

# Creating An Endangered Subspecies: A Comment on Smith et al. (2024)

Authors: Piaggio, Antoinette J., Heffelfinger, James R., Meyers, Paul M., and Hopken, Matthew W.

Source: Northwest Science, 97(4): 306-312

Published By: Northwest Scientific Association

URL: https://doi.org/10.3955/046.097.0406

The BioOne Digital Library (<u>https://bioone.org/</u>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<u>https://bioone.org/subscribe</u>), the BioOne Complete Archive (<u>https://bioone.org/archive</u>), and the BioOne eBooks program offerings ESA eBook Collection (<u>https://bioone.org/esa-ebooks</u>) and CSIRO Publishing BioSelect Collection (<u>https://bioone.org/csiro-ebooks</u>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Antoinette J. Piaggio<sup>1</sup>, USDA/APHIS/WS/National Wildlife Research Center, 4101 LaPorte Ave, Fort Collins, Colorado 80521

James R. Heffelfinger, Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, Arizona 85086

Paul M. Meyers<sup>2</sup>, Julia Butler Hansen NWR, P.O. Box 566, Cathlamet, Washington 98612

and

Matthew W. Hopken, USDA/APHIS/WS/National Wildlife Research Center, 4101 LaPorte Ave, Fort Collins, Colorado 80521

# Creating an Endangered Subspecies: A Comment on Smith et al. (2024)

The original paper "Reconsidering subspecific taxonomy of *Odocoileus virginianus* in Orgeon and Washington" is available at <u>https://doi.org/10.3955/046.097.0110</u>.

The reply "Acknowledging an Allopatric, Genetically Isolated Endemic Population: A Response to Piaggio et al. (2024)" is available at https://doi.org/10.3955/046.097.0407.

## Introduction

Smith et al. (2024) created a new subspecies of white-tailed deer (Odocoileus virginianus) occupying Douglas County, Oregon. The authors should be commended for assembling all available information on the Columbian white-tailed deer (O. v. leucurus) to support their argument. Unfortunately, the author's interpretation of the data is not compelling nor entirely accurate. Their justification for subspecific distinction is based on: 1) a misinterpretation or exclusion of relevant genetic analyses (Hopken et al. 2015, Piaggio et al. 2016, Piaggio and Taylor 2022); and 2) an untenable definition of subspecies based on those genetic analyses and on clinal skull morphology of three small, isolated, and fragmented sampling localities

#### Genetic Data

## Mitochondrial Sequence Data

Genetic data and historical records tell us subpopulations of Columbian white-tailed deer (O. v. leucurus) share a very recent common ancestor and that anthropogenic actions resulted in population isolation and interrupted gene flow in recent history, likely within the last 100 years (Hopken et al. 2015, Federal Register 81 FR71386 2016-24790). Initial genetic analyses were based on allozymes across 35 genomic loci (Gavin and May 1988); no significant differentiation was detected between deer from Douglas County, Oregon (DCOR) and Lower Columbia River (LC)/Julia Butler Hansen National Wildlife Refuge (JBH) subpopulations. Later, mitochondrial DNA (mtDNA) haplotypes from the rapidly evolving hypervariable Region I of the control region (HVI: 614 base pairs) were obtained from O. v. leucurus samples collected from the LC/JBH, DCOR, northeastern Oregon, southeastern Washington, Idaho, and Wyoming subpopulations. These samples largely grouped in a single Clade A (Hopken et al. 2015: their Figure 2) with a mean sequence divergence of 0.74%. Relationships of the 23 haplotypes within this clade are unresolved as there is very little genetic diversity or genetic distance among haplotypes (range 0.163–1.47% sequence divergence). Hopken et al. (2015) recovered only four haplotypes from individuals sampled at LC/JBH (except one that fell into a Columbian black-tailed deer [O. hemionus columbianus] clade, denoting introgression between these species at JBH) and DCOR (LC/JBH = 3, DCOR = 1). Hopken et al.

306 Northwest Science, Vol. 97, No. 4, 306–312, 2024, https://doi.org/10.3955/046.097.0406

© This open access article is licensed under a Creative Commons Attribution-Noncommercial-Noderivatives 4.0 International License [https://creativecommons.org/licenses/by-nc-nd/4.0/]. The authors of this paper include U.S. federal government employees whose contributions to the paper are in the public domain in the U.S.

