

# Inherit the kingdom or storm the castle? Breeding strategies in a social carnivore

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## Abstract

Breeding opportunities are inherently limited for animals that live and breed in groups. Turnover in breeding positions can have marked effects on groups of cooperative breeders, particularly social carnivores. We generally know little about how breeding vacancies are filled in social carnivores and what factors might influence an individual's ability to successfully fill a vacancy. I used a long-term (11 years) genetic dataset from gray wolves to ask whether breeding vacancies were filled by individuals from within groups or by adoptees (i.e., adult animals immigrating into the group) from outside the group. Males were three times more likely than females to be adopted into breeding positions outside their group. Females typically inherited breeding positions within their natal groups (80%,  $n = 20$ ), while males obtained breeding positions outside their group (76%,  $n = 17$ ). Group size did not influence whether a breeding vacancy was filled by an adoptee or inherited by an individual from within the group. Prior to adoption, genetic relatedness was 30% higher in groups when females were adopted into breeding positions compared to when they inherited breeding positions from within groups. Thus, genetic relatedness within groups appears to play a role in whether females are adopted into groups or not. Because of their strong reliance on dispersal to secure a breeding position, male wolves appear to be the couriers of genetic diversity in populations of gray wolves. Many states in the United States have recently implemented hunting and trapping seasons for gray wolves. If dispersing male wolves are disproportionately harvested, genetic connectivity and diversity in populations may be affected.

## KEYWORDS

breeding, *Canis lupus*, carnivore, cooperative breeding, inheritance, wolf

## 1 | INTRODUCTION

Some species, including humans, have evolved to live and breed in groups where individuals help rear young that are not their own (i.e., cooperative breeding; Dickinson & Koenig, 2016; Kramer, 2010). Group living often provides many advantages to individuals including increased food intake, enhanced ability to defend high-quality habitat, advantages during disease outbreaks, and ultimately, higher survival

and reproductive rates (Almberg et al., 2015; Cassidy et al., 2015; Clutton-Brock, 2006; Creel & Creel, 1995). Breeding opportunities are inherently limited for animals that live and breed in groups (i.e., the habitat can only support so many groups) and as a result reproductively mature individuals often delay dispersal (Clutton-Brock, 2006). In such populations, helping to rear related young can be a pathway to increased lifetime fitness (i.e., inclusive fitness; Hamilton, 1964) even in the absence of independent breeding opportunities for oneself.

Such individuals use various strategies to eventually secure breeding positions ranging from inheritance within their natal group to dispersing to an existing group or to vacant habitat to establish a new group (Jimenez et al., 2017; Kokko & Ekman, 2002; Walters & Garcia, 2016).

Because breeding opportunities are rare in such populations, competition for such positions can be fierce and the dynamics associated with breeder turnover often have marked effects on group size, composition, and breeder succession (Ausband et al., 2017; Brainerd et al., 2008). In some species, group size can influence whether an individual is adopted with smaller groups being more likely to adopt individuals than those in large groups (McNutt, 1996). Furthermore, the genetic relatedness of individuals within a group can affect their willingness to adopt new members (e.g., higher relatedness may favor adoption; Shen et al., 2017).

For individuals seeking to fill vacant breeding positions, sex can play a strong role on the strategy used. For example, in red-cockaded woodpeckers (*Picoides borealis*), most males remain on their natal territory as helpers and then inherit a breeding position once their father dies (Walters et al., 1992). Whereas in cooperatively breeding brown jays (*Cyanocorax morio*), females tend to remain on the natal territory and help rear young, although the overall lifetime fitness benefit of such behavior is unknown (Williams & Hale, 2007). We have a strong foundation for understanding how breeding vacancies are filled in many cooperatively breeding birds and many such species exhibit female-biased dispersal with males generally inheriting territories and breeding positions. We know considerably less about how breeding vacancies are filled in mammals where dispersal can be biased to either sex. We might expect to see unique patterns in how breeding vacancies are filled in mammals and particularly in social carnivores due to their inherent low densities and remarkable dispersal capabilities.

