

Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore

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Abstract

1. Breeder turnover can influence population growth in social carnivores through changes to group size, composition and recruitment.
2. Studies that possess detailed group composition data that can provide insights about the effects of breeder turnover on groups have generally been conducted on species that are not subject to recurrent annual human harvest. We wanted to know how breeder turnover affects group composition and how harvest, in turn, affects breeder turnover in cooperatively breeding grey wolves (*Canis lupus* Linnaeus 1758).
3. We used noninvasive genetic sampling at wolf rendezvous sites to construct pedigrees and estimate recruitment in groups of wolves before and after harvest in Idaho, USA.
4. Turnover of breeding females increased polygamy and potential recruits per group by providing breeding opportunities for subordinates although resultant group size was unaffected 1 year after the turnover. Breeder turnover had no effect on the number of nonbreeding helpers per group. After breeding male turnover, fewer female pups were recruited in the new males' litters. Harvest had no effect on the frequency of breeder turnover.
5. We found that breeder turnover led to shifts in the reproductive hierarchies within groups and the resulting changes to group composition were quite variable and depended on the sex of the breeder lost. We hypothesize that nonbreeding females direct help away from non-kin female pups to preserve future breeding opportunities for themselves. Breeder turnover had marked effects on the breeding opportunities of subordinates and the number and sex ratios of subsequent litters of pups. Seemingly subtle changes to groups, such as the loss of one individual, can greatly affect group composition, genetic content, and short-term population growth when the individual lost is a breeder.

KEYWORDS

breeder, *Canis lupus*, cooperative breeding, grey wolves, group size, helping, recruitment, social carnivore

1 | INTRODUCTION

Animals that live in groups and breed cooperatively can be affected by changes to group composition (i.e. number of individuals in different sex and age classes). Some changes to group composition may appear subtle, but the effects on remaining group members can be marked. For example, reproductively prime-aged females had low reproductive rates in groups of African elephants (*Loxodonta africana*) that had lost older females due to poaching (Gobush, Mutayoba, & Wasser, 2008). Additionally, female reproductive success was higher in groups of red howler monkeys (*Alouatta seniculus*) with fewer adoptees and higher genetic relatedness among members (Pope, 2000). Breeder turnover, particularly in groups of social carnivores that rely on experienced individuals and their familiarity and defence of resources within a territory, can yield diminished reproductive output, lowered group persistence and population growth (Borg, Brainerd, Meier, & Prugh, 2015; Brainerd et al., 2008; Gobush et al., 2008; Whitman, Starfield, Quadling, & Packer, 2004).

In addition to its effects on reproduction and population growth, breeder turnover can also affect group composition. Because breeding opportunities in many social carnivores are constrained by social hierarchies, breeder turnover can lead to dynamics among subordinates competing for vacant breeding positions. Experimental removals of breeders in cichlid fish (*Neolamprologus pulcher*) demonstrated that subordinate females typically inherited the vacant breeding position in their natal groups, whereas male vacancies were filled by immigrants (Stiver, Fitzpatrick, Desjardins, & Balshine, 2006). Such vacancies can lead to intragroup aggression and increased dispersal among subordinate group members seeking to improve their status in the social hierarchy and eventually breed (Sillero-Zubiri, Marino, Gottelli, & MacDonald, 2004; Stiver et al., 2006). A limited supply of breeding opportunities and high-quality territories within a population can lead to a polygyny threshold (Orians, 1969), where females choose polygamy over dispersing and breeding with another male on perhaps a lower quality territory. Age, sex and genetic relatedness to the new breeder are several additional factors that can influence resultant group composition after breeder turnover. The behaviour of new breeders can also influence whether subordinate members stay or leave. New breeders may attempt to retain sex and age classes of helpers that contribute strongly or that could eventually be mates (Kutsukake & Clutton-Brock, 2008; Loveridge, Hemson, Davidson, & MacDonald, 2010). Predictions arising from group augmentation theory (Kokko, Johnstone, & Clutton-Brock, 2001) would suggest that breeders and relatively philopatric helpers (e.g. female wolves) strive to maintain a large group size. Additionally, the 'helper repayment hypothesis' would suggest that individuals will help rear young that are more likely to reciprocate such help in the future (Emlen, Emlen, & Levin, 1986; Gowaty & Lennartz, 1985). In contrast, new breeders may try to expel unrelated individuals, particularly those of the same sex that might compete for breeding opportunities and resources. Dispersal decisions from the group could be a result of aggression by new breeders or simply decisions by subordinates to leave and attempt to breed elsewhere rather than staying to help rear non-kin young (Young et al., 2006).

