THE LANDSCAPE GENETICS OF AN INVASIIVE SPECIES: THE CASE OF FERAL PIGS

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Abstract: Biological invasions are one of the major threats to ecosystem function and conservation, agricultural lands, and human health. Within invasive mammal species, feral pigs (*Sus scrofa*) constitute one of the most aggressive and dangerous species. Feral pigs are considered an exotic invasive in the U.S.A., where conservative estimates indicate an annual loss of $200/pig due to agricultural damage. Feral pigs are also susceptible to diseases that affect livestock, humans, and wildlife (e.g., brucellosis, pseudorabies, foot and mouth). Population reduction (trapping or shooting) is the best current alternative for controlling swine damage and reducing opportunities for disease transmission. However, reduction is crude and inefficient in terms of manpower and resources because pigs from neighboring areas quickly re-colonize managed areas. To achieve long-term control, re-colonization of managed areas must be prevented. The new discipline of landscape genetics, the combination of genetic methods with GIS technologies, offers a powerful new tool for the large-scale management of wildlife. A landscape-genetic approach can facilitate the definition of management units and dispersal corridors, allowing control efforts to be concentrated where they will be the most effective. We expect landscape genetic approaches to become increasingly important to the management of feral pigs and other invasive species in coming decades.

Key words: geographical information systems, invasive species, feral pigs, landscape genetics, molecular markers

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INTRODUCTION

The spatial patterning, structure, and functioning of most of the ecosystems of the world have been altered by human activities. Biological invasions facilitated by the intentional or unintentional introduction of foreign species are one of the major threats to ecosystem function and conservation, agricultural lands, and human health worldwide (Mooney and Cleland 2001, Simberloff 2004). Research on species invasions has documented the far-reaching impacts of exotic species, including predation, competition, habitat alteration, extirpation of native species, and alteration of soil conditions, nutrient cycle, carbon budget, hydrology, and fire regimes by plant invaders (Mack et al. 2000). Accordingly, preventing the establishment and dispersal of invasive species constitutes both a major priority and an enormous challenge to conserving ecosystems, agriculture, and

human health. More information is needed on the large-scale population structure and dynamics and social behavior of invasive species to increase the effectiveness of management. Recent characterization of new genetic markers, automation of laboratory instrumentation, and improved analytical approaches has made large-scale genetic analyses of wildlife populations feasible. These new tools provide a means for increasing the effectiveness of invasive species management. Herein we describe some specific problems posed by the invasive feral pig in the United States of American (USA) and outline some potential benefits of using genetic methods in the management of this exotic invasive.

ORIGIN, DISTRIBUTION, AND ECOLOGY

Feral pigs (*Sus scrofa*) are the most abundant exotic ungulate in the United States (US) (Sweeney et al. 2003). Feral pigs are currently present in at least 32 states of the USA (Romero et al. 2003), with at least 2 million feral pigs in Texas alone (Mapston 1997). Pigs were domesticated in their native range of Europe and Asia and transported over much of the world by humans, where large feral populations have been established. In the US, feral pigs are the descendants of domestic swine, Eurasian wild boar, and hybrids of these two forms (Sweeney et al. 2003). The first introductions of feral pigs in North America dated from the 16th and 17th centuries during the Spanish, French, and English conquest of the new world (Mayer and Brisbin Jr. 1991). More recent introductions (since 1900's) may be attributed to free-range livestock husbandry practices, abandonment of herds during the Great Depression of the 1930's, and, recently, the intentional release or relocation for sport hunting (Mayer and Brisbin Jr. 1991).

Feral pig population dynamics at small to intermediate spatial scales reflect the high productivity of pigs relative to other ungulates (Taylor et al. 1998). Feral pigs are characterized by high population growth rates, early sexual maturity, and high survival (Sweeney et al. 2003). Feral pigs are capable of breeding year-round (Taylor 2003), with litter sizes ranging from 1–12 (reviewed in Sweeney et al. 2003). Feral pigs occur in a wide variety of habitats, from pine forests to arid thornscrub (Taylor 2003), but prefer bottomland hardwood forests with water bodies such as rivers and creeks (Sweeney et al. 2003, Taylor 2003). The social organization of feral pigs is characterized by small groups (sounders) composed of female relatives and their offspring, while adult males are typically solitary (Ilse and Hellgren 1997, Garbor et al. 1999).

