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Differential wolf-pack-size persistence and the role of risk when hunting dangerous prey

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Abstract
Risk to predators hunting dangerous prey is an emerging area of research and could account for possible persistent differences in gray wolf (*Canis lupus*) pack sizes. We documented significant differences in long-term wolf-pack-size averages and variation in the Superior National Forest (SNF), Denali National Park and Preserve, Yellowstone National Park, and Yukon, Canada ($p < 0.01$). The SNF differences could be related to the wolves' risk when hunting primary prey, for those packs ($N = 3$) hunting moose (*Alces americanus*) were significantly larger than those ($N = 10$) hunting white-tailed deer (*Odocoileus virginianus*) ($F_{1,8} = 16.50$, $p = 0.004$). Our data support the hypothesis that differential pack-size persistence may be perpetuated by differences in primary prey riskiness to wolves, and we highlight two important extensions of this idea: (1) the potential for wolves to provision and defend injured packmates from other wolves and (2) the importance of less-risky, buffer prey to pack-size persistence and year-to-year variation.

Keywords
alternate prey, defence, group size, hunting, pack size, risk, social provisioning, wolves.

1. Introduction

Many hypotheses, not necessarily mutually exclusive, exist regarding optimal pack size in wolves (see Fuller et al., 2003 for review). A relatively new idea and emerging area of research related to optimal-pack size is risk

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to the predator (injury or death) while hunting dangerous prey (MacNulty et al., 2012, 2014; Mukherjee & Heithaus, 2013; Mech et al., 2015). Recently, the concept of foraging risk for predators hunting large, dangerous prey has been applied to hunting-group size (subset of pack members that were at least superficially participating in a hunt) and hunting success in grey wolves in Yellowstone National Park (YNP) (MacNulty et al., 2012, 2014). There, MacNulty et al. (2012) demonstrated non-linear effects of group size on hunting success of elk (*Cervus elaphus*). Specifically, hunting success of elk did not measurably improve beyond 3–4 wolves due to free-riding (wolves withholding effort) apparently because the cost of hunting prey exceeded the increased hunting success with each additional wolf beyond that threshold (MacNulty et al., 2012). Additional wolves beyond 4 appeared to only superficially participate, probably to gain access to the kill (MacNulty et al., 2012). Wolves hunting elk face increasing risk (dangerous hooves kicking and trampling, antlers stabbing) as the hunt progresses from attacking (lowest risk) to selecting and killing (highest risk) (MacNulty et al., 2009). Interestingly, the withholding of effort varied according to the risk of the task with active participation declining most rapidly with the riskiest task (killing) and most slowly with the safest task (attacking) (MacNulty et al., 2012). MacNulty et al. (2012) concluded that "the influence of group size on hunting success per se is unlikely to promote the formation and maintenance of larger predator groups" (MacNulty et al., 2012: 7). However, subsequent YNP research showed that hunting-group size levelled off at a larger size for successful bison (*Bison bison*) capture (riskier) than for elk (MacNulty et al., 2014). Bison were considered riskier because they are larger, were three times more difficult to kill than elk in YNP (MacNulty et al., 2014), and were more likely to injure or kill wolves (MacNulty, 2002). Models, based on observations of hunting-group sizes up to 16, indicated that success levelled off at 4 wolves for attacking bison and 11 for capturing them (MacNulty et al., 2014). Thus, MacNulty et al. (2014: 1) concluded (in contrast to MacNulty et al., 2012) that "improved ability to capture formidable prey could therefore promote the formation and maintenance of large predator groups".

However, research has not focused on whether differential-group sizes related to risky prey persist long term and has not explored potential post-hunt dynamics (e.g., provisional care and defence from neighbouring wolves of injured group members, changes in primary hunting roles) related to group-size persistence. During our long-term wolf and white-tailed deer study in the

Superior National Forest (SNF) (Mech, 2009), some packs seemed to persist at larger sizes while others remained smaller. We wondered if this apparent pattern was statistically detectable and whether it might also be present in other study systems. We hypothesized that relative risk while hunting prey, the possibility of packmate provisioning and defence of injured members, in combination with the availability of, or lack of, less risky prey may drive differential pack-size persistence.

