

Linking age and social status of cooperative breeders to vulnerability throughout the harvest season

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Abstract

Individual behaviors are influenced by environmental, genetic, and demographic factors. Some animals choose to live in groups and cooperatively breed, and their behaviors can change depending on dynamic factors such as group size and composition that affect group persistence. In Idaho, USA, gray wolves (*Canis lupus*) are harvested annually, providing an opportunity to investigate the effects of harvest and seasonal behaviors on a population of cooperative breeders. These annual hunting and trapping seasons overlap with the dispersal and breeding periods for wolves and we do not know how harvest affects the vulnerability of different sex and age classes during these important biological periods. We applied 9 years (2009–2018) of genetic, age, and harvest data from harvested wolves to investigate how behaviors (dispersal and breeding) and biological drivers might influence the vulnerability of wolves to harvest. We created pedigrees from genotypes of non-invasively collected scats to estimate the expected proportion of the wolf population composed of 3 different age classes (pup, yearling, and sexually mature or ≥ 2 years old) and compared them to the observed number of each age class harvested during biologically significant periods (i.e., dispersal and breeding). We found that pups were more vulnerable to harvest in December when wolf harvest transitioned largely to trapping (accounts for 66% of harvest), and found evidence that adults were more vulnerable to harvest during their breeding season in January and February. In contrast, we found no difference in the expected versus

observed number of wolves ≥ 2 years old in the harvest during peak dispersal season (December), or in the expected versus observed number of yearlings in the harvest during September and October when pups are mobile and groups of wolves abandon the use of pup-rearing sites. Some age classes were disproportionately harvested during certain periods for specific years, but this was not consistent across all years, suggesting there is more to learn about the vulnerability of different age classes to harvest. We found harvest can disproportionately affect some demographic classes of individuals depending on year, biological period, and harvest type. With wolves continuing to recolonize historical ranges, our approach can benefit managers and future studies with the goal of identifying how interannual harvest affects groups of wolves.

KEYWORDS

Canis lupus, cooperative breeding, gray wolf, harvest, hunting, trapping

Cooperative breeding generally refers to the shared care of related, or even unrelated, young by helpers (i.e., non-breeding individuals) within a group (Solomon and French 1997). Many species that live in groups are cooperative breeders, and the complex social structures of these groups can affect the behavior of individuals within the group (Solomon and French 1997). These behaviors are influenced by the role each group member plays and these roles are vital for the group's success. For example, breeding pairs will suppress other adults within the group (through physical, olfactory, and vocal displays) from taking part in breeding; however, those non-breeding individuals will directly and indirectly care for the breeders' young, which is vital for the group's reproductive success and stability (Solomon and French 1997, Gobush et al. 2008). Human-caused mortality in cooperatively breeding species can directly and indirectly affect the success of these social groups, and who dies in the group and when may influence group persistence (Ausband et al. 2017, 2025; Ausband 2019).

In cooperatively breeding groups, the social hierarchies may affect individual behavior and group stability. For example, younger males and females typically remain nonreproductive while staying with their natal group (Solomon and French 1997). Additionally, for mature nonbreeding adults, acquiring a chance to reproduce can be challenging and costly, and typically acquired by dispersing from their natal group to join another. In groups of cooperatively breeding vertebrates, such as meerkats (*Suricata suricatta*), cichlids (*Neolamprologus obscurus*), and African wild dogs (*Lycaon pictus*), an increased number of helpers (nonbreeding members of the group) can increase recruitment, individual survival, and fitness (Tardif et al. 1984, Clutton-Brock et al. 1999, Clutton-Brock 2006, Tanaka et al. 2018, Downing et al. 2021). The helpers in these species aid the group through territory maintenance (guarding) and food provisioning, and all members of the group can benefit from group living, but participation varies among group members (Ausband et al. 2017, Ausband 2019). For example, on hunts, some members in a group will cooperate equally by engaging and improving hunting ability against larger dangerous prey while other individuals will withhold effort (MacNulty et al. 2014). Additionally, Jarvis (1981) showed that the size and age of helpers within cooperatively breeding colonies of naked mole rats (*Heterocephalus glaber*) dictated their participation in territory defense or maintenance.

