



RESEARCH PAPER

Individual, Group, and Environmental Influences on Helping Behavior in a Social Carnivore

David E. Ausband^{*1}, Michael S. Mitchell[†], Sarah B. Bassing^{*}, Andrea Morehouse[§], Douglas W. Smith[¶], Daniel Stahler[¶] & Jennifer Struthers^{**}

* Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA

† US Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA

§ Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

¶ Yellowstone Center for Resources, Yellowstone National Park, WY, USA

** Idaho Department of Fish and Game, Coeur d' Alene, ID, USA

Correspondence

David E. Ausband, Montana Cooperative Wildlife Research Unit, University of Montana, 205 Natural Sciences Building, 59812 Missoula, MT, USA.
E-mail: david.ausband@idfg.idaho.gov

¹Present address:

Idaho Department of Fish and Game, 2885 West Kathleen Avenue, 83185 Coeur d' Alene, ID, USA

Received: July 19, 2016

Initial acceptance: August 25, 2016

Final acceptance: September 15, 2016

(L. Ebensperger)

doi: 10.1111/eth.12566

Keywords: *Canis lupus*, cooperative breeding, groups, helping, pup-guarding, wolves

Abstract

Variation in group composition and environment can affect helping behavior in cooperative breeders. Understanding of how group size, traits of individuals within groups, food abundance, and predation risk simultaneously influence helping behavior is limited. We evaluated pup-guarding behavior in gray wolves (*Canis lupus*) to assess how differences in individuals, groups, and environment affect helping behavior. We used data from 92 GPS-collared wolves in North America (2001–2012) to estimate individual pup-guarding rates. Individuals in groups with low helper-to-pup ratios spent more time guarding young than those in groups with more helpers, an indication of load-lightening. Female helpers guarded more than male helpers, but this relationship weakened as pups grew. Subset analyses including data on helper age and wolf and prey density showed such factors did not significantly influence pup-guarding rates. We show that characteristics of individuals and groups have strong influences on pup-guarding behavior in gray wolves, but environmental factors such as food abundance and predation risk from conspecifics were not influential.

Introduction

Cooperative breeding refers to the care of related or unrelated young by non-breeding individuals in a group (Solomon & French 1997). In cooperatively breeding animals, both manipulative and observational studies have shown that the presence of helpers is critical to fitness of the breeders and persistence of the group as well (Mumme 1997; Solomon & French 1997; Courchamp et al. 2000, 2002; Courchamp & Macdonald 2001). Variation in group composition and environment can affect helping behavior (Russell 2004; Clutton-Brock 2006), but understanding is limited about how group size, individual traits, food

abundance, and predation risk might simultaneously influence an individual's decision to help.

In cooperatively breeding carnivores, foraging must often be performed at great distances from relatively immobile young. In such species, the ability to adequately guard young while other members in the group forage can be important for successful reproduction (Moehlman 1979; Pusey & Packer 1987; Courchamp & Macdonald 2001). For example, when group size dropped below five animals in African wild dogs (*Lycaon pictus*), groups reproduced less successfully than larger groups in part because of increased predation on unguarded young (Courchamp & Macdonald 2001; Courchamp et al. 2002). Group size can affect

how much time an individual devotes to guarding young (Courchamp & Macdonald 2001; Ruprecht et al. 2012). Distributing the workload of rearing young among members of a group (i.e., load-lightening; Crick 1992) has positive effects that have been documented across a broad range of taxa including birds (Crick 1992), mongooses (Clutton-Brock et al. 2001), and monkeys (Sanchez et al. 1999; Bales et al. 2001). Load-lightening can lead to increased survival and growth of young and in improved condition and survival of female breeders (Sanchez et al. 1999; Bales et al. 2001; Russell et al. 2003; Sparkman et al. 2011).

Although group size can affect helping behavior, individual traits and environmental variation can also be influential. In some primates, non-breeding females help more than non-breeding males and may be learning to care for young giving them an advantage once they initiate their own reproduction (Tardif et al. 1984). Additionally, non-breeding female wolves frequently inherit breeding positions in their natal group (Vonholdt et al. 2008) and group augmentation theory would predict they would help more in such situations (Kokko et al. 2001). Helper age can also influence behavior because older helpers often assist more with young than younger helpers (Lawton & Guindon 1981; Tardif 1997). Older helpers may be gaining experience as they prepare for dispersal and subsequent breeding opportunities of their own. Perception of predation risk on young can affect reproductive decision-making (Martin 2011) and behaviors such as the guarding of young (Courchamp & Macdonald 2001). Lastly, kin selection theory (Hamilton 1964) predicts that genetic relatedness will have a positive influence on helping behavior. This is true for many species but can vary as resources and conditions (e.g., territories, food abundance, and individual condition) change (Clutton-Brock 2006; Cornwallis et al. 2010).

