High retention of genomic variation and fitness-related traits in the effective population of reintroduced wolves in Yellowstone National Park

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Abstract

Cooperatively breeding species exhibit numerous strategies to avoid mating with close relatives, inherently reducing effective population size. For species of management concern, accurate estimates of inbreeding and trait depression are crucial for the species' future. We utilized genomic and pedigree data for Yellowstone National Park gray wolves to investigate the contributions of foundation stock lineages, genetic architecture of the effective population, and putative fitness consequences of inbreeding. Our dataset spans 25 years and seven generations since reintroduction, encompassing 152 nuclear families and 329 litters. We found over 87% of the pedigree foundation genomes persisted and report influxes of allelic diversity from two translocated wolves from a divergent source in Montana. As expected for group-living species, mean kinship significantly increased over time, although we found high retention of genetic variation. Strikingly, the effective population carried a significantly lower level of genome-wide inbreeding coefficients and autozygosity with shorter decays for linkage disequilibrium relative to the non-breeding population. Lifespan and heterozygosity were higher in the effective population, although individuals who had their first litter at an older age also had higher inbreeding coefficients. Our findings highlight genetic contributions to fitness, and the importance of effective population size and gene flow to counteract loss of genetic variation in a wild, free-ranging social carnivore. It is crucial for managers to mitigate factors that significantly reduce effective population size and genetic connectivity, which supports the dispersion of genetic variation that aids in rapid evolutionary responses to environmental challenges.

Introduction

Territorial, cooperatively-breeding species can exhibit a diversity of breeding strategies (e.g. monogamy, polygamy, polyandry) and reproductive skew (Keller and Reeve 1994; Clutton-Brock 2016). Yet regardless of these patterns, access to reproduction is restricted and effective population size (N_e) is reduced (Jennions and Macdonald 1994; Frankham 1995; Komdeur and Deerenberg 1997). Estimates of N_e provide critical information during the application and interpretation of evolutionary and population genetic theory (Wright 1931, 1969; Crow and Kimura 1970; Lanfear et al. 2014), as well as for wildlife management programs (Rowe and Beebee 2004). Species that have experienced either a natural population decline or bottleneck are expected to have a dramatically reduced census and effective size, and an increased probability of inbreeding and genetic identity by descent or autozygosity (Hedrick and Kalinowski 2000; Charlesworth and Willis 2009). Consequently, inbreeding can dramatically impact N_e estimates through increased genetic correlations and decreased frequency of heterozygotes (Ellegren 1999; Wang et al. 2016). Viability is then threatened by inbreeding or trait depression, the negative fitness consequence expected in inbred offspring (Lynch and Walsh 1998; Charlesworth and Willis 2009; Hedrick and Garcia-Dorado 2016). Inbreeding depression is often measured in fitness-related traits of life history (e.g. fecundity, survival, morphological measurements) and often only in captive populations (Hedrick and Kalinowski 2000). Measuring autozygosity further provides an assessment of the full effect of deleterious alleles, as individuals that carry greater levels of autozygosity are expected to exhibit decreased fitness (Charlesworth and Willis 2009).

Although there has been much attention paid to inbreeding avoidance and trait depression in captive breeding programs from pedigree estimates (Ralls et al. 1988; Laikre and Ryman 1991; Laikre et al. 1993; Kalinowski et al. 2000; Kalinowski and Hedrick 2001; Jiménez-Mena et al. 2016), much less is known about the genetic basis of depression in wild populations, although it is expected to exist (Lacy 1997; Keller and Waller 2002; Curik et al. 2017). Further, pedigrees that are unbalanced, incorrect, or incomplete can lead to errors in estimating inbreeding coefficients and trait depression (Curik et al. 2017). One critical aspect of pedigree-based errors is the assumption that pedigree founders are unrelated. Genome data now provide an opportunity to directly and accurately measure autozygosity, which quantifies the fraction of the genome that is contained within long stretches of homozygosity delineated along chromosomes (F_{ROH}; McQuillan et al. 2008). Keller et al. (2011) also showed that F_{ROH} outperformed inbreeding estimates derived from pedigree data.

We studied the dynamic landscape of inbreeding and life-history traits in a pedigreed population of gray wolves (*Canis lupus*). As a cooperatively-breeding species, wolf populations are subdivided with limited access to reproduction that is reinforced by a social hierarchy and social rank-related stress reflected in glucocorticoid levels (Sands and Creel 2004; vonHoldt et al. 2008). Several studies of small, isolated, bottlenecked or captive gray wolf populations across their Holarctic range have found genetic evidence of high inbreeding levels with a corresponding reduction in fitness and related population genetic health metrics. Two primary examples of such isolated island populations of wolves are those inhabiting Isle Royale in Lake Superior and Scandinavia (Laikre and Ryman 1991, 1993; Ellegren 1999; Flagstad et al. 2003; Liberg et al. 2005; Räikkönen et al. 2009, 2013; Adams et al. 2011; Hedrick et al. 2014; Åkesson et al. 2016, 2021; Robinson et al. 2019).

Specific to the wolves inhabiting the contiguous United States, effective government wildlife control programs eradicated nearly all gray wolves by the early 1930s (except in Minnesota; Fritts et al. 1997). Over five decades later, substantial support developed to establish a reintroduction plan for gray wolf restoration to the Rocky Mountains (Fritts et al. 1997). During the winters of 1995 and 1996, the US Fish and Wildlife Service released 35 wolves in central Idaho, and in a joint effort with the National Park Service, released 31 wolves in Yellowstone National Park (YNP). Additionally, there was the translocation of 10 wolf pups from the Sawtooth pack in northwestern Montana to YNP where they were released in 1997. Foundation stock (a.k.a. YNP founders) were captured from two source locations in western Canada, and vonHoldt et al. (2008) utilized 26 microsatellites to provide valuable genetic insights with respect to their relatedness and population genetic health during the first decade of recovery. It was reported that YNP founder breeding pairs were unrelated with near absolute inbreeding avoidance despite living in groups of related individuals. Yet, given the resolution limits of microsatellite data for investigating genomic architecture, little is known about the nature of genetic variation or chromosomal regions that are identical by descent (IBD).

Building upon the recent release of their updated pedigree constructed using genome-wide SNP data (vonHoldt et al. 2020), we explore here the genetics of YNP founders' lineages, demography, genomic contributions, inbreeding, and consequences thereof in YNP gray wolves during their 25 years post-reintroduction. We assessed pedigree- and marker-based aspects of the wolf population with the unique opportunity to integrate life-history fitness correlates with respect to reproduction. With the pedigree reconstructed utilizing genomic data, these two perspectives have provided new details regarding the genetic viability, reproduction, and recovery status of this social carnivore.

Materials and Methods

Yellowstone National Park's reintroduced wolf population

We analyzed 474 YNP gray wolves with pedigree and 391 with genome-wide SNP data derived from blood and tissue samples collected between 1995 and 2020 (see below). After reintroduction, the YNP population rapidly expanded, reaching a high of 174 wolves in 2003. However, the population stabilized over the last decade (Smith et al. 2020), averaging 97.9 (±3.9 SE) at the year-end official census count. For this study, the original 31 wolves translocated to YNP and the parents of the 10 translocated orphaned pups were designated as *YNP founders*. This is not to be confused with the animals at the foundation of the pedigree, known as the *pedigree founders*, which included two wolves sampled in Canada who were not translocated but known to be related to YNP wolves. The original and updated genealogy for this population confirmed close kinships (e.g. parent/offspring of full-siblings) and genetic similarities among a subset of the YNP founders (vonHoldt et al. 2008, 2020). These kinship ties were expected given the nature of the wild capture methods and release. Several individuals were captured together, likely representing a pack or a subset thereof. These relationships are reflected by increased allele sharing in the genetic-based analysis below, while the pedigree-based analysis incorporated these known relationships. These relationships are critical to account for as most treatments of founders assume they are unrelated (i.e. their kinship f_{xy} and inbreeding coefficients F are set to 0; Jiménez-Mena et al. 2016).

Pedigree-based analysis

We updated the full YNP wolf pedigree by adding three new individuals indicated in Supplemental Table S1 and used the same genomic preparation and analytical methods described by vonHoldt et al. (2020). Briefly, we constructed a parentage-informative dataset of 736 SNPs through strict filtering in *PLINK v1.9* (Chang et al. 2015) with parameter settings recommended for pedigree reconstruction (Huisman 2017): Hardy-Weinberg equilibrium (HWE) (--hwe 0.001), minor allele frequency (MAF) (--maf 0.45), and statistical linkage disequilibrium (LD) (--indep-pairwise 50 5 0.2). We calculated pairwise relatedness coefficients (*r*) using the *coancestry* function within the R v3.6.0 (2019) package *related* and implemented the dyadic likelihood estimator (dyadml=1; Milligan 2003) with allowance for inbreeding (allow.inbreeding=TRUE) (Pew et al. 2015). We then used these estimates alongside observation data and likely parent-offspring (P-O) pairs assigned by the R v3.6.0 package *sequoia* (Huisman 2017) to update the full YNP wolf pedigree to include 871 P-O pairs among 474 wolves (n, females=226, males=239, unknown=9; Table S1) (vonHoldt et al. 2020). Wolves that lacked genetically-confirmed parents or offspring were excluded from the pedigree analysis. For individuals where the likely birthday was a range of years, we assigned it the earliest birth year. We completed several of the described methods for the full pedigreed population, as well as annually between 1995 and 2020.

We used *PedScope©* v.2.4.01, a proprietary program used for animal population management and breeding recommendations, to perform pedigree-based analyses. The pedigree contained 26 pedigree founders, defined as individuals where no parents are included in the pedigree (Table S1). Correlations were assessed using the product moment correlation coefficient (r). We estimated several measures of gene diversity in the pedigreed population. We estimated the number of founder equivalents (*fe*) and founder genome equivalents (*fg*). The former measured gene diversity in a specified set of the pedigree (*e.g.* pedigree founders, annual, or entire) and represents the number of equally contributing founders expected to produce the observed level of genetic diversity in the specified population. The latter is a related metric that accounts for drift, where *fg* represents an estimate that incorporates random loss of alleles. Further, we estimated the number of effective ancestors (*fa*) and identified influential ancestors as those with the greatest contributions towards *fa* using an algorithm developed by Boichard et al. (1997). Estimates of *fa* are similar to that of *fe* but account for bottlenecks in the pedigree.

We surveyed genome uniqueness (*GU*) defined as the animal's likelihood that it carries pedigree founder alleles not present in another individual in the pedigree. We also estimated mean kinship (*MK*), Wright's pedigree-based inbreeding coefficient (*F*), and Ballou's direct method for estimating ancestral inbreeding coefficient. In a pedigree-based approach, pairwise kinship values describe the probability that two alleles shared are IBD, a measure also estimated by the pedigreed population's inbreeding coefficient F. We obtained the pairwise additive genetic relationship matrix ("A" matrix) to also assess pairwise relatedness. Differences in pedigree metrics were assessed using a 1-way ANOVA in R v3.6.0.

We counted the number of litters per individual as the total number of years a specific mating pair reproduced and included only offspring where birth year was known. We also included litter counts if only one parent was known. We used the $\log_{10}$ of the number of genetic litters as a proxy for fitness, surveyed as a function of inbreeding coefficients, where the slope of the fitted line is inferred as the inbreeding load (-*B*) (Keller and Waller 2002). We further used the pedigree to estimate the total number of lethal equivalents (LE) per diploid genome (*2B*). The inbreeding load is often defined as the reduction in survival expected in a completely homozygous individual. We then estimated the expected depression in fitness (δ) following $\delta=1\text{-}e^{-B*F}$, where *B* is the estimated number of lethal equivalents per gamete and *F* is the inbreeding coefficient.

Genome-wide SNP genotype data

Although the pedigree relationships are valuable, we utilized a marker-based genomics approach to explore the impact of pedigree structure on genomic variation and life-history related traits (Kardos et al. 2015). A subset of wolves in the pedigree were excluded from the genetic analyses due to low sequence coverage or lack of a genetic sample (*i.e.* only observation data supported their pedigree information). As such, the pedigree contains more individuals than analyzed with RADseq data. Further, we included observational data regarding parentage and reproduction. Such an exception was made when reproduction was observed but a genetic sample was unavailable. We analyzed 56 576 SNP loci (referred to as 56K) genotyped across 391 gray wolves (n, females=193, males=195, unknown=3), which were previously collected using a modified restriction-site associated DNA sequencing (RADseq) protocol by Ali et al. (2016) and mapped to the reference dog genome Canfam3.1 (vonHoldt et al. 2020). These public data were previously filtered to exclude individuals with >20% missing data and sites with >10% per-site missing data, MAF<1%, or significant deviation from HWE (p<0.0001), leading to a final genotyping rate of 96.4%. We estimated LD decay using the --r2 flag across 391 YNP wolves genotyped for 56K SNPs. We further removed SNPs with a genotype correlation of r^2>0.5 using the --indep-pairwise 50 5 0.5 flag to construct a pruned set of 24,235 statistically unlinked SNPs (referred to as 24K). Individual wolves with confirmed offspring via genetics or observation were categorized as “breeding” individuals (n=152), while wolves lacking offspring were considered “non-breeding” individuals (n=235), with four wolves of unknown breeding status (Table S2). We also completed several of the described methods for the full pedigreed population overall as well as annually and censored, between 1995 and 2018, with the pruned SNP set. Differences in annual estimates were assessed using a 1-way ANOVA in R. We estimated standard observed and expected heterozygosity (H_O and H_E, respectively) in *PLINK* with the --hardy and --het flags.

We also obtained the predicted impact and consequence of each allele from *Variant Effect Predictor* (VEP) (McLaren et al. 2016). Based on *VEP* impact annotations, we grouped the 17 loci with "*high*" predicted impact and 381 loci with "*moderate*" impact into a category (n=398 loci) inferred to negatively impact the individual fitness. This category was further detailed as the "*high*" impact loci were annotated as the gain/loss of a stop, loss of a start, or a splice acceptor/donor, while loci with "*moderate*" impact were missense variants and splice regions. We also grouped 844 loci annotated as "*low*" impact and 29 213 loci with a "*modifier*" impact in a category inferred to unlikely impact fitness (n=30 057 loci).

Estimating the inbreeding coefficient from genotype data

We estimated individual inbreeding coefficients (F) from the pruned SNP set and runs of homozygosity (ROH) with the R v3.6.0 function *detectRUNS* (Biscarini et al. 2018) as:

$$F_{ROH} = \frac{\sum L_{ROH}}{L_{genome}}$$

where L_{ROH} is the summed length of all ROHs detected in an individual and L_{genome} is the length of the genome that is used. As RADseq data are inherently clustered as sequence stacks across the genome at restriction enzyme cut sites, we used the consecutive window-free option for detecting homozygous and heterozygous tracks (Marras et al. 2015). Tracks were detected by a minimum of 10 SNPs in a track of at least 10 000 nucleotides with a maximum gap of 10^6 nucleotides between SNPs, and allowed for a maximum of a single opposite or missing genotype in the track. We further annotated each ROH with respect to their composition of alleles with either a functional impact or consequence (see VEP methods above) using the *intersectBed* function of *Bedtools* v2.28.0 (Quinlan and Hall 2010).

Modeling reproduction, life history, and genetic parameters

We examined the age at first litter (*Age_first_litter*) using Cox proportional hazards regression for survival (*survival* version 3.2-11) with time (in years) to the earliest of three events first litter, death or last documented observation. Animals who died or were lost to observation before breeding were considered right censored data in the analysis. We used the exact method to deal with ties when two or more animals had the same survival times. We standardized the potential predictors (observed heterozygosity, F_{ROH} and VEP consequence categories), and included sex and the first five principle components (PCs) as covariates in all analyses. We fit the following model structure:

Fit=coxph(Surv(Age_litter,Censoring)~Predictor,ties="exact",data)

For the Cox proportional hazards regression analysis, although *p*-values are reported, we elected the best fit models through assessment of the Akaike information criterion (AIC).