Although some studies have documented the effects of breeder turnover on group size and reproduction in social carnivores (Borg et al., 2015; Brainerd et al., 2008; Loveridge et al., 2010), many studies lack the detailed data regarding the sex and age of nonbreeding members needed to understand group dynamics following a turnover. Although inferences about the effects of breeder turnover on group composition can be made from some exemplary long-term studies of social carnivores (Clutton-Brock & Manser, 2016; Clutton-Brock et al., 1998, 2001), such insights are limited to just a few species.

In social carnivores, human-caused mortality can negatively affect groups by reducing group size and increasing breeder turnover (Wallach, Ritchie, Read, & O'Neill, 2009; Whitman et al., 2004). For example, hunted populations of African lions (*Panthera leo*) exhibit increased rates of breeding male turnover and infanticide by newly adopted males can reduce population growth and increase extinction risk (Whitman et al., 2004). Human-caused mortality in African wild dog (*Lycaon pictus*) populations has also been identified as a major factor limiting population growth and recovery in many areas across the species' range (Woodroffe, 2011; Woodroffe et al., 2007). At reduced group sizes, African wild dogs exhibit decreased recruitment because of an inability to adequately guard young from predation while also securing food (Courchamp, Rasmussen, & MacDonald, 2002). Despite the influence that human-caused mortality can have on populations of social carnivores, studies that possess detailed data on the sex and age of individuals within groups have generally been conducted on species that are not subject to recurrent annual human harvest (Kutsukake & Clutton-Brock, 2008; Young et al., 2006). Thus, we do not know how breeder turnover and harvest might interact to affect group composition and recruitment in social carnivores.

Grey wolves (*Canis lupus*) live in groups (i.e. packs) and cooperatively breed. Generally, young will delay dispersal for 2–3 years and help rear young of the breeders in the group. Helping during the pup-rearing season typically involves providing food and guarding pups at den and rendezvous sites (i.e. locations where group members congregate for several weeks; Ausband et al., 2016; Packard, 2003). Recent changes in population status and management led to the initiation of a harvest season via rifle hunting and trapping beginning in 2009 in Idaho, USA (Ausband, 2016). Such a shift in management, from protected under the Endangered Species Act to harvested annually, provided an opportunity for a natural experiment. Using genetic sampling before and after harvest, we examined how breeder turnover affected group composition and how harvest, in turn, affected breeder turnover. We hypothesized that breeder turnover would be associated with short-term (<1 year) increases in group size due to polygamy within groups either because a new, unrelated male joined the group and bred multiple females or a new breeding female joined that would not be able to successfully deter reproductive behaviour of subordinate females. We further hypothesized that after turnover of a breeding male or female there would, through increased dispersal, be fewer mature (≥ 2 years) nonbreeding helpers and fewer pups of the same sex because the new breeders would want to exclude

subordinates from breeding opportunities in the group. Lastly, we hypothesized that harvest would be associated with an increase in the frequency of breeder turnover and would positively influence the number of breeders in a group. Newly adopted individuals would be unrelated to existing group members and inbreeding avoidance (Packard, 2003) would no longer constrain breeding between some individuals in the group.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in Idaho, USA. From 2008 to 2015, we genetically censused 8–10 wolf groups annually in Game Management Units (GMUs) 28 (3,388 km²), 33, 34 and 35 (three neighbouring GMUs total 3,861 km²) in central Idaho. Idaho is mountainous and dominated by a mix of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and spruce (*Picea engelmannii*) forests and sagebrush (*Artemisia tridentata*) steppe. Annual precipitation ranges from 89 to 178 cm and temperatures range from –34°C in winter to 38°C in summer (Western Regional Climate Center, 2014). Public harvest of wolves began in Idaho in 2009, temporarily ceased in 2010 and began again in 2011 (Ausband, 2016). Most harvest occurs during September–March with a peak during the big-game rifle hunting season. Annual population harvest rates in our Idaho study areas averaged 24% (Ausband, Stansbury, Stenglein, Struthers, & Waits, 2015). Control actions to address livestock depredations were rare in our study groups, accounting for five animals over the course of our study.

