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Demars, C.A., Breed, G.A., Potts, J. et al. (1 more author) (2016) Spatial patterning of prey at reproduction to reduce predation risk: what drives dispersion from groups? American Naturalist, 187 (5). pp. 678-687. ISSN 1537-5323

https://doi.org/10.1086/685856

Spatial patterning of prey at reproduction to reduce predation risk: what drives dispersion from groups?

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Manuscript Type: Article

Short running title: Spatial patterning of prey

Keywords: group-living, dispersion, predation risk, multiple kills, reproductive behaviour, spacing out

Word count: 6682 [main text + figures + literature cited; excludes appendices]

List of Manuscript Elements:

Main Text (including figures)
Literature Cited
Online Appendix A
Online Appendix B
Online Appendix C
Online Appendix D
Online Appendix E
Electronic Enhancement 1 (contains computer code for data analyses; separate zip file)

Abstract

Group-living is a widespread behaviour 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 behaviours 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 only becomes favourable 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 behaviour in many species and conservation strategies for such species will require protecting sufficient space to allow dispersion to effectively reduce predation risk.

Introduction

Predator-prey interactions can be important drivers in the evolution of social behaviour in organisms (Hamilton 1971; Alexander 1974). One outcome of such interactions is the adaptation of sociality, or group-living, a widespread behaviour occurring in birds, mammals, and fish (Krause and Ruxton 2002; Beauchamp 2014). Functional explanations for this behaviour 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 defence (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 behavioural 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 behaviour 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 behaviour 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 behaviour 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 (Appendix A), 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 away' of barren-ground caribou (*sensu* Bergerud and Page 1987) – are considered to be primarily 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 of 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 to 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 (Ioannu 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 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 favoured 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 minutes 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 this data to exclude locations with low precision (< 3-dimensional fixes; Lewis et al. 2007) and/or associated with biologically unrealistic movements (Bjørneraas et al. 2010). We further excluded locations between 10:00 and 18:00 hrs, 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 4900 km^2 (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 Appendix 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 travelling 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 modelled using a correlated random walk (Turchin 1998). Within this framework, we modelled 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

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

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

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

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 $g(\theta)$ 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

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

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 modelled 15 minutes 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 1200 steps, which given the 16-hr day due to excluding 10:00 – 18:00 locations, 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 one hour 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, Muhly et al. 2010; 1.3-km, 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 Appendix 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; Appendix 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 2-13 – 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. 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 modelled 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 $\sqrt{3} \approx 1.73$. Using this relationship, we again evaluated the effects of grouping on the mean LOS, assessing group sizes ranging from 2-13 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 modelled 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 < 1 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 (Appendix 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 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 to 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 (see Appendix E for further discussion). Simulations were coded in the C programming language while LOS calculations were performed in R, version 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. 2015).

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 favourable tactic when caribou occurred as individuals (Fig. 1A). 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; Appendix E Table E1) 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. 1B, Appendix E Table E2). Moreover, increasing group size led to an increasing trend in the mean (group size 2: $\bar{x}$ = 3.06; group size 13: $\bar{x}$ = 6.09) and a decreasing trend in variance (group size 2: σ^2 = 1.72; group size 13: σ^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, Appendix E Table E3). Small groups ($2 \leq n \leq 4$) had a lower mean LOS on average (group size 2: $\bar{x}$ = 1.92; group size 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, mean LOS was higher than dispersed individuals (group size 10: $\bar{x}$ = 2.15; group size 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, Appendix E 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, Appendix E 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.

Modelling a lowered rate of kill success (50%) with differential group detectability resulted in a consistent increase in mean LOS across group sizes (group size 2: $\bar{x} = 3.37$; group size 13: $\bar{x} = 4.23$, Fig. 4, Appendix E Table E6). As a consequence, results from this interaction were similar to 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 > 6 was steeper than when the kills-per-encounter is 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 favour dispersion as a tactic for reducing predation risk at reproduction in otherwise group-living prey. Dispersion only led 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 favoured because the vulnerability of neonatal 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 adults (DeMars et al. 2013) and thereby lowering their capture probability. This reduced capture probability lowers the risk of multiple kills and therefore favours living in larger groups (e.g. > 6 for boreal caribou) – as evidenced by simulations modelling 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 behaviours in addition to the potential effect demonstrated here. In common lizards (*Zootoca vivipara*), gravid females will maintain a static, cryptic behaviour longer than non-gravid females upon predator approach because the increased weight of

pregnancy makes fleeing less effective (Bauwens and Thoen 1981). In bream (*Abramis brama*), a freshwater fish, migratory behaviour 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 behaviours 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 behaviour at reproduction. For example, within ungulates – where calving behaviour has been primarily assessed in terms of habitat selection – offspring vulnerability may be an influencing factor in the dispersive behaviour 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 calving. 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 defence (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 grey kangaroos (*Macropus giganteus*) foraging in open areas with dependent young were more likely to occur in groups in areas where predators were present compared to 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. 1B); 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 modelled. 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 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. 1B & 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. 1B). Moreover, group-living becomes 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 only became effective when caribou occurred as individuals (Fig. 1A). 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 reproduction 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 behaviour to effectively reduce predation risk.