<sup>&</sup>lt;sup>1</sup>Author to whom correspondence should be addressed. Email: toni.j.piaggio@aphis.usda.gov <sup>2</sup>Current address: 40 Alger Creek Heights Cathlamet,

Washington 98612



Figure 1 Median-joining network generated in NETWORK v4.6.1 for 614 base pairs of the mitochondrial DNA control region from Odocoileus virginianus collected from the Pacific Northwest, USA (reprinted from Hopken et al. 2015: their Figure 3). Each circle represents a haplotype with the branch in between representing one base pair change. The size of each haplotype circle represents its frequency among all O. virginianus samples. The shades and patterns represent a particular sampling location and circles with two or more shades or patterns were found in multiple locations (see legend and insets). The squares represent missing/unsampled/extinct haplotypes. The insets show the location of each haplotype: Lower Columbia River/Julia Butler Hansen Refuge (LC/JBH); Douglas County, Oregon (DCOR); Eastern Oregon (OR); Eastern Washington (WA); Idaho (ID); and Wyoming (WY). Haplotypes found in O. v. leucurus are labeled and have designated letters (a-d). Note that haplotype b from DCOR is intermediate between a, c, and d, all from LC/JBH. Note also that a and b are one base difference from i, which is a Northwest white-tailed deer (NWWTD) from Washington. Finally, note that a is more closely related to i than to other haplotypes from LC/JBH (c and d). The circles within the insets demonstrate the geographical distribution of the haplotypes (see legend). The checkered pattern haplotypes in the Oregon/Washington/Idaho inset represent haplotypes shared with another location within the inset. For example, a grey/white checkered pattern means those haplotypes are shared among the locations marked with solid grey and solid white (see legend). A solid color in that inset means that those haplotypes were only found in that location. The triangle in the LC/JBHR inset represents the collection location of the O. v. leucurus individuals with the Columbia black-tailed deer (O. h. columbianus) haplotype (Hopken et al. 2015: their Figure 2). The abbreviations in the LC/JBHR inset represent: Julia Butler Hansen National Wildlife Refuge on the Washington mainland (JBHR); Puget Island, Washington (P.I.); Tenasillahe Island, Oregon (T.I.). Letters at nodes are haplotype designations and correspond to those in Hopken et al. (2015: their Table A3).

(2015; their Figure 3) was not used in Smith et al. (2024) but is included here (Figure 1). This figure demonstrates that these four *O. v. leucurus* haplotypes are 1–4 base pairs (bp) different from one another with haplotype *c* from LC/JBH being only 1 bp different from haplotype b in DCOR, but 3 bp different from another haplotype (a) in LC/ JBH. Further, haplotype a from LC/JBH is 2 bp different from the DCOR haplotype (b). Remarkably, there is a haplotype of the Northwest white-

Comment on Smith et al. (2024) 307

tailed deer (NWWTD, *O. v. ochrourus*) that is a single bp different from both *a* (LC/JBH) and *b* (DCOR) haplotypes. Earlier work by Cronin (1991) was the first to identify a shared mtDNA haplotype among DCOR, LC/JBH, and NWWTD (haplotype c). These data clearly illustrate the recent shared ancestry among these haplotypes representing two subspecies (*O. v. ochrourus* and *O. v. leucurus*) including both subpopulations of *O. v. leucurus*. Smith et al. (2024) ignored the fact that the DCOR haplotype (*b*) they sampled is intermediate among the three haplotypes at LC/JBH and 1 bp different from LC/JBH and NWWTD (Figure 1).

Smith et al. (2024) based the subspecific distinctiveness of their proposed new subspecies, O. v. douglasi, on the fact that haplotypes detected in each O. v. leucurus subpopulation were not shared. This approach ignores clearly shared ancestry and the effects of the processes of random mutation and genetic drift in a small population that likely led to the single base change between the haplotypes of O. v. leucurus subpopulations and between them and O. v. ochrourus. The HVI is often used for infraspecific analyses specifically because of its high mutation rate and phylogenetic resolution (Hasegawa et al. 1993, Wakeley 1993). Separating the DCOR population from LC/JBH and those from O. v. ochrourus taxonomically creates a paraphyletic relationship among haplotypes that have a mean sequence divergence of  $\leq 1\%$ (Hopken et al. 2015).

