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The effect of group size on reproduction in cooperatively breeding gray wolves depends on density

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Abstract

In cooperatively breeding species, large group size is often positively related to reproductive success and group persistence. We have a poor understanding, however, of how group sizes within a population affect reproduction particularly as density varies. We hypothesized that at low densities, wolves in both small and large groups would have similar reproductive rates. At high densities, however, wolves in small groups would have lower reproductive rates compared to those in large groups. Using empirical data from radio-collared wolves in Idaho and Yellowstone National Park, WY, USA (1996–2012), we compared reproductive rates (i.e. proportion reproducing, litter size, pup survival) among small and large groups of wolves as density fluctuated within the populations. Reproductive rates were generally lower for individuals in small groups compared to those in large groups, particularly as density increased. Pup survival, however, was slightly higher for wolves in small groups compared to large groups except at very high densities. Polygamy increased with density regardless of group size, suggesting a polygamy threshold for wolves. Large group size resulted in less parturition failure, more breeding females per group, larger litter sizes, and ultimately more pups recruited per group. Large group size appears advantageous for several, but not all, aspects of reproduction particularly when population density is high.

Introduction

Cooperative breeding generally refers to the shared caring for related or unrelated young within a group (Solomon and French, 1997). In mammals, both manipulative and observational studies have shown that the presence of non-breeding helpers in a group enhances reproductive success, fitness of breeders, and persistence of the group (Clutton-Brock, 2006; Courchamp et al., 2000; Courchamp and Macdonald, 2001; Courchamp et al., 2002; Solomon and French, 1997).

The benefits of living in a large group may be particularly marked for territorial carnivores. Large group size can increase hunting success (Carbone et al., 2005; Creel and Creel, 1995; Fanshawe and Fitzgibbon, 1993; MacNulty et al., 2014) although there can be intermediate group sizes that lead to maximum per capita benefits for group members (Creel and Creel, 1995). Larger group size can also increase the ability to successfully defend a territory and offspring from predation (Cassidy et al., 2015; Courchamp et al., 1999; Courchamp et al., 2002; Creel and Creel, 1995; Packer et al., 1990; Whitman et al., 2004). Yet the benefits of larger group size may vary with conspecific density when resources are patchy and limited. For example, as density increases, individuals in large groups may be able to secure and defend high quality territories (i.e. those with abundant limiting resources) and provision and guard offspring more successfully than those in small groups (Ausband et al., 2016; Cassidy et al., 2015; Courchamp et al., 1999; Ruprecht et al., 2012).

In some populations, immigration can mitigate the effects of mortality over relatively short timescales, but such mortality may affect group social structure, learning, helping behavior and evolution over longer time periods (Haber, 1996; Rutledge et al., 2010). Because of their hierarchical structure and dependence on others in the group, mortality can affect group-living species in complex ways. For example, individuals in groups of African elephants (*Loxodonta africana*) that experienced higher rates of poaching, and particularly when they had lost older females, had lower reproductive rates despite the continued survival of reproductively prime females (Gobush et al., 2008). Additionally, the extinction rate for groups of cooperatively breeding gray wolves was 33–38% after breeder loss, but survival of the remaining pups was greater in groups that had more non-breeding helpers (Borg et al., 2015; Brainerd et al., 2008). The effects of mortality in such animals can be more than simply subtracting 1 animal from the group's size; effects can depend on the status of the animal lost but also which individuals remain in the group.

Bateman et al. (2011) asserted that knowing how births and deaths are affected by both population density and group size would enhance our understanding of populations of cooperative breeders. Considering Bateman et al., (2011) proposition, we estimated reproductive rates from individuals in a recolonizing population of cooperative breeders. We then used those reproductive rates to ask important questions about how the advantages of larger group size typically seen in cooperative breeders might vary with density. Specifically, we wanted to know how group size affects reproductive rates in a cooperative breeder as density varied.

