



Research Article

Lifetime reproductive characteristics of gray wolves

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Abstract

Female and male cooperative breeders can use different strategies to maximize reproduction and fitness over their lifetimes. Answering questions about fitness in cooperative breeders requires long-term studies as well as complete data on group composition and size which can be exceedingly difficult to obtain. Using a long-term genetic data set of complete group pedigrees, I asked how lifetime reproductive characteristics of female and male gray wolves (*Canis lupus*) differed. I predicted that genetic relatedness to helpers would be higher for females than males due to philopatric behavior of female wolves, group size would be similar between the sexes, females would inherit breeding positions from within groups more often than males due to differences in dispersal strategies between the sexes, males would have more lifetime mates and produce more young than females because of polygamy, and females would breed for more years than males due to the likelihood that females would still breed (with a new partner) after a mate died or was expelled from the group. I documented complete lifetime breeding histories for 11 male and 18 female wolves in Idaho, United States, 2008 to 2018. Genetic relatedness to helpers, group size, number of mates, pups, and years breeding did not differ between the sexes. Females, however, inherited breeding positions within groups far more often than males. Individuals who secured breeding positions generally reproduced for 2 seasons and commonly had more than 1 partner during their lifetimes if they were able to maintain their breeding position longer. Direct fitness varied greatly within female and male breeding wolves.

Key words: *Canis lupus*, cooperative breeding, mating, reproduction, wolf.

Características reproductivas de por vida de los lobos grises

Resumen

Las hembras y los machos que presentan crianza cooperativa pueden utilizar diferentes estrategias para maximizar la reproducción y la aptitud biológica a lo largo de sus vidas. Responder preguntas sobre la aptitud biológica de la crianza cooperativa requiere estudios a largo plazo, así como datos completos sobre la composición y el tamaño del grupo, que pueden ser extremadamente difíciles de obtener. Utilizando un conjunto de datos genéticos de largo plazo de genealogías grupales completas, investigué en qué se diferenciaban las características reproductivas a lo largo de la vida de las hembras y los machos de los lobos grises (*Canis lupus*). Predije que la relación genética con los ayudantes sería mayor para las hembras que para los machos; el tamaño del grupo sería similar entre los sexos; las hembras heredarían posiciones reproductivas dentro de los grupos con más frecuencia que los machos; los machos tendrían más parejas a lo largo de su vida y producirían más crías que las hembras debido a la poligamia; y que las hembras se reproducirían durante más años que los machos. Documenté la historia reproductiva a lo largo de la vida de 11 lobos machos y 18 hembras en Idaho, EE. UU., 2008-2018. La relación genética con los ayudantes, el tamaño del grupo, el número de parejas, las crías y los años de reproducción no difirieron entre los sexos. Sin embargo, las hembras heredaron posiciones reproductivas dentro de los grupos con mucha más frecuencia que los machos. Los individuos que aseguraron posiciones reproductivas generalmente se reprodujeron durante dos temporadas y comúnmente tuvieron más de una pareja durante su vida si pudieron mantener su posición reproductiva por más tiempo. La aptitud biológica directa varió mucho entre las hembras y los machos de los lobos reproductores.

Palabras clave: apareamiento, *Canis lupus*, cría cooperativa, lobo, reproducción.

For many group-living species, aggregations occur because offspring delay dispersal, thus generating highly related family groups. When genetic relatedness is high within groups, offspring may benefit from delayed dispersal by helping rear young that are

genetically related even if they are not their own (Hamilton 1964). Breeders can also benefit from increased genetic relatedness within groups because helpers provision and protect offspring from predation (Moehlman 1979; Barati et al. 2018). Similarly,

increased group size has been linked to higher reproductive success and breeder fitness across a wide variety of species and taxa (Bygott et al. 1979; Rood 1990; Balshine et al. 2001).

Males and females within a species can use different strategies to maximize reproduction and fitness over their lifetimes. For example, small groups of male Galapagos hawks (*Buteo galapagoensis*) will share breeding with 1 female. The males may benefit from such behavior because females are larger and can control the relative share of breeding attempts, whereas the females benefit because a team of males defends a high-quality territory and provides cooperative care for the young (Faaborg et al. 1995; Delay et al. 1996). In contrast, males who secure multiple mates (i.e., polygamy) can produce more offspring over a lifetime than females.

