Spatial Patterning of Prey at Reproduction to Reduce Predation Risk: What Drives Dispersion from Groups?

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ABSTRACT: Group living is a widespread behavior thought to be an evolutionary adaptation for reducing predation risk. Many group-living species, however, spend a portion of their life cycle as dispersed individuals, suggesting that the costs and benefits of these opposing behaviors vary temporally. Here, we evaluated mechanistic hypotheses for explaining individual dispersion as a tactic for reducing predation risk at reproduction (i.e., birthing) in an otherwise group-living animal. Using simulation analyses parameterized by empirical data, we assessed whether dispersion increases reproductive success by (i) increasing predator search time, (ii) reducing predator encounter rates because individuals are inconspicuous relative to groups, or (iii) eliminating the risk of multiple kills per encounter. Simulations indicate that dispersion becomes favorable only when detectability increases with group size and there is risk of multiple kills per encounter. This latter effect, however, is likely the primary mechanism driving females to disperse at reproduction because group detectability effects are presumably constant year-round. We suggest that the risk of multiple kills imposed by highly vulnerable offspring may be an important factor influencing dispersive behavior in many species, and conservation strategies for such species will require protecting sufficient space to allow dispersion to effectively reduce predation risk.

Keywords: group living, dispersion, predation risk, multiple kills, reproductive behavior, spacing out.

Introduction

Predator-prey interactions can be important drivers in the evolution of social behavior in organisms (Hamilton 1971; Alexander 1974). One outcome of such interactions is the adaptation of sociality, or group living, a widespread behavior occurring in birds, mammals, and fish (Krause and Ruxton 2002; Beauchamp 2014). Functional explanations for this behavior have primarily centered on its effects for reducing predation risk (Hamilton 1971; Hart and Freed

2005). For example, sociality may afford early predator detection (Pulliam 1973), decrease each individual's capture probability through dilution effects (Bertram 1978; Foster and Treherne 1981), or aid defense (Garay 2009). Sociality may also reduce the probability of predator encounter if increasing prey aggregation effectively lowers the number of groups available to predators (Travis and Palmer 2005; Ioannou et al. 2011).

Yet, given these apparent advantages to sociality, many organisms considered to be group living spend a portion of their life cycles as dispersed individuals (Alexander 1974). This behavioral shift suggests that the relative costs and benefits associated with group living can vary temporally. While other factors (e.g., access to food, parasite avoidance) may influence social behavior in animals (Krause and Ruxton 2002; Beauchamp 2014), here we focus on temporal trade-offs to sociality in terms of predation risk. In certain situations, the dispersion of individuals may be advantageous over group living: for example, if groups are more detectable than individuals (Hebblewhite and Pletscher 2002; Ioannou and Krause 2008), if aggregation leads to area-restricted search behavior from predators (Tinbergen et al. 1967; Scharf et al. 2011), or if the number of individuals predated per encounter is greater than one (Treisman 1975).

Within this context, we evaluated mechanistic hypotheses for explaining individual dispersion as a tactic for reducing predation risk at reproduction in an otherwise group-living animal. Specifically, we assessed the plausibility of these hypotheses for explaining the dispersive behavior of female boreal caribou (*Rangifer tarandus caribou*) at calving. For most of the year, boreal caribou occur in small groups of 5–10 individuals (Rettie and Messier 1998). During calving, however, parturient females disperse widely on the landscape (app. A; apps. A–E are available online), a spatial tactic that differs from barren-ground caribou (*Rangifer tarandus groenlandicus*), which undergo long-distance migrations and subsequently calve in large aggregations (Bergerud 1996). Both tactics—the "spacing out" of boreal caribou and the "spacing

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away" of barren-ground caribou (sensu Bergerud and Page 1987)—are considered primarily to be mechanisms for reducing predation risk, as they do not afford other maternal benefits, such as maximizing nutrition or minimizing parasite harassment (Russell et al. 1993; Bergerud et al. 2008). For barren-ground caribou, spacing away reduces predation risk because migration moves females from winter ranges with relatively high predator density to calving areas with lower predator density (Heard et al. 1996). For boreal caribou, spacing out may reduce predation risk by increasing the search time of predators and because solitary females with calves are less conspicuous than female-calf groups (Bergerud and Page 1987; Bergerud 1996). This latter point becomes increasingly advantageous in forested environments, where the benefits of early predator detection afforded by groups are minimized. To date, these mechanisms for spacing out have not been explicitly investigated.

Using simulation analyses, we assessed various hypotheses for explaining dispersion of boreal caribou at calving. We focused simulations on the interaction between female caribou with neonate calves (<4 weeks old) and wolves (*Canis lupus*), a primary predator of caribou calves. Simulations tracked caribou-wolf encounters, from which we calculated the mean number of calves surviving per female per generation (6.7 years for caribou; Thomas and Gray 2002) as a proxy for lifetime reproductive success (hereafter, long-term offspring survival [LOS]). Using this framework, we specifically evaluated the two hypotheses suggested by Bergerud and Page (1987). The first—the search time hypothesis—states that dispersion increases predator search time (see also Tinbergen et al. 1967) and thus predicts that increasing dispersion of individuals will correlate with increasing LOS. The second—the group detectability hypothesis—states that dispersion is driven by the relative inconspicuousness of individuals compared with groups. Note that this hypothesis runs counter to recent research suggesting that increasing prey aggregation leads to lowered visual detection by predators due to increasing distances between predator and prey as prey aggregate into larger, but fewer, groups (Ioannou et al. 2011). In forested environments, however, vision is limited and predator-prey encounters may be driven more by olfaction and/or audition, which may result in a positive relationship between prey group size and detection by predators (Hebblewhite and Pletscher 2002). The group detectability hypothesis predicts that dispersed individuals would have a higher LOS than grouped caribou and that the magnitude of this difference would be driven by differential detectability based on group size.