Gray wolves (*Canis lupus*) often leave adults at den and rendezvous sites to guard relatively sessile offspring while other adult wolves in the group forage or rest (Packard 2003). Pup-guarding behavior is crucial for increases in group size and stability in other species with similar life-history strategies to wolves (Moehlman 1979; Courchamp & Macdonald 2001). Both grizzly bears (*Ursus arctos*) and other wolves prey on young wolf (Hayes & Baer 1992; Smith et al. 2010), and wolves are commonly known to aggressively chase grizzly bears and other wolves away from pup-rearing sites (Murie 1944; Peterson et al. 1984; Hayes & Mossop 1987; Mech et al. 1998; Smith & Ferguson 2005; Smith et al. 2013). The breeding female spends the most time of any group member guarding the young, but this diminishes markedly after

weaning when guarding by non-breeding (i.e., helper) wolves increases (Ruprecht et al. 2012). Wolves within a group vary widely in how much time they spend guarding young (Thurston 2002; Ruprecht et al. 2012), but previous studies were understandably limited by sample size and an ability to measure many covariates of interest. Therefore, we have a poor understanding of how individual, group, and environmental variation interact to affect helping behavior.

We studied guarding behavior to provide insights into differences in individual, group, and environmental factors and their influence on helping behavior in gray wolves. Specifically, we hypothesized that (1) individuals in groups with relatively more helpers than young spend less time guarding pups, (2) female helpers spend more time guarding pups than male helpers, (3) older helpers help more than younger helpers, and (4) helping behavior is contingent on food availability and guarding of pups decreases as food becomes more scarce.

Study Areas

Our four study areas were in Idaho, Montana, Yellowstone National Park (YNP), Wyoming, and Alberta, Canada. Generally, Idaho and Montana are 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). Wolves were common and at moderate densities in both Idaho and Montana. Groups within our study areas in Idaho did not overlap the range of grizzly bears whereas some, but not all, of our groups in Montana did. Black bears (*U. americanus*), cougars (*Puma concolor*), coyotes (*C. latrans*), and wolves were present in all of our study areas. Public harvest of wolves began in both states in 2009, and control actions to address livestock depredations were rare in our study groups. YNP is dominated by lodgepole pine forests and expansive meadow systems. YNP is relatively dry and precipitation averages 47 cm annually, and temperature fluctuations range from -39°C in winter to 30°C in summer at Yellowstone Lake (Western Regional Climate Center 2014). Wolves and grizzly bears both exist at high densities, and there is no hunting by humans inside YNP. Lastly, southwest Alberta is a highly diverse landscape where mountainous forests meet the dry short-grass prairie region. Mountain forests are dominated by Douglas fir (*Pseudotsuga*

menziesii) and lodgepole pine forests. Expansive aspen (*Populus tremuloides*) forests are found where mountains meet prairie dominated by livestock grazing. Temperatures range from -32°C to 23°C and precipitation averages 40 cm annually on the prairie (Alberta Agriculture and Rural Development 2014). Wolf densities are thought to be low in southwest Alberta whereas grizzly bears are abundant, and wolf control actions and human harvest are common.

Methods

It was not possible to record data blindly because our study involved focal animals in the field. Gray wolves were captured by management agencies as part of monitoring and research efforts and by University of Montana personnel (Animal Use Protocol 008-09MMMCWRU and University of Alberta Animal Care Protocol no. 565712) from 2001 to 2012. Captured wolves were fitted with Global Positioning System (GPS) collars from 2001 to 2012 (Alberta 2008–2009; Idaho 2007–2012; Montana 2008–2010; YNP 2001–2012). GPS collars (Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA) were programmed to acquire three to eight locations at evenly spaced intervals daily. Several collars in Alberta and YNP were deployed as part of predation studies and acquired 48 or 24 locations daily spaced 0.5–1.0 h apart. Wolves were sexed and aged via tooth wear at the time of capture; breeding status was determined at time of capture or after subsequent monitoring (US Fish and Wildlife Service [USFWS] 2002–2013). We only used the age of helpers for analyses in this study, and they were generally aged as pups (0–1 yr), subadults (1–3 yr), or adults (≥ 3 yr) at the time of capture. We added a year to the age of the animal if it was marked for multiple years. Because it can be difficult to determine age from tooth wear >3 yr, we considered all such animals as one age class, >3 yr old.

