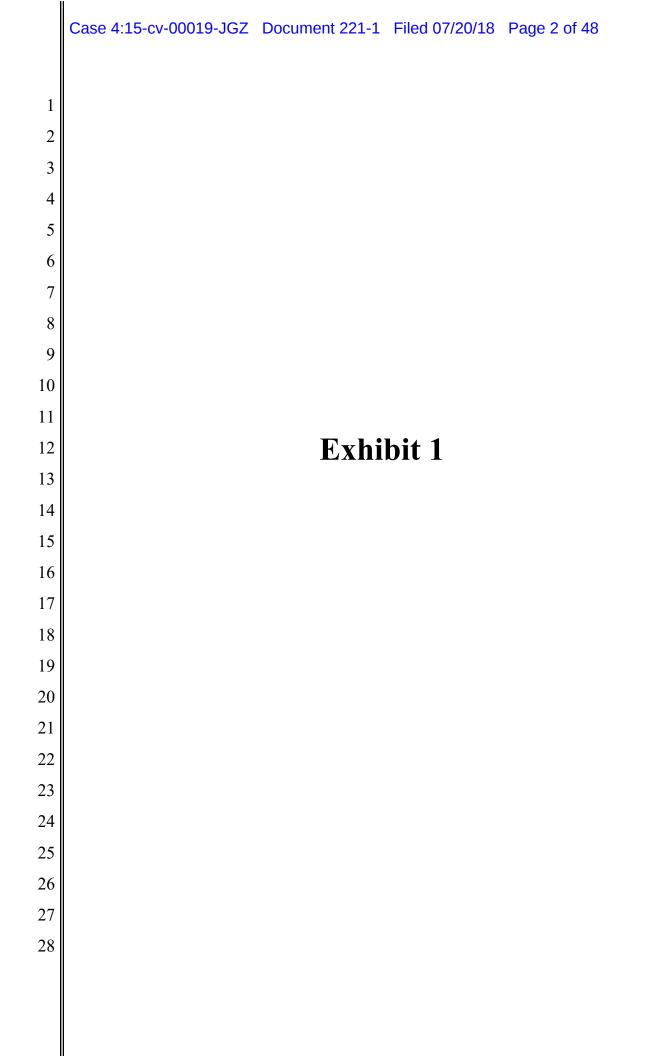
|          | Case 4:15-c | v-00019-JGZ    | Document 221-1       | Filed 07/20/18 | Page 1 of 48 |
|----------|-------------|----------------|----------------------|----------------|--------------|
| 1        |             |                |                      |                |              |
| 1        |             |                | NDEX OF ATTAC        |                | ſS           |
| 2        | Exhibit 1   |                | of Philip W. Hedric  |                |              |
| 3        | Exhibit 2   | Declaration of | of Carlos Carroll, P | h.D.           |              |
| 4        |             |                |                      |                |              |
| 5<br>6   |             |                |                      |                |              |
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|          |   |                |   |
| 1        | Timothy J. Preso (Montana Bar No. 5255)<br>Earthjustice       |                |   |
| 2        | 313 East Main Street  |                |   |
| 3        | Bozeman, MT 59715<br>tpreso@earthjustice.org                  |                |   |
| 4        | Fax: (406) 586-9695   |                |   |
| 5        | Phone: (406) 586-9699   |                |   |
| 6        | Heidi McIntosh (Utah Bar No. 6277)                            |                |   |
| 7        | Earthjustice<br>633 17th Street, Suite 1600                   |                |   |
| 8        | Denver, CO 80202  |                |   |
| 9        | hmcintosh@earthjustice.org<br>Fax: (303) 623-8083             |                |   |
| 10       | Phone: (303) 623-9466   |                |   |
| 11       | Attorneys for Plaintiffs Center for                           |                |   |
| 12       | Biological Diversity and Defenders of Wildlife                |                |   |
| 13       | Andrea Santarsiere (Idaho Bar No. 8818)                       |                |   |
| 14       | Center for Biological Diversity<br>P.O. Box 469               |                |   |
| 15       | Victor, ID 83455  |                |   |
| 16       | asantarsiere@biologicaldiversity.org<br>Phone: (303) 854-7748 |                |   |
| 17       | Attorney for Plaintiff Center for                             |                |   |
| 18       | Biological Diversity  |                |   |
| 10<br>19 | IN THE UNITED STATE   | ES DISTRICT C  | COURT                                   |
|          | FOR THE DISTRICT OF ARIZONA                                   |                |   |
| 20       | Center for Biological Diversity, et al.,                      | )              |   |
| 21       |   | ) (conso       | 15-cv-00019-TUC-JGZ blidated with Nos.  |
| 22       | Plaintiffs,   |                | v-00179-TUC-JGZ and<br>v-00285-TUC-JGZ) |
| 23       | VS.   | )              | ARATION OF PHILIP                       |
| 24       | Ryan Zinke, Secretary of the Interior, et al.,                |                | EDRICK, Ph.D.                           |
| 25       | Defendants.   | Ś              |   |
| 26       |   | )              |   |
| 27       |   |                |   |
| 28       |   |                |   |

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1

I, Philip W. Hedrick, Ph.D., declare as follows:

2 I am a Professor Emeritus in the School of Life Sciences at Arizona State 1. 3 University. My areas of expertise are population genetics and conservation biology with 4 a specific focus on genetic variation in populations, including how genetics can impact 5 the survival of rare and endangered species. In population genetics, I examine how 6 genetic variation in a population is affected by selection, inbreeding, migration between 7 populations, and random genetic change over time (genetic drift). In conservation biology, I study how genetics and evolutionary factors, such as inbreeding and genetic 8 9 drift, can be used to help prevent extinction in endangered species. I have authored ten 10 books and more than 250 articles in scientific journals and other publications about these 11 and related subject areas. I served on the Editorial Boards for the scientific journals Conservation Biology, Animal Conservation, Conservation Genetics, Heredity, Journal 12 13 of Heredity, Evolution, Evolutionary Applications, Journal of Theoretical Biology, 14 Genetica, and Molecular Ecology. I was the President of both the American Society of Naturalists and the American Genetics Association and am a Fellow of the American 15 Association for the Advancement of Science. In recent years, I have also worked on 16 17 conservation efforts for rare and endangered species including Mexican wolves, red wolves, Isle Royale wolves, winter run Chinook salmon, desert bighorn sheep, bison, 18 19 Gila topminnows, and other species. In particular, from 1994-2010 I served as a member of two Mexican wolf recovery teams assembled by the U.S. Fish and Wildlife Service. 20 My published work has been extensively cited and relied upon by the U.S. Fish and 21 Wildlife Service in connection with Mexican wolf recovery efforts, including in the 22 23 November 2014 Final Environmental Impact Statement for the Proposed Revision to the 24 Regulations for the Nonessential Experimental Population of the Mexican Wolf and the November 2017 Biological Report for the Mexican Wolf, which was prepared in 25 connection with the first revision of the Mexican Wolf Recovery Plan. I also was among 26 the Service's selected peer reviewers for that plan. Further detail and documentation of 27 28

my credentials is provided in my *curriculum vitae*, a copy of which is attached to this
 declaration as Exhibit 1.

3 2. I submit this declaration to explain the severe genetic problems imperiling the wild Mexican wolf population, to address the inadequacies of the U.S. Fish and 4 5 Wildlife Service's response to those problems to date, and to identify, based on my 6 knowledge and experience, the response needed to seize the opportunity that is available 7 today to rehabilitate the genetic impoverishment of the wild Mexican wolf population before it is too late. In this declaration, I cite and discuss a number of scientific 8 9 publications, referencing them by author and date as is customary in scientific literature. 10 A bibliography of these cited references is attached to this declaration as Exhibit 2.

3. 11 The Mexican wolf population existing today has severely depleted genetic integrity. The initial captive source population of Mexican wolves, originally called the 12 13 Certified Lineage because it had a well-documented and managed pedigree (since called 14 the McBride lineage), was descended from three founders. Two other putative captive Mexican wolf lineages whose history was less well documented, Ghost Ranch and 15 Aragón, were genetically evaluated and determined also to be Mexican wolf lineages 16 17 (Hedrick et al. 1997). These other two lineages were each descended from two founders and combined with the McBride lineage to form the present day Mexican wolf population 18 19 with seven total founders.

