Wild Pig Management Case Study:

The Pigs of Ossabaw Island: A Case Study of the Application of Long-term Data in Management Plan Development

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Introduction

Management programs to control feral pigs and/or make them available for hunter harvest frequently must be instituted without the benefit of long-term databases describing the characteristics of the animals to be managed. When available however, such long-term data can prove invaluable in helping to tailor the resulting management plan and goals to the specific habitat and population to be managed. In some rare instances moreover, such long-term data can also identify unique characteristics of the target population and may in turn raise important issues that need to be considered, beyond simply how best to exterminate or reduce numbers to the maximum extent possible. We describe one such case concerning the pigs of Ossabaw Island, Georgia, which long-term research has now shown to represent an important animal model for studies of obesity and diabetes, two diseases which have now become epidemic in many human populations worldwide (Marx 2002, Holden 2004). We also describe how properly coordinated data collections from animals being removed in control programs can serve the best interests of both research aimed at studying the pigs themselves, as well as conservation interests attempting to reduce pig numbers to the maximum extent possible.

Study Area

Ossabaw Island is one of the largest of the few remaining Georgia coastal barrier islands that are undeveloped and still largely uninhabited. The island is 16 kilometers in length and 13 kilometers wide and is located to the southeast of the city of Savannah (Chatham County), Georgia. In May, 1978, Ossabaw Island was sold/gifted to the State of Georgia whose Department of Natural Resources (DNR) now manages it as a State Heritage Preserve (Waller and Barrett 2001). The island encompasses 3,641 hectares of high ground and 6,499 hectares of tidal salt marsh. A detailed account of the flora, fauna and major habitat associations has been provided elsewhere (Waller and Barrett 2001, and references therein).

Population History

Throughout its recorded history Ossabaw Island has been inhabited by free-ranging feral swine which, as in the case of other southeastern coastal barrier islands, were first released by the earliest Spanish explorers of the New World. These releases were made in an effort to stock these islands with readily available sources of fresh meat to provision the Spanish missions and fortresses which were being established in this region in the early-mid 16th century (Mayer and Brisbin 1991). Mitochondrial DNA analysis of Ossabaw Island pigs captured in 2002 revealed an Asian DNA sequence in all individuals, not the European DNA sequence of Iberian pigs as previously thought (Lloyd et al. 2006b). This Asian haplotype was similar to that of pigs from the Canary Islands (Clop et al. 2008), which are known to have been the source of many pigs brought to the New World by Spanish explorers (Mayer and Brisbin 1991). Feral swine have continued to occupy Ossabaw Island through the following periods of colonial plantation development and subsequent private ownership by sportsmen who valued these animals as quarry for hunting. During their history of occurrence on the island, Ossabaw pigs have remained largely isolated from any significant introductions of mainland feral, domestic or other swine – certainly more-so than in the case of any other Georgia barrier island (Mayer and Brisbin 1991). Although several domestic boars were released on the island in the 1960's – 70's in an effort to "improve" the quality of the resident herd, these individuals were short-lived and although some phenotypic markers of their genetic input still exist in certain portions of the island, allozyme analyses have shown that Ossabaw feral swine, as a population, are genetically distinct from their mainland counterparts (Smith et al. 1980).

A Hampshire boar was introduced to Ossabaw Island and persistence of the belted coat color phenotype attests to its continuing genetic impact. Since the Ossabaw pig has no natural predators, coat color has relatively little impact on survival. However the "VQ" mutation (Arginine 200→Glutamine) in the PRKAG3 gene (the γ3 isoform of AMP-activated protein kinase), which is associated with high muscle glycogen and low intramuscular fat and is found in high frequency in Hampshires (Andersson 2003), was not found in any of the Ossabaw pigs sampled (Lloyd et al. 2006b). This finding suggests that the unpredictable island food supply selects against the Hampshire "unthrifty" metabolic genotype, i.e., propensity for leanness, not obesity. No adult pigs genotyped were homozygous for the wild-type "VR" allele (Valine 199—Arginine 200); in contrast, the Ossabaws were heterozygous or homozygous for the "IR" mutation (Valine 199→Isoleucine) in the PRKAG3 gene (Lloyd et al. 2006b). The IR allele is associated with low muscle glycogen and increased intramuscular fat, consistent with the obese Ossabaw pig "thrifty genotype" and their ability to survive the "feast and famine" ecology of Ossabaw Island. A piglet obtained by cesarean section was homozygous for the VR allele of the PRKAG3 gene and it is intriguing to know whether it would have survived to adulthood in the island environment (Sturek and Brisbin, unpublished).

