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Breeder Turnover, Harvest, and Food Affect Recruitment of Young Nonbreeders in Groups of Gray Wolves

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ABSTRACT

Groups of cooperative breeders typically have social hierarchies, with breeders at the top guiding group decisions and influencing the behavior of subordinates in the group. Because of breeders' strong influence on group dynamics and behaviors, breeder turnover can affect the survival of remaining group members. We lack a solid understanding of the nuanced but important effects of breeder turnover on group composition. I first asked how harvest (i.e., hunting and trapping) affected rates of breeder turnover in groups of gray wolves (*Canis lupus*) in Idaho, USA, from 2008 to 2020. Then, I asked how breeder turnover, group size, and food availability affected the recruitment of 1- and 2-year-old nonbreeders into groups. Harvest was associated with an increase in breeding female, but not breeding male, turnover. Breeding female turnover was negatively associated with the probability of 1-year-old, but not 2-year-old, nonbreeders being in a group the following year. The only significant variable associated with the recruitment of 2-year-old nonbreeders into groups was sex, as males were less likely than females to be present in groups at $time_{(t+1)}$. Finally, an index of prey biomass was positively associated with the probability of 1-year-olds being present in groups at $time_{(t+1)}$ (i.e., apparent pup survival to age 1). I show that harvest, social factors such as breeder turnover, and food availability influence the presence of young nonbreeders in groups, ultimately affecting group composition in a cooperative breeder.

1 | Introduction

Many species have evolved to live and breed in groups. Individuals born into such groups commonly delay dispersal, yielding multigenerational groups of related individuals. Such family groups typically have social hierarchies with breeders at the top guiding group decisions, such as when and where to forage, and influencing the behavior of subordinates in the group. For example, dominant individuals in groups of Kalahari meerkats (*Suricata suricatta*) rarely guard pups at the natal burrow while subordinates can spend an entire day pup-guarding, losing body weight as a consequence (Clutton-Brock and Manser 2016). Additionally, breeders in groups of gray wolves (*Canis lupus*) have been observed initiating and leading hunts that eventually involved subordinate group members (Mech et al. 2015).

Because of their strong influence on group dynamics and behaviors, breeder turnover can negatively affect group productivity. For example, poaching of older female African elephants (*Loxodonta africana*) led to low reproductive rates in groups

despite the continued presence of prime-aged females (Gobush et al. 2008). Similar cascading effects of breeder turnover have been observed in African lions (*Panthera leo*). Sport hunting of mature males led to increased infanticide and loss of cubs as new males attempted to take over prides after the death of the dominant male (Loveridge et al. 2007). The effects of breeder turnover on groups can vary and may influence groups differently depending on whether the loss was the breeding male or female (Petracca et al. 2019; Kern et al. 2023). Indeed, breeder loss can affect individual behaviors (e.g., infanticide) even in non-social species (Bellemain et al. 2006).

Breeder turnover can also affect group persistence. Groups of gray wolves disbanded 38% of the time after breeder turnover (Brainerd et al. 2008), for example. Even when breeder turnover does not affect group persistence, it can affect group composition by changing immigration and emigration patterns of individuals in groups (Duncan et al. 2023). Changes to group composition could have cascading effects on helping and foraging behavior, territory defense, and ultimately reproduction in the group (Brainerd et al. 2008). We lack a solid understanding of the nuanced but important effects of breeder loss on group composition.