4. The original goal in the combined captive population was a constitution of 20 80% McBride, 10% Ghost Ranch, and 10% Aragón (Hedrick et al. 1997). Given that 21 there were no problems in combining the lineages, Hedrick et al. (1997) suggested the 22 23 percentages for Ghost Ranch and Aragón should not be greater than 25% because the 24 McBride lineage was both genetically well managed and had a thoroughly documented history and had both more founders and more genetic variation than the other two 25 lineages. Hedrick (personal communication) suggested a secondary goal of ancestry 26 could be 60% McBride, 20% Ghost Ranch, and 20% Aragón. This combination would 27 28 both result in an increase in genetic variation (Hedrick et al., 1997) and provide for the

reduction of the lowered fitness (inbreeding depression) that had accumulated within the
 lineages (Fredrickson et al. 2007). The captive population in 2017 had ancestry of
 59.7%, 20.6%, and 19.6% for the McBride, Ghost Ranch, and Aragón lineages,
 respectively (Siminski and Spevak, 2017), very close to the above recommendation.

5 5. There are several overall measures of genetic diversity. Using known 6 pedigree information, gene diversity (GD) is often used. Typically, when captive 7 populations are established from wild populations, the goal is to retain at least 90% of the initial gene diversity (heterozygosity). However, given pedigree information, the 2017 8 9 current GD of the captive Mexican wolf population is only 0.830 (Siminski and Spevak, 2017), meaning that these wolves retain only 83% of the species' initial gene diversity, 10 11 well below this goal. A second overall genetic measure for the combination of the lineages is called the number of founder genome equivalents (FGE). Given that there 12 were seven founders, the maximum FGE for the Mexican wolf population is 7. However, 13 14 because of historical factors such as the unequal progeny contribution of individuals over generations and unequal contribution of the three lineages, this number has been reduced. 15 In the captive population, which is managed to retain genetic variation and avoid 16 17 inbreeding as much as possible, the FGE in 2017 was 2.94. A third overall genetic measure is mean kinship (MK), which measures the relatedness of individuals within a 18 19 population. This measure has a value of 0 when all individuals are unrelated and a value 20 of 0.25 when individuals are as closely related as full siblings. In the current captive population, the mean kinship is 0.170. 21

6. The reintroduced Mexican wolf population in the wild (MWEPA) is in
significantly worse genetic shape than the captive population. In 2017, the MWEPA
population had 77.0%, 15.8%, and 7.2% ancestry from the McBride, Ghost Ranch, and
Aragón lineages, respectively (Siminski and Spevak, 2017). This is more from the
McBride lineage and less from both the Ghost Ranch and Aragón lineages than in the
captive population (and the recommendation discussed above). In addition, the GD is
only 0.755 in the MWEPA population showing that it has lost 44% more variation than

the captive population. Also the FGE is only 2.04 in the MWEPA, 30.6% less than that
 in the captive population. In the reintroduced population, MK is 0.254, 49.4% higher
 than that in the captive population, and indicates that these wolves are as closely related
 as full siblings.

5 7. The low gene diversity, the very low number of effective founders and the high mean kinship of Mexican wolves in the reintroduced population appear to be as 6 7 extreme as in any reintroduced population of an endangered species, and portend severe 8 genetic problems. In addition, "all current known wild breeding pairs are producing pups 9 related to the Bluestem Pack, specifically breeding female F521" (Mexican Wolf 10 Interagency Field Team (IFT), 2017). This is particularly worrisome and could result in 11 fast genetic degradation. For example, inbreeding in descendants of this breeding female could result in lowered survival, fecundity, etc., and a high proportion of ancestry from 12 13 this female could greatly reduce genetic variation in the population. This highlights the 14 importance of prompt action to improve the genetic diversity of the MWEPA population.

8. As discussed above, when captive populations are established from wild 15 populations, typically the goal is to retain at least 90% of the initial gene diversity 16 17 (heterozygosity) of the wild members of the species that are taken into captivity. It is important to note that the initial population might have much less genetic variation than it 18 had ancestrally before the wild population became endangered. This appears to be the 19 case for Mexican wolves, which have a very low base level of genetic diversity in the 20 captive population compared to other wolf populations. This low base level of genetic 21 diversity likely reflects low population numbers before the captive population was 22 23 initiated. The observed heterozygosity estimated over all the genes in the genome in 24 Mexican wolves averaged only 0.12, about 55% that of northern gray wolves, which had a heterozygosity of 0.22 (vonHoldt et al. 2011). This level of variation in Mexican 25 wolves is about the amount of genetic variation expected if a pair of wolves were taken at 26 random from northern gray wolves, this pair reproduced and had two progeny, and those 27 28 progeny had offspring to produce a population. In other words, the level of genetic

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variation in Mexican wolves is only that expected from an extreme two-generation
 bottleneck of two individuals each generation from northern gray wolves. This indicates
 that there is very limited genetic variation in Mexican wolves for future adaptation to
 environmental challenges, such as new diseases and climate change, and further
 highlights the importance of a prompt, effective response to the Mexican wolf's genetic
 imperilment.

- 9. Available scientific information indicates that genetic rescue of the
  Mexican wolf population remains possible. Specifically, Fredrickson et al. (2007) found
  that there was inbreeding depression for litter size in both captive and wild Mexican
  wolves and also found that crosses between the three lineages (McBride, Ghost Ranch,
  and Aragón) showed an increased fitness, resulting in temporary genetic rescue.
- 10. More recently, the U.S. Fish and Wildlife Service, relying on Miller (2017), 12 asserted in the first revision of the Mexican Wolf Recovery Plan that inbreeding 13 depression is impacting the probability of a breeding pair producing a litter, but not to a 14 degree that is limiting population growth. However, since 2009, there has been extensive 15 artificial supplemental feeding of wild denning Mexican wolves that has greatly 16 17 increased the survival of pups. It is probable that this supplemental feeding masks some of the detrimental effects of inbreeding, an impact that would be evident if feeding was 18 19 discontinued. The present-day members of the captive and wild Mexican wolf 20 populations, which are three generations advanced from those examined by Fredrickson 21 et al. (2007), would be expected to still exhibit as much or more inbreeding depression as earlier. A recent analysis of all the wild Mexican wolves that were not fed 22 supplementally showed statistically significant inbreeding depression (Carroll, personal 23 24 communication). These effects were not evident in the analysis associated with Miller (2017) because data from unfed wolves were analyzed together with data from 25 supplementally fed wolves; feeding masked inbreeding depression effects in this latter 26 group. In terms of inbreeding depression effect, this analysis predicts that the litter size 27 28 for a 6-year-old female would be reduced by 0.72 pups per litter as inbreeding increased
  - 5

from 0.15 to 0.25, which is within the range of inbreeding currently shown by wolves in
 the wild population (Carroll, personal communication).

11. Releasing more genetically diverse wolves from the captive Mexican wolf
population is essential to positively influence the genetic diversity of the wild population.
To evaluate generally the impact of any releases genetically, in addition to examining the
level of gene diversity, the improvement in FGE and MK should also be incorporated as
concurrent goals.