Gray wolves (*Canis lupus*) in Idaho, USA, are an excellent study species for asking questions about how breeding vacancies are filled in social carnivores. Group size and composition have marked effects on wolf survival and reproduction (Ausband et al., 2017). Furthermore, wolf populations in Idaho, USA, are dynamic with both natural and human-caused mortality creating breeding vacancies (Ausband et al., 2017). I used a long-term (11 years) genetic dataset of pedigrees for gray wolves to examine how breeding vacancies are filled in a cooperatively breeding social carnivore. I asked whether breeding vacancies were inherited by individuals within groups or filled by adoptees from outside the group. I predicted that females would inherit breeding positions in their natal groups more than males, the probability of adoption would decrease with increasing group size, and increased genetic relatedness of individuals within a group would positively influence the probability of adoption into a breeding position for individuals outside the group.

## 2 | MATERIALS AND METHODS

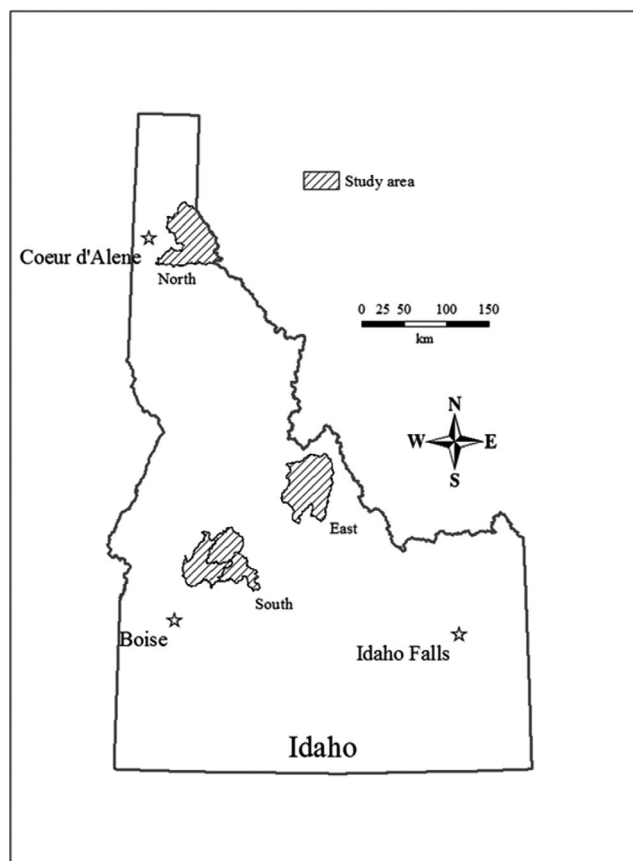
### 2.1 | Study areas

I sampled wolves in three study areas (north, east, and south) encompassing five Idaho Department of Fish and Game Management Units

(GMUs 4 "North", 28 "East", and 33–35 "South"; Figure 1). Idaho, USA, lies at latitude 44.06820 and longitude -114.74204. Annual temperatures ranged from -13 to 36°C (Western Regional Climate Center, 2016), precipitation ranged from 30 to 130 cm (Western Regional Climate Center, 2016), and elevation ranged from 646 to 3219 m. The northern study area (GMU 4; 3189 km<sup>2</sup>) was dominated by western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). The eastern (GMU 28; 3388 km<sup>2</sup>) and southern (GMUs 33–35; 3861 km<sup>2</sup>) study areas consisted of ponderosa pine (*Pinus ponderosa*), lodgepole pine, spruce mixed forests, and sagebrush (*Artemisia tridentata*) steppe (Mack et al., 2010). Public harvest of wolves began in Idaho in 2009 and occurred annually each year since 2011 (brief cessation in 2010). September–March constituted the bulk of harvest with a peak in October–November (Ausband, 2016). The population of wolves in Idaho was large during my study (approx. 1000 wolves; Idaho Department of Fish & Game, 2020) and adjacent to neighboring populations in western United States and Canada.