How an individual obtains its breeding position in a group can both affect and be affected by group composition. For example, an individual may bide its time and ultimately breed in its natal territory where it is already highly related to helpers in the group (Kokko and Ekman 2002). By contrast, usurping a breeder in a group can yield considerable social instability, increased dispersal of group members, and ultimately a smaller and less genetically related group (Whitman et al. 2004; Brainerd et al. 2008).

Answering questions about fitness in cooperative breeders requires long-term studies as well as complete (or nearly so) data on group composition and size which can be exceedingly difficult to obtain. Gray wolves (*Canis lupus*) are well-studied cooperative breeders that live and breed in groups typically comprised of family members (Boyd et al. 2023). Existing long-term genetic data from Idaho, United States, can provide insights about lifetime reproductive characteristics and direct fitness in this cooperative breeder.

Dispersal in wolves is often male-biased (Boyd et al. 2023). Thus, we might expect female wolves to inherit breeding positions within their natal groups more often than males and as a result have higher genetic relatedness to the existing group which is comprised largely of siblings. Additionally, male wolves may have increased direct fitness over their lifetimes compared to females because males can mate with >1 female in a group (i.e., polygamy). By contrast, females could conceivably have higher direct lifetime fitness because of the likelihood that they will breed even when they are older and experiencing senescence or even when there is an existing dominant breeding female in a group (i.e., polygamy). I asked how lifetime reproductive characteristics of female and male wolves differ. I predicted that genetic relatedness to helpers would be higher for females than males due to philopatric behavior of female wolves, group size would be similar between the sexes, females would inherit breeding positions from within groups more often than males due to differences in dispersal strategies between the sexes, males would have more lifetime mates and produce more young than females because of polygamy, and females would breed for more years than males due to the likelihood that females would still breed (with a new partner) after a mate died or was expelled from the group.

Methods

Study area.

We (author and field staff) sampled wolves in 3 study areas (north, east, and south) in Idaho, United States (Fig. 1). Annual temperatures ranged from -13°C to 36°C (Western Regional Climate Center 2016), precipitation ranged from 30 to 130 cm, and elevation ranged from 646 to 3,219 m. The northern study area (3,189

km², Fig. 1) was comprised of forests of Western Red Cedar (*Thuja plicata*), Douglas Fir (*Pseudotsuga menziesii*), Engelmann Spruce (*Picea engelmannii*), and Lodgepole Pine (*Pinus contorta*). The eastern (3,388 km²; Fig. 1) and southern (3,861 km²; Fig. 1) study areas were comprised largely of Ponderosa Pine (*Pinus ponderosa*), lodgepole pine, spruce mixed forests, and Big Sagebrush (*Artemisia tridentata*) steppe. Wolves were hunted and trapped for much of the duration of this study, beginning in 2009 and annually each year thereafter. There was no hunting and trapping in 2008 and 2010, however. Hunting and trapping averaged 18.4% of the population over the study period and ranged from 10.4% to 27.6% annually. Wolf density averaged 20.3 wolves/1,000 km² and ranged between 10.1 and 26.6 wolves/1,000 km² during my study.

Field methods.

We collected wolf scats at wolf pup-rearing sites during June to August, 2008 to 2018. When available, we used Global Positioning System (GPS) or radio-telemetry locations of wolves to locate pup-rearing sites. Wolves were radio-collared as part of population monitoring efforts by the U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, and the Nez Perce Tribe. When no radio-collared wolves existed, we surveyed historical pup-rearing sites and sites predicted by a habitat model that had a high probability ($\geq 70\%$ suitability) of being a pup-rearing site (Ausband et al. 2010). At sites of both collared and uncollared wolves, technicians howled (Harrington and Mech 1982) and attempted to find an activity center (area where pups congregate) by searching the area or through searches around wolf GPS clusters (>5 locations within 1 km for >7 days) and radio-telemetry locations when available. After the activity center was located, 4 to 8 technicians collected wolf scats (pup and adult) for 3 to 5 h, radiating out from the activity center on existing wolf trails up to 500 m to ensure that an adequate number of adult scats were collected (Ausband et al. 2010; Stenglein et al. 2010b). We also collected incidental scats found outside of pup-rearing sites and we attempted to resample each group every year. We collected 125 to 200 samples per group per year, which generally detected every individual in the group (Stenglein et al. 2011). Sampling was conducted under University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU).

