




Letter To The Editor

Defense of an Expanded Historical Range for the Mexican Wolf: A Comment on Heffelfinger et al.

SARAH A. HENDRICKS , Department of Biological Sciences and Institute of Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, ID, USA

STEPHAN KOBLMÜLLER, Institute of Zoology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria

RYAN J. HARRIGAN, Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, 300 LaKretz Hall, Los Angeles, CA 90095, USA

JENNIFER A. LEONARD, Conservation and Evolutionary Genetics Group, Estación Biológica de Doñana (EBD-CSIC), 41092 Sevilla, Spain

RENA M. SCHWEIZER, Division of Biological Sciences, University of Montana, 32 Campus Dr., Missoula, MT 59812, USA

BRIDGETT M. VONHOLDT, Department of Ecology and Evolutionary Biology, Princeton University, M151 Guyot Hall, Princeton, NJ 08544, USA

ROLAND KAYS, North Carolina Museum of Natural Sciences, Biodiversity Lab, Raleigh, NC 27601, USA; and Department of Forestry & Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

ROBERT K. WAYNE,¹ Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 610 Charles E. Young Drive East, Los Angeles, CA 90095, USA

In a recent review, Heffelfinger et al. (2017) question the utility of currently available genetic data and habitat suitability evidence as being sufficient justification for a proposed historical range expansion of the Mexican wolf (*Canis lupus baileyi*). According to these authors, the opinions of experts who observed wolves in the wild prior to extirpation and subsequent morphologic analysis of historical specimens should have more weight than genomic data in designation of a historical range. We assert that reintroductions and wildlife management plans should develop definitive expectations based on evolutionary hypotheses, and use genetic data to test them. The field of evolutionary genetics has experienced a revolution, given genome-wide typing and sequencing approaches, and we hope that Heffelfinger et al. might value this dramatic shift when considering conservation recommendations and future research possibilities. We have 4 main concerns with the work of Heffelfinger et al., which could be detrimental to the successful conservation and management of the subspecies.

MORPHOLOGY AND EVOLUTIONARY INFERENCE

Heffelfinger et al. (2017: 770) conclude that “differences in skull morphometrics are valuable indices to the geographic barriers to gene flow.” However, skull size, which is the principle phenotypic character used to deduce the original

historical distribution of Mexican wolves (Bogan and Melhop 1983, Nowak 1995), is not a reliable indicator of evolutionary distinction at the subspecies level because it can be plastically altered by habitat or prey size and abundance, or simply vary through time (Gortázar et al. 2000, Huston and Wolverson 2011, McNutt and Gusset 2012, Meachen and Samuels 2012). Taxonomy is best served by a focus on characters that have near perfect heritability, such as DNA sequence changes, which define evolutionary groups in a web-of-life framework (Arnold 2016, vonHoldt et al. 2017). The use of size as a diagnostic indicator of ancestry for Mexican wolves presumes that it maps to phylogeny. However, this is often not the case in wolves (Fan et al. 2016). In fact, none of the 5 currently supposed North American gray wolf subspecies based on morphologic characters are well matched with partitions based on genome-wide nuclear genetic markers (vonHoldt et al. 2011, Schweizer et al. 2016). A single genetic unit may contain wolves of varying size; hence, slightly larger wolves outside the original Mexican wolf range may share a common ancestry with them, which is consistent with the genetic findings of Leonard et al. (2005) and Hendricks et al. (2016).

THE OPINION OF EXPERTS AND TYPOLOGICAL THINKING

Heffelfinger et al. (2017) suggest that field observations made during the period of extirpation and subsequent cranial morphometric studies should dominate definitions of geographic range. However, early historical observations are weak data for range inference and opinions of experts (as defined by Heffelfinger et al. [2017]) were developed under a typological framework in large part prior to acceptance of the