Finally, we highlight that our results yields testable predictions of the social behaviour 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 modelled no group defence effects. Nevertheless, given these constraints, our results predict that if the probability of multiple kills is an important driver of dispersive behaviour, 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, modelling wolves as packs would increase the probability of multiple kills, further favouring dispersion of prey (Fig. 4). These examples illustrate the importance of accounting for the behavioural ecology of both predator and prey – and the environmental context in which their interactions take place – when testing predictions of social behaviour in novel predator-prey systems.

Acknowledgements

We thank J-M. Gaillard and three anonymous reviewers whose constructive comments significantly improved this manuscript. We acknowledge the funding and in-kind support of the Science and Community Environmental Knowledge Fund, Penn West Exploration, the Alberta Upstream Petroleum Research Fund, the Canadian Wildlife Federation, and BC Ministry of Forests, Lands, and Natural Resource Operations. We thank Mark Lewis (ML) and members of the Lewis lab for helpful comments. CAD was supported by postgraduate scholarships from the

Natural Sciences and Engineering Research Council (NSERC) of Canada and Nexen, Inc. GAB was funded through an NSERC Banting postdoctoral fellowship and JRP was partly funded by an NSERC Discovery and Acceleration grant awarded to ML.

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Figure Legends

Main Text

Figure 1: The effect 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; with standard error bars) 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 to dispersed caribou groups.

Figure 2: The effect 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; with standard error bars) 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.

Figure 3: The effect 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; with standard error bars) tracking caribou-wolf encounters during the calving season. Here, we show the effects when caribou occur in groups of seven, 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.

Figure 4: The effects of multiple mechanisms on the mean number of surviving calves per female per generation (7 years) during simulations (n = 250 / scenario or group size; with standard error bars) 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 (grey 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.

Appendices

Figure A1: A female boreal caribou accompanied by a neonate calf in the boreal forests of northeast British Columbia. During the calving season (mid-May to mid-July) females disperse from groups to calve in isolation.

Figure A2: Spatial locations of five female boreal caribou during winter (blue dots) and calving (red dots) within the Maxhamish caribou range of northeast British Columbia. The average distance between caribou increased from 2.7 km in winter to 41.5 km during calving.

Figure B1: The effects of varying the number of caribou and wolves used in simulation analyses to test the search time hypothesis, which states that increasing dispersion by females increases predator search time. The detection radius of wolves was fixed at 1-km for all simulations. [Note: standard error bars are not shown as all fall within the size of the point symbols].

Figure B2: The effects of varying the number of caribou and wolves used in simulation analyses to test the group detectability hypothesis, which states that caribou groups are more detectable than individuals and thus groups should have lower mean number of calves surviving. The detection radius of wolves varied as a function of caribou group size (see main text). [Note: standard error bars are not shown as all fall within the size of the symbol].

Figure B3: The effects of varying the number of caribou and wolves used in simulation analyses to test the multiple kills hypothesis, which states that dispersion of individuals should be favoured when more than one individual per group is killed per predator encounter. Here we show the effects on a group size of seven, the mean group size of caribou in northeast British Columbia. The detection radius of wolves was fixed at 1-km for all simulations. [Note: standard error bars are not shown as all fall within the size of the symbol].

Figure B4: The effects (with standard error bars) of varying the detection radius of wolves used in simulation analyses to test the search time hypothesis, which states that increasing dispersion by females increases predator search time. All simulations were initially populated with 300 caribou and 10 wolves.

Figure B5: The effects (with standard error bars) of varying the detection radius of wolves used in simulation analyses to test the group detectability hypothesis, which states that caribou groups are more detectable than individuals and thus groups should have lower mean number of calves surviving. The detection radius of wolves varied as a function of caribou group size (see main text). All simulations were initially populated with 300 caribou and 10 wolves.