Moreover, periods of biological significance (e.g., breeding season, rearing young, peak dispersal time) can further change how individuals behave. Gray wolves (*Canis lupus*) roam widely across large territories; how far and how often individuals travel from the rendezvous site (locations where wolf group members congregate for several

weeks) is dependent upon the time of year and the age, sex, and role of an individual in their group. As the pups mature and become more independent, the care provided by helpers can change (Thornton and Clutton-Brock 2011, Ausband et al. 2016). After the breeding female dens, the group will move pups to rendezvous sites for the next 8 to 20 weeks (June–August). Like other cooperatively breeding carnivores such as silver-backed jackals (*Lupulella mesomelas*) and African wild dogs (Moehlman 1979, Malcolm and Marten 1982), the nonbreeding adult wolves (typically 1–2 years old) are left to guard the pups and rendezvous site as babysitters while the breeding pair is hunting (Mech and Boitani 2003, Packard 2003, Ruprecht et al. 2012). Wolf pups, like the young of other cooperatively breeding species such as meerkats, spend their time at the homesite developing fundamental skills for territory protection and obtaining food through social learning and teaching within the group (Clutton-Brock et al. 1999). By mid-September, pups will have reached approximate adult size and can travel with the adults, leaving their rendezvous sites and joining the pack on hunts (Packard 2003). However, at this time they may be particularly vulnerable to harvest (hunting and trapping) and predation because they are still naïve to their environment and the risks outside of the rendezvous site. Adult wolves may be more aware of these hazards, but they may have greater vulnerability during biologically significant times of year. For example, adults will increase daily movement when dispersing (i.e., leaving their natal family group and territory) and might be more inclined to use riskier avenues of travel (e.g., roads and trails used by hunters and trappers) and investigate foreign sounds and scents during the breeding season. Wolf trappers commonly trap wolves on developed roads and trails that are baited with natural and artificial lures that mimic wolf urine and carrion. Harrington and Asa (2003) report that wolves exhibit scent-marking behavior and investigation of foreign wolf scents far more frequently during the breeding season. Adults may be more vulnerable to harvest at this time of year given wolf scents are commonly used as lures by trappers.

In cooperative breeders, individuals can perform different roles that may affect behavioral decisions made throughout the year. There is evidence that social and environmental factors such as group size, group composition, food abundance, and predation risk can influence an individual's decision to help or stay within the group (Clutton-Brock 2006). In cooperatively breeding species like gray wolves, individuals will disperse throughout the year, but dispersal peaks with social competition and environmental factors that influence food availability (Mech and Boitani 2003). For example, dispersal peaks in the fall and early winter when social competition and aggression related to breeding within a group of wolves is maximized (Rabb et al. 1967, Zimen 1976, Mech and Boitani 2003). At the same time, the young of the year of ungulate prey are more mobile and difficult to obtain, adding pressure to wolf groups because pups are nearly adult-sized and beginning to travel with the adults and thus require more food. Male and female wolves can disperse >850 km to find a mate or receptive pack with an opportunity to become a breeder (Fritts et al. 1983, Girman et al. 1993, Mech and Boitani 2003). However, leaving the group and traveling alone is risky; exposure to unfamiliar landscapes can increase the chances of starvation and predation (Pusey 1987). These risks may increase in areas with annual harvest, low population sizes, and fragmented habitat where mortality risks are higher or the opportunity to join established packs is lower.

It is currently unknown how the vulnerability of wolves relates to the timing of harvest season and the coinciding biological periods when there are changes in individual behavior. Gray wolf management in the American Northwest has high public interest and the debate is fierce, but empirical data regarding the effects of hunting and trapping on wolf behavior are rare (Gude et al. 2009). Wolves in Idaho, USA, are managed as a big game species and are harvested presumably opportunistically across all sex and age classes. Additionally, harvest seasons overlap breeding, dispersal, and pup-rearing periods. This provides an ideal opportunity to investigate how the cooperative breeding behaviors displayed during these 3 biologically significant periods relate to harvest vulnerability. Wolves are defensive of their established territories, group, and breeding positions (Mech and Boitani 2003). Hunters and trappers can exploit defensive and communicative behaviors (e.g., howling) that may be biased toward certain sex and age classes of wolves. For example, a dominant male or female breeder might be more enticed or responsive to auditory or olfactory lures displayed by hunters and trappers during their breeding season. Dispersing adult males in search of a mate may react in a similar manner at this time; while focused on encountering a mate they may ignore more risks than other age classes and social groups of wolves in the area.

