

DEMOGRAPHIC AND GENETIC EVALUATION OF AN AMERICAN MARTEN REINTRODUCTION: A COMMENT ON SWANSON ET AL.

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Molecular genetic techniques have been widely used to evaluate management actions, including the success of species reintroductions. However, conclusions drawn from genetic characterizations must be interpreted in the context of the sampling design and degree of uncertainty underlying genetic parameter estimation and assumptions of analyses performed. For example, failure to correctly identify and sample appropriate groups of individuals for comparative analyses will bias estimates of summary measures of genetic diversity, intersample variance in gene frequency, and derivations of effective population size or degree of reduction or bottlenecks in numerical abundance. We critically evaluate the foundational assumptions underlying the sampling design and analytical methods employed by Swanson and colleagues. Inaccuracies in reporting the founding population history of American marten (*Martes americana*) in Michigan and high levels of uncertainty underlying estimates of effective population size, bottleneck history, and demographic sustainability suggest that the authors' genetic data are misrepresented.

Key words: effective population size, genetic variability, marten, *Martes americana*, microsatellites, reintroduction, translocation

Reintroductions of extirpated species or populations are an important and widely used management and conservation tool (Griffith et al. 1989). Increasingly, population genetic theory and molecular genetic markers are providing the theoretical foundations on which reintroduction prescriptions are based, and allow retrospective examination of the success of management actions (Bodkin et al. 1999; Larson et al. 2002; Maudet et al. 2002; Williams et al. 2002). Recently, Swanson et al. (2006) presented background information on reintroductions of American martens (*Martes americana*) into the Upper Peninsula of Michigan. This contribution is of potential importance in that the paper adds to a growing literature on reintroductions that employ molecular techniques, and secondly because genetic data from reestablished martens in Michigan were placed into a broader geographic context using comparable data from extensive collections made previously across North America (Kyle and Strobeck 2003). However, because of inaccuracies in reporting founding population history, and due to inadequacies in the presentation of experimental

protocols and lack of verification of assumptions for parameters estimated, the results and conclusions described by Swanson et al. (2006) are suspect. Given the importance of this species' recovery to agencies around the Great Lakes region, we critically examine assumptions and data presented in the paper by Swanson et al. (2006) in the context of misreported founding population history.

Swanson et al. (2006) incorrectly stated that a single source population from Chapleau, Ontario, Canada, was used for all reintroductions of martens into the Upper Peninsula. All subsequent comparisons of genetic data from this reported single "source" and "recipient" Michigan population were based on this erroneous assertion. This fundamental misrepresentation casts considerable doubt on the validity of the sampling design, analytical methods, and causal basis for conclusions made in the paper.

The stocking history for martens introduced into the Upper Great Lakes regions is well documented (Churchill et al. 1981; Davis 1983; Harger and Switzenberg 1958; Kohn 1991; Ludwig 1986; Michigan Department of Natural Resources 1970; Wisconsin Department of Natural Resources 1986; summarized in Williams et al. 2007; Fig. 1) but inaccurately portrayed by Swanson et al. (2006). Swanson et al. (2006) stated that a single source population was used. In reality, multiple source populations were used from widely geographically

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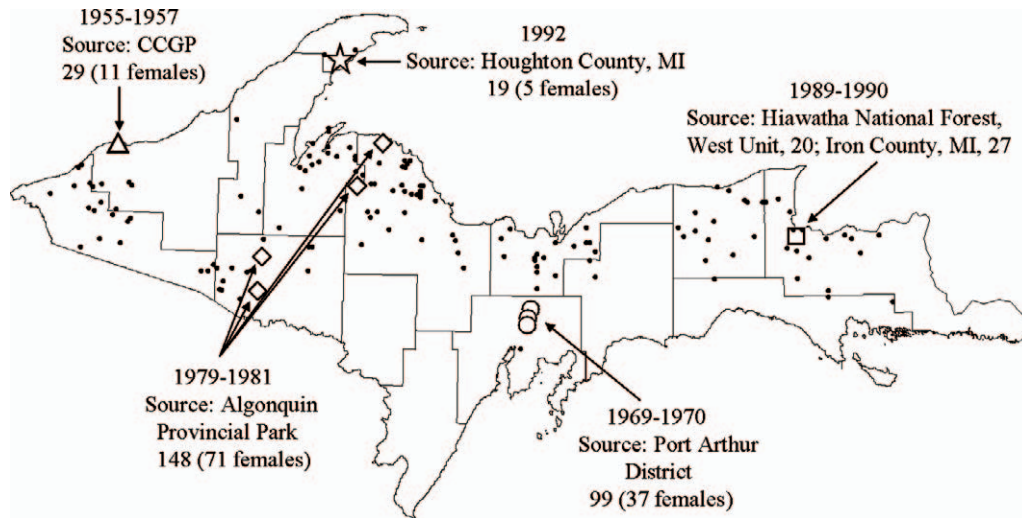