I first asked how harvest affected breeder turnover in groups of gray wolves in Idaho, USA. Then I asked how breeder turnover, group size, and food availability affected the presence of 1 and 2-year-old nonbreeders in groups of gray wolves. Specifically, I monitored the transition of pups (approx. 3-months-old) as they aged to 1-year-old nonbreeders, and 1-year-olds (approx. 1 year, 3 months) as they aged to 2-year-old nonbreeders (approx. 2 year, 3 months). The potential effects of harvest on turnover of certain age and sex classes were studied previously in this population for a limited duration and by treating harvest as a binary variable (harvest vs. no harvest; Ausband, Mitchell, Stansbury, et al. 2017). I reevaluated these data by adding data from additional years, treating harvest as a rate, and assessing the effect of food as well. Specifically, I predicted harvest (i.e., hunting and trapping) would be positively associated with breeder turnover. I also predicted that the recruitment of 1-year-olds (i.e., approx. 3-month-old pup at $\text{time}_{(t)}$ still in their natal group at $\text{time}_{(t+1)}$) would be negatively associated with breeder turnover and negatively associated with group size due to intragroup competition influencing individual dispersal behavior. Additionally, I hypothesized that the recruitment of 2-year-old females (i.e., approx. 1 year, 3-month-old at $\text{time}_{(t)}$ still in their natal group at $\text{time}_{(t+1)}$) in groups would increase after breeder turnover due to female-biased breeding inheritance in wolves (Ausband 2022). Consequently, I also hypothesized that the presence of 2-year-old male nonbreeders in groups would decline after breeder turnover due to an increase in dispersal as genetic relatedness declines and the selective forces of kin selection (Hamilton 1964) are weakened. Finally, I predicted increasing prey biomass would yield increased recruitment of both 1 and 2-year-old nonbreeders into groups.

2 | Materials and Methods

2.1 | Study Area

Field crews surveyed for wolf packs to obtain genetic samples in three study areas (Idaho Department of Fish and Game [IDFG], Game Management Units 4, 28, and 33–35) in Idaho, USA from 2008 to 2020 (Figure 1). Annual temperatures varied between −13°C and 36°C (Western Regional Climate Center 2023), annual precipitation varied 30–130 cm (Western Regional Climate Center 2023), and elevation varied 646–3,219 m. The north study area (3189 km^2, 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*). The east (3388 km^2, Figure 1) and south (3861 km^2, Figure 1) study areas were mixed forests comprising ponderosa pine (*Pinus ponderosa*), lodgepole pine, spruce mixed forests, and sagebrush (*Artemisia tridentata*) steppe. Hunting and trapping (wolf harvest) began in 2009 and occurred annually every year thereafter with a one-year pause in 2010.

2.2 | Field Methods

Field staff collected wolf scats for genetic analyses at pup-rearing sites. Staff located wolf packs by surveying sites predicted by a pup-rearing habitat model (Figure 1; Ausband et al. 2010). At each site, we gave a series of howls (Harrington and Mech 1982; Jacobs and Ausband 2019) to attempt to get wolves to respond and then searched for the activity center (area where pups congregate) where fecal samples would be most abundant. Pup scats were < 2.5 cm in diameter and adult scats were > 2.5 cm (Weaver and Fritts 1979; Ausband et al. 2010; Stenglein et al. 2011). Staff resampled each group every year. Repeated annual sampling of groups allowed us to track individuals over time. Fieldwork was performed under University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU) and University of Idaho IACUC-2018-73.

2.3 | Laboratory Methods

DNA analyses were conducted at the University of Idaho's Laboratory for Ecological, Evolutionary, and Conservation Genetics (Moscow, ID, USA). I used mitochondrial DNA to remove non-target species 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 Stenglein, De Barba, et al. (2010), Stenglein, Waits, et al. (2010), Stenglein et al. (2011), and Stansbury et al. (2014).

2.4 | Analytical Methods

Parentage was determined from pedigree analyses using Program COLONY, version 2.0.5.5 (Jones and Wang 2010). All adult males and females were included as potential parents, and all sampled pups were included as potential offspring each year. Allele frequencies were calculated for each year using Program COANCESTRY version 1.0.1.5 (Wang 2011) and then imported into Program COLONY for use in pedigree analyses. An allelic dropout rate of 0.01 and other genetic error rates (including mutations) of 0.01 were assumed. Resulting pedigrees and recurrent annual sampling allowed me to track individuals through time, estimate group size, and determine if there was breeder turnover (i.e., detected at $\text{time}_{(t)}$ but not $\text{time}_{(t+1)}$) in groups. Breeders needed to be detected during scat sampling to be considered present.