8 12. The Mexican wolf release schemes addressed by the U.S. Fish and Wildlife Service to date do not adequately respond either to the severe nature of the Mexican 9 10 wolf's genetic imperilment or the urgency of the available opportunity to positively 11 influence the Mexican wolf's genetic diversity. The U.S. Fish and Wildlife Service's most recent assessment of opportunities to utilize releases to improve the genetic 12 diversity of the wild Mexican wolf population consists of a population viability analysis 13 14 (PVA) presented in Miller (2017), which accompanied the Service's November 2017 final Biological Report for the Mexican wolf (a document prepared in connection with 15 the first revision of the Mexican Wolf Recovery Plan). The PVA simulations by Miller 16 17 (2017), which addressed only the level of gene diversity, examined how different numbers of releases from the captive population might impact the genetic variation in the 18 19 MWEPA population. Strikingly, the prediction is that the levels of releases examined in 20 Miller (2017) would have very little impact on the expected genetic variation in the wild 21 population. For example, for a parameter combination discussed by Miller (2017) (management target of 379 wolves and annual adult mortality rate of 24.9%), the level of 22 23 gene diversity after 100 years in the MWEPA population, without any releases, is expected to be 0.665 (Table 4 in his report). In comparison, for the release scheme 24 discussed by Miller (2017) which reflects the level of releases discussed in the 25 environmental impact statement ("EIS") for the January 2015 Mexican wolf 10(j) rule 26 (EIS20 20), the expected gene diversity is 0.684 (Table 7 in his report), only 2.9% 27 28 higher. The expected gene diversity in the captive population after 100 years is 0.785

(Table 4 in his report) so the EIS20 20 release scheme is predicted to move the gene 1 2 diversity of the MWEPA population only 15% of the way to that in the captive 3 population, marking very small progress. In other words, these release goals are inadequate to meaningfully address the genetic imperilment of the Mexican wolf 4 5 population. Miller (2017) does not evaluate the impact of these releases on either FGE or 6 MK. However, Carroll (personal communication) has done so and the MK value for the 7 EIS20 20 release scheme is 48.8% higher and FGE value is 33.0% lower in the wild 8 population than in the captive population. These results further demonstrate that these 9 release goals are inadequate to meaningfully address the genetic imperilment of the Mexican wolf population. 10

11 13. In addition, Miller (2017) also simulated a doubling of the various release schedules into the MWEPA and measured the expected impact on GD. The GD for the 12 same EIS20 20 demographic and release schedule combination with doubled releases 13 14 ([EIS X 2]20 20) was 0.700 (his Table 17 in the Addendum to the Mexican Wolf PVA 15 Report). When the releases are doubled, then the expected gene diversity is 5.3% higher than when there are no releases and these releases were predicted to move the gene 16 17 diversity 29% of the way to the level expected in the captive population. Again, Miller (2017) does not evaluate the impact of these releases on either FGE or MK but Carroll 18 (personal communication) has done so and the MK value is 39.1% higher and FGE value 19 is 28.2% lower in the wild population than in the captive population. Even in this 20 21 doubled release schedule, the expected gene diversity was inadequate to address the Mexican wolf's genetic imperilment. 22

14. It appears that the U.S. Fish and Wildlife Service is depending upon crossfostering of Mexican wolf pups to counter the genetic problems discussed above.
Specifically, the Service's November 2017 Mexican Wolf Recovery Implementation
Strategy does not appear to adopt any of the release schemes analyzed in Miller (2017)
but instead identifies an objective to "[c]ross-foster 12 wolf pups/year" as a means to
"[i]mprove gene diversity and maintain the health of Mexican wolves." It is possible that

specifically designed cross-fostering could be beneficial but the number of cross-fostered 1 2 wolves since 2014 has been only 2 in 2014, 6 in 2015, 4 in 2017, and, I understand, 8 in 3 2018, much below the goal stated in the Recovery Implementation Strategy of 12 pups annually. In addition, not all of these pups survived to the end of the year and many are 4 5 members of the same litter. This high relatedness among released pups would predictably have much less genetic impact than if unrelated pups were introduced. This 6 suggests that cross-fostering, a labor-intensive and very time-dependent option, would 7 not have a large genetic impact unless it was greatly increased or specifically targeted to 8 9 produce genetically important animals. Cross-fostering was not considered by Miller 10 (2017) and, given its logistical challenges, it appears that it would have less effect than 11 the planned, and inadequate, releases that he evaluated. In addition, because the individuals that are cross-fostered are pups, it generally takes two or more years after 12 their introduction for them to make a genetic contribution as breeders. By contrast, adult 13 14 wolves released from captivity may make a genetic contribution as breeders right away.

15. In conclusion, the Mexican wolf reintroduced population is critically 15 endangered because of its low genetic variation, low number of founder genome 16 equivalents, high mean kinship, and significant inbreeding depression. In the past few 17 years, there have been an inadequate number of releases of captive wolves into the wild 18 population to offset these problems. When the McBride, Ghost Ranch, and Aragón 19 lineages were combined, it provided an opportunity window to increase fitness as shown 20 by the genetic rescue documented by Fredrickson et al. (2007), an opportunity that was 21 not capitalized on and now is less available. Nevertheless, there remains an opportunity 22 to positively influence the Mexican wolf's genetic diversity. The plans detailed in Miller 23 24 (2017) do not provide sufficient releases to significantly counteract the genetic problems in the wild Mexican wolf population. For the Mexican wolf release program to have a 25 meaningful, timely, and positive impact on the genetic diversity of the wild Mexican wolf 26 population, several changes need to be made: 27

28

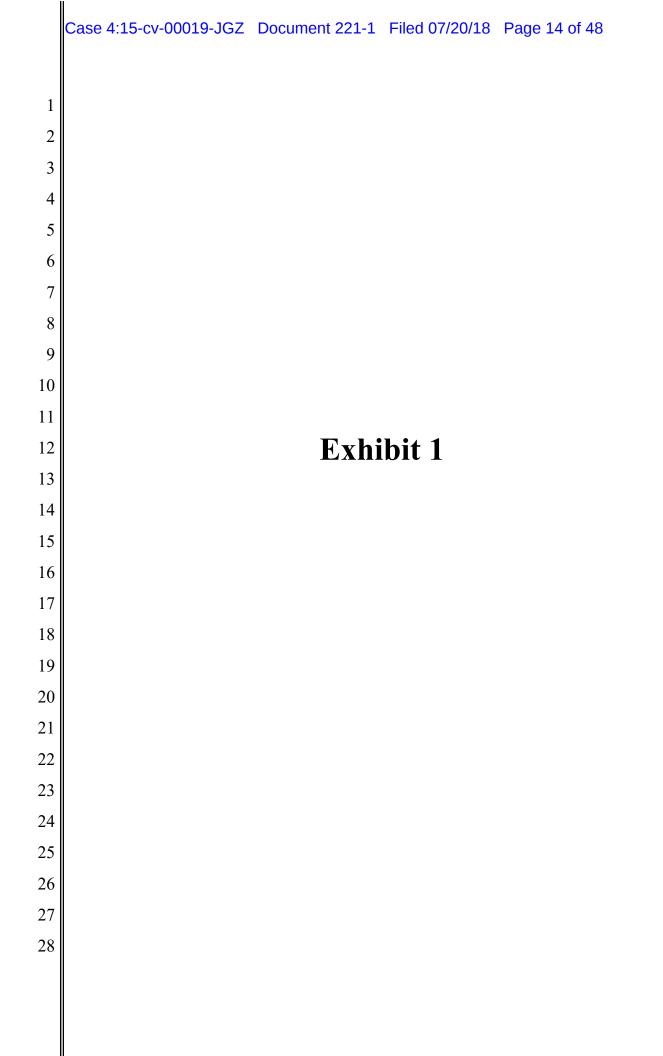
More releases need to be planned. At a minimum, these releases 1 (a) 2 should result in increasing the level of GD, FGE, and MK to a level at least 50% between 3 that expected in the captive population and that expected in the wild population, given no releases, for example, a GD level of 0.725. Based on my knowledge and experience, this 4 5 objective represents a reasonable and achievable target for rehabilitating the depleted genetic integrity of the wild Mexican wolf population through releases from the captive 6 population and, if achieved, could relieve some of the deleterious impacts of inbreeding 7 depression in the wild population. None of the release programs analyzed by Miller 8 9 (2017) would have a significant impact on the genetic imperilment of the wild 10 population. However, a GD of nearly 0.725 could be achieved with double the EIS 11 releases ([EIS X 2]20 20) plus the cross-fostered pup releases proposed in the Recovery Implementation Strategy (Carroll, personal communication). A figure graphically 12 13 illustrating this result, along with the outcomes of the release scenarios examined in Miller (2017) and the Recovery Implementation Strategy, is attached as Exhibit 3. 14

15 (b)**These releases need to start immediately**. If the wild population grows more before substantial genetic augmentation occurs, then more releases would be 16 necessary to have a given impact on the population. For example, it would take 20 17 wolves released into a population of size 200 to have the same impact as 10 wolves 18 released into a population of size 100, given other factors are equivalent. For this reason, 19 20 time is of the essence to begin an adequate release program and the window of 21 opportunity to maximize the impact of any such program will be irretrievably lost if not immediately pursued. 22

(c) Delay threatens further detrimental genetic changes. If an
adequate release program is delayed, then the wild population would be expected to
further decay genetically due to chance effects of genetic drift and unequal contributions
from a few individuals. In addition, natural selection is presumably occurring in the wild
population and to a lesser extent in the captive population (lesser in the captive
population because of detailed management). As a result, the wild population would be

9

expected to have both adaptive selection (selection for gene variants which are adaptive in the wild environment, such as disease resistance, etc.) and purifying selection (selection against detrimental gene variants that can cause low survival, genetic disease, etc.) operating and a delay would result in fewer generations of these beneficial effects. Also there may be some selection for captivity in the captive population (selection favoring gene variants that are advantageous only in captivity and not in the wild environment, such as selection for tameness, domestication traits, etc.), a factor that should be avoided as much as possible by making the releases sooner than later. I declare under penalty of perjury that the foregoing is true and correct. Executed day of June, 2018, at Winksingh Arizona. this Philip W. ledrick, Ph.D. 