FIG. 1.—Years and locations of releases of martens in the Upper Peninsula of Michigan: Porcupine Mountains State Park (triangle); Hiawatha National Forest, West Unit (circles); Huron Mountain Club, Carrol-Paul Forest in Marquette County McCormick Experimental Forest, and Webb Lake and Perch Lake areas of Iron County (diamonds); Tahquamenon Bay area, Hiawatha National Forest, East Unit (square); and Keweenaw Peninsula (star). Sources of martens included in each release are indicated, as well as the number of individuals released. Locations of martens harvested in Michigan in 2001–2002 and 2002–2003 are shown as points. Adapted from Williams et al. (2007).

separated locales (Fig. 1). Furthermore, Swanson et al. (2006) incorrectly stated that an approximately equal ratio of males to females was released. From 1955 to 1957, 29 martens (11 females) were released into the Porcupine Mountains State Park, Ontonagon County, Michigan, including 23 from the Crown Chapleau Game Preserve, Ontario, 4 from the Algoma District of Ontario, and 2 originally from British Columbia but raised on a fur farm in Delta County, Michigan (Harger and Switzenberg 1958; Michigan Department of Conservation, in litt.; Michigan Department of Conservation 1957). In 1969 and 1970, a 2nd marten reintroduction was made into Delta County consisting of 99 martens (37 females) from the former Port Arthur Ontario Ministry of Natural Resources District, Ontario, north of Thunder Bay (Michigan Department of Natural Resources 1970). A 3rd reintroduction from 1979 to 1981 consisted of release of a total of 148 martens (71 females) from Algonquin Provincial Park into 4 discrete areas of west-central Upper Peninsula, including the Huron Mountain Club and Carrol-Paul Forest in Marquette County ($n = 79$; 31 females), the McCormick Experimental Forest, Ottawa National Forest ($n = 22$; 13 females), and Webb Lake ($n = 10$; 6 females) and Perch Lake ($n = 38$; 21 females) areas of Iron County (Churchill et al. 1981). Three marten translocations occurring between 1989 and 1992 were correctly recorded by Swanson et al. (2006; Fig. 1), but the vast majority of martens released in Michigan from outside sources (91.7% or 253 of 276 martens) originated from geographic locales not sampled by the authors.

Furthermore, concomitant reintroductions in the Nicolet National Forest in northern Wisconsin used founders from Crown Chapleau Game Preserve ($n = 33$; 7 females—Davis 1983), Algonquin Provincial Park ($n = 109$; 29 females—Davis 1983), and Colorado ($n = 30$; 15 females—J. George, Colorado Division of Wildlife, pers. comm.). Migration has been documented between martens from the Nicolet National

Forest population and populations in the Upper Peninsula (Churchill et al. 1982). Proximity to harvested martens in the Upper Peninsula indicates migration also may have occurred between populations in the Michigan and a reintroduced population on the Chequamegon National Forest founded by individuals from Minnesota ($n = 139$; 45 females—Kohn 1991). These releases, the heterogeneous genetic background of additional founding populations, and subsequent movements should be taken into account when evaluating the spatial genetic structure of martens in the Upper Peninsula of Michigan.

Misrepresentation of the number, geographic representation, and concomitantly genetic backgrounds, of founding individuals biases any comparisons of genetic diversity made between Michigan and the single (Crown Chapleau Game Preserve) founder population reported by Swanson et al. (2006). Data presented in figures 2, 3, and 5 in Swanson et al. (2006) and all text corresponding to levels of genetic variation in 1 source (Crown Chapleau Game Preserve) and Michigan may be relevant to the small region of the Upper Peninsula where animals from the Crown Chapleau Game Preserve founding population were released (Fig. 1). However, the genetic data from Crown Chapleau Game Preserve martens are not directly comparable with martens collected across the entire Upper Peninsula.

Swanson et al. (2006) claimed that the high genetic diversity and high incidence of private alleles (9.5% of alleles in martens from Michigan were not detected in martens from Chapleau) were due to contributions from 2 individuals introduced from British Columbia. The authors failed to realize that other source populations contributed the majority of animals introduced. Not all populations from which founders were removed were sampled by Kyle and Strobeck (2003) or subsequently analyzed by Swanson et al. (2006). High levels of genetic differentiation expected among the 3 marten source populations

suggest that elevated levels of genetic diversity, including allelic richness, and presence of private alleles reported by Swanson et al. (2006) would be the result of sampling individuals descended from founders obtained from genetically different source populations. With regard to the martens from British Columbia in particular, martens were brought to a game farm before release. One of the 2 animals was known to have died within 5 months of release in Masonville, Michigan, 225 km from the release site, and approximately 10 km from the fur farm where it had been raised (Harger and Switzenberg 1958).