2.2 | Field methods

We collected scats for genetic analysis at rendezvous sites of reproductively active wolf groups. When available, we used radiotelemetry locations of wolves to locate rendezvous sites. In areas that did not contain radiocollared wolves, we surveyed at historic and highly suitable (≥70%) rendezvous sites predicted by a habitat model (Ausband et al., 2010). Technicians typically gathered 125–200 samples per group per year and attempted to locate and resample each group every year. Detailed methods and field protocols can be found in Ausband et al. (2010), Stenglein, De Barba, Ausband, and Waits (2010), Stenglein, Waits, Ausband, Zager, and Mack (2010, 2011), and Stansbury et al. (2014).

2.3 | Laboratory methods

DNA analyses were performed at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, ID). We used nine nuclear DNA microsatellite loci and sex identification primers to identify individuals and gender (Stansbury et al., 2014). We generated genotypes at an additional nine microsatellite loci on the best sample for each unique individual (i.e. total = 18 loci) and for samples that differed at only one locus out

of initial nine loci to verify matches or mismatches (Stansbury et al., 2014; Stenglein et al., 2011). For each locus, we required ≥2 independent PCR amplifications for consensus of a heterozygote and ≥3 independent PCR amplifications for consensus of a homozygote. In 2008 and 2009, we analysed all collected samples. After 2010, we analysed 40 adult and 25 pup scats from each pack based in part on rarefaction results regarding sampling effort (Stenglein et al., 2011). We analysed additional samples to obtain 10 more consensus genotypes if a pack had >2 individuals detected only once and additional collected samples were available. Further details regarding laboratory methods used 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 | Analysis methods—Pedigrees

For each year, we included all sampled adult males and females as potential parents and all sampled pups as potential offspring and then determined breeders and their offspring by constructing pedigrees using maximum-likelihood in Program COLONY version 2.0.5.5 (Jones & Wang, 2009). We calculated allele frequencies for each year in Program COANCESTRY version 1.0.1.5 (Wang, 2011) and then imported those into Program COLONY for use in pedigree analyses. We allowed for polygamy in both males and females and assumed an allelic dropout rate of 0.01. In cases where parentage was undetermined from COLONY, we further examined offspring genotypes against the likely parents of the remaining offspring in the group and allowed for a two allele mismatch owing to allelic dropout between parent and offspring to verify parentage across the 18 loci using exclusion methods (Allendorf, Luikart, & Aitken, 2013).

We sampled the same groups of wolves across consecutive years and from the resulting pedigrees, estimated for each sex the number of breeders, 1-year-old nonbreeders, ≥2-year-old nonbreeders, pups, pups alive at 15 months and adult individuals of unknown age. We documented breeder turnover (i.e. loss of a breeding position through death, expulsion or usurpation) between years and estimated the number of adults present in the group when pups were 3 months and 15 months old (Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vc6p9>). The timing of breeder turnover can affect whether a group can replace and recover from such losses before the next breeding season (Brainerd et al., 2008). While such timing data were available for some of our sampled wolves, they were not available for all breeder turnover events and we could not include timing of turnover in our analyses. Ages of pups were approximate assuming an average birthdate of 15 April and an average sampling date of 15 July (age = 3 months) with an average of 362 days until subsequent sampling (age = 15 months; Ausband et al., 2015). We defined adults as any non-pup individual (i.e. helpers; nonbreeding females and males, and breeders). For each sampled pup, we determined whether they were alive or dead 15 months after birth. Fewer than 4% of wolves disperse within their first year in our study population (Jimenez et al., 2017) and we assumed absence

at 15 months meant death. We note that we examined genotypes of harvested wolves throughout the state in the event wolves dispersed early and were harvested (no pups, early dispersers, were discovered this way).

