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ARTICLE
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Reproduction partially compensates for human-caused mortality in a cooperative breeder

David E. Ausband

U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, Idaho, USA

Correspondence
David E. Ausband
Email: dausband@uidaho.edu

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Abstract

Reproductive output can vary widely among mammalian species. There are many drivers that affect reproductive output including evolutionary, environmental, population, social, and individual traits. Although several factors, including human-caused mortality, can affect reproductive output, we generally have a poor understanding of how such factors interact to affect reproduction, particularly in cooperative breeders. Gray wolves (*Canis lupus*) in Idaho, USA, are exposed to annual hunting and trapping. Thus, they are an ideal species to answer questions about how turnover within groups affects reproduction in cooperative breeders. I hypothesized that the reproductive output of wolves would be affected by individual, social, and environmental factors. Contrary to my prediction, mid-summer litter size was positively associated with wolf harvest density, suggesting a compensatory response to harvest in cooperatively breeding gray wolves. Such compensation is only partial, however, and does not fully account for all the individuals lost from harvest. At the very highest harvest densities observed, mean litter size increased nearly 28%. In contrast, mid-summer litter size was negatively associated with multiple breeding in groups, suggesting resource limitation and competition within groups. I show that characteristics associated with harvest and breeding strategies predict variations in litter size in a cooperative breeder.

KEYWORDS
Canis lupus, gray wolf, harvest, hunting, litter size, reproduction, trapping

INTRODUCTION

Reproductive output (e.g., litter size) can vary widely among mammalian species. The reproductive output observed in a species is rooted in its evolutionary history, with some species investing in reproduction at the expense of survival (r-selected) and vice versa (k-selected). Such reproductive output can even vary dramatically within a species or population in space and time. Lemming (*Lemmus* spp.) and vole (*Microtus* spp.) populations, for example, can fluctuate wildly over time in part because of density-dependent effects on reproduction (Mills, 2013). Such cycles of "boom and bust" in populations have intrigued ecologists for decades (Schaffer & Tamarin, 1973). Changes in the environment also affect annual reproductive output, with some populations producing very few young in years of disease outbreaks or drought (Mech et al., 2008;

Paniw et al., 2019). Many drivers affect reproductive output, including evolutionary, environmental, population, social, and individual traits.

For species that live and breed in groups (i.e., cooperative breeders), reproductive output can be strongly affected by social influences. Cooperative breeders commonly live in multigenerational family groups where offspring delay dispersal and help rear young that are not their own (Solomon & French, 1997). Thus, social influences on reproduction in such groups can be profound. For example, female meerkats (*Suricata suricatta*) who lived in groups with more helpers produced more pups because they were able to breed more often in such groups (Russell et al., 2003). Conversely, dominant females in groups of Southern Pied Babblers (*Turdoides bicolor*) had their reproductive output diminished when subordinate females in the group bred (Nelson-Flower et al., 2013). Such within-group competition led dominant females to attempt to suppress breeding by subordinate females (Nelson-Flower et al., 2013). While limited resources and evolutionary history can constrain reproductive output, social factors are an additional constraint—and sometimes benefit—for reproduction in group-living animals.

Individual traits and mating systems can also affect reproductive output. Gray wolves (*Canis lupus*) are cooperative breeders that live and breed in groups where reproduction is typically, although not always, dominated by a breeding male and female. Nonbreeding individuals in groups of wolves can help rear pups in the group through both provisioning (Packard, 2003) and pup-guarding behaviors (Ausband et al., 2016). Litter size of female wolves increased with age until age 4 after which it decreased, although it was highly variable in the oldest individuals (Stahler et al., 2013). Additionally, similar to other largely monogamous species such as Short-tailed Shearwaters (*Ardenna tenuirostris*; Bradley et al., 1995), breeding pairs of gray wolves who were together longer (i.e., pair bond duration) had higher pup survival than newly mated pairs (Ausband, 2019).