Laboratory methods.

We (author and laboratory staff) performed DNA analyses at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, Idaho). We extracted DNA from scat samples with Qiagen kits (Qiagen, Valencia, California) and included a negative control to test for contamination. We initially screened all samples in a species-identification test using co-amplification and fragment analysis of 3 short segments of the mitochondrial DNA control region to remove nontarget species and low-quality samples. We then attempted to genotype all samples identified during the mtDNA test as wolf or dog (*C. familiaris*) using 18 nuclear DNA microsatellite loci (AHT103, AHT109, AHT121, AHT200, C05.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725; Holmes et al. 1994; Breen et al. 2001; Guyon et al. 2003; Salim et al. 2007; Ostrander et al. 2017). We first amplified all samples twice for genotyping and required successful amplification of alleles at ≥ 5 loci for the sample to continue for an additional 1 to 3 PCRs until 18 total loci were amplified, whereas we discarded samples that amplified at <5 loci. At each locus, we required ≥ 2 independent PCR amplifications for consensus of a heterozygote and ≥ 3 independent PCR

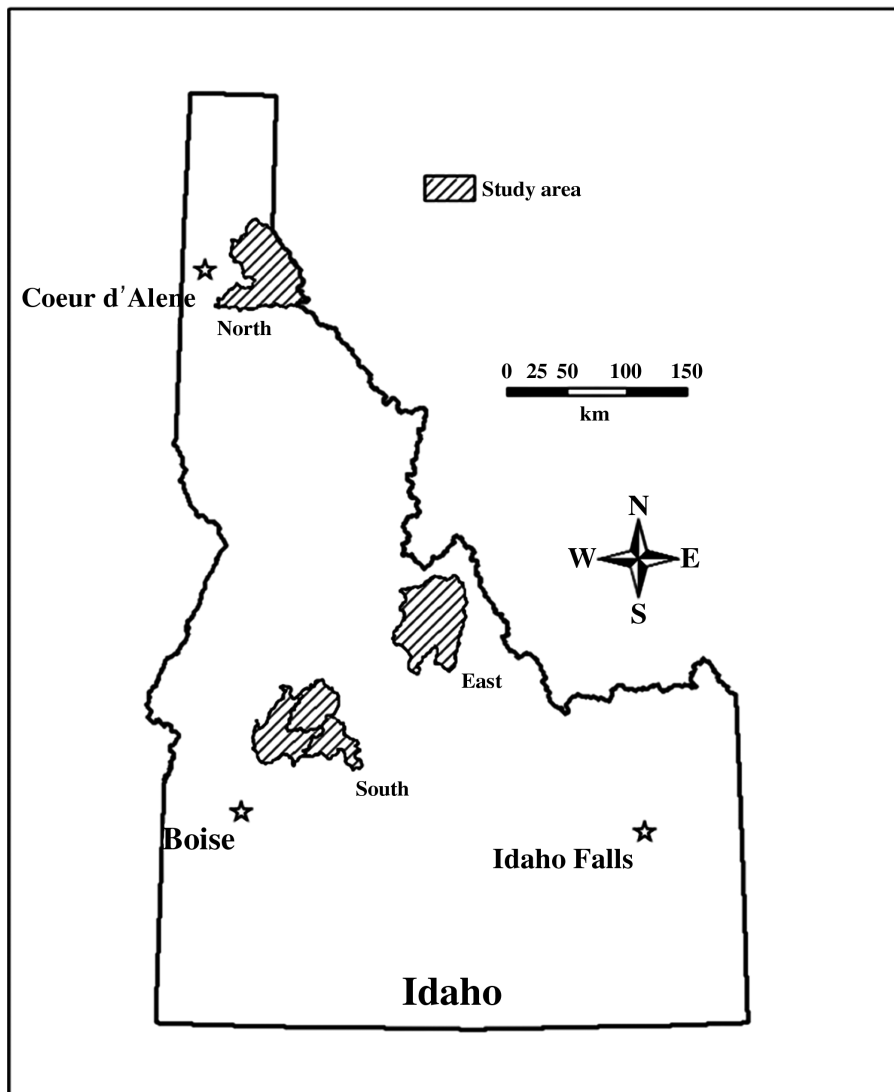


Fig. 1. Three study areas in Idaho, United States, where wolves were genetically sampled, 2008 to 2018.