2.5 | Analysis methods—Predictive models

We used generalized linear mixed effects models (GLMM) to examine the influence of breeder turnover on group composition and to explore the subsequent effects of harvest on breeder turnover. Models included breeder turnover (by sex, male and female) as an explanatory

TABLE 1 Results from mixed effects models addressing questions (Q) about the effects of breeder turnover on group composition in grey wolves, Idaho, USA (2008–2015). Bold indicates influential variables where 90% confidence intervals (CI) of odds ratios did not overlap 1.0

Variable	Coefficient	Odds ratio (90% CI)	<i>n</i>
Q: Does breeder turnover increase the number of pups per group?			
Breeding Female turnover	1.37	3.95 (1.81–28.48)	43
Breeding Male turnover	-0.62	0.56 (0.15–2.50)	43
Q: Are there multiple breeding females per group after breeding female turnover?			
Breeding Female turnover	0.54	1.71 (1.35–2.18)	43
Q: Are there short-term increases in group size due to polygamy after breeding female turnover?			
Breeding Female turnover	0.03	1.03 (0.20–6.89)	43
Q: Are there fewer mature nonbreeding male helpers after breeding male turnover?			
Breeding Male turnover	0.27	1.31 (0.66–2.62)	43
Q: Are there fewer mature nonbreeding female helpers after breeding male turnover?			
Breeding Male turnover	0.46	1.59 (0.81–3.20)	43
Q: Are there fewer male pups recruited after breeding male turnover?			
Breeding Male turnover	-0.46	0.63 (0.28–1.43)	105
Q: Are there fewer female pups recruited after breeding male turnover?			
Breeding Male turnover	-1.36	0.26 (0.11–0.60)	102
Q: Are there fewer mature nonbreeding female helpers after breeding female turnover?			
Breeding Female turnover	-0.19	0.83 (0.40–1.73)	43
Q: Are there fewer mature nonbreeding male helpers after breeding female turnover?			
Breeding Female turnover	0.32	1.38 (0.67–2.80)	43
Q: Are there fewer female pups recruited after breeding female turnover?			
Breeding Female turnover	0.03	1.03 (0.47–2.30)	102
Q: Are there fewer male pups recruited after breeding female turnover?			
Breeding Female turnover	0.79	2.20 (0.97–5.31)	105

variable but had different response variables (number of breeders, recruits, mature nonbreeding males and females, rate of breeder turnover and group size) depending on the question being asked (Table 1). We included random effects for pack and year in each model. For response variables that were binary (e.g. breeding female turnover, pup alive at 15 months), we used GLMM with a binomial distribution and a logit link function.

To test whether harvest affected breeder turnover, we also used GLMM models with a binomial distribution and a logit link function. Harvest (binary = present, absent) was an explanatory variable for either breeding male or female turnover as well as the number of breeders per group. We used the `LME4` and `GLMM` packages in Program R (Version 3.3.0, R Core Team 2016) for our analyses. We considered variables influential when the 90% CI of their predicted odds ratios ($OR = e^{\beta}$) did not overlap 1.0.

3 | RESULTS

All study packs experienced harvest of ≥ 2 individuals (range = 0–9 annually). The peak number of individuals harvested occurred during the 2011–2012 season (Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vc6p9>). Turnover of breeding females, but not breeding males, was associated with an increased number of pups per group during the parturition period following turnover ($OR = 3.95$; 1.81 – 28.48 , 90% CI; Table 1). The increased number of potential recruits (i.e. number of young born per group) was associated with an increased number of breeding females per group during the parturition period following breeding female turnover ($OR = 1.71$; 1.35 – 2.18 , 90% CI; Table 1). However, breeding female turnover did not predict group size 1 year later (Table 1). The number of mature nonbreeding helpers per group was unaffected by breeder turnover (Table 1). The lack of an association between breeder turnover and the number of mature nonbreeding helpers remained even for cases where the new breeder was an unrelated adoptee ($OR = 0.46$, 0.14 – 1.46 , 90% CI for predicting number of nonbreeding females; $OR = 0.50$, 0.18 – 1.37 , 90% CI for predicting number of nonbreeding males). Turnover of breeding males, however, led to a decline in the number of female pups ($OR = 0.26$; 0.11 – 0.60 , 90% CI; Table 1) but not male pups recruited during the following parturition period. There was no difference in the number of male and female pups recruited during the parturition period after breeding female turnover. For groups that experienced breeding male turnover and a reduction in the number of female recruits (i.e. number survived to 15 months old) under the new male, sex ratios in subsequent years were not female-biased to compensate for such losses (potential recruits = 22 females:27 males; recruited = 13 females:18 males).

Average group size declined from 9.2 adults ($SE = 0.97$) before harvest to 5.2 adults ($SE = 0.46$) at the end of our study (Figure 1). Harvest, however, was not associated with an increase in the frequency of breeder turnover nor did the number of breeders per group increase in years after harvest (Table 2).