Results

Pedigree structure

Using *Pedscope*©, the pedigree composed of 26 founders of the pedigree (individuals where no parents are found within the pedigree), 152 nuclear families (individuals that share the same parents), and 319 litters. Compared to the census size of 41 YNP founder individuals, we inferred 19.92 pedigree founder equivalents (*fe*), 18.53 founder genome equivalents (*fg*), and 18.79 effective ancestors (*fa*) in the pedigree analysis. There was a maximum ancestry depth of seven generations (Average±s.d.=3.8±1.6), with an average kinship (MK) of 3.2%. We restricted the founder analysis to the wolves translocated in years 1995 and 1996, which included the individuals translocated from the Sawtooth pack in northwestern Montana. We found that wolf 009F had the highest contribution as measured by the percent contribution in the current pedigree due to that individual (*pC*=12%; average=3.8%), followed by 005F with 9% to the full pedigree of 474 wolves, and then by their respective mates 010M and 004M both with 8% contributions each (Table 1).

Nearly all pedigree founders had ≥87% of their alleles retained in the total pedigree (Average±s.d.=88%±20%), with only three individuals at 50% retention (015M, 036F, and a Canada source wolf Y38 whose offspring were translocated to the Chief Joseph pack in YNP) (Table 1).

Average levels of founder genome uniqueness were low (*GU*=0.10±0.3), with only a single pedigree founder (036F) displaying absolute uniqueness (*GU*=1), and four additional individuals with non-zero values (013M, 015M, 035M, Y53) indicating the likelihoods that alleles are not present in another individual in the pedigree (Table 1). A survey of the total pedigree also revealed 20 influential pedigree founders, similarly highlighting the largest marginal contributions by mated pair 009F (12%) and 010M (8%), and mated pair 004M and 005F (8% and 9%, respectively) (Table 2).

We found a significant increase in annual MK with decreasing size of the genotyped population analyzed ($F_{(1,22)}=14.6$, $p=0.0009$), an increase of genomic uniqueness over time (F=9.6, $p=0.0053$), an increase in founder equivalents (F=38.4, $p=3.063\text{x}10^{-6}$), and a decrease in the number of founder genome equivalents over time (F=15.8, $p=0.0006$) (Table 3). The number of effective founders did not significantly change over time (F=0.7, $p=0.395$) (Table 3).

When we excluded observations of 0 litters, 153 observations remained with low levels of inbreeding coefficients (average F=0.009±0.03; range=0.0-0.25) and was negatively correlated to the number of litters (Pearson r=-0.076, p=0.35) (Fig. 1A). From this, we estimated the inbreeding load as the slope of the trendline between $\log_{10}$ litter number and inbreeding coefficient (y=-0.595x+0.292, -B=0.595), and thus 2B=0.595 lethal equivalents (LE) in a diploid genome. Following, we estimated fitness (δ) is expected to be depressed in 14% of progeny from a mating of first-degree relatives (F=0.25).

Lower inbreeding coefficients in the effective population

We obtained genome-wide SNP-based estimations for linkage, heterozygosity, and inbreeding for 391 Yellowstone gray wolves, 387 of which have known breeding status within the study period of 1995-2018 (Table S2). Linkage disequilibrium in the total YNP wolf population extended for an average of 150Kb before decaying below r^2=0.5, with a similar length of LD decay found in the breeding population (230Kb) and substantially longer LD decay in non-breeding wolves (750Kb) (Fig 1B). We found no significant differences in heterozygosity between wolves with a confirmed breeding status and non-breeding wolves across the 56K SNP genotypes (Average±s.d. H_O: breeding=0.792±0.02, non-breeding=0.794±0.02, 1-tailed t-test of equal variance *p*=0.0917). However, the breeding population had significantly lower levels of inbreeding estimates than non-breeding individuals (F_{ROH}: breeding=0.376±0.06, non-breeding=0.387±0.06, *p*=0.0462) (Fig. 1C). We found statistical evidence for enrichment of longer ROH blocks in non-breeding individuals relative to the effective population (mean=1,311,428bp and 1,347,336bp, respectively; 1-tailed Mann-Whitney U=7868x10^{9}, *p*=0.8.854x10^{-5}) (Fig. 1D).

We observed stable annual heterozygosity estimates that were not significantly different between breeding and non-breeding wolves for 21 of the 24 years surveyed, likely due to small intra-annual genetic sample size relative to the census size (Table 4). During three years (2011-2013), non-breeding wolves carried significantly higher observed heterozygosity than the effective population (*p*~0.05), although this trend can be noted in nearly every year surveyed and should be interpreted with caution given the small annual sample sizes. A similar but opposite trend was noted for inbreeding coefficients estimated from F_{ROH}, where non-breeding wolves had a significantly higher inbreeding coefficient than breeding wolves for a single year (2012) (F=5.64, *p*=0.0210) (Table 4).

Individuals with higher autozygosity estimates are older at first litter

We restricted the dataset to explore fitness and genetic data for 387 pedigreed wolves with sufficient life history information (known years of birth and known years of reproduction, death or last observation). We found that lifespan (average breeding=6.1 and non-breeding=2.1 years, 1-tailed t-test *p*=9.31x10^{-43}) was on average higher in the effective population concomitant with lower inbreeding coefficients (average breeding=0.37 and non-breeding=0.38 years, 1-tailed t-test *p*=0.0466), and that breeding wolves were on average 2.9±1.2 years old (males=3.2±1.3, females=2.7±1.1; 1-tailed t-test *p*=0.0086) at the time of their first litter (Figs. 2A,B). However, several life-history and genetic traits show strong correlations, with positive correlations noted between lifespan, age at first litter, and number of litters while inbreeding coefficients were negatively correlated (Fig. 2C).

We further explored the relationship of similar genetic parameters with respect to a wolf’s age at first litter using Cox proportional hazards survival analysis. In all analyses we included sex as a covariate along with the first five PCs from SNPs covering the genome to account for the relatedness; similar results were obtained without these covariates (results not shown). There were 139 animals with known ages at their first litter and 235 non-breeding animals with known age at death or last observation for a total of 374 animals with PCs and phenotype data used in this analysis. Individuals who had their first litter at an older age had higher inbreeding coefficients (Fig. 2D). We found that a higher inbreeding coefficient significantly reduced the Cox proportional hazard and was associated with later reproduction. Thus, F_{ROH} was a significant predictor of age at first litter (Log hazard coefficient=-0.2406, p=0.0203 Table 5). Sex was also significant, with males having a later age to their mate's first litter than females (Log hazard coefficient=-0.5674, p=0.0012 Table 5).

Discussion

The reintroduced gray wolves of Yellowstone National Park are unique in that they are observed every single year, with life events documented and supported by a wealth of molecular data. Despite the rising accessibility of genome sequencing, Yellowstone wolves stand among only a few other systems with similar multidimensional datasets that merge static, dynamic, and molecular perspectives (Stahler et al. 2020). We explored this interface by conducting a pedigree- and marker-based assessment of genetic variation over time within the effective population and modeled fitness-related traits. The pedigree is large and complex, capturing seven generations since the reintroduction of gray wolves to the Rocky Mountains of the United States in 1995 and 1996. Although Canadian founders were carefully selected and indeed have contributed to the genetic success of the population, equally important was the translocation of gray wolf pups from northwest Montana in 1997 that carried divergent genetics (vonHoldt et al. 2008, 2010). As two of these pups matured and assumed a social rank with reproductive access, this lineage continues to provide an influx of genetic variation distinct from the Canadian founders into YNP wolves through their descendants. This finding illustrates the critically positive impact that a few successful breeders have on gene flow into a population. Further, this is exemplary as a design for reintroduction programs to establish a genetically diverse founding population.

Given the known genealogy of this population, we identified a handful of founders that contributed a significant amount of kinship and genome uniqueness, with over 87% of the founders' genomes persisting in the pedigree. The remaining fraction was lost through random drift or emigration. As expected for group-living species, mean kinship significantly increased over time; however, this appears to be mitigated by the continued reproductive success of the translocated individuals from northwest Montana (now the Nez Perce lineage). Further, concordant with vonHoldt et al. (2008), mate choice and inbreeding avoidance also mitigates the degree to which mean kinship increased over time in the pedigree, which is expected to be significantly higher under random breeding alone. We found that the number of effective founders and genomic uniqueness increased over time; this positive consequence is expected in a social species with structured mating, which can alleviate the potentially strong impacts of the reintroduction event which inevitably forces a population genetic bottleneck.

We utilized genome-wide SNP data to explore the distribution of genetic variation across the pedigree relative to time, reproduction, and fitness-related traits (e.g. litters, inbreeding). Overall, we document high retention of genetic variation over the 25 years since reintroduction. We found that the effective population of breeding wolves carried a significantly shorter distances at which LD decays. This is consistent with past findings that the YNP effective gray wolf population carried a higher mean allelic richness, which is expected to show more immediate changes than other allele diversity metrics like heterozygosity, than the census in nearly all years surveyed (1995-2015) (Cornuet and Luikart 1996; DeCandia et al. 2021).

We hypothesized that reproductive status reflected overall fitness and predicted that the effective population showed increased genetic variation, reduced autozygosity levels, and that fitness-related traits reduced in value with increasing autozygosity levels. Elevations of autozygosity levels indicate both a lack of genetic diversity and inflation of alleles that are identical by descent via inbreeding and are often associated with increased expression of recessive deleterious traits (Keller 2002; Charlesworth and Willis 2009).

Indeed, we found remarkably lower levels of autozygosity and inbreeding coefficients in the effective population relative to the non-breeding population. Such a trend is far more significant on overall inference of genetic health than levels of homozygosity. Our finding is in direct contrast to the gray wolf population in Isle Royale National Park (IRNP; Michigan, USA), which had persisted at exceedingly low numbers for over a decade with negative fitness and genome-wide consequences recently documented (Robinson et al. 2019). We do not suggest the genetic health of YNP wolves is similar to IRNP; rather, they represent differences along the complex gradient of interactions between effective population size, genetic isolation, and fitness.

The suggested traits impacted by autozygosity in YNP gray wolves were reflected in reproduction, a fitness consequence concordant with studies of IBD and complex diseases in humans (Ceballos et al. 2018; Pemberton et al. 2018; Szpiech et al. 2013). After controlling for sex-specific differences in primiparity, individuals that are older at the time of their first litter carried higher levels of autozygosity, which was also positively associated with a significant reduction in the total number of litters for that individual. Proximate mechanisms for why these older individuals were unable to breed during previous years may be due to intra-pack composition (e.g. lower social status or no access to unrelated mates) or challenges with finding potential mates through dispersal. Ultimately, individuals with higher levels of autozygosity that breed later in life may be losing out to higher quality competitors before eventually breeding, indicating a fitness cost. Sex-specific differences in age at first litter likely reflect differential breeding opportunities through male-biased dispersal and female natal philopatry documented in YNP wolves (Stahler et al. 2020; Smith et al. 2020).

Albeit such trait depression is difficult to acquire a large enough sample size for a well-powered study in natural populations, especially those with longer generation times, similar trends have been reported in other systems (Keller and Waller 2002). Nielsen et al. (2012) utilized a long-term pedigree-based design for meerkats (*Suricata suricatta*), a cooperative and group-living species, and found that increased inbreeding coefficients were associated with negative morphologic consequences for pups with higher inbreeding coefficients. Increased pathogen load was found in Soay sheep (*Ovis aries*) in sheep with reduced genetic diversity (Coltman et al. 1999) and depressed fitness across developmental stages for the endangered red-cockaded woodpecker (*Picoides borealis*) (Daniels and Walters 2000). We also recently found similar trends for the YNP wolves whereas reductions in genome-wide diversity estimates are associated with increased disease severity with respect to sarcoptic mange infections (DeCandia et al. 2021). While YNP wolves overall are genetically diverse, we detected reproduction consequences associated with moderate increases in autozygosity as a result of reduced genetic variation. Similar patterns of reproductive consequences were found with maternal inbreeding levels in red deer (*Cervus elaphus*) being correlated with reduced offspring survival, further suggesting that depression of fitness traits in adult individuals is likely to be more accurately estimated from marker-based data (Huisman et al. 2016). Chu and colleagues (2019) reported a negative correlation between fecundity and autozygosity in a longitudinal study of domestic dogs, which also supported pedigree-based assessments of such (LeRoy et al. 2015).

Surveying lethal equivalents (LE) assumes that trait depression is caused by deleterious recessive variation found in the homozygous state (or the equivalent of alleles across loci with a similar contribution towards trait depression). Pedigree-based estimates of inbreeding revealed a negative correlation to the number of litters, with an estimation that each wolf likely carries nearly two LEs in their genome, similar to previous estimates made for humans, *Drosophila*, and great tits (Szulkin et al. 2007; Gao et al. 2015). This directly translated to an expected decrease in offspring survival to maturity by 22% due to a full-sibling mating. Nietlisbach and colleagues (2018) conducted a literature survey and reported that wild vertebrate populations carried on average 3.5 LEs. However, 13 of the 18 studies analyzed represented bird species, likely across a diversity of mating systems relative to the highly structured one of gray wolves.

Long-term implications

These results provide a valuable baseline through which continued monitoring can evaluate long-term genetic health of wolves in YNP. Similar approaches could be applied across a larger geographic scale to monitor genetic health and connectivity of wolf populations throughout the contiguous U.S., a task that is identified in the final ESA delisting requirements (USFWS 2020). In light of our findings, the future genetic health of wolves in YNP depends upon the critical role of gene flow and preserving landscape corridors to support effective dispersal. The YNP wolf population, which represents the core of a larger population throughout the Greater Yellowstone Ecosystem, serves as an important source for wolves that disperse beyond the protective boundaries (vonHoldt et al. 2010). As the YNP wolf population has stabilized at lower densities over time, the pedigreed population exhibited an increase in genome uniqueness (e.g. Table 3), suggestive of successful effective dispersal that has been documented through field observations of radio-collared dispersers (Stahler et al. 2020). Although this study does not evaluate gene flow into YNP, our findings suggest that immigration of effective dispersers over time will be essential for safeguarding their future through the incorporation of new and adaptive genetic variation. Such variation provides an important mechanism for rapid evolutionary response to changing environmental challenges caused by disease, climate change and human alteration of habitats (Kardos et al. 2021).

To maintain larger-scale wolf population connectivity and counteract loss of genetic variation, natural dispersal dynamics should be promoted and anthropogenic factors that significantly reduce genetic connectivity and effective population size should be mitigated (vonHoldt et al. 2010). These goals face increased challenges under recent wolf management directives in some northern Rocky Mountain states that aim to significantly reduce the number of wolves on the landscape. For example, recent legislative actions in Montana (2021 Montana Code Annotated 87-1-901) and Idaho (2021 Idaho Senate Bill No.1211) include aggressive policies to reduce wolf population sizes to levels close to minimum threshold requirements to prevent ESA relisting (e.g. Idaho SB 1211). These actions include regulations that allow for killing wolves using methods beyond shooting, such as baiting, snaring, trapping, night-time hunting on private land, aerial gunning, unlimited quotas, large numbers of wolf tags per hunter (20 wolves in Montana) or unlimited

(Idaho), and extensive hunting seasons (e.g. year-round in Idaho and 6 months in Montana). If continued, these specific regulations have the potential to significantly reduce regional wolf population sizes, not only limiting gene flow into YNP, but disrupting the genetic connectivity that was demonstrated to have occurred across a larger regional scale following the first decade of wolf recovery in the western U.S. (vonHoldt et al. 2010). Such management policies that fail to incorporate larger meta-population dynamics of dispersal and inter-regional connectivity with adequate effective population sizes could jeopardize the tremendous success of wolf recovery efforts and genetic health in the Western United States over the last 25 years.

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Conflict of Interest

The authors declare that this work was conducted under no competing financial interests.

Data Archiving

The previously published data analyzed in this study is publicly available on NCBI's Sequence Read Archive (PRJNA577957). The mapped bam files for three newly collected individuals can be found at PRJNA743299 with additional metadata found in Supplemental Table S1.

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Figure 1. A) Number of litters (log10) as a function of pedigree-based inbreeding coefficient (*F*) estimates with data from 158 Yellowstone gray wolves (product moment correlation coefficient, r=-0.11; Spearman rank correlation coefficient, rs=0.27). **B)** Linkage disequilibrium decay for Yellowstone gray wolves (n, all=391, breeding=122, non-breeding=235, unknown=4) genotyped at 56K SNPs. **C)** Number of runs of homozygosity (ROH; minimum of 10 SNPs per 10Kb track) detected in 6Mb tracks and the related inbreeding coefficients (F_{ROH}) estimated for 391 gray wolves. The length of the genome used for ROH estimates is 2 323 956 222bp for the pruned 24K SNP set. (Abbreviations: n, number of individuals). **D)** Violin box-and-whisker jitter plots of genome-wide inbreeding coefficients estimated from runs of homozygosity (F_{ROH}) detected in 6Mb tracks for 24K pruned SNPs (minimum of 10 SNPs per 10Kb track). Welch two sample t-test statistics are provided.