Figure B6: The effects (with standard error bars) of varying the detection radius of wolves used in simulation analyses to test the multiple kills hypothesis, which states that dispersion of individuals should be favoured when more than one individual per group is killed per predator encounter. Here we show the effects on a group size of seven, the mean group size of caribou in northeast British Columbia. Note the different scales of the y-axes. Dotted lines indicate the reference scenario where females occurred as highly dispersed individuals. All simulations were initially populated with 300 caribou and 10 wolves.

Figure C1: Nine scenarios with varying spatial dispersion of female boreal caribou (n = 300) during the calving season. These scenarios were used to evaluate the search time hypothesis.

Figure D1: Distribution of the number of boreal caribou calves killed from simulations of caribou-wolf encounters during the calving season. Here, we show two distributions from simulations evaluating the search time hypothesis: one where female caribou are highly clumped (top) and one where they are highly dispersed (bottom).

Appendix A: Spatial Behaviour of Boreal Caribou at Calving

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) spends its entire life cycle within the boreal forest biome of Canada. Outside of the calving season, boreal caribou typically occur in groups of 5-10 individuals (range: 1-36; Stuart-Smith et al. 1997; Rettie and Messier 1998; Culling and Culling 2013). During calving (mid-May to mid-July), however, females disperse from groups and distribute themselves widely on the landscape to give birth in isolation (Fig. A1), a behaviour known as "spacing out" (Bergerud and Page 1987). Here, we illustrate this behaviour with GPS radio-collar data from five females occurring within the Maxhamish caribou range of northeast British Columbia (~ lat: 59.2000 to 60.0000, ~ long: -124.0000 to -122.0000). During the winter of 2011, the average distance between these females was 2.7 km (range: 0.07 – 4.5; Fig. A2). At calving, the average distance had increased to 41.5 km (range: 5.9 – 79.9). We further note that upon capture for radio-collar deployment earlier in the winter (February 2011) all females occurred in groups (range: 5 – 12) while aerial surveys conducted during calving found all females with calves to be in isolation.

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Appendix B: Sensitivity Analyses of Simulation Outputs

We used simulation analyses to evaluate the plausibility of three hypotheses for explaining individual dispersion as a tactic for reducing predation risk at reproduction in an otherwise group-living animal, the boreal ecotype of woodland caribou (*Rangifer tarandus caribou*; see main text for descriptions of each hypothesis). Simulations tracked encounters between caribou and wolves (*Canis lupus*), a main predator of caribou calves, and we used simulation outputs to estimate the mean number of neonate calves surviving per female per generation (7 years) as a proxy of individual fitness (hereafter, long-term offspring survival [LOS]). We assessed the sensitivity of simulation inferences to variation in the number of caribou and wolves used within each simulation and to variation in the sensory radius within which wolves detected caribou (i.e. the detection radius).

Evaluating Sensitivity to Variation in Caribou and Wolf Numbers

In general, simulation inferences were robust to variation in the number of caribou and/or wolves used (Figs. B1-3). Varying the number of caribou caused little change in mean LOS across the three hypotheses evaluated. Varying the number of wolves proportionately changed mean LOS in all simulations but in most instances did not alter simulation inferences (e.g. increasing dispersion of individuals remained advantageous across the number of wolves assessed; Fig. B1). Note that we restricted the upper range of wolf numbers assessed to 15 as increasing wolf numbers above this threshold resulted in a relatively high proportion of simulations with all calves killed, creating a biologically unrealistic boundary effect that caused the distribution of calves killed to be left-skewed (see Appendix D) and thus prevented robust evaluation of each hypothesis.

Evaluating Sensitivity to Variation in Detection Radius

Varying the detection radius also had minimal influence on simulation outputs. For the search time hypothesis, lowering the detection radius resulted in a higher mean LOS but did not change the inference that increasing dispersion is favourable when caribou occur as individuals (Fig. B4). For the group detectability hypothesis, lowering the detection radius resulted in a left shift of the curvilinear relationship between LOS and group size, causing a few more group sizes to be advantageous over individuals compared to our original detection radius of 1-km (Fig. B5). Lowering the detection radius had minimal effect on the multiple kills hypothesis, only strengthening the advantage of groups over individuals when less than all of the calves were killed on initial encounter (Fig. B6).

Appendix C: Dispersion Scenarios to Test the Search Time Hypothesis

To test the search time hypothesis, which assessed the effectiveness of female caribou spacing out during calving, we evaluated nine scenarios representing varying degrees of dispersion ranging from highly clumped (Scenario 0) to highly dispersed (Scenario 8; Fig. C1). Each scenario was populated with 300 caribou in a simulated caribou range of 4900 km^2 at a grid cell resolution of 50-m.