IMPACTS ON ECOSYSTEMS AND NATIVE WILDLIFE

The most dramatic effect of feral pigs over the ecosystem is the destruction of habitats by excessive rooting and wallowing (Taylor 2003). The rooting behavior of feral pigs may cause extensive damage to natural plant assemblages by accelerating soil erosion, inhibiting plant succession, and accelerating the spread of exotic plants (Bratton 1975, Howe et al. 1976, Wood and Barrett 1979, Stone and Keith 1987, Mungall 2001). Most damage caused by feral pigs occurs in riparian zones, which may be very sensitive to disturbance (Engeman et al. 2004).

Feral pigs may severely affect native wildlife species through direct and indirect means. Feral pigs compete for resources with native species of reptiles, birds, and mammals (Gipson et al. 1998). Feral pigs may predate fawns, young lambs, and consume eggs of ground-nesting birds, such as wild turkey (*Melagris gallopavo*), and

bobwhite quail (*Colinus virginianus*) (Synatzske 1979, Tolleson et al. 1993, Gipson et al. 1998, Kammermeyer et al. 2003, Taylor 2003). Pig predation on threatened species has also been documented, including the Texas horned lizard (*Phrynosoma cornutum*) and the Texas tortoise (*Gopherus berlandieri*) (Taylor and Hellgren 1997). Pigs were an important factor in the decline of four amphibian species listed as rare, threatened, endangered, or of special concern in Florida through predation and habitat alteration (USDA 2002). Feral pigs also predate on the nests of marine turtles, many species of which are considered threatened or endangered (USDA 2002).

DISEASE RISK

Feral pigs are host to many endo- and ecto-parasites, including nematodes, roundworms, flukes, lice, and ticks (Samuel et al. 2001, Witmer et al. 2003). In addition, feral pigs are reservoirs of many diseases transmissible to livestock, humans, and wildlife (Samuel et al. 2001). Of particular concern is the pigs' ability to harbor bovine tuberculosis, leptospirosis, and vesicular stomatitis (Witmer et al. 2003). Accordingly, there has been increasing alarm about the role that feral pigs would play in infectious disease outbreaks (Witmer et al. 2003). Diseases with lesser critical severity that pose risk to livestock production are also a concern. For example, pseudorabies is present in a wide range of populations: 43-46% (Hawaii), 36% (Texas), 35% (Florida), 19-22% (southeastern states), 7-10% (Georgia), and 3% (California) (Mueller et al. 2000). Similarly, brucellosis is widespread through their range in feral pigs: 53% (Florida), 18% (South Carolina), 4% (California), and 3% (Texas) (Mueller et al. 2000).

The United States Department of Agriculture - Animal, Plant, and Health Inspection Service (USDA-APHIS) has established a national eradication program with the goal of eliminating swine brucellosis, bovine tuberculosis, pseudorabies, and other diseases of concern, as well as potential routes of transmission to humans, livestock, and wildlife (Witmer et al. 2003). Because of the wide and expanding geographic distribution of feral pig populations in the U.S., it is important to communicate the potential threat to humans, livestock, and natural resources posed by feral pig populations.

ECONOMIC IMPACTS

Feral pigs provide some economic benefits, primarily in the form of hunting and meat products. Feral pigs can be hunted year-round in most U.S. states (Bach and Connor 1993). Hunting may provide a bonus during unsuccessful big game hunts (Hudman 1993) and also draws many out-of-state hunters, providing revenue to state wildlife agencies (Chambers 1999). Furthermore, the market for feral pig meat is rapidly growing in the U.S. (Weems 1999). An increasing number of landowners have found niche markets for feral pig meat, which is prized for the nutritional quality including low fat content, and "wild" aspect (e.g. organic nature) of the meat. Meat production is also attractive due to the low production cost (e.g., no maintenance, feed) (Degner et al. 1983, Weems 1999).

Unfortunately, the economic benefits of feral pigs pale in comparison to the damage caused by the pigs. Feral pigs may be the most destructive ungulate species in the U.S. (Gabor et al. 1999). Conservative estimates predict that the 4 million feral pigs in the U.S. cause damage to crops and the environment costing $200/pig/year (Pimentel et al. 2005). Agricultural damage includes the destruction of crops, damage to wildlife feeders, predation and disease transmission to other livestock, and damage

to fences resulting in the escape and loss of livestock (Bach and Connor 1993, Gipson et al. 1998, Dickson et al. 2001).