We also evaluated a third hypothesis: that female dispersion is favored when more than one individual per group is predated per predator encounter (multiple kills hypothesis; Treisman 1975). This hypothesis, in effect, is the opposite of the dilution effect proposed by Bertram (1978), where per

capita predation risk is lower in larger groups (see also Foster and Treherne 1981). Here, the positive individual effect of dilution is negated—and in fact reversed—when high vulnerability of prey causes a concentrative effect from the predator, resulting in multiple kills on group encounter. Multiple kills on encounter have been documented in many predator-prey interactions (Kruuk 1972), and for caribou the killing of multiple calves per wolf encounter has been observed in the barren-ground subspecies, which congregates at calving (Miller et al. 1985). Under the multiple kills hypothesis, dispersed females are predicted to have a higher LOS than those in groups.

Methods

Wolf GPS Data

To model wolf movements, we used location data from GPS radio-collared wolves ($n = 15$) captured within boreal caribou ranges of northeast British Columbia, Canada (~lat 58.2500 to 60.0000, long −120.9000 to −123.5000). Animals were captured by aerial darting from a helicopter in either March 2012 ($n = 3$) or March 2013 ($n = 12$) and fitted with iridium satellite GPS collars (Advanced Telemetry Systems; model 2110E). All capture and handling procedures followed approved institutional animal care protocols (University of Alberta animal use protocol 748/02/12). GPS collars were programmed to acquire one location (or fix) every 15 min during the calving season of caribou (May 1–June 30) and once per day otherwise. For all analyses, we used only location data from the calving season ($n = 2$ seasons), and we screened these data to exclude locations with low precision (less than three-dimensional fixes; Lewis et al. 2007) and/or associated with biologically unrealistic movements (Bjørneraas et al. 2010). We further excluded locations between 1000 and 1800 hours, an interval coinciding with limited movement, presumably due to animals bedding down to avoid warm daytime temperatures.

Simulation Model Setup and Parameterization

We assessed caribou-wolf encounter rates under varying spatial conditions by creating a simulated caribou range of 4,900 km² (50-m grid cell resolution), a size that approximates the median range size of caribou herds in northeast British Columbia. We populated the simulated range with 300 caribou calves and 10 wolves (sensitivity analyses varying the number of caribou and wolves did not fundamentally alter simulation inferences; see app. B). Caribou-wolf encounters were primarily driven by individual wolves searching for stationary calves. We considered wolves to be individuals rather than packs, as pack cohesion is lower during the spring denning period, with pack members often traveling

alone (Fuller et al. 2003; see also "Discussion"). Calves were considered to be stationary because of their limited movement during the neonate period (<1-km displacement from the calving site; Gustine et al. 2006). In simulations where calves occurred in groups, we considered all individuals in the group to be occupying the same grid cell.

Wolf movements were modeled using a correlated random walk (Turchin 1998). Within this framework, we modeled the distribution of step lengths (distance between successive fixes) as a Weibull distribution, which is a generalization of the exponential distribution and has the following form:

$$f(r) = \frac{a}{b}\left(\frac{x}{b}\right)^{a-1} e^{-(x/b)^a}, \tag{1}$$

where r is the step length, a is the shape parameter, and b is the scale parameter. To model the turning angles between successive steps, we used a von Mises distribution,

$$g(\theta) \propto e^{k\cos(\theta)}, \tag{2}$$

where θ is the turning angle, k measures the amount of correlation between the direction of successive steps, and the constant of proportionality is chosen to ensure that $g(\theta)$ integrates to 1 between 0 and 2π. Maximum likelihood estimation (MLE) was used to determine the values of a, b, and k for each wolf. For the simulations, we picked a single set of parameters (a, b, k) that was representative because parameters did not vary much among wolves. For each likelihood maximization calculation, we used the Nelder-Mead simplex algorithm (Lagarias et al. 1998), as implemented in the Python maximize() function from the SciPy library (Jones et al. 2001). Assuming the wolf stays within the simulated caribou range, we used the following probability density function for a single step:

$$p(\boldsymbol{x}_n | \boldsymbol{x}_{n-1}, \theta_{n-1}) = f(|\boldsymbol{x}_n - \boldsymbol{x}_{n-1}|) g(\theta_{n-1} - \theta_n), \tag{3}$$

where $\boldsymbol{x}_1, \boldsymbol{x}_2, \ldots, \boldsymbol{x}_N$, are the successive positions of the wolf and θ_n is the bearing from $\boldsymbol{x}_{n-1}$ to $\boldsymbol{x}_n$. Each time step in the simulations modeled 15 min of wolf movement, mirroring the resolution of the GPS data. Successive positions were found by drawing from the probability distribution in equation (3). Each simulation lasted a total of 1,200 steps, which, given the 16-h day due to exclusion of locations between 1000 and 1800 hours, equates to a time period of 18.75 days.