Finally, humans can also strongly influence reproductive output in animal populations largely through mortality. Hunting of male brown bears (*Ursus arctos*) in Sweden increased infanticide and reduced reproductive output of females in the population (Swenson, 1997). At times, the effects of humans on one species can affect the ecological community and cascade to other species in the system. For example, Green et al. (2018) found that human-caused mortality of African lions (*Panthera leo*) reduced lion density and allowed a competitor, the spotted hyena (*Crocuta crocuta*), to increase via increased survival of young. Human-caused mortality does not affect all populations equally, however. Canids, in particular, are widely recognized as fecund and their populations commonly capable of withstanding light-to-moderate levels of human-caused mortality (Adams et al., 2008; Knowlton, 1972). Coyote (*Canis latrans*) populations, for example, were relatively unaffected by high levels of human-caused mortality because they appeared to compensate for such mortality through increased litter sizes (Knowlton, 1972). Although several factors, including human-caused mortality, can affect reproductive output, we generally have a poor understanding of how such factors interact to affect reproduction, particularly in cooperative breeders.

Gray wolves in Idaho, USA, are an ideal species for studying how harvest and individual, social, and environmental factors potentially drive reproduction in a cooperative breeder. Furthermore, gray wolves are exposed to annual hunting and trapping (i.e., harvest). Thus, they are an ideal species to answer questions about how high rates of turnover within groups affect reproduction in cooperative breeders. Additionally, fluctuating environmental conditions can affect the large herbivores (Mech et al., 2001) that wolves commonly prey upon and thus, potentially affect wolves' reproductive output. Finally, wolf harvest is a fiercely debated topic and some proponents of harvest may argue that wolves, like other canids, compensate for harvest mortality through increased reproductive output.

I hypothesized that wolf reproductive output (i.e., mid-summer litter size per breeding female) would be affected by harvest as well as individual, social, and environmental factors. Specifically, I predicted that litter size would not compensate for harvest mortality (Knowlton, 1972) and that breeding female age (individual factor; Stahler et al., 2013), group size (social factor; Russell et al., 2003), and prey biomass (environmental factor; Paniw et al., 2019) would positively affect litter size. By contrast, I hypothesized that litter size would be negatively associated with the presence of multiple breeding (i.e., multiple breeding females in a group; social factor) in a group potentially due to competition for resources within groups.

METHODS

Study area

Field technicians surveyed wolf packs to obtain genetic samples in three study areas (Idaho Department of Fish and Game, Game Management Units [IDFG GMUs; 4, 28, and 33–35]) in Idaho, USA during 2008–2020 (Figure 1). Temperatures varied from −13–to 36°C (Western Regional Climate Center, 2024) and elevation

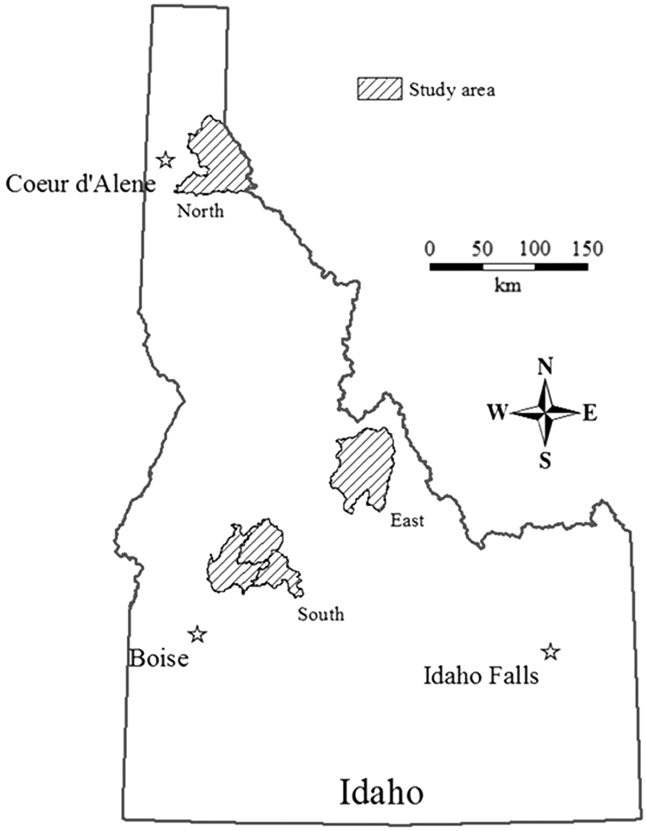

FIGURE 1 Three study areas in Idaho, USA, where gray wolves (*Canis lupus*) were genetically sampled, 2008–2020.