Received: 2 June 2017; Accepted: 20 July 2017

¹E-mail: rwayne@eeb.ucla.edu

modern evolutionary synthesis and did not incorporate evolutionary thinking. Even minor variations, often observed in just a few specimens, were used to define subspecies and races, and this Victorian legacy has carried over into modern times. For example, in the southern United States, historically black wolves were morphologically defined as a distinct species and then subspecies (*Canis rufus niger*). However, genetic analysis of gray wolves and closely related canids now suggest that the black coat coloration came from past hybridization with dogs, and gray and black wolves are the same species (Leonard et al. 2002, Anderson et al. 2009). The modern systematic framework for taxonomy uses shared-derived traits to define clades, such as those based on mtDNA or nuclear sequence data. These clades are then the basis for evolutionary taxonomic units (Moritz 1994). As such, size is a dubious character for evolutionary inference at best and average size may differ between populations depending on how they are defined and sample size. The classic text by (Young and Goldman 1944) cited by Heffelfinger et al. (2017) advocated 24 subspecies based on the sort of traits Heffelfinger et al. (2017) suggest can be used to define the Mexican wolf. This number was reduced to only 5 in recent analyses using a subset of skull measurements (Bogan and Melhop 1983, Nowak 1995). Some populations, such as the Mexican wolf, may be so narrowly defined that size does not overlap with other populations despite sharing a close evolutionary history. Under a modern view of admixture in current wolves, larger wolves observed by past naturalists may have been admixed or, despite size differences, are genetically and evolutionarily Mexican wolves. Large intergradation zones likely existed between Mexican wolves and other adjoining populations as suggested by the historical genetic data (Leonard et al. 2005, Hailer and Leonard 2008). Hence, a simple typological model as advocated by Heffelfinger et al. (2017) is not appropriate for informing either conservation or reintroduction decisions.

LIMITATIONS OF GENETIC DATA

Heffelfinger et al. (2017) indicate that the sample sizes included in Leonard et al. (2005) and Hendricks et al. (2016) are inadequate for genetic data to delineate historical range. Specifically, the authors suggest that it is impossible to rule out the process of genetic drift and incomplete lineage sorting to explain the distinct mtDNA clade for Mexican wolves. We maintain the Mexican wolf is one of the best defined groupings below the species level of any large North American vertebrate, which is supported by mtDNA sequence, microsatellite loci, genome-wide single nucleotide polymorphisms, and complete genome sequence data (Hedrick et al. 1997, Leonard et al. 2005, vonHoldt et al. 2011, 2016, Fan et al. 2016). The clade has a geographic coherence not expected for incomplete lineage sorting and recent analyses place the mtDNA clade in a worldwide context showing that it is highly distinct from other modern North American wolves (Koblmüller et al. 2016). The lack of geographic sampling is in part compensated by the large number of polymorphisms used to reconstruct evolutionary

history (Morin et al. 2004, Landguth et al. 2011, vonHoldt et al. 2011, 2016). In fact, a single genome can reveal much of the history of an entire species (Gronau et al. 2011, Li and Durbin 2011), and whole genome data support the distinctiveness of the Mexican wolf (Freedman et al. 2014, Fan et al. 2016, vonHoldt et al. 2016). Further, Hendricks et al. (2016) uses a combined approach of molecular, morphological (skull), and habitat suitability modeling data to incorporate evolutionary and ecological evidence to compensate for the paucity of available historical samples. Using multiple lines of scientific evidence, rather than single traits or *ad hoc* descriptions of one or few specimens, has similarly been used to characterize the taxonomic standings of the tiger (*Panthera tigris*), a system plagued with controversy that has hindered management efforts (Wilting et al. 2015).

HISTORICAL RANGE DEFINITION

In the absence of more extensive genetic data and given the questionable inferences from body size and historical observations, habitat suitability estimates in Hendricks et al. (2016) provide an alternative hypothesis for geographic range. Several conclusions by Heffelfinger et al. (2017) seem to misrepresent habitat suitability models. For instance, these models cannot provide evidence regarding the historical demography of populations. The fact that suitable habitat for Mexican wolves are predicted east and west of the Nevada and Arizona deserts implies only that suitable habitats exist for this species in these regions. Whether populations share a common history, or as Heffelfinger et al. (2017: 772) state “parallel changes driven by common ecological forces,” is not a question that these models, nor the conclusions of Hendricks et al. (2016), attempt to answer. These models do, however, identify habitat, outside the traditionally defined historical range of the Mexican wolf, that are currently suitable for this species. Heffelfinger et al. (2017) also argue against the ecological modeling results in Hendricks et al. (2016) because we predict suitable habitat exists as far north as southern Oregon. That areas far from the historical geographic range have suitable habitat, does not contradict its use for a guide to historical range, rather, criteria such as continuity or possible dispersal must be used in addition to defend an expanded historical geographic range. Much of the additional range we find in the Grand Canyon ecoregion and Southern Rockies, is confirmed by other landscape-scale analysis (Sneed 2001) and niche-based studies (Carroll et al. 2014) and with observations of long-range dispersal and admixture zones in modern wolves. Further, a web-of-life framework explains the evidence for a historical hybridization of *C. l. baileyi* and *C. l. mogollonensis*, which extends the historical range northwards, and allows for future admixture in this region (vonHoldt et al. 2017). Natural admixture zones should be part of reintroduction plans and admixed individuals providing ecosystem functionality should receive protection (Arnold 2016, Wayne and Shaffer 2016, vonHoldt et al. 2017).