At low population densities and in suitable habitat, individuals in small groups may be able to secure the resources they need just as well as individuals in large groups. Selection, however, has favored many cooperatively breeding species to live in relatively large, multi-generational family groups (Solomon and French, 1997). Thus, at high population densities the benefits of living in a larger group should become more pronounced as competition for limited resources between groups increases. Alternatively, large groups may experience higher intragroup competition yielding lower offspring survival and higher dispersal rates. Optimal group size may also be lower at high population densities. Finally, if recruitment is simultaneously influenced by group size and density, the distribution of group sizes within a population can affect population trajectory and thus management and conservation decisions.

Gray wolves are territorial, and sexually mature individuals (≥22 months) disperse from their natal groups establishing their own territories or joining existing groups. Reintroductions to vacant habitat in the northern Rocky Mountains of the U.S. (Bangs and Fritts, 1996) provide an ideal framework for assessing the relative influence of density on reproduction. Harvest of the Rocky Mountain wolf population began in 2009. Although declines in group size and density have been documented (Ausband et al., 2017; Bassing et al., 2020), we do not know how such declines might affect the reproductive potential of this population, if at all. We estimated and compared several reproductive rates for individuals in both small and large groups using empirical data collected from radio-collared wolves in Idaho and Yellowstone National Park (YNP), Wyoming, USA during a period of wolf recovery and recolonization (1996–2012).

We hypothesized that large group size in cooperative breeders is beneficial to reproductive rates primarily at higher-than-average population densities. Specifically, we predicted that (1) reproductive rates of wolves would be similar between small and large groups at below average densities, and (2) as density increased, reproductive rates would decline for small groups, whereas reproductive rates would be maintained in large groups.

Materials and methods

In Idaho and Yellowstone National Park, data were derived by tracking radio-collared individuals and observing groups and pups from fixed-wing aircraft and ground surveys at pup-rearing sites (i.e. dens, rendezvous sites; Mack et al., 2002; Mack and Holyan, 2003; Mack and Laudon, 1998; Phillips and Smith, 1997; Smith and Guernsey, 2002; Smith et al., 1999; Smith et al., 2000; Smith et al., 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013). Groups were considered distinct when radio-collared members were not observed by tribal and agency personnel together at pup-rearing sites or during radiotelemetry monitoring flights. Groups generally occupied the same territory and areas over time. If an entire group dissolved or was removed (e.g. control action) any wolves reoccupying the area became a new group. Counts of individuals were frequent, particularly in December when pup and group size counts were made as part of annual requirements under Endangered Species Act regulations. We ceased using Idaho data after 2002 because the population exceeded 300 animals and monitoring became more difficult resulting in groups without radio-collared members and gradually more incomplete data over time. The wolf population in Yellowstone National Park is generally quite small (approx. 100–150 wolves) with >1 radio-collared member in each group. Many of Yellowstone's wolves occupy a landscape with relatively open habitat and long views, thus many groups of wolves are sighted several times per week by the public and agency personnel. We tabulated parturition success (i.e. pups observed at a pup-rearing site), the number of breeding females in a group (i.e. number of separate den sites documented), litter sizes (i.e. number of pups observed at pup-rearing sites), probability of pup survival (i.e. over the period 15 April–31 December) for wolf groups and populations using counts reported to the U.S. Fish and Wildlife Service for documentation of wolf recovery in Idaho and Yellowstone National Park. We estimated wolf density (wolves/1000 km^2) by summing the number of adult wolves and dividing by the area separately for Yellowstone's northern range (inside YNP only; 1562 km^2), Yellowstone's interior (7458 km^2), and Idaho's wolf recovery area (75 070 km^2). Reproductive rates were compiled per wolf group (e.g. number of breeding females per group) except for litter size which was tabulated per breeding female in a group.