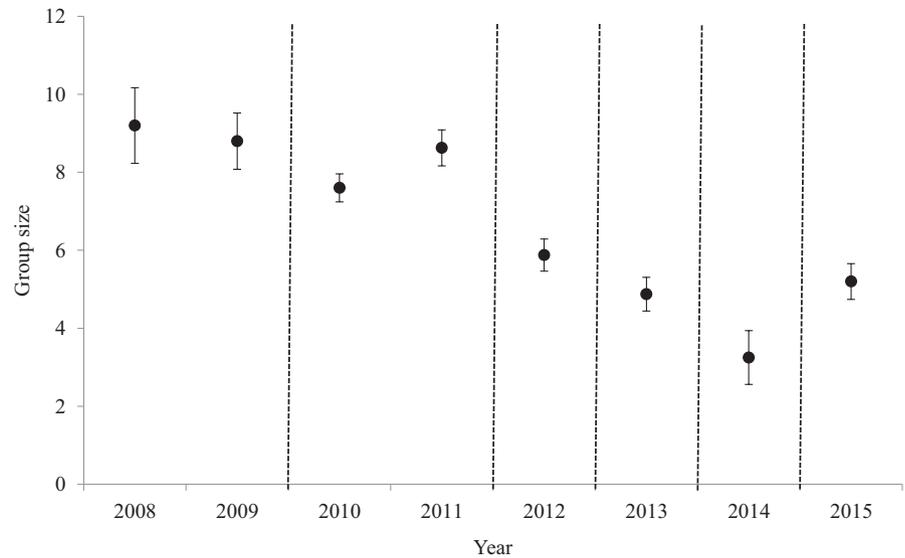


FIGURE 1 Mean number of adults for study groups of grey wolves in Idaho, USA (2008–2015). Dashed lines indicate when harvest occurred. There was no harvest prior to 2009. Error bars represent the SE

TABLE 2 Results from mixed effects models addressing questions (Q) about the effects of harvest on breeder turnover in grey wolves, Idaho, USA (2008–2015)

Variable	Coefficient	Odds ratio (90% CI)	n
Q: Does the frequency of breeding female turnover increase after harvest?			
After harvest	-0.06	0.94 (0.32–2.83)	43
Q: Does the frequency of breeding male turnover increase after harvest?			
After harvest	-0.25	0.78 (0.26–2.37)	43
Q: Does the number of breeders per group increase after harvest?			
After harvest	-0.10	0.90 (0.68–1.20)	44

4 | DISCUSSION

Breeder turnover had marked effects on the breeding opportunities of subordinates and the number and sex ratios of subsequent litters of pups. Breeder turnover led to shifts in the reproductive hierarchies within groups and the resulting changes to group composition were highly variable and depended on the sex of the breeder lost. Harvest, however, had no effect on the frequency of breeder turnover. This suggests that even in unharvested wolf populations, breeder turnover is common.

Our hypothesis that breeder turnover would be associated with short-term (<1 year) increases in group size due to polygamy was supported. In years when there was breeding female turnover, multiple females reproduced and the number of potential recruits born into groups increased during the subsequent parturition period. Our finding suggests there is a polygyny threshold (Orians, 1969) in grey wolves where females choose polygamy over dispersal but only when behavioural constraints (i.e. reproductive suppression) are removed. The availability of multiple reproductive females is in part a function

of group size and we would not expect small groups to always exhibit similar patterns of polygamy. Increases to group size from polygamy were short-lived, however, because group size was unaffected 1 year following breeder turnover. We do not know the mechanism behind the apparent short duration of boosts in group size but posit it may relate to food availability and competition among pack members for limited resources. Turnover of breeding males was not associated with increases in polygamy suggesting that in groups of grey wolves breeding opportunities are regulated by the breeding female. Breeding female meerkats (*Suricata suricatta*), for example, can monopolize reproduction in groups by behaving aggressively to subordinate females that are most likely to breed (Young et al., 2006). In some species, infanticide by breeders can negate reproduction by subordinates (Clutton-Brock et al., 1998). If subordinate females in wolf groups are all simply sexually immature, we should have found no evidence for increased polygamy after breeding female turnover. We did find an increase in polygamy after breeding female turnover, however, and it appears that sexually mature subordinates (not all are sexually mature) are actively discouraged from breeding by dominant breeding females. Physiological constraints on breeding by subordinates are unlikely in grey wolves (Packard, 2003) but the mechanism (i.e. direct behavioural interference, infanticide) by which reproductive suppression occurs in our study areas is unknown.