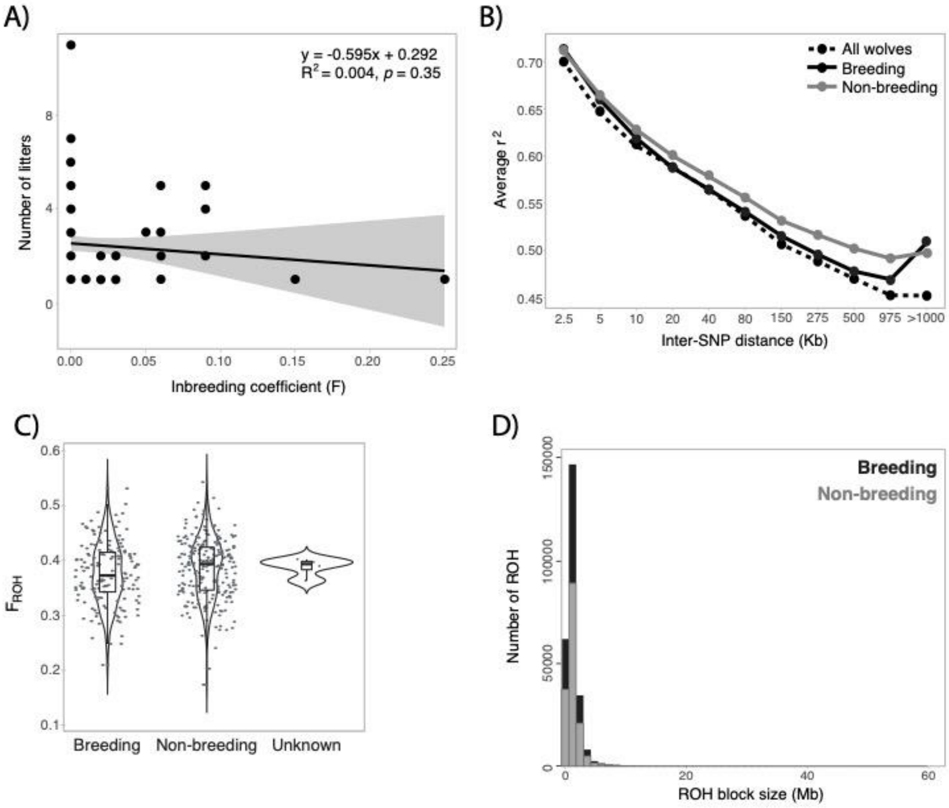

Figure 2. A) Distribution of the number of individuals per age at event of first litter (age_first_litter) when born after 1995, stratified by sex. The **B)** density plot of traits with respect to reproductive status (Abbreviations: N_{litters}, number of litters; Ho, observed heterozygosity, prop_Low, proportion of SNPs with low predicted impact; prop_Moder, proportion of SNPs with moderate predicted impact; prop_High, proportion of SNPs with high predicted impact; prop_Modif, proportion of SNPs predicted to be modifiers), and **C)** pairwise correlation plot (scale bar indicates direction and magnitude of correlation) of life-history traits for 276 wolves with known year of birth and death. **D)** Box-and-whisker plot of genome-wide inbreeding coefficients estimated from runs of homozygosity (*F_{ROH}*) as a function of age at first litter.

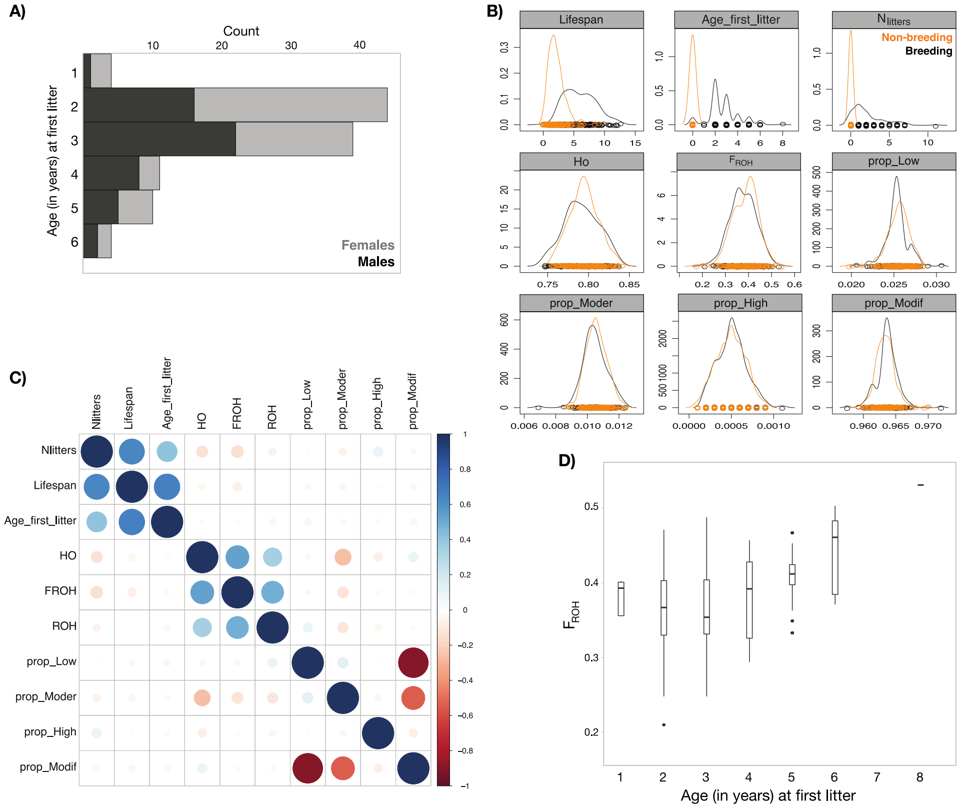

Table 1. Estimates of the pedigree founder contributions and genomic uniqueness in Yellowstone gray wolves. Genome uniqueness (*GU*) is the probability that a gene from the pedigree foundation was inherited ‘uniquely’ with respect to other pedigree founders. (Abbreviations: *pAR*, proportion of alleles retained; *pC*, proportion of genes in the pedigreed population due to that founder; YNP, Yellowstone National Park)

Founder ID	Source Pack (age class and sex)*	YNP Pack	*pC*	*pAR*	*GU*
004M	Petite Lake (adult male)	Mollies	0.08	0.94	0.00
005F	Petite Lake (adult female)	Mollies	0.09	1.00	0.00
009F	Mcleod (adult female)	Rose Creek	0.12	1.00	0.00
010M	Rick’s (adult male)	Rose Creek	0.08	0.99	0.00
013M	Berland (adult male)	Yellowstone Delta	0.02	0.98	0.01
014F	Berland (adult female)	Yellowstone Delta	0.02	0.99	0.00
015M	Berland (male pup)	Yellowstone Delta	0.00	0.50	0.33
027F	Halfway (adult female)	Nez Perce	0.04	0.99	0.00
028M	Halfway (adult male)	Nez Perce	0.04	0.99	0.00
035M	Chief (adult male)	Lone Star	0.00	0.88	0.25
036F	Besa (adult female)	Lone Star	0.00	0.50	1.00
038M	Prophet (adult male)	Druid Peak	0.02	0.99	0.00
039F	Besa (adult female)	Druid Peak	0.03	0.88	0.00
Y38	Unknown (adult male)	***	0.02	0.50	0.00
Y53	Kravac (adult female)	***	0.01	0.87	0.06
Sawtooth F**	Sawtooth (adult female)	Nez Perce	0.04	1.00	0.00
Sawtooth M**	Sawtooth (adult male)	Nez Perce	0.04	1.00	0.00

* The name of the pack in Canada from which the founder was captured.

** These two entries represent the known (and unsampled) parents of 10 full-sibling pups translocated (and genetically sampled) from the Sawtooth pack in northwestern Montana and fostered by the Nez Perce pack. Two of the translocated Sawtooth individuals assumed a breeding status in Yellowstone and represent gene flow (outbreeding) events.

*** Offspring of these individuals were translocated to the Chief Joseph pack in YNP.

Table 2. Influential ancestors identified by their marginal contribution (MC) to the total pedigree of YNP wolves. (Abbreviations: F, female; M, male)

Field ID	Source Pack (age class)	YNP pack	MC
004M	Petite Lake (dominant)	Mollies	0.08
005F	Petite Lake (dominant)	Mollies	0.09
006M	Petite Lake (pup)	Mollies	0.02
007F	Mcleod (pup)	Rose Creek	0.03
009F	Mcleod (dominant)	Rose Creek	0.12
010M	Rick’s (dominant)	Rose Creek	0.08
013M	Berland (dominant)	Yellowstone Delta	0.01
014F	Berland (dominant)	Yellowstone Delta	0.01
027F	Halfway (dominant)	Nez Perce	0.01
028M	Halfway (dominant)	Nez Perce	0.01
034M	Unknown (dominant)	Chief Joseph	0.04
038M	Prophet (dominant)	Druid Peak	0.02
039F	Besa (dominant)	Druid Peak	0.03
040F	Besa pack (pup)	Druid Peak	0.01
042F	Besa pack (pup)	Druid Peak	0.01
048F*	-	Nez Perce	0.07
072M	Sawtooth pack (pup)	Nez Perce	0.07
Y53	Kravac (female)	***	0.01
Sawtooth F**	Sawtooth (female)	Nez Perce	0.01
Sawtooth M**	Sawtooth (male)	Nez Perce	0.01

* The first generation of offspring born in YNP’s Nez Perce pack by founders 027F and 028M.

** These two entries represent the known (and unsampled) parents of 10 full-sibling pups translocated (and genetically sampled) from the Sawtooth pack in northwestern Montana and fostered by the Nez Perce pack. Two of the translocated Sawtooth individuals assumed a breeding status in Yellowstone and represent gene flow (outbreeding) events.

*** Offspring of these individuals were translocated to the Chief Joseph pack in YNP.

Table 3. Annual metrics of the pedigreed gray wolf population in Yellowstone National Park with known birth and death dates. Genomic uniqueness (*GU*) is an intra-annual population metric. (Abbreviations: *fa*, number of effective founders; *fe*, number of found equivalents; fg, number of founder genome equivalents; *MK*, mean kinship; N, annual sample size analyzed)

Year	N	*MK*%	*GU*%	*fe*	*fg*	*fa*
1995	18	7.4	20.2	8.3	7.8	8.3
1996	36	5.2	9.0	11.4	10.9	11.4
1997	59	4.9	4.9	13.1	12.2	12.9
1998	67	6.9	4.7	10.0	9.2	9.9
1999	72	7.3	5.5	9.7	8.8	9.6
2000	86	6.0	4.3	11.7	10.4	11.3
2001	89	5.9	3.0	12.4	10.8	11.9
2002	88	6.1	3.5	12.6	10.6	11.9
2003	92	6.3	3.4	12.6	10.3	11.7
2004	91	5.8	3.8	13.8	11.2	12.3
2005	78	6.3	5.3	13.6	10.7	12.1
2006	70	7.3	5.4	12.8	9.3	11.0
2007	84	7.0	5.0	14.4	9.8	12.4
2008	76	7.6	5.4	14.1	9.1	11.5
2009	65	8.1	7.1	13.3	8.6	10.9
2010	58	8.4	5.5	13.3	8.3	10.8
2011	53	8.1	8.9	14.2	8.6	12.0
2012	40	8.3	11.2	14.6	8.4	13.1
2013	29	8.2	13.4	15.8	8.3	12.3
2014	30	7.2	16.9	16.8	9.4	13.8
2015	28	7.4	13.1	17.0	9.2	14.5
2016	22	8.5	15.1	15.4	7.9	11.5
2017	16	10.2	18.0	13.5	6.6	10.2
2018	10	12.0	28.5	13.8	5.3	7.8
2019	1	--	--	6.4	0.9	2.0

Table 4. Annual population averages of observed heterozygosity (H_O) estimated from 56K SNPs and inbreeding coefficients (F_{ROH}) from 24K pruned SNPs genotyped in breeding and non-breeding gray wolves of Yellowstone National Park (B and NB, respectively) with known years of birth and death. When census size also includes individuals of unknown breeding status. Significance was assessed by a 1-way ANOVA. (Abbreviations: N_G, number of individuals genotyped; NS, not significant)

Year	N_B, N_{NB} (N_G)	H_O	F_{ROH}	ANOVA *F*, *p*
1995	23, 6 (29)	0.78, 0.79	0.34, 0.31	NS
1996	27, 16 (43)	0.78, 0.79	0.33, 0.34	NS
1997	38, 24 (62)	0.78, 0.79	0.35, 0.36	NS
1998	37, 28 (65)	0.79, 0.80	0.36, 0.39	NS
1999	36, 35 (71)	0.79, 0.80	0.37, 0.39	NS
2000	49, 37 (86)	0.79, 0.79	0.36, 0.37	NS
2001	50, 37 (88)	0.79, 0.79	0.37, 0.38	NS
2002	52, 39 (92)	0.79, 0.79	0.37, 0.38	NS
2003	58, 44 (103)	0.79, 0.80	0.38, 0.36	NS
2004	58, 52 (111)	0.79, 0.80	0.38, 0.38	NS
2005	52, 49 (101)	0.80, 0.80	0.38, 0.39	NS
2006	57, 36 (93)	0.80, 0.80	0.39, 0.39	NS
2007	62, 46 (108)	0.79, 0.79	0.38, 0.39	NS
2008	57, 42 (99)	0.79, 0.79	0.39, 0.38	NS
2009	56, 27 (83)	0.80, 0.79	0.39, 0.40	NS
2010	48, 26 (74)	0.80, 0.80	0.39, 0.40	NS
2011	46, 29 (75)	0.80, 0.81	0.39, 0.41	H_O 4.19, p=0.0444
2012	34, 24 (58)	0.79, 0.81	0.38, 0.42	H_O 9.58, p=0.0031; F_{ROH} 5.64, p=0.0210
2013	33, 13 (46)	0.79, 0.80	0.38, 0.40	H_O 3.80, p=0.0576
2014	32, 18 (50)	0.79, 0.79	0.39, 0.40	NS
2015	28, 18 (46)	0.79, 0.79	0.39, 0.39	NS
2016	23, 19 (42)	0.79, 0.79	0.39, 0.40	NS
2017	20, 20 (40)	0.79, 0.80	0.39, 0.40	NS
2018	12, 12 (24)	0.79, 0.79	0.40, 0.40	NS

Table 5. Cox proportional hazards regression with age at first litter as the outcome response. Time is recorded in years and represents time to first litter (n=139) or time to last observation or death (n=238) whichever is sooner. Data from animals who die or are no longer observed before reproducing are considered censored. The predictors are time invariant and have been standardized. The best fitting model (bolded) has the lowest Akaike information criterion (AIC). (Abbreviations: H_O, observed heterozygosity)

Predictor	Log hazard coefficient	Model *p*	AIC
Base model Sex	-0.5702	0.0012	1264.4
H_O	0.0186	0.8800	1266.4
Sex	-0.5721	0.0012	
F_{ROH}	**-0.2406**	**0.0203**	**1261.4**
Sex	**-0.5674**	**0.0012**	
propHigh	0.1103	0.2222	1264.9
Sex	-0.5526	0.0017	
propModer	-0.0563	0.5554	1266.1
Sex	-0.5558	0.0017	
propModif	0.1226	0.1697	1264.6
Sex	-0.5955	0.0008	
propLow	-0.1299	0.1432	1264.3
Sex	-0.6172	0.0006	

Supplemental Table S1. Sample information and meta-data for 474 Yellowstone gray wolves in pedigree analysis. Genetic or field-confirmed parentage as well as their natal pack name is provided. Individuals with genetic data included in this study are indicated in the “RADseq data” column. Individuals that founded the population are noted with one or both parents listed as “Canada” as per unknown pedigree information. (Abbreviations: F, female; M, male; YOB, year of birth; YOD, year of death)