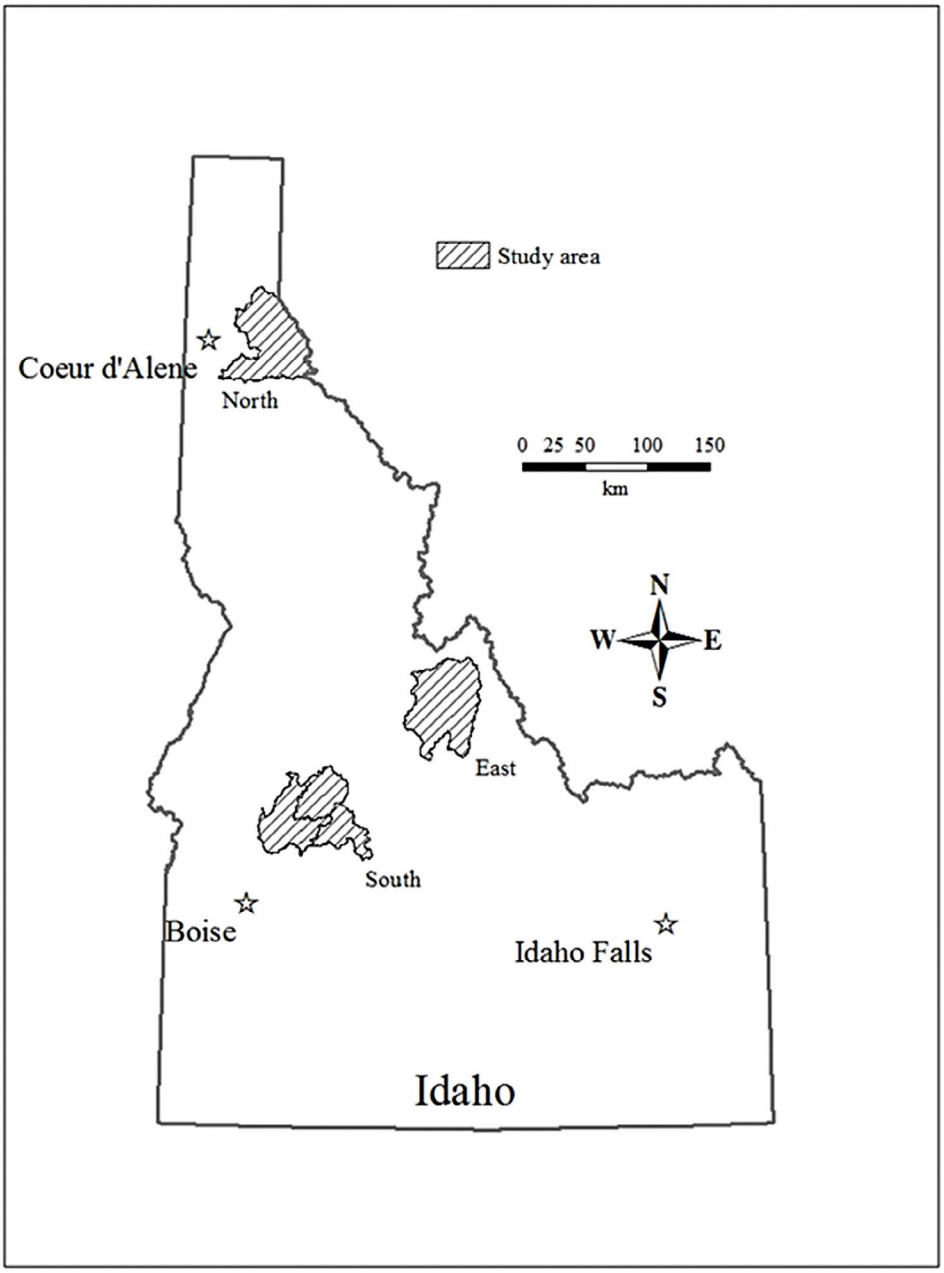

FIGURE 1 | Study areas (hatched) in Idaho, USA, where gray wolves were genetically sampled, 2008–2020.

I calculated wolf harvest for each study area annually 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 plot harvest locations per hunting GMU and calculate the number of wolves harvested/km^2 for each study area (which were based on GMU boundaries). I scaled the resulting estimates to wolves harvested/1000 km^2 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 from mandatory hunter harvest reporting to calculate the number of deer and elk harvested/100 km^2 for each study area (GMU) annually. I then divided the number of deer and elk harvested/100 km^2 by hunter days to account for effort. Finally, I multiplied the number of deer and elk harvested/100 km^2/100 hunter days by estimates of prey size (kg) from the literature (Silver et al. 1959; Greer and Howe 1964; Mackie 1964) to obtain an index of prey biomass (kg/100 km^2/100 hunter days). I standardized all numerical covariates using a Z-score for ease of resulting coefficient comparisons.