For the initial simulations, we started with the following assumptions. First, if a wolf encountered a calf, the calf was killed (i.e., the probability of death given encounter = 1.0). This assumption is not unreasonable given the small size of neonate calves and their high vulnerability to predation (Adams et al. 1995). Owing to the calf's small size, we imposed a 1-h handling time—or pause in wolf movement—to reflect the time required to process captured prey (Holling

1959). Second, we assumed that wolves could detect a calf at a distance up to 1 km. This distance is similar to detection distances used in other wolf studies (1.5 km in Muhly et al. 2010; 1.3 km in Whittington et al. 2011) and within the sensory detection range reported for wolves (Mech and Boitani 2003). We further note that sensitivity analyses conducted using different detection radii did not affect overall inferences (i.e., simulation outputs changed linearly with detection radius; see app. B).

Evaluating the Search Time Hypothesis

We assessed the search time hypothesis, which states that dispersion by females increases predator search time, in two ways. First, we evaluated how the magnitude of dispersion by individual females affected the mean LOS. For this analysis, we assessed nine scenarios representing varying degrees of dispersion from highly clumped (scenario 0) to highly dispersed (scenario 8; app. C). We maintained the basic assumptions as outlined above, specifically that the detection radius of wolves was 1 km and that once a calf was detected, the wolf killed it. We then evaluated how dispersed calves (scenario 8; hereafter, the reference scenario) compared against calves that were grouped. We evaluated group sizes ranging from 2 to 13, running independent simulations for each group size while maintaining a constant total population size of 300, and groups were randomly dispersed within the simulated range prior to each run. We maintained the 1-km detection radius regardless of group size, and when a wolf encountered a caribou group, only one calf was killed per encounter. After a wolf encounter, caribou groups were relocated within the simulated range, with the distance moved determined by randomly drawing from an exponential distribution with a mean of 8 km, a value based on observations of movements made by radio-collared maternal females following apparent predator or human-mediated disturbance (C. A. DeMars, unpublished data).

Evaluating the Group Detectability Hypothesis

We assessed the group detectability hypothesis by varying the detection radius of wolves as a function of group size. For this analysis, we assumed that the primary means of prey detection by wolves is by olfaction or audition, particularly in forested environments (Mech and Boitani 2003). We assumed that detection distances for these senses are predominantly influenced by the olfactory or auditory intensity of the point source and that this intensity increases linearly with the number of caribou in a group (Andersson et al. 2013). We therefore modeled the relationship between group size and detectability using the inverse square law, which states that the influence of a point source emitting a physical quantity will decay as the square root of the distance from the

point source (Self et al. 2009). For example, where we assumed that wolves could detect an individual calf at a distance of 1 km, a group of three calves would have a detection radius of $3^{1/2} \approx 1.73$. Using this relationship, we again evaluated the effects of grouping on the mean LOS, assessing group sizes ranging from 2 to 13 independently, and comparing these effects to the reference scenario, where individuals are highly dispersed. For these simulations, we maintained the rules that only one calf was killed per wolf encounter and that groups were randomly relocated following each encounter.

Evaluating the Multiple Kills Hypothesis

To assess the multiple kills hypothesis, we varied the number of calves killed per group encounter while holding the detection radius constant at 1 km regardless of group size and randomly relocating groups after each encounter. We varied kills per encounter by including a parameter in the simulation model that specified the number of encounters needed to kill all the calves in a group. We varied the kills-per-encounter parameter from one kill per encounter to values where all calves were killed on first encounter and evaluated the multiple kills hypothesis on group sizes of 3, 7, and 13.

Evaluating Multiple Mechanisms

We further evaluated the effects of multiple mechanisms by combining differential group detectability with variation in the number of kills per encounter. For these simulations, we modeled group detectability using the inverse square law as above and varied the number of kills per encounter from one to where all calves in a group were killed. We also tested scenarios where less than one individual was killed per encounter by substituting the kills-per-encounter parameter with a parameter specifying the probability of a calf being killed on encounter. We set this kill success parameter at 50%, a value close to empirical values of kill success for wolves when encountering groups of adult caribou (Haber 1977). Thus, this latter scenario provides a specific assessment of how the effects of grouping might differ between adults and neonate calves.

Simulation Analysis

For each scenario, we ran 250 simulations to generate a distribution of the number of calves killed per calving season (app. D). Note that for analyses assessing group size or kills-per-encounter effects, we ran 250 simulations for each group size and for each change in the number of calves killed per encounter. We used the distribution of kills to calculate the mean LOS for each scenario. For a given female, we randomly drew from the distribution of kills, used this proportion ($x/300$ calves) as the probability of a binomial draw to determine whether a calf survived, and repeated this seven times (the approximate generation time for caribou), summing the total to calculate LOS. We repeated this process 50,000 times and then calculated the mean LOS and its associated variance. To evaluate each hypothesis, we assessed for trends in the mean and variance of LOS and specifically noted how group living compared with the reference scenario. We emphasize that calculated LOS rates are for comparative purposes only and are not estimates of actual offspring survival rates in the wild (for further discussion, see app. E). Simulations were coded in the C programming language and are provided in a zip file (available online),[1] while LOS calculations were performed in R (ver. 3.1.2; R Core Team 2014). Data used to parameterize simulations are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.vr0kc (DeMars et al. 2016).