A new era in the history of Ossabaw Island feral swine began in the late 1960's when scientists from the University of Georgia and a number of other research institutions began to study the Ossabaw Island pigs and publish the results in the peer-reviewed literature of a number of scientific disciplines. This contrasts strongly with the history of most other populations of feral swine which are usually subjected to control measures without the benefit of a significant body of published literature concerning the biology of the animals themselves. Usually, previously published studies if any, are limited to issues of general ecology, and particularly, possible strategies for management/control of the population (e.g., Bratton 1975, Singer et al. 1984).

At the time that in-depth studies of the general biology of the Ossabaw Island pigs began, the population had been existing for at least a number of decades in a state of periodic cycles of "boom or bust" response to cycles of the island's acorn mast crop abundance. Although no quantitative data were collected during this period, collaborated reports of a number of former island residents confirmed that any sport hunting pressure by the island's previous owners had failed to control population growth to the point of eliminating severe over-abundance, resulting in consequential malnutrition and starvation. Even into the early 1970's, the senior author personally observed fully-grown adult pigs that were so weakened by malnutrition that they would fall to the ground and be unable to rise when pursued by humans or dogs. As will be indicated later however, these periodic episodes of overabundance and exceeding of the island's food resources undoubtedly favored adaptations that would enhance survival during such periods of food shortage and malnutrition. Beginning in the late 1980's, more intensive efforts were made to control pig numbers on the island. Information from the Department of Natural Resources (1992) indicated that from 1989 through mid-1992, pigs were being removed from the island at an average rate of 1,147/year. Pigs removed from the island were used for various purposes including research and/or slaughter, or sale to mainland hunting preserves (R. Parker, pers. comm.). However despite this removal of over a thousand pigs per year, discernible damage to other island resources continued to occur in the form of depredation of sea turtle nests and the rooting of oak hammock and salt marsh vegetation (Department of Natural Resources 1992).

Previous Studies

Taken together, three decades of research have documented the following unique traits in the Ossabaw Island pig, which (to our knowledge) have never been reported in any other population of feral swine. These unique traits include:

1. Ossabaw Island pigs have the smallest adult body size of any feral population of swine anywhere in the world, with the possible exception of the pigs of the Andaman Islands in the Bay of Bengal (Brisbin et al. 1977, Mayer and Brisbin 1991). A full-grown sexually mature female Ossabaw Island pig, carrying a full-term litter of fetuses can weigh less than 100 pounds!

2. Ossabaw Island pigs have been shown to contain higher levels of body fat reserves (mass of fat/mass of lean-dry body) than those from any other population of feral swine or, for that matter, than any other species of terrestrial wild mammal (Stribling et al. 1984). Recent studies on pigs removed from Ossabaw Island in 2002 have verified the propensity to obesity that far exceeds other laboratory research and domestic swine (Talbott et al. 2006, Dyson et al. 2006, Witczak et al. 2005).

3. Controlled captive studies at the Pennsylvania State University have shown Ossabaw Island pigs to be able to tolerate high concentrations of salt in their diet, and the water they drink (i.e., high concentrations of seawater) compared to other swine (Zervanos et al. 1983).

4. Ossabaw Island pigs have unique lipid-handling enzyme and hormone systems, which allow them to rapidly and efficiently mobilize body fat reserves (Martin et al. 1973, Martin and Herbein 1976, Wangsness et al. 1977, Buhlinger et al. 1978, Hoffman et al. 1983, Scott et al. 1981a, 1981b). Closely related to this trait is the following:

5. Ossabaw Island swine show the "metabolic syndrome" which is largely driven by their outstanding propensity to obesity. When allowed high levels of caloric intake in captivity obesity, insulin resistance, glucose intolerance, dyslipidemia, and hypertension develop (Sturek et al. 2006). Ossabaw swine are the only miniature pigs to develop type 2 diabetes, as evidenced by elevated fasting blood glucose (Bratz et al. 2008). In essence, the metabolic syndrome expressed on Ossabaw Island seems vital to survival, while in captivity, continued excess food supply available to Ossabaws, like the case with their modern day human counterparts, results in the expression of type 2 diabetes pathology (Chobanion et al. 1982, Dyson et al. 2006).