MANAGEMENT STRATEGIES

Control methods have traditionally involved lethal means aimed at population reduction or non-lethal methods aimed at exclusion of feral pigs from areas prone to damage. Lethal methods include intensive harvest (hunting, aerial shooting, trained dogs), snares, poisoning, and cage or pen traps (Mapston 1997, Geisser and Reyer 2004). Exclusion areas are constructed using non-electric and electric fences. Non-electric fences are expensive and require constant maintenance to serve as effective barriers to feral pigs (Mapston 1997). Electric fences, although requiring more maintenance to control vegetation, are portable and less costly and have been recommended as a very successful method for small areas (Mapston 1997, but see Geisser and Reyer 2004). The primary drawbacks of traditional control methods are high labor cost, reduced success over time, and limited area of population impact. The eradication of feral pig populations is seldom possible, and a combination of lethal and non-lethal techniques (shooting, trapping, hunting, fencing) on a recurring basis has been proposed as the most effective control for feral pigs (Kammermeyer et al. 2003).

GENETIC TOOLS IN WILDLIFE MANAGEMENT

Over the past 20 years, the development of new molecular markers and the increasing automation of laboratory instrumentation has enabled the widespread use of genetic tools in wildlife studies (Honeycutt 2000). Coupled with improved computing power and analytical methods, molecular markers allow biologists to quantify the genetic diversity of species and populations, track the movements of individuals, estimate the degree of inbreeding, characterize new species, and investigate contemporary and historical patterns of dispersal (Freeland 2005). Genetic variation can be assessed at the individual, population, or species level, depending on the question to be answered, the sample size, the genetic marker available for the species, and the amount of variation at marker loci (DeYoung and Honeycutt 2005).

Knowledge of animal movements and population structure is particularly important for the control and management of invasive species such as feral pigs. We contend that molecular techniques provide a means of assessing animal movements and population structure, but have thus far been vastly underutilized in the context of applied wildlife management. For instance, molecular-based approaches have been successfully employed in Australia to study genetic structure and dispersal patterns of feral pigs (Hampton et al. 2004). Similar to the situation in the USA, Australian feral pig populations were continuously distributed over a broad geographic area such that management units were difficult to define and local control efforts were stymied by high rates of immigration. However, genetic marker data revealed that populations were structured along watersheds such that high rates of movements occurred within watersheds, with little or no movement between adjacent watersheds. Obviously, this is important information for management of animal damage as well as the formulation of disease containment strategies (Hampton et al. 2004).

LANDSCAPE GENETIC APPROACH TO MANAGEMENT

The recent improvements in the number and type of molecular genetic markers available and increased rates of data

acquisition has resulted in lowered costs and widespread application of the technology. Concurrently, advances in computing power and the development of new statistical tools (e.g., maximum likelihood and Bayesian approaches) have increased the inferential power of many studies. The combination of fine-scale genetic data with spatial data via geographic information systems (GIS) has fostered the emergence of a new discipline, termed landscape genetics. This combination of molecular data and landscape ecology provides a great degree of promise for wildlife management (Manel et al. 2003). Under this new discipline it is possible to gather information about the interaction of microevolutionary processes (acquired by molecular markers) and landscape features (Manel et al. 2003). Landscape genetics is especially useful for deciphering the effects of terrain features on animal distribution and movements. Thus, it is possible to quantify the factors influencing the spatial distribution of wildlife, information that is requisite for the success of many management strategies (Sarre et al. 2000).

MANAGEMENT IMPLICATIONS

Genetic population structure

The movement or exchange of individuals across the landscape determines the degree of population genetic structure. In continuous populations, allele frequencies often become dissimilar with geographic distance, through genetic drift, a process known as isolation by distance (Wright 1943). However, landscape features may act as dispersal barriers or corridors (e.g. mountains, waterways), and thus may have a profound influence on the genetic structure of animal populations (Sacks et al. 2004). Furthermore, complex patterns of fine-scale genetic structure may arise due to habitat heterogeneity, especially for species with specific habitat preferences (Sacks et al. 2004). Feral pigs depend on the availability of free water for thermoregulation, and often exploit food resources and cover in the vicinity of free water sources (Sweeney et al. 2003, Hampton et al. 2004). For instance, an Australian study indicated that feral pigs were poor dispersers across arid habitats between water drainages (Hampton et al. 2004).