We plotted wolf locations from 15 Apr. to 1 Sept. for each year. Because guarding rates between age classes shift markedly before and after weaning (Ruprecht et al. 2012), we separated locations into pre-weaning (15 Apr.–1 Jun.) and post-weaning (2 Jun.–1 Sept.) seasons (Kreeger 2003). Wolves rear pups at den sites prior to weaning; once pups are weaned but too small to travel with adults, packs relocate pups to rendezvous sites (Joslin 1967) where pups remain while adults leave to hunt and return with food (Mech & Boitani 2003). We assumed distances >500 m from pup-rearing sites would make detecting and alerting the pups to predators ineffective. Additionally, pups are mobile around denning and rendezvous sites, and

it is likely that adults were near pups when within 500 m of a pup-rearing site. Although subjective, we assumed an individual wolf was in a position to guard pups if its location fell within a 500-m buffer of the group's den or rendezvous site location (Ruprecht et al. 2012). We estimated the proportion of time spent guarding pups for each individual in each year as the ratio of locations <500 m from den or rendezvous site to the total number of locations, before and after weaning. Because of the coarse spatial scale of our analyses (i.e., whether a location fell in or out of a 500-m buffer), we assumed that location error and variation due to collar brands and location schedules had minimal effects on our estimates. Where den and rendezvous site locations were not known from ground surveys and monitoring work (64% $n = 312$), we defined a cluster of GPS locations as a pup-rearing site when >10 locations were within 500 m of one another for >6 d. Clusters of locations can also indicate kill sites for wolves, but 85% of kills in YNP were abandoned after 3 d and none were found active after 5 d (Metz et al. 2011). GPS-collared wolves generally spent much more time clustered at a site than our minimum definition averaging 33.2 d at pup-rearing sites (SE = 2.3; Ausband et al. 2016). Using this definition of a pup-rearing site, we found that 87% ($n = 15$) of clusters defined as rendezvous sites from 2011 GPS collar data were within 150 m of highly suitable rendezvous site habitat in Idaho (Ausband et al. 2010). Two sites included in our analyses that were not in highly suitable habitat were ground-surveyed in 2012 and did appear to have been occupied the previous year as demonstrated by abundant old pup and adult scat, pup chew toys, bed sites, and devegetated pup play areas and trails.

The numbers of helpers and pups in each group were acquired via radiotelemetry flights or ground surveys conducted in summer (US Fish and Wildlife Service [USFWS] 2002–2013). Some group counts in Idaho were derived from non-invasive genetic sampling of scats at rendezvous sites (Ausband et al. 2010; Stenglein et al. 2011; Stansbury et al. 2014). Scats <2.5 cm were considered pup and >2.5 cm adult (Stenglein et al. 2011; Stansbury et al. 2014). We subtracted two (to represent the breeding pair) from the number of adults in each group to estimate the number of helpers that were present. It is plausible that individuals died over the pup-rearing season and our helper counts could be biased high. Hunting and trapping did not overlap the pup-rearing season in our study areas and dispersal generally occurs later in the fall/early winter (Jimenez et al. In Review); thus, we assume our helper counts were accurate.

In the northern range of YNP, however, counts of wolves approximated a census (D. Smith, YNP, unpublished data); we therefore used estimated wolf density (wolves/1000 km²) as a measure of predation risk for YNP. We estimated prey density (elk/km²) annually for 10 focal groups in the YNP northern range using aerial elk counts from the prior winter (Northern Yellowstone Cooperative Wildlife Working Group 2012).

We arcsine-transformed the proportions to ensure we met assumptions of regression and normally distributed data. We used a generalized linear mixed-effects model (GLMM) with proportion of time spent guarding pups as the dependent variable. We included explanatory covariates of the ratio of helpers (i.e., non-breeding adults) to pups in the group, and breeding status and sex of each wolf as a factor (four levels, breeding female, breeding male, non-breeding female, non-breeding male) with non-breeding males as the reference category to test for differences between male and females. We performed analyses using the lme4 package in Program R (Version 3.2.2).

We did not have covariates of prey density, wolf density, and helper age for every collared individual. Rather than impute these values, we conducted two additional GLMM analyses on individuals for which these covariates were available. These models included prey and wolf density (YNP northern range) and helper age (Montana, portions of Idaho, YNP). The reference category for breeding status and sex was set as breeding females in the prey and wolf density models and non-breeding females in the helper age model. We included random effects for individuals (18 individuals were included >1 yr), groups, study area, and year in all models (no study area random effect included in prey and wolf density model because data were from just one area, YNP). Because food abundance can affect group size, we tested for correlation using Pearson's product moment estimator between elk density and number of adults in groups using package Rcmdr in Program R.

Results

We collected location data from 92 GPS-collared wolves from 34 wolf groups for a total of 123 wolf-summer (Table 1). Non-breeding females guarded pups significantly more than non-breeding males before pups were weaned, but not after weaning (Fig. 1, Table 2). The ratio of helpers to pups did not influence guarding rates before pups were weaned, but strongly influenced guarding rates after pups were weaned (Table 2).

In our subset analyses, prey density varied widely (0.35–14.9 elk/km²) but did not influence the time spent guarding pups (Table 3). Wolf density did not predict pup-guarding before or after weaning in YNP (Table 3). Number of adults in each group was not correlated with prey abundance ($T = 0.001$, $p = 0.99$, correlation = 0.001). Age of helpers ($n = 47$ wolf-summer) did not predict guarding rates before or after pups were weaned (Table 4).