We used generalized mixed effects models to test for the influence of classes of group size (i.e. number of adults) and density on the six reproductive rates mentioned above: parturition success, presence of >1 breeding female, number of breeding females, litter size, pup survival, and total number of pups recruited per group annually. We did not suspect that a 1 unit increase in group size would yield effects on reproduction. Rather, we were interested in the advantage of relative group size and whether large groups outcompeted smaller groups, thus we defined 1–4 adults as a small group (Smith et al., 2010b) and ≥8 adult wolves constituted a large group. In addition to our desire to test for the relative advantage of group size, these breakpoints were chosen in part based on splines relating group size and various components of reproduction in individual wolves (Stahler et al., 2013). We included a covariate of 'density $\times$ group size' to test for an interaction effect of density and group size on reproductive rates. The Pearson correlation coefficient between density and group size was 0.45. Density was centered by

Table 1 Reproductive rates as a function of increasing group size and population density for gray wolves in Idaho and Yellowstone National Park, USA, 1996–2012

Reproductive rate	*n*	Covariate β (SE)	95% CI
Successful parturition (pups observed)	160	**Density: 0.06 (0.04)**	**0.0 to 0.16**
		Small: −1.14 (0.57)	**−2.46 to −0.05**
		Small*Density: −0.10 (0.04)	**−0.20 to −0.03**
		Group RE: variance = 0.0, SD = 0.0	
Presence of >1 breeding female[a]	160	**Density: 0.06 (0.02)**	**−0.01 to 0.10**
		Small: −0.48 (0.84)	−1.93 to 3.94
		Group RE: variance = 3.3, SD = 1.8	
No. of breeding females[a]	160	**Density: 0.01 (0.004)**	**0.00 to 0.02**
		Small: −0.14 (0.15)	−0.44 to 0.16
		Group RE: variance = 0.0, SD = 0.0	
Litter size	262	Density: 0.003 (0.003)	−0.003 to 0.01
		Small: −0.34 (0.10)	**−0.54 to −0.15**
		Small*Density: −0.01 (0.006)	**−0.03 to 0.00**
		Group RE: variance = 0.09, SD = 0.30	
Pup survival	849	**Density: −0.07 (0.01)**	**−0.09 to −0.05**
		Small: 0.78 (0.32)	**0.17 to 1.43**
		Small*Density: −0.04 (0.02)	**−0.08 to 0.00**
		Group RE: variance = 2.7, SD = 1.6	
Total pups recruited	161	Density: 0.00 (0.00)	−0.01 to 0.00
		Small: −0.20 (0.11)	−0.43 to 0.03
		Small*Density: −0.02 (0.00)	**−0.03 to 0.00**
		Group RE: variance = 0.18, SD = 0.43	

Parameters β (SE) for the influence of covariates on Reproductive rates derived from mixed effects models. Small groups = 1–4 adults and large groups = ≥8 adult wolves. Large groups were the reference category. Sample size (*n*) is the number of group years used in analyses. Covariates in bold with 95% CIs that did not overlap 0 were considered influential. We considered density and its influence on the Presence of >1 breeding female significant although it slightly overlapped 0 (i.e., 0.01). We report modeled variance and SD for the effect of random intercepts (RE).

[a] Indicates top model contained no density x group size interaction term.

subtracting the overall mean density from each value so that modeled interaction covariates were readily interpretable. For models where the response variable was count data we assumed a Poisson distribution and employed a log link function (O'Hara and Kotze, 2010). We found no evidence of overdispersion in our data (values < 1.5) and considered Poisson models appropriate. In models with binary response variables, we assumed a binomial distribution with a logit link function. We included a crossed random intercept for group in all models. Groups were allowed to occupy both 'small' and 'large' states in our model depending on group size in any given year. We used the glmm and lme4 packages in Program R (V. 3.2.2) for statistical tests and considered covariates biologically influential if the 95% profile likelihood confidence intervals did not overlap 0.