Specifically, we examined:

(1) Whether apparent long-term-pack sizes were consistently and statistically larger or smaller among wolf packs in the SNF.

(2) Whether these apparent long-term-pack sizes were associated with primary prey in the SNF.

(3) Whether wolf packs in other study sites (i.e., Denali National Park and Preserve, Yellowstone National Park, and the Yukon) showed similar consistency in long-term-pack sizes, both within and among sites.

(4) Which factor (study site, pack, year) across study areas was the greatest source of variation in pack size.

2. Material and methods

Our primary study area comprised 2060 km^2 in the Superior National Forest, Minnesota, USA (48°N, 92°W; see Nelson & Mech, 1981 for a detailed description). We recorded maximum, winter, wolf-pack sizes during aerial surveys in the SNF from 1967 to 2012. The SNF harbours a long-established wolf population that feeds primarily on deer and moose (Nelson & Mech, 1981, 1986; Mech, 2009). After approximately 1977, likely owing to habitat and climatic conditions, the ungulate composition of our study area changed such that wolf packs in the northeast of our study area fed primarily on moose, whereas those in the southwest fed mainly on deer (Nelson & Mech, 1981, 1986; Mech, 2009).

We also analysed annual wolf-pack-count data (winter or early spring before parturition) from 3 other study sites with varying wolf population origins (1 recovering population, 1 reintroduced population, and 1 established population). We used published data following wolf control in the Yukon (1991–1996) from a recovering wolf population when wolf harvest was negligible (Hayes & Harestad, 2000). The primary prey was woodland caribou

(*Rangifer tarandus*) (Hayes & Harestad, 2000). We used data from publically available annual reports (1997–2013) on the reintroduced wolf population in Yellowstone National Park (YNP) (Yellowstone Wolf Project Reports, 1997–2013). Wolves inside YNP were legally protected, and their primary prey for most packs was elk (*Cervus elaphus*) (Yellowstone Wolf Project Reports, 1997–2013). We used published (Meier, 2009; Borg & Burch, 2014; Borg et al., 2015) and personally communicated (L. Adams, USGS; B. Borg, NPS; S. Arthur, NPS) data from Denali National Park and Preserve (DNPP) from 1986–2014 on the established wolf population where moose was the primary prey although some packs have access to caribou and Dall sheep (*Ovis dalli*) (Mech et al., 1998; L. Adams, USGS, pers. comm.). Subsistence and sport hunting and trapping of wolves were permitted in the Preserve and new park additions to DNPP, but all harvest (hunting and trapping) was prohibited in the area of the original Mt. McKinley National Park.

We considered a wolf pack as the same pack over time if it had not moved entirely out of its original territory. Some year-to-year territory shifting was expected, but we only considered it a different pack if the shift meant the pack was in a different environmental context and no longer using its former territory. Thus, for our analysis a pack's name was a spatial reference that was not necessarily based on genetic relationships (but could be, especially in the short term).

We used maximum wolf pack counts (either winter or early spring before parturition) as determined by the authors of each study and included only packs with at least 5 years of data. We deleted pack counts of 2 anytime it began a string of data so that the analysed data would include packs that had at least 1 year to reproduce.

We analysed data from 13 packs over 49 years in the SNF from 1967–2015 (306 pack years), 28 packs spanning 29 years in DNPP from 1986–2014 (249 pack years), 14 packs spanning 17 years in YNP from 1997–2013 (136 pack years) and 9 packs in the Yukon from 1991–1996 (40 pack years) (Figure 1).

We investigated pack-size characteristics both within and among the 4 study sites and assessed differential pack-size persistence (i.e., whether there were differences in the long-term pack-size averages and variation). We first parsed the total variation in pack size into 3 variance components: site-to-site, pack-to-pack nested within sites, and year-to-year nested within packs to assess where the major source of variation occurs in pack size. For the below mentioned analysis of variances tests (ANOVAs), we considered the

