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RESEARCH ARTICLE

Gray wolf breeders are more vulnerable to harvest during the breeding season

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Abstract

In cooperatively breeding carnivores, breeders are vital to perpetuating the group; the death or removal of an individual breeder can greatly affect group composition, genetic content, and short-term population growth. Understanding the number of breeders harvested and timing of harvest can increase our knowledge of how mortality affects groups of cooperative breeders. Gray wolves (*Canis lupus*) in Idaho, USA, are exposed to annual harvest and are an ideal species for studying the effects of harvest on breeder turnover. We combined genotypes from tissue samples of harvested wolves with parentage analyses and cementum annuli ages and estimated when and how many breeding wolves were harvested. We genotyped and aged 229 adults and 203 pups using tissue and tooth samples from wolves harvested between 2014 and 2016. We identified a minimum count of 33 breeders in the harvest and found that they were disproportionately harvested more during the breeding season. We estimated that a minimum of ~14.5% of adult wolves harvested annually, or approximately 1 in 7, were breeders. We posit their behavior during breeding season may increase their vulnerability to harvest. By linking animal life history with vulnerability to human-caused mortality we show that managers could structure harvest seasons so there is less overlap with wolves' breeding season if there is concern about the demographic consequences of harvesting breeders.

KEYWORDS
breeder, *Canis lupus*, cooperative breeding, gray wolf, harvest, hunting, trapping

INTRODUCTION

Certain species have evolved to live in groups in part because it lessens the workload of rearing young and increases fitness (Solomon and French 1997). Such cooperatively breeding species live in groups wherein 1 or more of the nonbreeding members (helpers) aid the breeders (i.e., the individuals who produced the young of year) in rearing and protecting their young through territory defense, food provisioning, and teaching fundamental skills for long-term survival (Solomon and French 1997, Clutton-Brock 2006). Behavioral strategies vary among species and are influenced by environmental, genetic, and demographic factors. For example, group size and composition are dynamic factors that can affect a group's persistence because the amount of effort an individual contributes to the group may vary as a function of the different roles they perform as well as their sex and age class (Russell 2004, Ausband et al. 2015, Ausband et al. 2017*a*, Downing et al. 2021).

Breeders, in particular, can have a disproportionate influence on group persistence and population growth (Brainerd et al. 2008). In some cooperatively breeding species, the breeding males and females spend more time than other group members directly and indirectly aiding in rearing young. For example, in packs of gray wolves (*Canis lupus*) both male and female breeders show increased care for pups compared to other pack members in the first month after they are born (Mech and Boitani 2003). Breeding females will directly care for and feed the pups during the early months after birth, and the male breeder will contribute indirectly to pup care by provisioning the lactating mother with food and through territory defense (Mech and Boitani 2003, Boyd et al. 2023). Similarly, nonbreeding individuals may also help rear young through behaviors such as provisioning and pup-guarding (Packard 2003, Ausband et al. 2016). Studies of gray and red wolves (*C. rufus)* show that the removal of individuals of certain sex and age classes from a group can have direct and indirect consequences for a population by decreasing recruitment and group size after breeders die (Brainerd et al. 2008, Sparkman et al. 2017).

Group-living carnivores have been established as model species for studying the role that each individual plays within a social cooperative breeding group and how some roles are critical to breeder fitness and group persistence (Loveridge et al. 2007; Ausband et al. 2017*a*, *b*; Sparkman et al. 2017; Tanaka et al. 2018). In many group-living carnivores, breeders are vital to perpetuating the group, and the death or removal of an individual breeder can greatly affect group compositions, genetic content, and short-term population growth (Ausband et al. 2015, Bohling and Waits 2015). Harvest of African lions (*Panthera leo*) increased the frequency of breeder turnover, because harvest was disproportionally targeting large males that typically sired cubs of multiple resident females in the group (Loveridge et al. 2007). Human-caused mortality can have compounding effects on group-living wolves. Studies have shown that harvest has both direct (removing an individual from a population) and indirect effects on fitness and recruitment of wolves at the individual and group levels (Ausband et al. 2017*a*, *b*). The indirect effects of harvest can reduce fitness by limiting pair-bond duration and group size and increasing breeder turnover, all factors that have been correlated with a group's performance in alloparenting, predator avoidance, hunting, and pup recruitment (Clutton-Brock 2006).