Information on the genetic structure of feral pigs is limited to one study in U.S. (Gabor et al. 1999), one in Europe (Vernesi et al. 2003), and a handful of studies in Australia (Hampton et al. 2004, Spencer and Woolnough 2004, Hampton et al. 2005. In Western Australia, six populations were genetically differentiated, suggesting a discontinuous distribution (Hampton et al. 2004). Although feral pigs are considered habitat generalists, populations in arid regions are generally restricted to major watercourses and catchments dams (Hampton et al. 2004). Australian feral pig populations were not genetically different within three major river systems, indicating that gene flow was high within watercourses (Hampton et al. 2004). However, there was little movement among watercourses, even where separated by < 20 km (Hampton et al. 2004). Other geographic factors that affect the structuring process of feral pigs include rainfall and elevation (Cowled et al. 2007). Thus, although isolation by distance may be a factor influencing the genetic structure of continuous populations, geographic features appear to contribute strongly to the gene flow and genetic variability of some feral pig populations. Thus, it is probable that the identification of factors influencing population structure could be used to define management units and improve the effectiveness of control strategies.

Dispersal and movements

Dispersal is a permanent movement from an individual's natal area to a new home range. Within a species, dispersal is often sex-biased, where one sex is philopatric and remains near its natal area, while the other sex disperses to a new range, sometimes many km away (reviewed in Prugnolle and de Meeus 2002). In mammals, dispersal is typically male-biased (Greenwood 1980), and feral pigs are no exception (Sweeney et al. 2003).

Clearly, dispersal behavior can have an important influence on the distribution and abundance of organisms (Johnson and Gaines 1990). Dispersal routes and distances often depend on the behavior of the species, including, social structure, habitat preferences, and sex-bias of dispersal tendencies. The rate of dispersal or exchange among populations is proportional to the similarity in allele frequencies among populations. Molecular marker data, especially microsatellite data, are useful for testing patterns of dispersal. The combination of genetic data from microsatellite markers and GIS layers of landscape features (agricultural lands, water bodies, etc.) would allow the definition of neighborhood size and identify the landscape features that affect dispersal distances and rates.

Epidemiology and management of infectious disease

Disease outbreaks involving risk to livestock, humans and other wildlife are serious threats that can be minimized or alleviated only through advance planning and preparation. Once an outbreak occurs, reliable real-time information on the distribution and advance of positive cases is critical to containment. Molecular markers and GIS methods can verify the geographic origin of animals that carry the disease and delineate routs of transmission. For example, assignment methods provide an estimate of dispersal and gene flow by assigning individuals to populations based on multilocus genotypes (Manel et al. 2003). Individuals can be assigned to a population based on the genotype's likelihood of occurrence in several presumed populations (Waser and Strobeck 1998, Blanchong et al. 2002, Manel et al. 2003). Once the population of origin is identified, a GIS layer of landscape features and positive individuals can be overlaid to identify possible routes of transmission and delineate management units for containment. This represents a substantial improvement over the arbitrary boundaries that are often used in containment, consisting of concentric circles around positive individuals, where the diameter of the circle represents an average home range of an individual.

A Bayesian assignment method based on multilocus genotypes was employed successfully to determine the population of origin of white-tailed deer infected with bovine tuberculosis (TB) in Michigan (Blanchong et al. 2002). Deer affected by TB were expected to form a particular Deer Management Unit (DMU); however two positive individuals were assigned to different DMUs with high statistical likelihood, suggesting that TB is not exclusive to one DMU and resulting in increased surveillance for TB and changes in management policies of deer populations in Michigan (Blanchong et al. 2002).

Management based on genetic data

The application of genetic data derived from molecular markers could increase the effectiveness of feral pig management through the identification of dispersal corridors, dispersal distance, and landscape features that affect dispersal. Importantly, the spatial scale of the population structure can also be defined. Thus, genetic data can aid in the

development of contingency plans in case of a disease outbreak, evaluation of control or eradication programs, and the definition of management units. As a result, planning and implementation of management and control methods become more effective. The integration of demographic information, spatial data, and molecular techniques discussed in this paper will help develop our understanding of population structure and dynamics, and the social behavior of feral pigs. This information will allow managers to more effectively implement feral pig control.

LITERATURE CITED

BACH, J.P., AND J.R. CONNOR. 1993. Economics and human dimensions of the wild hog in Texas. Pages 88-100 *in* Proceedings of Feral Swine: a compendium for resource managers. Texas Animal Health Commission, Austin, TX. 88-100.