Discussion

Helping behavior in wolves can take several forms: guarding, provisioning, and social development of pups. We show that characteristics of individuals and groups have strong influences on pup-guarding behavior in gray wolves, but we detected no effect from environmental factors such as food abundance and predation risk from conspecifics. Our work only partially supports findings from previous studies of helping behavior in cooperatively breeding species. Similar to other studies (Crick 1992; Clutton-Brock et al. 2001; Ruprecht et al. 2012), we observed load-lightening where individuals in large groups spent less time guarding young than their counterparts in smaller groups. Additionally, our hypothesis that pup-guarding rates would decline as food became less abundant was not supported. Our results did not support other findings from previous studies, chiefly, that helper age and the density of wolves have strong influences on helping behavior (Tardif et al. 1984; Tardif 1997; Clutton-Brock 2006). A helper's experience or ability may be less important than maintaining a large group size in highly territorial species such as wolves that breed once a year. A group of experienced helpers may not be as important to breeder fitness as maintaining an adequate number of helpers to reduce workload.

Table 1: Number of GPS-collared wolves used to estimate guarding rates of pups in Alberta, Canada, Idaho, Montana, and Yellowstone National Park, Wyoming, USA, 2001–2012

Study area	No. breeding females	No. breeding males	No. non-breeding females	No. non-breeding males	No. wolf groups
Alberta	2	0	1	0	2
Idaho	10	9	26	11	12
Montana	4	3	4	1	8
Yellowstone	5	3	11	7	12
Total ^a	21	15	42	19	34

^a $n > 92$ wolves because five wolves changed breeding status over the course of the study.

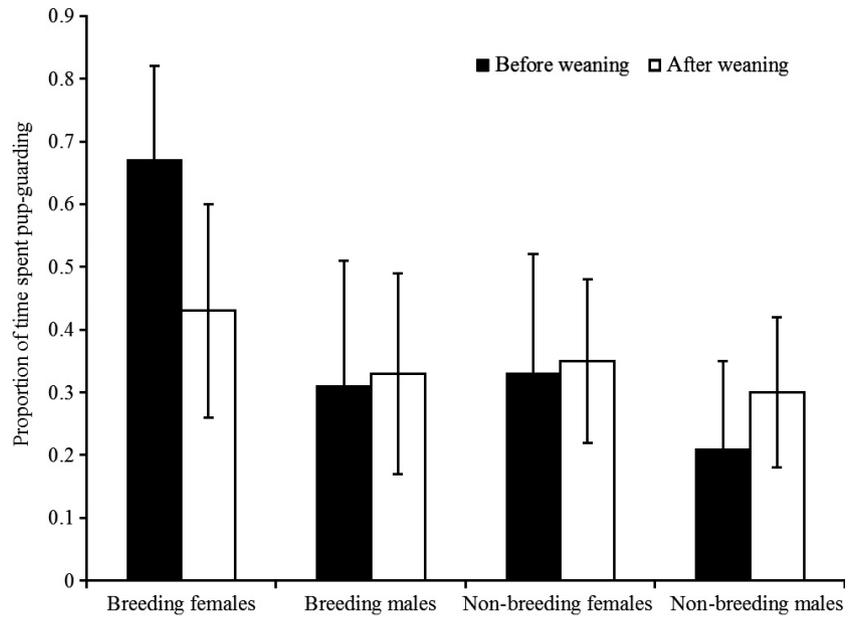


Fig. 1: Pup-guarding rates for gray wolves before and after weaning in Alberta, Canada, Idaho, Montana, and Yellowstone National Park, Wyoming, USA, 2001–2012. Error bars represent the 95% CI.

Table 2: Coefficients for covariates and sample sizes from generalized linear mixed models predicting guarding rates of wolf pups as a function of breeding status and sex, and helper:pup ratio. Models predict pup-guarding rates before and after weaning in Alberta, Canada, Idaho, Montana, and Yellowstone National Park, Wyoming, 2001–2012

	Intercept	Breeding status and sex ^a	Helper:pup ratio	n
Pre-weaning	0.22	BF: 0.58 (p < 0.0001) BM: 0.12 (p = 0.04) NBF: 0.14 (p = 0.007) NBM: 0	0.0008 (p = 0.97)	80
Post-weaning	0.38	BF: 0.17 (p = 0.0003) BM: 0.02 (p = 0.68) NBF: 0.06 (p = 0.12) NBM: 0	−0.05 (p = 0.003)	84

^aBF, breeding females; BM, breeding males; NBF, non-breeding females; NBM, non-breeding males.