# Curriculum Vitae: Philip W. Hedrick (May, 2018)

Personal Data: Born - 21 November 1942, Swampscott, Massachusetts

## Education:

| 1960-1962 | Hanover College, Indiana   |
|-----------|--|
| 1962-1963 | American University of Beirut, Lebanon                                 |
| 1963-1964 | B.A. Hanover College - Biology   |
| 1964-1966 | M.S. Univ. Minnesota - Genetics  |
| 1966-1968 | Ph.D. Univ. Minnesota - Genetics                                       |
|           | Dissertation: Selection in Finite Populations (Advisor, R.E. Comstock) |

# Experience:

# **Primary Appointments**

| 1964-1965 | Research Assistant, Univ. Minnesota                               |
|-----------|---|
| 1965-1968 | N.I.H., Predoctoral Fellow, Univ. Minnesota (with R. E. Comstock) |
| 1968-1969 | N.I.H., Postdoctoral Fellow, Univ. Chicago (with R. C. Lewontin)  |
| 1969-1973 | Assistant Professor, Univ. Kansas                                 |
| 1973-1979 | Associate Professor, Univ. Kansas                                 |
| 1975-1976 | Visiting Associate Professor, Univ. Calif Davis                   |
| 1979-1988 | Professor, Univ. Kansas   |
| 1982-1983 | Visiting Professor, Univ. Calif Berkeley                          |
| 1988-1992 | Professor of Biology, Pennsylvania State Univ.                    |
| 1992-2016 | Ullman Professor, Arizona State Univ.                             |
| 2016-     | Emeritus Ullman Professor, Arizona State Univ.                    |

## **Other Appointments**

| 1970 (summer)      | Visiting Professor, Univ. Groningen, Groningen, Netherlands |
|--------------------|---|
| 1979 (summer)      | Visiting Professor, Univ. Groningen, Groningen, Netherlands |
| 1980 (summer)      | Visiting Professor, Univ. Texas, Houston                    |
| 1981 (summer)      | Visiting Professor, Univ. Washington                        |
| 1982 (summer)      | Visiting Professor, Washington Univ.                        |
| 1982-1983          | Visiting Professor, Univ. Calif Berkeley                    |
| 1984-1988 (summer) | Visiting Professor, Univ. Calif Berkeley                    |
| 1986 (January)     | Visiting Lecturer, Nordic Graduate Course in Plant Breeding |
|                    | Univ. Helsinki, Finland                                     |
| 1988-1989(Dec-Feb) | Visiting Professor, Univ. New England, Armidale, Australia  |
| 1990 (JanMarch)    | Distinguished Research Fellow, Bodega Marine Lab.           |
| 1991 (March)       | Visiting Professor, Kyushu Univ., Fukuoka, Japan            |
| 1992 (summer)      | Visiting Professor, Oulu Univ., Oulu, Finland               |
|                    |   |

| Visiting Professor, Aarhus University, Aarhus, Denmark             |
|--|
| Adjunct Professor, Department of Ecology and Evolutionary Biology, |
| Univ. Arizona  |
| Visiting Professor, Univ. Zurich, Zurich, Switzerland              |
| Visiting Professor, Donana Biological Station-CSIC, Seville, Spain |
|  |

# Offices and Elected Positions

| 1970-1975    | Managing Editor, Evolution                              |
|--------------|---|
| 1977-1979    | Council Member, Evolution                               |
| 1978-1990    | Editor, Drosophila Information Service                  |
| 1986-1989    | Secretary, American Society of Naturalists              |
| 1987-present | Fellow, American Association for Advancement of Science |
| 1992         | President, American Society of Naturalists              |
| 2002         | President, American Genetics Association                |
|              |   |

## Editorial Positions

| Associate Editor, Evolution                     |
|---|
| Editorial Board, Journal of Theoretical Biology |
| Editorial Board, Genetica                       |
| Board of Editors, Conservation Biology          |
| Board of Editors, Animal Conservation           |
| Editorial Review Board, Conservation Genetics   |
| Board of Editors, Journal of Heredity           |
| Board of Editors, Heredity                      |
| Associate Editor, Molecular Ecology             |
| Board of Editors, Molecular Ecology             |
| Board of Editors, Evolutionary Applications     |
|   |

# Panels, Recovery Teams, and Committees

| 1983       | Panel Member, NSF-Population Biology and Physiological Ecology |
|------------|--|
| 1986-1991  | Technical Board, American Livestock Breeds Conservancy         |
| 1987-1988  | Scientific Advisor, Hooded Crane Species Survival Plan         |
| 1992       | Panel Member, NSF - Conservation Biology                       |
| 1992-1998  | Winter-Run Chinook Salmon Recovery Team                        |
| 1992-1997  | Board of Directors, Institute for Agricultural Biodiversity    |
| 1994-2010  | Mexican Wolf Recovery Team                                     |
| 1994       | Genome Resource Banking Committee - CBSG                       |
| 1994, 1999 | Florida Panther Genetics Committee - CBSG                      |
| 1999       | Whooping Crane Review Team                                     |
| 1999       | Red Wolf Program Review Committee                              |
| 1999       | PHVA of Desert Bighorn Sheep in New Mexico                     |
| 2000       | PHVA of Wolves in the Southern Rockies                         |
| 2000-2003  | Red Wolf Recovery Team   |

| 2001-2002<br>2001<br>2001 | Nevada Genomics Center Advisory Board<br>Committee on the Genetics of Wild Horses<br>PHVA of Mexican wolves |
|---------------------------|---|
| 2001 2002                 | Organizer of Molecular Evolutionary Genetics Symposium  |
| 2003-2010                 | Chiricahua Leopard Frog Recovery Team   |
| 2005-2008                 | Pallid Sturgeon Recovery Team Genetics Advisory Group   |
| 2005                      | Salmon in Alaska Review, Center for Independent Experts   |
| 2006-2007                 | Expert witness for World Wildlife Fund on wolves in Norway  |
| 2006                      | Outside Expert for the Finnish Centre of Excellence in Population   |
|                           | Genomic Research  |
| 2008                      | Workshop on Applying Conservation Biology to Endangered Species   |
|                           | Recovery Goals: The Wolf as a Case Study  |
| 2008                      | Panel on Artificial Propagation of Delta Populations (CA)   |
| 2008                      | Bison Genetics Advisory Panel   |
| 2010                      | Assessing Techniques for Bison Genetics Evaluation Panel  |
| 2012-2014                 | Isle Royale Wolf Genetics Panel   |
| 2017                      | Mexican Wolf Recovery Plan Review Panel   |

## Invited Symposium Lectures:

1975. Annual Drosophila Conference - Baton Rouge, Louisiana. *Simulation of X-linked Selection in* Drosophila.

1980. Population Genetics Workshop - Stanford, California. Factors Affecting Rates of Chromosomal Evolution.

1980. Midwest Population Biology Meeting - West Lafayette, Indiana *Genetic Hitchhiking:* A New Evolutionary Factor?

1983. Behavior Genetics Meeting - London, England. *Regulatory Gene Variation: Adaptation or Genetic Hitchhiking?* 

1983. XV International Congress of Genetics - New Delhi, India. *Speciation: A Population Genetics Perspective.* 

1984. Population Genetics in Forestry - Gottingen, Germany. *Inbreeding and Selection in Natural Populations*.

1984. Workshop on Genetic Management of Captive Populations - Front Royal, Virginia. *Protein Variation, Fitness, and Captive Propagation.* 

1985. Evolutionary Processes and Theory - Jerusalem, Israel. *Evolutionary Genetics: HLA as an Exemplary System*.

1985. Founder Effect in Evolution - Honolulu, Hawaii. *Founder Effect and Genetic Variance*.

1986. Applied Population Biology Symposium (Sloan Foundation) - Davis, California. *Genetics of Conservation in Zoos and Nature Reserves* 

1986. European Population Genetics Group (20th Anniversary Meeting) - Nottingham, England. *Evolutionary Genetics: HLA as an Exemplary System*.