Field_ID	Mother_ ID	Father_ID	YOB	YOD	Natal Pack	Pedigree _F	Number of litters from pedigree	RADseq data	Notes	Sample_ID in SRA
002M	005F	004M	1994	2002	Crystal/Mollies	0	6	Yes	YNP founder	227
003M	005F	004M	1994	1996	Crystal/Mollies	0	0		YNP founder	003M
008M	005F	004M	1994	2000	Crystal/Mollies	0	6	Yes	YNP founder	228
118M	005F	006M	1997	1999	Crystal	0	1	Yes		222
120M	005F	006M	1997	2000	Crystal	0	1	Yes		275
122M	005F	006M	1997	1999	Crystal	0	0	Yes		8749
136F	005F	006M	1997	2000	Crystal	0	0	Yes		223
303M	005F	006M	1997	2008	Mollie's	0	7	Yes		339
243M	005F	006M	1998	2002	Crystal	0	1	Yes		306
256M	005F	006M	2000		Crystal	0	1			256M
055M	007F	002M	1996	2000	Leopold	0	0	Yes		689
207M	007F	002M	1996	2003	Leopold	0	1	Yes		207M
095F	007F	002M	1997	1998	Leopold	0	0	Yes		224
151F	007F	002M	1997	2008	Leopold	0	6	Yes		151F
165M	007F	002M	1997	1999	Leopold	0	2	Yes		573
148F	007F	002M	1998	2001	Leopold	0	0	Yes		5409
150M	007F	002M	1998	2004	Leopold	0	0	Yes		632

152F	007F	002M	1998	2005	Leopold	0	5	Yes		233
300M	007F	002M	1999	2003	Leopold	0	0	Yes		336
209F	007F	002M	2000	2008	Leopold	0	3	Yes		284
259F	007F	002M	2000	2003	Leopold	0	1	Yes		320
296M	007F	002M	2000	2003	Leopold	0	1	Yes		335
302M	007F	002M	2000	2009	Leopold	0	4	Yes		5421
288F	007F	002M	2001	2006	Leopold	0	2	Yes		230
301M	007F	002M	2001	2006	Leopold	0	1	Yes		337
007F	009F	Canada	1994	2002	Rose Creek	0	6	Yes	YNP founder	231
016F	009F	010M	1995	2000	Rose Creek	0	5	Yes	YNP founder	246
017F	009F	010M	1995	1997	Rose Creek	0	1	Yes	YNP founder	247
018F	009F	010M	1995		Rose Creek	0	4		YNP founder	018F
019F	009F	010M	1995	1997	Rose Creek	0	0	Yes	YNP founder	248
020M	009F	010M	1995	1996	Rose Creek	0	0	Yes	YNP founder	249
021M	009F	010M	1995	2004	Rose Creek	0	11	Yes	YNP founder	250
022M	009F	010M	1995	1995	Rose Creek	0	0	Yes	YNP founder	251
155F	009F	008M	1998	2001	Rose Creek	0	0	Yes		695
161M	009F	008M	1998	2001	Rose Creek	0	0	Yes		7887
024F	014F	013M	1995	1998	Soda Butte	0	1	Yes	YNP founder	252
043M	014F	013M	1996	1999	Soda Butte	0	0	Yes		255
044F	014F	013M	1996	2005	Soda Butte	0	0	Yes		256
045F	014F	013M	1996	1996	Soda Butte	0	0	Yes		257
123M	014F	013M	1997	1999	Soda Butte	0	0	Yes		276

124M	014F		1997	2000	Soda Butte	0	0	Yes	8750
126F	014F	013M	1997	2009	Soda Butte	0	7	Yes	1261
240M	016F	165M	0	2003	Sheep Mountain	0.06	0	Yes	304
052M	016F	008M	1996	2003	Rose Creek	0	0		052M
078F	016F	008M	1997	1999	Rose Creek	0	0	Yes	267
085F	016F	008M	1997	1998	Rose Creek	0	0	Yes	7927
108M	016F	034M	1997	1997	Chief Joseph	0	0		273
111F	016F	034M	1997	1998	Chief Joseph	0	0	Yes	274
167F	016F	165M	1998	1999	Sheep Mountain	0.06	0		167F
168F	016F	165M	1998	1999	Sheep Mountain	0.06	0	Yes	279
188F	016F	165M	1998	2000	Sheep Mountain	0.06	0	Yes	576
195M	016F	165M	1998	2001	Sheep Mountain	0.06	0		195M
196M	016F	165M	1998	2001	Sheep Mountain	0.06	0	Yes	367
182M	016F	165M	1999	1999	Sheep Mountain	0.06	0	Yes	4666
183F	016F	165M	1999	1999	Sheep Mountain	0.06	0	Yes	4671
184F	016F	165M	1999	1999	Sheep Mountain	0.06	0	Yes	702
189M	016F	165M	1999	2001	Sheep Mountain	0.06	0	Yes	704
197F	016F	165M	1999	2000	Sheep Mountain	0.06	0	Yes	1527
113M	017F	034M	1997		Chief Joseph	0	7		630
147M	017F	034M	1997	2000	Chief Joseph	0	1	Yes	693
204M	017F	034M	1997	2005	Chief Joseph	0	2		204M
206M	017F	034M	1997	2004	Chief Joseph	0	4	Yes	282
077F	018F	008M	1997	2000	Rose Creek	0	0	Yes	266

082M	018F	008M	1997	1999	Rose Creek	0	0	Yes		268
083M	018F	008M	1997	1998	Rose Creek	0	0	Yes		269
192M	018F	008M	1997	2009	Rose Creek	0	1	Yes		372
193M	018F	008M	1997		Rose Creek	0	7			417
194M	018F	008M	1997	2004	Rose Creek	0	1			194M
208M	018F	008M	1997	2003	Rose Creek	0	0			160
153F	018F	008M	1998	1999	Rose Creek	0	0	Yes		690
154F	018F	008M	1998	2000	Rose Creek	0	0	Yes		7885
156F	018F	008M	1998	2000	Rose Creek	0	0	Yes		696
160F	018F	008M	1998	1999	Rose Creek	0	0	Yes		697
162M	018F	008M	1998	2002	Rose Creek	0	0	Yes		699
271F	018F	008M	1998	2006	-	0	2	Yes		324
190F	018F	008M	1999	2004	Rose Creek	0	0	Yes		371
260F	018F	207M	2001	2003	Rose Creek	0.06	0	Yes		321
228F	024F		1999		Teton	0	0			228F
229M	024F		1999	2001	Teton	0	0	Yes		301
026F	027F	028M	1995	1996	Nez Perce	0	0	Yes	YNP founder	622
029M	027F	028M	1995	1998	Nez Perce	0	2	Yes	YNP founder	7855
030F	027F	028M	1995	1998	Nez Perce	0	1		YNP founder	625
037F	027F	028M	1995	1997	Nez Perce	0	1	Yes	YNP founder	254
047M	027F	028M	1996	1996	Nez Perce	0	0			047M
048F	027F	028M	1996	2005	Nez Perce	0	6	Yes		258
128M	030F	035M	1997	1998	Thorofare	0	0	Yes		277

129F	030F	035M	1997	2000	Thorofare	0	0			129F
277F	033F	034M	0	2002	Chief Joseph	0	0			277F
115F	033F	034M	1998	1999	Chief Joseph	0	0	Yes		692
185M	033F	034M	1999	1999	Chief Joseph	0	0	Yes		5299
186M	033F	034M	1999	1999	Chief Joseph	0	0	Yes		4668
187F	033F	034M	1999	2000	Chief Joseph	0	0	Yes		700
201F	033F	034M	1999	2001	Chief Joseph	0	0	Yes		7913
202M	033F	034M	2000	2002	Chief Joseph	0	0			202M
203M	033F	034M	2000	2001	Chief Joseph	0	0	Yes		5413
205M	033F	034M	2000	2004	Chief Joseph	0	1	Yes		1529
248M	033F	034M	2001	2002	Chief Joseph	0	0	Yes		311
058F	036F	035M	1996	1996	Lone Star	0	0	Yes		261
092M	037F	029M	1997	2001	Nez Perce	0.25	0			092M
040F	039F	Canada	1995	2000	Druid Peak	0	2	Yes	YNP founder	369
041F	039F	Canada	1995	1997	Druid Peak	0	2	Yes	YNP founder	8787
042F	039F	Canada	1995	2004	Druid Peak	0	5	Yes	YNP founder	629
199M	040F	021M	1999	2000	-	0	0	Yes		4669
217F	040F	021M	2000	2004	Druid Peak	0	1	Yes		291
218F	040F	021M	2000	2002	Druid Peak	0	0	Yes		292
221M	040F	021M	2000	2002	Druid Peak	0	0	Yes		221M
251F	040F	021M	2000	2003	Druid Peak	0	2	Yes		313
472F	040F	021M	2000	2010	Druid Peak	0	7	Yes		378
103F	041F	038M	1997	2004	Druid Peak	0	1	Yes		271

422F	041F		2003	2004	Druid Peak	0	0		7623
105F	042F	038M	1997	2003	Druid Peak	0	1	Yes	7877
106F	042F	038M	1997	2005	Druid Peak	0	4	Yes	272
104M	042F	038M	1997	2000	Druid Peak	0	0	Yes	226
163M	042F	021M	1998	2000	-	0	0		163M
216F	042F	021M	2000	2002	Druid Peak	0	0	Yes	290
254M	042F	021M	2000	2002	Druid Peak	0	0	Yes	316
386F	042F	021M	2000	2004	-	0	1	Yes	1528
255F	042F	021M	2001	2005	Druid Peak	0	1	Yes	151
424M	042F	021M	2001	2004	Druid Peak	0	2		366
350M	042F	021M	2003	2004	Druid Peak	0	0	Yes	346
627M	042F	021M	2003	2008	Druid Peak	0	4	Yes	1268
212F	048F	029M	1998	2001	Nez Perce	0.25	1	Yes	287
191M	048F	072M	1999	2001	Nez Perce	0	0	Yes	705
215M	048F	072M	2000	2002	Nez Perce	0	0	Yes	289
249M	048F	072M	2000	2002	Nez Perce	0	0	Yes	312
340F	048F	072M	2000		Nez Perce	0	1		340F
534M	048F	072M	2000	2008	Nez Perce	0	7	Yes	5501
540F	048F	072M	2000	2007	Nez Perce	0	2	Yes	411
305M	048F	072M	2002	2005	Nez Perce	0	0	Yes	340
306F	048F	072M	2002		Nez Perce	0	0		306F
341F	048F	072M	2002	2008	Nez Perce	0	0	Yes	659
537F	048F	072M	2002	2009	Gibbon Meadows	0	7	Yes	1279

342F	048F	072M	2003	2004	Nez Perce	0	0		587
467M	048F	072M	2003	2004	Nez Perce	0	0	Yes	374
476F	048F	072M	2003	2005	Nez Perce	0	0		476F
484M	048F	072M	2004	2005	Nez Perce	0	0	Yes	386
485F	048F	072M	2004	2006	Nez Perce	0	1	Yes	387
486F	048F	072M	2004	2011	Nez Perce	0	6	Yes	388
381M	103F	296M	2002	2005	Leopold	0	1	Yes	358
219M	105F	021M	2000	2005	Druid Peak	0	0		293
253M	105F	021M	2000	2005	Druid Peak	0	0	Yes	315
353F	105F	021M	2000	2007	Druid Peak	0	2	Yes	349
222M	106F	021M	2000	2001	Druid Peak	0	0	Yes	296
224M	106F	021M	2000	2002	Druid Peak	0	1	Yes	297
351M	106F	294M	2002	2004	Geode Creek	0	0		347
391F	106F	294M	2002	2005	Druid Peak	0	0	Yes	364
392M	106F	294M	2002	2004	Geode Creek	0	0	Yes	365
483F	106F	294M	2003	2005	Geode Creek	0	0	Yes	385
488M	106F	227M	2004	2005	Geode Creek	0	0	Yes	4772
498F	106F	227M	2004	2005	Geode Creek	0	0	Yes	395
1104F	1091F	1015M	2017	2018	Wapiti Lake	0.02	0	Yes	9581
831F	1093F	712M	2011	2013	Canyon	0.05	0	Yes	5389
225M	126F	120M	2000	2001	Yellowstone Delta	0	0	Yes	225M
226M	126F	120M	2000	2001	Yellowstone Delta	0	0	Yes	7894
227M	126F	120M	2000	2005	Yellowstone Delta	0	1	Yes	299

245M	126F	243M	2001	2001	Yellowstone Delta	0	0	Yes	308
246M	126F	243M	2001	2001	Yellowstone Delta	0	0	Yes	309
247M	126F	243M	2001	2001	Yellowstone Delta	0	0	Yes	310
572F	126F		2001	2007	Yellowstone Delta	0	0	Yes	678
542F	126F		2003	2006	Yellowstone Delta	0	0	Yes	5415
493M	126F		2004	2005	Yellowstone Delta	0	0	Yes	662
659M	126F		2004	2008	Yellowstone Delta	0	0	Yes	1251
634F	126F		2006	2008	Yellowstone Delta	0	0	Yes	1253
635F	126F		2006	2008	Yellowstone Delta	0	0	Yes	1270
660F	126F		2006	2008	Yellowstone Delta	0	0	Yes	1254
633F	126F		2007	2014	Yellowstone Delta	0	1	Yes	1267
713F	126F		2007	2009	Yellowstone Delta	0	0	Yes	1487
257M	151F	303M	2001	2005	Cougar Creek	0.09	0	Yes	318
482M	151F	303M	2001	2010	Cougar Creek	0.09	5	Yes	482M
538M	151F	303M	2001	2007	Cougar Creek	0.09	0	Yes	409
291M	151F	303M	2002	2004	Cougar Creek	0.09	0	Yes	330
388F	151F	303M	2002	2005	Cougar Creek	0.09	0	Yes	361
389M	151F	303M	2002	2004	Cougar Creek	0.09	2	Yes	362
479M	151F	303M	2002	2005	Cougar Creek	0.09	0	Yes	384
477M	151F	303M	2003	2005	Cougar Creek	0.09	0	Yes	382
478F	151F	303M	2003	2015	Cougar Creek	0.09	4	Yes	478F
546M	151F	303M	2004	2006	Cougar Creek	0.09	0	Yes	412
632F	151F	303M	2004	2009	Cougar Creek	0.09	0		1272

636M	151F	303M	2007	2011	Cougar Creek	0.09	2	Yes	1274
SW798M	151F	303M	2009	2010	Cougar Creek	0.09	0		SW798M
SW804M	151F	303M	2009	2010	Cougar Creek	0.09	0		SW804M
541M	152F	206M	2000	2007	Swan Lake	0.03	2	Yes	404
292M	152F	206M	2001	2004	Swan Lake	0.03	1	Yes	292M
347M	152F	204M	2002	2003	Swan Lake	0.03	0	Yes	589
355F	152F	206M	2002	2005	Swan Lake	0.03	0	Yes	156
515U	152F		2005	2005	Swan Lake	0	0		515U
387U	174F	193M	1999	2001	Mollie's	0	0		387U
263M	174F	193M	2000		Mollie's	0	0		1517
378M	174F	193M	2000		Mollie's	0	0		378M
261M	174F	194M	2001	2004	Mollie's	0	2	Yes	322
264F	174F	193M	2001	2002	-	0	0		581
377M	174F	193M	2001	2006	Mollie's	0	2	Yes	355
379M	174F	193M	2001	2005	Mollie's	0	0	Yes	356
489M	174F	193M	2001	2006	Mollie's	0	1	Yes	489M
490M	174F	193M	2001	2006	Mollie's	0	2	Yes	391
586M	174F	193M	2002	2011	Mollie's	0	1	Yes	7928
587M	174F	193M	2002	2011	Mollie's	0	1	Yes	681
343M	174F	193M	2003	2005	Mollie's	0	0	Yes	342
495M	174F	193M	2003	2011	Mollie's	0	6	Yes	1485
496F	174F	193M	2004	2005	Mollie's	0	0	Yes	8753