In Idaho, USA, gray wolves are harvested annually, and harvest seasons overlap breeding, dispersal, and pup-rearing periods. Wolves defend established territories, groups, and breeding positions through howling, scent-marking, or even direct conflict (Mech and Boitani 2003, Boyd et al. 2023). Such behaviors (e.g., howling) can be exploited by hunters and trappers and may lead to bias toward certain sex and age classes in the wolf harvest. For example, breeders might be more responsive to auditory or olfactory lures used by hunters and trappers during the breeding season. Similarly, dispersing adults in search of mates may also be especially vulnerable (Nichols et al. 2014). Therefore, dispersing adults may ignore more risks than other age classes and social groups of wolves in the area (Pusey 1987). How the timing of harvest coincides with these life-history stages and their influence on individual behavior and vulnerability to harvest is poorly understood. Although gray wolf management in the Northwestern United States is hotly debated (Gude et al. 2012), the effects of wolf behavior on vulnerability to hunting and trapping are not well understood. Additionally, despite some inferences about how removing breeders from a group affects population demography, little is known about temporal patterns of breeder vulnerability to regulated public harvest and what time of year they are likely to be harvested in established populations. Many cooperatively-breeding species are not subject to recurrent annual harvest, thus much of the existing literature does not yield such inferences about their vulnerability (Ausband et al. 2024).

We sought to estimate the relative frequency of breeders (i.e., the individuals who produced the young of year) in the wolf harvest in Idaho, and to test whether breeders were disproportionately harvested during the breeding season. In Idaho, the state requires wolves to be checked in after they are harvested, at which time Idaho Department of Fish and Game (IDFG) personnel can record the sex of the individual and collect samples to determine the age and obtain a genetic sample for individual identification. Using such samples and associated data multilocus genotypes can be used to reconstruct pedigrees and estimate relatedness among individuals, which can then be used to investigate mating systems and relationships among harvested individuals (Stenglein et al. 2011, Clendenin et al. 2020, Shimozuru et al. 2022). Such genetic approaches can give biologists insights into whether who dies in a group and when matters for group persistence and reproductive success (Ausband et al. 2017b). Here, we used genetic data and parentage analysis to develop a useful method for estimating the number of breeders in the wolf harvest and to determine when breeders were most vulnerable to harvest.

We posited that by using parentage analyses and harvest tissue samples we could estimate the frequency of breeders harvested because wolves of all age classes are harvested annually and there would be multiple individuals harvested from the same family group. We predicted that a sufficient number of packs would have both breeders and pups harvested to determine the frequency of breeders in harvest. We also hypothesized that breeders would be more vulnerable to harvest during the breeding season (i.e., January–early February in Idaho) because they would be focused on finding a mate or defending their position as a breeder and less focused on threats presented by hunters, and thus more likely to investigate auditory and olfactory cues displayed by hunters. We predicted breeders would be most likely to be harvested during the breeding season.

METHODS

Study area

Our study area comprised Idaho, USA, (216,632 km^2) and included a wide variety of landscapes, including mountainous forests, desert shrub, prairies, and open valleys. Elevations in the state range from 217 m to >3,859 m. Public forests and private timber holdings were dominated by western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). Public harvest of wolves began in Idaho in 2009, temporarily ceased in 2010, and began again in 2011. During 2014–2016 (the study period) most harvest occurred during September–March, with a peak during the big-game rifle hunting season (September–December; Ausband 2016). Wolf trapping (foothold and snare; accounted for 66% of the harvest in December) also occurred during the 3 study years in all 13 Wolf Management Zones created by IDFG.