1988. The Genetics and Evolutionary Biology of Meiotic Drive - Honolulu, Hawaii. *Segregation Distortion: Effect on Gametic Disequilibrium and Evidence at HLA.* 

1988. Genetic Conservation Symposium - Toronto, Ontario. *Conservation Genetics: An Overview*.

1988. Research Priorities in Conservation Biology - Miami, Florida. *Population Viability Analysis - Minimum Viable Population*.

1989. Ecological and Evolutionary Genetics of *Drosophila* - Armidale, Australia. *Habitat* Selection and Maintenance of Genetic Variation.

1989. Analytical Methods for Population Viability Analysis and Management - Front Royal, Virginia. *Allelic Diversity and Heterozygosity*.

1990. Conservation of Genetic Resources for Sustainable Development - Roros, Norway. *Population Genetics Theory in Genetic Conservation*.

1992. Presidential Address, American Society of Naturalists - Berkeley, California *Evolutionary Genetics of the Major Histocompatibility Complex.* 

1992. Finnish-American/International Plant Genetics Symposium - Oulu, Finland. Evolutionary Genetics and the Major Histocompatibility Complex: Another Classic Example.

1993. Conservation Genetics - Aarhus, Denmark. *Relevance of the Major Histocompatibility Complex (MHC) to Conservation Genetics*.

1993. Conservation Genetics of Endangered Pacific Salmon - Bodega Bay, California. *Estimation of Effective Population Size in Winter Run Chinook Salmon.* 

1994. Ecology and Genetics in Spatially Structured Populations - Tvarmine, Finland. *Metapopulation Dynamics and the Effective Population Size*.

1994. Metapopulations and Wildlife Conservation and Management - Albuquerque, New Mexico. *The Genetics of Metapopulations*.

1994. Navajo-Churro Sheep Association - Chinle, Arizona. *Conservation Breeding in Navajo-Churro Sheep*.

1995. 4th International Workshop on MHC Evolution - St. Augustine, Florida. *Conservation Genetics and MHC*.

1995. European Society of Evolutionary Biology - Edinburgh, Scotland. *Effective Population Size in a Metapopulation*.

1995. The Role of Captive Breeding / Artificial Propagation in the Restoration of Endangered Species - Newport, Oregon. *Conservation Genetics: Gila Topminnow, Florida Panther, and Mexican Wolf.* 

1995. Captive Breeding in Pacific Salmon - Bodega Bay, California. *Genetics and Conservation of Salmon*.

1995. Society for Conservation Biology - Fort Collins, Colorado. *Directions in Conservation Biology*.

1995. Southwestern Rare and Endangered Plants - Flagstaff, Arizona. *Molecular and Adaptive Variation: A perspective for Endangered Plants.* 

1996. MHC and Behavior - Kiel, Germany. Balancing Selection and MHC Variation

1996. The Genetic and Physiological Basis of Heterosis - Bodega Bay, California. *Balancing Selection and the Major Histocompatibility Complex (MHC)*.

1997. Unanswered Questions about Small Populations - Baltimore, Maryland. *Conservation Genetics: Gila Topminnow and Mexican Wolf.* 

1997. Arizona Heritage Alliance Seminar - Phoenix, Arizona. Conservation Genetics and Endangered Species.

1997. The Effects of Captivity on Endangered Species - Albuquerque, New Mexico. *Genetic Change and Captivity* 

1998. Conservation Genetics - Phoenix, Arizona. Southwest Working Group of Declining Amphibians.

1998. Inbreeding Depression and Conservation Biology - Sydney, Australia. *Conservation Genetics*.

1998. A General Framework for Genetics, Demography, and Population Viability in Conservation - Sydney, Australia. *Conservation Biology*.

1998. Conservation Genetics Examples, from Gila Topminnows, Winter-run Chinook Salmon, and Other Endangered Species - El Escorial, Spain. *Conservation of Genetic Resources*.

1998. Conservation Genetics Examples, from Gila Topminnows, Winter-run Chinook Salmon, and Other Endangered Species - Uppsala, Sweden. *Conservation Genetics*.

1999. Application of Molecular Genetics to Managing Endangered Species – San Diego. *Population Viability Analysis: Assessing Models for Recovering Endangered Species.* 

2000. ESUs and MUs within Species. Missoula, Montana. Conservation Biology

2000. Wolf MHC. Manchester, England. Comparative Evolution of MHC.

2000. MHC and Captive Breeding. London, England. *Reproduction and Integrated Conservation Science*.

2000. Using Evolutionary Genetic Principles in Conservation Biology. Groningen, Netherlands. *Festshrift for Wilke Van Delden*.

2001. Neutral, Detrimental, and Adaptive Genetic Variation in Conservation Genetics. New York. *Conservation Genetics in the Age of Genomics* 

2001. Conservation Genetics. Lausanne, Switzerland. Conservation Genetics

2002. Inbreeding Depression in Conservation Biology. Farna, Sweden. *Conservation of Small Wolf Populations* 

2002. Research Challenges for Naturalists in the Era of Genomics. Banff, Canada. *Research Challenges for Naturalists in the 21st Century* 

2002. Recent Developments in Conservation Genetics. Strasbourg, France. *Population and Conservation Genetics of Forest Trees* 

2003. Aquatic Resources in Arid Lands. Las Cruces, New Mexico. *Conservation Genetics in Aquatic Species* 

2003. Recent Developments in Conservation Genetics. Leeds, England. *Genetic Biodiversity in Natural Populations: Implications for Management - European Society for Evolutionary Biology*.

2003. MHC and Endangered Species. Leeds, England. Evolutionary Dynamics of the Major Histocompatibility Complex (MHC) - European Society for Evolutionary Biology

2005. Genetics in the Florida Panther. Live Oak, Florida. Past effective population size in Florida panthers.

2005. Conservation Genetics in the European Union. Berlin, Germany. *Effective Population Size and Genetic Differentiation in Conservation Genetics*.

2005. *Recent Developments in Conservation Genetics*. Asilomar, California. Second International Meeting on Conservation Genetics.

2005. *Recent Developments in Conservation Genetics*. Derbyshire, UK. Conservation of Genetic Diversity: Science and Policy Needs in a Changing World.

2006. *Measuring Diversity Among Breeds and Populations*. Minneapolis, MN. 2006 Joint ADSA-ASAS Annual Meeting.

2006. Recent Developments in Conservation Genetics: Examples from Endangered Topminnows, Wolves, and Florida Panthers. Flagstaff, AZ. 33<sup>rd</sup> Natural Areas Conference

2006. *Conservation Genetics*. Madrid, Spain. IUFRO Conference Population Genetics and Genomics of Trees: From Gene Function to Evolutionary Dynamics and Conservation.

2007. *Captive Breeding and the Recovery of the Mexican and Red Wolves*. Los Angeles, CA. Microevolutionary Change in Human-altered Environments.

2007. *Population and Conservation Genetics of the Endangered Sonoran Topminnow*. Durham, NC. Developing New Model Systems for Evolutionary Genetics and Genomics Using Poeciliid Fishes.

2007. *Recent Developments in Conservation Genetics*. Moriela, Mexico. Association for Tropical Biology and Conservation.

2007. *Captive Breeding and the Recovery of the Mexican Wolves*. Moriela, Mexico. Association for Tropical Biology and Conservation.

2008. *Captive Breeding of Delta Smelt: Overview of Genetic Issues*. Davis, CA. CABA-CALFED Workshop on Establishment of Delta Smelt Refugial Populations.

2008. *Artificial Propagation and Genetics: Examples, General Principles, and Guidelines.* Sacramento, CA. CALFED Workshop on Artificial Propagation.