amplifications for consensus of a homozygote. We compared all consensus genotypes and all unique genotypes of previously identified individuals using Program Genalex (Peakall and Smouse 2006) to match samples and distinguish unique genotypes. To account for undetected genotyping errors, we grouped samples mismatching by allelic dropout at only 1 locus (e.g., 102, 102 vs. 102, 106) as a single individual (Adams and Waits 2007). We used Reliotype (Miller et al. 2002) to test the accuracy of unique genotypes captured once by ensuring that the genotype attained a 95% accuracy threshold. Further details regarding laboratory methods can be found in Stenglein et al. (2010a, 2010b), Stenglein et al. (2011), and Stansbury et al. (2014). We analyzed all collected samples in 2008 and 2009. After 2010, we used rarefaction analyses (Stenglein et al. 2011) to subsample for economic efficiency and analyzed 40 adult and 25 pup samples from each group. If a group had more than 2 individuals detected only once we analyzed additional samples when available to obtain 10 more consensus genotypes.

Analytical methods.

In addition to estimating observed heterozygosity for individuals and group size from the resulting genotypes, I determined

maternity and paternity from pedigree analyses using Program COLONY, version 2.0.5.5 (Jones and Wang 2009). I included all adult males and females as potential parents and all sampled pups as potential offspring for each year. I first calculated allele frequencies for year in Program COANCESTRY version 1.0.1.5 (Wang 2011) and then imported those into Program COLONY for use in pedigree analyses. I allowed polygamy in both sexes and assumed an allelic dropout rate of 0.01. Lastly, I used Program COANCESTRY (Wang 2011) to estimate Trio ML genetic relatedness between breeders and adult helpers within each group for each year.

For each breeding male and female for which I knew both the start and end of their breeding, I tested for differences in genetic relatedness to helpers, group size (i.e., number of adults), number of mates, number of pups produced (i.e., lifetime direct fitness), number of years breeding, for both male and female wolves using t-tests. Finally, I used a binomial logistic regression to test for differences between females and males and whether they had been adopted as a breeder from outside of the group or inherited the breeding position from within the group. Analyses were conducted in Program R, version 4.0.4 (The R Foundation for Statistical Computing 2021).

Results

The probability of identity for siblings (i.e., chance that 2 individuals would have the same genotype) was small and ranged from 3.54×10^{-4} to 1.18×10^{-3} . I documented complete breeding histories for 11 male and 18 female wolves over their lifetimes (Ausband 2023). The probability of parent-pair matches was 0.99 (SD = 0.03) across all 29 breeders. Female breeders were in my study an average of 4.6 years (range = 2 to 9 years) while males averaged 4.5 years (range 2 to 6 years). Females averaged 3.3 years old at first reproduction (SD = 1.3) while males averaged 2.9 years old (SD = 0.7).

Genetic relatedness between breeders and helpers was roughly 0.25 and did not differ between females and males (Tables 1 and 2). Average group size was slightly larger for females (6.4, SD = 2.8) than males (5.8, SD = 1.9) but this was not statistically significant (Table 2). Females inherited breeding positions from within groups nearly 4.5 times more often than males ($P = 0.004$; Tables 1 and 2). Approximately 28% ($n = 8$) of female and male wolves had more than 1 mate in their lives, sometimes within the same reproductive attempt (i.e., polyandry and polygamy). Both female and male wolves had 1 to 5 partners during their lifetimes and the average number of partners did not differ between sexes (Tables 1 and 2). Females produced an average of 7.1 pups over their lifetime (SD = 5.5) with a range of 1 to 20 pups, whereas males sired 10.8 pups (SD = 7.5) with a range of 1 to 25 pups and there was no significant difference between the sexes (Tables 1 and 2). There was also no difference in breeding tenure (Table 2); the average number of years breeding for females was 1.7 years (SD = 1.2), whereas males averaged 2.4 years (SD = 1.3). Finally, wolves that reproduced ≥ 3 years were likely (71%, $n = 5$) to have >1 partner during their lifetimes.

Discussion

Breeding opportunities in populations of cooperative breeders are few and most individuals do not become breeders. Although in some cases wolves can be reasonably long-lived (e.g., 14-15 years; Ausband et al. 2009), and individuals can occupy breeding spots for several years, tenure was typically short for wolves that

achieved breeder status. Wolves frequently re-paired with other individuals after the death or expulsion of a mate with some wolves pairing with as many 5 individuals over their lifetimes. Ultimately, direct fitness varied greatly within female and male breeding wolves.