### 2.2 | Field methods

I collected wolf scats at occupied or recently occupied wolf pup-rearing sites during June–August 2008–2018. When available, I



**FIGURE 1** Study areas in Idaho, USA, where wolves were genetically sampled, 2008–2018

used GPS or radio-telemetry locations of wolves to locate pup-rearing sites. When no radio-collared wolves existed, I surveyed historical pup-rearing sites and sites predicted by a habitat model that had a high probability ( $\geq 70\%$  suitability) of being a pup-rearing site (Ausband et al., 2010). During 2008–2010, we used no radio-collar information to find wolves, from 2011 to 2014 approximately 65% of our study groups contained collared individuals, although their locations did not always help us find pups. From 2015 to 2018, we again used no collar information. At sites of both collared and uncollared wolves, technicians howled (Harrington & Mech, 1982) and attempted to find an activity center (area where pups congregate) by searching the area or through searches around wolf GPS clusters ( $>5$  locations within 1 km for  $>7$  days) and radio-telemetry locations when available. After the activity center was located, 4–8 technicians collected wolf scats (pup and adult) for 3–5 h, radiating out from the activity center on existing wolf trails up to 500 m to ensure a sufficient sample of adult scats (Ausband et al., 2010; Stenglein et al., 2010a). Surveying the site with more people (e.g., 8 vs. 2) for shorter durations of time reduced the overall length of time we were in sites and potentially stressing wolves. We also collected incidental scats found outside of pup-rearing sites. We collected 125–200 samples per group per year, which generally detected every individual in the group (Stenglein et al., 2011). We attempted to resample each group every year. Sampling was conducted under University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU).

### 2.3 | Laboratory methods

We performed DNA analyses at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, ID, USA). We extracted DNA from scat samples with Qiagen kits (Qiagen) and included a negative control to test for contamination. We first screened all samples in a species identification test using co-amplification and fragment analysis of three short segments of the mitochondrial DNA control region to remove non-target species and low-quality samples. We then attempted to genotype all samples identified during the mtDNA test as wolf or dog (*C. familiaris*) using 18 nuclear DNA microsatellite loci (AHT103, AHT109, AHT121, AHT200, C05.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, and FH3725; Holmes et al., 1994, Breen et al., 2001, Guyon et al., 2003, Salim et al., 2007, Ostrander et al., 2017). We first amplified all samples twice for genotyping and required successful amplification of alleles at  $\geq 5$  loci for the sample to continue for an additional 1–3 PCRs, whereas we discarded samples that amplified at  $< 5$  loci. At each locus, we required  $\geq 2$  independent PCR amplifications for consensus of a heterozygote and  $\geq 3$  independent PCR amplifications for consensus of a homozygote. We compared all consensus genotypes and all unique genotypes of previously identified individuals using Program Genalex (Peakall & Smouse, 2006) to match samples and distinguish unique genotypes. To account for undetected genotyping errors, we grouped samples mismatching by allelic dropout at only

one locus (e.g., 102, 102 vs. 102, 106) as a single individual (Adams & Waits, 2007). We used Reliotype (Miller et al., 2002) to test the accuracy of unique genotypes that were captured just once by ensuring the genotype attained a 95% accuracy threshold. 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). We analyzed all collected samples in 2008 and 2009. After 2010, we used rarefaction analyses (Stenglein et al., 2011) to subsample for economic efficiency and analyzed 40 adult and 25 pup samples from each group. If a group had more than two individuals detected only once, we analyzed additional samples when available to obtain 10 more consensus genotypes.

### 2.4 | Analyses

I did not include pups in my analyses and used genotypes of wolves  $\geq 1$ -year-old because wolf pups do not breed in their first year. I included all sampled adult males and females as potential parents and all sampled pups as potential offspring for each year and study area and then determined breeders and their offspring by constructing pedigrees using maximum likelihood and Program COLONY version 2.0.5.5 (Jones & Wang, 2009). I first calculated allele frequencies for each study area and year in Program COANCESTRY version 1.0.1.5 (Wang, 2011) and then imported those into Program COLONY for use in pedigree analyses. I allowed polygamy in both sexes and assumed an allelic dropout rate of 0.01. In cases where parentage was undetermined from COLONY, I 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. Lastly, I used Program Co-ancestry (Wang, 2011) to estimate Trio ML genetic relatedness between all possible pairs of adult individuals within each group each year.