BLANCHONG, J.A., K.T. SCRIBNER, AND S.R. WINTERSTEIN. 2002. Assigment of individuals to populations: bayesian methods and multilocus genotypes. Conservation Biology 66:321-329.

BRATTON, S.P. 1975. The effects of European wild boar, *Sus scrofa*, on gray beech forest in the Great Smoky Mountains. Ecology 56:1356-1366.

CHAMBERS, M. 1999. Conserving a resource. Proceedings of First National Feral Swine Conference. Ft. Worth, TX. 115-116.

COWLED, B.D., J. ALDENHOVEN, O. INAKWU, T. GARRETT, C. MORAN, AND S.J. LAPIDGE. 2007. Feral pig population structuring in the rangelands of eastern Australia: applications for optimal management units. Conservation Genetics DOI 10.1007/s10592-007-9331-1.

DEGNER, R.L., L.W. RODAN, W.K. MATHIS, AND E.P.J. GIBBS. 1983. The recreational and commercial importance of feral swine in Florida: relevance to possible introduction of African swine fever into the U.S.A. Preventative Veterinary Medicine 1:371-381.

DEYOUNG, R.W., AND R.L. HONEYCUTT. 2005. The molecular toolbox: genetic techniques in wildlife ecology and management. Journal of Wildlife Management 69:1362-1384.

DICKSON, J.G., J.J. MAYER, AND J.D. DICKSON. 2001. Wild hogs. Pages 191-208 *in* J.G. Dickson, editor. Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

ENGEMAN, R.M., H.T. SMITH, R. SEVERSON, M.A. SEVERSON, S.A. SHWIFF, B. CONSTANTIN, AND D. GRIFFIN. 2004. The amount and economic cost of feral swine damage to the last remnant of a basin marsh system in Florida. Journal of Nature Conservation 12:143-147.

FREELAND, J. 2005. Molecular Ecology. John Wiley & Sons, Ltd., West Sussex, England.

GABOR, T.M., E.C. HELLGREN, R.A. VAN DEN BUSSCHE, AND N.J. SILVY. 1999. Demography, socio-spatial behavior and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. Journal of Zoology 247:311-322.

GEISSER, H., AND H.U. REYER. 2004. Efficacy of hunting, feeding, and fencing to reduce 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 26:279-286.

GREENWOOD, P.J. 1980. Mating systems, phlopatry, and dispersal in birds and mammals. Animal Behaviour 28:1140-1162.

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.

_____, T. KNIGHT, AND P.B.S. SPENCER. 2005. The impact of feral pigs in Australian

ecosystems. Ecological Management and Restoration 6:76-78.

HONEYCUTT, R.L. 2000. Genetic applications for large mammals. Pages 233-252 *in* S. Demarais, and P.R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, NJ.

HOWE, T.D., F.J. SINGER, AND B.B. ACKERMAN. 1976. Foraging relationships of European wild boar invading northern hardwood forest. Journal of Wildlife Management 45:748-754.

HUDMAN, J. 1993. Marketing feral hog hunts on the Nail Ranch. Proceedings of Feral Swine: a compendium for resource managers. Texas Animal Health Comission, Austin, TX. 134-136.

ILSE, L., AND E.C. HELLGREN. 1997. Spatial use and group dynamics of sympatric collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76:993-1002.

JOHNSON, M.L., AND M.S. GAINES. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449-480.

KAMMERMEYER, K., J. BOWERS, B. COOPER, D. FORSTER, K. GRAHL, T. HOLBROOK, C. MARTIN, S. MCDONALD, N. NICHOLSON, M. VANBRACKLE, AND G. WATERS. 2003. Feral hogs in Georgia: disease, damage, and control. Georgia Department of Natural Resources. GA.

MACK, R.N., W. SIMBERLOFF, W.M. LONSDALE, H. EVANS, M. CLOUT, AND F.A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Monographs 10:689-710.

MANEL, S., M.K. SCHWARTZ, G. LUIKART, AND P. TABERLET. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution 18:189-197.

MAPSTON, M.E. 1997. Feral hog control in Texas. USDA, Animal and Plant Health Inspection Service. Texas, USA.

MAYER, J.J., AND I.L. BRISBIN JR. 1991. History of the introduction. Pages 6-71 *in* Wild pigs in the United States: their history, comparative morphology, and current status. The University of Georgia Press, Athens, GA.

MOONEY, H.A., AND E.E. CLELAND. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the United States of America 98:5446-5451.