I tested whether breeding male and female turnover (0 = no turnover between time$_{(t)}$ and time$_{(t+1)}$, 1 = turnover between time$_{(t)}$ and time$_{(t+1)}$) for each group and year was associated with annual wolf harvest rate in each study area for each breeder sex separately using logistic regression.

I also used a logistic regression model to estimate the probability of recruitment for 1-year-olds (i.e., pup at time$_{(t)}$ still in their natal group at time$_{(t+1)}$, approx. 1 year, 3 months old) as a

function of breeding female turnover (binary, 0 or 1) number of adults in the group, and an index of prey biomass. I included a random effect for group/year in candidate models. Lastly, I modeled the probability a pup would still be in their natal group at $time_{(t+1)}$ as a function of a null model that included only an intercept and the random effect for group/year.

Similarly, I used a logistic regression model to estimate the probability of recruitment for 2-year-olds (i.e., 1-year old from $time_{(t)}$ still present in natal group at $time_{(t+1)}$) as a function of sex, breeding male and breeding female turnover (binary, 0 or 1) in the group, group size, and an index of prey biomass. I included a random effect for group/year in candidate models. I also modeled whether 1-year-old wolves were still present in the same group the following year as a function of an intercept-only null model with a random effect for group/year.

I used Akaike's Information Criterion (AIC) to assess support among candidate models (Burnham and Anderson 2002). Regression analyses were conducted using the lme4 package in Program R (R Core Team 2022; R version 4.0.4). I assessed model fit using the Area Under the Curve (Hosmer Jr. and Lemeshow 2000).

3 | Results

I estimated the probability of recruitment for 435 (239 males, 196 females) 1-year-old nonbreeders and 191 (101 males, 90 females) 2-year-old nonbreeders across 22 wolf groups during 2008–2020. Litter sizes (as estimated in July) averaged 4.47 pups/breeding female (SD = 1.9). Group size averaged 6.3 (SD = 3.2) adults per group across study areas and years.

During their first year of life, 220 pups (50.6%) experienced breeding female turnover, 223 (51.3%) experienced breeding male turnover, and 160 (36.8%) experienced turnover in both sexes of breeders. For 1-year-olds aging to 2-year-olds, 90 (47.1%) experienced breeding female turnover and 86 (45.0%) experienced breeding male turnover between $time_{(t)}$ and $time_{(t+1)}$. Wolf harvest ranged from 0.00 to 16.62 wolves harvested/1000 km^2 across study areas and years (Figure 2). The north study area generally had the highest harvest, whereas the east and south were relatively similar (Figure 2). Finally, a prey biomass index ranged from 11.75 to 42.39/kg/100 km^2/100 days across study areas and years (Figure 3). Overall, the east study area had the highest index of prey biomass, followed by the south and north study areas, respectively (Figure 3).

Harvest was associated with a significant increase in breeding female ($\beta = 0.14$, SE = 0.05, $p = 0.009$), but not breeding male turnover ($\beta = 0.06$, SE = 0.05, $p = 0.24$). The probability of recruitment of 1-year-olds averaged 0.46 (SE = 0.03) for males, 0.50 (SE = 0.04) for females and did not differ between the sexes ($\beta = 0.17$, SE = 0.19, $p = 0.36$). The top model for predicting recruitment of 1-year-olds into groups included breeding female turnover between $time_{(t)}$ and $time_{(t+1)}$ an index for prey biomass, and a random effect for group/year (Tables 1 and 2). This model had excellent discrimination (AUC = 0.86). Another candidate model that also included breeding male turnover was within 0.9 AIC of the top model, but I considered the most parsimonious of the two as the top model (Table 1). The odds that 1-year-olds were in their natal group at $time_{(t+1)}$ were 42% lower after breeding female turnover, although this effect was not particularly strong ($p = 0.10$). In contrast, the odds that 1-year-olds were in their natal group at $time_{(t+1)}$ increased 63% (17–227%, 95% CI) for every SD increase in standardized prey biomass index (Figure 4).

