. 2005	h004
AY884762	2	EAST	M2	M2	Domestic Large White	United Kingdom	Larson et al. 2005	h004

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884786	2	EAST	M2	M2	Domestic Large White	Germany	Larson et al. 2005	h004
AY884788	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884789	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884790	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884791	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884792	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884793	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884794	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884811	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884812	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884813	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
AY884814	2	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h004
JF702105	2	EAST	M2	M2	Wild-living	U.S., Idaho	CHAPTER II, III	-
JF702109	2	EAST	M2	M2	Wild-living	U.S., Michigan	CHAPTER II, III	-
JF702110	2	EAST	M2	M2	Wild-living	U.S., Michigan	CHAPTER II, III	-
AB015086	2	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h004
AB015092	2	EAST	M2	M2	Domestic Okinawa, Berkshire	Japan	Okumura et al. 2001	h004
AB041468	2	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h004
D42180	2	EAST	M2	M2	Wild and domestic Landrace, Large White	Europe	Okumura et al. 2001	h004
D42185	2	EAST	M2	M2	Domestic Berkshire, Hampshire	Europe	Okumura et al. 2001	h004
AB473816	2	EAST	M2	M2	Okinawa Native Pig	Japan	Tanaka et al. 2008	-
AM779928	2	EAST	M2	M2	Thai Native Pig	Thailand	unpublished	-
GQ169775	2	EAST	M2	M2	Domestic Taoyuan	Taiwan	unpublished	-
AB015087	3	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h005
D42184	3	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h005
AB015088	4	EAST	W5	W5	Wild	Japan	Okumura et al. 2001	h006

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AB015089	5	EAST	W5	W5	Wild	Japan	Okumura et al. 2001	h007
AB015090	6	EAST	W5	W5	Wild	Japan	Okumura et al. 2001	h008
AY232882	7	EAST	M2	M2	Domestic Large White	Europe	Alves et al. 2002	h009
AY232890	7	EAST	M2	M2	Domestic Spotted Black Jabugo	Spain	Alves et al. 2002	h009
DQ152868	7	EAST	M2	M2	Domestic Zang	China	Fang and Andersson 2006	h018
DQ152869	7	EAST	M2	M2	Domestic Xiangxi	China	Fang and Andersson 2006	h018
DQ152874	7	EAST	M2	M2	Domestic Zang	China	Fang and Andersson 2006	h018
DQ152882	7	EAST	M2	M2	Domestic Qianbei	China	Fang and Andersson 2006	h018
DQ152890	7	EAST	M2	M2	Domestic TiaMeslan	China	Fang and Andersson 2006	h009
DQ152895	7	EAST	M2	M2	Domestic Xiangxi	China	Fang and Andersson 2006	h018
DQ379101	7	EAST	M2	M2	Domestic Zang	China	Fang and Andersson 2006	h018
DQ379102	7	EAST	M2	M2	Domestic Zang	China	Fang and Andersson 2006	h018
DQ379103	7	EAST	M2	M2	Domestic Bamei	China	Fang and Andersson 2006	h018
DQ379104	7	EAST	M2	M2	Domestic Bamei	China	Fang and Andersson 2006	h018
DQ379181	7	EAST	M2	M2	Domestic Longlin	China	“ “	h009
DQ379182	7	EAST	M2	M2	Domestic Longlin	China	“ “	h009
DQ379183	7	EAST	M2	M2	Domestic Longlin	China	“ “	h009
DQ379184	7	EAST	M2	M2	Domestic Longlin	China	Fang and Andersson 2006	h009
DQ379185	7	EAST	M2	M2	Domestic Longlin	China	Fang and Andersson 2006	h009
DQ379186	7	EAST	M2	M2	Domestic Shanggao	China	Fang and Andersson 2006	h009
DQ379187	7	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h009
DQ379188	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379189	7	EAST	M2	M2	Domestic Manchado de Jabugo	Spain	Fang and Andersson 2006	h009
DQ379190	7	EAST	M2	M2	Domestic Manchado de Jabugo	Spain	Fang and Andersson 2006	h009
DQ379191	7	EAST	M2	M2	Domestic Berkshire	United Kingdom	Fang and Andersson 2006	h009

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379192	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379193	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379194	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379195	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379196	7	EAST	M2	M2	Domestic Creole	France	Fang and Andersson 2006	h009
DQ379197	7	EAST	M2	M2	Domestic Creole	France	Fang and Andersson 2006	h009
DQ379198	7	EAST	M2	M2	Domestic Large White	Europe	Fang and Andersson 2006	h009
DQ379199	7	EAST	M2	M2	Domestic Laconie	France	Fang and Andersson 2006	h009
DQ379240	7	EAST	M2	M2	Wild	Belgium	Fang et al. 2006	h009
DQ379265	7	EAST	M2	M2	Wild	China	Fang et al. 2006	h018
AY884646	7	EAST	M2	M2	Wild	Malaysia	Larson et al. 2005	h018
AY884677	7	EAST	M2	M2	Feral	Mariana Islands	Larson et al. 2005	h009
AY884683	7	EAST	M2	M2	Wild	China	Larson et al. 2005	h018
AY884692	7	EAST	M2	M2	Wild	Russia-Vladivostok	Larson et al. 2005	h009
AY884707	7	EAST	M2	M2	Wild	China	Larson et al. 2005	h009
AY884715	7	EAST	M2	M2	Domestic Ossabaw Hog	USA	Larson et al. 2005	h009
AY884760	7	EAST	M2	M2	Domestic Landrace	France	Larson et al. 2005	h009
AY884767	7	EAST	M2	M2	Domestic Tamworth	United Kingdom	Larson et al. 2005	h009
AY884779	7	EAST	M2	M2	Domestic Creole	France	Larson et al. 2005	h009
AY884782	7	EAST	M2	M2	Domestic Manchado de Jabugo	Spain	Larson et al. 2005	h009
AY884785	7	EAST	M2	M2	Domestic Large White	United Kingdom	Larson et al. 2005	h009
JF701990	7	EAST	M2	M2	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702054	7	EAST	M2	M2	Wild-living	U.S., South Carolina	CHAPTER II, III	-
JF702060	7	EAST	M2	M2	Wild-living	U.S., North Carolina	CHAPTER II, III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702063	7	EAST	M2	M2	Wild-living	U.S., Pensylvania	CHAPTER II, III	-
JF702073	7	EAST	M2	M2	Wild-living	U.S., Ohio	CHAPTER II, III	-
JF702106	7	EAST	M2	M2	Wild-living	U.S., Michigan	CHAPTER II, III	-
JF702107	7	EAST	M2	M2	Wild-living	U.S., Michigan	CHAPTER II, III	-
JF702108	7	EAST	M2	M2	Wild-living	U.S., Michigan	CHAPTER II, III	-
AB015091	7	EAST	M2	M2	Domestic Moncai, Berkshire, Large White	Japan	Okumura et al. 2001	h009
AB041479	7	EAST	M2	M2	Domestic Potbelly	East Asia	Okumura et al. 2001	h018
D42183	7	EAST	M2	M2	Wild and domestic	Japan, East Asia	Okumura et al. 2001	h018
AB473815	7	EAST	M2	M2	Domestic Ayoh	Japan	Tanaka et al. 2008	-
AM748933	7	EAST	M2	M2	Wild	Bergamo,Italy	unpublished	-
AM748937	7	EAST	M2	M2	Wild	Bergamo,Italy	unpublished	-
FM244687	7	EAST	M2	M2	Wild	Thailand	unpublished	-
AF486859	7	EAST	M2	M2	Domestic Xiang	China	Yang et al. 2003	h018
AF486860	7	EAST	M2	M2	Domestic Rong Chang	China	Yang et al. 2003	h018
AB015093	8	WEST	M1	M1	Domestic Yucatan Miniture	Mexico	Okumura et al. 2001	h010
AY884717	9	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h011
AY884718	9	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h011
AY884722	9	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h011
AY884723	9	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h011
AB015094	9	WEST	W2	W2	Wild	Italy	Okumura et al. 2001	h011
EU362413	9	WEST	W2	W2	Wild	Arezzo, Italy	Scandura et al. 2008	h011
EU362416	9	WEST	W2	W2	Wild	Arezzo, Italy	Scandura et al. 2008	h011
EU362455	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362456	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362457	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362458	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362459	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362460	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362462	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362465	9	WEST	W2	W2	Wild	Maremma RP, Italy	Scandura et al. 2008	h011
EU362469	9	WEST	W2	W2	Wild	San Rossore RP, Italy	Scandura et al. 2008	h011
EU362476	9	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h011
AM773234	9	WEST	W2	W2	Wild	Italy	unpublished	-
AF136563	10	WEST	W2	W2	Wild	Italy	Giuffra et al. 2000	h012
AF304201	10	WEST	W2	W2	Wild	Italy	Kijas and Andersson 2001	-
AY884719	10	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h012
AY884720	10	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h012
AY884721	10	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h012
AB015095	10	WEST	W2	W2	Wild	Italy	Okumura et al. 2001	h012
EU362443	10	WEST	W2	W2	Wild	Salerno, Italy	Scandura et al. 2008	h012
EU362453	10	WEST	W2	W2	Wild	Florence, Italy	Scandura et al. 2008	h012
EU362478	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
EU362479	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
EU362480	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
EU362481	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
EU362482	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
EU362483	10	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h012
AB041467	11	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h013
AB041472	12	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h014
DQ152870	13	EAST	M2	M2	Domestic Leping	China	Fang and Andersson 2006	h015
DQ152871	13	EAST	M2	M2	Domestic Yushan	China	Fang and Andersson 2006	h015
DQ152891	13	EAST	M2	M2	Domestic Xiang	China	Fang and Andersson 2006	h015

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ152893	13	EAST	M2	M2	Domestic Xiang	China	Fang and Andersson 2006	h015
DQ152896	13	EAST	M2	M2	Domestic Tamworth	United Kingdom	Fang and Andersson 2006	h015
DQ379105	13	EAST	M2	M2	Domestic Jiaozhou	China	Fang and Andersson 2006	h015
DQ379106	13	EAST	M2	M2	Domestic Jiaozhou	China	“ “	h015
DQ379107	13	EAST	M2	M2	Domestic Jiaozhou	China	“ “	h015
DQ379108	13	EAST	M2	M2	Domestic Jiaozhou	China	“ “	h015
DQ379109	13	EAST	M2	M2	Domestic Jiaozhou	China	“ “	h015
DQ379110	13	EAST	M2	M2	Domestic Leping	China	Fang and Andersson 2006	h015
DQ379111	13	EAST	M2	M2	Domestic Leping	China	Fang and Andersson 2006	h015
DQ379112	13	EAST	M2	M2	Domestic Qianbei	China	Fang and Andersson 2006	h015
DQ379113	13	EAST	M2	M2	Domestic Shanggao	China	Fang and Andersson 2006	h015
DQ379114	13	EAST	M2	M2	Domestic Shengxian	China	Fang and Andersson 2006	h015
DQ379115	13	EAST	M2	M2	Domestic Tongcheng	China	Fang and Andersson 2006	h015
DQ379116	13	EAST	M2	M2	Domestic Xiang	China	Fang and Andersson 2006	h015
DQ379117	13	EAST	M2	M2	Domestic Hampshire	Europe	Fang and Andersson 2006	h015
DQ379118	13	EAST	M2	M2	Domestic Large Black	United Kingdom	Fang and Andersson 2006	h015
DQ379119	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379120	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379121	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379122	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379123	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379124	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379125	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379126	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379127	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379128	13	EAST	M2	M2	Domestic LargeWhite	Europe	Fang and Andersson 2006	h015
DQ379129	13	EAST	M2	M2	Domestic NegroCanario	Spain	Fang and Andersson 2006	h015
DQ379130	13	EAST	M2	M2	Domestic Yushan	China	Fang and Andersson 2006	h015
DQ379200	13	EAST	M2	M2	Domestic Jiangquhai	China	Fang and Andersson 2006	h015
DQ379201	13	EAST	M2	M2	Domestic Xiang	China	Fang and Andersson 2006	h015
DQ379202	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379203	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379204	13	EAST	M2	M2	Domestic Large Black	United Kingdom	Fang and Andersson 2006	h015
DQ379215	13	EAST	M2	M2	Domestic British Saddleback	United Kingdom	Fang and Andersson 2006	h015
DQ379216	13	EAST	M2	M2	Domestic British Saddleback	United Kingdom	Fang and Andersson 2006	h015
DQ379217	13	EAST	M2	M2	Domestic British Saddleback	United Kingdom	Fang and Andersson 2006	h015
DQ379218	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379219	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379220	13	EAST	M2	M2	Domestic Gloucester Old Spot	United Kingdom	Fang and Andersson 2006	h015
DQ379221	13	EAST	M2	M2	Domestic Glouceste Old Spot	United Kingdom	Fang and Andersson 2006	h015
DQ379222	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379223	13	EAST	M2	M2	Domestic Landrace	Europe	Fang and Andersson 2006	h015
DQ379224	13	EAST	M2	M2	Domestic Tamworth	United Kingdom	Fang and Andersson 2006	h015
AF276923	13	EAST	M2	M2	Domestic Tong Cheng	China	Kim et al. 2002	h015
AF276925	13	EAST	M2	M2	Domestic Wannanhua	China	Kim et al. 2002	h015
AF276934	13	EAST	M2	M2	Domestic Cheju	Korea	Kim et al. 2002	h015
AY884613	13	EAST	M2	M2	Feral	Hawaii	Larson et al. 2005	h015
AY884642	13	EAST	M2	M2	Wild	China	Larson et al. 2005	h015

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884750	13	EAST	M2	M2	Domestic Landrace	United Kingdom	Larson et al. 2005	h015
AY884772	13	EAST	M2	M2	Domestic Large White	Germany	Larson et al. 2005	h015
AY884784	13	EAST	M2	M2	Domestic Large Black	United Kingdom	Larson et al. 2005	h015
AY884803	13	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h015
AY884804	13	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h015
AY884810	13	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h015
AB041474	13	EAST	M2	M2	Domestic Meishan, Berkshire	Europe-Asia	Okumura et al. 2001	h015
AB041490	13	EAST	M2	M2	Domestic Large White	Europe	Okumura et al. 2001	h015
AB059652	13	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h015
D42182	13	EAST	M2	M2	Wild and Domestic Berkshire, MiddleWhite	Japan-Europe	Okumura et al. 2001	h015
AY968797	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968798	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968799	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968800	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968801	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968802	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968803	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
AY968805	13	EAST	-	M2	Wild-living	U.S., California	CHAPTER III	-
EU362440	13	EAST	M2	M2	Wild	Salerno, Italy	Scandura et al. 2008	h015
EU362441	13	EAST	M2	M2	Wild	Salerno, Italy	Scandura et al. 2008	h015
EU362444	13	EAST	M2	M2	Wild	Salerno, Italy	Scandura et al. 2008	h015
AM777925	13	EAST	M2	M2	UNK	Thailand	unpublished	-
AM777926	13	EAST	M2	M2	UNK	Thailand	unpublished	-
EU979146	13	EAST	M2	M2	Domestic Licha Black	China	unpublished	-
EU979149	13	EAST	M2	M2	Domestic Yimeng black	China	unpublished	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU979165	13	EAST	M2	M2	Domestic Luyan White	China	unpublished	-
GQ169778	13	EAST	M2	M2	Domestic Berkshire	UNK	unpublished	-
AF486862	13	EAST	M2	M2	Domestic Tong Cheng	China	Yang et al. 2003	h015
AF486868	13	EAST	M2	M2	Domestic Yimenghei Black	China	Yang et al. 2003	h015
AF486871	13	EAST	M2	M2	Domestic Yushanheu Black	China	Yang et al. 2003	h015
AF486872	13	EAST	M2	M2	Domestic Jiangquhai	China	Yang et al. 2003	h015
AF486873	13	EAST	M2	M2	Domestic Wannanhua	China	Yang et al. 2003	h015
AF486874	13	EAST	M2	M2	Domestic Large White	Europe	Yang et al. 2003	h015
DQ152883	14	EAST	M2	M2	Domestic Yimeng	China	Fang and Andersson 2006	h016
DQ379175	14	EAST	M2	M2	Domestic Yimeng	China	Fang and Andersson 2006	h016
DQ379176	14	EAST	M2	M2	Domestic Jinhua	China	Fang and Andersson 2006	h016
DQ379177	14	EAST	M2	M2	Domestic Jinhua	China	Fang and Andersson 2006	h016
AB041475	14	EAST	M2	M2	Domestic Jinhua	East Asia	Okumura et al. 2001	h016
AB041476	14	EAST	M2	M2	Domestic Jinhua	East Asia	Okumura et al. 2001	h016
AB041477	14	EAST	M2	M2	Domestic Jinhua	East Asia	Okumura et al. 2001	h016
AF486863	14	EAST	M2	M2	Domestic Jinhua	China	Yang et al. 2003	h016
DQ152872	15	EAST	M2	M2	Domestic Neijang	China	Fang and Andersson 2006	h017
DQ152873	15	EAST	M2	M2	Domestic Yushan	China	Fang and Andersson 2006	h017
DQ379131	15	EAST	M2	M2	Domestic Neijang	China	Fang and Andersson 2006	h017
DQ379132	15	EAST	M2	M2	Domestic Neijang	China	Fang and Andersson 2006	h017
DQ379133	15	EAST	M2	M2	Domestic Jiangquhai	China	Fang and Andersson 2006	h017
DQ379134	15	EAST	M2	M2	Domestic Leping	China	Fang and Andersson 2006	h017
DQ379135	15	EAST	M2	M2	Domestic Qianbei	China	Fang and Andersson 2006	h017
DQ379136	15	EAST	M2	M2	Domestic Shengxian	China	Fang and Andersson 2006	h017
DQ379137	15	EAST	M2	M2	Domestic Shengxian	China	Fang and Andersson 2006	h017

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379138	15	EAST	M2	M2	Domestic Tongcheng	China	Fang and Andersson 2006	h017
DQ379139	15	EAST	M2	M2	Domestic Xiang	China	Fang and Andersson 2006	h017
DQ379140	15	EAST	M2	M2	Domestic Xiangxi	China	Fang and Andersson 2006	h017
DQ379141	15	EAST	M2	M2	Domestic Yushan	China	Fang and Andersson 2006	h017
DQ379142	15	EAST	M2	M2	Domestic Neijang	China	Fang and Andersson 2006	h017
DQ379143	15	EAST	M2	M2	Domestic Neijang	China	Fang and Andersson 2006	h017
AF136565	15	EAST	M2	M2	Wild	Japan	Giuffra et al. 2000	h017
AB041478	15	EAST	M2	M2	Domestic Yontsuan	East Asia	Okumura et al. 2001	h017
AB041481	15	EAST	M2	M2	Domestic Moncai	East Asia	Okumura et al. 2001	h020
AB041482	15	EAST	M2	M2	Domestic Moncai	East Asia	Okumura et al. 2001	h017
AB059650	15	EAST	M2	M2	Domestic Berkshire	Europe	Okumura et al. 2001	h017
D42173	15	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h017
D42176	15	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h017
AB505855	15	EAST	M2	M2	Wild	Japan	unpublished	-
DQ466081	15	EAST	M2	M2	Domestic Nuogo	UNK	unpublished	-
EU979181	15	EAST	M2	M2	Domestic Wulian Black	China	unpublished	-
GQ220329	15	EAST	M2	M2	Domestic Dahe	UNK	unpublished	-
EF545569	15	EAST	M2	M2	Wild	China	Wu et al. 2007	-
AF486856	15	EAST	M2	M2	Domestic Zang	China	Yang et al. 2003	h017
AF486867	15	EAST	M2	M2	Domestic Wuzhistan	China	Yang et al. 2003	h017
DQ152875	16	EAST	M2	M2	Domestic TongCheng	China	Fang and Andersson 2006	h019
DQ152885	16	EAST	M2	M2	Domestic Shanggao	China	Fang and Andersson 2006	h019
DQ379144	16	EAST	M2	M2	Domestic Middle White	United Kingdom	Fang and Andersson 2006	h019
DQ379145	16	EAST	M2	M2	Domestic Middle White	United Kingdom	Fang and Andersson 2006	h019
DQ379178	16	EAST	M2	M2	Domestic Shanggao	China	Fang and Andersson 2006	h019

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884643	16	EAST	M2	M2	Wild	India	Larson et al. 2005	h019
AB041480	16	EAST	M2	M2	Domestic Moncai	East Asia	Okumura et al. 2001	h019
AB041483	16	EAST	M2	M2	Domestic Moncai, Berkshire	Europe-Asia	Okumura et al. 2001	h019
GQ169777	16	EAST	M2	M2	Domestic Yorkshire	UNK	unpublished	-
EF545570	16	EAST	M2	M2	Wild	China	Wu et al. 2007	-
AF486857	16	EAST	M2	M2	Domestic Ningxiang	China	Yang et al. 2003	h019
AF486870	16	EAST	M2	M2	Domestic Dahuabai	China	Yang et al. 2003	h019
AY232864	17	WEST	M1	M1	Domestic Black Hairy	Iberia	Alves et al. 2002	h021
DQ152847	17	WEST	M1	M1	Domestic Bunte Bentheimer	Germany	Fang and Andersson 2006	h021
DQ152849	17	WEST	M1	M1	Domestic Hampshire	Germany	Fang and Andersson 2006	h021
DQ152856	17	WEST	M1	M1	Domestic Retinto	Spain	Fang and Andersson 2006	h021
DQ379027	17	WEST	M1	M1	Domestic Bunte Bentheimer	Germany	Fang and Andersson 2006	h021
DQ379028	17	WEST	M1	M1	Domestic Bunte Bentheimer	Germany	Fang and Andersson 2006	h021
DQ379071	17	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h021
DQ379072	17	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h021
DQ379073	17	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h021
DQ379074	17	WEST	M1	M1	Domestic Leicoma	United Kingdom	Fang and Andersson 2006	h021
DQ379075	17	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h021
DQ379076	17	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h021
DQ379077	17	WEST	M1	M1	Domestic Negro Iberico	Spain	Fang and Andersson 2006	h021
DQ379078	17	WEST	M1	M1	Domestic Negro Iberico	Spain	Fang and Andersson 2006	h021
DQ379079	17	WEST	M1	M1	Domestic Negro Iberico	Spain	Fang and Andersson 2006	h021
DQ379080	17	WEST	M1	M1	Domestic Retinto	Spain	Fang and Andersson 2006	h021
DQ379081	17	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h021