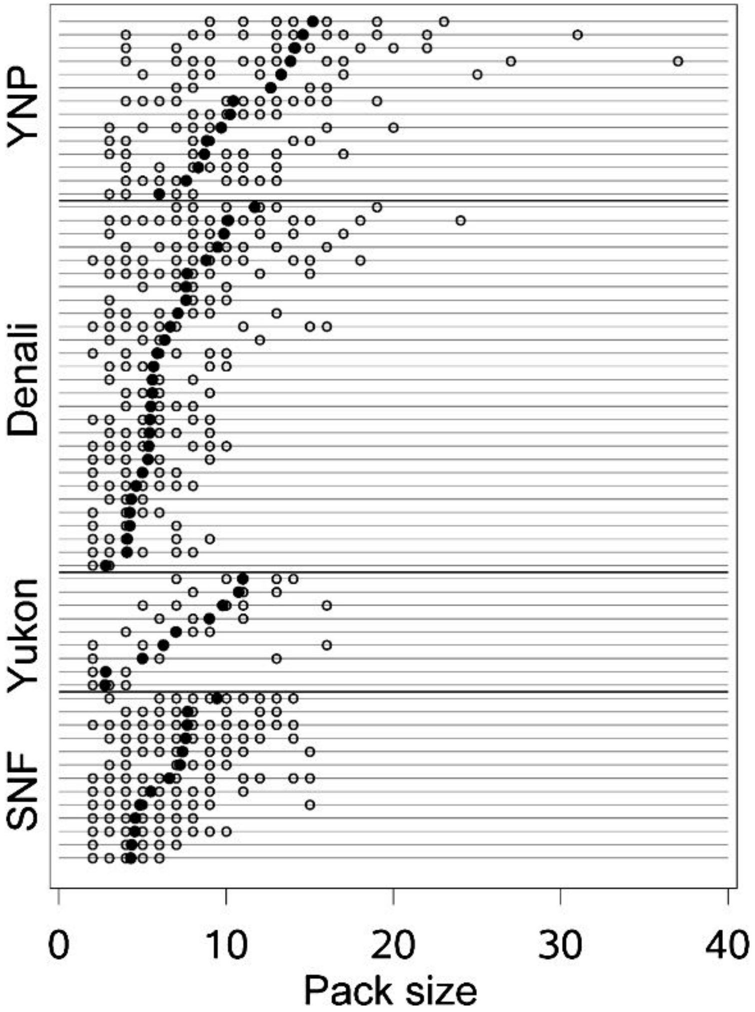

Figure 1. Overview of wolf-pack-size data from study sites (Yellowstone National Park (YNP), Denali National Park and Preserve (Denali), Yukon, and the Superior National Forest (SNF)), pack sizes (open circles) and mean pack sizes (filled circles). Circles may represent more than one data point. Each horizontal line with circles along the *y*-axis represents a different pack with each study site.

repeated-measures factor year as subsampling in time (Steel & Torrie, 1980). We used the mixed linear models procedure (PROC MIXED) in SAS (SAS Institute, 2014) to estimate variance components using the restricted maximum likelihood (REML) method and for all ANOVAs. Because elk population fluctuations dampened 10 years following wolf reintroduction to YNP (Mech & Barber-Meyer, 2015), we also used that procedure to independently assess whether YNP data from 1997–2004 and 2005–2013 needed to be analysed separately. Post-ANOVA comparisons of least-squares means (LSMEANS) among packs (or sites) were done in a Fisher's least significant difference (LSD) framework (Milliken & Johnson, 2009). ANOVAs with F-statistic p-values < 0.05 were considered as an indication of strong evidence for differences. Where applicable, we used Levene's Test (Milliken & Johnson, 2009) to compare variances in pack sizes among sites and within sites. To accommodate the repeated-measures factor year, we accounted for potential serial autocorrelation by using an assumed autoregressive lag-1 covariance structure and adjusted the degrees-of-freedom using the Kenward–Roger correction (Littell et al., 2006). We conducted separate ANOVAs (1) among all wolf packs within each study site, (2) among the 4 study sites and (3) among a reduced set of wolf packs within the SNF in which either moose or deer was the dominant prey for 1978–2015. We calculated simple correlations of the standard deviation of pack size versus mean pack size for each study site to assess whether larger packs tended to have larger variance.