Over all years, male 2-year-olds were still present in the same group the following year 34.7% of the time (SE = 4.8), whereas females were still present 62.2% of the time (SE = 5.1). The most supported model for predicting whether 2-year-olds would be present in the same group the following year (i.e., 1-year olds at $time_{(t)}$ aging to 2-year olds at $time_{(t+1)}$) included just sex and a random effect for group/year (Table 3). This model had good discrimination (AUC = 0.81). Another candidate model that also included breeding female turnover was within 1.7 AIC of the top model, but I considered the most parsimonious of the two as the

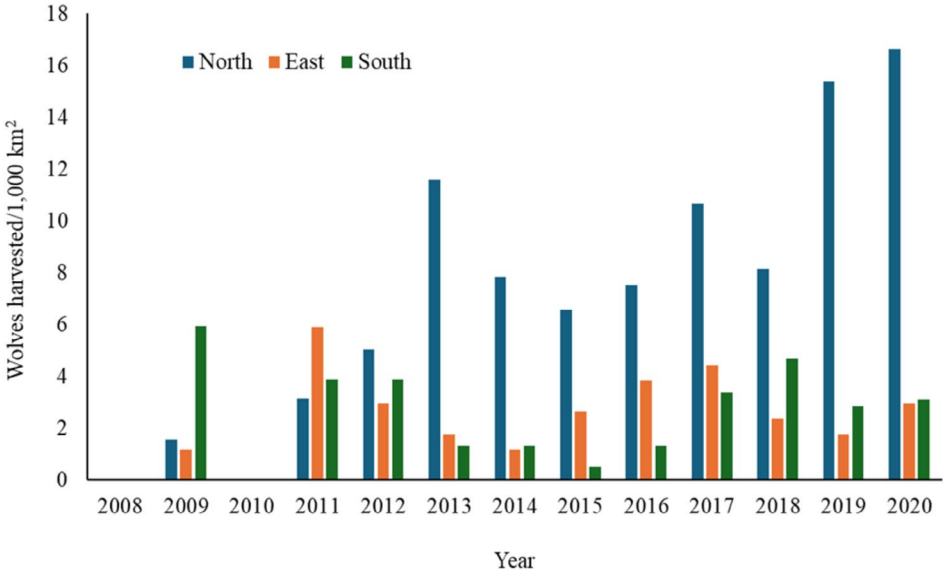

FIGURE 2 | Number of gray wolves harvested/1000 km^2 in three study areas in Idaho, USA, 2008–2020.

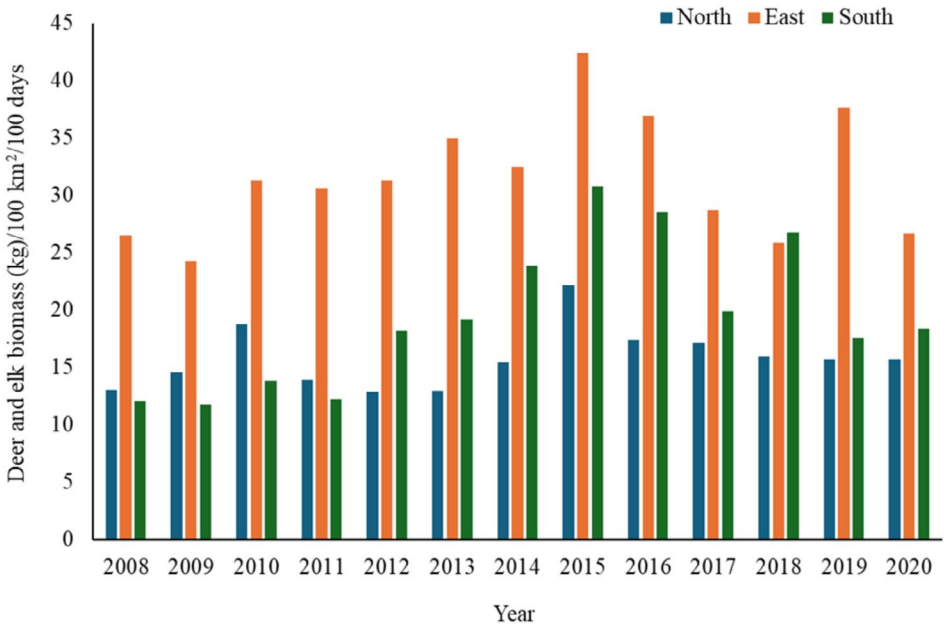

FIGURE 3 | Prey biomass index (kg/100 km^2/100 hunter days) in three study areas in Idaho, USA, 2008–2020.