Sampling

Idaho Department of Fish and Game personnel collected tissue samples during mandatory check-in of harvested wolves and extracted premolar tooth samples to age wolves using cementum analysis (Matson's Laboratory,

TABLE 1 Counts of harvested gray wolves in Idaho, USA, 2014–2016. Wolves were assigned by age class using cementum aging from tooth samples collected by Idaho Department of Fish and Game. Harvest year is from metadata collected from hunters at mandatory harvest check-in by Idaho Department of Fish and Game. Identified breeders (*n* = 33) and wolves dispatched by Wildlife Services (*n* = 5) are included in the adults in harvest.

	2014–2015	2015–2016
Adults	276	314
Pups	98	105
Total	374	419

Manhattan, MT, USA). Idaho Fish and Game personnel also recorded location, date of harvest, means of take, animal condition, and affixed a pelt tag to the animal hide. Data on sampled wolves were separated into harvest years 2014–2015 and 2015–2016 (Table 1). We considered any wolf born between June 1st and April 10th of a given biological year (2014–2015 or 2015–2016) as a pup from that biological year and any adult harvested during that time as a potential parent.

Laboratory methods

We extracted DNA from 20-mg tissue samples using Qiagen DNeasy Blood and Tissue kits (Qiagen, Inc., Valencia, CA, USA). For every DNA extraction set, we included a DNA extraction negative control to monitor for contamination. We combined 18 dye-labeled nuclear DNA microsatellite loci into 2 polymerase chain reaction (PCR) multiplexes with a product size of <300 base pairs. We genotyped samples in duplicate with 9 microsatellite loci and sex identification primers to identify individuals and sex (Stansbury et al. 2014, Clendenin et al. 2020). To verify matches or mismatches for samples different by only 1 locus and to obtain sufficient data for parentage analyses, we generated genotypes in duplicate at 9 additional microsatellite loci for each individual (total = 18 loci; AHT103, AHT109, AHT121, AHT200, CO5.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725; Stansbury et al. 2014, Clendenin et al. 2020). We used an Applied Biosystems 3130xl capillary machine (Applied Biosystems, Foster City, CA, USA) to separate PCR products and Genemapper 5.0 software (Applied Biosystems) to score genotypes. We required 2 independent amplifications for a consensus of heterozygotes and homozygotes at each locus and conducted additional PCR replicates when necessary to resolve inconsistencies. We included a positive and negative control for each PCR amplification. Each individual was assigned a unique wolf identification number that could be matched to the unique pelt tag number given by IDFG at the time of the harvest report.

Analysis methods-parentage

We took a conservative approach and only used samples that had >16 confirmed loci, and excluded all 1-year-old wolves from the parentage analysis, because wolves <2 years old are highly unlikely to have acquired a position as a breeder in the group (Ausband 2022). We included all adult (≥2 years old) males and females as potential parents and all sampled pups as potential offspring; samples were excluded if they were missing age data. We extended the sample set and techniques of Clendenin et al. (2020) for sibship reconstruction by estimating a minimum number of breeders. Once consensus genotypes were obtained at 17–18 loci, we imported them into the Program COLONY (version 2.0.6.8; Jones and Wang 2009, Wang 2011) to calculate allele frequencies and run parentage analyses. We used the demographic (age and sex) and related data (harvest date) to separate individuals into groups based on harvest year, age, and sex then entered the genetic data for those groups into COLONY to generate a minimum population size of breeders that were harvested in each year's annual harvest season (Clendenin et al. 2020). We allowed for polygamy in both sexes and assumed an allelic dropout rate of 0.01 and other genetic error rates (including mutations) of 0.01 and determined resulting parentage using maximum likelihood.