3. Results

Across all study sites and years, year was the largest source of pack-size variation (68.0%), followed by study site (20.6%). Variation in wolf-pack sizes among packs only accounted for 11.4% of the total variation in pack sizes. Further, only YNP had statistically greater variation ($F_{3,60} = 10.62$, $p < 0.001$) and a larger mean pack size than the other sites ($F_{3,29.6} = 8.69$, $p < 0.001$) (Table 1 and Figure 1). YNP data from $\leqslant$2004 and $\geqslant$2005 were appropriate to analyse as one period because variation attributed to 'site' (in this case the 2 periods) was $<1\%$.

Correlations of the standard deviation of pack size with mean pack size indicated variation in pack size increased with mean pack size across all study sites (Table 1, Figure 2). The strongest association occurred at Denali ($r = 0.78$) with much less but still a positive association for packs from the Yukon ($r = 0.17$) (Table 1, Figure 2).

Within each site, differences in the persistence in pack sizes were detected ($p = 0.001$, Table 2), both with respect to variances in pack size and mean

Table 1.
Homogeneity of variances (Levene's Test: $F_{3,60} = 10.62$, $p < 0.001$) and means (ANOVA: $F_{3,29.6} = 8.69$, $p < 0.001$) of packs among Denali National Park and Preserve (DNPP), the Superior National Forest (SNF), Yellowstone National Park (YNP) and Yukon.

Study site	*N*	Variances of pack sizes		Mean pack sizes		Correlation	
		LSMean	SE	LSMean	SE	*r*	*p*
DNPP	28	2.21^a	0.19	6.19^a	0.44	0.78	<0.001
SNF	13	1.93^a	0.24	6.29^a	0.43	0.54	0.058
YNP	14	3.77^b	0.26	10.77^b	0.82	0.62	0.019
Yukon	9	2.24^a	0.40	7.63^a	1.26	0.17	0.665

N, number of packs; LSMeans (least squares means) followed by common superscript letter within columns are strongly similar; correlation is between mean pack size and standard deviation of pack size.

pack size (Table 2) (except the SNF did not show strong evidence of significant differences in pack-size variances among packs). All sites exhibited significant variation in mean pack size across years. In particular within the SNF, mean pack sizes followed a gradient of overlapping mean pack sizes from the smallest (mean pack size = 4.3, 14 years) to the largest (mean pack size = 9.5, 37 years) (Table 3). Other sites show a similar overlapping gradient in both mean pack size and large differences in variances among packs across study years (Figure 1). An analysis of a subset of the SNF site (10 packs from 1978–2015) indicated that packs preying primarily on moose (rather than deer) were larger ($F_{1,8} = 16.50$, $p = 0.004$) although only 3 'moose' packs were available for this subset analysis (Table 4 and Figure 3).

4. Discussion

Given that year contributed the greatest source of variation to pack size and because there are many confounding variables when examining wolf-pack-size persistence (e.g., both within and across study site, changes in prey and sympatric predator populations, diseases, climate, etc.) it is likely that there is not a single reason behind the differential pack-size persistence that we found in all study sites we examined. Primary-prey size and risk, prey suite, prey density, prey vulnerability (e.g., weather conditions such as snow depth, snow duration, icing events, etc.; Mech & Peterson, 2003), and territorial acquisition and defence (Cassidy, 2013; Cassidy et al., 2015; Smith et al., 2015), all contribute to determine persistent pack sizes. Indeed, wolf