I sampled the same groups of wolves across consecutive years and from the resulting pedigrees, I estimated the number of individuals and breeders in each group. Causes of breeding vacancies were not always known and included loss of a breeding position through death, expulsion from the group, or having a breeding position behaviorally usurped.

I used both generalized linear mixed and fixed effects models in Program R (version 3.6.2, R Core Team, 2019) to test whether sex, group size, and genetic relatedness ( $r$ ) of adults in a group influenced whether a breeding vacancy was inherited by an existing group member or filled by an adopted individual from outside the group. The response variable in all models was binary (e.g., was breeding vacancy filled by an adoptee or not) and I assumed a binomial distribution with logit link function. I included a random effect for "group" in mixed effects models. I evaluated the relative support for competing models (e.g., sex, group size, genetic relatedness, and combinations thereof as well as a null model) using Akaike's information criteria ( $AIC_c$ ) adjusted for small sample size and model weights ( $w_i$ ; Burnham & Anderson, 2002). Models within two  $AIC_c$  values were

equally supported; however, I considered the most parsimonious (i.e., fewest parameters) among them as the top model. I assessed the fit of my most supported model using the receiver operating characteristic statistic (Hosmer & Lemeshow, 2000). To test for influences on breeding inheritance patterns within (rather than between) sexes, I tested whether genetic relatedness or group size differed when a breeding position was inherited or filled by an adoptee for both males and female separately using a t-test. Sample sizes were too limited for logistic regression analyses (e.g., only four females were adopted into breeding positions outside their natal group).

### 3 | RESULTS

I documented 37 breeder turnover events (20 breeding females and 17 breeding males) in 10 wolf groups during 2008–2018. Within these groups, I genotyped 151 unique individuals. Group size averaged 7.6 (SD = 2.9) adults per group and the genetic relatedness of adults in groups averaged 0.34 (SD = 12.2). The most supported and parsimonious model for predicting whether a breeding vacancy was filled by an adoptee or inherited from within the group contained a variable for “sex” and had good fit to the data (AUC = 0.76; Table 1). When breeding vacancies occurred, males were three times more likely ( $\beta = -2.27$ , SE = 0.77; model prob. = 0.75; 0.40–0.93, 95% CI) than females (model prob. = 0.24; 0.06–0.58, 95% CI) to be adopted into a breeding position outside their group. Females typically inherited breeding positions within their natal groups (80%,  $n = 20$ ), while males obtained breeding positions outside their group (76%,  $n = 17$ ).

Within males, neither group size ( $T = 1.26$ ,  $df = 16$ ,  $p = 0.22$ ) nor genetic relatedness ( $T = 0.62$ ,  $df = 16$ ,  $p = 0.53$ ) influenced whether a male inherited or was adopted into a breeding position in a group. Within females, however, genetic relatedness before adoption was 30% higher ( $T = 1.85$ ,  $df = 19$ ,  $p = 0.08$ ) in groups when females were adopted from outside the group ( $r = 0.43$ ; SE = 0.03) than when

females from within groups inherited breeding positions ( $r = 0.33$ ; SE = 0.03). Group size was not associated with inheritance or adoption into breeding positions in groups for females ( $T = 0.18$ ,  $df = 19$ ,  $p = 0.86$ ).

### 4 | DISCUSSION

Generally, few individuals breed in populations of cooperative breeders. Vacant breeding positions and related territories can be filled quickly, and various strategies have evolved for individuals competing for such opportunities (Kokko & Ekman, 2002). I found differences in breeding strategies by sex in gray wolves with females typically staying in their natal group and attempting to inherit a breeding position and males dispersing and being adopted into another group when a breeding vacancy occurred. Instances of females being adopted into breeding vacancies outside their natal group were infrequent. Genetic relatedness among adults in such groups was generally high when it did occur, however. Furthermore, in three of four cases where females were adopted into breeding positions, the existing breeding male was the father of all the adult female helpers in the group indicating inbreeding avoidance.