varied from 646 to 3219 m. The north study area (3189 km^2, GMU 4, Figure 1) was mixed conifer forests of largely western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Precipitation in the north study area averaged 95.3 cm annually (Western Regional Climate Center, 2024). The east (3388 km^2, GMU 28, Figure 1) and south (3861 km^2, GMUs 33, 34, 35, Figure 1) study areas were mixed forests comprising spruce mixed forests, ponderosa pine (*Pinus ponderosa*), lodgepole pine, and sagebrush (*Artemisia tridentata*) steppe. Annually, precipitation averaged 54.4 cm in the east study area and 35.6 cm in the south (Western Regional Climate Center, 2024). Turnover within groups of wolves in this study system was common. Hunting and trapping (i.e., harvest) began in 2009 and occurred annually every year thereafter except for 2010. Most wolf harvest occurs during September–March (Ausband, 2016).

Field methods

Technicians collected wolf scats for genetic analyses at pup-rearing sites when pups were approximately 3 months old. Scats that appeared old, mostly hair with little fecal matter, were not sampled. Since 2008, we have attempted to locate every wolf pack in each study area (8–16 annually). Wolf packs were located during summer by surveying sites predicted by a pup-rearing habitat model (Ausband et al., 2010). Upon reaching 500 m from each predicted site, we first gave a series of howls (Ausband et al., 2020; Harrington & Mech, 1982) in an attempt to receive a chorus howl response (i.e., pups and adults). If we received a response, we triangulated the howl direction and hiked in immediately to sample. We then searched in a grid manner for the activity center (i.e., area where pups congregate) where fecal samples would be most abundant. Once an activity center was found, we gathered the entire crew for sampling to decrease the amount of time spent in a site. In sites where we did not elicit a howl response, two technicians separated after howling and searched the site for 30–45 min hiking all roads and trails, including game trails found in site. Pup scats were <2.5 cm diameter and adult scats were >2.5 cm (Ausband et al., 2010; Stenglein et al., 2011; Weaver & Fritts, 1979). We further confirmed scat classifications (pup vs. adult) based on size when we performed pedigree analyses (see below). Scat sizes can vary within pups and adults, sometimes pup scats can be >2.5 cm and sometimes adults can be less. Most individuals were detected several times, thus providing some certainty as to age class. Sampling packs consecutively across years also provided some certainty about pup versus adult age classification because newly sampled individuals were either pups of the year or unrelated adult adoptees, which could be discerned from relatedness metrics. At each site, we collected 100–150 scats per group. Rarefaction analyses and concurrent independent counts showed that roughly 65 samples (40 adults, 25 pups) are necessary to detect every individual in a group (Stenglein et al., 2011). We resampled groups annually to allow us to track (and age) individuals over time. We performed fieldwork under University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU) and University of Idaho IACUC-2018-73.

Laboratory methods

I used genetic analyses to identify individual wolves from scats collected in the field. I conducted DNA analyses at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, ID, USA). I used mitochondrial DNA to remove nontarget species (e.g., Black bear, *Ursus americanus*) and low-quality samples. I then attempted to genotype all remaining samples using 18 nuclear DNA microsatellite loci. Further details regarding laboratory methods can be found in Stansbury et al. (2014), Stenglein et al. (2011), Stenglein, De Barba, et al. (2010), and Stenglein, Waits, et al. (2010).