Results

Population density varied widely over the course of our study ranging from 0.57 wolves/1000 km^2 in Idaho in 1996 to a high of 54.9 wolves/1000 km^2 on Yellowstone National Park's northern range in 2008. Mean density was 14.1 wolves/1000 km^2. For three of the five reproductive components we considered, there was a significant interaction between group size and density (Table 1; Figs 1–3). There was not a significant interaction effect between density and group size for either the probability of multiple breeding females or the total number of breeding females (Table 1). The probability a group contained >1 breeding female and the total number of breeding females per group increased with population density across all group sizes (Table 1). We found that small groups had lower successful parturition rates (i.e. more likely to fail to produce pups) and smaller average litter size when they did breed than large groups and there was a negative interaction with density (Table 1; Figs 2 and 3). Density had a negative effect on pup survival for all groups, although small groups generally had higher or equal pup survival compared to large groups. Ultimately, small groups recruited fewer pups than large groups because of smaller litter sizes and parturition failure. Such effects were more pronounced as density increased (Table 1).

Discussion

Wolves in larger groups generally had higher reproductive rates, but this effect was most pronounced when density was higher than average. Ultimately, fitness of individuals in a population of cooperative breeders reliant on patchily

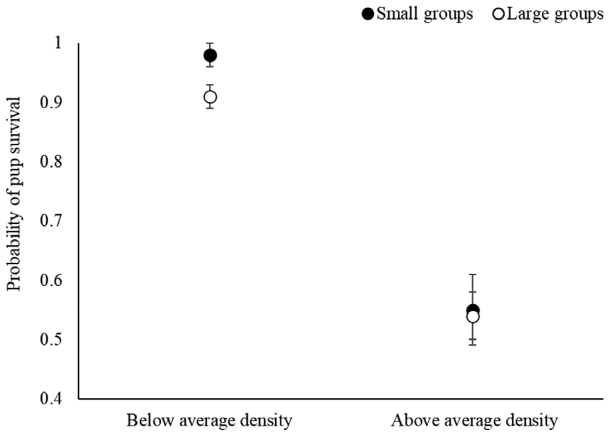

Figure 1 Estimated probability of pup survival (approx. 8 months) using a mixed effects model for wolves in small and large groups as a function of population density in Idaho (1996–2002) and Yellowstone National Park, WY, USA (1996–2012). Error bars represent the 95% CI

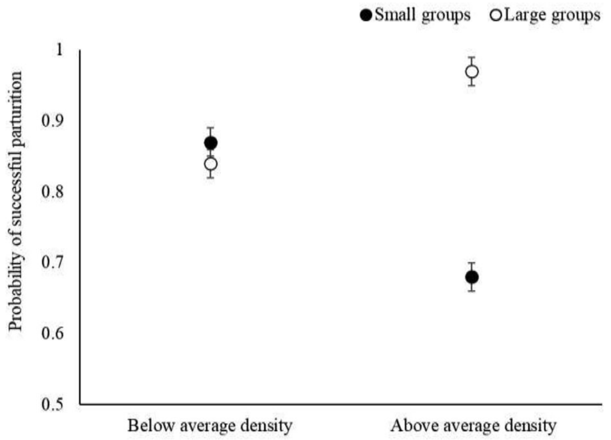

Figure 2 Estimated probability of successful parturition (i.e. pups observed) using a mixed effects model for wolves in small and large groups as a function of population density in Idaho (1996–2002) and Yellowstone National Park, WY, USA (1996–2012). Error bars represent the 95% CI

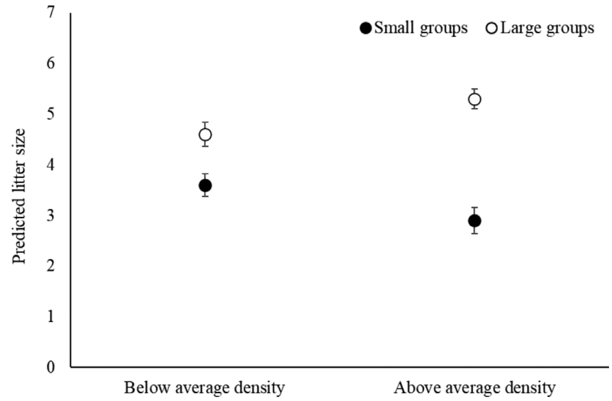

Figure 3 Estimated litter size using a mixed effects model for individual female wolves in small and large groups as a function of population density in Idaho (1996–2002) and Yellowstone National Park, WY, USA (1996–2012). Error bars represent the 95% CI

distributed resources (Macdonald et al., 2004) should be strongly affected by group size and population density. Increasing density yielded higher rates of polygamy (i.e. multiple breeding females) across all group sizes, however, suggesting a polygamy threshold in wolves (Ausband, 2018; Orians, 1969).