Program COLONY uses pairwise likelihood methods to infer parentage among individuals from multilocus genotypes while allowing for allelic dropout and false alleles in genotypes. The probability of identity for siblings (i.e., chance that two individuals would have the same genotype) was very low using the 18 loci and ranged from 3.54×10^{24} to 1.18×10^{23} (Ausband et al. 2017*a*, *b*). If parentage was undetermined in COLONY, we further examined offspring genotypes against the likely parents of the remaining offspring in the group to allow for up to a 2-allele mismatch owing to allelic dropout between parent and offspring to verify parentage across the 18 loci (Allendorf et al. 2013). We only accepted parent-offspring relationships produced by COLONY when $P \geq 0.90$. We divided the total number of breeders detected by the total number of successfully genotyped adults to estimate the minimum percent of breeders in the annual harvest.

To test the validity of parentage assignments, we compared the harvest locations of breeders and their pups to see if they were geographically near one another as one would expect for breeders and pups during their first year of life. We used the metadata provided by hunters to assess the timing of harvest and separated the breeders from the nonbreeding wolves. Samples with missing harvest dates were excluded from the analysis. We compared the observed proportion of breeders found in the harvest in each ecological time period (January–February = breeding season, March–April = gestation, May–September = pup-rearing, October–December = dispersal) to the observed proportion of nonbreeders harvested throughout the state in each ecological time period. We then used a 2-sample test for equality of proportions with continuity correction in Program R (version 4.3.3; R Core Team 2020) to compare the observed proportions of breeders and nonbreeders harvested in each biologically significant period to test our hypothesis about the relationship between vulnerability of breeders and the timing of harvest (Figure 1).

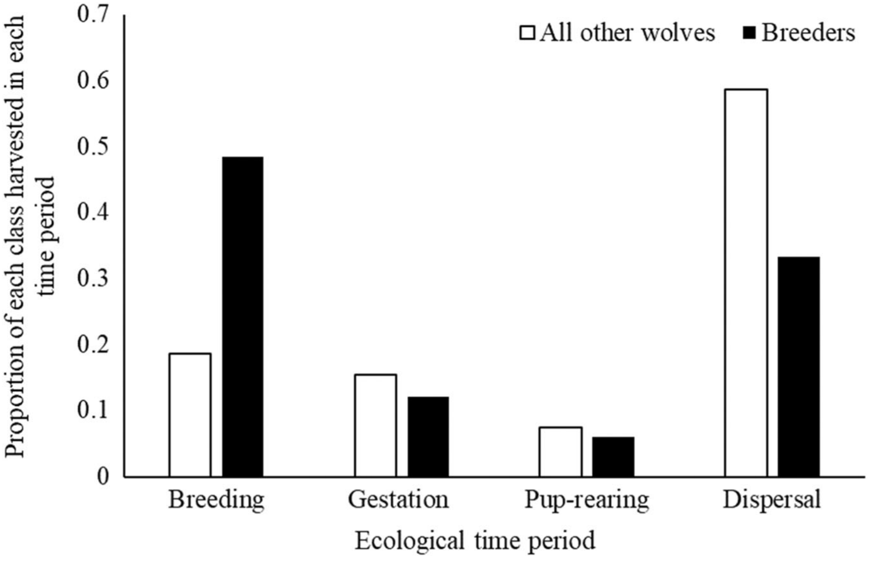

FIGURE 1 Estimated proportion of harvested wolves during biologically significant time periods in Idaho, USA, 2014–2016. Wolves were assigned by breeding status and time period harvested. Time periods were as follows: January–February = breeding season, March–April = gestation, May–September = pup-rearing, October–December = dispersal.

TABLE 2 Adults and pups successfully genotyped at 17–18 microsatellite loci and estimated minimum breeder counts from parentage analyses of harvested gray wolves in Idaho, USA, 2014–2016. Estimates of breeding status are based on the relationship assignments in Program COLONY and age is from metadata collected from hunters at mandatory harvest check-in by Idaho Department of Fish and Game.