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379082	17	WEST	M1	M1	Domestic Angler Sattelschwein	Germany	Fang and Andersson 2006	h021
DQ379241	17	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h021
AY884670	17	WEST	M1	M1	Wild	Macedonia	Larson et al. 2005	h021
AY884672	17	WEST	M1	M1	Wild	Norway	Larson et al. 2005	h021
AY884749	17	WEST	M1	M1	Domestic Landrace	Iceland	Larson et al. 2005	h021
AY884778	17	WEST	M1	M1	Domestic Duroc	Germany	Larson et al. 2005	h021
JF701993	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF701995	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702000	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702001	17	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702002	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702009	17	WEST	M1	M1	Wild-living	U.S., Mississippi	CHAPTER II, III	-
JF702017	17	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702025	17	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702026	17	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702027	17	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702028	17	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702029	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702030	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702031	17	WEST	M1	M1	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF702040	17	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702046	17	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702049	17	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702066	17	WEST	M1	M1	Wild-living	U.S., Arkansas	CHAPTER II, III	-
JF702076	17	WEST	M1	M1	Wild-living	U.S., North Dakota	CHAPTER II, III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702081	17	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702112	17	WEST	M1	M1	Wild-living	U.S., Nevada	CHAPTER II, III	-
JF702113	17	WEST	M1	M1	Wild-living	U.S., Nevada	CHAPTER II, III	-
AB041484	17	WEST	M1	M1	Domestic Berkshire	Europe	Okumura et al. 2001	h021
JF702004	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702005	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702007	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702008	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702015	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702016	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702019	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702020	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702021	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702022	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702043	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702045	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702047	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702048	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702051	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702053	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702055	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702080	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702083	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702085	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702086	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702095	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702097	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702098	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702099	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702100	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702101	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702104	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968701	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968702	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968703	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968704	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968705	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968706	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968708	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968709	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968710	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968714	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968715	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968716	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968717	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968718	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968719	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968720	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968721	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968722	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY968723	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968724	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968725	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968726	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968727	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968729	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968806	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968713	17	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
EU362507	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362508	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362509	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362510	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362511	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362512	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362513	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362514	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362515	17	WEST	M1	M1	Wild	Spain	Scandura et al. 2008	h021
EU362561	17	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h021
EU362568	17	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h021
EU362569	17	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h021
AF486858	17	WEST	M1	M1	Domestic Duroc	Europe	Yang et al. 2003	h021
AB041491	18	WEST	M1	M1	Domestic Large White	Europe	Okumura et al. 2001	h026
AY232856	19	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h022
AY232867	19	WEST	M1	M1	Domestic Iberian Blond	Iberia	Alves et al. 2002	h022
AY232877	19	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY232884	19	WEST	M1	M1	Domestic Landrace	Europe	Alves et al. 2002	h022
AY232885	19	WEST	M1	M1	Domestic Landrace	Europe	Alves et al. 2002	h022
AY232886	19	WEST	M1	M1	Domestic Pietrain	Europe	Alves et al. 2002	h022
AY232891	19	WEST	M1	M1	Domestic Basque	Iberia	Alves et al. 2002	h022
AY232892	19	WEST	M1	M1	Domestic Hungarian Mangalitza	Hungary	Alves et al. 2002	h022
DQ152848	19	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h022
DQ152854	19	WEST	M1	M1	Domestic AnglerSattelschwein	Germany	Fang and Andersson 2006	h022
DQ152855	19	WEST	M1	M1	Domestic Linderodssvin	Sweden	Fang and Andersson 2006	h022
DQ152858	19	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h022
DQ152861	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h027
DQ379029	19	WEST	M1	M1	Domestic Bunte Bentheimer	Germany	Fang and Andersson 2006	h022
DQ379030	19	WEST	M1	M1	Domestic Bisaro	Portugal	Fang and Andersson 2006	h022
DQ379031	19	WEST	M1	M1	Domestic Berkshire	United Kingdom	Fang and Andersson 2006	h022
DQ379032	19	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h022
DQ379033	19	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h022
DQ379034	19	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h022
DQ379035	19	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h022
DQ379036	19	WEST	M1	M1	Domestic Duroc	Europe	Fang and Andersson 2006	h022
DQ379037	19	WEST	M1	M1	Domestic Hampshire	Europe	Fang and Andersson 2006	h022
DQ379038	19	WEST	M1	M1	Domestic Hampshire	Europe	Fang and Andersson 2006	h022
DQ379039	19	WEST	M1	M1	Domestic Hampshire	Europe	Fang and Andersson 2006	h022
DQ379040	19	WEST	M1	M1	Domestic Leicoma	United Kingdom	Fang and Andersson 2006	h022
DQ379041	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379042	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379043	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379044	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379045	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379046	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379047	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h022
DQ379048	19	WEST	M1	M1	Domestic GermanLandrace	Europe	Fang and Andersson 2006	h022
DQ379049	19	WEST	M1	M1	Domestic German Landrace	Europe	“ “	h022
DQ379050	19	WEST	M1	M1	Domestic German Landrace	Europe	“ “	h022
DQ379051	19	WEST	M1	M1	Domestic Large White	Europe	“ “	h022
DQ379052	19	WEST	M1	M1	Domestic Large White	Europe	“ “	h022
DQ379053	19	WEST	M1	M1	Domestic Pietrain	Europe	“ “	h022
DQ379068	19	WEST	M1	M1	Domestic Linderodssvin	Sweden	“ “	h022
DQ379069	19	WEST	M1	M1	Domestic Linderodssvin	Sweden	Fang and Andersson 2006	h022
DQ379070	19	WEST	M1	M1	Domestic Linderodssvin	Sweden	Fang and Andersson 2006	h022
DQ379084	19	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h027
DQ379085	19	WEST	M1	M1	Domestic British Lop	United Kingdom	Fang and Andersson 2006	h027
DQ379086	19	WEST	M1	M1	Domestic British Lop	United Kingdom	Fang and Andersson 2006	h027
DQ379087	19	WEST	M1	M1	Domestic British Lop	United Kingdom	Fang and Andersson 2006	h027
DQ379088	19	WEST	M1	M1	Domestic British Lop	United Kingdom	Fang and Andersson 2006	h027
DQ379089	19	WEST	M1	M1	Domestic Creole	France	Fang and Andersson 2006	h027
DQ379090	19	WEST	M1	M1	Domestic Creole	France	Fang and Andersson 2006	h027
DQ379253	19	WEST	M1	M1	Wild	France	Fang et al. 2006	h022
AF136558	19	WEST	M1	M1	Domestic Hampshire	Sweden	Giuffra et al. 2000	h022
AF535161	19	WEST	M1	M1	Domestic	Finland	Gongora et al. 2003	h022
AF535162	19	WEST	M1	M1	Domestic	Finland	Gongora et al. 2003	h022
AF304203	19	WEST	M1	M1	Wild	Sweden	Kijas and Andersson 2001	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AF276937	19	WEST	M1	M1	Domestic Welsh	United Kingdom	Kim et al. 2002	h027
AY884626	19	WEST	M1	M1	Wild	Germany	Larson et al. 2005	h022
AY884665	19	WEST	M1	M1	Wild	Germany	Larson et al. 2005	h022
AY884667	19	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h022
AY884668	19	WEST	M1	M1	Wild Feral	Sardinia	Larson et al. 2005	h022
AY884669	19	WEST	M1	M1	Wild	Holland	Larson et al. 2005	h022
AY884724	19	WEST	M1	M1	Wild	Italy	Larson et al. 2005	h022
AY884728	19	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h022
AY884729	19	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h022
AY884732	19	WEST	M1	M1	Wild Feral	Sardinia	Larson et al. 2005	h022
AY884746	19	WEST	M1	M1	Domestic Duroc	United Kingdom	Larson et al. 2005	h022
AY884751	19	WEST	M1	M1	Domestic Swedish LinderOdssvin	Sweden	Larson et al. 2005	h022
AY884754	19	WEST	M1	M1	Domestic German Bunte	Germany	Larson et al. 2005	h022
AY884755	19	WEST	M1	M1	Domestic Portugal Bisaro	Portugal	Larson et al. 2005	h022
AY884758	19	WEST	M1	M1	Domestic Hampshire	Germany	Larson et al. 2005	h022
AY884759	19	WEST	M1	M1	Domestic Leicoma	United Kingdom	Larson et al. 2005	h022
AY884761	19	WEST	M1	M1	Domestic Large White	United Kingdom	Larson et al. 2005	h093
AY884766	19	WEST	M1	M1	Domestic Pietrain	France	Larson et al. 2005	h022
AY884777	19	WEST	M1	M1	Domestic Hampshire	United Kingdom	Larson et al. 2005	h022
AY884783	19	WEST	M1	M1	Domestic Berkshire	United Kingdom	Larson et al. 2005	h022
AY884787	19	WEST	M1	M1	Domestic Landrace	Germany	Larson et al. 2005	h022
AF034253	19	WEST	M1	M1	Domestic Landrace	Europe	Lin et al. 1999	h022
JF701994	19	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF701999	19	WEST	M1	M1	Wild-living	U.S., North Dakota	CHAPTER II, III	-
JF702010	19	WEST	M1	M1	Wild-living	U.S., Michigan	CHAPTER II, III	-
JF702024	19	WEST	M1	M1	Wild-living	U.S., Florida	CHAPTER II, III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702036	19	WEST	M1	M1	Wild-living	U.S., Texas	CHAPTER II, III	-
JF702037	19	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702056	19	WEST	M1	M1	Wild-living	U.S., Wisconsin	CHAPTER II, III	-
JF702058	19	WEST	M1	M1	Wild-living	U.S., Alabama	CHAPTER II, III	-
JF702059	19	WEST	M1	M1	Wild-living	U.S., Arkansas	CHAPTER II, III	-
JF702061	19	WEST	M1	M1	Wild-living	U.S., Oklahoma	CHAPTER II, III	-
JF702065	19	WEST	M1	M1	Wild-living	U.S., Texas	CHAPTER II, III	-
JF702067	19	WEST	M1	M1	Wild-living	U.S., Hawaii, Kauai	CHAPTER II, III	-
JF702068	19	WEST	M1	M1	Wild-living	U.S., Texas	CHAPTER II, III	-
JF702069	19	WEST	M1	M1	Wild-living	U.S., Georgia	CHAPTER II, III	-
JF702070	19	WEST	M1	M1	Wild-living	U.S., Louisiana	CHAPTER II, III	-
JF702072	19	WEST	M1	M1	Wild-living	U.S., Ohio	CHAPTER II, III	-
JF702078	19	WEST	M1	M1	Wild-living	U.S., Alabama	CHAPTER II, III	-
JF702087	19	WEST	M1	M1	Wild-living	U.S., West Virginia	CHAPTER II, III	-
JF702090	19	WEST	M1	M1	Wild-living	U.S., Colorado	CHAPTER II, III	-
JF702091	19	WEST	M1	M1	Wild-living	U.S., West Virginia	CHAPTER II, III	-
JF702092	19	WEST	M1	M1	Wild-living	U.S., Georgia	CHAPTER II, III	-
JF702114	19	WEST	M1	M1	Wild-living	U.S., Kentucky	CHAPTER II, III	-
AB041485	19	WEST	M1	M1	Domestic Berkshire	Europe	Okumura et al. 2001	h022
AB041489	19	WEST	M1	M1	Domestic Pietrain	Europe	Okumura et al. 2001	h022
AB041492	19	WEST	M1	M1	Domestic Hampshire, Large White	Europe	Okumura et al. 2001	h027
AB041494	19	WEST	M1	M1	Domestic Large White	Europe	Okumura et al. 2001	h022
AB041496	19	WEST	M1	M1	Domestic Landrace	Europe	Okumura et al. 2001	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
D16483	19	WEST	M1	M1	Domestic Duroc, Landrace, LargeWhite	Europe-America	Okumura et al. 2001	h022
JF702013	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702014	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702018	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702038	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702039	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702041	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702042	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702044	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702050	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702052	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702079	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702082	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702084	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702096	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702103	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968707	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968731	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968732	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968733	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968734	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968735	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968736	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968737	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY968738	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968739	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968740	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968741	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968742	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968744	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968745	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968746	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968747	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968748	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968749	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968750	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968752	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968753	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968754	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968755	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968756	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968757	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968758	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968759	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968760	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968761	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968763	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968765	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968766	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968767	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY968768	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968769	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968770	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968771	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968772	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968773	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968774	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968775	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968776	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968777	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968778	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968779	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968780	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968789	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968794	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968795	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JQ792040	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968762	19	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AJ314544	19	WEST	M1	M1	Wild Feral	Sardinia	Randi et al. 2002	h022
EU362412	19	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h022
EU362414	19	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h022
EU362415	19	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h022
EU362421	19	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h022
EU362424	19	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h022
EU362448	19	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h022
EU362449	19	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362450	19	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h022
EU362452	19	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h022
EU362466	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362467	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362468	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362470	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362471	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362472	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362473	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362474	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362475	19	WEST	M1	M1	Wild	San Rossore RP, Italy	Scandura et al. 2008	h022
EU362487	19	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h022
EU362488	19	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h022
EU362489	19	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h022
EU362493	19	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h079
EU362496	19	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h022
EU362559	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362560	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362562	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362563	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362564	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362565	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362566	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362567	19	WEST	M1	M1	Domestic Cinta Senese	Italy	Scandura et al. 2008	h022
EU362577	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362579	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362580	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362581	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362582	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362583	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362584	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362585	19	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h022
EU362591	19	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h022
AM748930	19	WEST	M1	M1	Wild	Bergamo,Italy	unpublished	-
AM748932	19	WEST	M1	M1	Wild	Bergamo,Italy	unpublished	-
AM748938	19	WEST	M1	M1	Wild	Arezzo, Italy	unpublished	-
AM773230	19	WEST	M1	M1	Wild	Italy	unpublished	-
AM773231	19	WEST	M1	M1	Wild	Italy	unpublished	-
AY230819	19	WEST	M1	M1	Domestic Schwabisch-Hallisches	Germany	unpublished	-
EF122155	19	WEST	M1	M1	Domestic Bisara	UNK	unpublished	-
EF122197	19	WEST	M1	M1	Domestic GochuAsturcelta	UNK	unpublished	-
AF486866	19	WEST	M1	M1	Domestic Landrace	Unknown	Yang et al. 2003	h027
AY232875	20	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h028
AY232876	20	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h028
DQ152864	20	WEST	M1	M1	Domestic Tamworth	United Kingdom	Fang and Andersson 2006	h028
DQ379093	20	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h028
DQ379094	20	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h028
DQ379095	20	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h028
DQ379096	20	WEST	M1	M1	Domestic Tamworth	United Kingdom	Fang and Andersson 2006	h028
DQ379097	20	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h028
AY884763	20	WEST	M1	M1	Domestic Large White	France	Larson et al. 2005	h028

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III^a	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF701996	20	WEST	M1	M1	Wild-living	U.S., North Dakota	CHAPTER II, III	-
JF701998	20	WEST	M1	M1	Wild-living	U.S., North Dakota	CHAPTER II, III	-
JF702012	20	WEST	M1	M1	Wild-living	U.S., South Carolina	CHAPTER II, III	-
AB041493	20	WEST	M1	M1	Domestic Large White	Europe	Okumura et al. 2001	h028
AY232849	21	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h030
DQ152860	21	WEST	M1	M1	Domestic Bisaro	Portugal	Fang and Andersson 2006	h030
DQ152867	21	WEST	M1	M1	Domestic Retinto	Spain	Fang and Andersson 2006	h030
AB041497	21	WEST	M1	M1	Domestic Landrace	Europe	Okumura et al. 2001	h030
AY232880	22	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h031
DQ379234	22	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h031
AB041498	22	WEST	M1	M1	Domestic Landrace	Europe	Okumura et al. 2001	h031
AB505854	22	WEST	M1	M1	Wild	Ryuku	unpublished	-
DQ152845	23	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h032
DQ379025	23	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h032
DQ379026	23	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h032
AF136561	23	WEST	M1	M1	Domestic Landrace	Sweden	Giuffra et al. 2000	h032
AB041499	23	WEST	M1	M1	Domestic Landrace	Europe	Okumura et al. 2001	h032
DQ152887	24	EAST	M2	M2	Domestic Huzhu	China	Fang and Andersson 2006	h033
DQ379179	24	EAST	M2	M2	Domestic Huzhu	China	Fang and Andersson 2006	h033
DQ379180	24	EAST	M2	M2	Domestic Huzhu	China	Fang and Andersson 2006	h033
AB059651	24	EAST	M2	M2	Wild	Italy	Okumura et al. 2001	h033
AB089478	25	EAST	M2	M2	Ancient	Japan	unpublished	-
AB252819	26	EAST	M3	M3	Native Pig	Laos	Tanaka et al. 2008	-
AB252822	27	EAST	M2	M2	Wild	Myanmar	Tanaka et al. 2008	-
AB252823	28	EAST	W4	W4	Wild	Cambodia	Tanaka et al. 2008	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AB306903	29	EAST	M2	M2	Wild	Vietnam	Ishiguro et al. 2008	-
AB306904	30	EAST	W4	W4	Wild	Vietnam	Ishiguro et al. 2008	-
AB306915	31	EAST	M3	M3	Domestic	Vietnam	Ishiguro et al. 2008	-
GQ220328	31	EAST	M3	M3	Domestic Banna Mini	UNK	unpublished	-
AF486869	31	EAST	M3	M3	Domestic Diannan Short Ear	China	Yang et al. 2003	h048
AB306916	32	EAST	M3	M3	Domestic	Vietnam	Ishiguro et al. 2008	-
AB505852	33	EAST	W5	W5	Wild	Ryuku	unpublished	-
AB505853	34	WEST	M1	M1	Wild	Ryuku	unpublished	-
AF136564	35	EAST	M2	M2	Wild	Japan	Giuffra et al. 2000	h002
AY884711	35	EAST	M2	M2	Wild	Russia-Siberia	Larson et al. 2005	h002
AB015084	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
AB041469	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
AB041470	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
AB041471	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
AB041473	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
D42172	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
D42175	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
D42177	35	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h002
AB505856	35	EAST	M2	M2	Wild	Japan	unpublished	-
AB505857	35	EAST	M2	M2	Wild	Japan	unpublished	-
AF136555	36	WEST	W1	W1	Wild	Poland	Giuffra et al. 2000	h034
AF535163	36	WEST	W1	W1	Wild	Finland	Gongora et al. 2003	h034
AY232844	37	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h029
AY232845	37	WEST	M1	M1	Domestic Portugese Red	Portugal	Alves et al. 2002	h029
AY232850	37	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h029
AY232853	37	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h029

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY232855	37	WEST	M1	M1	Domestic Black Hairless	Iberia	Alves et al. 2002	h029
AY232857	37	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h029
AY232859	37	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h029
AY232866	37	WEST	M1	M1	Domestic Black Hairy	Iberia	Alves et al. 2002	h029
DQ152844	37	WEST	M1	M1	Domestic Retinto	Spain	Fang and Andersson 2006	h029
DQ379019	37	WEST	M1	M1	Domestic Middle White	United Kingdom	Fang and Andersson 2006	h029
DQ379020	37	WEST	M1	M1	Domestic Middle White	United Kingdom	Fang and Andersson 2006	h029
DQ379021	37	WEST	M1	M1	Domestic Large Black	United Kingdom	Fang and Andersson 2006	h029
DQ379022	37	WEST	M1	M1	Domestic Large Black	United Kingdom	Fang and Andersson 2006	h029
DQ379023	37	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h029
DQ379024	37	WEST	M1	M1	Domestic Bisaro	Portugal	Fang and Andersson 2006	h029
AF136556	37	WEST	M1	M1	Wild	Poland	Giuffra et al. 2000	h029
AY884635	37	WEST	M1	M1	Wild	Morocco	Larson et al. 2005	h029
AY884666	37	WEST	M1	M1	Wild	Germany	Larson et al. 2005	h029
AY884697	37	WEST	M1	M1	Wild	Spain	Larson et al. 2005	h029
AY884756	37	WEST	M1	M1	Domestic British Lop	United Kingdom	Larson et al. 2005	h029
AY884765	37	WEST	M1	M1	Domestic Iberian Black	Spain	Larson et al. 2005	h029
AY884770	37	WEST	M1	M1	Domestic Middle White	United Kingdom	Larson et al. 2005	h029
JF701997	37	WEST	M1	M1	Wild-living	U.S., North Dakota	CHAPTER II, III	-
JF702006	37	WEST	M1	M1	Wild-living	U.S., California	CHAPTER II, III	-
JF702011	37	WEST	M1	M1	Wild-living	U.S., New Mexico	CHAPTER II, III	-
JF702033	37	WEST	M1	M1	Wild-living	U.S., Nebraska	CHAPTER II, III	-
JF702034	37	WEST	M1	M1	Wild-living	U.S., Oklahoma	CHAPTER II, III	-
JF702035	37	WEST	M1	M1	Wild-living	U.S., Texas	CHAPTER II, III	-
JF702057	37	WEST	M1	M1	Wild-living	U.S., Kansas	CHAPTER II, III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III^{a}	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702062	37	WEST	M1	M1	Wild-living	U.S., Arizona	CHAPTER II, III	-
JF702075	37	WEST	M1	M1	Wild-living	U.S., Louisiana	CHAPTER II, III	-
JF702088	37	WEST	M1	M1	Wild-living	U.S., Virginia	CHAPTER II, III	-
JF702089	37	WEST	M1	M1	Wild-living	U.S., New Jersey	CHAPTER II, III	-
JF702093	37	WEST	M1	M1	Wild-living	U.S., Pensylvania	CHAPTER II, III	-
AB041495	37	WEST	M1	M1	Domestic Landrace	Europe	Okumura et al. 2001	h029
AJ314542	37	WEST	M1	M1	Wild	Bulgaria	Randi et al. 2002	h029
EU362490	37	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h029
EU362491	37	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h029
EU362492	37	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h029
EU362527	37	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h029
EU362536	37	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h029
EU362538	37	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h029
EU362542	37	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h029
EU362543	37	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h029
EU362544	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362545	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362546	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362547	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362548	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362549	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362550	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362551	37	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h029
EU362575	37	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h029
EU362576	37	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h029
EU362578	37	WEST	M1	M1	Domestic Casertana	Italy	Scandura et al. 2008	h029

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AJ854426	37	WEST	M1	M1	UNK	Indonesia	unpublished	-
AY785146	37	WEST	M1	M1	Wild	Germany	unpublished	-
AY879794	37	WEST	M1	M1	Native Pig	Korea	unpublished	-
AY232858	38	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h023
AY232878	38	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h023
DQ152852	38	WEST	M1	M1	Domestic Gloucester Old Spot	United Kingdom	Fang and Andersson 2006	h023
DQ152853	38	WEST	M1	M1	Domestic Mangalica	Germany	Fang and Andersson 2006	h023
DQ379057	38	WEST	M1	M1	Domestic Gloucester Old Spot	United Kingdom	Fang and Andersson 2006	h023
DQ379058	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379059	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379060	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379061	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379062	38	WEST	M1	M1	Domestic Mangalica	Germany	Fang and Andersson 2006	h023
DQ379063	38	WEST	M1	M1	Domestic Mangalica	Germany	Fang and Andersson 2006	h023
DQ379064	38	WEST	M1	M1	Domestic Mangalica	Germany	Fang and Andersson 2006	h023
DQ379065	38	WEST	M1	M1	Domestic Bisaro	Portugal	Fang and Andersson 2006	h023
DQ379066	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379067	38	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h023
DQ379232	38	WEST	M1	M1	Wild	France	Fang et al. 2006	h023
DQ379233	38	WEST	M1	M1	Wild	France	Fang et al. 2006	h023
AF136557	38	WEST	M1	M1	Domestic Mangalica	Europe	Giuffra et al. 2000	h023
AY884664	38	WEST	M1	M1	Wild	Germany	Larson et al. 2005	h023
AY884731	38	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h023
AY884733	38	WEST	M1	M1	Wild Feral	Sardinia	Larson et al. 2005	h023
AY884747	38	WEST	M1	M1	Domestic Landrace	Denmark	Larson et al. 2005	h023

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884764	38	WEST	M1	M1	Domestic Hungarian Mangalica	Hungary	Larson et al. 2005	h023
AY884773	38	WEST	M1	M1	Domestic Landrace	United Kingdom	Larson et al. 2005	h023
AY884774	38	WEST	M1	M1	Domestic Landrace	United Kingdom	Larson et al. 2005	h023
AY884776	38	WEST	M1	M1	Domestic Landrace	Denmark	Larson et al. 2005	h023
AY884795	38	WEST	M1	M1	Wild Feral	Sardinia	Larson et al. 2005	h023
AY884796	38	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h023
JF702115	38	WEST	M1	M1	Wild-living	U.S., Kentucky	CHAPTER II, III	-
AB041486	38	WEST	M1	M1	Domestic Duroc	Europe	Okumura et al. 2001	h023
D42170	38	WEST	M1	M1	Domestic Landrace, Duroc	Europe-America	Okumura et al. 2001	h023
AY968712	38	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968728	38	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
EU362410	38	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h023
EU362418	38	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h023
EU362419	38	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h023
EU362420	38	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h023
EU362426	38	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h023
EU362427	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362428	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362429	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362430	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362431	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362432	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362433	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362434	38	WEST	M1	M1	Wild	Siena, Italy	Scandura et al. 2008	h023
EU362436	38	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h023
EU362439	38	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h023