TABLE 1 Predictions for vulnerability of different age classes of wolves to harvest methods and seasons in Idaho, USA. Predictions correspond to Idaho hunting and trapping seasons and biologically significant periods for wolves.

Period	Age class with increased vulnerability	Rationale
Jan-Feb	Sexually mature (>2 years)	Breeding season (Pusey 1987)
Dec	Pups and sexually mature	First exposure to trapping and increased dispersal for sexually mature individuals (Rabb et al. 1967, Zimen 1976, Pusey 1987, Mech and Boitani 2003)
Sep-30 Oct	Pups and yearlings (<16 months)	Naïve to the dangers outside of rendezvous sites (Packard 2003, Thornton and Clutton-Brock 2011)

Our goal was to determine how complex wolf social structures and behaviors affect vulnerability to harvest. We used long-term genetic data to create pedigrees of wolves and tested how vulnerability of different age classes to harvest might be affected by different biologically significant periods throughout the year. We hypothesized that sexually mature wolves (≥ 2 years old) would be more vulnerable to harvest during peak periods of dispersal and breeding. We predicted that sexually mature wolves would be disproportionately represented in harvest during January-February during the breeding season and would be disproportionately represented in harvest during December while dispersal is high, trapping season begins (accounting for 66% of harvest), and breeding season is near (Table 1). We also hypothesized that pups and yearlings (<16 months old) would be more vulnerable to harvest during autumn because they are naïve to dangers presented by hunters from September to October in their environment outside of the homesites. We predicted that pups and yearlings would be disproportionately represented in harvest from September to October. We hypothesized that pups would be more vulnerable in December because they would be more naïve to dangers presented by trappers at the start of trapping season. We predicted that pups would be disproportionately represented in harvest in December (Table 1).

STUDY AREA

All study areas were in mountainous regions of primarily United States Forest Service (USFS) lands. Yearly temperatures ranged from -13°C in the winter to 36°C in the summer (Western Regional Climate Center 2020). Annual precipitation ranged from 30 cm to 130 cm (Western Regional Climate Center 2020). Elevation ranges from 646 m to 3,219 m. The northern study area (GMU 4; 3,189 km²) has a maritime climate and is dominated by western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). The eastern (GMU 28; 3,388 km²) and southern (GMUs 33–35; 3,861 km²) study areas have a continental climate and are dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine, spruce mixed forests, and sagebrush (*Artemisia tridentata*) steppe (Mack et al. 2010). We collected wolf scats in 3 study areas (North, South, East) encompassing 5 Idaho Department of Fish and Game (IDFG) Management Units (GMUs) within Idaho (GMUs 4, 28, 33–35; Figure 1).

We also used tissue samples collected from harvested wolves throughout Idaho (216,632 km²) and in a wide variety of landscapes, including mountainous forests, desert shrubs, prairies, and open valleys. Elevations in the state range from 217 m to >3,859 m. Public forests and private timber holdings dominated by western red cedar, western hemlock (*Tsuga heterophylla*), Douglas-fir, and ponderosa pine comprised most areas. Public harvest of wolves began in Idaho in 2009, temporarily ceased in 2010, and began again in 2011. Most harvest occurred during September–March with a peak during the big-game rifle hunting season (Ausband 2016). Wolf trapping (foothold and snare; accounted for >50% of harvest in December) also occurred during the 3 study years in all 13 Wolf Management Zones created by IDFG.