2009. *Genetic Rescue and Hybridization*. Trondheim, Norway. Conservation Genetics Symposium.

2009. *Conservation Genetics and North American Bison*. Flagstaff, AZ. 10<sup>th</sup> Biennial Conference of Research on the Colorado Plateau.

2010. MHC, Inbreeding, and Disease. St. Louis, MO. Symposium on Mate Choice.

2010. Conservation Genetics: Its Impact on Conserving Endangered Species. Emmental, Switzerland. Retreat for Evolutionary Biology, Univ. Zurich.

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2011. Bison Conservation Genetics. Tulsa, OK. Meeting on Bison Ecological Restoration.

2011. *Conservation Genetics: How it Can Contribute to Recovery*. College Station, TX. Ecological Integration Symposium.

2012. *Conservation Genetics*. Univ. Calif. – Davis. Conservation of Extremely Small Populations.

2012. *Population Genetics of Malaria Resistance in Medicine*. Arizona State Univ., Tempe. Phylomedicine Conference.

2014. *Genetic Rescue in Isle Royale Wolves*. Missoula, MT. Genetic Rescue Symposium, Society for Conservation Biology.

#### Federal and State Research Grants:

| NSF      | Undergraduate Research Participation (1972) - \$15,000  |
|----------|---|
| NSF      | Genetic Variation in Temporally and Spatially Heterogeneous Environments (1973-1975) - \$38,000   |
| NSF      | Genetic Variation in Temporally and Spatially Heterogeneous Environments (1975-1978) - \$47,500   |
| NIH      | Disease Association and the HLA Region (1982-1984) with G. Thomson - U.C. Berkeley - \$180,000  |
| NIH      | Disease Association and the HLA Region (1984-1987) with G. Thomson - U.C. Berkeley - \$280,000  |
| NIH      | Population Genetics of the HLA Region (1985-1988) with G. Thomson - U.C. Berkeley - \$240,000   |
| NIH      | Disease Association and the HLA Region (1987-1992) with G. Thomson - U.C. Berkeley - \$450,000  |
| NIH      | Population Genetics of the HLA Region (1989-1994) with G. Thomson - U.C. Berkeley - \$750,000   |
|          | Menzies Wallflower Research Program (1989-1991), Contract with Humboldt<br>State University - \$12,900  |
| NSF      | Conservation Genetics and Inbreeding Depression (1990-1993) - \$140,000   |
| UC-Davis | Captive Broodstock Breeding Program in Winter-Run Chinook Salmon<br>(1993-1998), Contract with University California - Bodega Bay - \$115,000 |

| NSF   | Inbreeding Depression and Adaptive Genetic Variation in Gila Topminnows (1994-1997) - \$225,000  |
|-------|--|
| AZDGF | Mexican Wolf Genetics (1994-1996) with Philip Miller - Arizona Heritage<br>Program - \$28,000  |
| NSF   | Inbreeding Depression and Adaptive Genetic Variation in Gila Topminnows-<br>REU Supplement (1994) - \$5,000  |
| AZDGF | Microsatellite Variation in Topminnows (1995-1997) with Ruby Sheffer-<br>Arizona Heritage Program - \$33,200.  |
| AZDGF | Genetic Variation in Bighorn Sheep (1996-1998) with Steven Kalinowski-<br>Arizona Heritage Program - \$36,520.   |
| USFWS | Recommendation for Establishing and Maintaining a Broodstock for Bonytail<br>Chub (1996) – US Fish and Wildlife Service - \$4280.                              |
| USBR  | Gila Topminnow Diseases from Non-native Fishes (1996-1997) - Bureau of Reclamation - \$10,000  |
| AZDGF | MHC and Parasite Resistance in Gila Topminnows (1997-1999) with Timothy Kim - Arizona Heritage Program - \$38,000.   |
| USFWS | Evaluation of the Merging of the Three Mexican Wolf Lineages (1997-1998) - U.S. Fish and Wildlife - \$22,000.  |
|       | Genetic Variation for Disease Resistance Genes in the Arabian Oryx (1998) -<br>Phoenix Zoo - \$6,875.  |
| USBR  | Genetic Characterizations of Sonoran Topminnow Populations (1998) - Bureau of Reclamation - \$21,171.  |
| NSF   | Parasite Resistance in Gila and Yaqui Topminnows (1998-2002) - \$200,000   |
| AZDGF | Microsatellite and MHC variation to distinguish natural lineages of the Sonoran topminnow with Karen Parker (1998-2000) - Arizona Heritage Program - \$40,170. |
| USFWS | The Impact of Hybridization on Reintroduced Red Wolves (2000-2002) – US Fish and Wildlife Service - \$75,128.  |
|       | Winter Run Chinook Salmon Captive Propagation/Broodstock Program (1999-2001) – UC Davis - \$130,000.   |

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|   | AZDGF | Genetic Variation in the Gila Topminnow with Rhonda Lee (2000 – 2002) –<br>Arizona Heritage Program - \$40,130  |
|---|-------|---|
|   | USBR  | Maintenance of Gila Topminnow Stocks (2000-2004) - \$11,050.  |
|   |       | Winter Run Chinook Salmon Genetics (2001-2003) – UC Davis – \$80,000  |
|   | AZDGF | Genetic Variation in Arizona Springsnails with Carla Hurt (2001-2003) –<br>Arizona Heritage Program - \$47,167  |
|   | AZDGF | Shell Dyskeratosis in Sonoran Desert Tortoises: Genetic Causes and<br>Population Effects with Rhonda Lee (2002-2004) – Arizona Heritage Program<br>- \$41,063               |
|   | NSF   | Dissertation Research: Tempo and Mode of HLA Evolution in the Americas (written by Daniel Garrigan) (2002-2004) - \$9,307   |
|   | AZDGF | Conservation Genetics of Arizona Springsnails: Identifying Management Units<br>and Regions of Endemism with Carla Hurt (2003-2005) - Arizona Heritage<br>Program - \$33,050 |
|   | USFWS | Maintenance of Gila Topminnow Stocks (2005-2006) - \$5,000  |
|   | AZDGF | Conservation Genetics of Arizona Talussnails with Rhonda Lee (2005-2008) – Arizona Heritage Program - \$60,694.   |
| 1 | USFWS | Genetics of Pallid Sturgeon with Ed Heist (2008) - USFWS - \$40,000   |

## **Publications:**

### Books

- (1) 1983 Hedrick, P.W. Genetics of Populations. Jones and Bartlett, Boston, MA. 629 p.
- (2) 1984 Hedrick, P.W. *Population Biology: The Evolution and Ecology of Populations*. Jones and Bartlett, Boston, MA. 445 p.
- (3) 1989 Weaver, R., and P. W. Hedrick. Genetics. W. C. Brown, Dubuque, IA., 569 p.
- (4) 1991 Weaver, R., and P. W. Hedrick. Basic Genetics. W. C. Brown, Dubuque, IA. 518p.
- (5) 1992 Weaver, R., and P. W. Hedrick. *Genetics* (Second Edition). W. C. Brown, Dubuque, IA. 649 p.

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- (6) 1995 Weaver, R., and P.W. Hedrick. *Basic Genetics* (Second Edition). W.C. Brown, Dubuque, IA, 498 p.
- (7) 1997 Weaver, R., and P. W. Hedrick. *Genetics* (Third Edition). W.C. Brown, Dubuque, IA, 638 p.
- (8) 2000 Hedrick, P.W. *Genetics of Populations* (Second Edition). Jones and Bartlett, Boston, 553 p.
- (9) 2005 Hedrick, P.W. *Genetics of Populations* (Third Edition). Jones and Bartlett, Boston, 737p.
- (10) 2011 Hedrick, P.W. *Genetics of Populations* (Fourth Edition). Jones and Bartlett, Boston. 675p.