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362445	38	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h023
EU362446	38	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h023
EU362447	38	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h023
EU362516	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362517	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362518	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362519	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362520	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362521	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362522	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362523	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362524	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362525	38	WEST	M1	M1	Wild	France	Scandura et al. 2008	h023
EU362534	38	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h023
EF122168	38	WEST	M1	M1	Domestic Hampshire	UNK	unpublished	-
DQ152843	39	WEST	M1	M1	Domestic Hampshire	Germany	Fang and Andersson 2006	h025
DQ379016	39	WEST	M1	M1	Domestic Hampshire	Europe	Fang and Andersson 2006	h025
DQ379017	39	WEST	M1	M1	Domestic AnglerSattelschwein	Germany	Fang and Andersson 2006	h025
DQ379018	39	WEST	M1	M1	Domestic Hampshire	Europe	Fang and Andersson 2006	h025
AF136559	39	WEST	M1	M1	Domestic Hampshire	Sweden	Giuffra et al. 2000	h025
AY884781	39	WEST	M1	M1	Domestic German Angler	Germany	Larson et al. 2005	h025
JF702032	39	WEST	M1	M1	Wild-living	U.S., Ohio	CHAPTER II, III	-
JF702071	39	WEST	M1	M1	Wild-living	U.S., Florida	CHAPTER II, III	-
JF702077	39	WEST	M1	M1	Wild-living	U.S., Michigan	CHAPTER II, III	-
AB041488	39	WEST	M1	M1	Domestic Hampshire	Europe	Okumura et al. 2001	h025

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AF136560	40	WEST	M1	M1	Domestic Landrace	Sweden	Giuffra et al. 2000	h035
AY884775	40	WEST	M1	M1	Domestic Landrace	Finland	Larson et al. 2005	h035
EU362528	40	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h035
EU362532	40	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h035
EU362533	40	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h035
EU362552	40	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h035
EU362553	40	WEST	M1	M1	Wild	Hungary	Scandura et al. 2008	h035
AM748935	40	WEST	M1	M1	Wild	Bergamo,Italy	unpublished	-
GU226424	40	WEST	M1	M1	Wild	Romania	unpublished	-
AF136562	41	WEST	M1	M1	Domestic Large White	Sweden	Giuffra et al. 2000	h036
AY232888	42	EAST	D1	D1	Domestic Meishan	Asia	Alves et al. 2002	h037
AY232889	42	EAST	D1	D1	Domestic Meishan	Asia	Alves et al. 2002	h037
DQ152878	42	EAST	D1	D1	Domestic Yushan	China	Fang and Andersson 2006	h037
DQ379153	42	EAST	D1	D1	Domestic Yimeng	China	Fang and Andersson 2006	h037
DQ379154	42	EAST	D1	D1	Domestic Yimeng	China	Fang and Andersson 2006	h037
DQ379155	42	EAST	D1	D1	Domestic Jinhua	China	Fang and Andersson 2006	h037
DQ379156	42	EAST	D1	D1	Domestic Jiangquhai	China	Fang and Andersson 2006	h037
DQ379157	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
DQ379158	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
DQ379159	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
DQ379160	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
DQ379161	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
DQ379162	42	EAST	D1	D1	Domestic Meishan	Asia	Fang and Andersson 2006	h037
AF136567	42	EAST	D1	D1	Domestic Meishan	China	Giuffra et al. 2000	h037
DQ152897	43	EAST	M2	M2	Domestic Berkshire	United Kingdom	Fang and Andersson 2006	h024

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AF136568	43	EAST	M2	M2	Domestic Duroc	Sweden	Giuffra et al. 2000	h024
AB041487	43	EAST	M2	M2	Domestic Berkshire, Duroc	Unknown	Okumura et al. 2001	h024
AY232852	44	WEST	M1	M1	Domestic Black Hairless	Iberia	Alves et al. 2002	h038
AY232862	44	WEST	M1	M1	Domestic Black Hairy	Iberia	Alves et al. 2002	h038
DQ152859	44	WEST	M1	M1	Domestic Manchado de Jabugo	Spain	Fang and Andersson 2006	h038
DQ379083	44	WEST	M1	M1	Domestic Manchado de Jabugo	Spain	Fang and Andersson 2006	h038
AF182446	44	WEST	M1	M1	Domestic	Cook Islands	Giuffra et al. 2000	h038
AF276922	45	EAST	M2	M2	Domestic Erhualian	China	Kim et al. 2002	h039
AF276928	46	EAST	M2	M2	Domestic Gondonghei	China	Kim et al. 2002	h040
AF276929	47	EAST	M2	M2	Domestic Neijang	China	Kim et al. 2002	h041
AF276933	48	EAST	M2	M2	Domestic Cheju	Korea	Kim et al. 2002	h042
AF276935	49	EAST	M2	M2	Domestic Cheju	Korea	Kim et al. 2002	h043
AF304200	50	EAST	M2	M2	Domestic Meishan	China	Kijas and Andersson 2001	-
AF304202	51	EAST	M2	M2	Domestic Landrace	Unknown	Kijas and Andersson 2001	-
AF486855	52	EAST	M2	M2	Domestic Zhong Meishan	China	Yang et al. 2003	h044
AF486861	53	EAST	D1	D1	Domestic Erhualian	China	Yang et al. 2003	h045
DQ152880	54	EAST	M2	M2	Domestic Yimeng	China	Fang and Andersson 2006	h046
DQ379165	54	EAST	M2	M2	Domestic Laiwu	China	Fang and Andersson 2006	h046
DQ379166	54	EAST	M2	M2	Domestic Laiwu	China	Fang and Andersson 2006	h046
DQ379167	54	EAST	M2	M2	Domestic Laiwu	China	Fang and Andersson 2006	h046
DQ379168	54	EAST	M2	M2	Domestic Laiwu	China	Fang and Andersson 2006	h046
DQ379169	54	EAST	M2	M2	Domestic Min	China	Fang and Andersson 2006	h046
DQ379170	54	EAST	M2	M2	Domestic Min	China	Fang and Andersson 2006	h046
DQ379171	54	EAST	M2	M2	Domestic Min	China	Fang and Andersson 2006	h046
DQ379172	54	EAST	M2	M2	Domestic Min	China	Fang and Andersson 2006	h046

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ379173	54	EAST	M2	M2	Domestic Min	China	Fang and Andersson 2006	h046
EU979127	54	EAST	M2	M2	Domestic Laiwu Black	China	unpublished	-
AF486864	54	EAST	M2	M2	Domestic Min	China	Yang et al. 2003	h046
AF486865	55	EAST	D2	D2	Domestic Qing Ping	China	Yang et al. 2003	h047
AF535164	56	WEST	W1	W1	Wild	Finland	Gongora et al. 2003	h049
AY232881	57	WEST	M1	M1	Domestic Duroc	Europe	Alves et al. 2002	h001
AJ002189	57	WEST	M1	M1	Domestic	Sweden	Ursing and Arnason 1998	h001
AM744976	58	WEST	M1	M1	Wild	Tuscany,Italy	unpublished	-
AM748931	59	WEST	M1	M1	Wild	Bergamo,Italy	unpublished	-
AM748936	59	WEST	M1	M1	Wild	Arezzo, Italy	unpublished	-
AM773232	59	WEST	M1	M1	Wild	Italy	unpublished	-
AM773233	59	WEST	M1	M1	Wild	Italy	unpublished	-
EU362409	60	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h075
EU362411	60	WEST	M1	M1	Wild	Arezzo, Italy	Scandura et al. 2008	h075
EU362417	60	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h075
EU362422	60	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h075
EU362423	60	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h075
EU362425	60	WEST	M1	M1	Wild	Forli', Italy	Scandura et al. 2008	h075
EU362438	60	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h075
EU362442	60	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h075
EU362451	60	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h075
EU362454	60	WEST	M1	M1	Wild	Florence, Italy	Scandura et al. 2008	h075
EU362461	60	WEST	M1	M1	Wild	Maremma RP, Italy	Scandura et al. 2008	h075
EU362463	60	WEST	M1	M1	Wild	Maremma RP, Italy	Scandura et al. 2008	h075
EU362464	60	WEST	M1	M1	Wild	Maremma RP, Italy	Scandura et al. 2008	h075

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AM748934	60	WEST	M1	M1	Wild	Arezzo, Italy	unpublished	-
AM779936	61	EAST	M3	M3	Wild	Thailand	unpublished	-
AM779937	61	EAST	M3	M3	Wild	Thailand	unpublished	-
AY230823	62	WEST	M1	M1	Domestic German Landrace	Germany	unpublished	-
AY232842	63	WEST	M1	M1	Domestic Blond Alentajano	Spain	Alves et al. 2002	h050
AY232843	63	WEST	M1	M1	Domestic Blond Alentajano	Spain	Alves et al. 2002	h050
AY232861	63	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h050
EU117375	63	WEST	M1	M1	Domestic Iberian	UNK	unpublished	-
AY232846	64	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h051
AY232847	64	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h051
AY232848	64	WEST	M1	M1	Domestic Black Hairless	Spain	Alves et al. 2002	h051
AY232851	64	WEST	M1	M1	Domestic Black Hairless	Iberia	Alves et al. 2002	h051
AY232854	64	WEST	M1	M1	Domestic Black Hairless	Iberia	Alves et al. 2002	h051
AY232860	64	WEST	M1	M1	Domestic Iberian Red	Iberia	Alves et al. 2002	h051
AY232863	65	WEST	M1	M1	Domestic Black Hairy	Iberia	Alves et al. 2002	h052
AY232865	66	WEST	M1	M1	Domestic Black Hairy	Iberia	Alves et al. 2002	h053
AY463089	66	WEST	M1	M1	Feral	Australia	unpublished	-
AY232868	67	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h054
AY232869	67	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h054
AY232870	67	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h054
DQ379235	67	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h054
DQ379236	67	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h054
DQ379237	67	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h054
AY232871	68	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h055
AY232872	68	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h055

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
GQ141902	68	WEST	M1	M1	Domestic HybridLiaoningWild	UNK	unpublished	-
AY232873	69	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h021
AY232874	70	WEST	M1	M1	Wild	Spain	Alves et al. 2002	h056
AY232879	71	EAST	M2	M2	Domestic Duroc	Europe	Alves et al. 2002	h057
AY334492	72	EAST	M2	M2	Jeju Native Black	UNK	unpublished	-
AY463088	73	EAST	M2	M2	Feral	Australia	unpublished	-
DQ379264	74	EAST	W3	W3	Wild	China	Fang et al. 2006	h067
AY884691	74	EAST	W3	W3	Wild	Russia-Vladivostok	Larson et al. 2005	h067
AY751460	74	EAST	W3	W3	Wild	China	unpublished	-
AY785145	75	WEST	M1	M1	Wild	Germany	unpublished	-
EF533685	76	EAST	W4	W4	Wild	Korea	unpublished	-
EF533686	76	EAST	W4	W4	Wild	Korea	unpublished	-
EF533690	76	EAST	W4	W4	Wild	Korea	unpublished	-
EF533692	76	EAST	W4	W4	Wild	Korea	unpublished	-
EF533693	76	EAST	W4	W4	Wild	Korea	unpublished	-
AY879783	76	EAST	W4	W4	Wild	Korea	unpublished	-
AY879784	76	EAST	W4	W4	Wild	Korea	unpublished	-
AY879793	77	WEST	M1	M1	Jeju Native Pig	Korea	unpublished	-
AY884612	78	EAST	M2	M2	Wild	India	Larson et al. 2005	h059
AY884674	78	EAST	M2	M2	Wild	India	Larson et al. 2005	h059
AY884675	78	EAST	M2	M2	Domestic Indian	India	Larson et al. 2005	h059
AY884616	79	WEST	M1	M1	Wild	Spain	Larson et al. 2005	h089
AY884622	80	WEST	M1	M1	Wild	Iran	Larson et al. 2005	h060
AY884680	80	WEST	M1	M1	Wild	Armenia	Larson et al. 2005	h060
AY884710	80	WEST	M1	M1	Wild	Armenia	Larson et al. 2005	h060

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884727	80	WEST	M1	M1	Wild	Armenia	Larson et al. 2005	h060
AY884628	81	WEST	W2	W2	Wild Feral	Sardinia	Larson et al. 2005	h061
AY884690	81	WEST	W2	W2	Wild Feral	Sardinia	Larson et al. 2005	h061
EU362486	81	WEST	W2	W2	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h061
AY884632	82	-	Outgroup Clades	W8	Wild	Malaysia	Larson et al. 2005	h062
AY884648	82	-	Outgroup Clades	W8	Wild	Indonesia	Larson et al. 2005	h062
AY884659	82	-	Outgroup Clades	W8	Wild	Indonesia	Larson et al. 2005	h062
AY884676	82	-	Outgroup Clades	W8	Wild	Malaysia	Larson et al. 2005	h062
AY884644	83	-	Outgroup Clades	W7	Wild	Indonesia	Larson et al. 2005	h063
AY884657	83	-	Outgroup Clades	W7	Wild	Indonesia	Larson et al. 2005	h063
AY884678	84	EAST	F1	F1	Feral	Hawaii	Larson et al. 2005	h064
AY884704	84	EAST	F1	F1	Feral	Vanuatu	Larson et al. 2005	h064
AY884822	84	EAST	F1	F1	Feral	Papua-New Guinea	Larson et al. 2005	h064
JF702074	84	EAST	F1	F1	Wild-living	U.S., Hawaii, Oahu	CHAPTER II, III	-
JF702003	84	EAST	-	F1	Wild-living	U.S., California	CHAPTER III	-
AY968796	84	EAST	-	F1	Wild-living	U.S., California	CHAPTER III	-
AY968804	84	EAST	-	F1	Wild-living	U.S., California	CHAPTER III	-
DQ779310	84	EAST	F1	F1	*S. verrucosus*	Indonesia	Larson et al. 2007	-
AY884633	85	WEST	M1	M1	Wild	France	Larson et al. 2005	h065
AY884682	85	WEST	M1	M1	Wild	Sardinia	Larson et al. 2005	h065
AY884639	86	EAST	M2	M2	Wild	China	Larson et al. 2005	h066
AY884684	86	EAST	M2	M2	Wild	China	Larson et al. 2005	h066
AY884696	87	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h090
AY884623	88	EAST	M2	M2	Wild	Burma	Larson et al. 2005	h068
AY884629	88	EAST	M2	M2	Wild	Burma	Larson et al. 2005	h068

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AY884630	88	EAST	M2	M2	Wild	Thailand	Larson et al. 2005	h068
AY884712	88	EAST	M2	M2	Wild	Burma	Larson et al. 2005	h068
AY884714	89	WEST	M1	M1	Wild	Spain	Larson et al. 2005	h091
AY884716	90	WEST	W2	W2	Wild	Italy	Larson et al. 2005	h069
DQ152865	91	WEST	M1	M1	Domestic TiaMeslan	China	Fang and Andersson 2006	h094
DQ379098	91	WEST	M1	M1	Domestic Laconie	France	Fang and Andersson 2006	h094
DQ379099	91	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h094
DQ379100	91	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h094
AY884769	91	WEST	M1	M1	Domestic Pietrain	Germany	Larson et al. 2005	h094
AY884800	92	EAST	M2	M2	Feral	Australia	Larson et al. 2005	h070
DQ379254	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379255	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379256	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379257	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379258	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379259	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379260	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
DQ379261	93	WEST	M1	M1	Wild	France	Fang et al. 2006	h092
AY884815	93	WEST	M1	M1	Wild	France	Larson et al. 2005	h092
D42171	94	EAST	M2	M2	Wild	Japan	Okumura et al. 2001	h071
D42174	95	EAST	M2	W6	Wild	Japan	Okumura et al. 2001	h072
D42178	96	EAST	M2	W6	Wild	Japan	Okumura et al. 2001	h073
DQ152886	97	EAST	M2	M2	Domestic Huzhu	China	Fang and Andersson 2006	h074
D42181	97	EAST	M2	M2	Domestic	Japan	Okumura et al. 2001	h074
DQ152842	98	WEST	M1	M1	Domestic British Saddleback	United Kingdom	Fang and Andersson 2006	h098

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ152846	99	WEST	M1	M1	Domestic LargeWhite	Europe	Fang and Andersson 2006	h099
DQ152850	100	WEST	M1	M1	Domestic Negro Canario	Spain	Fang and Andersson 2006	h100
DQ379054	100	WEST	M1	M1	Domestic Negro Canario	Spain	Fang and Andersson 2006	h100
DQ379055	100	WEST	M1	M1	Domestic Negro Canario	Spain	Fang and Andersson 2006	h100
DQ152857	101	WEST	M1	M1	Domestic Large White	Europe	Fang and Andersson 2006	h101
DQ152862	102	WEST	M1	M1	Domestic Landrace	Europe	“ “	h102
DQ379091	102	WEST	M1	M1	Domestic Landrace	Europe	“ “	h102
DQ152863	103	WEST	M1	M1	Domestic Landrace	Europe	“ “	h103
DQ379092	103	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h103
JF702064	103	WEST	M1	M1	Wild-living	U.S., Mississippi	CHAPTER II, III	-
DQ152866	104	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h104
DQ379229	104	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h104
DQ379230	104	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h104
DQ379231	104	WEST	M1	M1	Domestic Pietrain	Europe	Fang and Andersson 2006	h104
DQ379238	104	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h104
DQ379239	104	WEST	M1	M1	Wild	Belgium	Fang et al. 2006	h104
DQ152877	105	EAST	M2	M2	Domestic Shengxian	China	Fang and Andersson 2006	h105
DQ379152	105	EAST	M2	M2	Domestic Shengxian	China	Fang and Andersson 2006	h105
DQ152879	106	EAST	M2	M2	Domestic Bamei	China	Fang and Andersson 2006	h106
DQ379163	106	EAST	M2	M2	Domestic Bamei	China	Fang and Andersson 2006	h106
DQ379164	106	EAST	M2	M2	Domestic Bamei	China	Fang and Andersson 2006	h106
DQ152881	107	EAST	M2	M2	Domestic Qianbei	China	Fang and Andersson 2006	h107
DQ152892	107	EAST	M2	M2	Domestic Zang	China	Fang and Andersson 2006	h107
DQ379174	107	EAST	M2	M2	Domestic Qianbei	China	Fang and Andersson 2006	h107
DQ152888	108	EAST	D2	D2	Domestic Huzhu	China	Fang and Andersson 2006	h108

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Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
DQ152889	109	EAST	D1	D1	Domestic Jiangquhai	China	Fang and Andersson 2006	h109
DQ152899	110	EAST	M2	M2	Domestic Berkshire	United Kingdom	Fang and Andersson 2006	h110
DQ379244	111	WEST	M1	M1	Wild	France	Fang et al. 2006	h111
DQ379262	112	EAST	M2	M2	Wild	China	Fang et al. 2006	h112
DQ379263	112	EAST	M2	M2	Wild	China	Fang et al. 2006	h112
DQ379266	113	EAST	M2	M2	Wild	China	Fang et al. 2006	h113
DQ379267	114	EAST	M2	M2	Wild	China	Fang et al. 2006	h114
EF122154	115	WEST	M1	M1	Domestic Alentejano	Spain	unpublished	-
EF122191	116	WEST	M1	M1	Domestic PorcoCeltaGalego	UNK	unpublished	-
EF533687	117	EAST	M2	M2	Wild	Korea	unpublished	-
EF533689	117	EAST	M2	M2	Wild	Korea	unpublished	-
EF533688	118	EAST	M2	M2	Wild	Korea	unpublished	-
EF533691	119	EAST	W4	W4	Wild	Korea	unpublished	-
EU333163	120	WEST	M1	M1	Wild	China	unpublished	-
EU362435	121	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h076
EU362437	122	WEST	M1	M1	Wild	Salerno, Italy	Scandura et al. 2008	h077
EU362477	123	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h078
EU362484	123	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h078
EU362485	123	WEST	W2	W2	Wild	Castel Porziano PR, Italy	Scandura et al. 2008	h078
EU362494	124	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h080
EU362495	125	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h081
EU362555	125	WEST	M1	M1	Domestic Sarda	Sardinia, Italy	Scandura et al. 2008	h087
EU362556	125	WEST	M1	M1	Domestic Sarda	Sardinia, Italy	Scandura et al. 2008	h087
EU362597	125	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h087
EU362497	126	WEST	M1	M1	Wild Feral	Sardinia, Italy	Scandura et al. 2008	h082
AY884681	127	WEST	M1	M1	Wild	Corsica	Larson et al. 2005	h083

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362498	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362499	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362500	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362501	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362502	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362503	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362504	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362505	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362506	127	WEST	M1	M1	Wild	Gorizia, Italy	Scandura et al. 2008	h083
EU362570	127	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h083
EU362571	127	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h083
EU362572	127	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h083
EU362573	127	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h083
EU362574	127	WEST	M1	M1	Domestic Calabrese	Italy	Scandura et al. 2008	h083
EU362526	128	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h084
EU362529	128	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h084
EU362530	128	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h084
EU362531	128	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h084
EU362535	128	WEST	M1	M1	Wild	Austria	Scandura et al. 2008	h084
EU362554	129	WEST	M1	M1	Domestic Sarda	Sardinia, Italy	Scandura et al. 2008	h086
EU362557	130	WEST	M1	M1	Domestic Sarda	Sardinia, Italy	Scandura et al. 2008	h088
EU362558	130	WEST	M1	M1	Domestic Sarda	Sardinia, Italy	Scandura et al. 2008	h088
EU362586	131	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h095
EU362592	131	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h095
EU362594	131	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h095
EU362595	131	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h095

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
EU362596	131	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h095
EU362587	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362588	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362589	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362590	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362593	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362599	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
EU362600	132	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h096
DQ152851	133	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h097
DQ379056	133	WEST	M1	M1	Domestic Landrace	Europe	Fang and Andersson 2006	h097
EU362598	133	WEST	M1	M1	Domestic Nera Siciliana	Sicily, Italy	Scandura et al. 2008	h097
GQ141892	134	EAST	M2	M2	Domestic Mashen	UNK	unpublished	-
GQ141894	135	EAST	M2	M2	Domestic LargeYorkshire	UNK	unpublished	-
GQ141899	136	WEST	M1	M1	Domestic Jinyang white	UNK	unpublished	-
GQ141900	137	EAST	M2	M2	Wild	China	unpublished	-
GU226423	138	WEST	M1	M1	Domestic Mangalitza	Romania	unpublished	-
HM010475	139	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010476	139	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010477	139	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010479	139	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010485	139	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010478	140	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010482	140	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010484	140	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010480	141	EAST	M2	M2	Wild	Russia	Ramayo et al.	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
HM010481	141	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010488	141	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
HM010483	142	EAST	W3	W3	Wild	Russia	Ramayo et al.	-
HM010487	142	EAST	W3	W3	Wild	Russia	Ramayo et al.	-
HM010486	143	EAST	M2	M2	Wild	Russia	Ramayo et al.	-
DQ379242	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379243	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379245	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379246	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379247	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379248	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379249	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379250	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379251	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
DQ379252	144	WEST	M1	M1	Wild	France	Fang et al. 2006	h085
AY884698	144	WEST	M1	M1	Wild	Portugal	Larson et al. 2005	h085
EU362537	144	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h085
EU362539	144	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h085
EU362540	144	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h085
EU362541	144	WEST	M1	M1	Wild	Poland	Scandura et al. 2008	h085
JF701989	145	EAST	M2	M2	Wild-living	U.S., North Carolina	CHAPTER II, III	-
JF701991	146	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF701992	147	WEST	M1	M1	Wild-living	U.S., Tennessee	CHAPTER II, III	-
JF702023	148	WEST	M1	M1	Wild-living	U.S., Kansas	CHAPTER II, III	-
JF702111	148	WEST	M1	M1	Wild-living	U.S., Indiana	CHAPTER II, III	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
JF702102	149	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
JF702094	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968711	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968781	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968783	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968784	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968785	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968786	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968787	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968788	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968790	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968792	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968793	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY973042	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968791	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968782	150	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
AY968751	151	WEST	-	M1	Wild-living	U.S., California	CHAPTER III	-
DQ779401	-	Outgroups	Outgroup Clades	sb	*S. barbatus*	Phillipines	Larson et al. 2007	-
DQ779501	-	Outgroups	Outgroup Clades	sb	*S. barbatus*	Indonesia	Larson et al. 2007	-
DQ779502	-	Outgroups	Outgroup Clades	sb	*S. barbatus*	Indonesia	Larson et al. 2007	-
DQ779397	-	Outgroups	Outgroup Clades	sc	*S. celebensis*	Indonesia	Larson et al. 2007	-
DQ779398	-	Outgroups	Outgroup Clades	sc	*S. celebensis*	Indonesia	Larson et al. 2007	-
DQ779515	-	Outgroups	Outgroup Clades	sc	*S. cebifrons*	Phillipines	Larson et al. 2007	-
DQ779517	-	Outgroups	Outgroup Clades	sc	*S. cebifrons*	Phillipines	Larson et al. 2007	-
DQ779396	-	Outgroups	Outgroup Clades	sp	*S. philippensis*	Phillipines	Larson et al. 2007	-
DQ779400	-	Outgroups	Outgroup Clades	sp	*S. philippensis*	Phillipines	Larson et al. 2007	-
DQ779520	-	Outgroups	Outgroup Clades	sv	*S. verrucosus*	Indonesia	Larson et al. 2007	-

Supplemental table 1 cont.