497M	174F	193M	2004	2007	Mollie's	0	0	Yes	7901
528M	209F	534M	2003	2006	Leopold	0	0	Yes	403
591F	209F	534M	2006	2008	Leopold	0	0	Yes	683
593F	209F	534M	2006	2008	Leopold	0	0	Yes	8754
623M	209F	534M	2007	2008	Leopold	0	0		1277
624F	209F	534M	2007	2008	Leopold	0	0	Yes	1260
252M	212F	072M	2000	2002	Nez Perce	0	0	Yes	314
309F	212F	072M	2000	2003	Nez Perce	0	0	Yes	586
453M	217F	261M	2003	2005	Slough Creek	0.03	0	Yes	5497
344F	220F		2002	2007	Leopold	0	1	Yes	343
239M	233F	147M	2001		-	0	0	Yes	303
295M	251F	113M	2002	2007	Agate Creek	0.06	5	Yes	334
361M	251F	301M	2003	2003	-	0.03	0	Yes	590
349M	255F	302M	2003	2005	Druid Peak	0.03	0	Yes	345
480M	259F	534M	2003	2010	Leopold	0	3	Yes	4773
307M	271F	424M	2000	2003	Mill Creek	0.06	0	Yes	584
308F	271F	424M	2002	2003	Mill Creek	0.06	0	Yes	585
435U	286F	021M	2004	2004	-	0.12	0		435U
382F	288F	534M	2003	2004	Leopold	0	0	Yes	359
468M	288F	534M	2003	2007	Leopold	0	0	Yes	4774
469F	288F	534M	2003	2012	Leopold	0	4	Yes	375
536F	288F	534M	2003	2009	Leopold	0	3	Yes	407
507U	288F	534M	2005	2005	Leopold	0	0		507U

508U	288F	534M	2005	2005	Leopold	0	0		508U
466U	340F		2004	2004	Biscuit Basin	0	0	Yes	466U
474M	340F		2004	2005	Biscuit Basin	0	0	Yes	380
475F	340F		2004	2005	Biscuit Basin	0	0	Yes	381
670U	344F		2007	2008	-	0	0		1519
352M	353F	294M	2002	2003	Druid Peak	0	0	Yes	348
568U	353F	287M	2006	2006	Hellroaring	0.09	0		568U
502U	380F	377M	2004	2004	Slough Creek	0.12	0		502U
526F	380F	377M	2004	2008	Slough Creek	0.12	0		401
631F	380F	615M	2007	2008	Slough Creek	0.02	0		1271
976F	380F	615M	2007	2015	Slough Creek	0.02	1	Yes	5882
286F	386F	214M	2002		Druid Peak	0	1		326
523F	469F	381M	2005	2008	Leopold	0.06	0	Yes	523F
639M	469F	SW147M	2006	2008	Hayden Valley	0.02	0	Yes	1278
821F	469F	695M	2009	2017	Quadrant	0.01	1	Yes	5874
871M	469F	295M	2010	2014	-	0.02	1	Yes	5394
733F	470F	627M	2006	2009	Oxbow Creek	0.05	0	Yes	1515
524F	471F	113M	2005	2007	Agate Creek	0.03	0	Yes	408
643F	471F	383M	2007	2008	Agate Creek	0.02	0	Yes	1259
644F	471F	383M	2007	2008	Agate Creek	0.02	0	Yes	1265
715F	471F	383M	2007	2011	Agate Creek	0.02	0	Yes	1489
384F	472F	113M	2003		Agate Creek	0.06	0		5591
385M	472F	113M	2003		Agate Creek	0.06	0		5592

471F	472F		2003	2012	Agate Creek	0	2	Yes	7898
525F	472F	113M	2004	2008	Agate Creek	0.06	0	Yes	400
SW147 M	472F	113M	2004	2010	Agate Creek	0.06	1	Yes	7912
615M	472F	113M	2005	2007	Agate Creek	0.06	3		1257
590M	472F	113M	2006	2008	Agate Creek	0.06	0	Yes	682
692F	472F	113M	2006	2011	Agate Creek	0.06	2	Yes	1507
693F	472F	113M	2006	2013	Agate Creek	0.06	2	Yes	1495
832F	472F	113M	2006	2012	Agate Creek	0.06	2		832F
642F	472F	383M	2007	2011	Agate Creek	0.03	0	Yes	1266
775M	472F	641M	2010	2011	Agate Creek	0.02	0	Yes	7903
757F	478F	689M	2009	2013	Cougar Creek	0.15	0	Yes	5373
910M	478F	689M	2009	2018	Cougar Creek	0.15	0	Yes	5871
825F	478F	689M	2011	2012	Cougar Creek	0.15	0	Yes	5383
962M	478F	689M	2011	2019	Cougar Creek	0.15	1		8764
953F	478F	689M	2013	2018	Cougar Creek	0.15	1	Yes	953F
1204F	478F	689M	2014		-	0.15	0		7921
754M	485F		2008	2012	755M Group	0	1	Yes	1504
755M	485F		2008	2017	755M Group	0	4	Yes	1502
712M	486F	193M	2006	2017	Mollie's	0	2	Yes	5418
640F	486F	586M	2007	2010	Mollie's	0	1	Yes	1280
641M	486F	586M	2007	2011	Mollie's	0	1	Yes	1273
686F	486F	586M	2007	2013	Mollie's	0	0	Yes	7856

870F	486F	587M	2008	2015	Mollie's	0	2	Yes	5392
812M	486F	495M	2009	2011	Mollie's	0	0	Yes	4665
779F	486F	495M	2010	2018	Mollie's	0	3	Yes	7906
970F	486F	495M	2010	2016	-	0	2	Yes	8771
823F	486F	495M	2011	2012	Mollie's	0	0	Yes	5381
824M	486F	495M	2011	2012	Mollie's	0	0	Yes	5382
889F	486F	495M	2011	2014	Junction Butte	0	0	Yes	5422
949M	486F	495M	2011	2017	-	0	0	Yes	9074
621F	527F	490M	2005	2007	Slough Creek	0.25	0	Yes	2056
716F	527F	490M	2005	2009	Slough Creek	0.25	0	Yes	1490
618F	527F	615M	2007	2007	Slough Creek	0.02	0		618F
620M	527F	615M	2007	2007	Slough Creek	0.02	0	Yes	1255
589F	536F	627M	2006	2008	Oxbow Creek	0.02	0	Yes	7929
628M	536F	627M	2006	2008	Oxbow Creek	0.02	0		628M
626F	536F	627M	2007	2008	Oxbow Creek	0.02	0	Yes	1264
672U	536F	627M	2008	2008	-	0.02	0		672U
451F	537F	256M	2004	2004	Gibbon Meadows	0	0	Yes	599
481M	537F	256M	2004	2006	Gibbon Meadows	0	0	Yes	166
539F	537F	482M	2005	2009	Gibbon Meadows	0	0	Yes	410
794F	537F	482M	2005	2012	Gibbon Meadows	0	2	Yes	5314
577M	537F	482M	2006	2008	Gibbon Meadows	0	0	Yes	679
578F	537F	482M	2006		Gibbon Meadows	0	0		680
689M	537F	482M	2006	2014	Gibbon Meadows	0	4	Yes	1493

646F	537F	482M	2007	2009	Gibbon Meadows	0	0	Yes	1269
647M	537F	482M	2007	2011	Gibbon Meadows	0	0	Yes	1276
687M	537F	482M	2008	2009	Gibbon Meadows	0	0	Yes	7618
688M	537F		2008	2010	Gibbon Meadows	0	0	Yes	1492
729M	537F	482M	2008	2009	Gibbon Meadows	0	0	Yes	1522
769M	537F	482M	2008	2010	Gibbon Meadows	0	0	Yes	1509
768F	537F	482M	2009	2010	Gibbon Meadows	0	0	Yes	5375
1093F	540F	541M	2006	2017	-	0	1	Yes	8782
622F	540F	541M	2007	2007	Hayden Valley	0	0	Yes	5302
1116U	545F		2011	2018	-	0	0		9587
570M	569F	302M	2006	2007	Druid Peak	0.03	0	Yes	676
571F	569F	480M	2006	2010	Druid Peak	0.02	0	Yes	677
629M	569F	480M	2006	2008	Druid Peak	0.02	0	Yes	1262
691F	569F	480M	2006	2010	Druid Peak	0.02	0	Yes	1494
694F	569F	480M	2006	2009	Druid Peak	0.02	0	Yes	1496
756F	569F	480M	2006	2010	Druid Peak	0.02	0	Yes	1511
645F	569F	480M	2007	2009	Druid Peak	0.02	0	Yes	1275
734M	569F	480M	2007	2009	Druid Peak	0.02	0	Yes	1512
761F	569F	480M	2007	2010	Druid Peak	0.02	0	Yes	1525
778M	569F	480M	2007	2015	Druid Peak	0.02	1	Yes	7905
815M	569F	480M	2007	2012	Druid Peak	0.02	2		815M
838M	569F	480M	2007	2012	Druid Peak	0.02	1	Yes	7867
690F	569F	480M	2008	2010	Druid Peak	0.02	0	Yes	7617

676M	588F	295M	2008	2008	-	0	0	Yes		1518
872F	633F	760M	2011	2014	Yellowstone Delta	0	0	Yes		5395
758M	640F	495M	2009	2013	Mollie's	0.12	0	Yes		5374
822F	640F	495M	2009	2012	Mollie's	0.12	0	Yes		5380
777M	692F	815M	2010	2012	Blacktail	0.05	0	Yes		8759
810F	692F	778M	2010	2011	Blacktail	0.05	0	Yes		4661
752F	693F	302M	2009	2012	Blacktail	0.03	0	Yes		5372
830F	693F	302M	2009	2012	Blacktail	0.03	0	Yes		5388
911M	693F	815M	2010	2016	Blacktail	0.05	3	Yes		7931
763F	696F	614M	2007	2012	Madison	0	0	Yes		1500
924F	779F		2013	2014	Mollie's	0	0	Yes		7924
978F	779F		2013	2018	Mollie's	0	0	Yes		5369
1014M	779F		2013	2018	-	0	0	Yes		5870
979F	779F		2014	2015	Mollie's	0	0	Yes		5370
1015M	779F		2014	2018	Mollie's	0	3	Yes		5875
1090F	779F		2014	2018	-	0	0	Yes		8779
1118F	779F		2014	2018	-	0	0	Yes		9589
1155M	779F		2014	2021	-	0	0		Newly collected in this study	10927
1013M	779F		2015	2017	-	0	0	Yes		5881
772U	794F	754M	2009	2010	-	0.06	0	Yes		5309
819F	794F	636M	2010	2012	Mary Mountain	0.15	0	Yes		5377
996M	821F	SW763M	2015	2018	-	0.01	0	Yes		5877

1012M	821F	SW763M	2015	2016	-	0.01	0	Yes	5873
1048M	821F	SW763M	2015	2018	Junction Butte	0.01	0	Yes	8775
776F	832F	755M	2010	2014	Lamar Canyon	0	0		776F
820F	832F	755M	2011	2013	Lamar Canyon	0	0	Yes	5378
759F	870F	495M	2009	2013	Mollie's	0.12	0	Yes	8758
961M	870F	890M	2014	2014	-	0	0	Yes	5884
968F	870F	890M	2014	2015	Junction Butte	0	0	Yes	8769
995F	870F	890M	2014	2016	-	0	0	Yes	5880
992M	909F	SW763M	2011	2016	-	0	0	Yes	5879
908F	909F	SW763M	2013	2014	8 Mile	0	0	Yes	7926
993M	909F	SW763M	2013	2016	-	0	0	Yes	5872
963F	909F	871M	2014	2018	8 Mile	0	1	Yes	8765
964M	909F	871M	2014	2018	8 Mile	0	0	Yes	8766
966M	909F	871M	2014	2017	8 Mile	0	0	Yes	8767
1047M	909F	871M	2014	2018	Junction Butte	0	0	Yes	8774
1005F	909F		2015	2018	-	0	0	Yes	5878
1096M	909F	962M	2017	2017	-	0	0	Yes	8785
967M	926F	925M	2014	2015	Lamar Canyon	0	0	Yes	8768
1016F	926F	925M	2015	2016	Lamar Canyon	0	0	Yes	5883
1050F	953F		2016	2017	Cougar Creek	0	0	Yes	8777
1051M	953F		2016	2017	Cougar Creek	0	0	Yes	8778
1049F	963F		2016	2018	8 Mile	0	0	Yes	8776
1107M	963F		2016	2019	-	0	0		9584

1108M	963F		2016	2018	-	0	0	Yes		9585
994M	970F	911M	2015	2016	-	0.03	0	Yes		5876
1109F	970F	911M	2016		Junction Butte	0.03	0			9586
977F	976F		2012	2015	-	0	0	Yes		5868
013M	Canada	Canada	1985	1997	Soda Butte	0	3	Yes	Pedigree founder; YNP founder	5289
004M	Canada	Canada	1989	1996	Crystal/Mollies	0	2		Pedigree founder; YNP founder	004M
027F	Canada	Canada	1989	1997	Nez Perce	0	2	Yes	Pedigree founder; YNP founder	368
038M	Canada	Canada	1989	1997	Druid Peak	0	2	Yes	Pedigree founder; YNP founder	627
039F	Canada	Canada	1989	1998	Druid Peak	0	1		Pedigree founder; YNP founder	039F
005F	Canada	Canada	1990	2000	Crystal/Mollies	0	4	Yes	Pedigree founder; YNP founder	244
009F	Canada	Canada	1990	1999	Rose Creek	0	3	Yes	Pedigree founder; YNP founder	7861
010M	Canada	Canada	1990	1995	Rose Creek	0	1		Pedigree founder; YNP founder	5290
011F	Canada	Canada	1991	1996	Soda Butte	0	0		YNP founder	011F
012M	Canada	Canada	1991	1996	Soda Butte	0	0		YNP founder	012M
035M	Canada	Canada	1992	1998	Lone Star	0	2	Yes	Pedigree founder; YNP founder	253
014F	Canada	Canada	1993	2000	Soda Butte	0	4	Yes	Pedigree founder; YNP founder	229
028M	Canada	Canada	1993	1997	Nez Perce	0	2		Pedigree founder; YNP founder	623
036F	Canada	Canada	1993	1996	Lone Star	0	1	Yes	Pedigree founder; YNP founder	556
006M	Canada	004M	1994	1998	Crystal/Mollies	0	3	Yes	YNP founder	245
015M	Canada	Canada	1994	1996	Soda Butte	0	1	Yes	Pedigree founder; YNP founder	555
034M	Canada	Y38	1994	2001	Chief Joseph	0	6	Yes	YNP founder; father is Pedigree founder	570

063F	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	262
064F	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	263
065F	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	264
066M	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0		YNP founder; parents are Pedigree founders	066M
067F	SawtoothF	SawtoothM	1996	1998	Nez Perce	0	0		YNP founder; parents are Pedigree founders	559
068F	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	560
069M	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	561
070M	SawtoothF	SawtoothM	1996	2005	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	563
071F	SawtoothF	SawtoothM	1996	1997	Nez Perce	0	0	Yes	YNP founder; parents are Pedigree founders	265
072M	SawtoothF	SawtoothM	1996	2003	Nez Perce	0	7	Yes	YNP founder; parents are Pedigree founders	562
032F	Y53	038M	1992	1996	Chief Joseph	0	0		YNP founder; mother is Pedigree founder	032F
031M	Y53	038M	1995	1997	Chief Joseph	0	0	Yes	YNP founder; mother is Pedigree founder	626
033F	Y53	038M	1995	2001	Chief Joseph	0	4	Yes	YNP founder; mother is Pedigree founder	154
285M				2003	Lone Bear	0	0	Yes		325
614M		192M		2007	Bechler	0	1	Yes		5305

023M		1995		Rose Creek	0	0		YNP founder	023M
233F	015M	1997		Soda Butte	0	1			302
174F		1998	2004	Crystal	0	7		Pedigree founder	174F
487M		1998	2006	Yellowstone Delta	0	1		Pedigree founder	389
294M		1999	2003	-	0	3	Yes	Pedigree founder	333
210M	303M	2000	2003	Leopold	0	0	Yes		285
214M	072M	2000	2004	Nez Perce	0	1			288
220F	303M	2000	2003	Leopold	0	1	Yes		294
555F	021M	2000	2006	-	0	0			555F
241M	118M	2001	2002	Sheep Mountain	0	1	Yes		305
434F		2001	2004	-	0	0	Yes		597
287M	224M	2002	2007	Leopold	0	1	Yes		327
289M	224M	2002	2003	Leopold	0	1	Yes		328
293F	206M	2002	2004	Swan Lake	0	0	Yes		332
356M	204M	2002	2005	Swan Lake	0	0	Yes		351
348M	302M	2003	2005	Druid Peak	0	0	Yes		344
373M	302M	2003		Druid Peak	0	0			2049
374M	302M	2003	2009	Druid Peak	0	0			2050
375F	302M	2003	2005	Druid Peak	0	0	Yes		354
380F	489M	2003	2008	Slough Creek	0	2	Yes		357
383M	113M	2003	2010	Agate Creek	0	2	Yes		7895
527F	490M	2003	2009	-	0	2	Yes		402
535M		2003	2006	Leopold	0	0	Yes		406