Our hypothesis that new breeders would decrease the number of same-sex nonbreeders in the group was not supported. This remained true even when the new breeder was an unrelated adoptee. This finding is consistent with group augmentation theory (Kokko et al., 2001) where breeders strive to maintain a large group size even if the individuals in the group are unrelated to them. Group size in many social carnivores such as grey wolves can positively influence territory defence and hunting success (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Creel & Creel, 1995; MacNulty, Tallian, Stahler, & Smith, 2014); thus, providing benefits to both subordinates and new breeders in groups. During our study (i.e. 2009), the population of wolves was at its greatest size (U.S. Fish and Wildlife

Service [USFWS], Nez Perce Tribe, National Park Service, Montana Fish, Wildlife and Parks, Blackfeet Nation, Confederated Salish and Kootenai Tribes, 2010) as wolves were reintroduced to Idaho in 1995–1996 (Bangs & Fritts, 1996) and breeding opportunities may have been limited. In a saturated population, subordinate wolves may remain in their natal groups regardless of relatedness to breeders because they are biding their time until a breeding position becomes vacant (Mech & Boitani, 2003).

Our hypothesis that recruitment of male and female pups would be biased after male and female breeder turnover, respectively, was not supported. For breeding male turnover, we found the opposite of our prediction—female pup recruitment was lower in the new breeding male's litter of pups. Female helpers in grey wolves have been shown to help more than males during some parts of the pup-rearing season (Ausband et al., 2016) and such differential help by the philopatric sex is predicted by group augmentation theory (Kokko et al., 2001). One could reasonably expect that in grey wolves, breeders would desire to recruit at least some future female helpers. Losses of female recruits, however, were not offset by biased sex ratios of litters nor biased survival of female recruits in the following year. We posit that nonbreeding females that remain in a group after turnover of the breeding male may not assist in rearing females of the new male's litter because his young are more distantly related to them, particularly if there has been recent breeding female turnover as well. A lack of cooperation in rearing non-kin female pups can decrease competition for future breeding opportunities with the new male. Although wolves generally avoid incest (Smith et al., 1997), it does occur (Packard, 2003; Stenglein et al., 2011), and we suggest that nonbreeding females behave in a way that ultimately reduces the number of competitors for mating with the new male or with future unrelated males should turnover occur again. Some cooperatively breeding birds care for and produce more individuals of the sex that will help more in the future, dubbed the 'helper repayment hypothesis' (Emlen et al., 1986; Gowaty & Lennartz, 1985). Our findings do not support the helper repayment hypothesis. We posit that breeder turnover and its effects on present and future breeding opportunities in highly related family groups add complexity to reproductive hierarchies and affect an individual's decision to stay or leave.

Contrary to our hypotheses, harvest was not associated with increased breeder turnover and did not affect rates of polygamy in our study groups. This finding supports recent interpretations of a study that found no effect of harvest on breeder loss and group persistence in Alaskan wolves (Borg, Brainerd, Meier, & Prugh, 2017). Although group size declined after harvest began, the frequency of breeder turnover was unaffected in our study. Harvest in African lions greatly increased the frequency of breeder turnover, but harvest was disproportionately targeted towards large males that typically hold prides and sire cubs of multiple resident females in the group (Loveridge et al., 2010). Harvest in grey wolves appears to be opportunistic (Ausband, 2016) and overall rates in our study may have been low enough (c. 24%; Ausband et al., 2015) that the frequency of breeder turnover did not exceed levels observed in naturally regulated populations (i.e., most of the data in Brainerd et al. (2008), Idaho prior to harvest).

We show that polygamy is likely constrained by behavioural mechanisms, sex-biased recruitment after breeder turnover may be the result of subordinates protecting future breeding opportunities for themselves, and subordinates do not exhibit increased dispersal after breeder turnover. The combination of these findings suggests breeding opportunities and high-quality territories are limiting; thus, the influences of helping and cooperative breeding on lifetime fitness in grey wolves should not be ignored. We hypothesize that higher harvest rates than those we observed could lead to a change in life-history strategy where subordinates help less and disperse more as breeding opportunities arise due to harvest mortality. If true, cooperative breeding may exist in some species as a continuum ultimately influenced by the population-level effects of harvest.