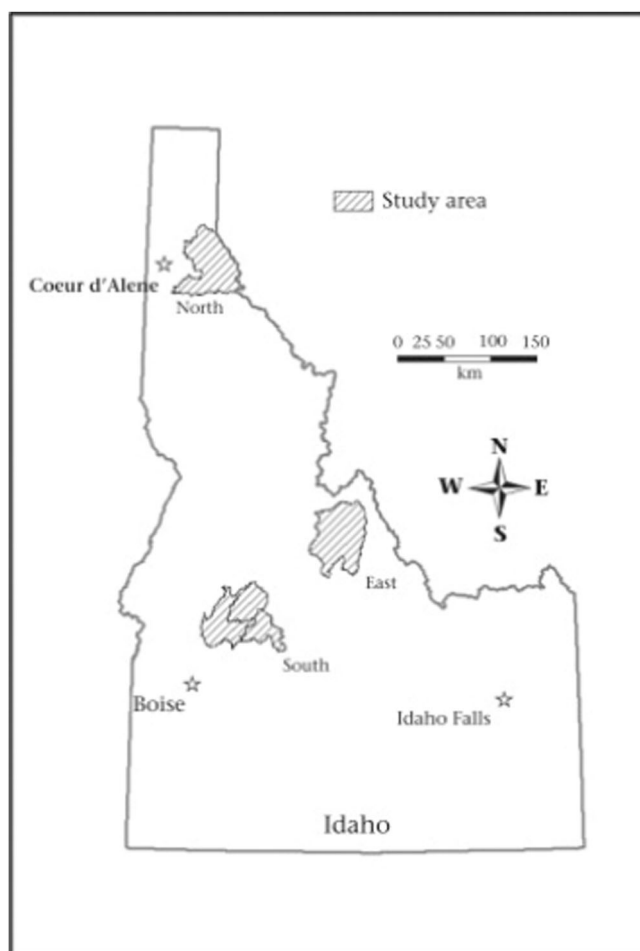


FIGURE 1 Long-term gray wolf study areas in Idaho, USA, used to assess the expected proportions of wolves in harvest, 2009–2018.

METHODS

Field methods

To obtain scat samples and generate genotypes that could be used to estimate the expected proportion of each age class in the harvest, each year (2009–2018), 6 technicians surveyed for the same 10–18 wolf packs residing across 3 study areas. We surveyed for wolves using a predicted habitat model and sampled wolf packs genetically using noninvasive methods developed since 2007. Briefly, each year we collected scats for genetic analysis at active rendezvous sites of the same reproductively active wolf groups between June–August. In these areas, technicians surveyed historical and highly suitable rendezvous sites predicted by a habitat model (Ausband et al. 2010). This model used the normalized difference vegetation index (greenness), roughness, and curvature to predict areas that are highly likely ($\geq 70\%$ suitability) to be rendezvous sites. We located active rendezvous sites during surveys by giving a series of howls and triangulating the location of the pack through call and response, or by following wolf track and sign (Ausband et al. 2010). Once we located the rendezvous site, we attempted to find an activity center (area where pups congregate) by backtracking wolf sign (tracks, scat, hair, chew toys; Harrington and Mech 1982).

After we found the activity center, 4–8 technicians collected wolf scats (pup and adult) for 3–5 hours and searched radiating out from the activity center on existing wolf trails up to 500 m to ensure we collected a sufficient sample of adult scats. Technicians typically gathered 125–200 samples (~60% adult samples, ~40% pup), which generally detected every individual in the group (Stenglein et al. 2011). We considered scat samples >2.5 cm in diameter to be from adult wolves (Weaver and Fritts 1979) and those <2.5 cm to be from wolf pups. We attempted to locate and resample each group annually, which allowed us to age individuals as they were detected in repeat sampling in later years (Ausband et al. 2010, Stenglein et al. 2010, Stenglein et al. 2011). Refer to Ausband et al. (2010) for more detailed information on field procedures.

We used genotypes from tissue samples from harvested wolves and cementum ages from teeth to calculate the observed number of wolves harvested by age class. During harvest seasons 2009–2010 and 2011–2018, IDFG personnel collected tissue samples and tooth samples during mandatory check-in of harvested wolves from across the state of Idaho. Tooth samples collected by IDFG personnel were sent to Matson's Laboratory (Manhattan, MT, USA) for cementum analysis to age harvested wolves. Personnel from IDFG also recorded sex, date of harvest, means of take, location, and animal condition, and affixed a pelt tag to the animal hide. Data on sampled wolves were recorded by IDFG personnel, and we separated them based on harvest year, harvest month, and age.

Laboratory methods scat and tissue

We extracted DNA from scat samples using Qiagen kits (Qiagen, Valencia, CA, USA) in a facility dedicated to low-quality DNA at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (LEECG) in Moscow, Idaho. For every set of scat samples, we used negative controls to monitor for contamination. We used 9 microsatellite loci and sex identification primers to identify individuals and sex (Stansbury et al. 2014). To verify matches or mismatches, we generated 9 additional microsatellite loci on the best sample from each unique individual (18 loci: AHT103, AHT109, AHT121, AHT200, CO5.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725) and samples that differed at only 1 locus out of the original 9 loci (Stansbury et al. 2014, Clendenin et al. 2019). We assigned each unique individual a unique wolf ID number. We used a capillary machine (3130xl; Applied Biosystems, Foster City, CA, USA) to separate polymerase chain reaction (PCR) products; we conducted a minimum of 2 independent amplifications for a consensus of a heterozygote and at least 3 amplifications for a consensus of a homozygote at each locus. We included a positive and negative control for each PCR amplification. We analyzed 40 adult and 25 pup scats from each pack; if a group had >2 individuals detected only once, we analyzed additional samples to obtain 10 more consensus genotypes (if additional samples were available). For additional details on laboratory methods, refer to Stenglein et al. (2010, 2011) and Stansbury et al. (2014).