	2014–2015	2015–2016
Adult males successfully genotyped	46	71
Adult females successfully genotyped	61	51
Pups successfully genotyped	98	105
Female breeders	9	10
Male breeders	6	8

RESULTS

We genotyped 229 breeding-age adults and 203 pups from the 2014–2015 and 2015–2016 harvest seasons in Idaho (Table 2). We documented 33 breeders in the harvest between the 2 harvest years and the average probability of parentage was 0.99 (SD = 0.01; Table S1, available in Supporting Information). The minimum number of breeders harvested each year was 15 individuals (9 females and 6 males) in 2014–2015 and 18 (10 females and 8 males) in the 2015–2016 season (Table 2). We estimated that approximately 1 in 7 (14.4%) harvested adult wolves were breeders.

The locations of potential breeders and their offspring identified in our parentage analyses were typically within the same Game Management Unit (GMU) and offspring were generally harvested on the same day as their identified parent suggesting our parentage analyses were accurate. Of the observed matched pairs of breeders and their offspring, 94% (31 out of 33) of the breeders were harvested in the same GMU as their offspring, whereas 2 adults were harvested in an adjacent GMU to where the breeder was (Table S1). We also compared the identified breeders from the harvest analysis to the pedigrees from our summer rendezvous site sampling data and identified 1 mutual breeder and pup pair from the same year (i.e., SZC8; Table S1). Of the 33 breeders harvested, 16 were harvested during the breeding season (48%; Figure 1). Breeders were disproportionately harvested more than expected (48.5% of breeders vs. 18.7% all other wolves) during the breeding season ($\chi^2_{(df)} = 15.79$, $P < 0.0001$). In contrast, breeders were significantly less vulnerable than expected (33.3% of breeders vs. 58.5% all other wolves; Figure 1) to harvest during the dispersal season ($\chi^2_{(df)} = 7.22$, $P = 0.007$; Figure 1). We also identified 5 additional breeders that were not included in the analysis because they were harvested by U.S. Department of Agriculture, Wildlife Services. Two of those individuals were identified as a breeding pair that shared the same 2 offspring and were all harvested on the same day (Table S1).

DISCUSSION

We found evidence that wolf breeders were routinely harvested and were more vulnerable to harvest during the breeding season (January–February in Idaho, USA). Furthermore, we found a contrasting decrease in breeder vulnerability to harvest during the dispersal season relative to other nonbreeding wolves in the population. Nonbreeders generally comprise the dispersing individuals in a wolf population, thus breeders may be less vulnerable to harvest than nonbreeding wolves traveling through unfamiliar habitats during dispersal. We show that the minimum number of breeders harvested can be accurately and reliably identified from parentage analyses using harvest samples. Our approach is useful for identifying the minimum number of breeders harvested in a population and for identifying when breeders are more likely to be harvested.

Gray wolves continue to recolonize their historic range in the lower 48 states and state agencies are and will be tasked with setting harvest quotas should they initiate wolf trapping and hunting seasons. Agencies might consider establishing mandatory harvest checks where state agency personnel can collect relevant data (e.g., genetic samples, tooth samples for age, harvest date, and harvest location). Collecting relevant biological data and using our method to create pedigrees from the harvested wolves will give wildlife agencies the ability to use opportunistic data and inform management and conservation of wolf populations. Nonbreeding and breeding adult wolves are often not physically distinguishable. Our work provides managers with a tool to identify the breeding and social status of harvested individuals in a population. Creating pedigrees and determining parentage from harvest data can give agencies the potential to locate areas with newly established breeding packs in addition to identifying a minimum count of breeders harvested, and when breeders are likely to be harvested. Knowing how many breeders are harvested and when agencies can adjust regulations and craft seasons to alter the hunting or trapping pressure for this cohort. Breeder turnover in a population of cooperative breeders can influence population growth and affect offspring recruitment (Clutton-Brock 2006, Ausband et al. 2017b). Thorough consideration of the factors influencing cooperative breeding strategies is timely for regions where wolves are beginning to recolonize and harvest seasons are not yet in place (e.g., California, Colorado). Given the disproportionate influence breeders can have on population demography, managers concerned about the demographic consequences of harvesting breeders could structure harvest seasons so there is less overlap with wolves' breeding season.