Swanson et al. (2006) stated that martens sampled from across the entire Upper Peninsula represent a single genetically panmictic population. It is not clear where Swanson et al. (2006) sampled the reported 94 harvested animals. A considerably larger number of individuals was available from throughout the region for the years sampled by Swanson et al. (2006; Fig. 1). Dispersion of the samples used by Swanson et al. (2006), particularly relative to the release sites of different source populations, would be critical to evaluate the authors' claim of only 1 genetically contiguous population being in the region (e.g., $K = 1$ Michigan genetic population based on analysis using STRUCTURE [Pritchard et al. 2000]). Heavy sampling in an area surrounding release sites of founders from the same source population relative to other release areas would greatly bias subsequent analyses and conclusions.

Skepticism surrounding the claims by Swanson et al. (2006) of genetic panmixia and of explanations for high genetic diversity and presence and frequency of private allele are based on the potential for high levels of genetic differentiation between source populations based on analysis of genetic differentiation. Kyle and Strobeck (2003) sampled from the Chapleau and Pembroke regions of Ontario, which represent areas east and southeast of the Crown Chapleau Game Preserve source population and Algonquin Provincial Park source population, respectively. An estimate of interpopulation variance (F_{ST}) between martens from the Chapleau and Pembroke regions (regions of comparable interlocation geographic distance with known but unsampled source populations of martens) was 0.053 (Kyle and Strobeck 2003). The marten population from the former Port Arthur Ontario Ministry of Natural Resources District was not sampled by Kyle and Strobeck (2003). Areas located at geographic distances from Crown Chapleau Game Preserve comparable to the distance to the Port Arthur district displayed F_{ST} values of 0.028 (Kyle and Strobeck 2003). Given the interpopulation variation found by Kyle and Strobeck (2003) and dispersion of source populations used as founders in Michigan, any comparisons of variance in allele frequency made by Swanson et al. (2006) between the collective sample of martens from Michigan and martens from Crown Chapleau Game Preserve are clearly biased.

Swanson et al. (2006) contended, based on qualitative representation of population genetic data (their figure 4 neighborhood-joining tree), that the population of martens in Michigan has taken an independent evolutionary trajectory. There are several issues with the authors' statement. First, the authors failed to include the relevant source populations in these analyses. Second, given that each source population was released into

a separate region in Michigan, comparative analyses would most appropriately be conducted between subpopulations in different Michigan regions and their respective sources. It is difficult to interpret the authors' data when no mention is made of sampling distribution in Michigan and levels of statistical support are not provided for any branches of the tree (figure 4 in Swanson et al. 2006). Finally, one interpretation of the reported levels of genetic divergence of martens from Michigan relative to other martens sampled by Swanson et al. (2006) based on the topology and branch lengths of the population tree (figure 4 in Swanson et al. 2006) is that considerable drift in allele frequency has occurred subsequent to introductions. The interpretation of data presented in figure 4 in Swanson et al. (2006) is not consistent with other information presented in the paper (i.e., high estimates of effective population size). An alternative explanation for reported genetic divergence of the Michigan marten population (relative to other populations that the authors sampled) is that in totality, the samples genotyped represent a mixture of recent descendents from multiple and genetically heterogeneous source populations.

Several additional points are warranted regarding the discussion in Swanson et al. (2006) of the effects of repeated introductions on genetic diversity. In the absence of gene flow from external sources (as is believed to be the case in Michigan's Upper Peninsula), recovery of population levels of heterozygosity or allelic diversity can be an extremely long process. The only mechanism to recover variability is through mutations. Roughly speaking, the number of generations required for a population to recover lost heterozygosity back to an equilibrium level commensurate with prebottleneck or prefounder levels is in the order of the reciprocal of mutation rate (Nei et al. 1975). If a population is able to recover demographically from a bottleneck, the equilibrium level of heterozygosity that a population will attain over ecological time is a function of initial heterozygosity of the founding population (or populations), the intrinsic rate of increase during the population bottleneck, generation length, and the effective population size during the time period when the population was reduced (Chakraborty and Nei 1996).

The arguments of Swanson et al. (2006) concerning "temporally segregating reintroductions" and drift-mutation equilibrium, which cannot be attained over comparatively few generations of martens, is puzzling. The demographic records we describe above clearly show that low numbers of martens were originally released from genetically heterogeneous source populations. Repeated and small release events within reintroductions should have increased the loss of genetic diversity, particularly when animals from original release locales were subsequently used for other releases (i.e., translocations).

Swanson et al. (2006) found that martens in Michigan display high levels of genetic diversity. Based on examination of demographic and genetic data, the authors concluded that stocking efforts were a resounding success. The findings may indeed be correct, but the fundamental assumptions on which nearly all analyses and conclusions were based are fundamentally flawed. Caution should be taken when interpreting the applications of analytical methods by Swanson et al. (2006)

and subsequent conclusions. Many lessons can be learned from the reintroduction of martens in Michigan. However, greater scrutiny of historical evidence and greater emphasis on communication between research and management personnel is warranted to help prevent inaccuracies in parameter estimation and reporting that affect wildlife and forest management at local and regional scales.

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