For tissue samples, we assigned each individual 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. Additional details on laboratory methods are provided by Stenglein et al. (2010, 2011), Stansbury et al. (2014), and Clendenin et al. (2019).

Analysis

After each summer rendezvous site sampling season, we genotyped the scats from each pack's rendezvous site that we located in that biological year. We calculated the cumulative probability of identity based on siblings in GenAIX version 6.2 (Peakall and Smouse 2012). Once we obtained consensus genotypes at 18 loci, we imported them into COLONY (Jones and Wang 2010) to calculate allele frequencies and run pedigree analyses. After importing allele frequencies and genotypes for each individual, 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 pedigrees

using maximum likelihood. When parentage was undetermined from COLONY, we further examined offspring genotypes against the likely parents of the remaining offspring in the group to allow for a 2-allele mismatch owing to allelic dropout between parent and offspring to verify parentage across the 18 loci (Allendorf et al. 2013). From the resulting pedigrees we estimated the number of individuals in each age class for each group (1-year-old female, ≥2-year-old female, 1-year-old male, ≥2-year-old male, unknown age females, unknown age males, female pups, male pups).

We used 9 years of harvest data collected by IDFG personnel (harvest date, tissue samples, and tooth samples; 2009–2018) from gray wolves harvested throughout the state of Idaho. The number of wolves harvested annually differed between 2009–2010 ($n = 65\text{--}200$) and 2012–2018 ($n = 262\text{--}362$) because of seasonal quotas set by IDFG. We did not have harvest DNA that matched with previously collected scat DNA (i.e., recaptures) for every year, but from 2013–2018 the recapture rate of wolves sampled via scat in summer who were later detected in harvest DNA samples was 0.15 ($n = 479$ scat-sampled wolves). For each year, we separated harvested individuals by age class (pups, yearlings, and sexually mature adults ≥2 years old) and month, then calculated the number observed in harvest for each age class. We removed from analysis individual wolves that were harvested illegally or lethally removed from the population by a management agency for predator control.

We used pack pedigrees from the genetic data collected from reproductive wolf packs' scat samples in summers 2009–2018 to calculate the expected number of individuals of age classes in the harvest (Figure 2). We genotyped 955 individual wolf-years representing 501 unique individuals through scat collection and pedigree analyses. New individuals (i.e., adoptees) were uncommon; of those 955 individual wolf-year genotypes, there were 10% ($n = 103$) where the age was unknown. To obtain the expected number, we first separated pack pedigree data by year and pack and totaled the individuals for each age cohort (e.g., number of 1-year-old wolves). If the age of an individual was unknown (because of newly sampled adult individuals in a pack or newly sampled packs), we estimated their age using the existing proportion of adult age and sex in that year's population. We multiplied the proportion of individuals in each age class from the pack pedigrees by the number of harvested wolves that year