We analyzed 36 additional samples collected from LC/JBH during 2016–2021 (Piaggio and Taylor 2022). All but six matched two of the three haplotypes from Hopken et al. (2015) already found in LC/JBH (GenBank Accession # KP308222.1 from Cathlamet, Washington, and GenBank Accession # KP308266.1 from Westport, Oregon). The other six individuals had mtDNA haplotypes that were identical to two haplotypes (GenBank Accession # KP308229.1 and GenBank Accession # KP308236.1) from Tenasillahe Island, OR (Piaggio and Taylor 2022) that are more closely related to *O. h. columbianus* than to any white-tailed deer samples (Hopken et al. 2015). This apparent introgression of *O. h. columbianus*  into *O. v. leucurus* was previously described as an ongoing threat to the genetic diversity of the LC/JBH population which could be exacerbated by isolation from other shared ancestral gene pools (Gavin and May 1988, Cronin 1991, Hopken et al. 2015, Piaggio and Taylor 2022). Smith et al. (2024) do not address the potential for these hybrids to be included in their analyses and influence the morphological characteristics they analyzed (see below under Cranial Morphology).

## Microsatellites

Piaggio et al. (2016) identified 13 new alleles from LC/JBH in 101 samples collected in 2014 and 2015. These samples came from O. v. leucurus that were being translocated from LC/JBH to the Ridgefield National Wildlife Refuge and Cottonwood Island, Wahkiakum County, Washington. The US Fish and Wildlife Service had been translocating Columbia River O. v. leucurus among islands of the LC/JBH from both the Oregon and Washington mainland since 1984 to facilitate gene flow (Azerrad 2016) and to increase the number of subpopulations. Of the 13 new alleles identified in the LC/JBH samples, 9 were also seen in either O. v. leucurus DCOR or O. v. ochrourus. One of the new shared alleles between O. v. leucurus LC/JBH and DCOR subpopulations was previously documented as a private allele in DCOR (Hopken et al. 2015) and was used by Smith et al. (2024) to argue for taxonomic distinctiveness for the DCOR subpopulation. Further, in a larger analysis (Piaggio and Taylor 2022) across 409 samples, allele 192 at locus K had a frequency of 0.28 in DCOR and 0.007 in LC/JBH (specifically in the mainland Washington population), illustrating the difficulty of relying on rare private alleles in small subpopulations as the basis for taxonomic revision. Further, two individuals captured at LC/JBH clustered with the DCOR population, meaning they shared more allelic diversity with DCOR samples than with LC/ JBH (Piaggio et al. 2016). This result is not surprising given that in 2010, eight individuals were moved from DCOR to LC/JBH (Azerrad 2016) and seven of these were genotyped and included in the analyses (Piaggio et al. 2016). It is also predictable that Piaggio et al. (2016) found new alleles in LC/JBH in the 101 new samples in addi-

308 Piaggio et al.

tion to the 80 samples analyzed by Hopken et al. (2015) because greater sample size increases the chances of detecting rare alleles. Overall, the LC/JBH and DCOR subpopulations of *O. v. leucurus* do not meet the subspecies definition of Smith et al. (2024:101), given they have more shared alleles between them than private ones that separate them. Given the logic in Smith et al. (2024), each population with a private allele at a neutral locus would be a candidate for subspecies designation.

Piaggio and Taylor (2022) further analyzed 409 O. v. leucurus individuals and found allele 159 at locus BM4208 was still a private allele for the LC/JBH subpopulation of O. v. leucurus, and it was also found across all five sampling localities at LC/JBH. Smith et al. (2024) relied on a STRUCTURE plot (their Figure 4; Piaggio and Hopken 2009: their Figure 6; Hopken et al. 2015:642) to argue that the LC/JBH and DCOR populations are distinct. However, they state in the text (p. 106), which is verbatim from Hopken et al. (2015:642), that there are individuals with shared assignment between LC/JBH and DCOR. More importantly, STRUCTURE plots can appear to show clear differentiation in populations with low genetic diversity because they have different allele frequencies. Thus, further data and interpretation with an understanding of evolutionary processes (such as genetic drift in this case) are required to assess connectivity, rather than simply relying on a visual plot (Lawson et al. 2018). Further, there were two genetic clusters within LC/JBH using STRUCTURE (Piaggio and Taylor 2022: their Figure 2), rather than the single one identified previously (Piaggio and Hopken 2009, Hopken et al. 2015). It is clear that these two genetic clusters are not isolated breeding populations, but in fact share some gene flow given geographical proximity and known translocation history (Piaggio and Taylor 2022: their Figure 1). However, given Smith et al.'s (2024) subspecific designation of the DCOR subpopulation based on a structure plot, these too could be considered separate subspecies.