Because breeding strategies varied by sex, one might predict differences in the helping behavior displayed by male and female wolves. For example, male wolves may benefit from larger body size when dispersing and attempting to acquire a breeding position outside their natal group as seen in other carnivores (Kovach & Powell, 2003; Lührs & Kappeler, 2014; Zedrosser et al., 2007). Selection could favor individuals who consume more food per capita than other group members and perhaps provision pups less than others or even steal food brought back to pups by other group members. Indeed, Ausband et al. (2017) found a significant negative effect of older non-breeding male helpers on pup recruitment. Conversely, one might expect females to exhibit increased helping behavior

Model	K	-2LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
Sex <sup>a</sup>	2	41.0	45.4	0.0	0.38
Sex with RE for group	3	39.7	46.4	1.0	0.23
Sex and relatedness	3	40.8	47.5	2.1	0.13
Sex and relatedness with RE for group	4	38.9	48.1	2.7	0.10
Sex, relatedness, and group size with RE for group	5	36.6	48.6	3.2	0.08
Sex, relatedness, and group size	4	39.6	48.9	3.5	0.07
Null	1	51.3	53.4	8.0	0.00
Group size	2	50.1	54.5	9.1	0.00
Null with RE for group	2	50.6	55.0	9.6	0.00
Group size with RE for group	3	48.6	55.4	10.0	0.00
Relatedness	2	51.2	55.6	10.2	0.00
Relatedness with RE for group	3	50.5	57.2	11.8	0.00

TABLE 1 Comparisons of generalized fixed and mixed effects models testing what influences whether a breeding vacancy is filled via inheritance by an existing group member or filled by an adoptee to the group. Data are from 10 groups of gray wolves in Idaho, USA, 2008–2018. Akaike's information criterion (AIC<sub>c</sub>) adjusted for small sample size was used to assess relative support between models

Abbreviations: -2LL,  $-2 \times$  Log-Likelihood; RE, random effect.

<sup>a</sup> $y = 1.099 - 2.277$  (sex [reference category, Male]); AUC = 0.76.

particularly when genetic relatedness of adults in the group is  $\leq 0.33$  if group augmentation theory (Kokko et al., 2001) drives cooperative breeding behavior in wolves. Females that help rear pups prior to obtaining a breeding position may increase group size yielding subsequent benefits in territory defense, prey acquisition, and perhaps even reciprocal aid from pups once they age into adults (Cassidy et al., 2015; Creel & Creel, 1995; Wiley & Rabenold, 1984). There is some evidence that female wolves help more than males particularly when pups are young (Ausband et al., 2016), but the ultimate effect on pup survival is not clear (Ausband et al., 2017).

The rate at which breeding positions turnover in a population likely affects the strategy individuals deploy to secure such vacancies. Wolves are harvested in my study system and the harvest rate averaged 13.3% (range: 0.0%–27.6%) annually (Ausband, 2019). Ausband et al. (2017) showed that breeding positions are fairly dynamic in this population with frequent turnover even in the absence of harvest. When density is low and suitable habitat is abundant, both sexes may opt to disperse and secure a breeding position and territory of their own rather than bide time in their natal group. As habitat becomes saturated, such as in the population I studied, male-biased dispersal appears to be the emergent strategy for wolves to secure breeding opportunities. Dispersing and monopolizing a breeding position is not the only avenue to increased fitness, however. Male wolves can also gain fitness benefits from extra-pair paternity while waiting for breeding vacancies to open elsewhere (Li & Kokko, 2018). Such extra-pair paternity is not uncommon in the population I studied (Ausband, 2018).

Male wolves appear to be the couriers of genetic diversity in wolf populations because they typically disperse to seek breeding opportunities elsewhere rather than wait for a breeding vacancy in their natal group. This finding has conservation implications. For example, many states in the United States have recently implemented hunting and trapping seasons for gray wolves. These harvest seasons generally overlap the peak time of dispersal for wolves (Jimenez et al., 2017). If dispersing male wolves are disproportionately harvested, genetic connectivity and diversity in the population may be affected. Managers implementing harvest seasons for wolves might consider a monitoring program or mandatory harvest check-in that allows them to determine the proportion of adult males in the harvest if genetic diversity is a concern.

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#### CONFLICT OF INTEREST

The author has no conflict of interest to report.

#### DATA AVAILABILITY STATEMENT

Data used in this study are available in the File S1.

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## SUPPORTING INFORMATION

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

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