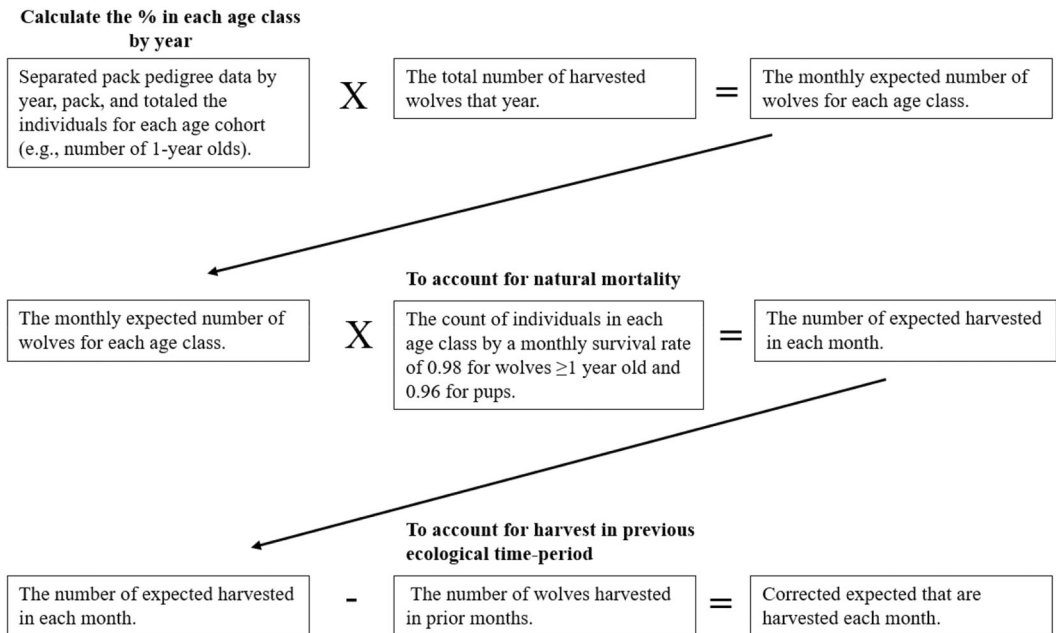


FIGURE 2 Description of how the scat collected from wolf rendezvous sites are used to calculate the expected number of wolves harvested each month in Idaho, USA.

to generate the monthly expected number of wolves for each age class. We multiplied the resulting count of individuals in each age class by a monthly survival rate of 0.98 for wolves ≥ 1 year old (Smith et al. 2010) and 0.96 for pups (Ausband et al. 2015, Ausband 2016) to account for natural mortality for each month prior to the biological period of interest. Additionally, we subtracted all harvested individuals from the months prior to the biological period of interest to get the corrected expected value for each age class in every month.

Using the age cohorts created from harvest data on cause-specific mortality, time of harvest, and age (tooth samples), we were able to compare the expected to the observed number in each biological period and determine whether an age class was disproportionately harvested. We used a chi-square test of independence in Program R (R Core Team 2020) to individually compare the number of expected versus number of observed for each class in each month's harvest during biologically significant periods: breeding (January-February), peak dispersal (December), and when the group is mobile after pup-rearing (September–October). For example, we compared the number of observed adult wolves harvested in January-February 2014 to the number of expected adult wolves harvested in January-February 2014, predicting that the ratio of observed:expected was approximately 1:1 if there was no statistical difference between observed and expected harvest. Because this generated many tests for each age class across years and seasons, we used a Bonferroni correction based on the number of tests run per age class (adult tests: $n = 19$, Bonferroni corrected alpha = 0.0026; yearling tests: $n = 10$, Bonferroni corrected alpha = 0.005; pup tests: $n = 20$, Bonferroni corrected alpha = 0.0025) to adjust our P -value and account for multiple significance tests over time. We considered to have strong evidence that the expected and observed number of wolves were different when P was less than or equal to the adjusted alpha and used this measure of significance for each age class during each year and for the total of all years in which harvest took place during biologically significant periods (2009, 2011–2018).

RESULTS

Of the 44 possible comparisons of biologically significant periods, we documented 5 instances (11.4%) where wolves were harvested more than expected: 3 times (6.8%) for wolves ≥ 2 years, once for yearlings (2.3%), and once for pups (2.3%; Table 2). In January-February of 2015 and December of 2009 and 2011, the number of adults observed in the harvest was higher than expected ($P < 0.0026$). Additionally, there was evidence ($P < 0.0029$) of a difference between the 10-year corrected expected value ($n = 153$) for wolves ≥ 2 years old harvested during breeding season compared to the observed ($n = 210$; Table 2). Wolves ≥ 2 years old were harvested as expected during peak dispersal (December) with all years combined (Table 2).

Pups were harvested more than expected during 2011 and with all years combined during December ($P < 0.0001$), which is the start of trapping season. Although statistical analysis did not support a difference for any other year–period combinations, the observed pup harvest was greater than the expected pup harvest in 7 of the 9 years during the September to October period and during peak dispersal (December), the most of any age class.

There was one year (2017) with a significant association between yearling vulnerability and the start of the harvest season between September and October ($P = 0.0036$). Yearlings were harvested more than expected in 5 years (2009, 2011, 2014, 2017) between September and October, but this was not statistically significant after accounting for Bonferroni correction (Table 2).