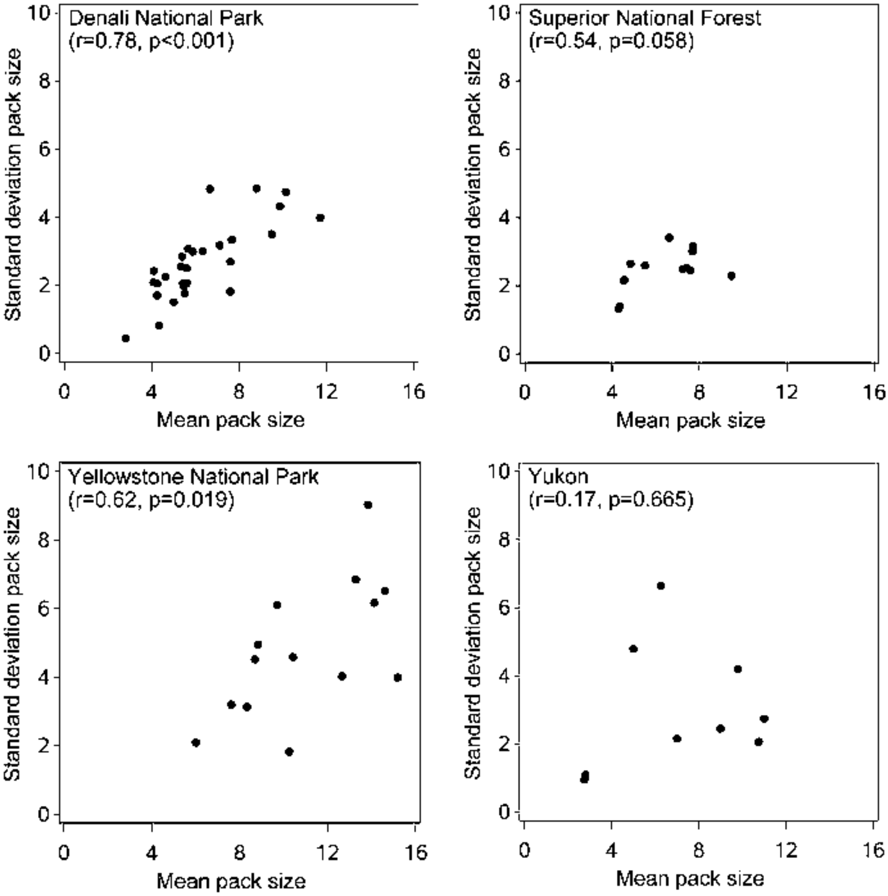

Figure 2. Correlations of the standard deviation of pack size versus mean pack size for Denali National Park and Preserve (Denali National Park), Superior National Forest, Yellowstone National Park and Yukon.

packs exist in dynamic and complex systems resulting in many confounding variables, especially when trying to compare across study sites.

However, despite the many sources of variation in our study area, we found evidence for persistent pack-size differences due to prey size and relative riskiness. We found that packs preying primarily on moose (mean pack size $= 8.2$, $N = 3$) were persistently larger than those preying primarily on deer (mean pack size $= 5.1$, $N = 10$) (even with small samples, $p < 0.01$). Although Fuller et al. (2003) found mean pack-size differences between packs that fed primarily on deer ($N = 10$) versus elk ($N = 3$) or versus cari-

Table 2.
Differential pack-size-persistence (variation in pack size and mean pack size) within Denali National Park and Preserve (DNPP), the Superior National Forest (SNF), Yellowstone National Park (YNP) and Yukon.

Study site	Variation in pack size		Mean pack size	
DNPP	$F_{27,221} = 2.27$	$p < 0.001$	$F_{27,206} = 4.16$	$p < 0.001$
SNF	$F_{12,293} = 1.48$	$p = 0.132$	$F_{12,269} = 11.30$	$p < 0.001$
YNP	$F_{13,122} = 1.85$	$p = 0.043$	$F_{13,95.1} = 2.93$	$p = 0.001$
Yukon	$F_{8,31.0} = 2.17$	$p = 0.058$	$F_{8,24.3} = 7.73$	$p < 0.001$

bou ($N = 2$) and moose ($N = 11$) versus elk ($N = 3$), they did not find a mean pack-size difference between packs that fed primarily on moose versus deer ($p = 0.24$) but they compared across 10 deer and 11 moose studies that varied in space and time. Thus, there were likely more confounding variables in the previous studies than in our within-SNF analysis. Nevertheless, the multiple-study-area data compiled by Fuller et al. (2003) showed that average maximum pack size for wolves preying on moose was larger (17,

Table 3.
Differential wolf-pack-size persistence (mean and SE) within the Superior National Forest ($F_{12,269.0} = 11.30$, $p < 0.001$).