Accession	Haplotype	Phylogeo-graphy	Phylogenetic assemblage CHAPTER II	Phylogenetic assemblage CHAPTER III[a]	Pig "type"	Geographic origin	Associated publication	Scandura et al. (2008) haplotype
AJ314538	-	Outgroups	Outgroup Clades	sv	*S. verrucosus*	Unknown	unpublished	-
AJ314539	-	Outgroups	Outgroup Clades	sv	*S. verrucosus*	Unknown	unpublished	-

[a] Phylogenetic results differred between Chapters 2 and 3, but only for h82, h83, h95 and h96.

LITERATURE CITED

Alves, E., Ovilo, C., Rodriguez, M. C. and Silio, L. 2003. Mitochondrial DNA sequence variation and phylogenetic relationships among Iberian pigs and other domestic and wild pig populations. Animal Genetics 34:319-324.

Fang, M. and Andersson, L. 2006. Mitochondrial diversity in European and Chinese pigs is consistent with population expansions that occurred prior to domestication. Proceedings of the Royal Society of Biological Sciences 273:1803-1810.

Fang, M., Berg, F., Ducos, A. and Andersson, L. 2006. Mitochondrial haplotypes of European wild boars with 2n = 36 are closely related to those of European domestic pigs with 2n = 38. Animal Genetics 37:459-464.

Giuffra, E., Kijas, J. M., Amarger, V., Carlborg, O., Jeon, J. T. and Andersson, L. 2000. The origin of the domestic pig: independent domestication and subsequent introgression. Genetics 154:1785-1791.

Gongora,J., Peltoniemi,O., Tammen,I., Raadsma,H. and Moran,C. Analyses of Possible Domestic Pig Contribution in Two Population of Finnish Farmed Wild Boar. Acta Agriculturae Scandinavica Section A-Animal Science 53:161-165.

Ishiguro, N., Sasaki, M., Iwasa, M., Shigehara, N., Hongo, H., Anezaki, T., Long, V. T., Lan, D. T. B. and Long, P. T. 2008. mtDNA variation in Vietnamese pigs, with particular emphasis on the genetic relationship between wild boars from Vietnam and the Ryukyu Islands. Mammal Study 33:51-58.

Kijas, J. M. and Andersson, L. 2001. A phylogenetic study of the origin of the domestic pig estimated from the near-complete mtDNA genome. Journal of Molecular Evolution 52:302-308.

Kim, K. I., Lee, J. H., Li, K., Zhang, Y. P., Lee, S. S., Gongora, J. and Moran, C. 2002. Phylogenetic relationships of Asian and European pig breeds determined by mitochondrial DNA D-loop sequence polymorphism. Animal Genetics 33:19-25.

Larson, G., Dobney, K., Albarella, U., Fang, M., Matisoo-Smith, E., Robins, J., Lowden, S., Finlayson, H., Brand, T., Willerslev, E., Rowley-Conwy, P., Andersson, L. and Cooper, A. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. Science 307:1618-1621.

Larson, G., Cucchi, T., Fujita, M., Matisoo-Smith, E., Robins, J., Anderson, A., Rolett, B., Spriggs, M., Dolman, G., Kim, T. H., Thuy, N. T., Randi, E., Doherty, M., Due, R. A., Bollt, R., Djubiantono, T., Griffin, B., Intoh, M., Keane, E., Kirch, P., Li, K. T., Morwood, M., Pedrina, L. M., Piper, P. J., Rabett, R. J., Shooter, P., Van den Bergh, G., West, E., Wickler, S., Yuan, J., Cooper, A. and Dobney, K. 2007. Phylogeny and ancient DNA of Sus provides insights into neolithic expansion in Island Southeast Asia and Oceania. Proceedings of the National Academy of Science 104:4834-4839.

Lin, C. S., Liu, C. Y., Wu, H. T., Sun, Y. L., Chang, L. C., Yen, N. T., Yang, P. C., Huang, M. C. and Mao, S. J. T. 1998. SSCP analysis in the D-loop region of porcine mitochondrial DNA as confirmed by sequence diversity. Journal of Animal Breed Genetics 115:73-78.

Okumura, N., Ishiguro, N., Nakano, M., Hirai, K., Matsui, A. and Sahara, M. 1996.Geographic population structure and sequence divergence in the mitochondrial DNA control region of the Japanese wild boar (*Sus scrofa leucomystax*), with reference to those of domestic pigs. Biochemical Genetics 34:179-189.

Ramayo, Y., Shemeret'eva, I. N. and Perez-Enciso, M. 2011. Mitochondrial DNA diversity in wild boar from the Primorsky Krai Region (East Russia). Animal Genetics 42:96-99.

Supplemental table 1 cont.

LITERATURE CITED cont.

Randi, E., d'Huart, J. P., Lucchini, V. & Aman, R. 2002. Evidence of two genetically deeply divergent species of warthog Phacochoerus africanus and P. aethiopicus (Artiodactyla: Suiformes) in East Africa. Mammalian Biology 67:91-96.

Scandura, M., Iacolina, L., Crestanello, B., Pecchioli, E., Di Benedetto, M. F., Russo, V., Davoli, R., Apollonio, M. and Bertorelle, G. 2008. Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: are the effects of the last glaciation still detectable? Molecular Ecology 17:1745-1762.

Tanaka, K., Iwaki, Y., Takizawa, T., Dorji, T., Tshering, G., Kurosawa, Y., Maeda, Y., Mannen, H., Nomura, K., Dang, V. B., Chhum-Phith, L., Bouahom, B., Yamamoto, Y., Daing, T. and Namikawa, T. 2008. Mitochondrial diversity of native pigs in the mainland South and South-east Asian countries and its relationships between local wild boars. Animal Science Journal 79: 417-434.

Ursing, B. M. and Arnason, U. 1998. The complete mitochondrial DNA sequence of the pig (*Sus scrofa*). Journal of Molecular Evolution 47: 302-306.

Watanobe, T., Ishiguro, N., Okumura, N., Nakano, M., Matsui, A., Hongo, H. and Ushiro, H. 2001. Ancient mitochondrial DNA reveals the origin of *Sus scrofa* from Rebun Island, Japan. Journal of Molecular Evolution 52:281-289.

Wu, G.S., Yao, Y.G., Qu, K.X., Ding, Z.L., Li, H., Palanichamy, M.G., Duan, Z.Y., Li, N., Chen,Y.S. and Zhang, Y.P. 2007. Population phylogenomic analysis of mitochondrial DNA in wild boars and domestic pigs revealed multiple domestication events in East Asia. Genome Biology 8 (11), R245 (Pubmed)

Yang, J., Wang, J., Kijas, J., Liu, B., Han, H., Yu, M., Yang, H., Zhao, S. and Li, K. 2003. Genetic diversity present within the near-complete mtDNA genome of 17 breeds of indigenous Chinese pigs. Journal of Heredity 94: 381-385

Appendix B

Single Nucleotide Polymorphism and Microsatellite Loci Information

Supplemental table 2. Chromosome location, flanking sequence/primers, and summary statistics for 96 Single Nucleotide Polymorphism (SNP) and microsatellite (MS) loci collected from 169 wild pigs sampled in 31 U.S. states and Iran during the period 1996-2010. Three tables are provided; SNP (top), MS (middle), combined chromosome associations (bottom). *denotes loci excluded for low amplification (<40%) or monomorphic allele frequency. Microsatellite loci were obtained from the International Society for animal genetics diversity panel and USDA MARC (Meat Animal Research Center); SNP are from MARC.

Ninety six Single Nucleotide Polymorphism (SNP) loci

Loci identifier	Chromosome	Major allele	Minor allele	Major allele frequency	Minor allele frequency	Percent heterozygous	No. amplifying	Percent amplifying	Flanking sequence 5' to 3' [SNP]
MARC0002500	13	A	G	74.83	25.17	22.52	151	89.35	TTATCCTCCATTAAACATGATGCTGACTCTGATTTTGAGATGTGTAGGTCTGTATAATGT[A/G]AAGGTGATCTAGACCTGTCTCATAATAGG
MARC0012087	6	G	A	59.18	40.82	31.01	158	93.49	ATTCTTATCAGCCTTTGGGCATTTGCTTTGTTTTGTGTCATTTCACAGAGTAGTGCATTT[A/G]GGATGTTAACTCATCAATACAATAGAATAAAAGAATAACCAAGTTAATCTCCTCTCTGCC
MARC0013873	5	A	G	71.30	28.70	36.42	162	95.86	TGTCCACTGCCCTGTCCCATTACTGAACAAGCACCACCAGTTCTATCTGTGTGGCACCTC[A/G]GCACAGTTCCCACATAGCGGACTATTCTCCAGGCACAAACATCCAGCTCGCAGTAGAGAG
MARC0014344	13	G	A	72.87	27.13	26.22	164	97.04	CAAAGTTTTTTAGTTTAACATAATTGAACTTGTACTAGATAGGGTTAATAGGCTAGAACA[A/G]AAGGTCAAAGCATAAGGCATTAGGCTTAATTAAGGGAGAGCAGGAGTGGCAGGAGTGTGT
MARC0015385	4	G	A	73.94	26.06	27.88	165	97.63	CCAGGTTTTCTCTCCGTGYGCTGAAGGCATTGTCYTCTCTT[A/G]CAGCCTCCATGGTCACTGCCAGAAATTCCACCATCAGGCTAATGTCTCTTTGTAAGTGAT
MARC0020951	6	C	T	79.43	20.57	21.28	141	83.43	CCACAGCCTTAAGAGCTTCCTTCTGAGCCCTTAAGTGGGC[A/G]GAGGAAACAGGTTTTGCACTTCATCAGCAAACACTTGTCACACCTGCTGCTGAAATGAAG
MARC0021307	4	C	T	71.25	28.75	42.50	80	47.34	TCCCACCAGTCATACTGATAAAATATCAGTCAATAATACTCTAGTGAGAATGGATTTCAG[A/G]GTTCAACCTGTTTGGCTGAGACTGTTAGCAGCCATTTCCCAAGACCTACTTAGATGTAGA
MARC0022388	6	C	T	70.86	29.14	28.83	163	96.45	AAAGAATTACCACAGCCGGCATACTGCTATATATTGGCAGAGATGATGTTTCGGGCTGCA[A/G]TAACCTGTGCTAATGGGCTCTTGTCCTCTGGCAGTAAGGTGGCAGGCTTTTTTTTTGTTA
MARC0025520	14	C	T	64.95	35.05	32.99	97	57.40	GGAGACCCAGAATCCAGTGTCTGCCTGCAGGGCGCAGAGCCAGCTGAATGATCAAACAGT[A/G]CGCTTAAAGGCAGGGTGCGCTGTGGGCTGGAATTCAGCTGGAGGGCAAAACAGAGGTCAG
MARC0026394*	UNK	G	NA	100.00	NA	0.00	167	98.82	TTATCTTAAATAAGTCATTTCTCATGTTTCAGATTATTTCCTCAGGCGGGATTTCTGGAG[A/G]GGAAAGAGGAAATGCTGGTCCTTTTGTCCTATTATTCCCCCCTTCTTAGGTCTTGATTTT
MARC0026950	6	T	C	62.65	37.35	40.12	162	95.86	ATGACTTTTTTATCACTGAAAACTGGAACTATCTGCACTGAAAAACAGATTTTAGGTAAC[A/G]AATTAACATTAAAAACCCCTTGGTCCTGAAATTAAATTGAAGTATCAGTGTGAACCCATA
MARC0028430	14	C	T	61.18	38.82	3.95	76	44.97	CCTTGTGAGCACCGGGCAGACAGCCT[A/G]AGAAAGGGTCATTAGCAGTCTTGACACCAGCAAAGTGGATGAGCAGAGCAGACACTGAAA
MARC0028812	UNK	G	A	95.06	4.94	7.41	162	95.86	CAAAAATAGGAACTTTTGTAATGATTTTCAGATGTATTTTTCAATTGAGTAAAGAAAAAC[A/G]TGGCATTAAATCCTTGTTCTTTGGCTTGCCTTTCCCCGTCACTCCCAGGG
MARC0028812	UNK	G	A	95.06	4.94	7.41	162	95.86	CAAAAATAGGAACTTTTGTAATGATTTTCAGATGTATTTTTCAATTGAGTAAAGAAAAAC[A/G]TGGCATTAAATCCTTGTTCTTTGGCTTGCCTTTCCCCGTCACTCCCAGGG

Supplemental table 2 cont.

Ninety six Single Nucleotide Polymorphism (SNP) loci

Loci idenfier	Chromosome	Major allele	Minor allele	Major allele frequency	Minor allele frequency	Percent heterozygous	No. amplifying	Percent amplifying	Flanking sequence 5' to 3' [SNP locus]
MARC0029459	10	G	A	55.94	44.06	41.88	160	94.67	TTCAAATGAATCTTCTCCAGTTTTGAAATGGGGCACAGAGGTCAGGGAACTCTGTTGAGA[A/G]AACGGTGTTACTAAAGAGATCTGCTGCTCTCTGCACTAAACCATCTGCTGCTCTARGATG
MARC0029665	3	C	T	53.99	46.01	39.26	163	96.45	NNNNNNNNGGNANTTNGNAACCCCAGCCTGACCTGGCTTTGGGATCCGGATAAAGTGCCT[A/G]TGGGTTGTGCATGGAAGGTGGTGTAACGGTGATATTTTGGTGAGCAGCTGTGCGAATCCC
MARC0029888	UNK	T	C	75.62	24.38	19.14	162	95.86	AGCACAGCAGTTCCAGAAGTACAAAAATAAAACATGCATCTACTCTAAAAAGCTGTTGCT[A/G]AAACAAAAGCTGCAGCACATGATTCTGGAAAGCATAAATGGTGGCTCAGGTACAGAAGCT
MARC0030180	12	A	G	78.33	21.67	30.00	150	88.76	AAGCAGACGGAGGCTGCTGCCCACCCTTGTAACTACCCAACAGGACGCGGTAGAAGAGCC[A/G]GGAGGTGGGAGCTTTTGGGGAGAAAATCCTTTCAGGTTTTGATCTTTTCCTTTTGCAGAA
MARC0030522	6	G	A	83.02	16.98	22.64	159	94.08	ATCTAATTTTGGAGGTGAAATTTAGCTCCAAACCTGGAGAAATCCCTTGATGCCAACTCT[A/G]ACTTTAAAACTGGGTGACTTCCATTCTTGCTCTTGGGGAAGGCATGAACCAGTGGGTCAG
MARC0030589	2	C	T	62.09	37.91	40.52	153	90.53	GTGAGGGGGCTCTGGGGACTGTGAGAGGGCTGGGGGACAGCGAGAG[A/G]AACCATGGGACATGAGAGGACCTATGAGGACACAAGGGGGCTGAGGGGACAGTGAGAGGA
MARC0030899	4	A	G	55.21	44.79	35.42	144	85.21	CCTGAACGTTGCCCTTACTATTTCTCACCTCATGTCACCATCACTACTGAAACCCTATGA[A/G]TTTACCTGTGGTTTGCTCTACTCTGAACCCATTTCTAAGGAGAGAAAGGTAAATAGCGCT
MARC0031510	5	C	T	80.12	19.88	28.92	166	98.22	CCAAATTAATAGGTGTCTAATACAAGAAAGAGTAAAAAATAGAAGCCCCCAAA[A/G]TAGGTCTGTTAACTCTTACTGAATCAGCCAACCCAGGACAATTGATTTATCTTTTGCNNN
MARC0031610	13	G	A	79.94	20.06	22.29	157	92.90	CAAAGATCTTGAGGTTTTTTGAGTGAAGATGGGAGTAAAAGAGACATTGTTTGTTTGTTT[A/G]TTTTTGCATCATCTCAGTTTCTTTCGAGCAAGTATTTAAATAATTCAAGGCTCAAATTTC
MARC0032048	10	A	G	90.52	9.48	13.79	116	68.64	NNANNAYGTTTTATGGGTGGTGAGAACATGAGTTAAATGTGTCAGCCTTGTCCTTGATGG[A/G]TAGATGATCATTTATTATCTCACTCTGTACTCACTCTTTAGTAGCTCATTCACTTTCCTT
MARC0032253	8	G	T	89.78	10.22	8.76	137	81.07	AAGTAGAATATTTCCTGACTACTAACGTTGGATTTGGATGCTCATAAGATGCTTAGATTG[A/C]GTCACTTTTCTTTCCAGGAGATTAGACTGGG
MARC0034983	13	G	A	67.97	32.03	28.76	153	90.53	CGAAAACTGCATCTTGACCCATAAATCATCTAATACAGAATTCACTGTTGCTAGCTTAGG[A/G]CTATCAGAAGTGAAATCAGAGAATGACATGGCTACAAAGGGACTTTTGAAGACCTGTAAC
MARC0035863	15	C	T	90.85	9.15	14.63	164	97.04	GACGCTGAAAGGTCATAGACATAGGTCTTGCGTATCAGATCCAGGTTTAATCATGTTATA[A/G]AGATTTCAATAATTTTTAACCAACACTAAAAAGTCATTAGATATCAGGTCAAAATCCCAA
MARC0035886	9	A	G	88.24	11.76	17.65	102	60.36	TGTATATTAAATGCATCTCCCATCACCTTCACCATCTCTTTCCCCAGATGCTTGCAAACC[A/G]TTTCCCTGACCACAGAGCACAGGGTGCTGGACGCTCTGGCTCCTTCTCATAATGAAATTG
MARC0036375	UNK	G	A	61.01	38.99	35.12	168	99.41	ACATTGACTCCAAACCTTTTAAAGTGGGTAAAGGGCTTTGAATTTGCTGACCGAGAAGAG[A/G]TCAGTGTCGCTGGAGTTTATTTATTTATTGGAACCAAAAATATCTTTATATAAACTATTA
MARC0036708	13	A	G	64.07	35.93	35.93	167	98.82	TATTTCGGAATATTCCTGGGCTTCCTCTTCCATTTTATATCTCTGTCCCCCACATAAGAG[A/G]GAGGTTTTATTTACTTAGCATTGTAATGTATTTATGTATCTAGTGGGATGAGTCCTATTC
MARC0036725	UNK	T	G	62.27	37.73	33.74	163	96.45	TTTCAATTGCTGTGAAAACAATCTTTGACTTTTTTGCAGTTCCACTTTAGTCCAAGTATG[A/C]GAAATTGAAAGTTCAGCTTCTGGA
MARC0037294	UNK	C	T	69.20	30.80	36.96	138	81.66	GCTCAGGAATGCTGAATTGTGTTTGGATCCAGCTTTTCACCTTAAATATGAACAAATTTA[A/G]GTCAAAATCAGGGAGGCTTGAGTCCAGGAAAATGTTATCAGTGGAGTCAGAAATGTATCT
MARC0037295	3	A	G	61.07	38.93	30.71	140	82.84	CCATCCTCTCTTCTATAAGCTTCAGGATATTTCTTAAGCATACTTTCCTTCTTTCATTAA[A/G]CAAATACATTTTCTAGGATTTGAATAATAAGTTAATGCAAAATGCATCAGGGTGATGGAT
MARC0040061	5	T	C	91.82	8.18	11.32	159	94.08	AGGATCAGGATCGGGTTGGCATTTTTGTTGCCTGATAAGATTATCTTAAAACATGCAGTC[A/G]CGTGGATCTCAAGCCACCGGGTACCTAGATCTTTTTGTTTTGTTCTGCGCTGACAGATTT
MARC0041890	8	A	G	54.41	45.59	26.47	136	80.47	CAGAGCAAAAGGAAAAATTATATTGTCACAAGATGAGTTCCCCAAAAGCAACTGAATTTG[A/G]GTTATTGAACATTTATTAGAAATCAACACTTGTGAAAGGAAAGGAGGAAAAGCAGGATTG
MARC0043859	16	T	C	83.14	16.86	23.08	169	100.00	GATTCTGTTTATGCCACAACAAACTGCATTGCCTTTCCCCACCTGTGGAATGCATTTGCC[A/G]CTTTCATTTTTGCAGATGAATACCCCTGTGGAGTGATCTGCCAATTTRAAATGGAAGGAG
MARC0044793	3	G	T	64.17	35.83	26.67	120	71.01	ATTTCAAGGAGGGCATTCTAACTCCACCATCCTCATAGGCTTCCCCCAAAAGGGAATTTT[A/C]GTGGGTACCTGCGAGCTACGCATGAAAACCAGTATTTTTTCAAGTTGTGAATCTATCAGG
MARC0045269	9	A	G	60.18	39.82	30.54	167	98.82	ATCTGATGGTTAAACTGAAGCATTATTTTAATCTGTTTAACTTATTCATACAGTGATCTC[A/G]CTATATTCCATGCACGTGCCATGGTATTCATTCATAGAAAATTGAGTGTGCCATGTAAAT
MARC0047165*	9	C	T	50.00	50.00	100.00	8	4.73	RGGAAAAGCTCTCTTAGAGAGAAAACAACAACACAGGTGCCAAAGGAGTGAGCATGCTGA[A/G]GCKGGGGACGGACAATGNMGTGAAGGTGTGGAGACAGTGTGCAGAGGGGGTGGTGGAGGG
MARC0048682	14	C	A	59.29	40.71	35.71	70	41.42	CCCCTAAACCTCGATGCTCCACGTTCAAGGTGAGGAAGGAGAGGTGAGCAGTTTGCCTGT[A/C]ACRCCCCCTGCAGMCAGAATCGCTGCTCTGTTCCCGGGCGGTAACCCTCACCCTCAATAC

Supplemental table 2 cont.