#### Articles

- (1) 1968 Hedrick, P. W., and R. E. Comstock. Role of linkage in gene frequency change of coat color alleles in mice. *Genetics* 58:297-303.
- (2) 1970 Hedrick, P. W. Selection in finite populations. I. The probability of fixation and rate of response using transition matrix iteration. *Genetics* 65:157-173.
- (3) 1970 Hedrick, P. W. Selection in finite populations. II. The selection limit and rate of response for a Monte Carlo simulation model. *Genetics* 65:175-186.
- (4) 1971 Hedrick, P. W. A new approach to measuring genetic similarity. *Evolution* 25:276-280.
- (5) 1971 Hedrick, P. W. Competition experiments between *Drosophila melanogaster* and *D. simulans. Dros. Inf. Serv.* 47:61-62.
- (6) 1971 Hedrick, P. W. A culture which allows sand pupation. Dros. Inf. Serv. 47:131.
- (7) 1972 Hedrick, P. W. Possible stable equilibrium for *D. melanogaster* and *D. simulans*. *Dros. Inf. Serv.* 48:128-129.
- (8) 1972 Hedrick, P. W. Maintenance of genetic variation with a frequency-dependent selection model as compared to the overdominant model. *Genetics* 72:771-776.
- (9) 1973 Hedrick, P. W. Factors responsible for a change in interspecific competitive ability in *Drosophila*. *Evolution* 26:513-522.
- (10) 1973 Hedrick, P. W. Genetic variation and the generalized frequency-dependent selection model. *Am. Natur.* 107:800-802.

- (11) 1974 Hedrick, P. W. Genetic variation in a heterogeneous environment. I. Temporal heterogeneity and the absolute dominance model. *Genetics* 78:757-770.
- (12) 1974 Hedrick, P. W. X-linked selection. Dros. Inf. Serv. 51:34-3.6.
- (13) 1975 Hedrick, P. W. Genetic similarity and distance: comments and comparisons. *Evolution* 29:362-366.
- (14) 1976 Hedrick, P. W. Simulation of X-linked selection in *Drosophila*. *Genetics* 83:551-571.
- (15) 1976 Hedrick, P. W., M. Ginevan, and E. Ewing. Genetic polymorphism in heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7:1-32.
- (16) 1976 Hedrick, P. W. Genetic variation in a heterogeneous environment. II. Temporal heterogeneity and directional selection. *Genetics* 84:145-157.
- (17) 1978 Hedrick, P. W., and E. Murray. Average heterozygosity revisited. *Am. J. Hum. Genet.* 30:377-382.
- (18) 1978 Hedrick, P. W. Genetic variation in a heterogeneous environment. V. Spatial heterogeneity in finite populations. *Genetics* 89:389-401.
- (19) 1978 Hedrick, P. W., S. Jain, and L. Holden. Multiple gene systems in evolution. *Evol. Biol.* 11:101-184.
- (20) 1978 Hedrick, P. W. Genetic variation in a heterogeneous environment. VI. A possible experimental system. *J. Hered.* 69:135-136.
- (21) 1979 Hedrick, P. W., and L. R. Holden. Hitch-hiking: An alternative to coadaptation for the barley and slender wild oat examples? *Heredity* 43:79-86.
- (22) 1979 Hedrick, P. W., and E. Murray. Competition between wild-caught *D. melanogaster* and *D. simulans. Dros. Inf. Serv.* 55:58-60.
- (23) 1980 Hedrick, P. W. Hitchhiking: A comparison of linkage and partial-selfing. *Genetics* 94:791-808.
- (24) 1980 Hedrick, P. W., and J. F. McDonald. Regulatory gene evolution. *Heredity* 45:85-99.
- (25) 1980 Hedrick, P. W. Selection in finite populations. III. An experimental test. *Genetics* 96:297-313.
- (26) 1981 Hedrick, P. W. The establishment of chromosomal variants. *Evolution* 35:322-332.

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- (27) 1982 Chakraborty, R., and P. W. Hedrick. Paternity exclusion and the paternity index for two linked loci. *Hum. Hered.* 33:13-23.
- (28) 1982 Hedrick, P. W. Genetic hitchhiking: A new factor in evolution? *Bioscience* 32:845-853.
- (29) 1983 Hedrick, P. W., and E. Murray. Selection and measures of fitness, p. 61-104. In Ashburner et al. (eds.) *The Genetics and Biology of Drosophila* Vol. 3d. Academic Press, NY.
- (30) 1983 Hedrick, P. W. Recombination and directional selection. *Nature* 302:727.
- (31) 1983 Hedrick, P. W., and G. Thomson. Evidence for balancing selection at HLA. *Genetics* 104:449-456.
- (32) 1983 Chakraborty, R., and P. W. Hedrick. Heterozygosity and genetic distance of proteins. *Nature* 304:155.
- (33) 1983 Hedrick, P. W. Neutrality or selection at HLA? Am. J. Hum. Genet. 35:1055-1057.
- (34) 1984 Hedrick, P. W., and E. Louis. Speciation: A population genetics perspective, p. 251-262. *Proc. XV International Congress of Genetics IV*.
- (35) 1984 Hedrick, P. W., and D. Levin. Kin founding and the fixation of chromosomal variants. *Am. Natur.* 124:789-797.
- (36) 1985 Hedrick, P. W. Coat variants in cats: Gametic disequilibrium between unlinked loci. *J. Hered.* 76:127-131.
- (37) 1985 Ahmad, M., and P. W. Hedrick. Electrophoretic variation in the common mussel, *Mytilus edulis*: No evidence for gametic disequilibrium. *Heredity* 55:47-51.
- (38) 1985 Hedrick, P. W. Inbreeding and selection in natural populations, p. 71-91. In H. R. Gregorius (ed.) *Population Genetics in Forestry*. Lecture Notes in Biomathematics 60, Springer-Verlag, New York.
- (39) 1985 Thomson, G., F. Nicholas, W. Bodmer, M. O'Neill, P. W. Hedrick, and E. Hudes. Analysis of negative and multiple HLA antigen disease associations: Multilocus models. *Tissue Antigens* 26:293-306.
- (40) 1985 Peetz, E. W., G. Thomson, and P. Hedrick. Charge changes in protein evolution. *Mol. Biol. Evol.* 3:84-94.
- (41) 1986 Hedrick, P. W., and G. Thomson. A two-locus neutrality test with applications to humans, *Escherichia coli*, and lodgepole pine. *Genetics* 112:135-156.

- (42) 1986 Hedrick, P. W., P. Brussard, F. W. Allendorf, J. Beardmore, and S. Orzack. Protein variation, fitness, and captive propagation. *Zoo Biol*. 5:91-99.
- (43) 1986 Hedrick, P. W., and C. C. Cockerham. Partial inbreeding: equilibrium heterozygosity and the heterozygosity paradox. *Evolution* 40:856-861.
- (44) 1986 Hedrick, P. W., G. Thomson, and W. Klitz. Evolutionary genetics: HLA as an exemplary system, p. 583-606. In Karlin and Nevo (eds.) *Evolutionary Processes and Theory*, Academic Press.
- (45) 1986 Hedrick, P. W. Average inbreeding or equilibrium inbreeding? *Am. J. Hum. Genet.* 38:965-970.
- (46) 1986 Hedrick, P. W. Genetic polymorphism in heterogeneous environments: A decade later. *Ann. Rev. Ecol. Syst.* 17:535-566.
- (47) 1987 Hedrick, P. W. Populations genetics of intragametophytic selfing. *Evolution* 41:137-144.
- (48) 1987 Hedrick, P. W. Estimation of the rate of partial inbreeding. *Heredity* 58:161-166.
- (49) 1987 Hedrick, P. W. Gametic disequilibrium in cats: epistasis is an unlikely cause. J. *Hered*. 78:204.
- (50) 1987 Hedrick, P. W. Genetic load and the mating system in homosporous ferns. *Evolution* 41:1282-1289.
- (51) 1987 Hedrick, P. W., G. Thomson and W. Klitz. Evolutionary genetics and HLA: Another classic example. *Biol. J. Linn. Soc.* 31:311-331.
- (52) 1987 Hedrick, P. W. Genetic disequilibrium measures: Proceed with caution. *Genetics* 117:331-341.
- (53) 1987 Hedrick, P. W. Genetic bottlenecks. Science 237:963.
- (54) 1988 Hedrick, P. W. HLA sharing, recurrent spontaneous abortion, and the genetic hypothesis. Genetics 119:199-204.
- (55) 1988 Hedrick, P. W., and G. Thomson. Maternal-fetal interactions and the maintenance of histocompatibility polymorphism. *Genetics* 19:205-212.
- (56) 1988 Hedrick, P. W. Does segregation distortion influence gametic disequilibrium? *Genet. Res.* 52:237-242.
- (57) 1988 Hedrick, P. W. Genetic variation in Przewalski's horses. J. Hered. 79:401.