Analytical methods

I determined parentage from pedigree analyses using Program COLONY, version 2.0.7.0 (Jones & Wang, 2010). All adult males and females were included as potential parents and all sampled pups included as potential offspring for each year. I calculated allele frequencies for each year using Program COANCESTRY version 1.0.1.11 (Wang, 2011) and imported them into Program COLONY for use in pedigree analyses. I assumed an allelic dropout rate of 0.01 and other genetic error rates (including mutations) of 0.01. Resulting pedigrees and recurrent annual sampling allowed me to track individuals through time to determine mid-summer litter sizes, minimum breeding female age, and document multiple breeding. I only accepted parent–offspring relationships produced by COLONY when $p \geq 0.90$. I used minimum breeding female age because I did not know the age of a breeding female if they were recently adopted into the group and had not been previously sampled. In such cases, I assumed that they were 2 years old (thus, 3 years old at $t + 1$), which is the earliest age at first breeding in my population (D. Ausband, unpublished data).

I calculated wolf harvest for each study area using IDFG hunting and trapping data gathered during mandatory wolf harvest check-in at IDFG offices and licensed affiliates. During check-in, hunters and trappers are required to report a harvest location. I used these spatial data to calculate the number of wolves harvested per square kilometer for each study area. I scaled the resulting estimates to wolves harvested per 1000 square kilometers to standardize estimates across study areas and match density estimates commonly reported for wolves in the literature. To generate an index of prey biomass, I used IDFG general season deer (*Odocoileus* spp.) and elk (*Cervus canadensis*) harvest data to calculate the number of deer and elk harvested per 100 square kilometers for each study area (e.g., IDFG, 2018). I then divided the number of deer and elk harvested per 100 square kilometers by hunter days to account for effort. To obtain an index of prey availability, I multiplied the number of deer and elk harvested per 100 square kilometers per 100 hunter days by estimates of prey size (in kilograms) from the literature (Greer & Howe, 1964; Mackie, 1964; Silver et al., 1959) to obtain an index of prey biomass (in kilograms per 100 square kilometers per 100 hunter days).

After standardizing numerical covariates using a *Z*-score for ease of resulting coefficient comparisons, I used a Poisson regression model to estimate litter size (i.e., total pups present at approx. 3 months of age) per breeding female as a function of minimum breeding female age (quadratic variable to assess potential nonlinear effects of age; Stahler et al., 2013), harvest density from time$_{(t-1)}$ to time$_{(t)}$, group size (i.e., number of adults in the group), prey biomass index, whether there was multiple breeding (i.e., >1 breeding female) present in the group (categorical 1,0), and a categorical covariate for study area (east, north, south). I also attempted to treat "study area" as a random effect using a mixed-effects model, but it would not converge. I tested for overdispersion between the data and resulting Poisson regression model using the AER package in Program R (R Core Team, 2022; R version 4.0.4). I used Akaike information criterion (AIC) to assess support between candidate models (Burnham & Anderson, 2002). Finally, to further assess differences among study areas, I conducted tests of whether the harvest density, group size, and a prey biomass index differed between study areas using a generalized liner model with a Gaussian distribution. I conducted regression analyses using the "glm" function in Program R.

RESULTS

I calculated litter sizes across 22 wolf groups and 13 years for a total of 109 wolf-group-years. Mid-summer litter size averaged 4.47 pups/breeding female (SD = 1.9; range = 1–11), average minimum breeding female age was 4.14 years (SD = 2.0; range = 2–10), average number of adults per group was 6.3 (SD = 3.2; range = 2–16), and multiple breeding was present in 23/109 (21.1%) of wolf-group-years. Wolf harvest density ranged from 0.00 to 16.62 wolves harvested/1000 km^2 across study areas and years. The north study area had significantly higher harvest than the east ($\beta = -9.52$, SE = 0.65, $p < 0.0001$) and south ($\beta = -9.20$, SE = 0.63, $p < 0.0001$) study areas. Finally, a prey biomass index ranged from 11.75 to 42.39 kg 100 km^{-2} 100 days^{-1} across study areas and years. Overall, the north study area had a lower index of prey biomass compared to the east ($\beta = 15.52$, SE = 1.26, $p < 0.0001$) but not south ($\beta = 1.40$, SE = 1.21, $p = 0.25$) study area. Lastly, the north study area had fewer adults per group compared to the east ($\beta = 0.39$, SE = 0.10, $p = 0.0001$) but not south ($\beta = 0.04$, SE = 0.11, $p = 0.74$) study area.