Ninety six Single Nucleotide Polymorphism (SNP) loci

Loci idenfier	Chromosome	Major allele	Minor allele	Major allele frequency	Minor allele frequency	Percent heterozygous	No. amplifying	Percent amplifying	Flanking sequence 5' to 3' [SNP locus]
MARC0048886	16	G	A	53.46	46.54	37.74	159	94.08	AAATGTTGGTGTGTCTGTAATTAGATCATTAACTTTATTGCTGTAATCATGGTATGAGGC[A/G]AAACTGTACCTAAGCAACACAATTAGTGTCCAGCTGTTTCAGGTGTCTCTTTAAGAATTT
MARC0049963	1	T	G	66.57	33.43	31.93	166	98.22	GCAGATAGTTTAGGACAAATATGTATGCCCAGCATTGACAATCAAAACTGGAAGTAAAAA[A/C]CCGAATGTCCAACAGGAGTGGAGATTGCCTCTTATTGACATAGTTGTAAGGTGG
MARC0050287	12	A	G	52.36	47.64	37.16	148	87.57	TCAACAGCTTTATCATTAACACTAGTAACTCTACTGTGAATGAGCCTTGTTCAATGCCCA[A/G]CACACAGGGAGGCTCAATATGGTAAATGATTAAATGGATAACACCGG
MARC0050788	2	G	A	69.81	30.19	33.12	154	91.12	GCCCAAGCCATTGTCCCTCTAGTTTTACACGCACTCTTTAGGGAGGCAATATTGACCAAG[A/G]AATTGGTTCATCACCTCAGTATCCCTGAGTTTAAAACTTTTGGCACACANCNATTTNNAA
MARC0052461	13	G	A	72.82	27.18	18.12	149	88.17	ATCTGGTCTGACAAGCAAAGAGATGGGGCAGTGTGATCATGCTGATAGTTCTACAGATAC[A/G]CCTCTGAGAGGCTGCTATTTCCCTTATGAATAAACTTGTCCAGATTTTTGAAACAGAATC
MARC0052559	8	T	C	69.28	30.72	27.45	153	90.53	TTACAATGACAGGTAAATATGAGACATACATTTTTTACTAGCTTTGGTAAAATTGTATTC[A/G]TTTTACATTTTGGACTGAGGTGAAGGTTGCAAATATTAACTGAATTGAGGYGAAAGCTGA
MARC0052855	9	T	C	84.69	15.31	20.63	160	94.67	TGGAAAAGAAGTTTCTCATATTGGCTGAGCAGGTCTGCGGATACAGACGCATATTTCTCT[A/G]GCGAGGAAAATCTCCATTTTTAACTTAGTGTTATTCTTAGTTTCAGTCCTGCTATCCTTT
MARC0053715	9	T	C	81.93	18.07	19.28	166	98.22	GNCTTNACCNTTNCTTNGTTNATNATGTATCACTGACTCACTCCAAATCATTTAATCTAA[A/G]CTCACTTCACAAGTGCTTTGTTATGTAAAACATTTGTGCATTTGTATATGAATTTTCACT
MARC0055700	7	T	C	86.73	13.27	16.67	162	95.86	TTTGTATGTATTTTTAAGACATCATTCTCAGCTATACTTGTATAACTGCAACTTAGAGGT[A/G]AGGGACATGAAGTGTTATATTTGTTAGATATGTTAACCGAAGCACGGAGATAGGATTTGT
MARC0057599*	6	G	A	51.72	48.28	41.38	29	17.16	CTCACTGTGTTATATCTTCCAAGTGACTAGGATCCCTGCTCACATGAGGATTTAAAAACT[A/G]CACTCCCTCGAGGCAGCCCCGTMGAAAMTCCTCTGCGTTGGCTCCCTGCCAAAGCCATGA
MARC0058294	14	A	G	92.47	7.53	10.24	166	98.22	GAAAACCAGAATAGATTCTCTCTGTCTGGGAAACCAGCTCTCACCCCCAACTTCTAGGCT[A/G]TTGGTCTGCTTGAAAGAGAATAATTTCACCACTTTAAAAAGGAACAGAATTAGAAATGCC
MARC0058847	7	G	A	54.19	45.81	34.13	167	98.82	TCTTTCAGTCTTGCAATTTCCAACCCAAAGTATCAAGAACAAGAAGACAAAAGGCATGGG[A/G]GGATGGATCAGCAGGTCTACTATCCAATTAAGTGGGGCTTTAGATAAAGTGATATGGAAA
MARC0059303	6	A	G	96.99	3.01	6.02	166	98.22	AATTAGACTGACCTACAGTTGTAAGCCCTAGAAGGAAGTAATTCTACATTAAAACTTTCT[A/G]TATCTGAGCCAAGTATCTTATAAGTAGCTGGTGAAAGATTATGCAATGATATTAGTTATC
MARC0060657	14	T	C	62.30	37.70	35.71	126	74.56	GTATTTCATTACCAAAATCAGAGCTGCAACAAAACACTCCACCCAAGTAAAACTGCTCCC[A/G]AATGAGAACTRCCTTTAAAGTCTCTATAGAGATTTCACCAGGATTACGCCACATAGTCGT
MARC0060820	1	A	G	55.03	44.97	34.59	159	94.08	AGGAGCAGAACTGGAACCAGCCCTCAACTAGCTGTTGAGTTTGCTCTTGGAGACAGTTAC[A/G]CAAATACCTAAATGTCTAATGTGAAATCTAYAAGCAAGTAAGGAGGGGATGTGAATGTGG
MARC0060957	6 | 3	T	G	71.82	28.18	32.12	165	97.63	CTGAGCCACGACRGGAACTCTTATAGTGTGTCTTTAAAAAAAGTCTTTGAAATCCAAAAA[A/C]GTTTCTAGAACCTAGCTAAGAAAGATGCCTCTTTGTAAGTACTACAGAGCCTTTGCAACT
MARC0062781	UNK	A	C	96.43	3.57	5.95	168	99.41	CCAGACCATCTTACTACCTTATGCTACA[A/C]ATTTTGGAATATTCAAGGGGTTAAAAAAGTTCCTAAGAGAACTGTGACAAGGAGGGAAAG
MARC0063986	12	T	C	99.41	0.59	1.18	169	100.00	CCGTCCTGCCCCCACCCAAAGCCTGGGCTGAACTGGACTGACCGGGCTAGAAAAGCAAGT[A/G]ATATGGAATTGCTGGGGCTCCACGGAGAGGGAGGGATCTCCCCGATGACAYGACCRTCTT
MARC0064308	UNK	A	G	75.50	24.50	28.86	149	88.17	NTTTNCNNANNNNNNNNNANTTTNGGCTCTTATGTCTGGAAATTGAAAATTATGCCACAT[A/G]AGGGCTTACTATCAAGATCCAGTTAGAAAGTGCTCATGACCTAGAAAGTGCCTTTTTCCT
MARC0064312	UNK	G	A	79.72	20.28	18.18	143	84.62	GCCACACCCCCTGTCCTCAGGCAGAGCTGGGTAGGCTGGTCATGCTAGTACCTTGTAACC[A/G]CGCTCTTGCTCTTCCTTTGGGTGTCTTCAATATAATACAGCCAAACTTCTAAAAAGGATG
MARC0066508	8	G	A	65.16	34.84	30.97	155	91.72	ACATCTACCAGTCCACCTAAGTGGTTGGTGGTGGTGTTTTGCTTAAACTATGGTCTTCTA[A/G]AATGCACTTACATCAGAATCACCCAAAAGACRTTTTTTAAAGATTTATTTGGG
MARC0067107	7	C	T	52.78	47.22	37.65	162	95.86	ACTGTTTTGTGGCTATTCGTAATAATTGCATGCAAGTTAGCATGGTAGAGTTCAAGCTGA[A/G]TTAGTAGTTGCCTGGGAGACCTAGAATAAAGGAGCAACTTAGAAGGGTTGAGGGCTGCCT
MARC0070868	13	T	C	90.32	9.68	8.06	124	73.37	TTTTCACACTAAAAATCTTTAGGCAATTTTTCAAAAATATGGCATTGTGTTAGGGACCAG[A/G]GGAGGCAACAATTTTTTTTTCCCCAGGG
MARC0070952*	9 | 1	A	NA	100.00	NA	0.00	3	1.78	GGAGCAGAGGAGCACCATTTCCTAATTCATACAAAACACTGGGTTCTGCTGGTCAGGCTG[A/G]CTGTTGTGAAGGGGAGACTTTTTAATGGAAGAACTGGCTCAGGGGACTGTTCAATTCCCT
MARC0071223*	17	G	NA	100.00	NA	0.00	89	52.66	TCCTCCAGTCCCCACCGCTTCAGATGATCATTTCTTCTTCACCAAAGAGACTGATCTCAC[A/G]TGACACAGACCCCCTGCCTCCTTCCCTCCAATTAATAAGACACTCATGATCCCTTTCTGT
MARC0071898	12	G	A	81.95	18.05	21.89	169	100.00	TCGATCTCTGAGTGCAGTGTGAGGAAGGGATCTAATTTTATGTTTTATGCACATTAGCCA[A/G]TCATTCTGCTATCACGATCATTTGGTGTCTTCTTTTCCCACTATGTGCAGTGACACCAAC

Supplemental table 2 cont.

Ninety six Single Nucleotide Polymorphism (SNP) loci

Loci idenfier	Chromosome	Major allele	Minor allele	Major allele frequency	Minor allele frequency	Percent heterozygous	No. amplifying	Percent amplifying	Flanking sequence 5' to 3' [SNP locus]
MARC0074362	9	C	T	99.10	0.90	1.80	167	98.82	CCCAGAAAGAGTGTTGGCTGTAGGT[A/G]TGGCTTAT GTGGGGACTTACATGATATAACCATAATGCAGTTCTC TCTGTGTCCGGGYTT
MARC0074610	16	A	C	68.95	31.05	26.61	124	73.37	AAATACATRTGTGTTTATACAGGTATCCATACAYGCT AAGGTTTATTAATCAATAATATT[A/C]TGAGAGTTTCC TAGATTTTAGACATGAGCTATTTTTAAAAATTCCCTTC TTTTCAGAGAT
MARC0075511	UNK	G	A	91.91	8.09	10.29	136	80.47	GCCATTCATCAGAGCAAGGCATCCCACTGTCTCCAAG GAGGGGGGAAATTCCTAAGCAAG[A/G]NGAGAAATA TTTTTTTGCCCCAAAACATGAAGAGCAAGTATAAAGA AAATCAGAGGCTGT
MARC0075587	7	C	T	52.52	47.48	26.05	119	70.41	TTTTTTTTTTTTTCCTATCTTTATCCTTTACTGTCACAC AGACTGCTTCACGTCTGACCC[A/G]TCTGGTCAGCAA GCAATTCTCTGACAGCAGCTGGGTGTCCTGCAGTTTA ACTCCGTTCTG
MARC0076403	UNK	C	T	59.49	40.51	17.72	79	46.75	GTGCACCCCTGTATCTATTTGGCAT[A/G]TGGTTTAAA CTGTTACGTGACTTCTGTATACTATCATGGGGAAATG AGTAGGCTATTTAT
MARC0077362	16 | 1	T	C	74.07	25.93	33.33	162	95.86	TCCGTATCCAGGTAAGCTTTGCTAAGCATCTAAGCAG GATAAGTAATAAGCCCTTATCAA[A/G]TGATTCCATCC ACCTGAAATCCCTTCTTGGGGTTTGTGCTTAACTCTTT CAAGTTACCAA
MARC0083543	10	G	A	59.39	40.61	27.88	165	97.63	NTNCNNNGGNTNNNGGNNNNTNNNNCNAACNCAGTT TCTGGACTGTGAAAGTTCTTGGGG[A/G]AATTTCATTT GGGGGAATGACAGGGTTTAGGACATGCTACCCCTAA ATATGG
MARC0085717	1	A	C	52.68	47.32	29.17	168	99.41	TGTCTTATACCTTTGGAGCTTTCAGTTTGAGCATGTGC AATATTTAAGGAAATTTCTCAC[A/C]GAATTTTGATAA TCAAGGGATATCTGAAGGAAAAAGCCAATGTCCTGG AATGTCAGGGCT
MARC0085722	UNK	G	A	85.63	14.37	22.75	167	98.82	GAAACCAACTACAACAACAAAGATAAGACCATGTAT TAAAAATGGCGTGGATGGAACGTG[A/G]AAGAATCTC TGTCTTGATGACACTGTTAAACATTGTACCAGCCTAG ACTACCTTCCCTGC
MARC0088091	15	T	C	67.83	32.17	38.85	157	92.90	TGAGTTAAAAGACGTTGAGCTCTAAAAACTAGGGGA ACAAAAAATTACATACACACACTT[A/G]TGAACACCC CAGAGCCATGGGCTGTCAGGTTTTGTTTGGTCTGGAC AGCATTTAAAGCAA
MARC0089437	7	C	T	80.84	19.16	22.73	154	91.12	GGCGGAGATCCCATGAATACATCTCACCTTATTTATT GAATTTGTAAGAAAGGAGGTAGT[A/G]AGGGGAAGG AAGCACTGAAGACTCGGAGCCCACATTAGACACTGG GGAGGGAAAAATTAA
MARC0089489	1	C	T	59.63	40.37	27.33	161	95.27	ACCTAGAGATTTAAAATCATGAATTGAACATGTAAAA TTCCAGTAAAATGTAAAGATGGN[A/G]TATGCATCGC TCTTAACCTTGAGCATAGTGACTTAGAGACACTGTGT ATCAGTATTGCCA
MARC0089921	12	C	T	79.73	20.27	9.46	148	87.57	AAAAGTGACTAATTTTGTTGTAGTCTGTACCCGTCAA GGGAAGAGAATTGTACGGAACCA[A/G]ATGCCTCTAA TTTAGAACCTGGACGGACTGCAGGCTGCAGGGCGG
MARC0089972	UNK	C	T	72.89	27.11	27.71	166	98.22	AAGCCCAACTGAATATTCCAGAGTATAAGGAGACGT AAAGTGAACATACTGGTTTTCCTC[A/G]ACTAAAGTG GNACCGGGCTAAATATTAAACCTATGGAAACTCATG AGAAATAGACTCGCA
MARC0091567	8	T	C	63.17	36.83	35.33	167	98.82	CAGGACACAAGCAAAGTGTCACTAAAAACAAAGAGC ACAGAGCCATTTTCCTGAAACTCG[A/G]TTTTGGTAGA AAGGGCAGCAAAGCCACTTCCYGCTGTGCACAAAAG CTTCCTCCTCTCAG
MARC0092163	1	C	A	67.28	32.72	33.33	162	95.86	GTGATCCCTCCTTATCCAAGCTCTACCCATTTCGTCTG GGAAACTGCCTCTTAGATCAAC[A/C]TGAATCAACCTT TCTCTTCCTCTTTACACTTATTATCGAAATCGCACCAT TAGCCCCATT
MARC0092210	13	A	G	56.29	43.71	27.04	159	94.08	CATCTTATACTGCCAAAGACTTCAAAAGGGAAATATT TTATTTCCTTGACTATTTTCATC[A/G]AGAACTGTATA CTCATTCTGAATTAAMGAACCAATAATGTCAGTGTTC ACTTTCATTYAG
MARC0092955	2	C	T	52.73	47.27	40.00	165	97.63	GAGACGGTGGATATGGTAACCCTATGAATTCTATAAC TAATTGTTTGTGTTTGTAGGACA[A/G]AATTAACTGAG TTGCAGGATAAAGTCAGTGATGACTGATGACAAGAG ACAGAAATTCATC
MARC0093055	13	T	C	60.86	39.14	28.29	152	89.94	ACGTACATATCATGTTAAAAATCAAGTTAATTTTATA TAGTAATTTGGTACCAAAAAATC[A/G]TCACATCATG ATACAGGAATTTGTAGAGACCTCACTAAAGGCACCTC AGGTGTTAAGCCA
MARC0094480	14	A	G	84.64	15.36	25.00	140	82.84	TCCCCTAACCCAACTTCTCACTACTGGGTCGCTGACA GAGTGGGACCACAGGTGCTAGAG[A/G]TGAGTTCTAG AGGGTTAAGGACAGAGTTTCACTCTGGAAACCAGAC AACAGGTGAGCAAG
MARC0094560	6	T	C	57.58	42.42	31.52	165	97.63	TGGTAGGTTTTTCTTTTCTCCCAACTAAGTGAGGTTAA CTACATGTGGCAGTTGTTTGCA[A/G]TTTGCTAGGTCC ATTGGCTTTGAAACGTTTGAATCCTGAAGATGTTTTA AAACATTTTGG
MARC0096049	3	A	G	63.38	36.62	26.11	157	92.90	GTAAGGTTTATTCCCAAGGCATTTTTCAGGCTCTTAG CCTGCTCTTGGCTTTGAGATGGT[A/G]GTATTGCCCTC TCTTCTGTGGAAAACCCTTCACAGCTGGAGTGTTAGT GACTGAGATGTG
MARC0102724	UNK	C	T	74.50	25.50	25.83	151	89.35	ATATTAAATACACATTTATAGGTGGATAGAATAGGAA ACTAAGGGCAGACAGTGATGTGG[A/G]CAAATAAAG AAGCAAGGGGGAAAGCAGACAAAGCCTGATTTAGGA GTCTTGTCAGTTTAA
MARC0102878	16	C	T	61.26	38.74	24.50	151	89.35	CCTCTGCTACATGATGACATAAGTAATTATCTAGGCT TTTCTGCATTAGAAGAGTGTTCT[A/G]TATTATAGAAA AAGTGTCACTGAGTGGGAAAACATGCTGAATTCTCTG TGGCTCATTTAT
MARC0104045*	1	A	G	50.00	50.00	23.40	47	27.81	TGTTACTGCTGAGCCACAATGGTAACTCCTCTTATAG CAATTTTTAAATACCATGAAAAT[A/G]TTTTTTCTTTTT TGGAAAAGTAATATTTGGGGGAGGCGAGTTTTTAAGT ATTTTTTGGAA
MARC0111751	UNK	C	T	74.83	25.17	32.65	147	86.98	GTGTCAGGTAAGTTCTGTGAAAATCCAACCACAGGG ACAGTAACCCTCGGGGCAGAGTCC[A/G]TGATGACCT TGGTAAACATTTGAAGTCGAAATCCAATTTGACCAGG GTTAGAGGCGAGTG
MARC0112888	2	C	A	94.28	5.72	4.22	166	98.22	GGAGCTGCAGAACCCAAATAAATGCCCACAAGGAGT GCCAGCACGTCACATGTGTCTTTG[A/C]TGGAGCTATG GGTGAACTGGGTAGGAAGTCAGGTAACAGCCCATCA GGCATGACGAGATG
MARC0112924	15	C	T	80.82	19.18	19.18	146	86.39	TCAGCTTCTCCCTGTCCCTCCCGCAGAACCGTGTCCA CGTTTCTTCGCAAACATTGAGAA[A/G]TAGGTGAGCTT CAGGACGCTGCCTTTCTACCAACCCTTCCAGTGTTAA TCGTGGGACCTT
MARC0113081	9	G	A	51.23	48.77	39.88	163	96.45	TTGCATCTAATTTTTGTGTGTCTCCTTTAACTGCTTAT TGTAGATACAGGTGATTTTACT[A/G]CTTTCGCTTTTA ACTTCCCTTCTAATTTGTGTGTGAATAATTTCTACCTT TAACGTATGT
MARC0114647	3	C	A	63.19	36.81	29.17	144	85.21	CCTTCATCTTTCATTCCTCCTAAAATAAAAGAATCATT GYAAC[A/C]AAAACCCACACAAAGGTCAATTTAGATT TAGATCTAAATAGGTCACTCACTCTAATTCAT
MARC0115474*	13	NA	NA	NA	NA	NA	NA	0.00	AGATGAGAGGGGAAATGTCAACTCCTCCAACAGGGG TATTTCCTTTGATATCAGGGTGGC[A/G]GTGTTCCAAT AACTCAGCACTCTGTGTGTTTCGGGGGGCAGGGAGG ACTTCAGTCAAGTC

Supplemental table 2 cont.

Fourteen microsatellite (MS) loci

Loci ID	Chromosome	No. alleles	Size	Percent heterozygous	No. amplifying	Percent amplifying	Forward primer / reverse primer
S0005	5	26	220-276	81.82	154	91.12	TCCTTCCCTCCTGGTAACTA/GCACTTCCTGATTCTGGGTA
S0026	16	9	107-123	32.54	169	100.00	AACCTTCCCTTCCCAATCAC/CACAGACTGCTTTTTACTCC
S0090	12	8	250-266	52.90	138	81.66	CCAAGACTGCCTTGTAGGTGAATA/GCTATCAAGTATTGTACCATTAGG
S0097	4	16	221-261	73.49	166	98.22	GACCTATCTAATGTCATTATAGT/TTCCTCCTAGAGTTGACAAACTT
S0155	1	10	163-183	50.90	167	98.82	TGTTCTCTGTTTCTCCTCTGTTTG / AAAGTGGAAAGAGTCAATGGCTAT
S0230	11	14	307-343	52.35	149	88.17	AACAGCCCAAGTGCCCATT/TCCCCCTCCACTTCCTTTC
SW147	7	11	212-241	56.02	166	98.22	TTGCCTTTCTCCATGTGACT/ACAACCTAACCATTTGTCACAGG
SW632	7	13	167-197	53.61	166	98.22	TGGGTTGAAAGATTTCCCAA/GGAGTCAGTACTTTGGCTTGA
SW72	3	9	118-136	50.30	167	98.82	ATCAGAACAGTGCGCCGT / TTTGAAAATGGGGTGTTTCC
SW776	2	17	107-145	68.06	144	85.21	TAATCCGTTGCACCCCAG/CCATATGCCACAGTTTCGG
SW857	14	10	160-178	61.01	159	94.08	TGAGAGGTCAGTTACAGAAGACC/GATCCTCCTCCAAATCCCAT
SW911	9	9	167-185	61.08	167	98.82	CTCAGTTCTTTGGGACTGAACC/CATCTGTGGAAAAAAAAAGCC
SW936	15	11	112-138	72.56	164	97.04	TCTGGAGCTAGCATAAGTGCC/GTGCAAGTACACATGCAGGG
SW951	10	15	141-155	25.00	168	99.41	TTTCACAACTCTGGCACCAG/GATCGTGCCCAAATGGAC

Supplemental table 2 cont.