Results

Search Time Hypothesis

Under the assumptions that wolves detected caribou at a constant radius of 1 km and killed one calf per encounter, dispersion appeared to be a favorable tactic when caribou occurred as individuals (fig. 1*A*). Increasing dispersion resulted in an increasing trend in mean LOS (scenario 0 [highly aggregated]: $\bar{x} = 1.88$; scenario 8 [highly dispersed]: $\bar{x} = 2.12$; table E1; tables E1–E6 are available online), and variance tracked the mean trend, albeit at a slower rate, in a Poisson-like distribution (σ^2 range: 1.37–1.49). Dispersing as individuals, however, was not advantageous over group living under these assumptions, as dispersed individuals had a lower mean LOS than grouped caribou (fig. 1*B*; table E2). Moreover, increasing group size led to an increasing trend in the mean (group size of 2: $\bar{x} = 3.06$; group size of 13: $\bar{x} = 6.09$) and a decreasing trend in the variance (group size of 2: $\sigma^2 = 1.72$; group size of 13: $\sigma^2 = 0.79$) of LOS.

Group Detectability Hypothesis

The advantage of group living greatly diminished when the detection radius of wolves varied as a function of caribou group size (fig. 2; table E3). Small groups ($2 \leq n \leq 4$) had a lower mean LOS on average (group size of 2: $\bar{x} = 1.92$; group size of 4: $\bar{x} = 1.75$) than dispersed individuals ($\bar{x} = 2.14$), and the mean for small groups trended lower with increasing group size. This trend, however, reversed at intermediate to large group sizes (≥ 5), and, as a result, when group size was ≥ 10 the mean LOS was higher than that for dispersed individuals (group size of 10: $\bar{x} = 2.15$;

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1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.
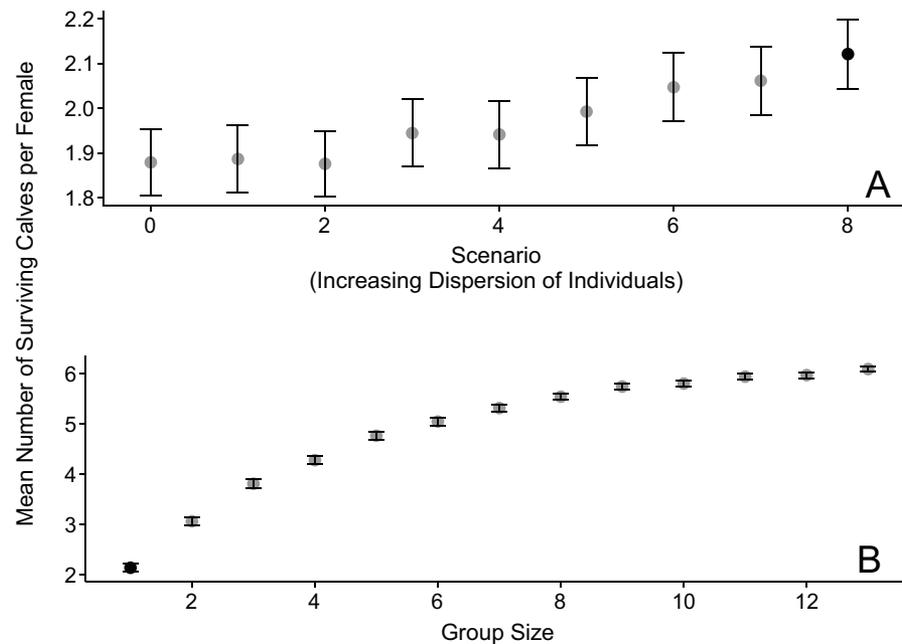
Figure 1: Effect (with standard error bars) of individual dispersion (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations ($n = 250$/scenario or group size) tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves was 1 km regardless of group size, and one calf was killed per encounter. Black circles refer to the values of the reference scenario, where caribou occur as highly dispersed individuals. In *A*, the spatial configuration of individual caribou was varied from highly clumped (scenario 0) to highly dispersed (scenario 8). In *B*, highly dispersed individuals are compared with dispersed caribou groups.

group size of 13: $\bar{x} = 2.35$). Variance in LOS remained relatively constant across group sizes (σ^2 range: 1.32–1.55).

Multiple Kills Hypothesis

Varying the number of kills per encounter while holding the detection radius constant resulted in grouped caribou having a higher mean LOS than dispersed individuals in all simulations except those where all calves were killed on initial encounter (fig. 3; table E4). Variance showed a slight curvilinear effect, being higher at middle values of mean LOS.

Multiple Mechanisms

Combining the effects of multiple kills per encounter and differential group detectability resulted in dispersed individuals having a higher mean LOS than grouped caribou (fig. 4; table E5). This outcome was evident even in simulations where only 1.5 calves were killed on average per encounter (dispersed individuals: $\bar{x} = 2.14$; all groups: $\bar{x} \leq 1.73$). Variance again showed a Poisson-like property, mirroring the trend in mean LOS.