470F	295M	2004	2011	Leopold	0	1	Yes		376
473M	205M	2004	2005	Swan Lake	0	0	Yes		379
491M	377M	2004	2006	Slough Creek	0	0	Yes		392
492F	487M	2004		Yellowstone Delta	0	0			7920
529F	021M	2004	2006	Druid Peak	0	0	Yes		405
569F	021M	2004	2009	Druid Peak	0	4	Yes		7902
658M		2004	2008	Yellowstone Delta	0	0	Yes		1252
685M	377M	2004	2011	Slough Creek	0	1	Yes		1491
695M	261M	2004	2011	-	0	1	Yes		1497
696F		2004	2009	-	0	1	Yes	Pedigree founder	1531
698M	241M	2004	2008	-	0	0	Yes		4664
543M	192M	2005	2007	Bechler	0	0	Yes		414
544M	192M	2005	2008	Bechler	0	0	Yes		415
545F	192M	2005	2010	Bechler	0	1	Yes		416
588F	534M	2005	2008	Leopold	0	1	Yes		7917
613M	295M	2005	2007	-	0	0	Yes		7866
625F	292M	2006	2009	Leopold	0	0	Yes		1281
661M		2006	2014	Butte Creek	0	0	Yes		1499
762M	289M	2006	2012	-	0	0	Yes		1510
630F	615M	2007	2008	Slough Creek	0	0	Yes		1263
638M	495M	2007	2008	Hayden Valley	0	0	Yes		1258
679F		2007	2008	-	0	0	Yes		1526
697M		2007	2009	-	0	0	Yes		1514

760M		2007	2014	Butte Creek	0	2	Yes	Pedigree founder	1508
SW763 M	295M	2007	2017	8 Mile	0	3	Yes		8772
684M	685M	2008		Everts	0	0			8755
753F		2009	2010	Silver	0	0	Yes		1503
809F	389M	2009	2011	-	0	0	Yes		4660
909F		2009	2017	Quadrant	0	5	Yes	Pedigree founder	7918
925M		2009	2015	-	0	2	Yes	Pedigree founder	7914
780M	760M	2010	2011	Yellowstone Delta	0	0	Yes		8760
811F	389M	2010	2011	-	0	0	Yes		4662
827M	760M	2010	2012	Yellowstone Delta	0	0	Yes		5385
905M		2010	2013	Blacktail	0	0	Yes		3185
808F		2011	2011	-	0	0	Yes		4659
813F	712M	2011	2011	Canyon	0	0	Yes		4663
818F	636M	2011	2012	Mary Mountain	0	0	Yes		5376
826F	636M	2011	2012	Mary Mountain	0	0	Yes		5384
828M	760M	2011	2013	Yellowstone Delta	0	0	Yes		5386
829F		2011	2012	Blacktail	0	0	Yes		5387
890M		2011	2018	Junction Butte	0	1	Yes	Pedigree founder	5398
926F	755M	2011	2018	Lamar Canyon	0	2	Yes		7915
869M	838M	2012	2014	-	0	0	Yes		5396
906M	838M	2012	2014	-	0	0	Yes		7922
907F	911M	2013	2018	Junction Butte	0	0	Yes		7925

969F	911M	2013	2018	Junction Butte	0	0	Yes		8770
1091F	755M	2015	2018	Wapiti Lake	0	1	Yes		8780
1119F		2016	2018	8 Mile	0	0	Yes		9910
1094M		2017	2017	-	0	0	Yes		8786
1095F		2017	2017	-	0	0	Yes		8784
1097F		2017	2017	-	0	0	Yes		8783
1098M		2017	2017	-	0	0	Yes		8781
1105M	1015M	2017	2020	Wapiti Lake	0	0			9582
1106M	1015M	2017	2018	Wapiti Lake	0	0	Yes		9583
1203F	1015M	2017	0	Wapiti Lake	0	0		Newly collected in this study	10923
1201F	1015M	2018	2020	Wapiti Lake	0	0		Newly collected in this study	10924

Supplemental Table S2. Sample information, meta-data, and descriptive values for each of the 391 Yellowstone National Park gray wolves in the genetic analysis. Reference to “end event” is either age at death or the last observation documented for that individual. Time in years to first observed litter; for animals that were translocated into YNP with offspring or reproduced after leaving YNP will lack an observed time of first litter and likely considered non-breeding individuals. All ROH estimates have at least 10 SNPs within the 10Kb tract and estimated from the 24K statistically unlinked set of SNPs. Asterisks indicate wolves with first observed litter dates older than age at end event that were excluded from the survival model analysis. (Abbreviations: F_{ROH}; inbreeding coefficient estimated from runs of homozygosity; HO, observed heterozygosity; ROH, runs of homozygosity; N_litters, number of litters identified from the pedigree; propr., proportion; YOB, year of birth; YOD, year of death)

Field_ID	Breeding status	Age (years) at end event	Time (years) to first [observed] litter	N_litters	HO	ROH	FROH	Propr. of Low impact SNPs	Propr. of Moderate impact SNPs	Propr. of High impact SNPs	Propr. of Modifying SNPs
016F	Breeder	5.3	1	5	0.7829	712	0.393	0.0243	0.0097	0.0003	0.9657
165M	Breeder	2.5	1	2	0.7985	763	0.402	0.0248	0.0107	0.0005	0.964
380F	Breeder	5.4	1	2	0.7898	701	0.401	0.0254	0.0115	0.0004	0.9628
870F	Breeder	6.9	1	2	0.7785	666	0.356	0.0253	0.0108	0.0006	0.9633
002M	Breeder	8.7	2	6	0.8244	658	0.311	0.0261	0.0117	0.0006	0.9616
007F	Breeder	8.1	2	6	0.7764	699	0.364	0.0236	0.0093	0.0006	0.9665
008M	Breeder	6.2	2	6	0.792	719	0.405	0.0255	0.0095	0.0007	0.9643
014F	Breeder	7.0	2	4	0.7861	678	0.349	0.0254	0.0106	0.0005	0.9635
017F	Breeder	2.2	2	1	0.8279	475	0.21	0.0206	0.0069	0.0005	0.972
019F	Breeder	2.0	2		0.7906	685	0.392	0.0261	0.0101	0.0005	0.9633
021M	Breeder	9.2	2	11	0.8177	704	0.328	0.0278	0.0105	0.0007	0.9611
029M	Breeder	3.5	2	2	0.7716	680	0.351	0.0246	0.0108	0.0006	0.964
037F	Breeder	2.6	2	1	0.758	603	0.309	0.025	0.0113	0.0009	0.9628

041F	Breeder	2.6	2	2	0.7821	641	0.348	0.0254	0.0109	0.0005	0.9633
042F	Breeder	8.8	2	5	0.7763	570	0.387	0.0262	0.0113	0.0007	0.9618
048F	Breeder	9.6	2	6	0.7512	593	0.3	0.0269	0.0123	0.0008	0.96
078F	Breeder	2.6	2		0.7859	689	0.408	0.0235	0.01	0.0005	0.9661
1091F	Breeder	2.7	2	1	0.7909	659	0.403	0.0236	0.0106	0.0006	0.9652
1093F	Breeder	11.0	2	1	0.777	668	0.359	0.0248	0.0099	0.0004	0.9649
148F	Breeder	2.9	2		0.7863	712	0.398	0.0238	0.0106	0.0007	0.9649
152F	Breeder	7.3	2	5	0.7877	703	0.402	0.025	0.0105	0.0008	0.9638
155F	Breeder	2.9	2		0.8124	766	0.387	0.025	0.0107	0.0004	0.9639
212F	Breeder	2.8	2	1	0.8066	554	0.459	0.0248	0.0103	0.0009	0.964
220F	Breeder	3.3	2	1	0.8041	713	0.427	0.0261	0.01	0.0005	0.9633
224M	Breeder	1.9	2*	1	0.7748	656	0.354	0.0248	0.012	0.0002	0.963
251F	Breeder	3.2	2	2	0.7735	653	0.348	0.0265	0.0119	0.0004	0.9612
255F	Breeder	4.6	2	1	0.7809	692	0.347	0.0276	0.0108	0.0002	0.9614
261M	Breeder	3.1	2	2	0.8204	791	0.471	0.0247	0.0101	0.0005	0.9648
271F	Breeder	8.4	2	2	0.8154	720	0.456	0.0243	0.01	0.0003	0.9654
288F	Breeder	4.7	2	2	0.8172	616	0.29	0.0253	0.009	0.0005	0.9651
295M	Breeder	5.2	2	5	0.7774	618	0.349	0.0254	0.0116	0.0007	0.9622
296M	Breeder	2.9	2	1	0.8083	771	0.407	0.0243	0.0091	0.0003	0.9663
301M	Breeder	4.9	2	1	0.8175	669	0.308	0.0263	0.0105	0.0009	0.9624
353F	Breeder	6.9	2	2	0.8054	606	0.285	0.0271	0.0085	0.0002	0.9642
386F	Breeder	3.8	2	1	0.7766	701	0.349	0.0278	0.0109	0.0002	0.961
469F	Breeder	8.9	2	4	0.7919	685	0.418	0.0274	0.0097	0.0004	0.9625

470F	Breeder	6.8	2	1	0.8202	709	0.355	0.0258	0.0103	0.0005	0.9634
471F	Breeder	9.0	2	2	0.7801	630	0.367	0.029	0.0115	0.0003	0.9592
480M	Breeder	6.9	2	3	0.7895	675	0.397	0.0253	0.0099	0.0008	0.9639
486F	Breeder	7.6	2	6	0.7602	635	0.33	0.0244	0.011	0.0004	0.9641
489M	Breeder	5.0	2	1	0.8134	645	0.448	0.0238	0.0098	0.0005	0.9659
490M	Breeder	5.7	2	2	0.8365	773	0.43	0.0236	0.0094	0.0003	0.9666
527F	Breeder	6.5	2	2	0.7851	668	0.377	0.0251	0.0103	0.0003	0.9642
529F	Breeder	2.6	2		0.8049	696	0.437	0.0253	0.0103	0.0006	0.9639
537F	Breeder	7.4	2	7	0.7529	612	0.314	0.0261	0.0101	0.0004	0.9634
569F	Breeder	5.5	2	4	0.8011	577	0.433	0.025	0.0115	0.0004	0.9631
571F	Breeder	4.0	2		0.8035	730	0.365	0.024	0.0115	0.0006	0.9639
590M	Breeder	2.7	2		0.7731	648	0.351	0.027	0.0124	0.0005	0.9602
625F	Breeder	2.9	2		0.8083	668	0.45	0.0245	0.0101	0.0008	0.9646
639M	Breeder	2.0	2		0.7859	700	0.403	0.0254	0.0109	0.0005	0.9632
640F	Breeder	3.0	2	1	0.7795	664	0.364	0.0219	0.0104	0.0003	0.9674
642F	Breeder	4.5	2		0.8326	532	0.248	0.0281	0.011	0.0003	0.9606
691F	Breeder	3.8	2		0.791	627	0.387	0.0255	0.0104	0.0005	0.9636
694F	Breeder	3.0	2		0.8086	729	0.393	0.0258	0.0101	0.0006	0.9635
733F	Breeder	3.5	2		0.7913	672	0.411	0.0254	0.0106	0.0006	0.9634
752F	Breeder	3.6	2		0.7903	722	0.39	0.026	0.0101	0.0008	0.9632
755M	Breeder	8.9	2	4	0.7659	602	0.329	0.0253	0.0111	0.0005	0.9631
820F	Breeder	2.4	2		0.7733	600	0.348	0.0258	0.0105	0.0005	0.9632
838M	Breeder	5.1	2	1	0.8137	707	0.353	0.0254	0.0094	0.0006	0.9645

889F	Breeder	3.6	2		0.7967	719	0.332	0.025	0.0103	0.0004	0.9642
890M	Breeder	6.8	2	1	0.7802	708	0.408	0.0275	0.0102	0.0005	0.9618
907F	Breeder	4.8	2		0.781	672	0.376	0.0222	0.012	0.0005	0.9653
909F	Breeder	8.0	2	5	0.8142	681	0.324	0.0259	0.0101	0.0004	0.9636
963F	Breeder	3.8	2	1	0.7991	657	0.428	0.0248	0.0099	0.0007	0.9647
966M	Breeder	3.5	2		0.803	689	0.446	0.0254	0.0111	0.0005	0.963
969F	Breeder	4.8	2		0.7845	622	0.367	0.025	0.0109	0.0006	0.9635
SW147M	Breeder	6.5	2	1	0.7982	633	0.39	0.0252	0.0106	0.0008	0.9635
006M	Breeder	4.4	3	3	0.802	724	0.362	0.0259	0.0107	0.0003	0.9631
033F	Breeder	6.3	3	4	0.7583	600	0.309	0.027	0.0115	0.0005	0.961
034M	Breeder	7.6	3	6	0.7668	501	0.259	0.0239	0.01	0.0006	0.9655
040F	Breeder	5.1	3	2	0.7507	582	0.304	0.0252	0.0094	0.0008	0.9647
070M	Breeder	9.1	3		0.8006	537	0.248	0.0271	0.0116	0.0002	0.9611
072M	Breeder	7.5	3	7	0.7796	621	0.347	0.0249	0.0108	0.0005	0.9638
1015M	Breeder	3.8	3	3	0.7749	635	0.354	0.026	0.0097	0.0004	0.9639
105F	Breeder	6.1	3	1	0.7553	593	0.313	0.024	0.0101	0.0003	0.9655
106F	Breeder	8.0	3	4	0.747	567	0.297	0.0258	0.0102	0.0006	0.9634
120M	Breeder	3.2	3	1	0.8174	618	0.472	0.0251	0.0105	0.0006	0.9639
126F	Breeder	11.9	3	7	0.7793	645	0.35	0.026	0.0105	0.0006	0.9629
206M	Breeder	6.9	3	4	0.7783	665	0.354	0.025	0.0095	0.0006	0.9649
209F	Breeder	8.4	3	3	0.8252	558	0.262	0.0243	0.011	0.0006	0.9641
217F	Breeder	3.7	3	1	0.7891	685	0.335	0.0268	0.0114	0.0004	0.9613
243M	Breeder	4.6	3	1	0.8321	694	0.333	0.0262	0.0094	0.0005	0.9639

259F	Breeder	3.0	3	1	0.7991	684	0.412	0.0258	0.0097	0.0006	0.9639
287M	Breeder	4.8	3	1	0.7936	736	0.373	0.0251	0.0101	0.0004	0.9643
294M	Breeder	4.0	3	3	0.8057	732	0.461	0.0247	0.0104	0.0007	0.9641
302M	Breeder	9.5	3	4	0.7939	710	0.422	0.0231	0.0104	0.0005	0.966
377M	Breeder	5.0	3	2	0.8176	667	0.486	0.0248	0.0103	0.0003	0.9646
381M	Breeder	3.3	3	1	0.776	718	0.362	0.0254	0.0105	0.0007	0.9634
472F	Breeder	10.6	3	7	0.7612	630	0.323	0.0274	0.01	0.0007	0.9619
482M	Breeder	8.9	3	5	0.7943	705	0.415	0.025	0.0099	0.0005	0.9647
534M	Breeder	8.4	3	7	0.7635	682	0.349	0.027	0.0111	0.0005	0.9615
536F	Breeder	6.6	3	3	0.7817	641	0.37	0.0248	0.0091	0.0008	0.9652
588F	Breeder	3.6	3	1	0.8068	709	0.426	0.0255	0.0101	0.0006	0.9638
627M	Breeder	5.4	3	4	0.7958	714	0.338	0.0263	0.0097	0.0006	0.9634
636M	Breeder	4.6	3	2	0.8246	715	0.488	0.0269	0.0104	0.0003	0.9623
641M	Breeder	4.7	3	1	0.7891	720	0.372	0.0256	0.0104	0.0004	0.9636
689M	Breeder	8.6	3	4	0.7698	665	0.343	0.0252	0.0114	0.0006	0.9627
692F	Breeder	5.6	3	2	0.7746	605	0.353	0.0306	0.0112	0.0007	0.9575
693F	Breeder	7.5	3	2	0.7677	631	0.327	0.0272	0.0109	0.0004	0.9614
696F	Breeder	4.8	3	1	0.8279	764	0.437	0.0255	0.0092	0.0003	0.965
712M	Breeder	10.8	3	2	0.789	727	0.362	0.0253	0.0105	0.0003	0.9639
715F	Breeder	4.6	3		0.8163	729	0.419	0.0254	0.0112	0.0005	0.9629
757F	Breeder	4.2	3		0.8274	793	0.41	0.0249	0.0106	0.0005	0.964
760M	Breeder	6.9	3	2	0.7822	640	0.363	0.0251	0.0117	0.0006	0.9627
778M	Breeder	8.7	3	1	0.7929	752	0.404	0.0254	0.0096	0.0006	0.9644