Summary: No. loci per chromosome

Chromosome	SNP	MS	Combined
1	6	1	7
2	4	1	5
3	5	1	6
4	3	1	4
5	3	1	4
6	8	0	8
7	5	2	7
8	5	0	5
9	7	1	8
10	3	1	4
11	0	1	1
12	5	1	6
13	10	0	10
14	6	1	7
15	3	1	4
16	4	1	5
17	1	0	1
18	0	0	0
19	0	0	0
Multiple	3	0	3
UNK	15	0	15
Total	96	14	110

Appendix C

Geographic Locations and Bayesian Clustering Results for Inferred Groupings

Supplemental table 3. Geographic location and inferred molecular population relationships for 169 wild pigs collected from 31 U.S. states and Iran during the period 1996-2010. Population membership determined through Bayesian analyses with programs BAPS and STRUCTURE; consensus populations determined through agreement of Bayesian clustering programs, Principal Components Analysis, FST relationships, and geographic associations. *Indicates differences in groupings between BAPS and STRUCTURE analyses, **indicates where nested STRUCTURE analyses identified additional population substructure but overarching group membership agreed between Bayesian clustering techniques.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
18	BM0018	USA	CA	Los Angeles	-118.40000	33.40000	Geographic coordinates	1	1	
523	RL108	USA	CA	Los Angeles	-118.40000	33.40000	Directions (Loggins 2007)	1	1	
524	RL109	USA	CA	Los Angeles	-118.42000	33.35200	“ “	1	1	
533	RL123	USA	CA	Santa Barbara	-119.84458	34.05620	“ “	2	2	
534	RL124	USA	CA	Santa Barbara	-119.78700	34.00000	“ “	2	2	
536	RL126	USA	CA	Santa Barbara	-119.74000	33.99000	“ “	2	2	
90	BM0090	USA	CA	Sutter	-121.78443	39.28721	Geographic coordinates	3	3	
91	BM0091	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
92	BM0092	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
94	BM0094	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
95	BM0095	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
97	BM0097	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
110	BM0110	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
112	BM0112	USA	CA	Sutter	-121.78443	39.28721	“ “	3	3	
443	BM0443	USA	NH	Sullivan	-72.23100	43.37800	Estimated county center	4	6	*
445	BM0445	USA	NH	Sullivan	-72.23100	43.37800	“ “	4	10	*
446	BM0446	USA	NH	Sullivan	-72.23100	43.37800	“ “	4	11	*

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
93	BM0093	USA	CA	Colusa	-122.25626	39.14887	Geographic coordinates	5	8	**
98	BM0098	USA	CA	Colusa	-122.25626	39.14887	“ “	5	8	**
324	BM0324	USA	CA	Colusa	-122.25626	39.14887	“ “	5	8	**
426	BM0426	USA	CA	Colusa	-122.54156	39.38630	“ “	5	8	**
321	BM0321	USA	CA	Contra Costa	-121.88209	37.79939	“ “	5	6	**
438	BM0438	USA	NV	Humboldt	-118.14800	41.40900	“ “	5	6	**
439	BM0439	USA	NV	Humboldt	-118.14800	41.40900	“ “	5	6	**
507	RL46	USA	CA	King	-119.79300	36.08500	“ “	5	6	**
36	BM0036	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
37	BM0037	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
38	BM0038	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
39	BM0039	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
40	BM0040	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
41	BM0041	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
42	BM0042	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
43	BM0043	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
44	BM0044	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
45	BM0045	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	6	**
322	BM0322	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
328	BM0328	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	6	**
389	BM0389	USA	CA	Mariposa	-120.21407	37.34495	“ “	5	4	**
20	BM0020	USA	CA	Monterey	36.47750	121.22388	“ “	5	6	**
323	BM0323	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
325	BM0325	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
327	BM0327	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
388	BM0388	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
398	BM0398	USA	CA	Monterey	-121.72049	36.57990	Geographic coordinates	5	5	**
399	BM0399	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
400	BM0400	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
427	BM0427	USA	CA	Monterey	-121.72049	36.57990	“ “	5	5	**
545	RL154	USA	CA	Monterey	-121.79523	36.46544	Directions (Loggins 2007)	5	6	**
587	RL205	USA	CA	Nevada	-121.27000	39.16180	“ “	5	7	**
387	BM0387	USA	CA	Placer	-121.07479	38.90028	Geographic coordinates	5	7	**
19	BM0019	USA	CA	San Benito	36.50766	121.18258	“ “	5	6	**
21	BM0021	USA	CA	San Benito	36.46729	121.15561	“ “	5	8	**
22	BM0022	USA	CA	San Benito	36.50780	121.18266	“ “	5	6	**
23	BM0023	USA	CA	San Benito	36.47580	121.15960	“ “	5	6	**
401	BM0401	USA	CA	San Benito	-121.40193	36.85563	“ “	5	6	**
494	RL16	USA	CA	San Louis Obispo	-120.80320	35.67148	Directions (Loggins 2007)	5	6	**
495	RL17	USA	CA	San Louis Obispo	-120.80340	35.67498	“ “	5	6	**
107	BM0107	USA	CA	Santa Clara	-121.72918	37.20675	Geographic coordinates	5	8	**
108	BM0108	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
109	BM0109	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
111	BM0111	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
114	BM0114	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
119	BM0119	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
390	BM0390	USA	CA	Santa Clara	-121.72918	37.20675	“ “	5	8	**
486	RL6	USA	CA	Santa Clara	-121.52849	37.19402	Directions (Loggins 2007)	5	8	**
505	RL31	USA	CA	Solano	-122.33526	38.09280	“ “	5	8	**
393	BM0393	USA	CA	Tehama	-122.21667	40.08399	Geographic coordinates	5	6	**
394	BM0394	USA	CA	Tehama	-122.21667	40.08399	“ “	5	6	**
521	RL104	USA	CA	Tehama	-122.40637	40.16150	Directions (Loggins 2007)	5	6	**

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
471	I1	IRAN	-	-	-	-	-	6	9	
472	I10	IRAN	-	-	-	-	-	6	9	
473	I2	IRAN	-	-	-	-	-	6	9	
474	I3	IRAN	-	-	-	-	-	6	9	
475	I4	IRAN	-	-	-	-	-	6	9	
476	I5	IRAN	-	-	-	-	-	6	9	
477	I6	IRAN	-	-	-	-	-	6	9	
478	I7	IRAN	-	-	-	-	-	6	9	
479	I8	IRAN	-	-	-	-	-	6	9	
480	I9	IRAN	-	-	-	-	-	6	9	
444	BM0444	USA	NH	Sullivan	-72.23100	43.37800	Estimated county center	6	9	
118	BM0118	USA	SC	Aiken	-81.64100	33.55900	“ “	7	11	
566	RL179	USA	CA	Alameda	-122.09997	37.77919	Directions (Loggins 2007)	7	11	
572	RL185	USA	CA	Alameda	-122.09050	37.76586	“ “	7	10	
381	BM0381	USA	PA	Bedford	-78.48965	39.91388	Geographic coordinates	7	10	
244	BM0244	USA	OH/WV	Belmont	-80.98000	40.01000	Estimated county center	7	11	
249	BM0249	USA	OH/WV	Belmont	-80.98000	40.01000	Estimated county center	7	11	
174	BM0174	USA	NC	Bertie	-77.15701	36.08034	Geographic coordinates	7	10	
10	BM0010	USA	ND	Billings	-103.42400	46.98500	Estimated county center	7	10	
11	BM0011	USA	ND	Billings	-103.42400	46.98500	Estimated county center	7	10	
12	BM0012	USA	ND	Billings	-103.42400	46.98500	Estimated county center	7	10	
7	BM0007	USA	TN	Blount	-83.90100	35.51500	Geographic coordinates	7	6	*
224	BM0224	USA	LA	Bossier	-93.61700	32.67900	Estimated county center	7	10	
203	BM0203	USA	TX	Brazoria	-95.50200	29.10400	Estimated county center	7	10	
184	BM0184	USA	OK	Caddo	-98.54950	34.86585	Geographic coordinates	7	10	
333	BM0333	USA	WV	Clay	-81.19685	38.48873	Geographic coordinates	7	10	

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
326	BM0326	USA	CA	Contra Costa	-121.88209	37.79939	Geographic coordinates	7	11	
131	BM0131	USA	KS	Cowley	-96.83200	37.23400	Estimated county center	7	11	
125	BM0125	USA	WI	Crawford	-90.91244	43.27959	Geographic coordinates	7	10	
337	BM0337	USA	VA	Culpeper	-77.93102	38.40676	Geographic coordinates	7	10	
206	BM0206	USA	AR	Desha	-91.16533	33.62304	Geographic coordinates	7	11	
376	BM0376	USA	GA	Dougherty	-84.38464	31.47056	Geographic coordinates	7	10	
212	BM0212	USA	TX	Duval	-98.52000	27.68500	Estimated county center	7	10	
267	BM0267	USA	LA	Evangeline	-92.28779	30.78971	Geographic coordinates	7	11	
238	BM0238	USA	FL	Franklin	-84.79600	29.89200	Estimated county center	7	11	
506	RL45	USA	CA	Fresno	-120.54321	36.18669	Directions (Loggins 2007)	7	10	
348	BM0348	USA	NJ	Gloucester	-74.92777	39.58789	Geographic coordinates	7	10	
79	BM0079	USA	TX	Hamilton	-98.09600	31.71300	Estimated county center	7	10	
76	BM0076	USA	NE	Harlan	-99.24484	40.03132	Geographic coordinates	7	11	
170	BM0170	USA	AR	Hempstead	-93.70335	33.54072	Geographic coordinates	7	10	
441	BM0441	USA	KY	Henry	-85.15300	38.45300	Estimated county center	7	11	
30	BM0030	USA	MI	Hillsdale	-84.40080	41.86893	Geographic coordinates	7	10	
286	BM0286	USA	AL	Jackson	-86.14945	34.67507	Geographic coordinates	7	1	*
437	BM0437	USA	IN	Jackson	-86.29392	38.81886	Geographic coordinates	7	10	
354	BM0354	USA	WV	Kanawha	-81.20584	38.52586	Geographic coordinates	7	11	
575	RL193	USA	CA	Kern	-118.63902	35.04125	Directions (Loggins 2007)	7	10	
576	RL194	USA	CA	Kern	-118.62586	35.02280	Directions (Loggins 2007)	7	10	
577	RL195	USA	CA	Kern	-118.69861	34.96110	Directions (Loggins 2007)	7	11	
352	BM0352	USA	CO	Kiowa	-102.47266	38.54150	Geographic coordinates	7	11	
430	BM0430	USA	MI	Marquette	-87.60300	46.43200	Estimated county center	7	10	
431	BM0431	USA	MI	Marquette	-87.60300	46.43200	Estimated county center	7	10	
432	BM0432	USA	MI	Marquette	-87.60300	46.43200	Estimated county center	7	10	

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations
433	BM0433	USA	MI	Marquette	-87.60300	46.43200	Estimated county center	7	10
434	BM0434	USA	MI	Marquette	-87.60300	46.43200	Estimated county center	7	10
560	RL172	USA	CA	Mendocino	-123.36397	38.97440	Directions (Loggins 2007)	7	11
72	BM0072	USA	OH	Mercer	-84.61900	40.54100	Estimated county center	7	11
46	BM0046	USA	KS	Miami	-95.05936	38.56444	Geographic coordinates	7	10
86	BM0086	USA	TX	Midland	-101.85396	31.90051	Geographic coordinates	7	10
190	BM0190	USA	AZ	Mohave	-114.53619	34.79189	Geographic coordinates	7	11
518	RL64	USA	CA	Monterey	-120.44064	35.93666	Directions (Loggins 2007)	7	11
429	BM0429	USA	ID	Owyhee	-115.81910	42.89459	Geographic coordinates	7	10
53	BM0053	USA	FL	Palm Beach	-80.50000	26.65600	Estimated county center	7	11
31	BM0031	USA	NM	Quay	-103.57800	35.10900	Estimated county center	7	10
32	BM0032	USA	SC	Richland	-80.62624	33.78556	Geographic coordinates	7	11
586	RL204	USA	CA	Riverside	-117.24640	33.96990	Directions (Loggins 2007)	7	10
13	BM0013	USA	ND	Rolette	-99.85300	48.77600	Estimated county center	7	11
280	BM0280	USA	MI	Saginaw	-84.36843	43.19050	Geographic coordinates	7	11
582	RL200	USA	CA	San Louis Obispo	-120.41900	35.40000	Estimated county center	7	11
485	RL5	USA	CA	Santa Cruz	-122.04408	37.06973	Directions (Loggins 2007)	7	11
77	BM0077	USA	OK	Seminole	-96.59584	35.08570	Geographic coordinates	7	10
29	BM0029	USA	MS	Sharkey	-90.73290	32.96548	Geographic coordinates	7	10
96	BM0096	USA	CA	Siskiyou	-122.80264	41.31010	Geographic coordinates	7	10
99	BM0099	USA	CA	Siskiyou	-122.80264	41.31010	Geographic coordinates	7	10
547	RL156	USA	CA	Sonoma	-122.90300	38.55900	Estimated county center	7	10
548	RL159	USA	CA	Sonoma	-123.06417	38.57431	Directions (Loggins 2007)	7	10
551	RL162	USA	CA	Sonoma	-123.06808	38.57904	Directions (Loggins 2007)	7	10
216	BM0216	USA	GA	Taliaferro	-82.88151	33.46587	Geographic coordinates	7	10
202	BM0202	USA	MS	Tallahatchie	-90.18600	33.95600	Estimated county center	7	10

Supplemental table 3 cont.

Sample No.	Specimen ID	Country of origin	State of origin	County of origin	Latitude	Longitude	Geographic reference	BAPS & Consensus Populations	Nested STRUCTURE Populations	
440	BM0440	USA	KY	Todd	-87.19100	36.84300	Estimated county center	7	10	
146	BM0146	USA	AL	Washington	-87.94177	31.47267	Geographic coordinates	7	11	
201	BM0201	USA	PA	Wyoming	-76.15173	41.63475	Geographic coordinates	7	10	
64	BM0064	USA	TN	Blount	-83.83670	35.59525	Geographic coordinates	8	12	
65	BM0065	USA	TN	Blount	-83.64622	35.68617	Geographic coordinates	8	12	
66	BM0066	USA	TN	Blount	-83.84533	35.58990	Geographic coordinates	8	12	
17	BM0017	USA	NC	Haywood	-83.07397	35.58582	Geographic coordinates	8	12	
69	BM0069	USA	NC	Haywood	-83.06863	35.57708	Geographic coordinates	8	12	
70	BM0070	USA	NC	Haywood	-83.10410	35.62917	Geographic coordinates	8	12	
6	BM0006	USA	NC	Jackson	-83.16613	35.56168	Geographic coordinates	8	12	
3	BM0003	USA	TN	Sevier	-83.38808	35.71641	Geographic coordinates	8	12	
4	BM0004	USA	TN	Sevier	-83.43488	35.73208	Geographic coordinates	8	12	
5	BM0005	USA	TN	Sevier	-83.38569	35.71371	Geographic coordinates	8	12	
16	BM0016	USA	TN	Sevier	-83.53727	35.68089	Geographic coordinates	8	12	
67	BM0067	USA	TN	Sevier	-83.63307	35.63601	Geographic coordinates	8	12	
2	BM0002	USA	NC	Sutter	-83.71610	35.54646	Geographic coordinates	8	12	
8	BM0008	USA	NC	Sutter	-83.17832	35.56652	Geographic coordinates	8	12	
15	BM0015	USA	NC	Sutter	-83.17956	35.56861	Geographic coordinates	8	12	
68	BM0068	USA	NC	Sutter	-83.71890	35.47242	Geographic coordinates	8	12	
210	BM0210	USA	HI	Kauai	-159.54900	22.05100	Estimated county center	9	11	*
264	BM0264	USA	HI	Honolulu	-158.06019	21.63978	Geographic coordinates	10	11	*
271	BM0271	USA	ND	Sheridan	-100.18204	47.57395	Geographic coordinates	11	11	*

Appendix D

Cell Reclassification for Habitat Variable in Geographic Information Systems

Supplemental table 4. Cell reclassification for land cover rater dataset; habitat quality and land cover impedance were assessed values as high (H), medium (M), and low (L) and used to rank land cover into eleven cost categories for use in Path Analysis in ARGIS. Rantionale for separation of land classes beyond quality and impedance values is provided under "Justification".

Land cover category	Habitat quality (H/M/L/U)	Habitat impedance (H/M/L/U)	Cost rankings	Justification
Blue Oak Woodland	H	L	1	Oak woodlands are viewed as most important; source of food that is linked to reproduction and survival.
Blue Oak-Foothill Pine	H	L	1	""
Coastal Oak Woodland	H	L	1	""
Valley Oak Woodland	H	L	1	""
Annual Grassland	H	L	2	High quality for foraging (invertebrates and roots); linked to survival during seasons when hard mast is not available.
Pasture	H	L	2	""
Perennial Grassland	H	L	2	""
Wet Meadow	H	L	2	High quality for foraging and source of water for hydration and wallowing; linked to survival during dry months.
Freshwater Emergent Wetland	H	L	3	""

Supplemental table 4 cont.

Land cover category	Habitat quality (H/M/L/U)	Habitat impedance (H/M/L/U)	Cost rankings	Justification
Montaine Riparian	H	L	3	High quality for rooting, source of water, and potential corridor for dispersal and refuge during dry months.
Valley Foothill Riparian	H	L	3	""
Bitterbrush	U	U	4	Low cover-important for refugia
Chamise-Redshank Chaparral	M	L	4	""
Coastal Scrub	M	L	4	""
Low Sage	M	L	4	""
Mixed Chaparral	H	L	4	""
Montane Chaparral	H	L	4	""
Sagebrush	M	L	4	""
Unk Shrub	M	L	4	""
Desert Riparian	M	L	5	Rivers may be important corridors for dispersal in desert areas; however it is unclear what role these habitats have in connecting pig populations in California. Because of this uncertainty, I have assigned a mid-range impedance value.
Estuarine	H	M	5	Lakes and Estuaries provide shorline that may be of high quaility for pigs; it is currently unclear what role these are playing in dispersal. As such I have assigned a mid-range impedance.
Lacustrine	H	M	5	""

Supplemental table 4 cont.

Land cover category	Habitat quality (H/M/L/U)	Habitat impedance (H/M/L/U)	Cost rankings	Justification
Riverine	H	L	5	Rivers may be viewed as corridors or barriers; pigs can swim across rivers but the relationship is unclear. Therefore, I have assigned a mid-range impedance.
Saline Emergent Wetland	M	L	5	Lakes and Estuaries provide shorline that may be of high quaility for pigs; it is currently unclear what role these are playing in dispersal. As such I have assigned a mid-range impedance.
Water	H	M	5	""
Agriculture	M	M	6	High quality forage but animals occupying agricultural areas may be highly persecuted. Therefore, I have given these areas a moderate impedance.
Montain Hardwood	H	L	7	Unknown quality; some tree seeds might be important for foraging, yet pigs are not occuring at high density in areas where this habitat occurs. Assume a moderate-high impedance.
Montain Hardwood-Conifer	M	L	7	""
Aspen	L	L	8	This would provide overstory cover but would not be optimal habitat.

Supplemental table 4 cont.

Land cover category	Habitat quality (H/M/L/U)	Habitat impedance (H/M/L/U)	Cost rankings	Justification
Closed-Cone Pine-Cypress	L	L	8	""
Douglas Fir	L	L	8	""
Eastside Pine	L	L	8	""
Eucalyptus	L	L	8	""
Jeffrey Pine	L	L	8	""
Juniper	L	L	8	This would provide mid-level cover for refuge, but would not be optimal habitat.
Klamath Mixed Conifer	L	L	8	This would provide overstory cover but would not be optimal habitat.
Lodgepole Pine	L	L	8	This would provide overstory cover but would not be optimal habitat.
Palm Oasis	L	L	8	Unknown quality; associated with arid locations. Not likely optimal habitat.
Pinyon Juniper	L	L	8	Mid-level cover
Ponderosa Pine	L	L	8	This would provide overstory cover but would not be optimal habitat.
Red Fir	L	L	8	This would provide overstory cover but would not be optimal habitat.
Redwood	L	L	8	""
Sierran Mixed Conifer	L	L	8	""
Subalpine Conifer	L	L	8	""
Unk Conifer	L	L	8	""
White Fir	L	L	8	""
Alkalai Desert Scrub	U	U	9	Anything with "alpine", "desert", or "barren" association not likely high quality for pigs. As such I have assigned high impedance values.

Supplemental table 4 cont.

Land cover category	Habitat quality (H/M/L/U)	Habitat impedance (H/M/L/U)	Cost rankings	Justification
Alpine Dwarf Shrub	U	U	9	""
Desert Scrub	U	M	9	""
Desert Succulent Shrub	U	M	9	""
Desert Wash	U	U	9	""
Joshua Tree	L	L	9	""
Barren	L	H	10	""
Marine	NA	NA	11	Ocean is an absolute barrier and ocean edge would not be an important dispersal corridor for inland invasions.
Urban	L	H	11	Urban areas would be barriers to natural movements of pigs.

Appendix E

Ranking of Pig Density Metric

Supplemental table 5. Pig density reclassification scheme with ten density categories used in cost surface for Path Analysis in ARCGIS.

Reclassification value	Break-point in No. pigs taken during 1992-2006	No. Cells
1	2351	49
2	1601	89
3	800	273
4	400	581
5	200	978
6	100	941
7	50	930
8	25	1358
9	10	4751
10	0	20930

REFERENCES

Acevedo-Delgado, J. H. 2010. Feral pig management in southern Texas: A landscape genetics approach. Dissertation, Texas A&M University, Kingsville, Texas, USA.

Acevedo-Whitehouse, K., J. Vicente, C. Gortazar, U. Hofle, I. G. Fernandez-de-Meria, and W. Amos. 2005. Genetic resistance to bovine tuberculosis in the Iberian wild boar. Molecular Ecology 14:3209-3217.

Adams, C. E., B. J. Higginbotham, D. Rollins, R. B. Taylor, R. Skiles, M. Mapston, and S. Turnman. 2005. Regional perspectives and opportunities for wild hog management in Texas. Wildlife Society Bulletin 33(4):1312-1320.

Adkins, R. N. and L. A. Harveson. 2007. Demographic and spatial characteristics of feral hogs in the Chihuahuan Desert, Texas. Human-Wildlife Conflicts 1:152-160.

Allen, M. S., E. Matisoo-Smith, and A. Horsburgh. 2001. Pacific ‘Babes’: Issues in the origins and dispersal of Pacific pigs and the potential of mitochondrial DNA analysis. International Journal of Osteoarchaeology 11:4-13.

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. Basic local alignment search tool. Journal of Molecular Biology 215:403-410.

Alexander, L. J., G. A. Rhorer, and C. W. Beattie. 1996. Cloning and characterization of 414 polymorphic porcine microsatellites. Animal Genetics 27:137-148.

Alves, E., C. Ovilo, M. C. Rodriguez, an dL. Silio. 2003. Mitochondrial DNA sequence variation and phylogenetic relationships among Iberian pigs and other domestic and wild pig populations. Animal Genetics 34:319-324.

Aranguren-Mendez, J., A. Beja-Pereira, R. Avellanet, K. Dzama, and J. Jordana. 2004. Mitochondrial DNA variation and genetic relationships in Spanish donkey breeds (Equus asinus). Journal of Animal Breeding Genetics 121:319-330.

Archibald, A. L., L. Bolund, C. Churcher, M. Fredholm, M. A. M. Groenen, B. Harlizius, K-T Lee, D. Milan, J. Rogers, M. F. Rothschild, H. Uenishi, J. Wang, L. B. Schook, the Swine Genome Consortium. 2010. Pig genome sequence-analysis and publication strategy. BMC Genomics 11:438.

Avise, J. C. 2004. Molecular markers, natural history, and evolution. Second Edition. Sinauer Associates Inc. USA.

Baber, D. W. and B. E. Coblentz. 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island Journal of Mammalogy 67:512-525.

Balkenhol N., F. Gugerli, S. A. Cushman, L. P. Waits, A. Coulon, J. W. Arntzen, R. Holderegger, H. H. Wagner, and Participants of the Landscape Genetics Research Agenda Workshop. 2009. Identifying future research needs in landscape genetics: where to from here? Landscape Ecology 24:455-463.

Ballard, J. W. O. and M. C. Whitlock. 2004. The incomplete natural history of mitochondria. Molecular Ecology 13:729-744.

Barrett, R. H. 1977. Wild pigs in California. in G. W. Wood, editor. Research and management of wild hog populations. Belle Baruch Forest Science Institute, Clemson University, Georgetown, South Carolina, USA.

Barrett, R. H. 1978. The feral hog on the Dye Creek Ranch, California. Hilgardia 46:283-355.

Barrett, R. H. and D. S. Pine. 1980. History and status of wild pigs, *Sus scrofa*, in San Benito County, California. California Fish Game 67:105-117.

Barrett, R. H. 1982. Habitat preferences of feral hogs, deer, and cattle on a Sierra foothill range. Journal of Range Management. 35:342-346.

Barrowclough, G. F. and R. M. Zink. 2009. Funds enough, and time: mtDNA, nuDNA and the discovery of divergence. Molecular Ecology 18:2934-2936.

Belisle, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86:1988-1995.

Benfield, D. A., J. E. Collins, S. A. Dee, P. G. Halbur, H. S. Joo, K. M. Lager, W. L. Mengeling, M. P. Murtaugh, K. D. Rossow, G. W. Stevenson, and J. J. Zimmerman. 1999. Porcine reproductive and respiratory syndrome. Pages 201-232 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Bensasson, D., M. W. Feldman, and D. A. Petrov. 2003. Rates of DNA duplication and mitochondrial DNA insertion in the human genome. Journal of Molecular Evolution 57:343-354.

Bieber, C. and T. Ruf. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42:1203-1213.

Bjornerfeldt, S., M. T. Webster, and C. Vila. 2006. Relaxation of selective constraint on dog mitochondrial DNA following domestication. Genome Research 16:990-994.

Boitani, L., L. Mattei, D. Nonis, and F. Corsi. 1994. Spatial and activity patterns of wild boars in Tuscany, Italy. Journal of Mammalogy 75:600-612.