Modeling a lowered rate of kill success (50%) with differential group detectability resulted in a consistent increase in mean LOS across group sizes (group size of 2: $\bar{x} = 3.37$; group size of 13: $\bar{x} = 4.23$; fig. 4; table E6). As a consequence, results from this interaction were similar to those of the group detectability simulations, where dispersed individuals ($\bar{x} = 3.51$) had a higher mean LOS than small groups (here, group sizes of 2–4: all $\bar{x} \leq 3.42$) but not large groups (>6 individuals: all $\bar{x} \geq 3.72$). Notably, the increasing trend in mean LOS associated with group sizes of >6 was steeper than when the kills per encounter was 1.0. Variance in LOS was relatively constant across group sizes (σ^2 range: 1.67–1.76).

Discussion

Our results suggest that multiple mechanisms interact to selectively favor dispersion as a tactic for reducing predation risk at reproduction in otherwise group-living prey. Dispersion led only to the highest number of offspring surviving when detectability increased with group size and predators killed more than one offspring per encounter. The risk of multiple kills per encounter, however, may be the primary mechanism causing females to disperse at reproduction, as differential group detectability is likely to remain relatively constant throughout the year for most species. During reproduction, dispersion is favored because the vulnerability of neonatal
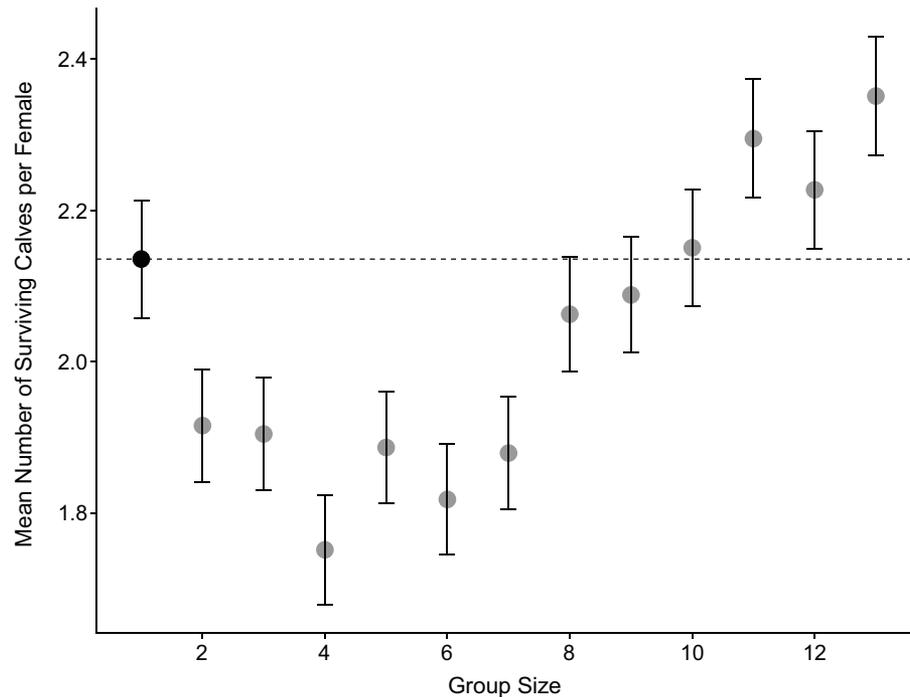
Figure 2: Effect (with standard error bars) of differential detectability by group size (group detectability hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations (*n* = 250/scenario or group size) tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves varied as the square root of caribou group size, and only one calf was killed per wolf encounter. The black circle and dashed line refer to the values of the reference scenario, where caribou occur as highly dispersed individuals.

offspring results in a high risk of multiple kills if offspring are grouped (Miller et al. 1985), and this risk outweighs the benefits afforded by group living. Outside of reproduction, the risk of multiple kills is greatly reduced because groups consist of adults and juveniles, individuals that are much more mobile with a considerably lower probability of capture than neonates. Indeed, the reforming of groups by caribou later in the summer is likely driven by calves attaining movement rates similar to those of adults (DeMars et al. 2013) and thereby lowering their capture probability. This reduced capture probability lowers the risk of multiple kills and therefore favors living in larger groups (e.g., >6 for boreal caribou)—as evidenced by simulations modeling a kill success of 50%—with the benefits of group living likely due to the increased search time and lowered predator encounter rates associated with increasing group size (Ioannou et al. 2011).

Temporal variation in predation vulnerability has been shown to be a driver in the evolution of other stage-specific behaviors in addition to the potential effect demonstrated here. In common lizards (*Zootoca vivipara*), gravid females will maintain a static, cryptic behavior longer than nongravid females on predator approach because the increased weight of pregnancy makes fleeing less effective (Bauwens and Thoen 1981). In bream (*Abramis brama*), a freshwater fish, migra-

tory behavior is thought to be a size-dependent response to predation risk, with smaller, high-risk individuals showing a greater propensity to migrate (Skov et al. 2011). In both examples, predation-sensitive behaviors likely evolved because of the positive effects on individual survival and, therefore, fitness. For caribou in forested environments, dispersion at calving may have become fixed over aggregation because of dispersion's positive effect on neonate survival, a contributing factor to overall fitness. This mechanism likely generalizes beyond caribou in explaining dispersive behavior at reproduction. For example, within ungulates—where calving behavior has been primarily assessed in terms of habitat selection—offspring vulnerability may be an influencing factor in the dispersive behavior of parturient moose (*Alces alces*; Poole et al. 2007) and elk (*Cervus elaphus*; Vore and Schmidt 2001). Within birds, offspring vulnerability could be a contributing mechanism in the dispersion of pairs at breeding in otherwise flocking species (Lima 2009).