MUELLER, U.G., F.J. CONRATHS, AND E.C. HAHN. 2000. Pseudorabies virus infections (Aujeszky's disease) in wild swine. Reviews of Infectious Diseases 2:27-34.

MUNGALL, E.C. 2001. Exotics. Pages 736-764 *in* S. Demarais, and P.R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, NJ.

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.

PRUGNOLLE, F., AND T. DE MEEUS. 2002. Inferring sex-biased dispersal from population genetic tools: a review. Heredity 88:161-165.

ROMERO, C.H., J.E. MEADE, B.L. HOMER, J.E. SHULTZ, AND G. LOLLIS. 2003. Potential sites of virus latency associated with indigenous pseudorabies viruses in feral swine. Journal of Wildlife Diseases 39:567-575.

SACKS, B.N., S.K. BROWN, AND H.B. ERNEST. 2004. Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. Molecular Ecology 13:1265-1275.

SAMUEL, W.M., M.J. PYBUS, AND A.A. KOCAN. 2001. Parasitic disease of wild animals. Iowa State University Press, Ames, IA.

SARRE, S.D., N. AITKEN, M.N. CLOUT, W.J. ROBINS, AND D.M. LAMBERT. 2000. Molecular ecology and biological control: the mating system of a marsupial pest. Molecular Ecology 9:723-733.

SIMBERLOFF, D. 2004. A rising tide of species and literature: a review of some recent

books on biological invasions. BioScience 54:247-254.

SPENCER, P.B.S., AND A.P. WOOLNOUGH. 2004. Size should matter: Distribution and genetic consideration for pest animal management. Ecological Management and Restoration 5:220-222.

STONE, C.P., AND J.O. KEITH. 1987. Control of feral ungulates and small mammals in Hawaii's National Parks: research and management strategies. Pages 277-287 *in* C.G.H. Richards, and T.Y. Ku, editors. Control of mammal pests. Taylor and Francis, London, United Kingdom.

SWEENEY, J.R., J.M. SWEENEY, AND S.W. SWEENEY. 2003. Feral hog. Pages 1164-1179 *in* G. Feldhamer, B. Thomson, and J. Chapman, editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, MD.

SYNATZSKE, D.R. 1979. Status of the feral hog in Texas. Texas Parks and Wildlife.

TAYLOR, R. 2003. The feral hogs in Texas. Texas Parks and Wildlife.

_____, AND E.C. HELLGREN. 1997. Diet of feral hogs in the Western South Texas plains. Southwestern Naturalist 42:33-39.

_____, _____, T.M. GARBOR, AND L. ILSE. 1998. Reproduction of feral pigs in southern Texas. Journal of Mammalogy 79:1325-1331.

TOLLESON, D., D. ROLLINS, M. PINCHAK, M. IVY, AND A. HIERMAN. 1993. Impact of feral hogs on ground-nesting gamebirds. Proceedings of Feral swine: A compendium for resource managers. College Station, TX, 76-83.

UNITED STATES DEPARTMENT OF AGRICULTURE. 2002. Environmental assessment: management of predation losses to state and federally endangered, threatened, and species of special concern; and feral hog management to protect other state and federally endangered, threatened, and species of special concern, and candidate species of flora and fauna in the state of Florida. United States Department of Agriculture, Animal, Plant, and Health Inspection Service, Wildlife Services.

VERNESI, C., B. CRESTANELLO, E. PECCHOILI, D. TARTARI, D. CARAMELLI, H. HAUFFE, AND G. BERTORELLE. 2003. The genetic impact of demographic decline and reintroduction in the wild boar (*Sus scrofa*): a microsatellite analysis. Molecular Ecology 12:585-595.

WASER, P., AND C. STROBECK. 1998. Genetic signatures of interpopulation dispersal. Trends in Ecology and Evolution 13:43-44.

WEEMS, J. 1999. Marketing feral swine meat. Proceedings of First National Feral Swine Conference. Ft. Worth, TX. 111-113.

WITMER, G.W., R.B. SANDERS, AND A.C. TAFT. 2003. Feral swine-Are they a disease threat to livestock in the United States? Proceedings of 10th Wildlife Damage Management Conference. Ft. Collins, CO. 316-325.

WOOD, G.W., AND R.H. BARRETT. 1979. Status of the wild pigs in the United States. Wildlife Society Bulletin 7:237-246.

WRIGHT, S. 1943. Isolation by distance. Genetics 28:114-138.