6. Subsequent to long-term obesity, metabolic syndrome, and progression to type 2 diabetes in Ossabaw swine, a constellation of modern human diseases are now being studied in pigs removed from Ossabaw Island in 2002. As indicated in Table 1, these diseases include non-alcoholic steatohepatitis (Lee et al. 2009), polycystic ovary syndrome (Krisher et al. 2006), and coronary artery atherosclerosis and restenosis (Edwards et al. 2008). Evidence suggests that Ossabaw swine are an ideal animal model for studying the efficacy of bariatric surgery (Flum et al. 2007).

The above traits have resulted in the International Union for the Conservation of Nature and Natural Resources (IUCN), in a 1991 survey of conservation priorities for world-wide wild and feral pig populations, naming the Ossabaw Island pig as one of only two forms of feral pigs in the world, which at that time were actually worthy of conservation consideration (Oliver and Brisbin 1993**)**. Of all of these traits however, the most important for consideration in the development of any management guidelines and goals for this population are those related to the metabolic syndrome controlling lipid metabolism and storage and the potential to develop type 2 diabetes and subsequent long-term health complications. These traits make the Ossabaw Island pig an extremely important animal model for applied biomedical and basic biochemical, physiological and genetic studies of these now epidemic conditions in humans (Grundy et al. 1999, Marx 2002). Above all, the Ossabaw pigs now offer researchers in these fields the opportunity, possibly for the first time, to study these conditions in the field under those conditions which likely provided natural selection for the development and/or maintenance of these traits in the first place.

As described by Neel (1962), the "thrifty genotype" leading to the condition shown by the Ossabaw pigs, would confer a selective advantage under environmental conditions of dependence on a fluctuating and unpredictable food supply such as the annual acorn mast crop of Ossabaw Island. As mentioned previously, during periods of mast crop failure or depletion in late winter months, Ossabaw pigs are often exposed to conditions of severe malnutrition and starvation. This was especially true when a past lack of population control and harvest led to unsustainable high population densities which were a consequence of the inability of this insular population to disperse to other areas such as would be the case with a mainland population. It is not possible however, to determine whether the metabolic syndrome currently shown by the Ossabaw pigs arose *de novo* after the pigs were released on the island by early Spanish explorers or whether this trait was already present in the pigs released to this and other coastal barrier islands as a result of prior adaptation to similar selection pressures to which these pigs' ancestors had been exposed in the Old World. Unfortunately, hybridization of the free-ranging pigs of other coastal barrier islands of the southeast with either wild boar hybrids or domestics (Mayer and Brisbin 1991) would compromise attempts to study this question by sampling free-ranging pigs from other barrier islands. Some insight however might be gained by studies seeking to document this trait in unselected free-ranging pigs of the Iberian peninsula and/or the Caribbean region where free-ranging populations of pigs were established by the Spanish and then used to subsequently stock expeditions to locations elsewhere in the new world (Mayer and Brisbin 1991). Stribling et al. (1984) concluded that the uniquely high levels of total body fat which they found in Ossabaw Island pigs were not likely to have been derived from earlier domestic ancestors, since more recently derived mainland feral pigs did not show such elevated fat levels.

There has been debate whether the thrifty genotype hypothesis explains the increasing prevalence of metabolic syndrome and type 2 diabetes in modern human society (Diamond 2003, Baschetti 2006, Gerstein and Waltman 2006). A "selection and adaptation" hypothesis that is almost the reverse of the thrifty genotype hypothesis, posits that Ossabaws and all pigs were always exposed to a "diabetogenic" environment in which food was plentiful and only those pigs that could tolerate the excess calorie environment could survive and reproduce. Even only a modest decrease in reproduction would select for resistance to diabetes over just 12-25 generations. Controlled laboratory studies clearly showed that Ossabaw neonates survived longer after food deprivation than leaner breed domestic Yorkshire pigs (Kasser et al. 1981). This finding suggests that "thriftiness" could be essential for Ossabaw Island pigs to reach reproductive age and, thus there would be a strong selection pressure. Whether genotype is related to survival before reproductive age is a critical piece of evidence to address the thrifty genotype hypothesis.