Table 3: Coefficients for covariates from generalized linear mixed models predicting guarding rates of wolf pups as a function of breeding status and sex, helper:pup ratio, and prey and surrounding wolf density. Models predict pup-guarding rates before and after weaning in Yellowstone National Park, Wyoming, 2001–2012. Analyses were based on 27 wolf-summers from Table 2, where estimates of prey density and wolf density were available for individual wolves

	Intercept	Breeding status and sex ^a	Helper:pup ratio	Prey density	Wolf density
Pre-weaning	0.58	BM: −0.23 (p = 0.02) NBF: −0.30 (p < 0.0001) NBM: −0.38 (p < 0.0001) BF: 0	−0.04 (p = 0.23)	−0.008 (p = 0.45)	0.16 (p = 0.65)
Post-weaning	0.77	BM: −0.17 (p = 0.08) NBF: −0.10 (p = 0.11) NBM: −0.12 (p = 0.08) BF: 0	−0.02 (p = 0.48)	−0.01 (p = 0.25)	−0.11 (p = 0.76)

^aBM, breeding males; NBF, non-breeding females; NBM, non-breeding males; BF, breeding females.

Guarding young from predation can be an important behavior that enhances reproductive success in group-living carnivores (Moehlman 1979; Courchamp et al. 2002). While wolves are known to kill

conspecifics, even the very young (Smith et al. 2015), we found that wolf density was not predictive of pup-guarding rates. Predation of pups by both grizzly bears and wolves, while uncommon, can lead to loss of

Table 4: Coefficients for covariates from generalized linear mixed models predicting guarding rates of wolf pups as a function of helper sex, age, and ratio to pups. Models predict pup-guarding rates before and after weaning in Idaho, Montana, and Yellowstone National Park, Wyoming, 2001–2012 and were based on 44 wolf-summers from Table 2, where estimates of helper age were available for individual wolves. Data from Montana were not available for pre-weaning analysis

	Intercept	Breeding status and sex ^a	Helper:pup ratio	Helper age
Pre-weaning	0.48	M: -0.17 (p = 0.0009) F: 0	-0.09 (p = 0.02)	Age=1: 0 Age=2: 0.0008 (p = 0.99) Age=3: -0.18 (p = 0.29) Age>3: 0.06 (p = 0.38)
Post-weaning	0.42	M: -0.05 (p = 0.18) F: 0	-0.06 (p = 0.03)	Age=1: 0 Age=2: -0.03 (p = 0.51) Age=3: 0.12 (p = 0.34) Age>3: -0.04 (p = 0.41)

^aM, non-breeding males; F, non-breeding females.

entire litters (Hayes & Baer 1992; Smith et al. 2010); thus, investing time in guarding regardless of predator densities could still be advantageous. The median number of adults available to guard pups was generally high ($\bar{x} = 7$) in our study; thus, groups may have had adequate protection of young regardless of the presence or abundance of predators. Furthermore, because wolves are territorial, they can decrease the chance that neighboring wolves will encounter their pups by not placing pup-rearing sites near the edges of their territories (Ciucci & Mech 1992). Territorial behaviors such as scent marking and howling may further decrease aggressive wolf encounters with a group's young. Lastly, our relatively small sample size ($n = 27$) may have affected our ability to measure an effect of conspecific density on guarding rates.

Our hypothesis that individuals in groups with relatively more helpers than young spend less time guarding pups was supported but only after pups were weaned. Before pups were weaned, pups were in relatively defensible dens and breeding females were frequently present (Fig. 1). Additionally, it appeared that both non-breeding females and breeding males were also present approximately 1/3 of the time before pups were weaned (Fig. 1). After weaning, breeding females were present less often, pups were more mobile, and groups no longer occupied dens. Pups may be more vulnerable to predation when wolf groups occupy aboveground rendezvous sites after weaning; thus, helping behavior in the form of pup-guarding may be more important during this time. Similar to Ruprecht et al. (2012), we found that individuals in groups with fewer helpers per pup spent more time guarding pups than those in groups with more helpers. Individuals in small groups, or those with low helper-to-pup ratios, increase their time spent guarding young, presumably at the cost of

obtaining food for both themselves and pups. Our findings suggest that load-lightening occurs within groups of wolves. The effects of such load-lightening on reproduction in wolves are not known, but it may explain in part why wolf pups have higher survival and breeding females have increased fitness in large groups than in small groups (Sparkman et al. 2011; Stahler et al. 2013). Our counts of individuals in groups may be slightly conservative particularly for larger groups where all individuals may not be visually or genetically detected during sampling. Consequently, the effect of group size on helping behavior may be more marked than we observed. Although still negative, we observed a weaker effect of helper:pup ratio on guarding rates in our subset predator/prey model (YNP only) and believe this could be due to decreased sample size and its effect on statistical significance.

Our hypothesis that female helpers gain experience rearing pups and thus spend more time guarding than male helpers was strongly supported ($p = 0.007$) before pups were weaned but only weakly supported after weaning ($p = 0.12$). Other studies have found non-breeding males to guard less often during weaning (Ballard et al. 1991) and our findings support this because non-breeding males guarded less than non-breeding females and both breeding males and females. After pups were weaned, however, non-breeding males appeared to help more and only differed significantly from breeding females in time spent pup-guarding (Table 2, Fig. 1). Group augmentation theory (i.e., helpers increase group productivity and thus increase their own fitness) predicts that the sex which is most philopatric will help most (Kokko et al. 2001) and female wolves are slightly philopatric in the US Rocky Mountains (Jimenez et al. In Review). Female philopatry, while present, may not

be marked enough in the wolves we studied to expect strong differences in helping behavior between the sexes. Alternatively, the relative equivalence of help between males and females post-weaning may be because help from males is higher than what might be expected (e.g., Tardif et al. 1984) due to social coercion or the threat of eviction from the group if they do not help (Clutton-Brock 2006).