TABLE 1 | Candidate models for predicting 1-year-old nonbreeder recruitment in gray wolf groups as a function of breeder turnover, number of adults in group, and a prey biomass index in Idaho, USA, 2008–2020.

	Model	*K*	*LL*	AIC	ΔAIC	AICw_i
1.	Breeding female turnover + prey biomass index + RE (group/year)[a]	4	−271.8	551.7	0	0.50
2.	Breeding male turnover + breeding female turnover + prey biomass index + RE (group/year)	5	−271.3	552.6	0.9	0.32
3.	Breeding male turnover + breeding female turnover + number of adults + prey biomass index + RE (group/year)	6	−271.0	554.0	2.3	0.16
5.	Null + RE (group/year)	2	−277.2	558.3	6.6	0.02

Abbreviation: RE, random effect.
[a]Indicates most supported model. AUC = 0.86.

TABLE 2 | Covariates from top model for predicting 1-year-old nonbreeder recruitment in groups of gray wolves as a function of breeding female turnover and a prey biomass index in Idaho, USA, 2008–2020.

Covariate	*β*	SE	*P*
Intercept	0.09	0.23	NA
Breeding female turnover	−0.55	0.33	0.10
Prey biomass index	0.49	0.18	0.006

Note: Random effect for group/year, SD = 1.47.

top model (Table 3). Male 2-year-olds were far less likely than females to still be present in the same group the following year ($p = 0.0003$; Table 4).

4 | Discussion

While harvest by humans can have direct effects on individuals in groups (e.g., lower survival via harvest), it can also have indirect effects on group members through the potential loss of breeders in groups. I found harvest was associated with increased breeding female turnover rates. Competition for breeding positions in wolf populations is fierce, and breeder turnover can be common even in protected wolf populations (D. Smith, U.S. National Park Service, unpublished data). Furthermore, male wolves typically disperse to secure breeding opportunities outside their natal packs (Ausband 2022) making breeding male turnover common. I suspect the harvest rates I observed during my study did not create conditions in male breeder turnover that exceeded the background level observed in the absence of harvest. Indeed, across study areas and study duration, the turnover rate for breeding females was 0.39, whereas it was 0.52 for males at below average harvest rates, suggesting breeding male turnover rates are high even when harvest is low.

Increased breeding female turnover rates were associated (albeit weakly) with decreased recruitment of 1-year-old nonbreeders at time$_{(t+1)}$. Previous work in this system showed no effect of female breeder turnover on the probability of 1-year-old recruitment in groups, although it did show male breeder turnover had negative effects on such probabilities (Ausband, Mitchell,