Closely related to the above is the question of whether any other extant populations of free-ranging feral pigs, particularly those isolated in other insular situations, might not also show the above biochemical and physiological traits which are being claimed as being "unique" to the pigs of Ossabaw Island. To date however, no data of this kind has ever been sought in any other free-ranging pig population, and again, the extensive history of hybridization of most all other feral pig populations (Mayer and Brisbin 1991) would suggest that there is little or no probability of such traits remaining detectable in any other population today, particularly in North America.

Management Plan Development

Whatever its origin, the metabolic syndrome shown by the Ossabaw pigs has important implications for the development and implementation of any plan for the long-term management and control of these animals as part of their island ecosystem. Preliminary studies suggest that some of the unique traits of these pigs may not be stable over time under conditions of captive propagation on the mainland and may be lost over time as the regime of natural selection favoring its development/maintenance on the island is removed. In response to concerns for the continued maintenance of a stable free-ranging population of pigs on Ossabaw Island for use in research in the areas described above, the Georgia DNR appointed a committee of experts in 1992 to make recommendations pertaining to the management of feral hogs on the island, and specifically to (1) evaluate the impact of the hogs on the native flora and fauna and (2) recommend the desired hog population level to control ecological damage to the island (Department of Natural Resources 1992). Although this committee recognized that an argument could be made for the eradication of pigs on the island because of their negative impacts on island resources, the committee did not make this recommendation for four reasons: (1) the history of feral pigs as part of the biota and culture of the southeastern coastal region for a long period of time, i.e., for the past nearly 500 years since introduction by Spanish explorers; (2) the value of these pigs as a resource for recreational hunting; (3) the prudence of maintaining a core population on the island as subjects for studies of their unique characteristics as outlined above; and (4) total eradication would be costly and likely would not succeed because of the likelihood of unauthorized/illegal restocking/releases that would almost certainly follow any successful eradication effort as a result of efforts by a "pro-wild pig" lobby of hunters in this region.

From 1998-2000 the Georgia DNR developed a comprehensive management plan (CMP) for Ossabaw Island in order to provide "clear direction to Department personnel and [their] partners in the management and protection of Ossabaw" (Waller and Barrett 2001). The portion of this plan dealing with the management of pigs on the island was developed within a "Management Subcommittee" whose area of responsibility included the management of all wildlife species and other natural resources on the island. This subcommittee was charged with examining all available scientific information, considering public comments made both in writing and orally at designated public meetings seeking public input on the CMP, and then writing a report that served as a chapter in the final plan. Following a procedure similar to that of the 1992 Hog Advisory Committee (see above), the Management Subcommittee of the CMP also considered and expressed strong sentiment for the option of total pig eradication on the island. Consensus could not be obtained on this option however, and thus the subcommittee's report, as published in the CMP, indicated that the DNR would "continue to remove feral hogs to result in no measurable ecological impact." The CMP further indicated that removal rates may, "at times need to exceed 2500 per year." However the CMP did not indicate how this particular removal level was calculated and no quantitative criteria were provided for determining when a level of "no measurable ecological impact" had been attained. The plan did however indicate that "Hunter harvest, observational data, exclosures, shorebird nesting success, sea turtle nesting success and other ecological data" would all serve as "indices" to monitor any ongoing impacts of the island's pigs.