The dominant mechanisms driving spatial distributions of organisms are likely context specific (Treisman 1975; Taylor 1976; Scharf et al. 2011; Beauchamp 2014). This idea is exemplified by caribou, where the surrounding environment likely plays an important role in determining whether to disperse (boreal caribou) or aggregate (barren-ground caribou) at calv-
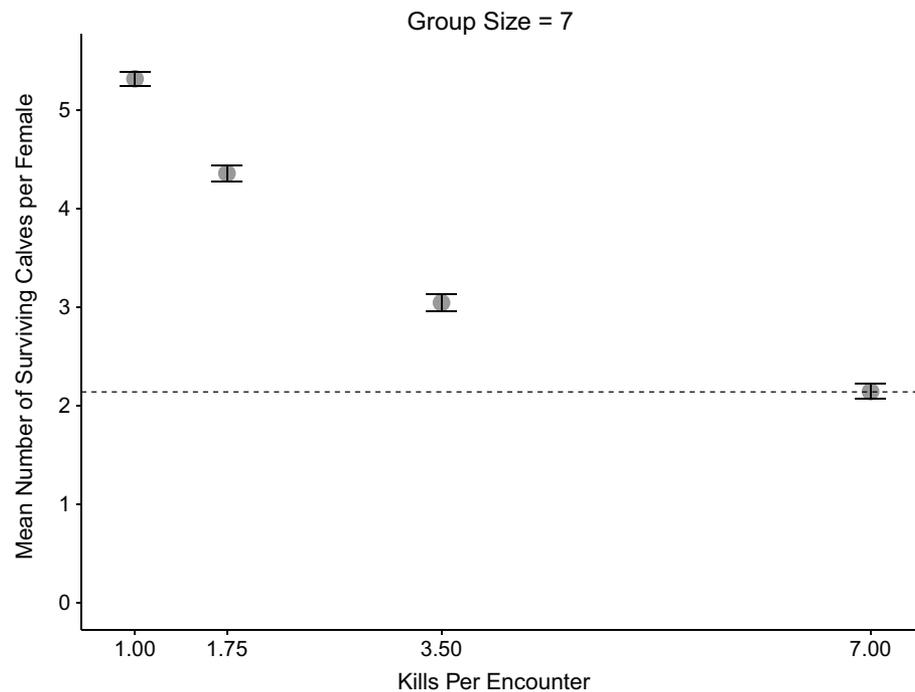
Figure 3: Effect (with standard error bars) of multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) during simulations ($n = 250$/scenario or group size) tracking caribou-wolf encounters during the calving season. Here we show the effects when caribou occur in groups of 7, the mean group size of caribou during the winter in northeast British Columbia. The dashed line indicates the mean number of surviving calves in the reference scenario, where caribou are dispersed as individuals.

ing. In our simulations, we assumed that wolves primarily detected caribou by olfaction and/or audition because forest cover limits visual detection. Environmental effects on vision may also determine the spatial distribution of prey, as it directly affects the benefit of early predator detection provided by groups (Pulliam 1973; Beauchamp 2014). In open environments, group living is likely maintained during reproduction because early visual detection of predators enhances predator evasion (e.g., bighorn sheep [*Ovis canadensis*], Berger 1978; common degu [*Octodon degus*], Ebsenperger and Wallem 2002) or the organization of group defense (e.g., muskoxen [*Ovibos moschatus*], Tener 1965; bison [*Bison bison*], Carbyn and Trottier 1988), and these benefits may outweigh the risk of multiple kills when offspring are grouped. Indeed, in a predator removal experiment Banks (2001) found that female eastern gray kangaroos (*Macropus giganteus*) foraging in open areas with dependent young were more likely to occur in groups in areas where predators were present compared with areas where they were removed. For boreal caribou, the weight of importance is placed on minimizing the risk of multiple kills because early visual detection of predators is limited by forest vegetation. The importance of vision in determining grouping patterns has also been demonstrated in other taxa, including freshwater fish (Emery 1973) and dolphins (Scott and Cattanach 1998).