Similar to wolves in this study, female meerkats (*Suricata suricatta*) showed great variation in breeding tenure and lifetime reproductive output (Hodge et al. 2008). Stahler et al. (2013) also showed substantial variation in the reproductive output of female wolves as a function of group and population-level influences and even individual age. Relatedly, wolves in Scandinavia show remarkable variation in age at first reproduction as a function of both population size and level of inbreeding estimated in the population (Wikenros et al. 2021), although the average age at first reproduction (3 years for females, 2 years for males) was similar to what I observed for both sexes.

I report direct fitness (i.e., pups produced) but some individuals may have benefitted from being in groups and helping rear related young that were not their own (i.e., inclusive fitness; Hamilton 1964). In some cases, inclusive fitness can yield higher fitness over a lifetime than breeding on a territory by oneself (Koenig et al. 2023). While I knew when an individual was present in a group, I did not know how much care they may have provided to the related young; thus, my inferences are limited to measures of direct fitness.

Similar to work from Poland (Jędrzejewski et al. 2005), female wolves tended to inherit breeding positions within their groups while males were commonly adopted into breeding positions from outside the group. Ausband (2022) found similar results for wolves in Idaho using a larger sample size of individuals than what is presented here. Such sex-biased dispersal has been widely documented across taxa and species and depends in part on inbreeding avoidance, competition between kin, and fluxes in food abundance or changes in habitat suitability (Li and Kokko 2019).

Breeding tenure was relatively short for wolves in Idaho (approx. 2 years). In Spain where wolf poaching was common, breeding tenure was surprisingly more than twice as long, although this estimate was derived from 6 breeders and may be an artifact of sample size (Blanco and Cortes 2007). Breeding

Table 1. Lifetime reproductive characteristics of breeding female ($n = 18$) and male ($n = 11$) gray wolves in Idaho, United States, 2008 to 2018.

	Years breeding (SD)	No. of partners (SD)	No. of pups produced (SD)	Genetic relatedness to helpers (SD)	No. of adults in group (SD)	Inherit breeding position from within group
Females	1.7 (1.2)	1.3 (0.7)	7.1 (7.5)	0.26 (0.13)	6.4 (2.8)	77.8%
Males	2.4 (1.3)	1.6 (0.8)	10.8 (7.5)	0.27 (0.12)	5.8 (1.9)	18.1%

Table 2. Differences between lifetime reproductive characteristics of breeding female ($n = 18$) and male ($n = 11$) gray wolves in Idaho, United States, 2008 to 2018.

Question	Answer
Did genetic relatedness to helpers differ between female and male breeders?	No ($T = -0.20$, $P = 0.84$)
Did group size differ between female and male breeders?	No ($T = 0.61$, $P = 0.54$)
Did females inherit breeding positions from within groups more often than males?	Yes ($Z = 2.76$, $P = 0.004$)
Did the number of lifetime mates differ between females and males?	No ($T = -0.72$, $P = 0.48$)
Did the total number of pups produced differ between females and males?	No ($T = -1.42$, $P = 0.17$)
Did the total number of years breeding differ between females and males?	No ($T = -1.46$, $P = 0.16$)

tenure in a population of wolves in Scandinavia and Poland where human-caused mortality was common (86% of known-fate pair dissolution events were human-caused in Scandinavia; 10% to 64% annual harvest in Poland was similar to Idaho; [Jędrzejewski et al. 2005](#); [Milleret et al. 2017](#)). Because breeding tenure in wolves is relatively short, we might expect food availability, group size and composition, and mating decisions (e.g., polygamy) to have profound effects on individual fitness.

Why do pairs dissolve? Several hypotheses exist for explaining the decision to divorce in pairs of monogamous birds including incompatibility, better options, and even forced divorce by a third individual ([Choudhury 1995](#)). In most cases, I did not know what ended tenure of a breeding pair. Mated wolf pairs in Scandinavia, however, typically dissolved due to the death of one of the individuals ([Milleret et al. 2017](#)) and I presume that such was the case for most of the observed pair dissolution events in this study.

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Conflict of interest

None declared.

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