DISCUSSION

We found that wolf vulnerability to harvest was associated with age class and whether harvest occurred during biologically significant periods for wolves. Pups, in particular, were more vulnerable to harvest at the start of the trapping season in December. This supports our hypothesis on pups' naivety to attractions associated with trapping

TABLE 2 Results for the number of wolves harvested (observed) and expected (from summer scat sampling) by age class during biologically significant periods in Idaho, USA, 2009–2018. The NA indicates that there was no public harvest season set for wolves across the state, some individual wolves were harvested because of conflict with livestock. The values with an asterisk indicate significant relationships after adjusting the alpha level with a Bonferroni correction based on the number of tests run per age class (adults adjusted Bonferroni alpha = 0.0026, juveniles adjusted Bonferroni alpha = 0.005, pups adjusted Bonferroni alpha = 0.0025).

Age class	Season	Parameters	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	All Years
Adult	Jan-Feb	Chi square	NA	0.16	NA	1.49	4.6	0.9	24.16	5.44	0.6	0.02	8.82
		df	NA	1	NA	1	1	1	1	1	1	1	1
	Dec	P	NA	0.6918	NA	0.2214	0.0320	0.3417	≤0.0001*	0.0196	0.4382	0.8837	0.0029
		Observed	NA	10	NA	58	29	31	25	24	15	18	210
Adult	Dec	Expected	NA	8	NA	46	47	39	0	10	19	19	153
		Chi square	9.07	NA	18.14	2.28	0.8	0.85	1.97	0.44	0.93	0.14	1.98
	df	1	NA	1	1	1	1	1	1	1	1	1	1
	P	0.0026*	NA	≤0.0001*	0.1311	0.3721	0.3571	0.1604	0.5055	0.3339	0.7062	0.1597	
Yearling	Sep-Oct	Observed	9	NA	18	13	16	13	12	11	17	9	118
		Expected	0	NA	0	22	21	18	6	8	12	10	98
	Sep-Oct	Chi square	6.51	NA	0.58	1.88	2.27	4.95	4.42	1.2	8.47	0.26	1.8
		df	1	NA	1	1	1	1	1	1	1	1	1
Pup	Sep-Oct	P	0.0107	NA	0.4474	0.1700	0.1320	0.0261	0.0355	0.2724	0.0036*	0.6089	0.1794
		Observed	22	NA	21	24	15	18	6	17	29	29	182
	Sep-Oct	Expected	8	NA	17	16	24	7	15	24	11	34	157
		Chi square	1.45	NA	2.44	5.49	1.37	0.22	0.84	0.31	0	1.73	1.02
Pup	Sep-Oct	df	1	NA	1	1	1	1	1	1	1	1	1
		P	0.2278	NA	0.1180	0.0191	0.2412	0.6408	0.3597	0.5798	0.9489	0.1890	0.3121
	Sep-Oct	Observed	24	NA	36	22	46	31	47	35	40	47	327
		Expected	16	NA	24	40	35	35	39	30	39	35	302

(Continues)

TABLE 2 (Continued)

Age class	Season	Parameters	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	All Years
Pup	Dec	Chi square	3.09	NA	16.35	0.22	7.82	2.39	0.27	2.8	2.51	8.97	23.07
		df	1	NA	1	1	1	1	1	1	1	1	1
		P	0.0785	NA	≤0.0001*	0.6410	0.0051	0.1223	0.6061	0.0942	0.1133	0.0027	≤0.0001*
		Observed	10	NA	26	17	29	25	10	19	26	29	190
		Expected	4	NA	4	20	11	15	12	10	16	10	107

such as lures and physical objects used to draw animals to traps. However, results for most age classes were highly variable across the 9 years and may depend on annual variation in hunter effort, changes in harvest regulations, and perhaps even wolf litter size. Additionally, harvesting one or multiple individuals from a group during one significant period may indirectly affect vulnerability of others within that group during another period. Wolf behavior is often influenced by their sociality, and the direct and indirect effects of removing individuals from a group may disrupt their complex hierarchies during these biologically important periods and decisions that individuals make throughout the year (Clutton-Brock 2006, Ausband et al. 2017). Some packs are likely more accessible to hunters and trappers than others and mortality risk is not equal across the state. We used a statewide approach, however, and were unable to address spatial variability of hunting and trapping because we did not have location data from hunters and trappers (i.e., we had location data for kills, but not effort).