Conclusion: Coordinating Research and Management

While the goal of removing pigs to minimize their numbers on Ossabaw Island might at first glance appear to conflict with research interests aimed at studying the biology of these animals in their natural island habitat, this need not necessarily be the case. In fact, both of these interests, despite their seemingly disparate goals, would benefit greatly if a coordinated effort could be made to collect even simple demographic data from the pigs which are removed as part of any control program. While feral pigs in general may be a scourge, only a pest, to most ecologists, these pigs in particular also represent a biomedical treasure (Mayer and Brisbin 1995). Ossabaw Island pigs, by all accounts, recapitulate the complex diseases of obesity, metabolic syndrome, and progression to type 2 diabetes and all the long-term health complications associated with these diseases. Demographic, biochemical, and genetic data could help to evaluate the effectiveness of removal/control efforts by enabling conservation interests to better "know thy enemy," while at the same time providing an invaluable data set of basic biological/demographic information needed by researchers, both ecological and biomedical. Such efforts are consistent with a recent plea to promote the use of farm animals in biomedical research (Roberts et al. 2009). Even the recording of several simple pieces of information (e.g., sex, date and location of collection, and body size/weight) could indicate which seasons, age classes and sexes of pigs would be the most effective to target in future removal efforts in order to most effectively achieve a goal of a given reduction in population size. Furthermore, if removed lethally, invaluable data could be obtained concerning age (using dental criteria summarized by Mayer and Brisbin 1991), reproductive condition and foraging habits (Brisbin and Mayer 2001). Genotyping pigs to gain insights about obesity and survival genes would provide an unprecedented opportunity to address the thrifty genotype hypothesis (Du et al. 2008, Neel 1962). The application of new stable isotope techniques to stomach content samples removed from pigs taken in control removal programs could provide important information on the types of habitats being impacted by the pigs and the dynamics of their trophic role in the island's various food webs (Brisbin et al 2003).

To be sure, the collection of this kind of information places additional time demands on personnel charged with pig removal, and state and federal agencies responsible for undertaking these kinds of removal programs often do not have sufficient financial resources to compensate for the additional resources that such sample collections and field data recording would require. This may however, be an example of being "penny-wise and pound foolish" in that the kinds of information provided by the collection of even minimal basic data could, when properly analyzed and incorporated into appropriate demographic models (Tipton 1977), make predictions that could in turn, result in substantial savings of personnel time and other resources. This would result from allowing future control efforts to be tailored to the specific population attributes of the pigs themselves and those island habitats from which they most need to be removed in order to realize management plan goals.

To our knowledge, the kind of close coordination of pig removal operations with basic biological research interests and data collection described above has yet to be successfully realized for any free-ranging pig population in the world. We see no reason however, why Ossabaw Island could not and should not be the first to be successful in this regard for several reasons: (1) the deed of transfer which established the island as a Heritage Trust property of the state requires that the interests of both research and island habitat protection be priorities in any management plan; (2) there are few if any pig populations for which the stakes are so high in terms of the potential for basic research to make a direct contribution to human welfare (through studies of obesity and diabetes, particularly the "thrifty genotype" hypothesis); and (3) there is probably no other free-ranging pig population in the world for which a comparable long-term base of published scientific information suggests such a potential for high-return scientific understanding which could be realized from a minimal investment of resources and proper management plan development.

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Table 1. Modern diseases and uses of Ossabaw miniature swine for biomedical research.

Disease and/or Use	Comments	References
● Adrenal medullary and cortical hormone regulation	-	Alloosh et al. 2008, Hu et al. 2009
● Alzheimer's disease, neurodegeneration	Lee, W. Indiana University School of Medicine, Indianapolis, IN	-
● Atherosclerosis	-	Kaser et al. 2004, Zafar et al. 2004a, Zafar et al. 2004b, Mokelke et al. 2005, Dyson et al. 2006, Edwards et al. 2006, Sheehy et al. 2006, Sturek et al. 2006, Le et al. 2007, Sturek et al. 2007, Bender et al. 2008, Bratz et al. 2008, Edwards et al. 2008, Langohr et al. 2008, Lloyd et al. 2008, Neeb et al. 2008, Kreutz et al. In Press, Wang et al. In Press
● Bariatric surgery	R.V. Considine, Indiana University School of Medicine, Indianapolis, IN	Flum et al. 2007
● Bladder function and disease	-	Mattern et al. 2007
● Cardiac innervation and arrhythmias	-	Han et al. 2009
● Cardiac ischemia	D. Lefer, Emory University, Atlanta, GA; L. Lerman, Mayo Clinic, Rochester, MN	Miller et al. 2007, Bender et al. 2008, Borbouse et al. 2008
● Cardiomyopathy	-	Dincer et al. 2006
● Cholesterol and lipid metabolism	-	Dyson et al. 2006, Sturek et al. 2007, Bratz et al. 2008, Lee et al. 2009
● Coronary artery pharmacology	-	Bender et al. 2008, Bratz et al. 2008
● Coronary collateral artery development	F. Sellke, Harvard University, Cambridge, MA	Sturek et al. 2007
● Diabetic eye disease	B.G. Kennedy, Indiana University School of Medicine, Gary, IN	-
● Dietary probiotics	G. Solano-Aguilar, U.S. Department of Agriculture, Beltsville, MD; P. Heegaard, National Veterinary Institute, Technical University of Denmark, Copenhagen, Denmark	-