Smith et al. (2010b) found that individuals in small groups had higher mortality rates (i.e. hazard ratios) than those in large groups but the effect was weak. We found pup survival was consistently higher for wolves in small groups than large groups except at very high densities (i.e. >27 wolves/1000 km^2). Pups in large groups may have reduced survival due to competing with subadult wolves in their group who may intercept food at pup-rearing sites or preclude smaller pups of the year from feeding at kills. Many of the reproductive rates we estimated (i.e. successful parturition, litter size) were higher, however, for wolves in large groups than those in small groups, particularly as density increased. At high density, reproduction for wolves in small groups appeared to be most influenced by increased breeding failure and smaller litter sizes when they did successfully breed. Stahler et al. (2013) also showed that breeding females in large groups produced larger litters of pups, but this effect attenuated after group size was >8 wolves. Increased ability of large groups to successfully compete with conspecifics as well as other species may explain these differences. Infanticide can occur during the pup-rearing season (Smith et al., 2015b) and wolves benefit from increased group size during confrontations with other wolves (Cassidy et al., 2015) and possibly other species as well. It is possible that breeding failure could have been the result of infanticide early in the pup-rearing season. Adequately guarding young in a predator-rich environment may be difficult for small groups and, coupled with poorer breeding female body condition, could have contributed to the lower reproductive rates we estimated for individuals living in small groups.

Populations of cooperative breeders can be particularly sensitive to variations in the reproductive vital rates of individuals within groups (Bateman et al. 2013; Bourne et al., 2020). Thus, we focused on the relative advantage of group size to reproductive success. Although we included pup survival in our definition of reproductive success, demography can also be affected by other important vital rates such as adult survival. While Smith et al. (2010b) did not find group size influenced individual survival, Almberg et al. (2015) showed that adult survival was higher for wolves in large groups during a disease outbreak. Group size may also influence an individual's decision to disperse and may influence how successful they are during such events (e.g. body size advantages when attempting to join an existing group). Conceivably, small group size may actually be advantageous during times with low food availability assuming there is increased per capita food consumption for individuals in small groups compared to large groups. Pup survival can vary widely in gray wolves (Miller et al., 2002) and breeding opportunities are inherently limited in wolf populations. Focusing on the effects of group size and density on reproductive success should provide strong inference for understanding gray wolf population demography.

Implications

Our findings apply most directly to cooperatively breeding species that are fecund, territorial, and in relatively stable environments. The overall advantage of large group size may decline when there are insufficient resources available for all group members. In extreme cases of environmental variability such as drought, the majority of groups in a population of cooperative breeders can go extinct (Clutton-Brock, 2006) independent of group size, density, and immigration.

Finally, because we show that components affecting recruitment are influenced partly by group size, the distribution of group sizes within a population can affect population trajectory and thus management and conservation. Idaho has observed a decline in average group size since wolf harvest began in 2009 (Ausband et al., 2017) and concurrent declines in recruitment have been documented as well (Ausband et al., 2015). Declines in recruitment were documented only for groups that reproduced, however, and we do not know the overall population level effect of failed breeding attempts since harvest began. Our findings suggest that as average group size declines the frequency of groups that fail to breed will increase, litter sizes will be smaller, and recruitment will ultimately be lower. Such effects on groups should become less apparent as overall population density declines, however.

Conflict of interest

None to declare.

Author contribution

DA formulated hypotheses, performed analyses, and wrote manuscript. MM helped with hypothesis development and wrote large portions of the manuscript.

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