A model with a quadratic term for breeding female age, presence of multiple breeding in groups, and harvest density was the most supported among the candidate set for predicting litter sizes (Table 1). I found no effect of overdispersion between the data and most supported model ($Z = -0.63$, $p = 0.74$). The most supported model showed a positive association between mid-summer litter size and harvest density ($\beta = 0.13$, SE = 0.05, $p = 0.009$; Table 2; Figure 2a). In contrast, the presence of multiple breeding in groups was associated with smaller mid-summer litter sizes ($\beta = -0.26$, SE = 0.13, $p = 0.04$; Table 2; Figure 2b). Finally, a quadratic term for breeding female age was retained in the most supported model but was not statistically significant ($\beta = 0.04$, SE = 0.05, $p = 0.43$). Group size, prey biomass index, and study area were not included in the most supported model and were not significant covariates in any candidate models.

DISCUSSION

Reproductive output varies widely across mammalian species. For groups of species that are generally considered quite fecund, like canids, one might expect marked variability in reproduction among individuals over space and time as resources fluctuate. I found evidence that reproduction was affected by social factors and is partially compensating for harvest mortality in cooperatively breeding gray wolves. In addition to harvest, characteristics associated with individual factors such as breeding strategy and potentially within-group competition (social factor) predict variations in litter size in gray wolves.

Harvest density (at $t - 1$, the previous fall/winter) had a significant positive association with mid-summer litter size: as harvest increased, so did litter sizes. At below average harvest densities (<4.7 wolves/1000 km^2), mean litter size was 4.28 (SD = 1.85) pups, whereas mean litter size increased 15% to 4.91 (SD = 1.89) pups per litter at harvest densities above average. At the very highest harvest densities observed (>10.7 wolves/1000 km^2), mean litter size increased nearly 28% to 5.44 (SD = 1.99) pups per litter. Wolf territories in Idaho are approximately 686 km^2 (Ausband et al., 2014), an increase of >1.2 pups per litter when going from below-average harvest to high harvest would not wholly compensate for the concurrent increase in harvest mortality (~6 wolves/1000 km^2) even if those 1.2 pups survived to adulthood. Thus, similar to other canid species (Knowlton, 1972; Minnie et al., 2016), wolves appear to partially compensate for harvest mortality through increased reproduction. While I do not know the mechanism by which wolves appear to increase reproduction, I posit that temporarily lower overwinter densities as a result of harvest may yield abundant food for females going into breeding and gestation allowing them to grow in size and eventually give birth to larger litters in early spring. Reproduction is just one vital rate that could compensate for harvest mortality. I did not measure other vital rates that could have also been compensatory for harvest mortality such as survival or immigration rates. Other studies have found such compensation, or at least partial compensation, in wolf populations (Adams et al., 2008; Stenglein et al., 2018).

The presence of multiple breeding females in a group had one of the strongest effects measured on litter size.

TABLE 2 Most supported model with the parameters, estimated coefficients, SEs, and significance for predicting litter size in gray wolves (*Canis lupus*) in Idaho, USA, 2009–2020.

Parameter	Coefficient (SE)	*p*
Intercept	1.55 (0.05)	
Breeding female age^2	0.04 (0.05)	0.43
Harvest density from time $t - 1$ to time t	0.13 (0.05)	0.009
Multiple breeding in group	−0.26 (0.13)	0.04

Note: No multiple breeding occurred was the reference category for the "multiple breeding in group" parameter.

TABLE 1 Candidate models for predicting litter size in gray wolves (*Canis lupus*) in Idaho, USA, 2009–2020.