Our hypothesis that wolves ≥ 2 years old would be more vulnerable between January and February was not supported; however, there is some evidence that adult wolves are more vulnerable to hunting and trapping during the breeding season. Results from 2015 supported our hypothesis and across all years there was weak evidence for a relationship, with a *P*-value just slightly above the Bonferroni-corrected cutoff. Of the 3 different age classes considered, wolves ≥ 2 years old comprised the highest number of wolves harvested between January and February across all 9 years. This suggests that these numbers reflect the number of sexually mature wolves harvested but not the number of individuals actively expressing breeding behaviors and responding to hunter-induced stimuli. Little is known of reproductive suppression within our study area (Ausband 2022), and constraints on breeding by subordinates that are sexually mature may affect how individuals are actively participating in breeding during this time. Identifying the number of breeders in the annual harvest (Rebholz et al. 2024) may better predict how hunting and trapping stimuli during breeding season can affect their vulnerability.

Contrary to our hypothesis, wolves ≥ 2 years old were not more vulnerable to harvest during December when trapping season begins and dispersal is high. This trend was true for all subsequent years following 2011, but results from 2009 and 2011 supported our hypothesis, perhaps because the resident wolf population had not been previously exposed to annual harvest. During 2009, wolf populations were at their greatest (Bangs and Fritts 1996, Ausband et al. 2017) following their reintroduction into Idaho in 1995–1996 (Bangs and Fritts 1996) and annual statewide harvest seasons provided hunters with a large population of wolves that may have been unaccustomed to being hunted. Our results show that vulnerability of all wolves ≥ 2 years old was not influenced by the transition from opportunistic hunting into trapping during peak dispersal season; however, not all wolves harvested during that period would have been dispersing individuals. Wolves in the Rocky Mountains in the United States are reproductively mature at 22 months and typically do not disperse from the natal group until 3 years of age (although some have been recorded dispersing as early as 12 months; Jimenez et al. 2017). Typically, males choose to disperse between late fall and the start of the breeding season (mid-February) in search of a breeding position within another group but more commonly create their own pack in populations where vacant habitat exists (Mech and Boitani 2003). Female wolves are generally more philopatric and more likely than males to replace breeders within their natal packs (Ausband 2022). Our analysis grouped both male and female wolves ≥ 2 years old and may have missed the more common sex of dispersing wolves during this time. Future studies may better isolate dispersal behaviors by individual age classes by refining the scope to males ages 2–4.

Our hypothesis that pups and yearlings would be more vulnerable between September and October after they leave the summer rendezvous sites was not supported. However, our hypothesis that pups would be more vulnerable in December because they would be more naïve to dangers presented by hunters at the start of trapping season was supported. We found considerable variation in harvest vulnerability among years suggesting that there is still a gap in knowledge in what is causing some age classes to be disproportionately represented in the harvest. Litter size variation is unknown throughout much of Idaho but could be a driving factor for why we found variation among years. For example, using our observed versus expected approach, we would have surmised pups were harvested less than expected if there was a year of low pup production. Pair bond duration has been shown (Ausband 2019) to affect pup recruitment as well. Pups in a group with long-duration pair bonds may be less

vulnerable to harvest in these months because more experienced pairs will better be able to teach their offspring to avoid dangers associated with hunting and trapping.

Overall, harvest seemed to be opportunistic but there were year–period combinations for each age class where we found wolves were harvested more than expected. This finding suggests there is still much to learn about seasonal variation in wolf behavior and what management actions most strongly affect wolf vulnerability to harvest during those ecologically significant periods. The approach we used could benefit future studies with the goal of identifying how interannual variation affects groups of wolves. Additionally, this work can help determine thresholds where managers can manipulate harvest seasons to better isolate groups of wolves to avoid or target for harvest depending on management goals.

MANAGEMENT IMPLICATIONS

Pups are more vulnerable to harvest in December when wolf harvest transitions largely to trapping; thus, managers who are concerned about the potential negative effects of harvest on recruitment could craft their trapping seasons to avoid or be shorter during this period. Additionally, managers concerned about over-harvesting adults could consider lowering harvest during January and February when adults are slightly more vulnerable to harvest.

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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 used in this manuscript are available in Table 2.

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