Differential group detectability strongly influenced the relative differences between dispersion and group living in our simulations. When detectability was held constant for all group sizes, group living was highly advantageous over dispersion regardless of group size (fig. 1*B*); conversely, when detectability varied as a function of group size, dispersion was somewhat advantageous over small to intermediate groups but not large groups (fig. 2). These results are similar to empirical findings of encounter rates between wolves and elk groups, where intermediate group sizes of elk had higher encounter rates with wolves than individuals or large groups (Hebblewhite and Pletscher 2002). Together, these results suggest that at small to intermediate group sizes, group detectability effects have a stronger influence on encounter rates than the minimizing effect associated with increasing group size (Ioannou et al. 2011). Note, however, that the encounter-detectability relationship is dependent on how detectability is modeled. Because the nature of prey detections in our wolf-caribou system is unknown, we used the inverse square law to model detectability as the square root of group size (Andersson et al. 2013). This approach is likely not an exact representation of how wolves detect caribou and may be biologically liberal when group sizes are large (e.g., the detection radius of a group of 13 in our simulations is 3.6 km). If the true detection radius is smaller, then group living becomes
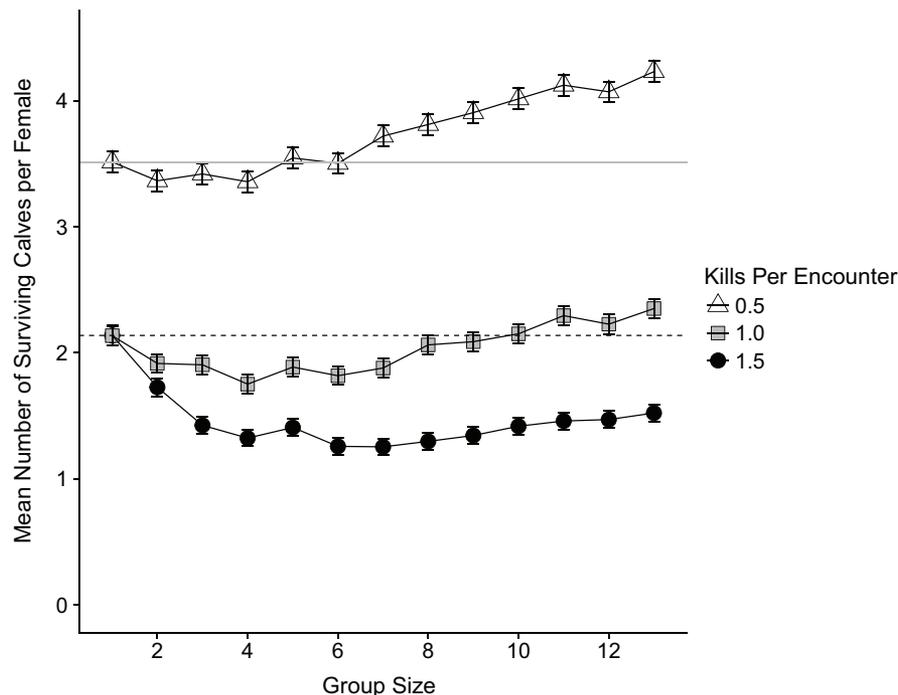
Figure 4: Effect (with standard error bars) of multiple mechanisms on the mean number of surviving calves per female per generation (7 years) during simulations ($n = 250$/scenario or group size) tracking caribou-wolf encounters during the calving season. Differential group detectability was separately combined with multiple kills per encounter (black circles) and a 50% rate of kill success (white triangles). For multiple kills, the average kills per encounter was 1.5. The results of simulations assessing only differential group detectability (gray squares; kills per encounter = 1.0) are also presented for comparison. Dashed lines represent the value of the reference scenario, where caribou are dispersed as individuals.

increasingly advantageous even at small group sizes. These relationships therefore suggest that while differential group detectability discounts the advantages of group living relative to dispersion (figs. 1*B*, 2), it is by itself an insufficient explanation for why female caribou disperse at calving unless detection radii exceed distances that may be biologically implausible.

Of the three a priori hypotheses evaluated, the search time hypothesis, which isolated the effect of simply spacing out, was the least informative for explaining dispersion at reproduction. In simulations comparing groups to dispersed individuals, group living was advantageous over individuals across all group sizes (fig. 1*B*). Moreover, group living became increasingly advantageous as group size increased, an effect caused by the increasing search time required for wolves to locate the decreasing number of available caribou groups (Travis and Palmer 2005; Ioannou et al. 2011). Dispersion became effective only when caribou occurred as individuals (fig. 1*A*). In these simulations, increasing dispersion resulted in increasing mean LOS. While this finding does not directly answer our central question of why organisms disperse from groups, it does have important ramifications for the management of species that disperse at repro-

duction to reduce predation risk. If human-altered landscapes force such species to become increasingly clumped, an effect that has been shown for boreal caribou (Fortin et al. 2013), then lowered or more variable offspring survival may result, potentially leading to population declines and increased extinction risk (Boyce et al. 2006). Thus, conservation strategies for species that disperse at reproduction will require the protection of sufficient space to allow their dispersive behavior to effectively reduce predation risk.

Finally, we highlight that our results yield testable predictions of the social behavior of prey at reproduction in other predator-prey systems. These predictions are predicated on the assumptions and inputs of our simulation approach; for example, we restricted our analysis to forested environments, where early predator detection by vision is limited and modeled no group defense effects. Nevertheless, given these constraints, our results predict that if the probability of multiple kills is an important driver of dispersive behavior, then group-living prey that can dissuade multiple kills should remain in groups at reproduction. Such prey could include those that emit a noxious substance to deter repeated attacks. Prey with a relatively small-sized primary predator should also remain in groups because multiple kills

are less likely. Conversely, group-hunting predators should exert a strong influence for prey dispersion. In our simulations, for example, modeling wolves as packs would increase the probability of multiple kills, further favoring dispersion of prey (fig. 4). These examples illustrate the importance of accounting for the behavioral ecology of both predator and prey—and the environmental context in which their interactions take place—when testing predictions of social behavior in novel predator-prey systems.

Acknowledgments

Literature Cited

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584–594.