Our hypothesis that older helpers help more than younger helpers was not supported; we found no evidence that the age of helpers affected guarding rates. For animals that forage for scattered prey that are difficult to capture, gaining experience locating and securing food may be more important to the success of future breeding attempts than learning how to protect young, which may be a comparatively easier behavior to learn. Alternatively, older helpers may not pup-guard more than younger helpers because their experience is needed for hunting. If this were the case, however, younger animals should be found at pup-rearing sites more frequently than older helpers. We did not find this to be true. Harrington et al. (1983) hypothesized that non-breeding wolves may not be helping when attending pup-rearing sites, but by being near a central location used by foraging group members, they are obtaining food and information on kills, particularly when prey densities are low.

Our hypothesis that helping behavior is contingent on food availability and that guarding of pups decreases as food becomes scarce was not supported. We found that prey density did not have a strong influence on an individual's time spent guarding pups. Harrington et al. (1983) hypothesized that a benefit of helping behavior is increased acquisition of food; thus, helpers may spend more time near pup-rearing sites when food is scarce. Moehlman (1979), however, found no evidence that helping behavior was contingent on food availability in black-backed jackals (*C. mesomelas*). Similarly, Potvin et al. (2004) found no relationship between time spent at den and rendezvous sites and prey density for wolves in the Midwest USA. Our subset predator/prey model had a smaller sample size than our full model (Table 2) and could have affected our ability to measure an effect of food availability on guarding rates.

We found individuals in groups with fewer helpers spent more time guarding pups, presumably resulting in reduced provisioning rates as well. This finding suggests that small groups may make trade-offs between time spent guarding young and foraging (Courchamp et al. 2002). Such trade-offs may be costly when individuals in small groups

are forced to forage and guard less, placing offspring at greater risk of predation (Harrington et al. 1983). Additionally, time spent guarding at the cost of foraging can affect growth rates of both helpers and young creating the potential for diminished lifetime fitness of helpers and breeders alike. Mortality of breeding females during the pup-rearing period, even after pups are weaned, would also place pups at a greater risk of predation unless other individuals in the group compensate by increasing their guarding rates.

Acknowledgements

Anonymous reviewers provided valuable suggestions and professional critiques. Our manuscript is greatly improved as a result of their time and effort and we thank them. We also thank L. Bradley, J. Gude, G. Hale, J. Holyan, J. Husseman, K. Laudon, C. Mack, M. Metz, M. Nordhagen, K. Oelrich, L. Rich, C. White, P. Zager, T. Martin, H. Cooley, and L.S. Mills helped with early hypothesis development and manuscript reviews. We received funding from the Regina Bauer Frankenberg Foundation for Animal Welfare, Eppley Foundation for Scientific Research, Idaho Department of Fish and Game, and a Wesley M. Dixon Fellowship at The University of Montana. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Literature Cited

- Alberta Agriculture and Rural Development. 2014 <<http://agriculture.alberta.ca/acis/alberta-weather-data-viewer.jsp>>. Accessed 10 April 2014.
- 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. *J. Wild. Mngmnt.* **74**, 1043–1049.
- Ausband, D. E., Mitchell, M. S., Bassing, S. B., Nordhagen, M., Smith, D. W. & Stahler, D. R. 2016: Dog days of summer: influences on decision of wolves to move pups. *J. Mamm.* **97**, 1282–1287. doi: 10.1093/jmammal/gyw114.
- Bales, K., O'Herron, M., Baker, A. J. & Dietz, J. M. 2001: Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Prim.* **54**, 211–221.
- Ballard, W. B., Ayres, L. A., Gardner, C. L. & Foster, J. W. 1991: Den site activity patterns of gray wolves *Canis lupus*, in Southcentral Alaska. *Can. Field Nat.* **105**, 497–504.