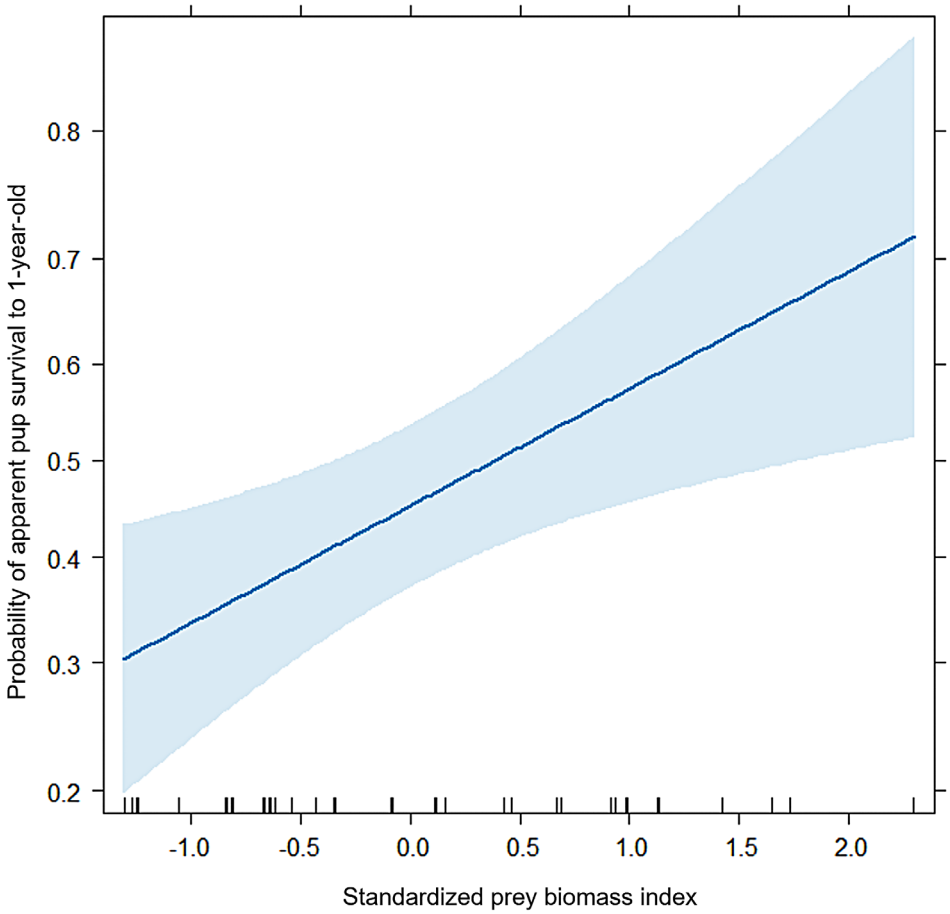

FIGURE 4 | Probability of recruitment for 1-year-old nonbreeders in groups of gray wolves as a function of prey biomass index in Idaho, USA, 2008–2020.

TABLE 3 | Candidate models for predicting the recruitment of 2-year-old nonbreeders in groups of gray wolves as a function of breeder turnover, group size, prey biomass index, and sex of the nonbreeder in Idaho, USA, 2008–2020.

	Model	*K*	*LL*	AIC	ΔAIC	AICw_i
1.	Sex (female as reference category) + RE (group/year)[a]	3	−123.4	252.7	0	0.52
2.	Breeding female turnover + sex (female as reference category) + RE (group/year)	4	−123.2	254.4	1.7	0.22
3.	Breeding male turnover + breeding female turnover + sex (female as reference category) + RE (group/year)	5	−122.8	255.5	2.8	0.13
4.	Breeding male turnover + breeding female turnover + prey biomass index + Sex (female as reference category) + RE (group/year)	6	−122.1	256.3	3.6	0.109
5.	Breeding male turnover + breeding female turnover + group size + prey biomass index + sex (female as reference category) + RE (group/year)	7	−122.1	258.1	5.4	0.4
6.	Null + RE (group/year)	2	−130.6	265.1	12.4	0.00

Abbreviation: RE, random effect.
[a]Indicates most supported model. AUC = 0.81.

Stansbury, et al. 2017). I posit the differences in findings are due to sample size limitations and the limited number of years with harvest present in earlier work. The work presented here used > 4 times the sample size of individuals, > 3 times the number of breeding female turnover events, and six more years of harvest estimated at the study area scale than Ausband, Mitchell, Stansbury, et al. (2017). Intuitively, one might expect breeding female turnover to negatively affect pup survival over their first year due to decreased provisioning, but the probability a 1-year-old was in its natal group at time$_{(t+1)}$ was estimated post-weaning (i.e., pups > 3 months old at time$_{(t)}$). Lower apparent survival of pups post-weaning may be due to newly adopted females not providing sufficient access to food over winter after the pups' mother has died or dispersed. Such limited access to food could be due to newly adopted breeding females being unfamiliar with the group's territory and resource locations.

TABLE 4 | Covariates from most supported model predicting the recruitment of 2-year-old nonbreeders in groups of gray wolves as a function sex of the onbreeder in Idaho, USA, 2008–2020.

Covariate	β	SE	*P*
Intercept	0.54	0.25	NA
Sex (Female as reference category)	−1.23	0.34	0.0002

Note: Random effect for group/year, SD = 0.70.

Alternatively, it may reflect direct deterrence of pups feeding at kill sites because the new breeding females are not genetically related to the pups. Currently, we do not know the mechanism behind the negative effect of breeding female turnover on the probability of 1-year-old recruitment into groups.