Brown, W. M., George Jr, M. & Wilson, A. C. 1979 Rapid evolution of mitochondrial DNA. Proceedings of the National Academy of Science 76:1967–1971.

Brisbin, I. L., Jr., R. A. Geiger, H. G. Graves, J. E. Pinder, III, J. M. Sweeney, and J. R. Sweeney. 1977. Morphological characteristics of two populations of feral swine. Acta Theriologica 22:75-85.

Caley, P. and B. Ottley. 1995. The effectiveness of hunting dogs for removing feral pigs (*Sus scrofa*). Wildlife Research 22:147-154.

Campbell, D. J. and M. R. Rudge 1984. Vegetation changes induced over ten years by goats and pigs at Port Ross, Auckland Islands (subAntarctic). New Zealand Journal of Ecology 7:103-118.

Campbell, K. J., G. S. Baxter, P. J. Murray, B. E. Coblentz, C. J. Donlan, and G. V. Carrion. 2005. Increasing the efficacy of Judas goats by sterilization and pregnancy termination. Wildlife Research 32:737–743.Cho et al. 2009

Cargil, C. and P. R. Davies. 1999. External parasites. Pages 669-684 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Clark, R. K., D. A. Jessup, D. W. Hird, R. Ruppanner, and Me. E. Meyer. 1983. Serologic survey of California wild hogs for antibodies against selected zoonotic disease agents. Journal of the American Veterinary Medical Association 183:1248-1251.

Clarke, C. M. H. and R. M. Dzieciolowski. 1991. Feral pigs in the northern South Island, New Zealand: I. Origin, distribution, and density. Journal of the Royal Society of New Zealand 21:237-247.

Clement, M., D. Posada, and K. S. Crandall. 2000. TCS: A computer program to estimate gene genealogies. Molecular Ecology 9:1657-1660.

Cliff, A. D. and J. K. Ord. 1973. Spatial Autocorrelation. London: Pion.

Chang, K-T. 2008. Introduction to Geographic Information Systems. Fourth Edition. McGraw-Hill Companies, New York, New York.

Choquenot, D., B. Kay, and B. Lukins. 1990. An evaluation of warfarin for the control of feral pigs. Journal of Wildlife Management 54:353-359.

Choquenot, D., and B. Lukins. 1996. Effect of pasture availability on bait uptake by feral pigs in Australia's semi-arid rangelands. Wildlife Research 23:421–428.

Choquenot, D., J. Hone, and G. Saunders. 1999. Using aspects of predator-prey theory to evaluate helicopter shooting for feral pig control. Wildlife Research 26:251-261.

Coblenzt, B. E. 1978. The effects of feral goats (Capri hircus) on island ecosystems. Biological Conservation 13:279-286.

Coblentz, B. E., and D. W. Baber. 1987. Biology and control of feral pigs on Isla Santiago, Galapagos, Ecuador. Journal of Applied Ecology 24:403–418.

Corn, J. L., P. K. Swiderek, B. O. Blackburn, G. A. Erickson, A. B. Thiermann, and V. F. Nettles. 1986. Survey of selected diseases in wild swine in Texas. Journal of the American Veterinary Medical Association 189:1028-1032.

Corrander, J., P. Marttinen, and S. Mantyniemi. 2006. A Bayesian method for identification of stock mixtures from molecular marker data. Fishery Bulletin 104:550-558.

Corrander, J., P. Marttinen, J. Siren, and J. Tang. 2008. Enhanced Bayesian modeling in BAPS software for learning genetic structures of populations. BMC Bioinformatics 9:539.

Corwin, R. M., and T. B. Stewart. 1999. Internal parasites. Pages 713-730 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Cousse, S., F. Spitz, M. Hewison, and G. Janeu. 1994. Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Canadian Journal of Zoology 72:1691-1694.

Cracraft, J., J. Feinstein, J. Vaughn, and K. Helm-Bychowski. 1998. Sorting out tigers (Pantera tigris): mitochondrial sequences, nuclear inserts, systematic, and conservation genetics. Animal Conservation 1:139-150.

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.

Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. The American Naturalist 168:486-499.

Cushman, S. A. and E. L. Landguth. 2010. Spurious correlations and inference in landscape genetics. Molecular Ecology 19:3592-3602.

Darwin, C. 1868 The variation of animals and plants under domestication. London: John Murry.

de Nevers, G. and B. Goatcher. 1990. Wild pigs kill knobcone pines. Fremontia 18:22-23.

Didion, J. and M. R. Lunsford. 1993. Management of wild pigs in the California State Park system. Pages 41-42 in W. Tietje and R. H. Barrett, technical coordinators. The wild pig in California oak woodland: ecology and economics. Symposium Proceedings, San Luis Obispo, California, USA.

Dinu, A. 2009. The action of the masticatory muscles and cranial changes in pigs as results of domestication. Documenta Praehistorica XXXVI. UDK 90316 “633/634”:636.01. DOI: 10.4312/dp.36.13.

Edwards, S. and S. Bensch. 2009. Looking forwards or looking backwards in avian phylogeography? A comment on Zink and Barrowclough 2008. Molecular Ecology 18:2930-2933.

Ehrlich, P. R. 1986. Which animal will invade? Pages 79-95. *in* H. A. Mooney and J. A. Drake Editors. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag New York Inc.

Ellis, W. A. 1999. Leptospirosis. Pages 483-494 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Engeman, R. M., H. T. Smith, S. A. Shwiff, B. Constantin, J. Woolard, M. Nelson, and D. Griffin. 2003. Prevalence and economic value of feral swine damage to native habitats in three Florida state parks. Environmental Conservation 30:319-324.

Engeman, R. M., S. A. Shwiff, H. T. Smith, and B. Constantin. 2004. Monetary valuation of rare species and imperiled habitats as a basis for economically evaluating conservation approaches. Endangered Species Update 21:66-73.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611-2620.

Evans, J. D., J. S. Pettis, W. M. Hood, and H. Shimanuki. 2003. Tracking an invasive honey bee pest: mitochondrial DNA variation in North American small hive beetles. Apidologie 34:103-109.

Everritt, J. H. and M. A. Alanis. 1980. Fall and winter diets of feral hogs in south Texas. Journal of Range Management 33:126-129.

Excoffier, L. G. Laval, and S. Schneider. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47-50

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.

Fang, M., X. Hu, T. Jiang, M. Braunschweig, L. Hu, Z. Du, J. Feng, Q. Zhang, C. Wu, and N. Li. 2005. The phylogeny of Chinese indigenous pig breeds inferred from microsatellite markers. Animal Genetics 36:7-13.

Fang, M., F. Berg, A. Ducos, and L. Andersson. 2006. Mitochondrial haplotypes of European wild boars with 2n=36 are closely related to those of European domestic pigs with 2n=38. Animal Genetics 37:459-464.

Fang, M., and L. Andersson. 2006. Mitochondrial diversity in European and Chinese pigs is consistent with population expansions that occurred prior to domestication. Proceedings of the Royal Society 273:1803-1810.

Feldhamer G. A., L. C. Drickamer, S. H. Vessey, J. F. Merritt, and C. Krajewski. 2007. Mammalogy: adaptation, diversity, ecology. The Johns Hopkins University Press, Baltimore, Maryland.

Fitzhugh, E.L., and J.B. Loomis. 1993. An economic analysis of fee hunting for wild pigs in California. Pages 21-22 in W.Tietje and R.H. Barrett, technical coordinators. The wild pig in California oak woodland: ecology and economics. Symposium proceedings, San Luis Obispo, California, USA.

Focardi, S., D. Cpizzi, and D. Monetti. 2000. Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. Journal of Zoology 250:329-334.

Focardi, S., R. Isotti, and A. Tinelli. 2002. Line transect estimates of ungulate populations in a Mediterranean forest. Journal of Wildlife Management 66:48-58.

Focardi, S., J-M. Galliard, F. Ronchi, and S. Rossi. 2008. Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. Journal of Mammalogy 89:1113-1123.

Frantz, A. C., S. Cellina, A. Krier, L. Schley, and T. Burke. 2009. Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? Journal of Applied Ecology 46:493-505.

Frederick, J. M. 1998. Overview of wild pig damage in California. Proceedings Vertebrate Pest Conference 18:82-86.

Gabor, T. C., E. C. Hellgren, and N. J. Silvy. 1997. Renal morphology of sympatric suiforms: implications for competition. Journal of Mammalogy 74:1089-1095.

Gabor, T. M., E. C. Hellgren, R. A. Van Den Bussche, and N. J. Silvy. 1999. Demography, sociospatial behaviour and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. Journal of the Zoological Society of London 247:311-322.

Garcelon, D. K., K. P. Ryan, and P. T. Schuyler. 2005. Application of techniques for feral pig eradication on Santa Catalina Island, California. Proceedings of the Sixth California Channel Islands Symposium. Ventura, California, December 1-3, 2003.

Geisser, H. and H-U. Reyer. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of Wildlife Management 68:939-946.

Gipson, P. S., B. Hlavachick , and T. Berger. 1998. Range expansion by wild hogs across the central United States. Wildlife Society Bulletin 26:274-278.

Gipson, P. S., J, K. Veatch, R. S. Matlack, and D. P. Jones. 1999. Health status of a recently discovered population of feral swine in Kansas. Journal of Wildlife Diseases 35:624-627.

Giuffra , E., J. M. H. Kijas, V. Amarger, O. Carlborg , J-T. Jeon, and L. Andersson. 2000. The origin of the domestic pig: Independent domestication and subsequent introgression. Genetics 154:1785-1791.

Goios, A., A. Carvalho, and A. Amorim. 2009. Identifying NUMT contamination in mtDNA analyses. Forensic Science International: Genetics Supplement Series 2, pages 278-280.

Gomez, J. M., D. Garcia, and R. Zamora. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean Quercus pyrenaica forest. Forest Ecology and Management 180:125–134.

Gongora, J., P. Fleming, P. B. S. Spencer, R. Mason, O. Garkavenko, J-N. Meyer, C. Droegemueller, J. H. Lee, and C. Moran. 2004. Phylogenetic relationships of Australian and New Zealand feral pigs assessed by mitochondrial control region sequence and nuclear GPIP genotype. Molecular Phylogenetics and Evolution 33:339-348.

Gray, M. L., F. Rogers, S. Little, M. Puette, D. Ambrose, and E. P. Hoberg. 1999. Sparagnosis in feral hogs (*Sus scrofa*) from Florida. Journal of the American Veterinary Medical Association 215:204-208.

Gray, M. M., J. M. Granka, C. D. Bustamante, N. B. Sutter, A. R. Boyko, L. Zhu, E. A. Ostrander, and R. K. Wayne. 2009. Linkage disequilibrium and demographic history of wild and domestic canids. Gnetics 181:1493-1505.

Gresham, C. S., C. A. Gresham, M. J. Duffy, C. T. Faulkener, and S. Patton. 2002. Increased prevalence of Brucella suis and pseudorabies virus antibodies in adults of an isolated feral swine population in coastal South Carolina. Journal of Wildlife Diseases 38:653-656.

Grinde, A. 2006. Ecological effects of wild pigs (*Sus scrofa*) in California Oak Ecosystems. Thesis, University of North Dakota, Grand Forks, ND, USA.

Groves, C. P. 1981. Ancestors for the pigs: taxonomy and phylogeny of the Genus *Sus*. Technical Bulletin No. 3, Department of Prehistory, Research School of Pacific Studies, Australian National University: 96 pages.

Groves, C. P. and P. Grubb. 1993. The Eurasian Suids *Sus* and *Babyrousa*. Pages 167-175. *in* W. L. R. Oliver, editor. Pigs, peccaries, and hippos: status survey and conservation action plan of the IUCN World Conservation Union, Gland, Switzerland.

Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52:696-704.

Haasl, R. J. and B. A. Payseur. 2010. Multi-locus inference of population structure: a comparison between single nucleotide polymorphisms and microsatellites. Heredity (2010) 1-14, Macmillan Publishers Limited 0018-067x/10

Hafez, E. S. E. and J. P. Signoret. 1969. The behavior of swine. In. The Behavior of Domestic Animals, 2nd edition. E. S. E. Hafez, editor. Pages 349-390. Baltimore, MD. Williams and Wilkins Co. 619 pages.

Hagen, D. R. and K. B. Kephart. 1980. Reproduction in domestic and feral swine. I. Comparison of ovulatory rate and litter size. Biology of Reproduction 22:550-552.

Halbert, N. D., T. Raudsepp, B. P. Chowdhary, and J. N. Derr. 2004. Conservation genetic analysis of the Texas state bison herd. Journal of Mammalogy 85:924-931.

Hall, T. 2001. Bioedit version 5.0.6 Department of Microbiology, North Carolina State University. <http://www.mbio.ncsu.edu/BioEdit/bioedit.html> Accessed November 2010.

Hampton, J. O., P. B. S. Spencer, D. L. Alpers, L. E. Twigg, A. P. Woolnough, J. Doust, T. Higgs, and J. Pluske. 2004. Molecular techniques, wildlife management and the importance of genetic population structure and dispersal: A case study with feral pigs. Journal of Applied Ecology 41:735-743.

Hanson, R. P., and L. Karstad. 1959. Feral swine in the southeastern United States. Journal of Wildlife Management 23:63-74.

Heeg, E. R. 2006. Landscape genetic study of feral pigs (*Sus scrofa*) in the central coast region of California. Thesis, University of California Davis, Davis, CA, USA.

Henry, V. G. 1968. Length of estrous cycle and gestation in European wild hogs. Journal of Wildlife Management 32:406-408.

Henry, V. G. 1969. Predation on dummy nest of ground-nesting birds in the southern Appalachians. Journal of Wildlife Management 33:169-172.

Henry, V. G. and R. H. Conley. 1972. Fall foods of European wild hogs in the southern Appalachians. Journal of Wildlife Management 36:854-860.

Hone, J. and G. E. Robards. 1980. Wild pigs: Ecology and control. Wool Technology and Sheepbreeding, 28:7-11.

Hone, J. and B. Atkinson. 1983. Evaluation of fencing to control feral pig movement. Australian Wildlife Research 10:499-505.

Hongo, H., N. Ishiguro, T. Watanobe, N. Shigehara, T. Anezaki, V. T. Long, D. V. Binh, N. T. Tien, and N. H. Nam. 2002. Variation in mitochondrial DNA of Vietnamese pigs: relationships with Asian domestic pigs and Ryukyu wild boars. Zoological Society of Japan 19:1329-1335.

Howe, T. D., F. J. Singer, and B. B. Ackerman. 1981. Forage relationships of European wild boar invading northern hardwood forest. Journal of Wildlife Management 45:748-754.

Hutchison, D. W. and A. R. Templeton. 1999. Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic variability. Evolution 53:1898-1914.

Ishiguro, N., M. Sasaki, M. Iwasa, N. Shighara, H. Hongo, T. Anezaki, V. T. Long, D. T. B. Lan, and P. T. Long. 2008. mtDNA variation in the Vietnamese pigs, with particular emphasis on the genetic relationship between boars from Vietnam and the Ryuku Islands. Mammal Study 33:51-58.

Isle, 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.

Jaarola, M. and Tegelström, H. 1996. Mitochondrial DNA variation in the field vole (*Microtus agrestis*): regional population structure and colonization history. Evolution 50: 2073–2085

Jones, G. F. 1998. Genetic aspects of domestication, common breeds and their origin. Pages 17-50. *in* M. F. Rothschild & A. Ruvinsky, Editors. The genetics of the pig. CAB International, Wallingford, Oxdordshire, United Kingdom.

Jones, P., K. Chase, A. Martin, P. Davern, E. A. Ostrander, and K. G. Lark. 2008. Single-Nucleotide-Polymorphism-Based association mapping of dog stereotypes. Genetics 179:1033-1044.

Jonsson, P. 1991. Evolution and domestication, an introduction. Pages 1-10. in: Maijala, K., editor. Genetic resources of pig, sheep and goat. Elsevier, Amsterdam, Oxford, New York, and Tokyo.

Katahira, L. K., P. Finnegan, and C. P. Stone. 1993. Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes National Park. Wildlife Society Bulletin 21:269-274.

Keegan, D. R., B. E. Coblentz, and C. S. Winchell. 1994. Feral goat eradication on San Clemente Island, California. Wildlife Society Bulletin 22:56–61.

Kerstens, H. H. D., S. Kollers, A. Kommadath, M. del Rosario, B. Dibbits, S. M. Kinders, R. P. Cooijmans, and M. A. M. Groenen. 2009. Mining for single nucleotide polymorphisms in pig genome sequence data. BMC Genomics doi:10.1 186/147 1-2164-10-4.

Kijas, J. M. H., R. Wales, A. Tornsten, P. Chardon, M. Moller, and L. Andersson. 1998. Melanocortin receptor 1 (MC1R) mutations and coat color in pigs. Genetics 150:1177-1185.

Kim, K-I., J-H. Lee, K. Li, Y-P. Zhang, S-S. Lee, J. Gongora, and C. Moran. 2002. Phylogenetic relationships of Asian and European pig breeds determined by mitochondrial DNA D-loop sequence polymorphism. Animal Genetics 33:19-25.

Kluge, J. P., G. W. Beran, H. T. Hill, and K. B. Platt. 1999. Pseudorabies. Pages 233-244 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology predicting invaders. Trends in Ecology and Evolution 16:199-204.

Kotanen, P. M. 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a California coastal prairie. Ecography 18:190–199.

Koutsogiannouli, E. A., K. A. Moutou, T. Sarafidou, C. Stamatis, and Z. Mamuris. 2010. Detection of hybrids between wild boars (*Sus scrofa scrofa*) and domestic pigs (*Sus scrofa f. domestica*) in Greece, using the PCR-RFLP method on melanocortin-1 receptor (MC1R) mutations. Mammalian Biology 75:69-73.

Kurz, J. C., and R. L. Marchinton. 1972. Radiotelemetry studies of feral hogs in South Carolina. Journal of Wildlife Management 36:1240-1248.

Larson, G., K. Dobney, U. Albarella, M. Fang, E. Matsoo-Smith , J. Robins , S. Lowden, H. Finlayson, T. Brand, E. Willerslev , P. Rowley-Conwy, L. Andersson, and A. Cooper. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. Science 307:1618-1621.

Larson, G., U. Albarella, K. Dobney, P. Rowley-Conwy, J. Schibler, A. Tresset, J. D. Vigne, C. J. Edwards, A. Schlumbaum, A. Dinu, A. Balacsescu, G. Dolman, A. Tagliacozzo, N. Manaseryan, P. Miracle, L. Van Wijngaarden-Bakker, M. Masseti, D. G. Bradley, and A. Cooper. 2007. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. Proceedings of the National Academy of Science 104:15276-15281.

Larson, G., R. Liu, X. Zhao, J. Yuan, D. Fuller, L. Barton, K. Dobney, Q. Fan, Z. Gu, X-H. Liu , Y. Luo, P. Lv, L. Andersson , and N. Li . 2010. Patterns of East Asian pig domestication, migration, and turnover revealed by modern and ancient DNA. Proceedings of the National Academy of Science 107:7686-7691.

Lavelle, M. J., K. C. Vercauteren, T. J. Hefley, G. E. Phillips, S. E. Hybnstrom, D. B. Long, J. W. Fischer, S. R. Swafford, and T. A. Campbell. 2011. Evaluation of fences for containing feral swine under simulated depopulation conditions. Journal of Wildlife Mangement 75:1200-1208.

Legendre, P. and M. Troussellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnology and Oceanography 33:1055–1067.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Legendre, P., D. Borcard and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75: 435-450.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2008. Analyzing or explaining beta diversity. Ecology 89:3238-3244.

Lewis, J. C. 1966. Observations of Pen-reared European hogs released for stocking. Journal of Wildlife Management 30:832-835.

Lichstein, J. W. 2007. Multiple regression of distance matrices: a multivariate spatial analysis tool. Plant Ecology 188:117-131.

Lin, C-S., Y-L. Sun, C-Y. Liu, P-C. Yang, L-C. Chang, I-C. Cheng, S. J. T. Mao, and M-C. Huang. 1999. Complete nucleotide sequence of pig (*Sus scrofa*) mitochondrial genome and dating evolutionary divergence within Artiodactyla. Genetics 236:107-114.

Loggins, R.E., J. T. Wilcox, D. H. Van Vuren, and R.A. Sweitzer. 2002. Seasonal diets of wild pigs in oak woodlands of the central coast region of California. California Fish and Game Quarterly 88:28-34.

Loggins, R. E. 2007. Historic origin, range expansion, and habitat suitability of introduced wild pigs (*Sus scrofa*) in California. Dissertation, University of North Dakota, Grand Forks, North Dakota, USA.

Lombardo, C. A., and K. R. Faulkner. 2000. Eradication of feral pigs, (*Sus scrofa*) from Santa Rosa Island, Channel Islands National Park, California. Pages 300–306. *in* D. R. Browne, K. L. Mitchell, and H. W. Chaney, Editors. Proceedings of 5th California islands symposium. U.S. Department of the Interior, Mineral Management Services Pacific Outer Continental Shelf Region, study MSS99–0038, Washington.

Lopez, J. V., N. Yuhki, R. Masuda, W. Modi, and S. J. Obrien. 1994. Numt, a recent transfer and tandem amplification of mitochondrial DNA to the nuclear genome of the domestic cat. Journal of Molecular Evolution 39:174-190.

Lowdon, S., H. A. Finlayson, A. A. Macdonald, A. C. Downing, S. J. Goodman, K. Leus, L. Kaspe, E. Wahyuni, and A. L. Archibald. 2002. Application of *Sus scrofa* microsatellite markers to wild suiformes. Conservation Genetics 3:347-350. D.C., USA.

Lucchini, V., E. Meijaard, C. H. Diong, C. P. Groves, and E. Randi. 2005. New phylogenetic perspectives among species of South-east Asian wild pig (*Sus* sp) based on mtDNA sequences and morphometric data. Journal of the Zoological Society of London 266:25-35.

Luetkemeier, E. S., M. Sodhi, L. B. Schook , and R. S. Malhi. 2010. Multiple Asian pig origins revealed through genomic analyses. Moleclar Phylogenetics and Evolution 54:680-686.

Luikart, G. and J-M. Cornuet. 1999. Estimating the effective number of breeders from heterozygote excess in progeny. Genetics 151:1211-1216.

Loggins, R. E., J. T. Wilcox, D. H. Van Vuren, and R. A. Sweitzer. 2002. Seasonal diets of wild pigs in oak woodlands of the central coast region of California. California Fish and Game 88:28-34.

Macmillan, A. P. 1999. Brucellosis. Pages 385-394 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220.

Martinez, A. M., J. V. Delgado, A. Rodero, and J. Vega-Pla. 2000. Genetic structure of the Iberian pig breed using microsatellites. Animal Genetics 31:295-301.

Mason, R. J., P. J. S. Fleming, L. D. Smythe, M. F. Dohnt, M. A. Norris, and M. L. Symonds. 1998. Leptospira interrogans antibodies in feral pigs from new south wales. Journal of Wildlife Diseases 34:738-743.

Massei, G., P. V. Genov, B. W. Staines, and M. L. Gorman. 1997. Factors influencing home range and activity of wild boar, *Sus scrofa*, in a mediterranean coastal area. Journal of Zoology, 242(3):411-423.

Mayer, J.J., and I. L. Brisbin. 1991. Wild Pigs in the United States: Their History, Comparative Morphology, and Current Status. University of Georgia Press, Athens, Georgia, USA.

Mayer, J. J., and I. L. Brisbin Jr. 2009. Wild Pigs: Biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, USA. SRNL-RP-2009-00869:1-400.

Mayer, W. and R. Hochegger. 2011. Discrimination of two alleles of the melanocortin receptor 1 gene to discern European wild bair (*Sus scrofa scrofa*) and domestic pig (*Sus scrofa domestica*) in meat products by real-time PCR. European Food Research Technology 232:687-692.

Mayer, K. E. and W. F. Laudenslayer, Jr. 1988. A guide to the wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento, California, USA.