Model	*K*	LL	AIC	ΔAIC	AICw_i
1. Breeding female age^2 + Harvest density + Multiple breeding in group	4	−201.89	411.78	0	0.75
2. Breeding female age^2 + Harvest density + Multiple breeding in group + Study area	6	−201.45	414.89	3.11	0.16
3. Breeding female age^2 + Harvest density + Multiple breeding in group + Prey biomass index + Study area	7	−201.38	416.75	4.97	0.06
4. Global model: Breeding female age^2 + Group size + Harvest density + Multiple breeding in group + Prey biomass index + Study area	8	−201.37	418.74	6.96	0.02
5. Null	1	−212.17	426.34	14.56	0.00

Abbreviations: AIC, Akaike information criterion; AICw_i, AIC model weight; *K*, number of parameters; LL, log-likelihood; ΔAIC, change in AIC.

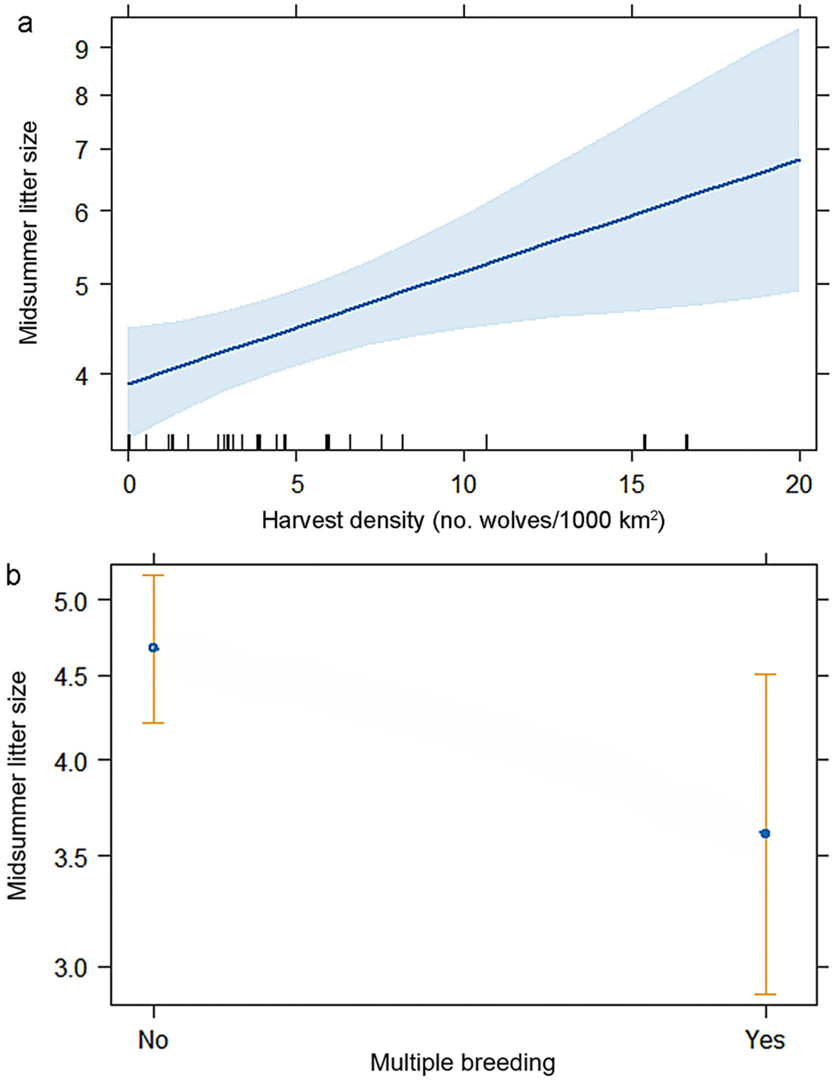

FIGURE 2 Litter size as a function of (a) harvest density (tick marks represent raw values) and (b) presence of multiple breeding in a group for gray wolves (*Canis lupus*) in Idaho, USA, 2008–2020. Error bars represent 95% CIs.