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AUTHORS' CONTRIBUTIONS

D.A. performed fieldwork, designed and tested hypotheses and wrote much of the manuscript, M.M. assisted with early hypothesis development and wrote text of the manuscript, and L.W. performed fieldwork, oversaw genetic analyses and contributed to text in the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.vc6p9> (Ausband, Mitchell, & Waits, 2017).

REFERENCES

Allendorf, F. W., Luikart, G., & Aitken, S. N. (2013). *Conservation and the genetics of populations*. Hoboken, NJ: Wiley-Blackwell.

- Ausband, D. E. (2016). Gray wolf harvest in Idaho. *Wildlife Society Bulletin*, 40, 500–505.
- Ausband, D. E., Mitchell, M. S., Bassing, S. B., Morehouse, A., Smith, D. W., Stahler, D. R., & Struthers, J. S. (2016). Individual, group, and environmental influences on helping behavior in a social carnivore. *Ethology*, 122, 963–972.
- Ausband, D. E., Mitchell, M. S., Doherty, K., Zager, P., Mack, C. M., & Holyan, J. (2010). Surveying predicted rendezvous sites to monitor gray wolf populations. *Journal of Wildlife Management*, 74, 1043–1049.
- Ausband, D. E., Mitchell, M. S., & Waits, L. P. (2017). Data from: Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.vc6p9>.
- Ausband, D. E., Stansbury, C., Stenglein, J. L., Struthers, J. L., & Waits, L. P. (2015). Recruitment in a social carnivore before and after harvest. *Animal Conservation*, 18, 415–423.
- Bangs, E. E., & Fritts, S. H. (1996). Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*, 24, 402–413.
- Borg, B. L., Brainerd, S. M., Meier, T. J., & Prugh, L. R. (2015). Impacts of breeder loss on social structure, reproduction, and population growth in a social canid. *Journal of Animal Ecology*, 84, 177–187.
- Borg, B. L., Brainerd, S. M., Meier, T. J., & Prugh, L. R. (2017). Corrigendum. *Journal of Animal Ecology*, <https://doi.org/10.1111/1365-2656.12631>.
- Brainerd, S. M., Andren, H., Bangs, E. E., Bradley, E. H., Fontaine, J. A., Hall, W., ... Wydeven, A. P. (2008). The effects of breeder loss on wolves. *Journal of Wildlife Management*, 72, 89–98.
- Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive inter-pack interactions of gray wolves in Yellowstone National Park. *Behavioral Ecology*, 26, 1352–1360.
- Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., ... McClrath, G. M. (2001). Contributions to cooperative rearing in meerkats. *Animal Behaviour*, 61, 705–710.
- Clutton-Brock, T. H., Brotherton, P. N. M., Smith, R., McClrath, G. M., Kansky, R., Gaynor, D., ... Skinner, J. D. (1998). Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society, B*, 265, 2291–2295.
- Clutton-Brock, T. H., & Manser, M. (2016). Meerkats: Cooperative breeding in the Kalahari. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 294–316). Cambridge, UK: Cambridge University Press.
- Courchamp, F., Rasmussen, G. S. A., & MacDonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycan pictus*. *Behavioral Ecology*, 13, 20–27.
- Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycan pictus*. *Animal Behaviour*, 50, 1325–1339.
- Emlen, S. T., Emlen, J. M., & Levin, S. A. (1986). Sex ratio selection in species with helpers-at-the-nest. *American Naturalist*, 127, 1–8.
- Gobush, K. S., Mutayoba, B. M., & Wasser, S. K. (2008). Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conservation Biology*, 22, 1590–1599.
- Gowaty, P. A., & Lennartz, M. R. (1985). Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. *American Naturalist*, 126, 347–353.
- Jimenez, M. D., Bangs, E. E., Boyd, D. K., Smith, D. W., Becker, S. A., Mack, C. M., ... Laudon, K. (2017). Wolf dispersal in the northern Rocky Mountains in western United States: 1993–2008. *Journal of Wildlife Management*, <https://doi.org/10.1002/jwmg.21238>.
- Jones, O., & Wang, J. (2009). COLONY: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources*, 10, 551–555.
- Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society, London B*, 268, 187–196.
- Kutsukake, N., & Clutton-Brock, T. H. (2008). The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats. *Proceedings of the Royal Society, B*, 275, 209–216.