Table 1. Modern diseases and uses of Ossabaw miniature swine for biomedical research. (Continued)

Disease and/or Use	Comments	References
● Diffuse idiopathic skeletal hyperostosis	J.J. Verlaan, University Medical Center Utrecht, Utrecht, The Netherlands	-
● Gastrointestinal tract, electrical stimulation of	E. Firestone, W. Starkenbaum, Medtronic, Inc., St. Paul, MN	-
● Endothelial progenitor cell biology	D.P. Basile, M. Yoder, K.L. March, Indiana University School of Medicine, Indianapolis, IN	-
● Exercise physiology	-	Lloyd et al. 2006a, Sturek et al. 2007
● Genetics	Z. Machaty, Purdue University, West Lafayette, IN; S. Fahrenkrug, University of Minnesota, St. Paul, MN	Smith et al. 1980, Andersson 2003, Lloyd et al. 2006b, Sturek et al. 2007, Clop et al. 2008
● Hypertension	-	Dyson et al. 2006, Sheehy et al. 2006, Sturek et al. 2007, Bratz et al. 2008
● Kidney function and disease	B. Molitoris, Indiana University School of Medicine, Indianapolis, IN; J. Strickland, FAST Diagnostics, Indianapolis, IN	Alloosh et al. 2008
● Lithotripsy treatment of kidney stones	A. Evan, Indiana University School of Medicine, Indianapolis, IN	-
● Metabolic syndrome	Includes other features listed (obesity, insulin resistance, glucose intolerance, dyslipidemia, hypertension)	Dyson et al. 2006, Lloyd et al. 2006b, Sturek et al. 2007, Bender et al. 2008, Bratz et al. 2008, Spurlock and Gabler 2008, Lee et al. 2009
● Neonatology, fetal imprinting	Pig is classical neonatology model; ideal for determining epigenetic effects of metabolic syndrome	-
● Non-alcoholic steatohepatitis (NASH), liver disease	D. Crabb, Indiana University School of Medicine, Indianapolis, IN	Lee et al. 2009

Table 1. Modern diseases and uses of Ossabaw miniature swine for biomedical research. (Continued)

Disease and/or Use	Comments	References
● Obesity and adipokines	-	Boullion et al. 2003, Witczak et al. 2005, Dyson et al. 2006, Flum et al. 2007, Sturek et al. 2007, Bender et al. 2008, Bratz et al. 2008, Spurlock and Gabler 2008, Lee et al. 2009
● Percutanous catheter interventions	-	Kaser et al. 2004, Zafar et al. 2004a, Zafar et al. 2004b, Edwards et al. 2006, Sturek et al. 2006, Sturek et al. 2007, Edwards et al. 2008, Lloyd et al. 2008
● Polycystic ovary syndrome (PCOS)	-	Krisher et al. 2006
● Pancreatic beta cell function and isolation	R. McCarthy, VitaCyte LLC, Indianapolis, IN	-
● Peripheral artery disease (PAD)	-	Lloyd et al. 2006a, Langohr et al. 2008, Wang et al. In Press
● Platelet aggregation and thrombosis	-	Kreutz et al. In Press
● Skeletal muscle metabolism	M. Perez-Enciso, Universitat Autonoma, de Barcelona, Bellaterra, SPAIN	Habegger et al. 2008, Kostrominova et al. 2008
● Testicular development	J. Ford, U.S. Department of Agriculture, Lincoln, NE	-
● Type 2 diabetes	-	Bender et al. 2008, Bratz et al. 2008
● Vascular stents	-	Sturek et al. 2007, Edwards et al. 2008, Lloyd et al. 2008, Kang et al. In Press

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