779F	Breeder	7.8	3	3	0.7774	686	0.368	0.0254	0.0101	0.0004	0.964
911M	Breeder	6.4	3	3	0.7869	703	0.382	0.0258	0.0105	0.0002	0.9635
926F	Breeder	6.8	3	2	0.7742	580	0.343	0.0254	0.0097	0.0005	0.9644
953F	Breeder	4.8	3	1	0.8185	619	0.461	0.0252	0.0108	0.0006	0.9635
1118F	Breeder	3.8	4*		0.7812	691	0.381	0.0248	0.0099	0.0006	0.9647
103F	Breeder	7.0	4	1	0.7469	586	0.294	0.0225	0.0116	0.0004	0.9655
151F	Breeder	11.5	4	6	0.8027	693	0.428	0.026	0.01	0.0004	0.9636
190F	Breeder	5.5	4		0.7942	675	0.407	0.0239	0.0102	0.0002	0.9656
205M	Breeder	4.5	4	1	0.7631	606	0.317	0.0271	0.0119	0.0007	0.9603
227M	Breeder	4.9	4	1	0.8078	737	0.392	0.0253	0.0112	0.0005	0.963
303M	Breeder	10.9	4	7	0.8201	793	0.432	0.0247	0.01	0.0005	0.9647
383M	Breeder	6.9	4	2	0.7734	572	0.326	0.0257	0.0112	0.0005	0.9626
540F	Breeder	7.5	4	2	0.7537	590	0.297	0.0269	0.0119	0.0003	0.9609
541M	Breeder	7.5	4	2	0.7787	663	0.369	0.0232	0.0111	0.0002	0.9654
685M	Breeder	6.9	4	1	0.8246	764	0.457	0.0259	0.0104	0.0003	0.9634
759F	Breeder	3.9	4*		0.812	583	0.454	0.0257	0.0097	0.0005	0.9641
871M	Breeder	4.5	4	1	0.8012	724	0.389	0.0259	0.0118	0.0006	0.9617
978F	Breeder	4.8	4		0.7763	644	0.357	0.0277	0.0101	0.0007	0.9615
SW763M	Breeder	9.9	4	3	0.7887	619	0.393	0.0242	0.0122	0.0006	0.963
192M	Breeder	12.1	5	1	0.8225	799	0.412	0.0247	0.01	0.0004	0.9649
207M	Breeder	7.4	5	1	0.7981	706	0.42	0.024	0.0098	0.0005	0.9657
344F	Breeder	5.3	5	1	0.8117	696	0.453	0.0255	0.0099	0.0004	0.9641
545F	Breeder	5.3	5	1	0.7995	745	0.412	0.0258	0.0107	0.0003	0.9631

586M	Breeder	9.5	5	1	0.8192	651	0.467	0.0246	0.0106	0.0003	0.9645
695M	Breeder	7.6	5	1	0.7949	674	0.409	0.0254	0.0103	0.0002	0.9641
794F	Breeder	7.1	5	2	0.7815	687	0.333	0.0255	0.0106	0.0005	0.9634
925M	Breeder	5.9	5	2	0.7749	564	0.363	0.0228	0.0111	0.0007	0.9653
970F	Breeder	6.0	5	2	0.7713	651	0.349	0.0252	0.0104	0.0005	0.9639
976F	Breeder	7.8	5	1	0.8082	716	0.417	0.0281	0.0103	0.0005	0.9611
992M	Breeder	5.0	5		0.7998	706	0.438	0.0251	0.0106	0.0005	0.9638
478F	Breeder	12.6	6	4	0.827	788	0.483	0.0258	0.0099	0.0005	0.9638
495M	Breeder	8.4	6	6	0.813	677	0.461	0.0252	0.0109	0.0005	0.9634
587M	Breeder	9.1	6	1	0.8304	720	0.503	0.0254	0.0112	0.0004	0.963
633F	Breeder	7.4	6	1	0.7971	676	0.395	0.0257	0.0105	0.0005	0.9634
686F	Breeder	6.4	6		0.7854	713	0.371	0.0256	0.0108	0.0003	0.9633
949M	Breeder	6.4	6		0.7792	670	0.381	0.0243	0.0103	0.0005	0.9649
910M	Breeder	8.8	8		0.837	596	0.531	0.025	0.0102	0.0004	0.9644
005F	Breeder	10.6		4	0.7975	765	0.418	0.0255	0.0108	0.0005	0.9633
009F	Breeder	9.6		3	0.8006	732	0.415	0.0258	0.0097	0.0006	0.9639
013M	Breeder	11.9		3	0.7674	593	0.298	0.0234	0.0095	0.0003	0.9667
027F	Breeder	8.5		2	0.7466	578	0.3	0.0253	0.0106	0.0007	0.9634
035M	Breeder	5.8		2	0.769	632	0.305	0.0268	0.0105	0.0006	0.9621
036F	Breeder	3.0		1	0.7595	611	0.312	0.0242	0.0101	0.0011	0.9646
038M	Breeder	8.7		2	0.7669	529	0.288	0.0219	0.0101	0.0008	0.9672
104M	Breeder	3.6			0.7483	574	0.29	0.025	0.0115	0.0003	0.9632
614M	Breeder			1	0.8043	674	0.436	0.0257	0.0101	0.0006	0.9637

821F	Breeder	8.0	1	0.7924	677	0.422	0.0242	0.011	0.0002	0.9645
1005F	Non-breeder	2.8		0.7905	675	0.391	0.0272	0.0097	0.0003	0.9628
1014M	Non-breeder	4.8		0.7793	684	0.386	0.0279	0.0105	0.0008	0.9609
1048M	Non-breeder	2.8		0.8006	725	0.434	0.0269	0.0111	0.0006	0.9615
1049F	Non-breeder	1.8		0.8007	662	0.396	0.027	0.0105	0.0004	0.9622
1090F	Non-breeder	3.8		0.7781	653	0.366	0.0244	0.0106	0.0008	0.9642
1104F	Non-breeder	0.8		0.8036	728	0.389	0.0281	0.011	0.0009	0.96
1106M	Non-breeder	0.8		0.7898	688	0.406	0.0259	0.0116	0.0003	0.9622
1119F	Non-breeder	1.8		0.7794	651	0.381	0.025	0.0107	0.0005	0.9638
118M	Non-breeder	2.0		0.8048	655	0.447	0.0271	0.0106	0.0004	0.9618
147M	Non-breeder	3.2		0.7666	603	0.323	0.025	0.0107	0.0007	0.9636
241M	Non-breeder	1.0		0.8142	748	0.456	0.0244	0.01	0.0002	0.9654
253M	Non-breeder	4.8		0.7847	704	0.369	0.0265	0.0087	0.0003	0.9645
289M	Non-breeder	1.7		0.7919	717	0.389	0.0273	0.0117	0.0004	0.9605
292M	Non-breeder	2.9		0.7846	650	0.373	0.0252	0.0113	0.0004	0.9632
350M	Non-breeder	1.4		0.7798	722	0.376	0.0281	0.0122	0.0005	0.9592
389M	Non-breeder	2.1		0.8258	701	0.506	0.0245	0.0104	0.0005	0.9646
485F	Non-breeder	1.9		0.7886	606	0.28	0.0227	0.01	0.0006	0.9668
525F	Non-breeder	3.7		0.7856	581	0.388	0.0257	0.0105	0.0005	0.9633
698M	Non-breeder	4.1		0.764	637	0.328	0.026	0.0104	0.0007	0.9628
015M	Non-breeder	2.1		0.8052	428	0.174	0.0251	0.0105	0.0005	0.964
020M	Non-breeder	1.2		0.7932	740	0.393	0.0275	0.0102	0.0007	0.9616
022M	Non-breeder	0.7		0.8016	758	0.392	0.0254	0.011	0.0006	0.963

024F	Non-breeder	3.5	0.7801	613	0.371	0.0258	0.0112	0.0005	0.9625
026F	Non-breeder	1.4	0.7753	514	0.274	0.0201	0.0099	0.0005	0.9694
031M	Non-breeder	2.6	0.7856	525	0.274	0.0197	0.01	0.0003	0.97
043M	Non-breeder	2.9	0.7819	685	0.362	0.024	0.0111	0.0004	0.9645
044F	Non-breeder	9.0	0.8019	648	0.318	0.0277	0.0116	0.0005	0.9602
045F	Non-breeder	0.4	0.7942	676	0.381	0.0255	0.0118	0.0007	0.962
055M	Non-breeder	3.9	0.7909	715	0.413	0.0242	0.01	0.0006	0.9652
058F	Non-breeder	0.0	0.8299	511	0.514	0.0249	0.0108	0.0003	0.964
063F	Non-breeder	1.5	0.7777	648	0.333	0.0238	0.0107	0.0004	0.9651
064F	Non-breeder	1.1	0.7754	609	0.345	0.0246	0.0109	0.0004	0.964
065F	Non-breeder	1.1	0.7765	629	0.354	0.0244	0.0107	0.0002	0.9647
068F	Non-breeder	1.4	0.7854	568	0.314	0.0212	0.0106	0.0001	0.968
069M	Non-breeder	1.2	0.7738	636	0.345	0.027	0.0103	0.0007	0.9619
071F	Non-breeder	1.1	0.7753	609	0.341	0.0261	0.0106	0.0002	0.9631
077F	Non-breeder	3.7	0.8109	678	0.347	0.0244	0.0105	0.0004	0.9647
082M	Non-breeder	2.1	0.804	781	0.417	0.0257	0.0099	0.0004	0.964
083M	Non-breeder	1.5	0.7931	696	0.406	0.0257	0.0102	0.0006	0.9635
085F	Non-breeder	1.6	0.8188	683	0.337	0.0264	0.0096	0.0003	0.9636
095F	Non-breeder	1.1	0.8311	537	0.24	0.0265	0.0092	0.0003	0.964
1012M	Non-breeder	0.9	0.7914	651	0.418	0.0251	0.0112	0.0006	0.9631
1013M	Non-breeder	2.7	0.7771	670	0.361	0.0256	0.0106	0.0006	0.9633
1016F	Non-breeder	0.8	0.7749	682	0.355	0.0259	0.0104	0.0008	0.963
1047M	Non-breeder	3.8	0.806	666	0.442	0.0268	0.0114	0.0006	0.9612

1050F	Non-breeder	1.0	0.8006	675	0.423	0.0267	0.0096	0.0005	0.9632
1051M	Non-breeder	0.8	0.8041	707	0.445	0.0247	0.0104	0.0006	0.9643
1094M	Non-breeder	0.0	0.8163	663	0.307	0.0258	0.0105	0.0005	0.9632
1095F	Non-breeder	0.0	0.8022	703	0.442	0.0268	0.0095	0.0004	0.9633
1096M	Non-breeder	0.0	0.792	685	0.404	0.0277	0.0098	0.0005	0.962
1097F	Non-breeder	0.0	0.7997	723	0.431	0.0276	0.0096	0.0005	0.9622
1098M	Non-breeder	0.0	0.8039	751	0.43	0.027	0.0098	0.0003	0.9629
1108M	Non-breeder	1.8	0.7964	704	0.411	0.0261	0.0105	0.0006	0.9627
111F	Non-breeder	1.2	0.768	614	0.309	0.0277	0.011	0.0006	0.9608
115F	Non-breeder	1.3	0.7818	632	0.309	0.0252	0.0114	0.0009	0.9625
122M	Non-breeder	2.3	0.8147	627	0.475	0.026	0.0105	0.0006	0.9629
123M	Non-breeder	2.6	0.7836	698	0.369	0.0254	0.0102	0.0006	0.9638
124M	Non-breeder	2.7	0.7722	599	0.356	0.0248	0.0121	0.0006	0.9624
128M	Non-breeder	1.1	0.7649	628	0.342	0.0255	0.0107	0.0005	0.9633
136F	Non-breeder	2.9	0.8176	673	0.461	0.027	0.0102	0.0005	0.9623
150M	Non-breeder	6.5	0.7871	673	0.399	0.0256	0.0099	0.0004	0.9641
153F	Non-breeder	1.6	0.7911	711	0.424	0.0273	0.0105	0.0003	0.9619
154F	Non-breeder	2.6	0.7887	707	0.413	0.0246	0.0096	0.0005	0.9653
156F	Non-breeder	2.3	0.7928	710	0.42	0.026	0.0102	0.0004	0.9634
160F	Non-breeder	0.8	0.8039	721	0.445	0.0257	0.0096	0.0005	0.9642
161M	Non-breeder	2.9	0.796	702	0.425	0.0252	0.01	0.0005	0.9643
162M	Non-breeder	4.0	0.8075	763	0.399	0.0251	0.0105	0.0001	0.9643
168F	Non-breeder	1.6	0.8204	780	0.412	0.0264	0.0107	0.0003	0.9627

182M	Non-breeder	0.5		0.7958	699	0.416	0.0254	0.0107	0.0004	0.9635
183F	Non-breeder	0.5		0.819	708	0.454	0.0256	0.0108	0.0006	0.963
184F	Non-breeder	0.5		0.8138	696	0.449	0.0265	0.011	0.0007	0.9618
185M	Non-breeder	0.6		0.7826	689	0.338	0.0249	0.0105	0.0004	0.9642
186M	Non-breeder	0.6		0.7632	609	0.33	0.025	0.0106	0.0007	0.9638
187F	Non-breeder	0.8		0.7899	602	0.277	0.0239	0.0123	0.0005	0.9634
188F	Non-breeder	2.2		0.7995	643	0.439	0.0253	0.0102	0.0006	0.964
189M	Non-breeder	1.9		0.8125	609	0.443	0.0261	0.0114	0.0003	0.9622
191M	Non-breeder	1.9		0.7716	658	0.325	0.0266	0.0108	0.0006	0.9621
196M	Non-breeder	3.3		0.8083	781	0.44	0.0256	0.0115	0.0002	0.9627
197F	Non-breeder	1.1		0.8348	618	0.279	0.0284	0.0094	0.0003	0.9619
199M	Non-breeder	1.1		0.7722	667	0.35	0.0277	0.0105	0.0002	0.9616
201F	Non-breeder	2.5		0.7574	619	0.321	0.0265	0.0109	0.0007	0.962
203M	Non-breeder	1.4		0.7584	619	0.306	0.0264	0.011	0.0005	0.962
210M	Non-breeder	3.0		0.8141	628	0.479	0.0253	0.0101	0.0006	0.964
211M	Non-breeder	2.8		0.8277	594	0.288	0.0235	0.009	0.0004	0.967
215M	Non-breeder	2.3		0.7769	669	0.325	0.0235	0.0109	0.0007	0.965
216F	Non-breeder	1.8		0.7862	682	0.324	0.0264	0.0117	0.0003	0.9616
218F	Non-breeder	2.3		0.7918	666	0.315	0.0258	0.0103	0.0004	0.9635
221M	Non-breeder	1.9		0.7656	640	0.325	0.024	0.0103	0.0002	0.9656
222M	Non-breeder	1.2		0.7613	626	0.342	0.0271	0.0108	0.0002	0.9619
225M	Non-breeder	0.9		0.7937	635	0.408	0.0263	0.0102	0.0005	0.963
226M	Non-breeder	0.8		0.788	684	0.391	0.0247	0.0105	0.0004	0.9645