- Loveridge, A. J., Hemson, G., Davidson, Z., & MacDonald, D. W. (2010). African lions on the edge: Reserve boundaries as 'attractive sinks'. In D. W. MacDonald, & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 284–304). Oxford, UK: Oxford University Press.
- MacNulty, D. R., Tallian, A., Stahler, D. R., & Smith, D. W. (2014). Influence of group size on the success of wolves hunting bison. *PLoS ONE*, <https://doi.org/10.1371/journal.pone.0112884>.
- Mech, L. D., & Boitani, L. (2003). Wolf social ecology. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology and conservation* (pp. 1–34). Chicago, IL: The University of Chicago Press.
- Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist*, 103, 589–603.
- Packard, J. M. (2003). Wolf behavior: Reproductive, social, and intelligent. In L. D. Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology and conservation* (pp. 35–65). Chicago, IL: The University of Chicago Press.
- Pope, T. (2000). Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, 48, 253–267.
- R Core Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Sillero-Zubiri, C., Marino, J., Gottelli, D., & MacDonald, D. W. (2004). Ethiopian wolves: Afroalpine ecology, solitary foraging, and intense sociality amongst Ethiopian wolves. In D. W. MacDonald, & C. Sillero-Zubiri (Eds.), *The biology and conservation of wild canids* (pp. 311–322). Oxford, UK: Oxford University Press.
- Smith, D., Meier, T., Geffen, E., Mech, L. D., Burch, J. W., Adams, L. G., & Wayne, R. K. (1997). Is incest common on gray wolf packs? *Behavioral Ecology*, 8, 384–391.
- Stansbury, C. S., Ausband, D. E., Zager, P., Mack, C. M., Miller, C. R., Pennell, M. W., ... Waits, L. P. (2014). A long-term population monitoring approach for a wide-ranging carnivore: Noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. *Journal of Wildlife Management*, 78, 1040–1049.
- Stenglein, J. L., De Barba, M., Ausband, D. E., & Waits, L. P. (2010). Impacts of sampling location within a faeces on DNA quality in two carnivore species. *Molecular Ecology Resources*, 10, 109–114.
- Stenglein, J. L., Waits, L. P., Ausband, D. E., Zager, P., & Mack, C. M. (2010). Efficient noninvasive genetic sampling for monitoring reintroduced wolves. *Journal of Wildlife Management*, 74, 1050–1058.
- Stenglein, J. L., Waits, L. P., Ausband, D. E., Zager, P., & Mack, C. M. (2011). Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. *Journal of Mammalogy*, 92, 784–795.
- Stiver, K. A., Fitzpatrick, J., Desjardins, J. K., & Balshine, S. (2006). Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour*, 71, 449–456.
- U.S. Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, Montana Fish, Wildlife and Parks, Blackfoot Nation, Confederated Salish and Kootenai Tribes (2010). *Rocky Mountain Wolf Recovery 2009 Interagency Annual Report*, C.A Sime, & E.E. Bangs (Eds.). Helena, MT: USFWS, Ecological Services.
- Wallach, A. D., Ritchie, E. G., Read, J., & O'Neill, A. (2009). More than mere numbers: The impact of lethal control on the social stability of a top-order predator. *PLoS ONE*, 4, e6861.

- Wang, J. (2011). COANCESTRY: A program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, 11, 141–145.
- Western Regional Climate Center. (2014). Historical climate information. Retrieved from <http://www.wrcc.dri.edu>
- Whitman, K., Starfield, A. M., Quadling, H. S., & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature*, 428, 175–178.
- Woodroffe, R. (2011). Demography of a recovering African wild dog (*Lycaon pictus*) population. *Journal of Mammalogy*, 92, 305–315.
- Woodroffe, R., Mostert, H. D., Ginsberg, J., Graf, J., Leigh, K., McCreery, K., ... Szykman, M. (2007). Rates and causes of mortality in endangered African wild dogs *Lycaon pictus*: Lessons for management and monitoring. *Oryx*, 41, 215–223.
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennet, N. C., & Clutton-Brock, T. H. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences USA*, 103, 12005–12010.

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