- (58) 1988 Hedrick, P. W. Letter to the editor. Bull. Ecol. Soc. Amer. 69:68.
- (59) 1988 Hedrick, P. W. Inference of recombinational hotspots using gametic disequilibrium values. *Heredity* 60:435-438.
- (60) 1989 Van Vuren, D., and P. W. Hedrick. Genetic conservation of feral populations of Livestock. *Cons. Biol.* 3:312-317.
- (61) 1989 Hedrick, P. W., M. S. Gaines and M. L. Johnson. Owl predation on small mammals. *Univ. Kansas Natural Hist. Occas. Papers.* 1-7.
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- (63) 1990 Hedrick, P. W. Mating systems and evolutionary genetics, p. 83-115. In K. Wohrmann and S. Jain (eds.), *Population Biology*. Springer-Verlag.
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- (65) 1990 Hedrick, P. W., and K. Ritland. Gametic disequilibrium and multilocus estimation of selfing rates. *Heredity* 65:343-347.
- (66) 1990 Hedrick, P. W. Evolution at HLA: Possible explanations for the deficiency of homozygotes in two populations. *Hum. Hered.* 40:213-220.
- (67) 1990 Hedrick, P. W. Theoretical analysis of habitat selection and maintenance of genetic variation, p. 209-227. In J. S. F. Barker, W. T. Starmer and R. J. MacIntyre. *Ecological and Evolutionary Genetics of Drosophila*. Plenum Press, NY.
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- (69) 1990 Hedrick, P. W., J. S. F. Barker and T. Armstrong. Effect of adult experience on oviposition choice and short-distance attraction in *Drosophila buzzatii*. J. Insect. Behav. 3:689-697.
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- (83) 1993 Miller, P. S., and P. W. Hedrick. Inbreeding and fitness in captive populations: lessons from Drosophila. *Zoo Biol.* 12: 333-351.
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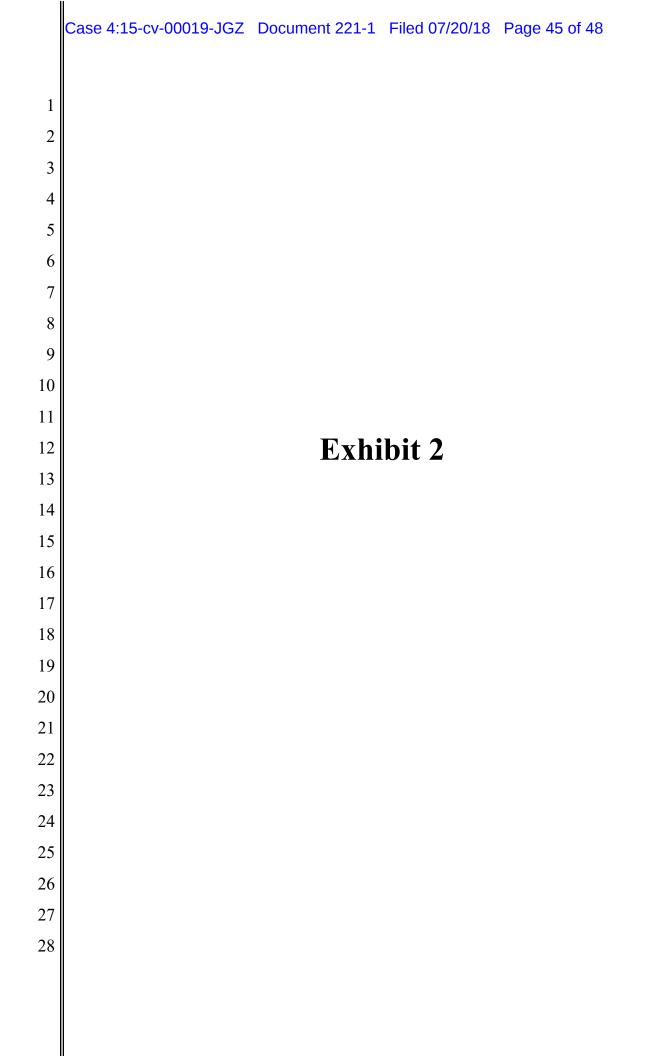
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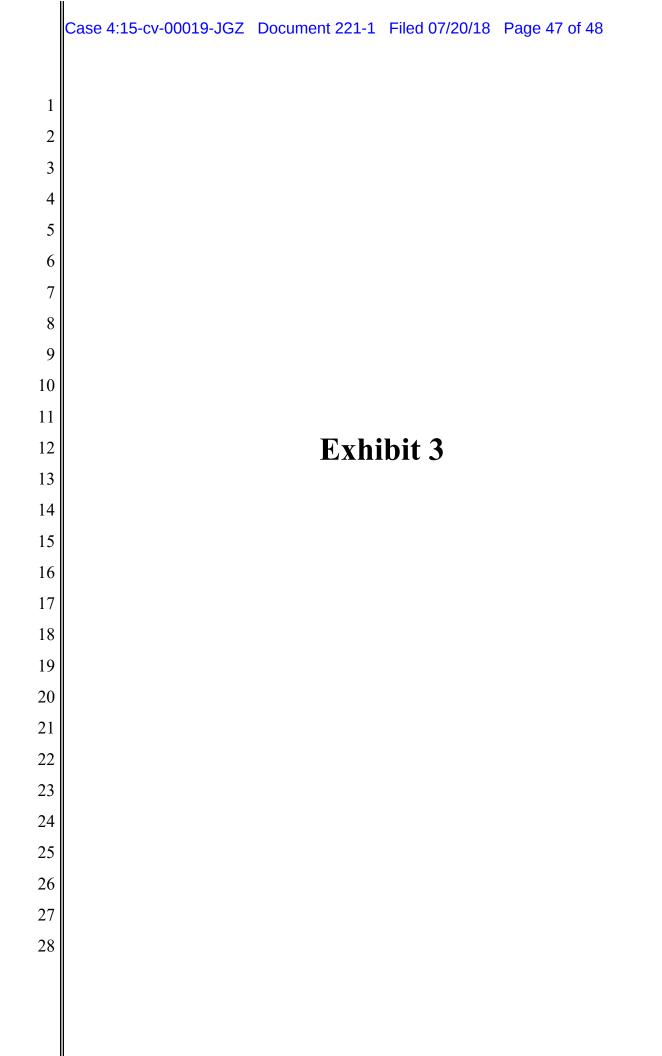
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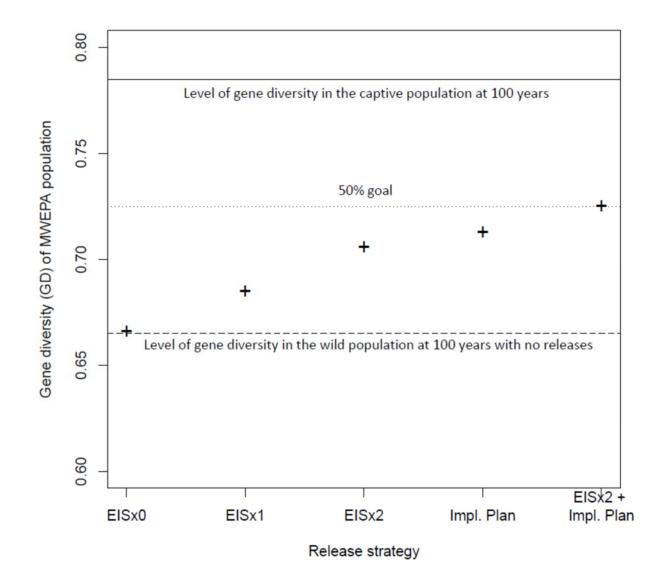


Figure 1. The expected level of gene diversity (GD) after 100 years in the wild population when there are no releases (bottom broken line), in the captive population (top solid line), and the proposed 50% goal (middle dotted line). The GD for five different levels of releases are given and only a scenario combining the EIS x 2 release level plus the cross-fostered pups proposed in the Implementation Plan reaches the 50% goal (Carroll, personal communication).