- Ciucci, P. & Mech, L. D. 1992: Selection of wolf dens in relation to winter territories in northeast Minnesota. *J. Mamm.* **73**, 899–905.
- Clutton-Brock, T. H. 2006: Cooperative breeding in mammals. In: *Cooperation in Primates and Humans: Mechanisms and Evolution*, (Kappeler, P. M. & vanSchaik, C. P., eds). Springer Publishing, Berlin, USA, pp. 173–190.
- Clutton-Brock, T. H., Brotherto, P. N. M., O’Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G. M. 2001: Contributions to cooperative rearing in meerkats. *Anim. Behav.* **61**, 705–710.
- Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. 2010: Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972.
- Courchamp, F. & Macdonald, D. W. 2001: Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Anim. Cons.* **4**, 169–174.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. 2000: Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. *Anim. Cons.* **3**, 277–285.
- 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 *Lycaon pictus*. *Behav. Ecol.* **13**, 20–27.
- Crick, H. Q. P. 1992: Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis* **134**, 56–61.
- Hamilton, W. D. 1964: The genetical evolution of social behavior. I. *J. Theo. Biol.* **7**, 1–16.
- Harrington, F. H., Mech, L. D. & Fritts, S. H. 1983: Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behav. Ecol. Sociob.* **13**, 19–26.
- Hayes, R. D. & Baer, A. 1992: Brown bear, *Ursus arctos*, preying upon gray wolf, *Canis lupus*, pups at wolf den. *Can. Field Nat.* **106**, 381–382.
- Hayes, R. D. & Mossop, D. H. 1987: Interactions of wolves, *Canis lupus*, and brown bears, *Ursus arctos*, at a wolf den in the Northern Yukon. *Can. Field Nat.* **101**, 603–604.
- Jimenez, M. D., Bangs, E. E., Boyd, D. K., Smith, D. W., Becker, S. A., Mack, C. M., Holyan, J., Sime, C. A., Ausband, D. E., Woodruff, S. P., Nadeau, S., Asher, V. J., Bradley, E. H. & Laudon, K. In Review: Wolf dispersal in the northern Rocky Mountains in western United States: 1993–2008. *J. Wild. Mngmnt.*
- Joslin, P. W. B. 1967: Movements and home sites of timber wolves in Algonquin Park. *Am. Zool.* **7**, 279–288.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001: The evolution of cooperative breeding through group augmentation. *Proc. Roy. Soc Lond. B.* **268**, 187–196.
- Kreeger, T. J. 2003: The internal wolf: physiology, pathology and pharmacology. In: *Wolves: Behavior, Ecology, and Conservation*, (Mech, L. D. & Boitani, L. eds). The Univ. of Chicago Press, Chicago, IL, pp. 192–217.
- Lawton, M. F. & Guindon, C. F. 1981: Flock composition, breeding success, and learning in the brown jay. *Condor* **82**, 27–33.
- Martin, T. E. 2011: The cost of fear. *Science* **34**, 1353–1354.
- Mech, L. D. & Boitani, L. 2003: Wolf social ecology. In: *Wolves: behavior, ecology, and conservation*. (Mech, L. D., Boitani, L., eds). The Univ. of Chicago Press, Chicago, IL, USA, pp. 1–34.
- Mech, L. D., Adams, L. G., Meier, T. J., Burch, J. W. & Dale, B. W. 1998: *The Wolves of Denali*. Univ. of Minnesota Press, USA.
- Metz, M. C., Vucetich, J. A., Smith, D. W., Stahler, D. R. & Peterson, R. O. 2011: Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PLoS One* **6**, e17332.
- Moehlman, P. D. 1979: Jackal helpers and pup survival. *Nature* **277**, 382–383.
- Mumme, R. L. 1997: A bird’s-eye view of mammalian cooperative breeding. In: *Cooperative Breeding in Mammals*. (Solomon, N. G., French, J. A., eds). Cambridge Univ. Press, UK, pp. 364–388.
- Murie, A. 1944: *The Wolves of Mount McKinley*. Univ. of Washington Press, Seattle, USA.
- Northern Yellowstone Cooperative Wildlife Working Group, 2012: Winter Classification of Northern Yellowstone Elk, January 2012 through March 2012
- Packard, J. M. 2003: Wolf behavior: reproductive, social, and intelligent. In: *Wolves: behavior, ecology, and conservation*. (Mech, L. D., Boitani, L., eds). The Univ. of Chicago Press, Chicago, IL, USA, pp. 35–65.
- Peterson, R. O., Woolington, J. D. & Bailey, T. N. 1984: *Wolves of the Kenai Peninsula, Alaska*. Wild. Mono. **88**, 3–52.
- Potvin, M. J., Peterson, R. O. & Vucetich, J. A. 2004: Wolf homesite attendance patterns. *Can. J. Zool.* **82**, 1512–1518.
- Pusey, A. E. & Packer, C. 1987: The evolution of sex-biased dispersal in lions. *Behav.* **101**, 275–310.
- Ruprecht, J. S., Ausband, D. E., Mitchell, M. S., Garton, E. O. & Zager, P. 2012: Homesite attendance based on sex, reproductive status and number of helpers in gray wolf packs. *J. Mamm.* **93**, 1001–1005.
- Russell, A. F. 2004: Mammals: comparisons and contrasts. In: *Ecology and Evolution of Cooperative Breeding in Birds*, (Koenig, W. D. & Dickinson, J. L. eds). Cambridge Univ. Press, New York, USA, pp. 210–227.
- Russell, A. F., Sharpe, L. L., Brotherton, P. N. M. & Clutton-Brock, T. H. 2003: Cost minimization by helpers in cooperative vertebrates. *Proc. Natl Acad. Sci. USA* **100**, 3333–3338.