## $F_{\rm ST}$

 $F_{\rm ST}$  is a metric that describes the reduction of heterozygosity due to genetic drift and thus can

identify population subdivision (Hartl 1981). It is used to estimate relative differences between subpopulations but should not be used as a basis for taxonomic revision. In fact, low overall genetic diversity within a population can lead to inflated  $F_{\rm st}$  between some genomic regions. If one population has a certain allele, or set of alleles, and another population has a different allele, this does not mean that there is no gene flow or that other regions do not show lower F ST (Cruickshank and Hahn 2014). Smith et al. (2024) lean heavily on an oversimplified interpretation of  $F_{ST}$  to describe their new infraspecific designation.  $F_{\rm ST}$  can be inflated by low genetic diversity (Jost 2008) due to genetic drift and inbreeding. Further,  $F_{\rm ST}$ between subpopulations of O. v. leucurus may be detecting historical isolation-by-distance, which is a common pattern of population structure in white-tailed deer (Cullingham et al. 2011, Bauder et al. 2021, Burbrink et al. 2022). As such, these subpopulation differences are not valid support for a new taxonomic designation for one of the subpopulations.

The genetic basis for creating a new subspecies consisting of the DCOR subpopulation of O. v. leucurus as argued by Smith et al. (2024) comes down to the single private allele across the LC/JBH subpopulation,  $F_{\rm ST}$  values, and a single haplotype that is found in only the DCOR population but is 1 bp different from LC/JBH and northeastern Oregon populations. The alternative and most parsimonious explanation of these patterns is random genetic drift in two subpopulations that were part of a larger historical population but have been isolated by habitat fragmentation resulting in lower genetic diversity and inbreeding.

## Cranial Morphology

Smith et al. (2024) identified statistically significant morphological differences between *O. v. leucurus* and *O. virginianus* from northern Idaho. These differences are primarily related to overall size of the skulls (basilar length, least interorbital breadth, zygomatic breadth, and mastoid breadth), which are subject to strong environmental influences. Smith et al. (2024: their Figures 1 and 2) show a general body size

Comment on Smith et al. (2024) 309

cline from larger deer in northern Idaho (Bonner County n = 8 and Latah County n = 1), then progressively smaller deer west into Wahkiakum County, Washington (n = 24) and Tenasillahe Island, northern Oregon (n = 1), with the smallest south into Douglas County in southern Oregon (DCOR, n = 63). This sampling scheme is noteworthy given that Bonner County, Idaho is approximately 500 miles from the next sampling locality (Wahkiakum County, Washington) and about 650 miles from the subpopulation in question in Douglas County, Oregon. Nonetheless, considering there is a well-established clinal size relationship in deer (Heffelfinger and Heffelfinger 2023) it should not be surprising that three small and isolated populations along that cline would show statistically significant differences. It is questionable, however, whether these represent taxonomically relevant differences or simply a difference in nutritional resource availability. They also claim that habitat differences between LC/JBH and DCOR "have imposed selective pressures" (p. 109); however, this is pure speculation as they assume that skull size is completely due to selection but no test for selection or heritability was attempted for these populations.

Smith et al. (2024; their Figure 3) describe the results of their principal component analysis (PCA) as representing "slightly overlapping morphological groups" (p. 105), however there is a considerable amount of overlap, likely owing to the recent gene flow of these populations before anthropogenic fragmentation of their habitat. Smith et al. (2024: their Figure 2B) show individuals from the LC region overlapping most of the samples from the other two populations. This overlap also counters the ability to diagnose individuals as one of the subspecies because it is based on a test of means rather than a diagnostic trait, which limits classification of a future, random individual. One quantifiable definition of subspecies is that 75% of individuals in one subspecies must fall outside 99% of the other (Amadon 1949, Patten and Unitt 2002). While not all taxonomists accept this definition, it is an attempt to make morphometric measurements diagnosable. A cursory review of the PCA indicates that it appears to violate this 75% rule; thus, there are no characters to distinctively classify most individuals as DCOR or LC/JBH. In addition, there is a danger of interpreting morphological information without considering the extent of hybridization in these samples. The LC/JBH subpopulation is known to contain individuals with O. h. columbianus genes, which may affect some morphological traits. Smith et al.'s (2024) Figure 2B contains several outliers from the LC/JBH subpopulation. The uncertainty of the lineage of these samples adds more ambiguity to the reliability of the morphological data. Given the environmental plasticity of skulls independent of phylogenetic decent and the potential for hybrids, analyses of a few small and recently isolated deer populations at this regional scale do not provide compelling support for creating a new subspecies of deer that is the O. v. leucurus subpopulation from DCOR.