Appendix D: Example Distributions of the Number of Calves Killed from Caribou-Wolf Encounter Simulations

Simulations of caribou-wolf encounters during the calving season tracked the number of calves killed (out of 300). For each scenario tested, we ran 250 simulations (i.e. 250 calving seasons), generating an estimated distribution of the number of calves killed during a calving season. Below are two example distributions when testing the search time hypothesis: one when caribou are highly clumped (scenario 0) and one when caribou are highly dispersed (scenario 8; Fig. D1).

Appendix E: Estimates of Long-term Offspring Survival from Simulations Tracking Caribou-Wolf Encounters during the Calving Season

The following tables list the long-term offspring survival [LOS] values (mean and standard error [SE] of the number of surviving neonate calves per female per generation) calculated from simulations evaluating the search time, group detectability and multiple kills hypotheses as well as their combined effects. We ran 250 simulations for each group size or scenario tested and each simulation started with 300 caribou calves and 10 wolves.

Note that the calculated LOS rates listed are for comparative purposes only as they are sensitive to the number of predators specified (see Appendix B) and therefore are not estimates of actual offspring survival rates in the wild. Nevertheless, simulation outputs (e.g. ~30% neonate survival for scenario 8; Table E1) are within the relatively wide range of values reported for boreal caribou populations (e.g. 26-65%, Pinard et al. 2012; see also Thomas and Gray 2002).

Table E1: The effect of individual dispersion (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. For these simulations, the detection radius of wolves was 1-km and one calf was killed per encounter.

	Number of Surviving Calves Per Female	
Scenario (Increasing Dispersion)	Mean	SE
0	1.88	0.07
1	1.89	0.07
2	1.88	0.07
3	1.94	0.07
4	1.94	0.07
5	1.99	0.08
6	2.05	0.08
7	2.06	0.08
8	2.12	0.08

Table E2: The effect of group size (search time hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations 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.

	Number of Surviving Calves Per Female	
Group Size	Mean	SE
1	2.14	0.08
2	3.06	0.08
3	3.81	0.08
4	4.28	0.08
5	4.76	0.08
6	5.04	0.07
7	5.31	0.07
8	5.54	0.07
9	5.74	0.06
10	5.80	0.06
11	5.94	0.06
12	5.97	0.06
13	6.09	0.06

Table E3: The effect of differential detectability by group size (group detectability hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations 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 one calf was killed per encounter.

	Number of Surviving Calves Per Female	
Group Size	Mean	SE
1	2.14	0.08
2	1.92	0.07
3	1.90	0.07
4	1.75	0.07
5	1.89	0.07
6	1.82	0.07
7	1.88	0.07
8	2.06	0.08
9	2.09	0.08
10	2.15	0.08
11	2.30	0.08
12	2.23	0.08
13	2.35	0.08

Table E4: The effect of multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. Group sizes of three, seven and thirteen were evaluated.

		Number of Surviving Calves Per Female	
Group Size	Average Kills Per Encounter	Mean	SE
3	1.0	3.80	0.08
	1.5	3.20	0.08
	3.0	2.20	0.08
7	1.0	5.32	0.08
	1.8	4.36	0.08
	3.5	3.04	0.08
	7.0	2.14	0.08
13	1.0	6.10	0.06
	2.2	5.00	0.08
	4.3	3.80	0.08
	6.5	2.96	0.08
	13.0	2.09	0.08

Table E5: The combined effects of differential group detectability (group detectability hypothesis) and multiple kills per encounter (multiple kills hypothesis) on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season. In these simulations, the number of kills per encounter averaged 1.5 for group sizes ≥ 2.

	Number of Surviving Calves Per Female	
Group Size	Mean	SE
1	2.14	0.08
2	1.73	0.07
3	1.42	0.07
4	1.32	0.07
5	1.41	0.07
6	1.26	0.06
7	1.25	0.06
8	1.30	0.06
9	1.34	0.07
10	1.42	0.07
11	1.46	0.07
12	1.47	0.07
13	1.52	0.07

Table E6: The combined effects of differential group detectability (group detectability hypothesis) and a kill success rate of 50% on the mean number of surviving calves per female per generation (7 years) from simulations tracking caribou-wolf encounters during the calving season.

	Number of Surviving Calves Per Female	
Group Size	Mean	Variance
1	3.51	1.76
2	3.37	1.77
3	3.42	1.73
4	3.36	1.75
5	3.55	1.73
6	3.50	1.74
7	3.72	1.74
8	3.81	1.73
9	3.91	1.73
10	4.02	1.71
11	4.12	1.69
12	4.07	1.70
13	4.23	1.67

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