Previous research has shown that breeders in group-living species have a disproportionate influence on group persistence and population growth (Whitman et al. 2004; Brainerd et al. 2008; Ausband et al. 2017*a*, *b*; Sparkman et al. 2017). Removing a breeder from these groups that breed once annually can directly (population size decreases by 1) and indirectly (population decreases because pack fails to reproduce) affect the population size and the subsequent recruitment. Disruption from breeder turnover and the time of year a breeder is removed from a group can cause the remaining group members to fail to reproduce or even disband (Brainerd et al. 2008). Breeders are more vulnerable during the breeding season due to innate behaviors that are exploited by hunting and trapping techniques. By contrast, during the dispersal season, pups are moving with the pack outside of their rendezvous sites for the first time and may be naïve to the dangers presented by hunters and trappers (Packard 2003). Additionally, some nonbreeding adults from a group will be dispersing and using roads and trails to travel longer distances during hunting and trapping season (Fritts 1983, Pusey 1987, Mech and Boitani 2003). Breeders, however, would not be expected to be dispersing and thus, may not encounter the conditions experienced by dispersing wolves.

We used data readily available to wildlife managers through mandatory harvest check-in (IDFG, state wildlife agency) and a combination of harvest samples, genotyping, cementum annuli aging, and parentage analyses using free software to assess the vulnerability of breeding and nonbreeding wolves. With samples failing due to degradation, dependency on both the pup and the breeder having been harvested in the same year for breeder identification, samples being excluded because of missing age and harvest month data, and only accepting samples from wolves >2 years old with >16 confirmed loci, there is a strong possibility that we underestimated the number of breeders harvested each year. Given our conservative approach, additional breeders may have been removed from the analysis because they did not meet our stringent criteria.

We estimated the minimum percent of harvested individuals that were breeders annually in Idaho and our methods can be used to determine how many breeders are harvested in other populations as long as the total number of individuals harvested is known. At the harvest rates we observed, nearly 1 in 7 adult wolves that were harvested annually in Idaho were breeders, and this ratio was higher during the breeding season. If the average number of wolves in a group is 12, roughly 1 in 6 wolves would be expected to be a breeder.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We used existing harvest data to answer our research questions. No live animals were captured or handled as part of this research.

DATA AVAILABILITY STATEMENT

All data are available in Supplemental Table 1.

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REFERENCES

Allendorf, F. W., G. Luikart, and S. N. Aitken. 2013. Conservation and the genetics of populations. John Wiley & Sons. Hoboken, New Jersey, USA.

Ausband, D. E. 2022. Inherit the kingdom or storm the castle? Breeding strategies in a social carnivore. Ethology 128:152–158.

Ausband, D. E. 2016. Gray wolf harvest in Idaho. Wildlife Society Bulletin 40:500–505.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Ausband, D. E., M. S. Mitchell, S. B. Bassing, A. Morehouse, D. W. Smith, D. Stahler, and J. Struthers. 2016. Individual, group, and environmental influences on helping behavior in a social carnivore. Ethology 122:963–972.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017*a*. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal Society B: Biological Sciences 284:1855.

Ausband, D. E., M. S. Mitchell, and L. P. Waits. 2017*b*. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. Journal of Animal Ecology 86:1094–1101.

Ausband, D. E., P. F. Rebholz, and L. Petrillo. 2024. The effects of human-caused mortality on mammalian cooperative breeders: a synthesis. Biol Reviews. in press.