# **Untenable Subspecies Concept**

Taxonomic separation of the proposed new subspecies O. v. douglasi out of what is now O. v. leucurus in Douglas County, Oregon is contrary to conservation community efforts to increase landscape connectivity and pools of genetic diversity for deer populations throughout western North America (Middleton et al. 2020, Kauffman et al. 2022). The genetic data from O. v. leucurus subpopulations support the historical record that they were all part of a regional panmictic population. Over-splitting taxonomic categories can invite activist litigation (Baier 2015), dilute resources available to imperiled taxa, and impede conservation by discouraging translocations and other efforts to foster evolutionary potential through restoring once-shared genetic diversity (Latch and Heffelfinger 2022). Further, introgression of O. hemionus genome into O. v. leucurus is a threat to the integrity of the unique genetic diversity remaining, given that in small populations rare and/or recessive alleles can become common (Rhymer and Simberloff 1996). Ralls et al. (2018) reviewed the genetic rescue literature and outlined an approach that reduces extinction risk of isolated populations that were once part of a larger widely distributed species. They determined that populations that

310 Piaggio et al.

are "chromosomally compatible, were isolated by human activities within the last 500 years and are not adapted to strongly different environments" (p. 4) should be managed in a way to increase genetic diversity rather than maintain isolation. The fact that translocated deer from DCOR have survived and increased the genetic diversity already in the LC/JBH population counters the argument that they are now uniquely adapted to DCOR and demonstrates that the populations are "chromosomally compatible." The question is: should we ignore anthropogenic alterations and support classifications that separate documented, natural gene flow corridors that erode genetic diversity? We argue that taxonomic distinction of the DCOR O. v. leucurus subpopulation is invalid, and that the evolutionary potential of white-tailed deer west of the Cascade Range would instead benefit from restoration of a shared gene pool.

# **References Cited**

- Amadon D. 1949. The seventy-five per cent rule for subspecies. The Condor 51:250–258.
- Azerrad JM. 2016. Periodic Status Review for the Columbian White-tailed Deer. Washington Department of Fish and Wildlife, Olympia, WA.
- Baier LE. 2015. Inside the Equal Access to Justice Act. Rowman and Littlefield Publishers, Lanham, MA.
- Bauder JM, Anderson CS, Gibbs HL, Tonkovich MJ, Walter WD. 2021. Landscape features fail to explain spatial genetic structure in white-tailed deer across Ohio, USA. Journal of Wildlife Management 85:1669–1684.
- Burbrink FT, Crother BI, Murray CM, Smith BT, Ruane S, Myers EA, Pyron RA. 2022. Empirical and philosophical problems with the subspecies rank. Ecology and Evolution 12:e9069.
- Cronin MA. 1991. Mitochondrial and nuclear genetic relationships of deer (*Odocoileus* spp.) in western North America. Canadian Journal of Zoology 69:1270–1279.
- Cruickshank TE, Hahn MW. 2014. Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. Molecular Ecology 23:3133–3157.

# Acknowledgements

The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy. This research was supported in part by the Arizona Game and Fish Department and the US Department of Agriculture, Animal Plant Inspection Service, Wildlife Services, and National Wildlife Research Center.

# **Conflict of Interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

# Author Contributions

AJP, JRH, PMM, and MWH all contributed to conceptualization and writing. AJP and MWH also did data analysis.