The negative association of breeding female turnover on 1-year-old recruitment was countered by a positive effect of food availability. Other studies have also shown positive effects of food availability on the survival of young (i.e., recruitment) across a wide variety of cooperative breeders (Clutton-Brock 2006; Koenig et al. 2016; Preston et al. 2016). I note that the prey biomass index I calculated did not include moose (*Alces alces*). This species is not harvested with a general season in Idaho, and limited tags are available for a controlled hunt only in the north study area. Despite this, moose are common in the north, but not in the east and south study areas. Thus, the prey biomass index I generated underestimated total prey available in the north study area.

The probability of fewer male nonbreeding 2-year-olds than females being present in groups likely reflects sex-biased dispersal in wolves. Wolves commonly disperse between 2 and 3 years, with some dispersing as 1-year-olds (Jimenez et al. 2017; Morales-González et al. 2022). Further, dispersal in wolves is commonly male-biased (although not always, Morales-González et al. 2022) and appears to be so in my study system (Jimenez et al. 2017). I do not know if 1-year-olds in my study dispersed or died as they aged to 2-year-olds. I only know they were no longer present in groups when they would have reached age 2. Model results showing fewer 2-year-old males than females in groups and wolf life history in the region suggest the number of 2-year-old males in a group at $\text{time}_{(t+1)}$ is likely a function of both mortality and dispersal behavior. Wolves have also been found to disperse at young ages in regions where food availability and vacant habitat permit dispersal (Nordli et al. 2023). Thus, the decisions by 1-year-olds to stay or disperse from groups as they age to 2-year-olds could also be a function of wolf density. Finally, in some systems, wolves disperse at younger ages (Morales-González et al. 2022) than is commonly observed in Idaho, USA. Thus, my inferences about the effects of sex on 2-year-olds remaining in their natal pack may be limited to certain wolf populations.

Genetic sampling is imperfect and individuals may have been present in groups yet gone undetected. I know, however, from rarefaction work that analyzing 65 scats per group commonly detects all the individuals present in a group (Stenglein et al. 2011). Despite this, the 1-and 2-year-old presence rates may be biased low if individuals were there and went undetected. This would be true for all years; however, both years with and without harvest. Across all individuals and years, I found just six 1-year-olds (1.4%) and five 2-year-olds (2.6%) that were missed at $\text{time}_{(t+1)}$ but were likely to have been there because they were later detected at $\text{time}_{(t+2)}$. Such small discrepancies are unlikely to change the inferences here. Finally, although I knew when there were breeder turnover events, I could not know with certainty that the missing breeder was harvested due to inadequate sample collection for 17% of samples at the time of harvest.

The potential effect of harvest on wolves is a fiercely debated topic (Creel and Rotella 2010; Gude et al. 2012). Wolves live in social groups, and individuals often participate differently from one another in behaviors such as hunting, territory defense, and guarding and provisioning pups (Boyd et al. 2023). Such complexity has led some to speculate that harvest can affect the social structure of wolf groups and thus have negative effects on populations (Haber 1996). Some studies have examined harvest effects on wolf group reproduction and persistence (Cassidy et al. 2023; Zubiria Perez et al. 2024), but few have explicitly defined or disentangled harvest effects on the social structure of wolf groups. Studies that have examined the effects of harvest on social structure have often done so through the lens of breeder loss (Borg et al. 2015; Ausband, Mitchell, and Waits 2017). Even when studies have explored the effects of harvest on social structure via other classes of individuals in groups, the population-level effects are not easily inferred (Ausband, Mitchell, Stansbury, et al. 2017). We generally do not know how changes to social structure influence wolves at the scale of the population.

Group composition in gray wolves is affected by evolutionary, environmental, and social factors. Evolutionarily, wolf group size and composition have likely been molded by forces such as kin selection (Hamilton 1964) or selective forces associated with the benefits of being in a group to secure large prey (Creel and Macdonald 1995). Clearly, environmental conditions such as prey availability can also affect group composition and size (Clutton-Brock et al. 1999). I show here that harvest, social factors such as breeder turnover, and food availability can influence the presence of younger age classes of individuals in groups and ultimately affect the composition of groups.

Author Contributions

The author takes full responsibility for this article.

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Foundation, U.S. Fish and Wildlife Service, Wolf Recovery Foundation, University of Idaho College of Natural Resources, and University of Idaho Environmental Science Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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