Given the difficulty of establishing Mexican wolves in the United States and Mexico, which contrasts with the

considerable success of Yellowstone-Idaho reintroduction (Wayne and Hedrick 2011), expanded historical range and suitable habitat is needed, and as discussed above, is supported by ecological and genetic evidence. Further, climate change is likely to increase the proportion of suitable range northwards. Contemporary species conservation needs to move beyond strict adherence to maintaining or restoring populations within their putative historical ranges. Emphasis on the realized contemporary and likely future range may enhance the long-term viability of the highly endangered Mexican wolf.

LITERATURE CITED

- Anderson, T. M., B. M. vonHoldt, S. I. Candille, M. Musiani, C. Greco, D. R. Stahler, D. W. Smith, B. Padhukasahasram, E. Randi, J. A. Leonard, C. D. Bustamante, E. A. Ostrander, H. Tang, R. K. Wayne, and G. S. Barsh. 2009. Molecular and evolutionary history of melanism in North American gray wolves. *Science* 323:1339–1343.
- Arnold, M. L. 2016. Divergence with genetic exchange. Oxford University Press, Oxford, United Kingdom.
- Bogan, M. A., and P. Melhop. 1983. Systematic relationships of gray wolves (*Canis lupus*) in southwestern North America. Occasional Papers of the Museum of Southwestern Biology 1:1–21.
- Carroll, C., R. J. Fredrickson, and R. C. Lacy. 2014. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. *Conservation Biology* 28:76–86.
- Fan, Z., P. Silva, I. Gronau, S. Wang, A. S. Armero, R. M. Schweizer, O. Ramirez, J. Pollinger, M. Galaverni, D. Ortega-Del Vecchyo, L. Du, W. Zhang, Z. Zhang, J. Xing, C. Vilà, T. Marques-Bonet, R. Godinho, B. Yue, and R. K. Wayne. 2016. Worldwide patterns of genomic variation and admixture in gray wolves. *Genome Research* 26:163–173.
- Freedman, A. H., I. Gronau, R. M. Schweizer, D. Ortega-Del Vecchyo, E. Han, P. M. Silva, M. Galaverni, Z. Fan, P. Marx, B. Lorente-Galdos, H. Beale, O. Ramirez, F. Hormozdiari, C. Alkan, C. Vilà, K. Squire, E. Geffen, J. Kusak, A. R. Boyko, H. G. Parker, C. Lee, V. Tadigotla, A. Siepel, C. D. Bustamante, T. T. Harkins, S. F. Nelson, E. A. Ostrander, T. Marques-Bonet, R. K. Wayne, and J. Novembre. 2014. Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics* 10:e1004016.
- Gortázar, C., A. Travaini, and M. Delibes. 2000. Habitat-related microgeographic body size variation in two Mediterranean populations of red fox (*Vulpes vulpes*). *Journal of Zoology* 250:335–338.
- Gronau, I., M. J. Hubisz, B. Gulko, C. G. Danko, and A. Siepel. 2011. Bayesian inference of ancient human demography from individual genome sequences. *Nature Genetics* 43:1031–1034.
- Hailer, F., and J. A. Leonard. 2008. Hybridization among three native North American *Canis* species in a region of natural sympatry. *PLoS ONE* 3:e3333.
- Hedrick, P. W., P. S. Miller, E. Geffen, and R. Wayne. 1997. Genetic evaluation of the three captive Mexican wolf lineages. *Zoo Biology* 16:47–69.
- Heffelfinger, J. R., R. M. Nowak, and D. Paetkau. 2017. Clarifying historical range to aid recovery of the Mexican wolf. *Journal of Wildlife Management* 81:766–777.
- Hendricks, S. A., P. R. S. Clee, R. J. Harrigan, J. P. Pollinger, A. H. Freedman, R. Callas, P. J. Figura, and R. K. Wayne. 2016. Re-defining historical geographic range in species with sparse records: implications for the Mexican wolf reintroduction program. *Biological Conservation* 194:48–57.
- Huston, M. A., and S. Wolverton. 2011. Regulation of animal size by eNPP, Bergmann's rule and related phenomena. *Ecological Monographs* 81:349–405.