Pack name	N (no. years)	Mean	SE
Farm Lk	14	4.3^{a}	0.7
Pagami Lk	10	4.3^{a}	0.8
Birch Lk	35	4.5^{a}	0.4
Little Gabbro Lk	19	4.6^{a}	0.6
Harris Lk	40	4.9^{ab}	0.4
Wood Lk	30	5.5^{b}	0.5
Quadga Lk	23	6.6^{c}	0.5
Perent Lk	8	7.3^{cd}	0.9
Ensign Lk	25	7.4^{d}	0.5
Sawbill Lk	24	7.6^{d}	0.5
Clear Lk	10	7.7^{d}	0.8
Jackpine Mtn	31	7.7^{d}	0.5
Malberg Lk	37	9.5^{e}	0.4

Shared superscript letters between packs after the 'Mean' indicate they are not significantly different.

Table 4.
Comparison of Superior National Forest packs (variation and mean pack size) after 1978 that fed mainly on moose or mainly on deer.

Main prey	N (no. packs)	Variation in pack size ($F_{1,6.17} = 0.84$, $p = 0.394$)		Mean pack size ($F_{1,8} = 16.50$, $p = 0.004$)	
		LSMean	SE	LSMean	SE
Deer	7	1.9	0.17	5.1	0.40
Moose	3	2.3	0.31	8.2	0.64

LSMean, least squares mean.

$N = 14$ populations) than those preying on deer (11, $N = 9$ populations) (Jędrzejewski et al., 2007). We suspect that, with pack-specific information on primary prey types, this difference in mean pack size by prey type may be present in the other study sites as well.

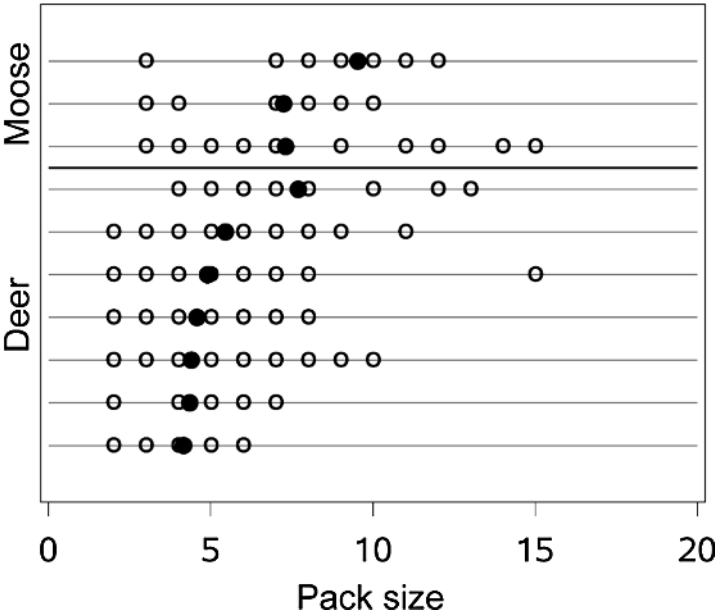

Figure 3. Comparison of Superior National Forest wolf-pack sizes after 1978 that fed mainly on moose or mainly on deer (separated by the dark line), pack sizes (open circles) and mean pack sizes (filled circles). Circles may represent more than one data point. Each horizontal line with circles along the y-axis represents a different pack.

Supplemental provisioning of small, low risk prey may also account for some variation within pack sizes. The moose packs evaluated in our SNF subset analysis live primarily in, or adjacent to, the Boundary Waters Canoe Area Wilderness. These wolves have greater access to beavers (*Castor canadensis*) (Barber-Meyer & Mech, unpublished data) than our deer packs. Although beavers are preyed upon more heavily during other seasons, they are also consumed during winter (Forbes & Theberge, 1996; Ibrahim, 2015; Mech et al., 2015). Beavers may be important to pack-size persistence because they are less risky to hunt compared to adult moose and even to calves that are defended by the dangerous hooves of their mothers. Also, supplemental beaver predation may allow wolves to enter fall at a higher nutritional plane, and beaver as a buffer prey may reduce within-pack competition for food, resulting in delayed dispersal, larger litters, and higher pup survival which would lead to larger packs. Similarly, in DNPP when snowshoe hares (*Lepus americanus*) were especially abundant, the hares may have supported relatively high wolf recruitment (a higher than average change from spring to fall) because of easier provisioning of young near the den site (Borg, unpublished data).