Bohling, J. H., and L. P. Waits. 2015. Factors influencing red wolf–coyote hybridization in eastern North Carolina, USA. Biological Conservation 184:108–116.

Boyd, D. K., D. E. Ausband, H. D. Cluff, J. R. Heffelfinger, J. W. Hinton, B. R. Patterson, and A. P. Wydeven. 2023. North American wolves. Pages 32.1–32.68 *in* T. L. Hiller, R. D. Applegate, R. D. Bluett, S. N. Frey, E. M. Gese, and J. F. Organ, editors. Wild furbearer management and conservation in North America. Wildlife Ecology Institute, Helena, Montana, USA.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg et al. 2008. The effects of breeder loss on wolves. The Journal of Wildlife Management 72:89–98.

Clendenin, H. R., J. R. Adams, D. E. Ausband, J. A. Hayden, P. A. Hohenlohe, and L. P. Waits. 2020. Combining harvest and genetics to estimate reproduction in wolves. The Journal of Wildlife Management 84:492–504.

Clutton-Brock, T. H. 2006. Cooperative breeding in mammals. Pages 173–190 *in* P. M. Kappeler and C. P. van Schaik, editors. Cooperation in primates and humans: mechanisms and evolution. Springer, Berlin, Germany.

Downing, P. A., A. S. Griffin, and C. K. Cornwallis. 2021. Hard-working helpers contribute to long breeder lifespans in cooperative birds. Philosophical Transactions of the Royal Society B: Biological Sciences 376:1823.

Fritts, S. H. 1983. Record dispersal by a wolf from Minnesota. Journal of Mammalogy 64:166–167.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Jones, O., and J. Wang. 2009. COLONY: a program for parentage and sibship inference from multilocus genotype data. Molecular Ecology Resources 10:551–555.

Loveridge, A. J., A. W. Searle, F. Murindagomo, and D. W. Macdonald. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biological Conservation 134:548–558.

Mech, L. D., and L. Boitani. 2003. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Nichols, H. J., M. A. Cant, J. I. Hoffman, and J. L. Sanderson. 2014. Evidence for frequent incest in a cooperatively breeding mammal. Biology Letters 10:12.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35–65 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution 2:295–299.

Russell, A. F. 2004. Mammals: comparisons and contrasts. Pages 210–227 *in* W. D. Koenig and J. L. Dickinson, editors. Ecology and evolution of cooperative breeding in birds. Cambridge University Press, Cambridge, UK.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Shimozuru, M., M. Jimbo, K. Adachi, K. Kawamura, Y. Shirane, Y. Umemura, T. Ishinazaka, M. Nakanishi, M. Kiyonari, M. Yamanaka, et al. 2022. Estimation of breeding population size using DNA-based pedigree reconstruction in brown bears. Ecology and Evolution 12:e9246.

Solomon, N. G., and J. A. French. 1997. Cooperative breeding in mammals. Cambridge University Press, New York, NY, USA.

Sparkman, A. M., M. Blois, J. Adams, L. Waits, D. A. W. Miller, and D. L. Murray. 2017. Evidence for sex-specific reproductive senescence in monogamous cooperatively breeding red wolves. Behavioral Ecology and Sociobiology 71: 1–11.

Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, C. R. Miller, M. W. Pennell, and L. P. Waits. 2014. A long-term population monitoring approach for a wide-ranging carnivore: noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. The Journal of Wildlife Management 78:1040–1049.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784–795.

Tanaka, H., M. Kohda, and J. G. Frommen. 2018. Helpers increase the reproductive success of breeders in the cooperatively breeding cichlid *Neolamprologus obscurus*. Behavioral Ecology and Sociobiology 72:1–9.

Wang, J. 2011. Coancestry: A program for simulating, estimating and analysing relatedness and inbreeding coefficients. Molecular Ecology Resources 11:141–145.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature 428: 175–178.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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