- Sanchez, S., Pelaez, F., Gil-Burmann, C. & Kaumanns, W. 1999: Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *Am. J. Prim.* **48**, 99–111.
- Smith, D. W. & Ferguson, G. 2005: Decade of the Wolf. The Lyons Press, Guilford, USA.
- Smith, D. W., Stahler, D. R., Albers, E., McIntyre, R., Metz, M., Cassidy, K., Irving, J., Raymond, R., Zaranek, H., Anton, C. & Bowersock, N. 2010: Yellowstone wolf project: Annual report 2009. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2010-06.
- Smith, D. W., Stahler, D. R., Stahler, E., Metz, M., Quimby, K., McIntyre, R., Ruhl, C., Martin, H., Kindermann, R., Bowersock, N. & McDevitt, M. 2013: Yellowstone wolf project: Annual report 2012. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2013-02.
- Smith, D. W., Metz, M. C., Cassidy, K. A., Stahler, E. E., McIntyre, R. T., Almberg, E. S. & Daniel, R. S. 2015: Infanticide in wolves: seasonality of mortalities and attacks at dens support evolution of territoriality. *J. Mamm.* **96**, 1174–1183.
- Solomon, N. G. & French, J. A. 1997: Cooperative Breeding in Mammals. Cambridge Univ. Press, Cambridge, UK.
- Sparkman, A. M., Adams, J., Beyer, A., Steury, T. D., Waits, L. & Murray, D. L. 2011: Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). *Proc. Roy. Soc. B.* **278**, 1381–1389.
- Stahler, D. R., MacNulty, D. R., Wayne, R. K., vonHoldt, B. & Smith, D. W. 2013: The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *J. Anim. Ecol.* **82**, 222–234.
- Stansbury, C. R., 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. *J. Wild. Mngmnt.* **78**, 1040–1049.
- Stenglein, J. L., Waits, L. P., Ausband, D. E., Zager, P. & Mack, C. 2011: Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. *J. Mamm.* **92**, 784–795.
- Tardif, S. D. 1997: Parental behavior and evolution of alloparental care. In: Cooperative Breeding in Mammals, (Solomon, N. G. & French, J. A. eds). Cambridge Univ. Press, Cambridge, UK, pp. 11–33.
- Tardif, S. D., Richter, C. B. & Carson, R. L. 1984: Effects of sibling-rearing experience on future reproductive success in two species in Callitrichidae. *Am. J. Prim.* **6**, 377–380.
- Thurston, L. 2002: Homesite attendance as a measure of alloparental and parental care by gray wolves (*Canis lupus*) in northern Yellowstone National Park. MS Thesis. Texas A and M Univ., College Station, TX, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2002: Rocky Mountain Wolf Recovery 2001 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2003: Rocky Mountain Wolf Recovery 2002 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2004: Rocky Mountain Wolf Recovery 2003 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2005: Rocky Mountain Wolf Recovery 2004 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2006: Rocky Mountain Wolf Recovery 2005 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2007: Rocky Mountain Wolf Recovery 2006 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, and USDA Wildlife Services 2008: Rocky Mountain Wolf Recovery 2007 Annual Report. Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, Montana Fish, Wildlife and Parks, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Idaho Fish and Game, and USDA Wildlife Services 2009: Rocky Mountain Wolf Recovery 2008 Interagency Annual Report. (Sime, C. A. & Bangs, E. E. eds.), Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Nez Perce Tribe, National Park Service, Montana Fish, Wildlife and Parks, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Idaho Fish and Game, USDA Wildlife Services 2010: Rocky Mountain Wolf Recovery 2009 Interagency Annual Report, (Sime, C. A. & Bangs, E. E. eds.), USFWS, Ecological Services, Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Montana Fish, Wildlife and Parks, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Washington Department of Wildlife, Oregon Department of Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services 2011: Rocky Mountain Wolf Recovery 2010 Interagency Annual Report. (Sime, C. A. & Bangs, E. E. eds.), Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife and Parks, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah

- Department of Natural Resources, and USDA Wildlife Services 2012: Northern Rocky Mountain Wolf Recovery Program 2011 Interagency Annual Report. (Jimenez, M. D. & Becker, S. A. eds.), Helena, MT, USA.
- US Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife and Parks, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services 2013: Northern Rocky Mountain Wolf Recovery Program 2012 Interagency Annual Report. (Jimenez, M. D. & Becker, S. A. eds.), Helena, MT, USA.
- Vonholdt, B. M., Stahler, D. R., Smith, D. W., Earl, D. A., Pollinger, J. P. & Wayne, R. K. 2008: The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Mol. Ecol.* **17**, 252–274.
- Western Regional Climate Center 2014: Historical climate information. <<http://www.wrcc.dri.edu>>. Accessed 10 April 2014.