- Cullingham CI, Merrill EH, Pybus MJ, Bollinger TK, Wilson GA, Coltman DW. 2011. Broad and fine-scale genetic analysis of white-tailed deer populations: estimating the relative risk of chronic wasting disease spread. Evolutionary Applications 4:116–131.
- Gavin TA, May B. 1988. Taxonomic status and genetic purity of Columbian white-tailed deer. Journal of Wildlife Management 52:1–10.
- Hartl DL. 1981. A primer of populations genetics. Sinauer Associates, Inc. Publishers, Sunderland, MA.
- Hasegawa M, DiRienzo A, Kocher TD, Wilson AC. 1993. Toward a more accurate time scale for the human mitochondrial DNA tree. Journal of Molecular Evolution 37:347–354.
- Heffelfinger LJ, Heffelfinger JR. 2023. Physical Characteristics. *In* JR Heffelfinger and PR Krausman (editors), Ecology and Management of Black-tailed and Mule Deer in North America. CRC Press, Boca Raton, FL. Pp. 43–70.
- Hopken MW, Lum TM, Meyers PM, Piaggio AJ. 2015. Molecular assessment of translocation and management of an endangered subspecies of white-tailed deer (*Odocoileus virginianus*). Conservation Genetics 16:635–647.
- Jost L. 2008. *G*<sub>st</sub> and its relatives do not measure differentiation. Molecular Ecology 17:4015–4026.

Comment on Smith et al. (2024) 311

- Kauffman MJ, Lowrey B, Beck J, Berg J, Bergen S, Berger J, Cain J, Dewey S, Diamond J, Duvuvuei O, Fattebert J, Gagnon J, Garcia J, Greenspan E, Embere H, Harper G, Harter S, Hersey K, Hnilicka P, Hurley M, Knox L, Lawson A, Maichak E, Meacham J, Merkle J, Middleton A, Olson D, Olson L, Reddell C, Robb B, Rozman G, Sawyer H, Schroeder C, Scurlock B, Short J, Sprague S, Steingisser A, Tatman N. 2022. Ungulate migrations of the western United States, Volume 2: U.S. Geological Survey. Scientific Investigations Report 2022–5008. 160 pp. https://doi.org/10.3133/sir20225008
- Latch EK, Heffelfinger JR. 2022. Genetics informs meaningful intraspecific taxonomy: the black-tailed and mule deer species complex. Animal Production Science 63:1615–1622.
- Lawson DJ, Van Dorp L, Falush D. 2018. A tutorial on how not to over-interpret STRUCTURE and ADMIX-TURE bar plots. Nature Communications 9:3258.
- Middleton AD, Sawyer H, Merkle JA, Kauffman MJ, Cole EK, Dewey SR, Gude JA, Gustine DD, McWhirter DE, Proffitt KM, White PJ. 2020. Conserving ungulate migrations across the Greater Yellowstone Ecosystem requires transboundary science, policy, and management. Frontiers in Ecology and the Environment 18:83–91. <u>https://doi.org/10.1002/ fee.2145</u>
- Patten MA, Unitt P. 2002. Diagnosability versus mean differences of sage sparrow subspecies. The Auk 119:26–35.
- Piaggio AJ, Hopken MW. 2009. Evolutionary relationships and population genetic assessment of Oregon whitetailed deer. Wildlife Genetics Lab Report. USDA, APHIS, WS National Wildlife Research Center, Ft. Collins, CO. <u>https://nwrc.contentdm.oclc.org/ digital/collection/NWRCPubs1/id/69269/rec/4474</u>

Submitted 27 February 2024 Accepted 15 July 2024

- Piaggio AJ, Hopken MW, Wostenberg DJ. 2016. Genetic assessment of a translocated population of Columbian white-tailed deer (*Odocoileus virginianus leucurus*). Report to the US Fish and Wildlife Service, USDA/APHIS/WS/National Wildlife Research Center Wildlife Genetics Lab, Fort Collins, CO. 16 pp.
- Piaggio AJ, Taylor DR. 2022. Genetic assessment of a translocated population of Columbian white-tailed deer (*Odocoileus virginianus leucurus*). Report to the US Fish and Wildlife Service, USDA/APHIS/ WS/National Wildlife Research Center Wildlife Genetics Lab, Fort Collins, CO. 15 pp.
- Ralls K, Ballou JD, Dudash MR, Eldridge MDB, Fenster CB, Lacy RC, Sunnucks P, Frankham R. 2018. Call for a paradigm shift in the genetic management of fragmented populations. Conservation Letters 11:e12412.
- Rhymer JM, Simberloff D. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.
- Smith WP, Carraway LN, Gavin TA, Jenks JA. 2024. Reconsidering subspecific taxonomy of *Odocoileus* virginianus in Oregon and Washington. Northwest Science 97:99–112.
- Wakeley J. 1993. Substitution rate variation among sites in hypervariable region 1 of human mitochondrial DNA. Journal of Molecular Evolution 37:613–623.

#### 312 Piaggio et al.