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics 5:328–383.

Andersson, P., C. Löfstedt, and P. A. Hambäck. 2013. How insects sense olfactory patches—the spatial scaling of olfactory information. Oikos 122:1009–1016.

Banks, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. Animal Behaviour 61:1013–1021.

Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. Journal of Animal Ecology 50:733.

Beauchamp, G. 2014. Social predation. Academic Press, London.

Berger, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behavioral Ecology and Sociobiology 4:91–99.

Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer 16:95–116.

Bergerud, A. T., S. N. Luttich, and L. Camps. 2008. The return of caribou to Ungava. McGill-Queen's University Press, Montreal.

Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65:1597–1606.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 64–96 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Sinauer, Sunderland, MA.

Bjørneraas, K., B. Van Moorter, C. M. Rolandsen, and I. Herfindal. 2010. Screening global positioning system location data for errors using animal movement characteristics. Journal of Wildlife Management 74:1361–1366.

Boyce, M., C. Haridas, and C. Lee; NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. Trends in Ecology and Evolution 21:141–148.

Carbyn, L. N., and T. Trottier. 1988. Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. Arctic 41:297–302.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3:4149–4160.

DeMars, C. A., G. A. Breed, J. R. Potts, and S. Boutin. 2016. Data from: Spatial patterning of prey at reproduction to reduce predation risk: what drives dispersion from groups? American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.vr0kc

Ebsenperger, L. A., and P. K. Wallem. 2002. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. Oikos 98:491–497.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. Canadian Journal of Zoology 30:761–774.

Fortin, D., P.-L. Buono, A. Fortin, N. Courbin, C. Tye Gingras, P. R. Moorcroft, R. Courtois, et al. 2013. Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. American Naturalist 181:827–836.

Foster, W. A., and J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293:466–467.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitani, eds. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

Garay, J. 2009. Cooperation in defence against a predator. Journal of Theoretical Biology 257:45–51.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165:1–32.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. PhD diss. University of British Columbia, Vancouver.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hart, P. J., and L. A. Freed. 2005. Predator avoidance as a function of flocking in the sexually dichromatic Hawaii akepa. Journal of Ethology 23:29–33.

Heard, D. C., T. M. Williams, and D. A. Melton. 1996. The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. Rangifer Special Issue 9:37–44.

Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology 80:800–809.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Ioannou, C. C., F. Bartumeus, J. Krause, and G. D. Ruxton. 2011. Unified effects of aggregation reveal larger prey groups take longer to find. Proceedings of the Royal Society B: Biological Sciences 278: 2985–2990.

Ioannou, C. C., and J. Krause. 2008. Searching for prey: the effects of group size and number. Animal Behaviour 75:1383–1388.

Jones, E., T. Oliphant, P. Peterson, et al. 2001. SciPy: open source scientific tools for Python. http://www.scipy.org/.

Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.

Kruuk, H. 1972. Surplus killing by carnivores. Journal of Zoology 166: 233–244.

Lagarias, J. C., J. A. Reeds, M. H. Wright, and P. E. Wright. 1998. Convergence properties of the Nelder-Mead simplex method in low dimensions. SIAM Journal on Optimization 9:112–147.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error: GPS collar performance. Journal of Applied Ecology 44:663–671.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

Mech, L. D., and L. Boitani. 2003. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

Miller, F. L., A. Gunn, and E. Broughton. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. Canadian Journal of Zoology 63:295–300.

Muhly, T. B., M. Alexander, M. S. Boyce, R. Creasey, M. Hebblewhite, D. Paton, J. A. Pitt, et al. 2010. Differential risk effects of wolves on wild versus domestic prey have consequences for conservation. Oikos 119:1243–1254.

Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139–150.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

Rettie, W. J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology 76:251–259.

Russell, D. E., A. M. Martell, and W. A. Nixon. 1993. Range ecology of the porcupine caribou herd in Canada. Rangifer 13:1–168.

Scharf, I., O. Ovadia, and S. Foitzik. 2011. The advantage of alternative tactics of prey and predators depends on the spatial pattern of prey and social interactions among predators. Population Ecology 54:187–196.

Scott, M. D., and K. L. Cattanach. 1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. Marine Mammal Science 14:401–422.

Self, D., B. Duncan, I. Sinclair, R. Brice, J. L. Hood, A. Singmin, D. Davis, E. Patronis, and J. Watkinson. 2009. Audio engineering: know it all. Newnes, Burlington, MA.

Skov, C., H. Baktoft, J. Brodersen, C. Bronmark, B. B. Chapman, L.-A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B: Biological Sciences 278:1414–1418.

Taylor, J. 1976. The advantage of spacing out. Journal of Theoretical Biology 59:485–490.

Tener, J. S. 1965. Muskoxen in Canada: a biological and taxonomic review. Department of Northern Affairs and National Resources, Canadian Wildlife Service, Ottawa.

Thomas, D. C., and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, *in* COSWEIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defence against predation. Behaviour 28:307–321.

Travis, J. M. J., and S. C. F. Palmer. 2005. Spatial processes can determine the relationship between prey encounter rate and prey density. Biology Letters 1:136–138.

Treisman, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. Animal Behaviour 23:779–800.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, MA.

Vore, J. M., and E. M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29: 720–725.

Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48:1535–1542.