- Koblmüller, S., C. Vilà, B. Lorente-Galdos, M. Dabad, O. Ramirez, T. Marques-Bonet, R. K. Wayne, and J. A. Leonard. 2016. Whole mitochondrial genomes illuminate ancient intercontinental dispersals of grey wolves (*Canis lupus*). *Journal of Biogeography* 43:1728–1738.
- Landguth, E. L., B. C. Fedy, S. J. Oyler-McCance, A. L. Garey, S. L. Emel, M. Mumma, H. H. Wagner, M.-J. Fortin, and S. A. Cushman. 2011. Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern. *Molecular Ecology Resources* 12:276–284.
- Leonard, J. A., C. Vilà, and R. K. Wayne. 2005. Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Molecular Ecology* 14:9–17.
- Leonard, J. A., R. K. Wayne, J. Wheeler, R. Valadez, S. Guillén, and C. Vilà. 2002. Ancient DNA evidence for Old World origin of New World dogs. *Science* 298:1613–1616.
- Li, H., and R. Durbin. 2011. Inference of human population history from individual whole-genome sequences. *Nature* 475:493–496.
- McNutt, J. W., and M. Gusset. 2012. Declining body size in an endangered large mammal. *Biological Journal of the Linnean Society* 105:8–12.
- Meachen, J. A., and J. X. Samuels. 2012. Evolution in coyotes (*Canis latrans*) in response to the megafaunal extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 109:4191–4196.
- Morin, P. A., G. Luikart, R. K. Wayne, and the SNP Workshop Group. 2004. SNPs in ecology, evolution and conservation. *Trends in Ecology & Evolution* 19:208–216.
- Moritz, C. 1994. Defining “evolutionarily significant units” for conservation. *Trends in Ecology & Evolution* 9:373–375.
- Nowak, R. M. 1995. Another look at wolf taxonomy. Pages 375–397 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.
- Schweizer, R. M., B. M. vonHoldt, R. Harrigan, J. C. Knowles, M. Musiani, D. Coltman, J. Novembre, and R. K. Wayne. 2016. Genetic subdivision and candidate genes under selection in North American grey wolves. *Molecular Ecology* 25:380–402.
- Sneed, P. G. 2001. The feasibility of gray wolf reintroduction to the Grand Canyon ecoregion. *Endangered Species Update* 18:153–158.
- vonHoldt, B. M., K. E. Brzeski, D. S. Wilcove, and L. Rutledge. 2017. Redefining the role of admixture and genomics in species conservation. *Conservation Letters* 10:in press.
- vonHoldt, B. M., J. A. Cahill, Z. Fan, I. Gronau, J. Robinson, J. P. Pollinger, B. Shapiro, J. Wall, and R. K. Wayne. 2016. Whole-genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf. *Science Advances* 2:e1501714.
- vonHoldt, B. M., J. P. Pollinger, D. A. Earl, J. C. Knowles, A. R. Boyko, H. Parker, E. Geffen, M. Pilot, W. Jedrzejewski, B. Jedrzejewska, V. Sidorovich, C. Greco, E. Randi, M. Musiani, R. Kays, C. D. Bustamante, E. A. Ostrander, J. Novembre, and R. K. Wayne. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. *Genome Research* 21:1294–1305.
- Wayne, R. K., and P. W. Hedrick. 2011. Genetics and wolf conservation in the American West: lessons and challenges. *Heredity* 107:16–19.
- Wayne, R. K., and H. B. Shaffer. 2016. Hybridization and endangered species protection in the molecular era. *Molecular Ecology* 25:2680–2689.
- Wilting, A., A. Courtiol, P. Christiansen, J. Niedballa, A. K. Scharf, L. Orlando, N. Balkenhol, H. Hofer, S. Kramer-Schadt, J. Fickel, and A. C. Kitchener. 2015. Planning tiger recovery: understanding intraspecific variation for effective conservation. *Science Advances* 1:e1400175.
- Young, S., and E. A. Goldman. 1944. *The wolves of North America*. American Wildlife Institute, Washington, D.C., USA.