229M	Non-breeder	2.2	0.8027	708	0.398	0.0262	0.0108	0.0005	0.9625
245M	Non-breeder	0.7	0.7889	617	0.394	0.0247	0.0106	0.0005	0.9642
246M	Non-breeder	0.7	0.7931	591	0.389	0.0275	0.0111	0.0004	0.9609
247M	Non-breeder	0.7	0.7925	643	0.404	0.0265	0.0106	0.0005	0.9624
248M	Non-breeder	1.3	0.7547	588	0.304	0.0256	0.0105	0.0005	0.9634
249M	Non-breeder	2.7	0.7648	593	0.32	0.0262	0.0119	0.0003	0.9616
252M	Non-breeder	2.1	0.7764	660	0.313	0.0265	0.0118	0.0003	0.9614
254M	Non-breeder	2.3	0.7723	720	0.353	0.0267	0.0101	0.0006	0.9626
257M	Non-breeder	4.5	0.8046	660	0.444	0.0259	0.0089	0.0006	0.9645
260F	Non-breeder	2.3	0.7906	657	0.404	0.0244	0.0097	0.0004	0.9655
291M	Non-breeder	2.3	0.8173	812	0.444	0.0257	0.0096	0.0004	0.9643
293F	Non-breeder	2.1	0.8181	707	0.427	0.0234	0.0102	0.0008	0.9656
300M	Non-breeder	4.5	0.8024	751	0.423	0.0253	0.0095	0.0005	0.9646
305M	Non-breeder	3.0	0.7556	613	0.315	0.0231	0.0104	0.0008	0.9657
307M	Non-breeder	2.8	0.7961	683	0.406	0.0267	0.0103	0.0006	0.9625
308F	Non-breeder	0.8	0.8021	696	0.421	0.0242	0.0105	0.0007	0.9646
309F	Non-breeder	2.8	0.7671	659	0.337	0.0258	0.0109	0.0006	0.9627
341F	Non-breeder	5.8	0.8084	583	0.263	0.0267	0.0124	0.0001	0.9608
343M	Non-breeder	1.7	0.8333	801	0.459	0.0257	0.0104	0.0006	0.9633
347M	Non-breeder	1.6	0.8053	593	0.427	0.0246	0.0116	0.0005	0.9634
348M	Non-breeder	1.7	0.7902	728	0.411	0.0259	0.0099	0.0007	0.9635
349M	Non-breeder	1.8	0.7956	733	0.422	0.0262	0.011	0.0002	0.9626
352M	Non-breeder	1.7	0.7967	648	0.436	0.0269	0.01	0.0006	0.9625

355F	Non-breeder	3.3		0.7942	659	0.419	0.0241	0.0104	0.0005	0.965
356M	Non-breeder	2.7		0.8168	751	0.441	0.0246	0.0107	0.0006	0.9641
361M	Non-breeder	0.7		0.8112	734	0.383	0.0257	0.0114	0.0008	0.9621
375F	Non-breeder	1.8		0.7912	700	0.406	0.0263	0.0103	0.0006	0.9628
379M	Non-breeder	4.6		0.8222	811	0.428	0.026	0.0116	0.0002	0.9622
382F	Non-breeder	1.2		0.7903	657	0.39	0.027	0.0097	0.0005	0.9629
388F	Non-breeder	3.3		0.8136	746	0.468	0.0253	0.0105	0.0006	0.9636
391F	Non-breeder	3.1		0.7631	642	0.342	0.0249	0.0108	0.0006	0.9637
392M	Non-breeder	2.6		0.7553	620	0.3	0.026	0.0102	0.0002	0.9636
451F	Non-breeder	0.4		0.7847	704	0.36	0.0242	0.0106	0.0004	0.9648
453M	Non-breeder	2.2		0.7842	657	0.402	0.0257	0.011	0.0006	0.9626
466U	Non-breeder	0.7		0.7878	703	0.344	0.0242	0.0112	0.0003	0.9642
467M	Non-breeder	1.6		0.7625	615	0.319	0.0231	0.0107	0.0004	0.9658
468M	Non-breeder	3.9		0.8037	741	0.405	0.0227	0.0101	0.0008	0.9664
473M	Non-breeder	1.0		0.8131	659	0.316	0.0259	0.01	0.0009	0.9632
474M	Non-breeder	1.2		0.7916	625	0.296	0.0251	0.0112	0.0002	0.9634
475F	Non-breeder	0.8		0.7748	647	0.344	0.0232	0.0109	0.0003	0.9656
477M	Non-breeder	2.5		0.8186	736	0.48	0.0256	0.0098	0.0004	0.9642
479M	Non-breeder	3.4		0.8104	679	0.455	0.0274	0.0101	0.0005	0.962
481M	Non-breeder	1.9		0.768	649	0.354	0.0243	0.0105	0.0006	0.9646
483F	Non-breeder	2.2		0.7608	660	0.337	0.0245	0.0101	0.0007	0.9648
484M	Non-breeder	1.3		0.7671	610	0.313	0.0277	0.0113	0.0009	0.9601
488M	Non-breeder	1.3		0.7736	665	0.349	0.0244	0.012	0.0003	0.9633

491M	Non-breeder	1.8			0.8272	721	0.492	0.0252	0.0103	0.0006	0.964
493M	Non-breeder	0.8			0.7927	649	0.398	0.0262	0.0104	0.0004	0.963
496F	Non-breeder	1.1			0.8077	654	0.445	0.0269	0.0106	0.0007	0.9618
497M	Non-breeder	3.1			0.818	643	0.484	0.0254	0.0103	0.0003	0.964
498F	Non-breeder	0.9			0.7785	654	0.317	0.0263	0.0106	0.0003	0.9628
523F	Non-breeder	3.0			0.796	576	0.406	0.0249	0.0097	0.0007	0.9646
524F	Non-breeder	2.2			0.7813	666	0.363	0.0273	0.011	0.0006	0.9611
528M	Non-breeder	2.8			0.7814	668	0.378	0.0284	0.0105	0.0008	0.9603
535M	Non-breeder	3.1			0.8011	644	0.348	0.0223	0.0096	0.0006	0.9675
538M	Non-breeder	6.1			0.8	735	0.43	0.0242	0.0109	0.0004	0.9645
539F	Non-breeder	3.9			0.774	658	0.354	0.0262	0.0107	0.0004	0.9627
542F	Non-breeder	3.0			0.7985	674	0.4	0.0259	0.01	0.0004	0.9636
543M	Non-breeder	2.6			0.8029	764	0.392	0.0256	0.0101	0.0005	0.9637
544M	Non-breeder	2.7			0.8039	635	0.436	0.0252	0.01	0.0005	0.9644
546M	Non-breeder	1.8			0.8302	762	0.433	0.0266	0.0107	0.0006	0.9621
570M	Non-breeder	1.5			0.7947	652	0.417	0.0259	0.0103	0.0003	0.9635
572F	Non-breeder	6.1			0.7995	634	0.396	0.0268	0.0108	0.0005	0.9619
577M	Non-breeder	1.9			0.7849	692	0.342	0.0241	0.0097	0.0006	0.9656
589F	Non-breeder	2.4			0.7977	668	0.435	0.0272	0.01	0.0004	0.9624
591F	Non-breeder	2.3			0.7913	684	0.389	0.0251	0.0115	0.0004	0.963
593F	Non-breeder	1.8			0.793	633	0.397	0.0264	0.0108	0.0007	0.9621
613M	Non-breeder	2.3			0.7918	647	0.393	0.0249	0.0106	0.0007	0.9638
620M	Non-breeder	0.6			0.7913	630	0.401	0.026	0.0113	0.0003	0.9623

621F	Non-breeder	2.6		0.791	661	0.408	0.0252	0.0102	0.0005	0.964
622F	Non-breeder	0.7		0.7624	619	0.316	0.0264	0.0111	0.0005	0.962
624F	Non-breeder	1.3		0.8167	772	0.415	0.0253	0.0111	0.0007	0.9628
626F	Non-breeder	1.4		0.8021	640	0.46	0.025	0.0105	0.0004	0.9642
629M	Non-breeder	2.3		0.7848	661	0.377	0.0251	0.0111	0.0005	0.9633
630F	Non-breeder	1.6		0.7881	648	0.397	0.0264	0.0109	0.0005	0.9623
634F	Non-breeder	1.9		0.7769	622	0.359	0.0253	0.0109	0.0007	0.9631
635F	Non-breeder	1.8		0.7994	656	0.416	0.0258	0.0105	0.0005	0.9632
638M	Non-breeder	1.0		0.7878	638	0.398	0.0261	0.0106	0.0007	0.9626
643F	Non-breeder	1.3		0.7868	593	0.38	0.0246	0.0109	0.0004	0.9642
644F	Non-breeder	1.5		0.7915	637	0.398	0.0278	0.0112	0.0002	0.9609
645F	Non-breeder	2.1		0.7974	734	0.4	0.0259	0.0104	0.0007	0.963
646F	Non-breeder	2.5		0.77	667	0.351	0.0244	0.0113	0.0003	0.964
647M	Non-breeder	3.9		0.7778	692	0.36	0.0263	0.0103	0.0003	0.9631
658M	Non-breeder	3.9		0.8222	707	0.349	0.0265	0.011	0.0005	0.962
659M	Non-breeder	3.9		0.8176	615	0.3	0.0266	0.0111	0.0006	0.9617
660F	Non-breeder	1.9		0.7801	642	0.365	0.0256	0.0103	0.0007	0.9634
661M	Non-breeder	8.4		0.7925	678	0.364	0.0229	0.0106	0.0008	0.9658
676M	Non-breeder	0.3		0.7905	663	0.392	0.0254	0.0116	0.0005	0.9626
679F	Non-breeder	1.6		0.8198	710	0.353	0.0243	0.0102	0.0007	0.9648
687M	Non-breeder	1.6		0.7849	619	0.291	0.0263	0.0099	0.0005	0.9634
688M	Non-breeder	2.0		0.8013	586	0.413	0.0271	0.0099	0.0007	0.9624
690F	Non-breeder	2.0		0.815	757	0.393	0.0258	0.0096	0.0005	0.9641

697M	Non-breeder	2.7	0.7961	712	0.408	0.0256	0.0109	0.0005	0.963
713F	Non-breeder	1.9	0.7993	609	0.405	0.0247	0.0096	0.0003	0.9654
716F	Non-breeder	4.4	0.7952	678	0.41	0.0255	0.0102	0.0004	0.9639
729M	Non-breeder	1.1	0.7931	659	0.411	0.025	0.0098	0.0007	0.9645
734M	Non-breeder	2.6	0.8	661	0.435	0.0256	0.0096	0.0004	0.9644
753F	Non-breeder	1.3	0.7768	669	0.355	0.0258	0.0107	0.0005	0.963
754M	Non-breeder	4.6	0.7694	648	0.333	0.024	0.0112	0.0002	0.9646
756F	Non-breeder	3.8	0.7936	726	0.411	0.0263	0.0104	0.0006	0.9627
758M	Non-breeder	3.9	0.8342	734	0.484	0.0241	0.0098	0.0002	0.9659
761F	Non-breeder	2.9	0.7954	733	0.419	0.0231	0.0099	0.0006	0.9664
762M	Non-breeder	6.3	0.8084	665	0.448	0.0265	0.0113	0.0004	0.9618
763F	Non-breeder	5.3	0.8066	664	0.447	0.0261	0.0101	0.0005	0.9634
768F	Non-breeder	0.9	0.7862	708	0.353	0.026	0.0113	0.0003	0.9624
769M	Non-breeder	1.9	0.7708	642	0.345	0.0243	0.0113	0.0002	0.9641
772U	Non-breeder	1.0	0.794	681	0.412	0.0245	0.0106	0.0005	0.9643
775M	Non-breeder	1.7	0.7968	715	0.383	0.0258	0.0096	0.0002	0.9644
777M	Non-breeder	2.3	0.8062	740	0.418	0.0255	0.0099	0.0003	0.9642
780M	Non-breeder	0.8	0.8156	635	0.464	0.0229	0.0118	0.0005	0.9648
808F	Non-breeder	0.4	0.8112	703	0.343	0.0264	0.0116	0.0005	0.9615
809F	Non-breeder	2.4	0.8096	643	0.462	0.026	0.0105	0.0004	0.9631
810F	Non-breeder	1.4	0.807	658	0.341	0.0278	0.0097	0.0006	0.9619
811F	Non-breeder	1.5	0.8175	763	0.426	0.0241	0.0089	0.0005	0.9664
812M	Non-breeder	2.5	0.7777	698	0.356	0.0258	0.0102	0.0003	0.9637

813F	Non-breeder	0.7	0.783	654	0.385	0.0258	0.0112	0.0004	0.9626
818F	Non-breeder	1.0	0.8299	684	0.495	0.0253	0.0101	0.0005	0.9641
819F	Non-breeder	2.0	0.8143	600	0.475	0.0249	0.0106	0.0005	0.964
822F	Non-breeder	3.3	0.8252	658	0.491	0.0255	0.0101	0.0007	0.9637
823F	Non-breeder	1.6	0.7738	680	0.335	0.0258	0.0112	0.0003	0.9627
824M	Non-breeder	1.5	0.7938	708	0.359	0.0246	0.0108	0.0007	0.9639
825F	Non-breeder	1.7	0.8367	752	0.464	0.0257	0.0103	0.0004	0.9636
826F	Non-breeder	1.1	0.8416	582	0.543	0.0259	0.01	0.0007	0.9634
827M	Non-breeder	2.0	0.8149	585	0.434	0.0267	0.0104	0.0003	0.9626
828M	Non-breeder	1.9	0.7992	583	0.411	0.0253	0.0109	0.0006	0.9633
829F	Non-breeder	1.5	0.7989	620	0.429	0.0249	0.0099	0.0007	0.9645
830F	Non-breeder	2.9	0.7829	679	0.376	0.0238	0.01	0.0004	0.9659
831F	Non-breeder	2.1	0.7994	713	0.422	0.0249	0.0109	0.0006	0.9636
869M	Non-breeder	2.0	0.8143	617	0.448	0.0254	0.0101	0.0005	0.964
872F	Non-breeder	2.9	0.8116	600	0.438	0.0236	0.0117	0.0007	0.964
905M	Non-breeder	3.6	0.8112	496	0.203	0.0277	0.0105	0.0001	0.9617
906M	Non-breeder	1.8	0.7988	617	0.411	0.0263	0.0115	0.0005	0.9617
908F	Non-breeder	0.8	0.8028	746	0.43	0.0262	0.0109	0.0004	0.9625
924F	Non-breeder	0.8	0.7871	704	0.394	0.0251	0.011	0.0005	0.9635
961M	Non-breeder	0.6	0.7726	638	0.381	0.0241	0.0114	0.0004	0.9642
964M	Non-breeder	3.7	0.7923	674	0.415	0.0254	0.011	0.0005	0.9631
967M	Non-breeder	1.5	0.7831	684	0.342	0.023	0.0112	0.0005	0.9653
968F	Non-breeder	1.6	0.7825	650	0.392	0.026	0.01	0.0005	0.9635

977F	Non-breeder	2.8		0.7963	649	0.429	0.0267	0.0099	0.0007	0.9627
979F	Non-breeder	1.5		0.8007	647	0.308	0.0253	0.0115	0.0007	0.9625
993M	Non-breeder	3.2		0.7955	707	0.433	0.0244	0.0114	0.0007	0.9635
994M	Non-breeder	1.6		0.7715	655	0.369	0.0256	0.0115	0.0004	0.9625
995F	Non-breeder	1.9		0.7891	677	0.404	0.0267	0.0104	0.0006	0.9623
996M	Non-breeder	2.8		0.7978	684	0.424	0.0242	0.0114	0.0003	0.964
239M	Unknown			0.7807	679	0.363				
240M	Unknown			0.8124	731	0.402	0.0256	0.0108	0.0006	0.963
285M	Unknown			0.8076	693	0.397	0.0255	0.01	0.0004	0.9642
434F	Unknown	3.3		0.7946	713	0.39	0.0259	0.0104	0.0004	0.9633