The strong negative effect of multiple breeding on litter size could be a reflection of limited resources in the environment and within-group competition for those resources. For example, Stahler et al. (2013) found a strong positive association between female body mass and litter size; thus, within-group conditions that reduce female body size may affect litter sizes as well. Also, multiple breeding in groups often led to social disruption and groups splitting in Yellowstone National Park, WY, USA (Stahler et al., 2020). Multiple breeding in wolf groups is strongly associated with increased group size (Ausband, 2018), but individuals in large groups may be food stressed and not able to grow large and produce large litters. Additionally, I did not find a strong association between group size and litter size, suggesting that helpers are not likely influencing at least the initial production of pups. Multiple breeding was commonly one breeding male with two breeding females in a group and the male may not have been able to adequately provision both females during the denning and lactation period. If this is true, pups may have died early in the denning period and litter size counts would have been low for females in groups where polygamy occurred. Lastly, provisioning multiple litters of pups in summer is likely more difficult than just one litter, and some early summer mortality may have occurred in groups with polygamy prior to our sampling. I note that multiple breeding was slightly more common (57%) early in the study when group sizes were large and harvest had just begun. Indeed, from 2011 to 2018, there was no documented multiple breeding in my study. Although the overall average rate of multiple breeding was 21%, it can be predicted by both group size and density (Ausband, 2018) and can be quite rare depending on the year.

Stahler et al. (2013) found that female wolves produced larger litters as they aged but litter size decreased after age 4. I note, however, that Stahler et al. (2013) showed both the highest and lowest litter sizes produced at the highest female ages (8–9 years) in their study suggesting that there is quite a bit of variability in reproductive output as wolves age. Although a quadratic term for breeding female age was not statistically significant as a covariate, and a model with breeding female age as a linear variable was equally supported, I retained it as a quadratic variable in my top model in part due to the strong findings of Stahler et al. (2013).

Perhaps surprisingly, I did not find an effect of prey biomass on mid-summer litter sizes even though the three study areas varied considerably. I do note that the prey biomass index I calculated did not include moose (*Alces alces*), which are common in the north study area but not the east and south study areas. Moose are not harvested with a general season in north Idaho, and limited tags are permitted each year, which did not allow me to use harvest as an index of abundance. Despite not being able to estimate moose prey density, including study area in models also had no effect on mid-summer litter sizes suggesting that the availability of moose as a prey item does not appreciably affect litter size, at least in Idaho.

I note that my findings about litter sizes do not reflect litter sizes at birth. We generally detected wolf packs in July when pups were 3 months old; thus, I have no inferences about litter sizes at birth and the mortality rate of pups in my study from 0 to 3 months old is unknown. Mills et al. (2008), however, found that early season mortality rates for wolf pups were generally quite low for eastern wolves (*Canis lycaon*) in Canada. Additionally, genetic sampling is imperfect. Although we tested our methods and techniques rigorously against independent data sources (Stenglein et al., 2011), there is still a chance we missed individuals during sampling. I have no reason, however, to suspect there is any directional bias in litter size counts by group or breeding pair. Finally, genotyping error can often be marked for noninvasive samples. The probability of identity for siblings (i.e., chance that two individuals would have the same genotype), however, was very low using the 18 loci and ranged from 3.54×10^{-4} to 1.18×10^{-3} (Ausband, Mitchell, et al., 2017; Ausband, Mitchell, and Waits, 2017). Thus, I suspect my genotyping results are robust. Finally, the reproductive output of individuals can vary based on underlying genetics or even episodic pulses in food availability coinciding with gestation that I was unable to measure.

I treated wolf harvest as an annually occurring experiment to answer questions about how harvest affects reproduction in a cooperative breeder. Multiple factors appear to affect reproduction in a population where turnover within groups is common. Wolves do appear to compensate for high levels of harvest with increased reproduction via larger litters. Such compensation is only partial, however, and does not fully account for all the individuals lost from harvest.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ausband, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.15041470.

ORCID

David E. Ausband https://orcid.org/0000-0001-9204-9837

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