We found a consistent pattern of persistent pack-size differences across the study sites we examined, which is compelling, and we propose another, not mutually exclusive, hypothesis to explain differential pack-size persistence. Extra wolves above the optimal hunting-group-size thresholds are needed when packs hunt larger, riskier prey, like moose, to provide substitute hunters when other wolves are injured (to maintain near-optimal hunting-group size) and to allow for pack provisioning and defence of the injured.

The general tendency is for free-riding in wolves to increase as hunting-group-size increases, with the threshold for withholding effort higher for groups hunting very risky prey (MacNulty et al., 2012, 2014). Similarly, research on other large, cursorial, social predators demonstrated predators were more cooperative when hunting larger, riskier prey (e.g., African lions (*Panthera leo*); Scheel & Packer, 1991). Additionally, large predators were more successful at hunting large, difficult-to-catch prey when in larger groups up to a threshold (e.g., wild dogs (*Lycaon pictus*); Creel & Creel, 2002). Thus, we hypothesize when effective hunting-group size diminishes due to injured wolves hunting risky prey, that frequently free-riding wolves would exert more hunting effort.

Almberg et al. (2015) found that wolves with mange survived better if in a larger pack than a smaller pack, and these authors attributed this increased survival to increased social care and provisioning. If wolves care for and provision diseased pack members while they recover, might they do the same for wolves traumatically injured while hunting? Parent wolves are known to provision even healthy offspring up to at least 13-months old (Mech, 1995), but we know of no records of such provisioning after that age.

Breeders were more likely to attack and kill in large groups in YNP than non-breeders (MacNulty et al., 2012), perhaps due to different cost–benefit ratios for hunting risky prey (Mukherjee & Heithaus, 2013) given differences in their average relatedness to packmates. When breeders are injured from hunting risky prey, do non-breeders (more often free-riders than breeders) in larger packs provision and defend them (from neighbouring wolves) and assume a more active role in attacking and killing risky prey? If breeders subsequently heal, do the non-breeders resume more frequent free-riding? More generally, it will be important to test whether the survival of injured wolves varies given pack size, whether packmates provision and defend injured wolves until they heal and can hunt again, and whether free-riders actively fill the injured wolf's role as a hunter. Of course, quantification of foraging-related injuries to predators is difficult to measure and likely underestimated being based mostly on teeth or bones, with very little information available on soft-tissue injuries and recovery rates (Mukherjee & Heithaus, 2013).

One of the problems in evaluating hypotheses that may explain differential pack-size persistence is that wolf packs exist in dynamic and complex systems resulting in many confounding variables, especially when trying to compare across study sites. For example, variation in wolf pack size fluctuated widely across years except in SNF (Table 2). Furthermore, mean pack size was correlated with variation across all study sites, but the strength of the correlation ranged from high in DNPP to much lower in the Yukon (Table 1, Figure 2). In DNPP, many of the larger packs are subject to hunting (because their territories extend beyond the park's boundary) and, depending on the time of year, when a large pack loses a female breeder the pack can collapse from say 16 wolves to 2 (a decrease of 87.5%) presumed to be because of the loss of social cohesion (DNPP, 2016). The same event for a pack of 4 collapsing to 2 would only reduce the pack size by 50%, highlighting how factors that influence pack size may have greater effect on large packs.

Further study of site-specific differences and temporal nuances will improve our understanding of pack-size-persistence dynamics.

We encourage researchers to collect additional data (e.g., risk and consequences of hunting various prey, social provisioning and defence allowing healing from traumatic injuries, the degree to which wolves rely on less risky prey) that may explain differential pack-size persistence in their systems. We also suggest that differential group-size persistence and the role of provisional care (i.e., post-hunt dynamics particularly when hunting very risky prey) and defence from conspecifics or other species, may extend to other social, large carnivores such as lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and spotted hyenas (*Crocuta crocuta*) that hunt large, risky prey. These ideas may even extend to marine mammals such as killer whales (*Orcinus orca*) hunting dangerous prey (Duignan et al., 2000).

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