McCann, B. E., D. K. Davie, and G. A. Feldhamer. 2003. Distribution, habitat use, and morphotypes of feral hogs (*Sus scrofa*) in Illinois. Transactions of the Illinois State Academy of Science 96:301-311.

McCann, B. E., K. Ryan, and D. K. Garcelon. 2004. Techniques and approaches for the removal of feral pigs from island and mainland ecosystems. Proceedings of Vertebrate Pest Conference 21:42–46.

McCann, B. E. and D. K. Garcelon. 2008. Eradication of feral pigs from Pinnacles National Monument. Journal of Wildlife Mangement 72:1287-1295.

McEvoy, B. P., J. E. Powell, M. E. Goddard, and P. M. Visscher. 2011. Human population dispersal "Out of Africa" estimated from linkage disequilibrium and allele frequencies of SNPs. Genome Research 21:821-829.

McGahern, A., M. A. M. Bower, C. J. Edwards, P. O. Brophy, G. Sulimova, I. Zakharov, M. Vizuete-Forster, M. Levine, S. Li, D. E. MacHugh, and E. W. Hill. 2006. Evidence for biogeographic patterning of mitochondrial DNA sequences in Eastern horse populations. Animal Genetics 37:494-497.

McIlroy, J. C. and R. J. Saillard. 1989. The effect of hunting with dogs on the numbers and movements of feral pigs, *Sus scrofa*, and the subsequent success of poisoning exercises in Namadgi National Park, Australian Capital Territory. Australian Wildlife Research 16:353-363.

McIlroy, J. C., E. J. Gifford, and R. I. Forrester. 1993. Seasonal patterns in bait consumption by feral pigs (*Sus scrofa*) in the hill country of Southeastern Australia. Wildlife Research 20:637–651.

McIlroy, J. C., and E. J. Gifford. 1997. The 'Judas' pig technique: a method that could enhance control programmes against feral pigs, *Sus scrofa*. Wildlife Research 24:483–491.

Mengeling, W. L. 1999. Porcine parvovirus. Pages 187-200 *in* B. E. Straw, editor. Diseases of Swine. Eighth edition. Iowa State University Press, Ames, Iowa, USA.

Miller, J. E. 1993. A national perspective on feral swine. Pages 9-16. *in* C. W. Hanselka and J. F. Cadenhead, Editors. Feral swine: a compendium for resource managers. Proceedings of a Conference, March 24-25, Kerrville, TX. .Texas Agricultural Extension Service, College Station.

Miller, L. A., B. E. Johns, and D. J. Elias. 1998. Immunocontraception as a wildlife management tool: some perspectives. Journal of Wildlife Management 26:237-243.

Miller, L. A., J. Rhyan, and G. Killian. 2004. GonaCon: A versatile GnRH contraceptive for a large variety of pest animal problems. Vertebrate Pest Conference 21:269-273.

Minchin, D., C. Maguire, and R. Rosell. 2003. The zebra mussel (Dreissena polymorpha pallas) invades Ireland: human mediated vectors and the potential for rapid intranational dispersal. Biology and Environment: Proceedings of the Royal Irish Academy 103:23-30.

Minor, E. 2005. Experts say ‘Hogzilla’ was real and big. Associated Press, March 22, 2005.

Mona, S., E. Randi, and M. Tommaseo-Ponzetta. 2007. Evolutionary history of the genus *Sus* inferred from cytochrome b sequences. Molecular Phylogenetics and Evolution 45:757-762.

Morrison, S. A., N. Macdonald, K. Walker, L. Lozier, and M. R. Shaw. 2007. Facing the dilemma at eradication's end: uncertainty of absence and the Lazarus effect. Frontiers in Ecology and the Environment 5(5):271–276.

Mount, L. E. 1968. Adaptation of swine. Pages 277-291, in Adaptation of domestic animals. E. S. E. Hafez, editor. Lea and Febiger, Philadelphia, 415 pages.

Murtskhvaladze, M., A. Gavashelishvili, and D. Tarkhnishvili. 2010. Geographic and genetic boundaries of brown bear (Ursus arctos) population in the Caucasus. Molecular Ecology 19:1829-1841.

New, J. C., K. Delozier, C. E. Barton, P. J. Moris, and L. N. D. Potgeiter. 1994. A serologic survey of selected viral and bacterial diseases of European wild hogs, Great Smoky Mountains National Park, USA. Journal of Wildlife Diseases 30:103-106.

Nikolov I. S., B. Gum, B. Markov, and R. Kuehn. 2009. Population genetic structure of wild boar *Sus scrofa* in Bulgaria as revealed by microsatellite analysis. Acta Theriologica 54:193-205.

Nilsson, R. H., M. Ryberg, E. Kristiansson, K. Abarenkov, K-H. Larsson, and U. Koljalg. 2006. Taxonomic reliability of DNA sequences in public sequence databases: a fungal perspective. PLoS ONE 1(1): e59. doi: 10.1371/journal.pone.000059.

NPS. 2006. Pointe Reyes National Seashore non-native deer management plan: protecting the seashore's native ecosystems. National Park Service, 2006. 431 pages.

Oliver, W. L. R., I. L. Brisbin Jr., and S. Takahashi. 1993. The Eurasian wild pig, *Sus scrofa*. Pages 175-189 *in* W. L. R. Oliver, editor. Pigs, peccaries, and hippos: status survey and conservation action plan of the IUCN World Conservation Union, Gland, Switzerland.

Oliver, W. L. R, and I. L. Brisbin Jr. 1993. Introduced and feral pigs: problems, policy, and priorities. Pages 269-286 *in* W. L. R. Oliver, editor. Pigs, peccaries, and hippos: status survey and conservation action plan of the IUCN World Conservation Union, Gland, Switzerland.

Okumura, N., N. Ishiguro, M. Nakano, K. Hirai, A. Matsui, and M. Sahara. 1996. Geographic population structure and sequence divergence in the mitochondrial control region of the Japanese wild boar (*Sus scrofa leucomystax*), with reference to those of domestic pigs. Biochemical Genetics 34:179-189.

O'Regan, H. J. and A. C. Kitchener. 2005. The effects of captivity on the morphology of captive, domesticated and feral animals. Mammal Review 35:215-230.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. Conservation Biology 12:418-429.

Parr, R. L., J. Maki, B. Reguly, G. D. Dakubo, A. Aguirre, R. Wittock, K. Robinson, J. P. Jakupciak, and R. E. Thayer. 2006. The pseudo-mitochondrial genome influences mistakes in heteroplasmy interpretation. BMC Genomics 7:185.

Patterson, N., A. L. Price, and D. Reich. 2006. Population structure and eigenanalysis. PLoS Genetics 2: 2074-2093.

Pavlov, P. M. and J. Hone. 1982. The behavior of feral pigs, *Sus scrofa*, in flocks of lambing ewes. Australian Wildlife Research 9:101-109.

Peart, D., D. T. Patten, and S. L. Lohr. 1994. Feral pig disturbance and woody species seedling regeneration and abundance beneath Coast Live Oaks (Quercus agrifolia) on Santa Cruz Island, California. Pages 313–322. *in* W. L. Halvorson and G. J. Maender, Editors. Fourth California Channel Islands symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Perez-Espona, S., F. J. Perez-Barberia, J. E. MCleod, C. D. Jiggins, I. J. Gordon, and J. M. Pemberton. 2008. Landscape features affect gene flow of Scottish Highland red deer (Cervus elaphus). Molecular Ecology 17:981-996.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53-65.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

Pimentel, 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. Fagerstone, Editors. Managing vertebrate invasive species: Proceedings of an international symposium. USDA APHIS Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, USA.

Pine, D. S. and G. L. Gerdes. 1973. Wild pigs in Monterey County. California Fish and Game 59:126-137.

Pirtle, E. C., J. M. Sacks, V. F. Nettles, and E. A. Rollor, III. 1989. Prevalence and transmission of pseudorabies virus in an isolated population of feral swine. Jurnal of Wildlife Diseases 25:605-607.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25:1253-1256.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of populations structure using multilocus genotype data. Genetics 155: 945-959.

Putnova, L., A. Knoll, V. Dvorak, and J. Dvorak. 2003. A novel porcine microsatellite panel for the identification of individuals and parentage control in the Czech Republic. Czech Journal of Animal Science 48:307-314.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org

Ramos, A. M., R. P. M. A. Crooijmans, N. A. Affara, A. J. Amaral, A. L. Archibald, J. E. Beever, C. Bendixen, C. Churcher, R. Clark, P. Dehais, M. S. Hansen, J. Hedegaard, Z-L. Hu, H. H. Kerstens, A. S. Law, H-J. Megens, D. Milan, D. J. Nonneman, G. A. Rohrer, M. F. Rothschild, T. P. L. Smith, R. D. Schnabel, C. P. Van Tassel, J. F. Taylor, R. T. Wiedmann, L. B. Schook, and M. A. M. Groenen. 2009. Design of a high density SNP genotyping assay in the pig using SNPs identified and characterized by next generation sequencing technology. PLoS ONE 4(8) e6524. doi10.1371/journal.pone.0006524.

Ramsey, D. S. L., J. Parkes , and S. A. Morrison. 2009. Quantifying Eradication Success: the removal of feral pigs from Santa Cruz Island, California. Conservation Biology 23:449-459.

Randi, E., M. Apollonio, and S. Toso. 1989. The systematics of some Italian populations of wild boar (*Sus scrofa* L.): a craniometric and electrophoretic analysis. Z. Saugetierkunde 54:40-56.

Randi, E., Lucchini, V., Diong, C.H., 1996. Evolutionary genetics of the Suiformes as reconstructed using mtDNA sequencing. Journal of Mammalian Evolution 3, 163–193.

Randi, E., N. Mucci, F. Claro-Hergueta, A. Bonnet, and E. J. P. Douzery. 2001. A mitochondrial DNA control region phylogeny of the Cervinae: speciation in Cervus and implications for conservation. Animal Conservation 4:1-11.

Raymond, M. and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Rhorer, G. A., B. A. Freking, and D. Nonneman. 2007. Single nucleotide polymorphisms for pig identification and parentage exclusion. Animal Genetics 38:253-258.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Roemer, G.W., T.J. Coonan, D.K. Garcelon, J. Bascompte, and L. Laughrin. 2001. Wild pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Animal Conservation 4:307-318.

Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Rosenberg, M. S. and C. D. Anderson. 2011. PASSaGE: Pattern analysis, spatial statistics and geographic exegesis. Version 2. Methods in Ecology and Evolution 2:229-232.

Rothschild, M. F. and A. Ruvinsky. 1998. The genetics of the pig. CAB International, Wallingford, Oxdordshire, United Kingdom.

Rousset, F. 2008. GENEPOP '007: a complete reimplementation of the GENEPOP software for Windows and Linux. Molecular Ecological Resources 8:103-106.

Roux, J. L. and A. M. Wieczorek. 2008. Molecular systematic and population genetics of biological invasions: towards a better understanding of invasive species management. Annals of Applied Biology 154:1-17.

Rubinsztien, D. C., W. Amos, J. Leggo, S. Goodburn, S. Jain, S-H. Li, R. L. Margolis, C. A. Ross, and M. A. Ferguson-Smith. 1995. Microsatellite evolution- evidence for directionality and variation in rate between species. Nature Genetics 10:337-343.

Rutherford, K. M. D., E. M. Baxter, B. Ask, P. Beerg, R. B. D'Eath, S. Jarvis, K. K. Jensen, A. B. Lawrence, V. A. Moustsen, S. K. Robson, R. Roehe, F. Thorup, S. P. Turner, and P. Sandoe. 2011. Project report 17 Danish centre for bioethics and risk assessment and SAC (Scottish Agricultural College). 148 pages.

Salmela, E., T. Lappalainen, I. Fransson, P. M. Andersen, K. Dahlman-Wright, A. Fiebig, P. Sistonen, M-L. Savontaus, S. Schreiber, J. Kere, and P. Lahermo. 2008. Genome-wide analysis of single nucleotide polymorphisms uncovers population structure in Northern Europe. PLoS ONE 3(10) e3519.

San Cristobal, M., C. Chevalet, C. S. Haley, R. Joosten, A. P. Rattink, B. Harlizius, M. A. M. Groenen, Y. Amigues, M-Y. Boscher, G. Russell, A. Law, R. Davoli, V. Russo, A. M. Martinez, M. Ramos, P. Glodek, J. N. Meyer, G. C. Gandini, D. Matassino, G. S. Plastow, K. W. siggens, G. Laval, A. L. Archibald, D. Milan, K. Hammond, and R. Cardellino. 2005. Genetic diversity within and between European pig breeds using microsatellite markers. Genetics 37:189-198.

Saunders, G., and H. Bryant. 1988. The evaluation of a feral pig eradication program during a simulated exotic disease outbreak. Australian Wildlife Research 15:73–81.

Saunders, G. 1993. Observation on the effectiveness of shooting feral pigs from helicopters in western New South Wales. Wildlife Research 20:771-776.

Saunders, G., B. Kay, and H. Nicol. 1993. Factors affecting bait uptake and trapping success for feral pigs (*Sus scrofa*) in Kosciusko National Park. Wildlife Research 20:653-665.

Scandura, M., L. Iacolina , G. Crestanello, E. Pecchili, M. F. Di Benedetto, V. Russo, R. Davoli, M. Apollonio, and G. Bertorelle. 2008. Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: Are the effects of the last glaciation still detectable? Molecular Ecology 17:1745-1762.

Scandura, M., L. Iacolina, and M. Apollonio. 2011. Genetic diversity in the European wild boar *Sus scrofa*: Phylogeography, population structure and wild x domestic hybridization. Mammal Review 41:125-137.

Schmitz, A., B. Chaput, P. Fouchet, M. N. Gully, G. Frelat, and M. Vaiman. 1992. Swine chromosomal DNA quantification by bivariate flow karyotyping and karyotype interpretation. Cytometry 13:703-710.

Schuyler, P. T., D. K. Garcelon, and S. Escover. 2002. Eradication of feral pigs (*Sus scrofa*) on Santa Catalina Island, California, USA. Pages 274–286. *in* C. R. Veitch and M. N. Clout, Editors. Turning the tide: the eradication of invasive species. World Conservation Union, Species Survival Commission, Invasive Species Specialist Group, Gland, Switzerland and Cambridge, United Kingdom.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. Mckelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology 90:3222-3232.

SCWDS. 2010. National Feral Swine Mapping System, Southeastern Cooperative Wildlife Disease Study, University of Georgia, http//:www.feralswinemap.org

Signoret, J. P., B. A. Baldwin, D. Fraser, and E. S. E. Hafez. 1975. The behavior of swine. Pages 295-329 in The Behavior of domestic animals. E. S. E. Hafaez, editor. Williams and Wilkins, Baltimore, Maryland, 532 pages.

Simmons, R. B., and S. J. Scheffer. 2004. Evidence of cryptic species within the pest *Copitarsia decolora* (Guenée) (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 97:675-680.

Singer, F. J., D. K. Otto, A. R. Tipton, and C. P. Hable. 1981. Home ranges, movements and habitat use of European wild boar in Tennessee. Journal of Wildlife Management 45:343-353.

Singer, F. J., W. T. Swank, and E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. Journal of Wildlife Management 48:464-473.

Smouse, P. E., J. C. Long, And R. R. Sokal. 1986. Multiple regression and correlation extension of the Mantel test of matrix correspondence. Systematic Zoology 35:627-632.

Sokal, R. R., N. L. Oden, and J. S. F. Barker. 1987. Spatial structure in Drosophila buzzatii populations: Simple and directional spatial autocorrelation. American Naturalist 129:122-142.

Soule, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. Conservation Biology 4:233-239.

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 Mangement 73:497-502.

Spencer, P. B. S. and J. O. Hampton. 2005. Illegal translocation and genetic structure of feral pigs in Western Australia. Journal of Wildlife Management 69:377-384.

Stephens, M., N. Smith, and P. Donnelly. 2001. A new statistical method for haplotype reconstruction from population data. American Journal of Human Genetics 68:978-989.

Stephens, M. and P. Scheet. 2005. Accounting for decay of linkage disequilibrium in haplotype inference and missing-data imputation. American Journal of Human Genetics 76:449-462.

Stiver, W. H. and E. K. DeLozier. 2009. Great Smoky Mountains National Park wild hog control program. Pages 341-352. *in* J. J. Mayer and I. L. Brisbin Editors. Wild Pigs: Biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, USA. SRNL-RP-2009-00869:1-400.

Storfer, A., M. A. Murray, S. F. Spears, R. Holderegger, and L. P. Waits. 2010. Landscape genetics: where are we now? Molecular Ecology 19:3496-3514.

Sweeney, J. M., J. R. Sweeney, and E. E. Provost. 1979. Reproductive biology of a feral hog population. Journal of Wildlife Management 43:555-559.

Sweeney, J. R., J. M. Sweeney, and S. W Sweeney. 2003. Feral hog. *in* G. A. Feldhamer, B.C. Thompson, and J. A. Chapman Editors. Wild Mammals of North America: Biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Sweitzer, R. A., B. J. Gonzales, I. A. Gardner, D. Van Vuren, J. D. Waithman, and W. M. Boyce. 1997. A modified panel trap and immobilization technique for capturing multiple wild pigs. Wildlife Society Bulletin 25:699–705.

Sweitzer, R. A., D. Van Vuren, I. A. Gardner, W. M. Boyce, and J. D. Waithman. 2000. Estimating sizes of wild pig populations in the north and central coast regions of California. Journal of Wildlife Management 64:531-543.

Sweitzer, R. A., and D. Van Vuren. 2002. Rooting and foraging effects of wild pigs on tree regeneration and acorn survival in California's oak woodland ecosystems. Pages 218–231 in R. B. Standiford, D. McCreary, and K. L. Purcell, technical coordinators. Proceedings of the 5th symposium on oak woodlands: oaks in California's changing landscape. U.S. Forest Service, General Technical Report PSW-GTR-184. Pacific Southwest Research Station, Albany, California, USA.

Sweitzer, R. A. and B. E. McCann. 2007. Natural areas ecological damage and economic costs survey report. Unpublished support submitted to all interested survey respondents. Prepared by R. A. Sweitzer and B. E. McCann. Department of Biology, University of North Dakota, Grand Forks, North Dakota, USA. 37 pages.

Swofford DL (2002) PAUP*-Phylogenetic analysis using parsimony. (Version 4.0b). Sinauer: Sunderland, MS.

Taylor, D. and L. Katahira. 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16:297-299.

Taylor, R. B., E. C. Hellgren, T. M. Gabor, and L. M. Ilse. 1998. Reproduction of feral pigs in southern Texas. Journal of Mammalogy 79:1325-1331.

Tisdell, C. A. 1982. Wild pigs: environmental pest or economic resource. Pergamon Press, Rushcutters Bay, New South Wales, Australia.

Tompkins, S. 2011. Three new Texas laws go into effect today. Houston Chronicle, August 31, 2011.

Tooman, L. K., C. J. Rose, C. Carraher, D. M. Suckling, S. R. Paquette, L. A. Ledezma, T. M. Gilligan, M. Epstein, N. B. Barr, and R. D. Newcomb. 2011. Patterns of mitochondrial haplotype diversity in the invasive pest Epiphyas postvittana (Lepidoptera: Tortricidae). Journal of Economic Entomology 104:920-932.

Toro, M., C. Barragan, C. Ovilo, J. Rodriganez, C. Rodriguez, and L. Silio. 2002. Estimation of coancestry in Iberian pigs using molecular markers. Conservation Genetics 3:309-320.

Towne, C. W., and E. N. Wentworth. 1950. Pigs: from cave to cornbelt. University of Oklahoma Press, Norman, Oklahoma, USA.

Truve, J., J. Lemel, and B. Soderberg. 2004. Dispersal in relation to population density in wild boar (*Sus scrofa*). Galemys 16:75-82. ISSN:1137-8700

Turakulov, R. and S. Easteal. 2003. Number of SNP loci needed to detect population structure. Human Heredity 55:37-45.

Twigg, L. E., T. Lowe, G. Martin, and M. Everett. 2005. Feral pigs in north-western Australia: basic biology, bait consumption, and the efficacy of 1080 baits. Wildlife Research 32:281–296.

TWRA. 2011. Tennessee Wildlife Resources “New wild hog regulations”. (http://www.eregulations.com/tennessee/hunting/new-wild-hog-regulations/) Accessed 10 February 2012.

USDA 2010. Risk assessment of the movement of firewood within the United States. United States Department of Agriculture Animal and Plant Health Inspection Service. http://www.emeraldashborer.info

Van der Leek, M. L., H. N. Becker, E. C. Pirtle, P. Humphrey, C. L. Adams, B. P. All, G. A. Erickson, R. C. Belden, W. B. Frankenberger, and E. P. J. Gibbs. 1993. Prevalence of pseudorabies (Aujeszky's Disease) virus antibodies in feral swine in Florida. Journal of Wildlife Disease 29:403-409.

Vigne, J-D., A. Zazzo, J-F. Saliege, F. Poplin, J. Guilaine, and A. Simmons. 2009. Pre-Neolithic wild boar management and introduction to Cyprus more than 11,400 years ago. Proceedings of the National Academy of Science 106:16135-16138.

Waithman, J. D. 1995. Wild pig management for California. The Resources Agency, California Department of Fish and Game. 99 pp.

Waithman, J. D., R. A. Sweitzer, D. Van Vuren, J. D. Drew, A. J. Brinkhaus , I. A. Gardner, and W. M. Boyce. 1999. Range expansion, population sizes, and management of wild pigs in California. Journal of Wildlife Management 63:298-308.

Wesche, P. L., D. J. Gaffney, and P. D. Keightley. 2004. DNA sequence error rates in Genbank records estimated using the mouse genome as a reference. DNA Sequence 15:362-364.

West, B. C., A. L. Cooper, and J. B. Armstrong. 2010. Managing wild pigs: a technical guide. Human-Wildlife Interactions Monograph 1:1-55.

Wilcox, J. T., E. T. Aschehoug, C. A. Scott, and D. H. Van Vuren. 2004. A test of the Judas technique as a method for eradicating feral pigs. Transactions of the Western Section of the Wildlife Society 40:120–126.

Wilcox, J. T. and D. H. Van Vuren. 2009. Wild pigs as predators in oak woodlands of California. Journal of Mammalogy 90:114-118.

Wood, G. W. and R. W. Brenneman. 1980. Feral hog movements and habitat use in coastal South Carolina. Journal of Wildlife Management 44:420-427.

Work, G. 1993. A rancher's view of the wild pig as an economic and ecological asset to the ranching enterprise. Pages 5-6 in W.Tietje and R.H. Barrett, technical coordinators. The wild pig in California oak woodland: ecology and economics. Symposium proceedings, San Luis Obispo, California, USA.

Xu, Y., B. Peng, Y. Fu, and C. I. Amos. 2011. Genome-wide algorithm for detecting CNV associations with diseases. BMC Bioinformatics 12:331

Xuebin, Q., H. Jianlin, B. Lkhagva, I. Chekarova, D. Badamdorj, J. E. O. Rege, and O. Hanotte. 2005. Journal of Animal Breeding Genetics 122:117-126.

Yang, S-L., Z-G. Wang, B. Liu, G-X. Zhang, S-H. Zhao, M. Yu, B. Fan, M-H. Li, T-A. Xiong, and K. Li. 2003. Genetic variation and relationships of eighteen Chinese indigenous pig breeds. Genetics of Selection and Evolution 35:657-671.

Zink, R. M. and G. F. Barrowclough. 2008. Mitochondrial DNA under siege in avian phylogeography. Molecular Ecology 17:2107-2121.

Zygmont, S. M., V. F. Nettles, E. B. Shotts, Jr. W. A. Carmen, and B. O. Blackburn. 1982. Brucellosis in wild swine: a serologic and bacteriographic survey in the southeastern United States and Hawaii. Journal of the American Veterinary Medical Association 181:1285-1287.